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Mechanisms of As, Cd, Pb, and Zn hyperaccumulation by plants and their effects on soil microbiome in the rhizosphere

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Excess potentially toxic elements (PTEs), including arsenic (As), cadmium (Cd), lead (Pb), and zinc (Zn), above permissible limits in the environment, have detrimental effects on trophic levels. Hence, imperative to devise advertent measures to address this situation, especially in the soil ecosystem: the major reservoir of many PTEs. Using aerial plant parts (shoot) to accumulate As, Cd, Pb, and Zn - hyperaccumulators are considered a permanent approach to PTE removal from soils. This communication expatiated the principles that govern the hyperaccumulation of plants growing on As, Cd, Pb, and Zn-contaminated soils. The contribution of soil microbial communities during hyperaccumulation is well-elaborated to support the preference for this remediation approach. The study confirms a flow direction involving PTE uptake–translocation–tolerance–detoxification by hyperaccumulators. Rhizosphere microbes exhibit a direct preference for specific hyperaccumulators, which is associated with root exudations, while the resultant formation of chelates and solubility of PTEs, with soil physicochemical properties, including pH and redox potential, promote uptake. Different compartments of plants possess specialized transporter proteins and gene expressions capable of influx and efflux of PTEs by hyperaccumulators. After PTE uptake, many hyperaccumulators undergo cellular secretion of chelates supported by enzymatic catalysis and high transport systems with the ability to form complexes as tolerance and detoxification mechanisms. The benefits of combining hyperaccumulators with beneficial microbes such as endophytes and other rhizosphere microbes for PTE removal from soils are vital in enhancing plant survival and growth, minimizing metal toxicity, and supplying nutrients. Inoculation of suitable rhizosphere microbes can promote efficient cleaning of PTEs contaminated sites utilizing hyperaccumulator plants.

KEYWORDS

above-ground biomass, hyperaccumulators, microbes, phytoremediation, transporter protein

1 Introduction

Potentially toxic elements (PTEs), not excluding arsenic (As), cadmium (Cd), zinc (Zn), and lead (Pb), exert antagonistic behavior in the soil ecosystem, associated growing plants, and biomagnifications in animals and humans through ingestion (Knabb et al., 2016; Landrigan et al., 2018). Elements such as copper (Cu) and Zn are ubiquitous and exhibit direct physiological and metabolic relevance in plants as micronutrients, while excess

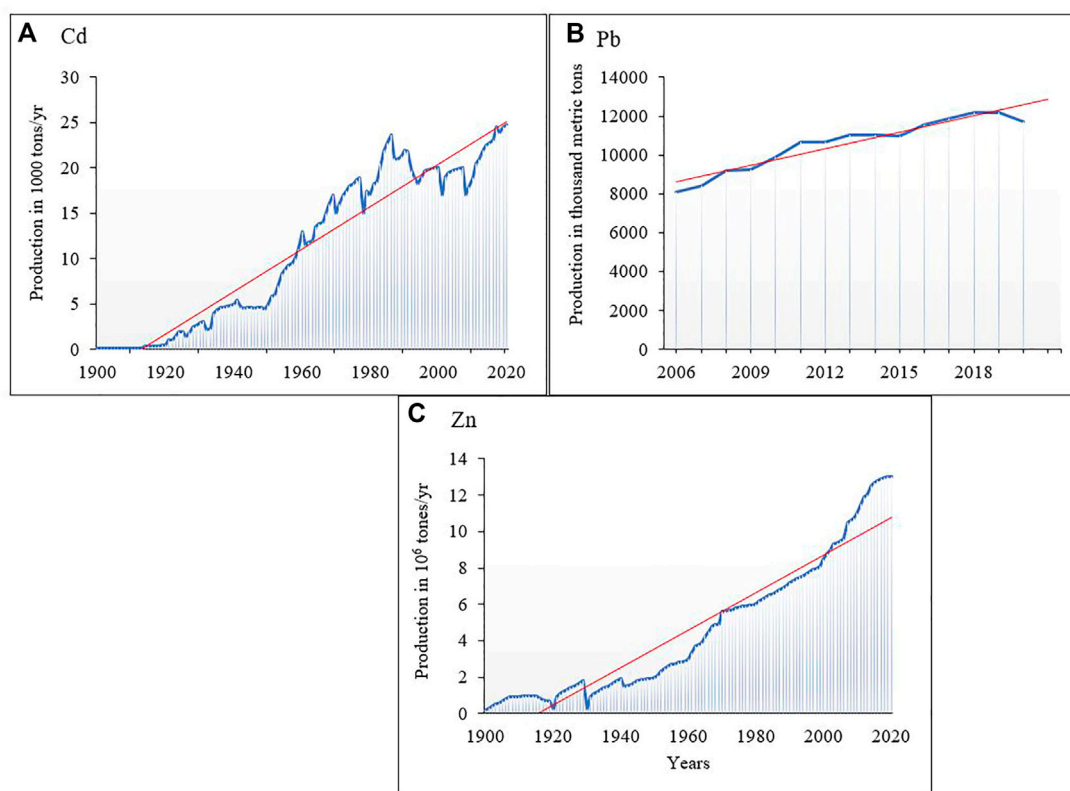


FIGURE 1

World production trend of (A) As, (B) Cd (adopted from Lucia Fernández, 2022), (C) Pb (Statista Research Department), and (D) Zn (U.S. Geological Survey, <http://minerals.usgs.gov/ds/2005/140>).

accumulation above threshold limits incurs growth dysfunctions and death (Liu et al., 2018). Arsenic, Pb, and Cd have no benefit to plants and humans with possible health disorders, e.g., cardiovascular disease and diabetes upon accumulation (Fuller et al., 2022), as their environmental exposure increases.

Despite the geogenic occurrence of PTEs, anthropogenic interferences, including mining and smelting (Knabb et al., 2016; Boente et al., 2022), the extended application of untreated organic wastes (e.g., sewage sludge and compost) and mineral fertilizers (e.g., phosphate fertilizers) application to arable lands (Bisht and Chauhan, 2020), and coal ash deposition (Shin et al., 2017) often release enormous contents in soils. Industrialization, war, and intensification of agriculture have left a legacy of soil contamination throughout, with 80,000 sites (in Australia), 1,300 in the United States, 3 million in Europe and the western Balkans, and 16% in China's soils representing the hot spot of global polluted sites (FAO/UN, 2018). Culminating these data reveals the extent of loss of land resources for agricultural sustainability and calls for more effective, efficient, and affordable removal methods. The vicinity of point sources of potentially toxic elements (PTEs), e.g., As, Cd, Pb, and Zn, become contaminated, affecting the quality of the water table via infiltration and the metabolism of soil microfauna/microflora (Cempel and Nikel, 2006; Ji et al., 2021). For example, mining and metallurgy of the 19th century in the Linares district (Jaén, South Spain) accumulated (mg kg^{-1}) As (42), Cd (140), Pb (4,244–35,899), and up to 768 Zn compared to

threshold limits of <20, 2, 100, and 200, respectively (Boente et al., 2022). Environmental exposure to PTEs results in hazardous effects as they are non-degradable (Woldetsadik et al., 2017; Landrigan et al., 2018). These raise significant awareness about the cleaning of affected soils as increases in human population parallel metalliferous activities (Figure 1). Considering climate change in recent decades and the consequences of its impacts (Hardy, 2003; National Academy of Sciences, 2020), removing PTEs in soils by plants offer adequate results over conventional technologies. Conventional strategies for cleaning up contaminated lands, e.g., soil washing (Shen et al., 2019), solidification (Matec industries, 2021), landfilling, soil flushing, and washing, capping, and vitrification (Koul and Taak, 2018; Liu et al., 2018; Khan et al., 2021), are often *ex-situ* and involve high treatment costs. These approaches often result in losing the fertility of soils and biodiversity, e.g., microfauna (Liu et al., 2022).

Some plants demonstrate Cd, Pb, and Zn accumulation in tissues and organs, especially shoots, providing evidence of their suitability in cleaning contaminated soils (Berhongeray et al., 2015; Yan et al., 2020). Hence, plant-based remediation techniques: phytoextraction, phytostabilization, phytodegradation, and phytovolatilization, most recently, have been adopted based on their success in revegetating PTE-polluted soils at an optimized cost and providing a greener ecosystem. Phytoremediation supports large field reclamations, prevents erosion and leaching by stabilizing metals, enhances organic matter (OM) accumulation, and builds up

soil fertility (Jacob et al., 2018; Yan et al., 2020). During the reclamation of contaminated lands, a selection of phytoremediation type depends on the contaminants and the intended purpose of the field.

Some plant species extract and accumulate PTEs in aboveground organs (stem, appendages, leaves, lateral buds, flowering stems, and flower buds), with minimal or no signs of toxicity, termed hyperaccumulators (Suman et al., 2018; Ashraf et al., 2019). In recent times, PTE-polluted soils have been well-used to grow high-biomass woody plants, e.g., *Salix* and *Populus* spp allowing the reduction of environmental mobility of PTE and producing polluted harvested woody biomass to produce income (Guerra et al., 2011; Mleczek et al., 2018). Extraction of PTEs in contaminated soils to aboveground organs of plants (phytoextraction) prevents surface soils from contaminating other areas via runoff and erosion (Yan et al., 2020). Many hyperaccumulators grow faster, with high-biomass, fast root-to-shoot translocation, PTE-tolerant, and detoxify PTEs (Balafrej et al., 2020). The possibility of other low biomass and slow-growth plant hyperaccumulators, e.g., *Solanum nigrum* L., exhibit high PTE accumulation under the assistance of microorganisms (Zhang et al., 2021). Plant species from families including Brassicaceae (e.g., *Brassica* sp. and *Noccaea* sp.), Pteridaceae (e.g., *Pteris vittata* L.), Lamiaceae (*Lamium maculatum* L.), Poaceae (*Deschampsia caespitosa* L.), and Crassulaceae, are often characterized by high accumulation of PTEs aboveground biomass (Małacka et al., 2019; Castañares and Lojka, 2020). For example, out of 970 mg kg⁻¹ total Zn content in soils, the leaf, stem, and root of *Cratogeomys sumatranum* (Jack) accumulated 223, 329, and 210 mg kg⁻¹ of Zn, respectively, in the mountain of Magdiwata, Philippines (Castañares and Lojka, 2020).

Furthermore, the extension of roots creates a microbe-rhizosphere community with bacteria, fungi, actinomycetes, protozoa, and algae that regulate the mobility and bioavailability of PTE (Jacob et al., 2018; DalCorso et al., 2019). Microbes that tolerate PTEs contribute to plant survival and growth in the rhizosphere. For example, *rhizobium* represents bacteria that capture groups of plant rhizosphere with symbiotic nitrogen (N) fixation in soils (Visioli et al., 2015) and promote OM decomposition (Geng et al., 2022). Generally, root exudates capture microbes in soils and colonize root surfaces or infiltrate root cortexes (Visioli et al., 2015).

Organic acids, phenolics, and siderophores affect the acidification process, and the dynamics of redox conditions change the potential in rhizospheres (Glick, 2010). Hence, adsorbed, precipitated, and residual fractions of PTEs solubilize by increasing acidity, chelation, and ligand-induced dissolution by microbes to become accessible to plants (Sessitsch et al., 2013). For example, under Cd, Pb, and Zn stress, *Enterobacter* sp. and *Klebsiella* sp. cause high accessibility in the root rhizosphere of *Brassica napus* L. (Jing et al., 2014). It is vital to understand microbial input during hyperaccumulation of PTEs and their extent of effects on hyperaccumulating plants. Such studies enable specific microbes culturing for plants suitable to alleviate PTEs contaminated soils. Although there is individual scattered literature on soil PTEs, hyperaccumulation, and microbial effects on PTE cleaning by plants, a compilation of such studies remains scarce. It is pertinent to treat environmental contamination with urgent

concern as the production rate of these metals, e.g., Cd, Pb, and Zn, keep increasing over the years (Figure 1). The end-products, such as litharge, after ore processing, are often disposed of and contribute to high PTE contents, especially in soils.

The current study presents an overview that describes in detail the principles governing the uptake, translocation, accumulation, and detoxification of As, Cd, Pb, and Zn by hyperaccumulating plants. We also answer questions that pertain to the extent of microbial participation in the accessibility of PTEs by hyperaccumulators. The implications of specific rhizosphere microbes in reworking PTEs during phytoextraction by hyperaccumulators deserve critical attention. Knowledge of the intensity of accumulation of exaggerated content of As, Cd, Pb, and Zn by plant hyperaccumulators is essential in avoiding the detrimental effects on soils and living things.

2 Data acquisition and proceedings

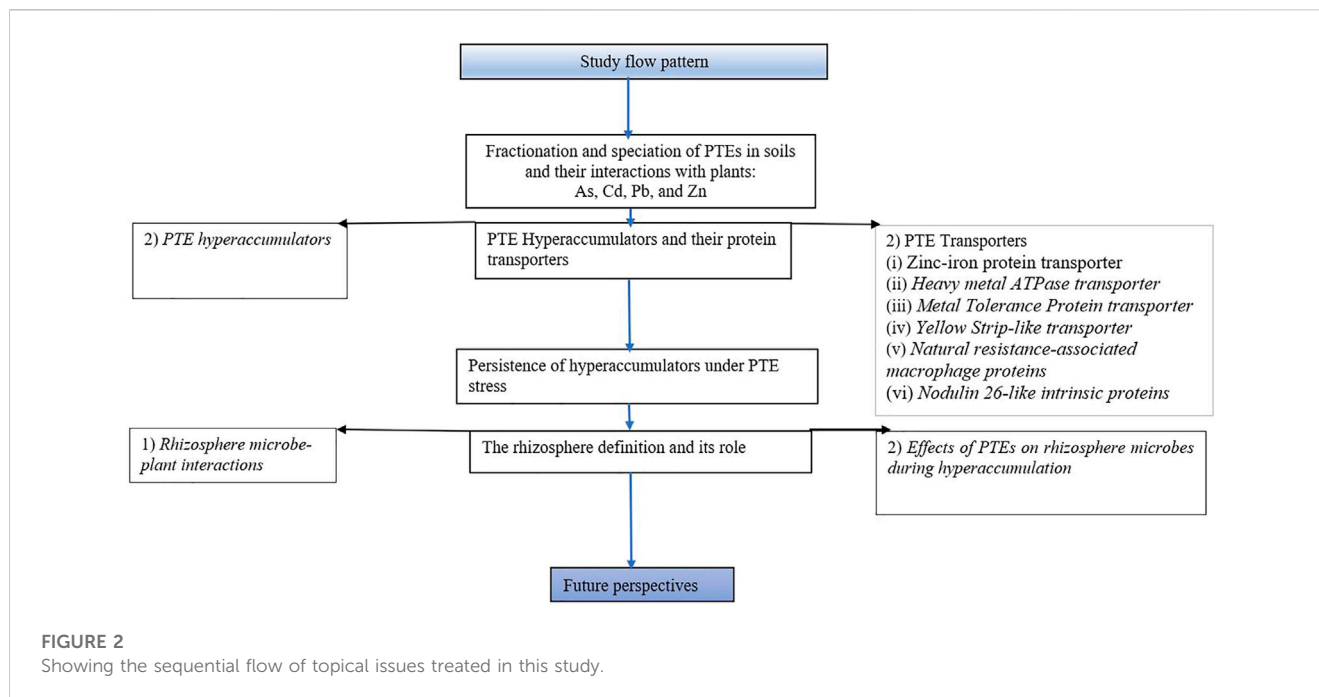
Relevant peer-reviewed publications covering sub-headings of this study were critically elucidated from ScienceDirect, Google Scholar, Web of Science, ResearchGate, and Scopus in the last decades to date to satisfy the flow chart in Figure 2. We used the search engines to elaborate on keywords, including the impacts of PTEs on the environment, processes of PTE uptake and translocation in plants, and effects of plant hyperaccumulators on microbes growing on PTE-contaminated soils.

3 Fractionation and speciation of PTEs in soils and their interactions with plants

Different elements are well-categorized by their physicochemical forms in soils, especially in organic complexes, adsorbed in solid phases or constituents of solid/mineral phases, with diverse solubility (Wu et al., 2019; Salman et al., 2021). Plant-accessible forms represent the exchangeable complexes (organic and inorganic components) and soluble forms in soil solution taken predominantly by plants as divalent ions.

The principles underlying the mobility (e.g., high pH, redox dynamics) and immobilization (e.g., high OM contents, soil colloids) may individually or collectively complement the dynamic of elements in soils (Wu et al., 2019; Zemanová et al., 2021). For example, PTEs undergo reactive dissolution leading to bioavailability in highly acidic soil (Kicińska et al., 2021). Again, OM reduces the mobility of PTE due to high negative charges that adsorb cationic elements (Sarkar et al., 2021).

- (i) **Arsenic (As):** Various forms of As in soils include free ionic species, precipitated as solids, adsorbed on organic or inorganic constituents, and the exchangeable and structural composition of primary and secondary minerals (Shahid et al., 2014; Joseph et al., 2015). Inorganic species of As (As^(III) and As^(V)) are present in forms such as fully protonated As or arsenous acids (Fayiga and Saha, 2016). Arsenate (AsO₃⁻⁴) is more stable and quickly adsorbed to surfaces of clay minerals and Fe/Mn (hydro) oxides (Khalid et al., 2017), while under reduced soil conditions,



arsenite ($\text{As}(\text{OH})_3^0$) becomes highly toxic, soluble, and mobile for easy plants availability (Zemanová et al., 2021). Both $\text{As}^{(\text{V})}$ and $\text{As}^{(\text{III})}$ are highly soluble in H_2O and may change valency states depending on the pH (Parvin et al., 2021) and Eh (da Silva et al., 2018).

In As contaminated soils, organoarsenicals, e.g., monomethylarsenic (MMA), dimethylarsenic (DMA), tetramethylarsonium (TMA), trimethylarsine oxide (TMAO), and tetramethylarsonium ion (TETRA) usually represent a minor component or are not detected in many soils (Shrivastava et al., 2015). Arsenic can undergo oxidation, reduction, methylation, and demethylation in soils under the modulation of microorganisms (Di et al., 2019). Arsenic mobility, availability, and toxicity in the soil-to-plant system depend on the oxidation states of As (da Silva et al., 2018).

(ii) **Cadmium (Cd)**: Cadmium occurs in a soluble and exchangeable portion, precipitated with carbonates, occluded in amorphous Fe/Mn oxides, complexed with OM, and residual forms (Wiggenhauser et al., 2021). In soils, Cd can bind with colloids and organic amendments (e.g., hydroxyapatite-phosphate materials) to reduce mobility (Zeng et al., 2020). High alkaline soils constitute Cd precipitates ($\text{Cd}(\text{OH})_2$), a condition for low accumulation by plants (Gong et al., 2021; Asare et al., 2023). Additionally, low Eh can induce reductive dissolution of Fe and Mn oxides, which release bonded Cd into soil solution and increase bioaccessibility (Izquierdo et al., 2017; Wu et al., 2019).

(iii) **Lead (Pb)**: Lead in soils exists as a free metal ion, mostly complexed with inorganic components (e.g., PbCO_3^{2-} , PbHCO_3^- , PbSO_4^{2-} , and PbCl_2^-), or occurs as organic ligands (e.g., humic and amino acids) (Lodygin et al., 2020). Ionic Pb, Pb^{II} , Pb oxides and hydroxides, and Pb-metal

oxyanion complexes are the general forms released into soils. Organo-Pb compounds of commercial and toxicological value are predominantly limited to the alkyl (methyl and ethyl) Pb compounds and their salts (e.g., diethyl-Pb-dichloride, dimethyl-diethyl-Pb, and trimethyl-Pb-chloride) (Wang and Mulligan, 2006). Lead shows a high affinity to soil OM and colloidal surfaces, thus, reduces, its availability in plants. Free Pb in soils often remains the only phyto-available form (Punamiya et al., 2010).

(iv) **Zinc (Zn)**: The mobility and immobilization of Zn in soils are associated with chemical fractions; Fe/Mn oxide bound, residual (immobile), OM bound, carbonate bound, exchangeable, and soluble in H_2O (Đurić et al., 2021). Soluble forms of Zn, such as ZnSO_4 , are moderately mobile in many soils. Zinc content in contaminated soils occurs in immobile forms (Sharma et al., 2013). Studies show that most agricultural and industrial activities result in a high fraction (>70%) of inaccessible Zn by plants with availability (exchangeable and carbonate forms) of >30% (Mertens and Smolders, 2013; Liao et al., 2019).

In soils with free molecular oxygen, reductive dissolution of Fe/Mn (hydr)oxides releases Zn into the aqueous phase, which repartitions with Zn into sulfide and carbonate solids. In dry oxidized soils, Zn relates with (hydr)oxide phases, and in flooded systems, sulfides and carbonates (Mondillo et al., 2018). In general, the speciation and bioavailability of As, Cd, Pb, and Zn in soils are individually or collectively associated with soil reaction (pH), redox potential (Eh), dissolved organic carbon, clay content, Fe/Mn/Al (hydr)oxides, and microbial processes (Dary et al., 2010; Sungur et al., 2020).

Meanwhile, plants modulate the mobility and accessibility of PTEs by discharging root exudates: oxalic, fumaric, malic, and acetic acids (Lapie et al., 2019), which enhance solubilization. However,

TABLE 1 Contents of As, Cd, Pb, and Zn in plant hyperaccumulators from different studies.

Hyperaccumulator/family	Frequent occurrence	Soil content (mg kg ⁻¹)	Content of elements in the plant (mg kg ⁻¹)		References
			Leaf	Shoot	
As					
<i>Pteris vittata</i> L./Pteridaceae	Indigenous Asia, southern Europe, tropical Africa, and Australia	18.8–1,603	4,240–6,030	3,280–4,980	Ma et al. (2001) Visoottivisetha et al. (2002)
<i>Pteris vittata</i> Linn/Pteridaceae		12,300			
<i>Isatis cappadocica</i> Desv./Brassicaceae	Native in Iran, Iraq, Lebanon-Syria, Transcaucasia, and Türkiye		>200	350	Karimi et al. (2009)
<i>Brassica juncea</i> L./Brassicaceae	Eastern Europe and China, where the range of its parent species	As-fed in hydroponics		>2000	Karimi et al. (2009)
<i>Pityrogramma calomelanos</i> L./Parkeriaceae	Native in Mexico, Central, and South America	12,300	8,350		Visoottivisetha et al. (2002)
<i>Berkheya coddii</i> Roessler/Asteraceae	Tropical Africa, especially in southern regions		4,100		Mesjasz-Przybyłowicz et al. (2004)
Cd					
<i>i. Viola baoshanensis</i> /Violaceae <i>ii. Lysimachia deltoidea</i> Wight/Primulaceae	(i) Native in Southeast China. (ii) Native in parts of China East Himalaya, India, Laos, Myanmar, Nepal, Sri Lanka, Thailand, Vietnam			(i) 1,090	Wu et al. (2010)
				(ii) 212	
<i>(i) Nocceae caerulenscens</i> (J.Presl & C.Presl)/Brassicaceae	(i) Native to Eastern and Central Europe. Introduced to Baltic States, Belarus, Central European Rus			(i) 160	Bridgwater et al. (1999)
<i>(ii) Euphorbia cheiradenia</i> Boiss. & Hohen/Euphorbiaceae	(ii) Native in Afghanistan, Iran, Iraq, Lebanon-Syria, Palestine, Türkiye			(ii) (ii) 237	
<i>Viola baoshanensis</i> /Violaceae		663		>1,000	Liu et al. (2004)
<i>Arabidopsis hellari</i> /Brassicaceae				>400	Mohiley et al. (2021)
			Leaf	Shoot	
Pb					
<i>(i) Viola baoshanensis</i> /Violaceae <i>(ii) Silene viscidula</i> Franch/Caryophyllaceae <i>(iii) Silene gracilicaulis</i> C. L. Tang/Caryophyllaceae	Native in parts of China, East Himalaya, India, Laos, Myanmar, Nepal, Sri Lanka, Thailand, Vietnam			(i) 1902 (ii) 3,930 (iii) 3,617	Wu et al. (2010)
<i>Betula occidentalis</i> Hook/Betulaceae			>1,000		Koptsik (2014)
<i>Euphorbia cheiradenia</i> Boiss. & Hohen/Euphorbiaceae	Native in Afghanistan, Iran, Iraq, Lebanon-Syria, Palestine, Turkey	-		967	Bridgwater et al. (1999)
Zn					
<i>Euphorbia cheiradenia</i> Boiss. & Hohen/Euphorbiaceae				3,614	Bridgwater et al. (1999)
<i>Nocceae caerulescens</i> (J.Presl & C.Presl)/Brassicaceae	Native to Eastern and Central Europe. Introduced to Baltic States, Belarus, Central European Rus		2,100		Lombi et al. (2002)

(Continued on following page)

TABLE 1 (Continued) Contents of As, Cd, Pb, and Zn in plant hyperaccumulators from different studies.

Hyperaccumulator/family	Frequent occurrence	Soil content (mg kg ⁻¹)	Content of elements in the plant (mg kg ⁻¹)	References
<i>Cratogeomys sumatranum</i> Jack/Hypericaceae	Indigenous to Southeast Asia		555	Castañares and Lojka. (2020)
(i) <i>Gentiana</i> sp./Gentianaceae (ii) <i>Potentilla griffithii</i> Hook. fl./Rosaceae (iii) <i>Silene viscidula</i> Franch/Caryophyllaceae	(i) Occur in north-western Africa, eastern Australia, and New Zealand (ii) Native in China South-Central, East Himalayas, Nepal, and Tibet (iii) Native in China and grows in the temperate biomes		(i) 19710 (ii) 8,748 (iii) 11,155	Wang et al. (2009)
<i>Pisum sativum</i>		1,656	18700	Wioleta et al. (2015)

root exudates can remove PTEs by chelating and complexation, altering the numbers and activity of rhizosphere microbes (Jing et al., 2014; Lapie et al., 2019). Uptake of PTE is partly possible via diffusion into the root epidermis. However, the primary passage occurs via the apoplast and symplast (Yan et al., 2020). Apoplastic movement involves several transporter proteins for uptake and translocation (Guerinot, 2000). Casparian strips represent an apoplastic restriction of PTE, especially Pb (Wang et al., 2015; Wilkins et al., 2016). The uptake of PTEs through the symplast is well-governed by metal carriers or complexing agents (Asare et al., 2023). Chelation resulting from the production of phytochelatin can result in the immobilization of PTEs in roots (Flores-Cáceres et al., 2015) while remaining PTEs sequester in cellular organelles. Cadmium, As, Pb, and Zn sequestered inside the vacuoles can transport into the stele and enter the xylem via the root symplast (Thakur et al., 2016). In the apoplast, many precipitated forms of compounds, e.g., CO²⁻³, get immobilized. However, the mobile fractions of PTEs at this point are translocated via the apoplast or symplast movement into leaves and sequestered in extracellular parts to stop compartmental cellular accumulation (Tong et al., 2004).

4 PTE hyperaccumulators and their protein transporters

4.1 PTE hyperaccumulators

Several plants can accumulate As, Cd, Pb, and Zn above threshold levels in aboveground organs. At the organ level, leaves are well-considered in establishing the hyperaccumulating statuses of plants (Yan et al., 2020; Lima et al., 2022). Hyperaccumulators of PTEs have distinguished physiological properties capable of sequestering high contents of PTEs at a high rate (Lima et al., 2022).

Due to health and ecotoxicological reasons, PTE contents in plants have assigned global and regional permissible limits. According to WHO (1996), the content of (in mg kg⁻¹) As- 0.1, Cd- 0.02, Pb- 2, and Zn- 0.60 should not exceed the standard reference in plants. The use of translocation (root-to-shoot quotient, TF) and bioaccumulation (plant-to-soil quotient, BF) factors over 1 are vital parameters when associated with permissible limits of PTEs determining plant hyperaccumulating abilities (Ghori et al., 2016; Souri et al., 2017). Many hyperaccumulating plant species, including *Lysimachia deltoidea* L., *Viola baoshanensis* (W. S. Shu), *Silene gracilicanlis* L., and *Gentiana* sp. exhibit translocation factors >1 for Cd, Zn, and Pb (Reeves and Baker, 2000; Table 1).

Studies show that Cd, Pb, and Zn-hyperaccumulator can accumulate (in mg kg⁻¹ dry weight) > 100 (Baker et al., 2000), >1,000 (Baker et al., 2000), and 3,000 (Reeves and Baker, 2000), respectively, in any above-ground organ. According to Baker and Whiting (2002), these high contents only provide guidelines in recognition of the extreme behavior of plants during PTE uptake. High consideration is, thus, given to the content of PTEs in contaminated soils and their respective accumulation by the aboveground biomass, especially in the case where BF > 1. Plant species such as *Pteris vittata* L. (Danh et al., 2014) and *Isatis cappadocica* Desv (Karimi et al., 2009), hyperaccumulate As. For example, *Pteris vittata* adopts a mechanism of arsenate and arsenite

uptake, translocation, and vacuolar sequestration (Danh et al., 2014), while the stem and shoot remain unaffected by As stress (Sridhar et al., 2011). Many hyperaccumulators possess multiple abilities in accumulating several PTEs. Wu et al. (2010) observed that *V. baoshanensis* accumulated (in mg kg⁻¹) 1,090 of Cd, 1,902 Pb, and 3,428 Zn in the shoots.

4.2 PTE transporters

Plant uptake and subsequent transport of PTEs are well-mediated by complex sequences. Many specialized protein transporters in different plant parts exhibit diverse abilities for PTE translocation, maintaining homeostasis, and controlling ion movements across cellular channels from roots to shoots (Ricachenevsky et al., 2013; Mishra et al., 2017). These transporters enable the re-mobilization of sugar molecules from photosynthetic tissues in leaves to roots, stems, and seeds through phloem loading. Primary protein transporter families for PTEs include;

Zinc/iron protein transporter (ZIP): Most divalent cationic elements (Cd, Ni, Cu, Co, and Fe), especially Zn, undergo uptake and active translocation in the plant system by ZIP and associated transcription genes (Table 2). Another subfamily, the iron-regulated transporters (IRTs), are implicated mainly in the transport of Fe (Verret et al., 2004). The IRT is also responsible for Cd transport in the *Arabidopsis* (Lee and An, 2009).

Metal tolerance protein (MTPs): This transporter transports metals at the whole plant level (Desbrosses-Fonrouge et al., 2005) and regulates homeostasis and active Zn translocation (Ricachenevsky et al., 2013). The MTP transporters have different sub-families; *Fe/Zn-MTP*, *Zn-MTP*, and *Mn-MTP* (Shirazi et al., 2019), and can exist in several accessions from *MTP1* to *MTP12* (Shirazi et al., 2019).

Members of this family and their accessions partly mediate Co, Ni, and Cd transport. Studies have previously shown *MTP1* in *Hordeum vulgare* (*HvMTP1*), *Oryza sativa*- (*OsMTP1*), and *Cucumis sativus* (*CsMTP1*), with *MTP3* and *MTP4* in *A. thaliana* and *Cucumis sativus*, respectively, into different compartments (Shahzad et al., 2010; Yuan et al., 2012).

Yellow Strip-like transporter family (YSL): YSL is well-known for the transport of Zn and Cd; described as an essential regulator of excess Zn together with Ferric Reductase Defective3 (*FRD3*), a MATE (multi-drug and toxin efflux) transporter (Pineau et al., 2012). They mediate the cellular uptake of metals that form complex to non-proteinogenic amino acids (Socha and Guerinot, 2014). According to DiDonato Jr et al. (2004), *YSL2* is expressed in many cell types in roots and shoots of *Arabidopsis* and represents a metal-regulated gene encoding transporter of nicotianamine-metal complexes. In *A. thaliana*, *YSL4* and *YSL6* buffer the adverse effects of excess Fe (Divol et al., 2013).

Natural resistance-associated macrophage protein (NRAMP): The functions of the NRAMP were previously related to Fe²⁺ uptake and translocation (Williams and Mills, 2005; Mishra et al., 2017). The NRAMPs are well-identified in varied compartments of *Arabidopsis*, and other monocot and dicot, governing the transport of divalent PTEs, e.g., Cd, Zn, and Pb (Bastow et al., 2018).

Nodulin 26-like intrinsic proteins (NIP): NIPs are cationic element transporters, including Si, Se, As, and Sb. Various species of As in soils are loaded into plants by NIP (Zhao et al., 2008; Chen et al., 2016). Evidence of As^(V) species transport in *P. vittate* and *I. cappadocica* was well-demonstrated by Su et al. (2008) and Karimi and Souri (2015).

Different groups of transporters control the transport of specific PTE (Figure 3).

i. Arsenic transporters

Plant roots select As species by distinct transporters. For instance, in *A. thaliana*, As^(V) uptake is mediated by phosphate (*PHT*) transporters *AtPHT1*, 4, 5, 7, 8, and 9, while the *NIP1-3*, 5, and 7 for As^(III) (Xu et al., 2015). Moreover, NIP has shown evidence in root-to-shoot translocation of As^(III) (LeBlanc et al., 2013), with *ACCC1* and 2 responsible for cellular transport of As^(III) in the cytosol while in the presence of phytochelatins (Song et al., 2010).

Another transporter pertinent in As^(III) is the tonoplast intrinsic protein (*TIP*) determined in *P. vittate* (He et al., 2016). Gene expressions, such as *NIP1;1*, *NIP1;2*, *NIP3;1*, *NIP5;1*, *NIP6;1*, and *NIP7;1*, are capable of coordinating H₃AsO₃ from the root and their subsequent transport (Bienert et al., 2008; Xu et al., 2015). The unanswered question so far is, are the same transporters solely for As species transport in hyperaccumulating plants?

ii. Cadmium transporters

Transporters *Nramp*, *HMA*, *ZIP*, *ATP*, *YSL*, and *ABC* (ATP Binding Cassette) families are involved in Cd distribution. The *Nramps* are well-identified in different compartments of *Arabidopsis*, and other monocots and dicots, Cd transport (Bastow et al., 2018). Meanwhile, *Nramp1*, 3, and 4 are often in charge of Cd above-organ accumulation in *A. thaliana*. *Nramp6* is a Cd transporter, which mediates Cd transport from storage into the toxic cellular compartment. Gene transcription *NcNramp1* in *N. caerulea* regulates Cd influx across the endodermal plasma membrane, which implies possible root-to-shoot transport (Milner et al., 2014).

HMA1 is an efflux transporter localized in the chloroplast and controls the export of Cd from the chloroplast. *HMA2* is a plasma membrane transporter involved in Cd root-to-shoot translocation, while overexpression of *AtHMA3* enhanced Cd tolerance and increased its accumulation (Morel et al., 2009). *AtHMA2* and *AtHMA4*, localized in the plasma membrane, are responsible for the xylem loading of Zn/Cd and play a key role in their accumulation in the shoots (Takahashi et al., 2012). Heavy-metal ATPase transporters are responsible for the long-distance transport of Cd from root to shoot. Additionally, gene expressions *HMA4* and *HMA2* regulate the influx of Cd into the stele to promote root-to-shoot transport in *Arabidopsis* (Mishra et al., 2017).

YSL family involved in Cd transport include *YSL1*, *YSL3*, *YSL6*, and *YSL7* (Curie et al., 2009). An excess of Cd can stimulate the expression of YLS. Overexpression of *YSL1* or *YSL3* in *Arabidopsis* increases the Cd translocation ratio under Cd stress (Tao and Lu, 2022).

iii. Lead transporters

TABLE 2 Examples of types of protein transporter and function.

Transporter (gene expression)	Example of hyperaccumulators	PTE	Part of plant	Function	References
Zinc-iron protein (ZIP) (<i>NcZNT1</i>)	<i>Noccaea caerulescen</i>	Zn	Stele in root	The radial movement to stele in roots	Van de Mortel et al. (2006)
<i>ZIP23</i> , <i>ZIP19</i> , <i>ZIP5</i> , and <i>IRT3</i>		Zn	Vacuole in the root	Vacuole storage and transported to the endodermis	Balafrej et al. (2020)
<i>ZNT2</i> , <i>ZNT5</i>		Zn	Root	Transport in the root cortex	Balafrej et al. (2020)
<i>ZIP4</i> , and <i>IRT3</i>			Root, shoot	Root-to-shoot translocation	Balafrej et al. (2020)
Heavy metal ATPases (HMA)					
<i>HMA3</i>	Many plants, e.g., <i>Arabidopsis halleri</i>	Zn, Cd, and Pb	Vacuole	Sequestration of Zn, Cd, and Pb into the vacuole	Hanikenne and Baurain (2014), Liu et al., 2018
<i>HMA4</i>	<i>N. caerulescens</i> and <i>Arabidopsis halleri</i>	Cd, Pb, Zn	Root and shoot	Xylem loading of Cd, Pb, and Zn for root-to-shoot transport	Mishra et al. (2017)
<i>HMA 2</i>	<i>Arabidopsis halleri</i>	Cd and Zn	Shoot	Hyper-tolerance	Frérot et al. (2018)
Metal Tolerance Protein (MTP)					
<i>MTP1</i>	<i>Arabidopsis thaliana</i> (Non-hyperaccumulator)	Zn	Vacuole and plasma membranes	Accumulation and tolerance	Desbrosses-Fonrouge et al. (2005)
Yellow Strip-like					
<i>YSL2</i>	<i>Arabidopsis</i>	Zn and Cd	Root and shoot	xylem loading	Curie et al. (2009)
Nodulin 26-like intrinsic proteins (NIP)					
<i>HvNIP1:2</i>	<i>Hordium Vulgaris</i>	As	Root	As uptake	Chen et al. (2016)
<i>NIP1;1</i> , <i>NIP1;2</i> , <i>NIP3;1</i> , <i>NIP5;1</i> , <i>NIP6;1</i> , and <i>NIP7;1</i>	<i>Oryza sativa</i> , <i>Hordium Vulgaris</i> , <i>Pteris vittata</i> 's	H ₃ AsO ₃	Root	root uptake	Chen et al. (2016); He et al. (2016)

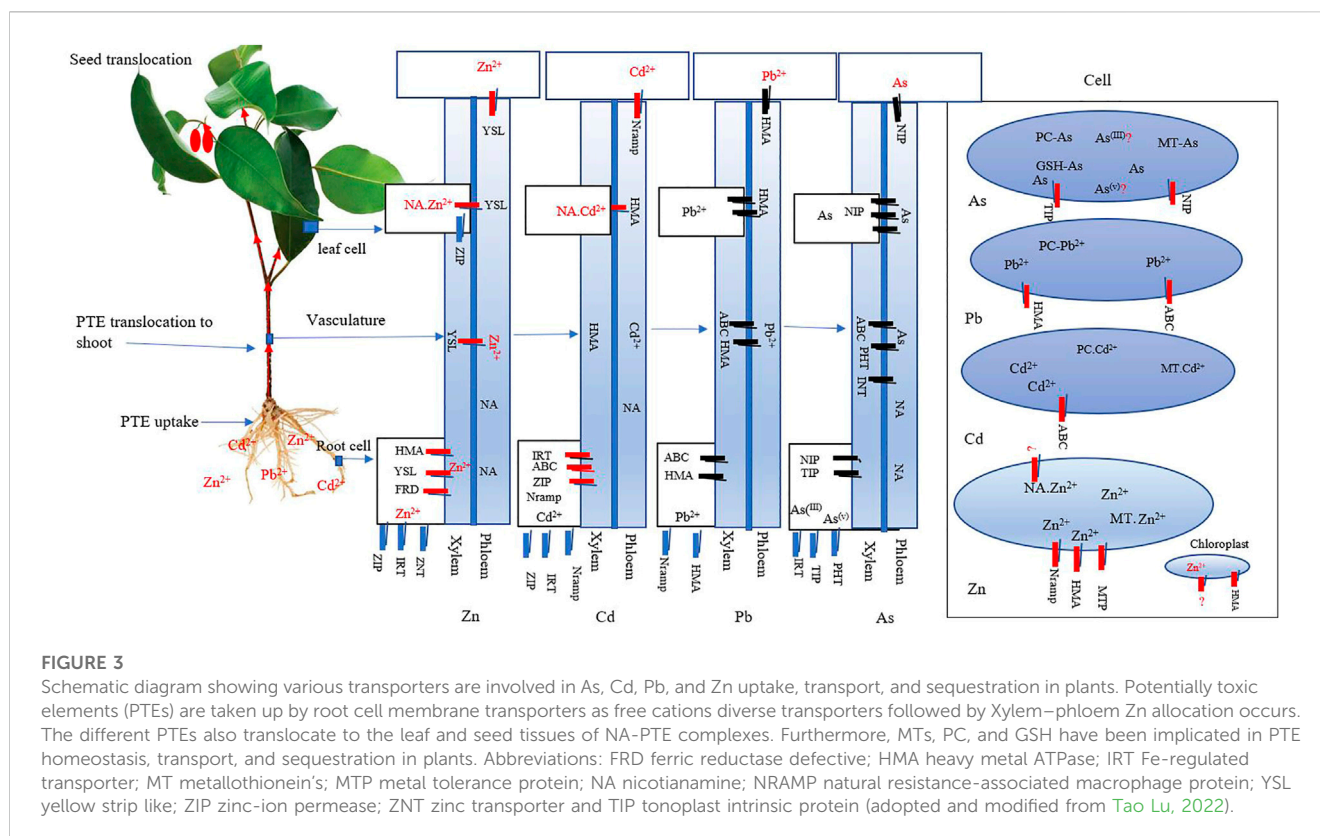
NRAMP transporter family has been noted with the uptake of Pb, e.g., in *O. sativa* (Qiao et al., 2021). *HMA3*, a vacuolar P1B-ATPase, mediates the sequestration of Pb²⁺ and other cationic metals, into the vacuole of different plant species (Liu et al., 2018). ABC transporters and their subfamilies also modulate Pb transport. For example, the transcription gene *ABCG36* of poplar hybrid located on the plasma membrane transports Pb²⁺ from the cytoplasm across the plasma membrane (Abolghassem et al., 2015). Expression *ABCG48* was upregulated in the shoots and roots of plants treated with Pb²⁺ (Abolghassem et al., 2015). A homolog of *HMA5* in poplar, *PtHMA4*, was also found to be localized at the plasma membrane. Meanwhile, the upregulation of Pb in the root by *PtHMA4*, suggests Pb from roots to shoots (Qiao et al., 2021). In *Arabidopsis halleri* L, *AtHMA3* participates in Pb²⁺ sequestration by transporting it to the vacuoles (Hasan et al., 2017).

iv. Zinc transporters

ZIP transfers Zn to the stele in roots. For example, *Noccaea caerulescens* (J. Presl. & C. Presl.) and *A. halleri* exhibit improved Zn uptake (Assunção et al., 2001) and are represented by *ZNT1* (Van de Mortel et al., 2006). The *NcZNT1* gene expression and *AtZIP4* for *A. thaliana* are active in the cortex, endodermis, and pericycle cells. These expressions are also in the same tissues of *N. caerulescens* but are not limited to Zn-deficient conditions (Van de Mortel et al., 2006; Lin et al., 2016). Zinc transporter 2 (*ZNT2*) and *ZNT5* are also responsible for Zn²⁺ transport in the root cortex or by diffusion (Lin

et al., 2016). The Zn ion is sequestered for vacuole storage and transported to the endodermis by *ZIP23*, *ZIP19*, *ZIP5*, and *IRT3*. Zinc ion transport stops by the apoplastic barrier (e.g., Casparian strip) and enters the endodermis via *ZNT1/ZIP4*. Transcriptional-level analysis shows that *HMA2* and *HMA4* form vital components of Zn hyperaccumulation and hyper-tolerance in *A. halleri* - *AhHMA2* and *AhHMA4* (Hanikenne et al., 2008; Frérot et al., 2018). Moreover, in the root pericycle, *AhHMA2* and *AhHMA4* promote Zn²⁺ efflux and loading in the root xylem (Hussain et al., 2004). Again, *HMA3* mediates the sequestration of cationic Zn into the vacuole.

Zinc can transport from the root to shoot by *ZIP4* and *IRT3*, form chelates, or possibly diffuse into the pericycle cells (the outermost part of the stele). Enhanced accumulation of Zn in the shoot by overexpression of *IRT3* was suggested by Balafrej et al. (2020). Meanwhile, Zn enters the leaf cell either in chelation with low-molecular-weight ligands or as free Zn²⁺ complemented by *ZIP4* and *ZIP6* (Sinclair and Kramer, 2012). Several gene transcriptions from different transporters (e.g., *MTP1* and 8, *HMA3* and 4, and *NRAMP3*) promote the transport of Zn into the vacuole. The long-distance root-shoot translocation of Cd and Zn is solely responsible for *HMA4* (Verret et al., 2004). Additionally, overexpression of *HMA4* enhances Zn²⁺ efflux from the root symplast into the xylem vessels and promotes metal tolerance (Verret et al., 2004). After Zn loading in the xylem by different transporters: *HMA*, *ZIP*, and *YLS*, Zn reaches the leaves, where it binds to organic acids, e.g., malate and citrate, and sequesters in vacuoles. Unchelated Zn at the



apoplastic barrier reaches the xylem through YSL or direct diffusion. Zn^{2+} crosses the xylem as free Zn or coupled with histidine, citrate, or malate (Tao and Lu, 2022). YSL transporters are also known for loading and unloading Zn in the xylem (Curie et al., 2009).

5 Persistence of hyperaccumulators under PTE stress

Plants, especially hyperaccumulators, either tolerate or detoxify PTEs to persist under high PTE (Dalvi and Bhalerao, 2013). Already taken ionic PTEs must undergo intracellular mechanisms to tolerance, including (a) cellular and subcellular compartmentalization of PTEs, (b) formation of chelates-reducing the toxicity of ionic forms of PTEs (Dalvi and Bhalerao, 2013), and (c) transportation capability. Meanwhile, other detoxification approaches involved in PTE tolerance in plants, such as PTE-immobilization in cell walls, impeded permeation across cell membranes, and active export into the apoplast (DalCorso et al., 2019).

Stress from PTEs triggers the production and accumulation of bioactive substances in plants. For instance, proline accumulation results from Cd, Pb, and Zn stress on plants (Roy and Bera, 2002). The detoxification process begins as proline (comprised of amino acids) chelates with PTE (Rai, 2002). Inadequate detoxification increases PTEs accumulation in the cytoplasm, enabling the release of reactive oxygen species (ROS). Excess production of ROS results in oxidative stress, may disrupt cell homeostasis, inhibit cellular processes, DNA damage, and protein oxidation

(DalCorso et al., 2019). In PTE-induced oxidative damage, plant cells activate the ROS-scavenging system, which induces antioxidant enzymes (e.g., superoxide dismutase, catalase, peroxidase, and glutathione reductase) and non-enzymatic antioxidant compounds, e.g., metabolites (DalCorso et al., 2019).

- Arsenic (As):** In the cells of roots, As is converted to less toxic forms, transported to vacuoles as As^{III} , and forms complexes with glutathione/phytochelatins (Souri et al., 2017). The formation of As^{III} complexes with γ -glutamyl-cysteinyl-glycine and phytochelatins (PC) and their transport into roots and shoots forms the dynamics of As coping (Souri et al., 2017). In the vacuole, As is predominantly sequestered in the form of phytochelatins (PC)-As or GSH (glutathione) conjugates (Kumar et al., 2015). Thus, the transporters responsible for vacuole sequestration of PC-As or GSH-As conjugate control As detoxification. Volatile fractions of reduced organo-arsenicals taken up by plants partly disappear via stomatal openings during phytovolatilization (Limmer and Burken, 2016).

For instance, As uptake by *P. vittata* is achieved through a high-affinity phosphate transport system, having the ability to store complexes in vacuoles of leaf cells (Singh et al., 2016). Ionic forms of PTE can sequester into petioles, sheathes, and trichomes of leaves (Eapen and D'souza, 2005; Yan et al., 2020). Transport systems with the ability to store complexes in vacuoles of leaf cells (Singh et al., 2016). Meanwhile, organic acids within cells prevent PTEs as free ions in the cytoplasm by forming complexes. However, this reduces the further availability of PTEs. For

example, Malate is involved in the chelation of Zn in *A. halleri* (Shanmugam et al., 2013). Translocated As species are partly detoxified by ABC and ACR3 (arsenite transporters), an arsenic transporter (Thounaojam et al., 2021).

(ii) *Cadmium* (Cd): Plants exhibit efficient strategies to respond to Cd in their environments. In the root, Cd forms chelate with ligands in the cell wall, cytoplasm, and vacuole resulting in its immobilization, thereby losing toxicity (Ali et al., 2013). Root vacuole storage of Cd reduces its toxicity and long-distance transport to shoot (Thakur et al., 2016). Cd is sequestered in shoots, and detoxification occurs in cell walls or plant vacuoles. The main mechanism of PC-mediated Cd detoxification is chelation by PCs to form a complex, which is then transported into the vacuoles by ABC transporters (Vatamaniuk et al., 2000; Zhang et al., 2018). Again, metallothionein, minute peptides that contain cysteine also act as cytoplasmic Cd chelation proteins (Zhang et al., 2013). Studies show that the cell wall, particularly pectin increases plant Cd tolerance by preventing Cd from entering root cells (Gutsch et al., 2018). The studies by Luo and Zhang, (2021) indicate that the expression of different genes occurs in the cell wall, which supports Cd hyperaccumulation and detoxification, e.g., in *Sedum plumbizincicola*.

In *Brassica napus* (*Bna*), ABC sub-transporters *BnaABCC3* and *BnaABCC4* were upregulated under Cd stress and enhanced Cd tolerance by limiting the entry of Cd inside the cells and their phytochelatin-mediated detoxification (Yamaji et al., 2013).

(iii) *Lead* (Pb): Pb in plant tissue activates cellular responses and changes in signaling mechanisms and gene expression (Kumar and Prasad, 2018). These mechanisms trigger the release of specific metabolites, e.g., phytochelatin (PC), glutathione, and metallothionein (Estrella-Gómez et al., 2009). These bioactive materials, e.g., PC effectively bind with Pb and transport it to the vacuole, where detoxification of Pb occurs. Reportedly, Pb accumulation in plant tissues increases the expression of the PCS gene with a concomitant increase in PCs in aquatic fern *Salvinia minima*, a known Pb-hyperaccumulator (Estrella-Gómez et al., 2009). Increased synthesis of PCs reduces free Pb content in the cytoplasm and shows a strong correlation with the suppression of stress-related responses in plants (Estrella-Gómez et al., 2009). Finally, PTE complexation with glutathione, amino acids, and PCs is transported to the tonoplast or vacuole, where active detoxification and cell removal occur.

(iv) *Zinc* (Zn): Firstly, Zn storage in root vacuoles is used as a mechanism of Zn exclusion from the shoot in the presence of excess Zn influx into roots or excess Zn supply in the soil (references). The accumulation of Zn in different cells, e.g., trichomes, is thought to act as a detoxification and storage strategy under excess Zn growth conditions (Ricachenevsky et al., 2021). Zinc import into subcellular compartments is also a vital detoxification strategy. Meanwhile, studies show that AtHMA3 is involved in the vacuole sequestration of Zn²⁺ and the overexpression of AtHMA3 resulting in hyper-tolerance in *A. thaliana* (Miyadate et al., 2010).

6 The rhizosphere definition and its role

The rhizosphere elaborates on the root system and its close soils that foster biological and chemical activities, e.g., by exudation, for plant security and growth (Hartmann et al., 2009; Chamkhi et al., 2022). Rhizosphere represents nutrient-rich zones in soils that exhibit the capacity to perform extended functions for plants during stress (Chamkhi et al., 2022). However, the region supports beneficial and non-cooperative associations between rhizosphere microbes and plants (Figure 4). Due to the diverse root structure, the rhizosphere may exhibit varied size ranges. Hence, the properties of this region change only along roots. Meanwhile, about 90% of plants have roots extending from 0.27 to 0.9 m in soils, with a few reaching 1.82 m (Gilman, 1990).

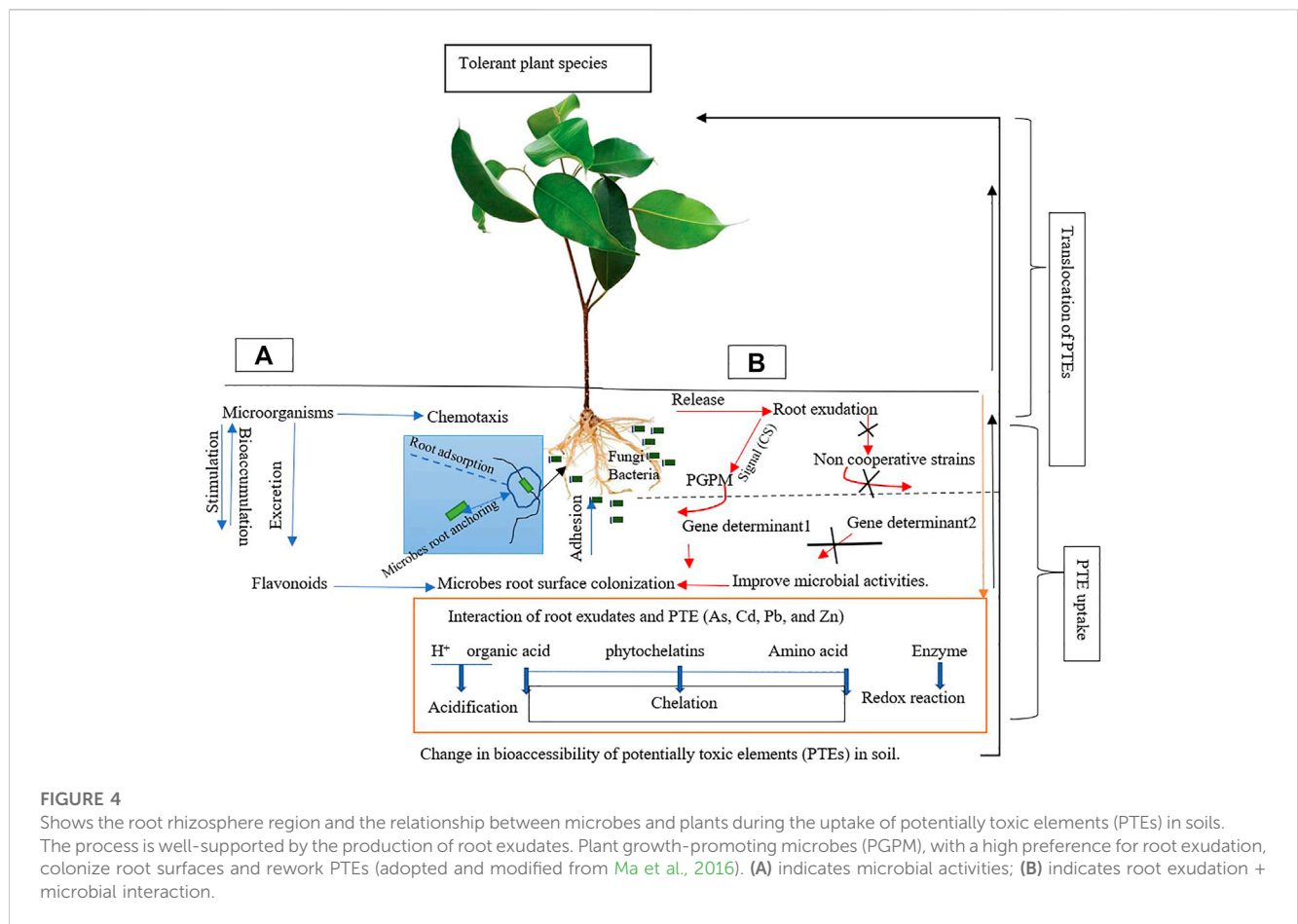
The secretion of different bioactive (metabolites) compounds directing depends on the type of plant (genotype) and stress elicitor (e.g., abiotic and biotic). For example, roots can discharge their photosynthetically fixed C- into the soil (Sasse et al., 2018). The composition of exudates significantly impacts the activities and microbial count and diversity. Increased microbial count and activities in rhizosphere regions are a function of metabolite discharge (Sasse et al., 2018). Microbial preferences in the rhizosphere also depend on the influence of root exudates, which can affect the dissolution of PTEs for effective uptake. Hence, exudate patterns are vital drivers that shape the rhizosphere microbiome (Zhalnina et al., 2018) and are plant species-specific (Gianfreda, 2015).

Knowledge of the soil–root interface is pertinent to managing microorganisms, increasing plant growth, and reducing the effect of plant production. However, with the identification of plant genomes and the genes induced under different PTE stress, e.g., encoding for transporter proteins, metal sequestering peptides, and enzymes metabolism in plants, the principles governing PTEs uptake, accumulation, transport, chelation, and detoxification provide vital information for effective soil decontamination.

6.1 Rhizosphere microbe-plant interactions

Rhizosphere microbes exhibit movement to discharge pulses along plant roots (Hünninghaus et al., 2019) and play a vital role in regulating nutrition in plants, e.g., N fixation (Xiong et al., 2021). These microbes can compete and populate the root rhizosphere (Schreiter et al., 2018; Mulero-Aparicio et al., 2019). The attraction of microbes to the rhizosphere depends on the characteristics of the roots. Microbe-plant interaction in the rhizosphere involves chemical processes that partly account for the chelation and solubilization/dissolution of PTEs to promote mobility or immobilization (Figure 4). Although some microbes may not show a direct affinity for root exudates and many physicochemical properties of soils, especially toward the dissolution of PTEs, but contribute to their detoxification in soils. For example, *Bacillus subtilis* shows high tolerance and adsorption for Cd and Pb, a means of detoxification and elimination (Li et al., 2022). Soil properties, e.g., OM, organic C, and clay contents, influence microbial functional diversity (Li et al., 2022).

Microbes exhibiting resistance to the long-term effect of PTE contamination provide a basis for selecting suitable microbial species



to assist in phytoremediation (Zubair et al., 2016; Table 2). Bacteria can help plants to resist stress and improve plant growth and productivity. For example, resistant bacteria can transform PTEs into less toxic forms and alter their availability for possible plant uptake or chelation (Whiting et al., 2001). Rhizosphere microbes such as *Acinetobacter*, *Bacillus*, *Gluconacetobacter*, and *Pseudomonas* affect the bioavailability of Zn (Costerousse et al., 2017), which involves pH reduction (acidic) and root growth. Additionally, the presence of mycelium fungi contributes to the increase in plants' tolerance to excess Cd and Zn in *Salix sp* (Hrynkiwicz et al., 2012). Some rhizosphere microbes promote plant growth by direct interactions with plants or indirect antagonistic activities against plant pathogens. Pathogens affect many bacteria and fungi.

A typical example is endophyte resistance toward pathogenic space and nutrients in the rhizosphere and plant tissues (Vogel-Mikuš et al., 2006). The apical roots are involved in the active selection of specific microbe. Studies show that the polysaccharide composition of root mucilage for microbes with suitable glycosyl hydrolase composition (Amicucci et al., 2019) and further by extracellular DNA, antimicrobial proteins, and secondary metabolites (Haichar et al., 2014). Meanwhile, arbuscular mycorrhiza and ectomycorrhiza avoid PTEs from root uptake via absorption or chelation, indicating resistance (Hall, 2002).

Loading of PTEs in plant cell walls represents an approach to metal avoidance (Memon and Schroder, 2009; Krzeszowska et al., 2021). Cell wall pectin made of negative carboxylic groups of

polygalacturonic acids can bond with cationic PTEs. The cation exchange reactions prevent free metallic ions from entering plant cells. Various interacting microbes produce phytohormones, which inhibit or promote root growth, protect plants against abiotic stress, and improve nutrient acquisition by roots (Gupta et al., 2014). One pertinent role of microbes in plant nutrition and health is the association between rhizosphere fluorescent *pseudomonas* and plants, while others suppress plant diseases and fungal pathogens from OM (Kumari and Kumar, 2018). For example, in soils suppressive to the fungal pathogen *Rhizoctonia solani*, Raza et al. (2016) reported that proteobacteria, firmicutes, and actinobacteria were prominent taxa involved in disease suppression.

Stable isotope study of plants and root-associated microbes shows dynamics in taxonomic composition and activities of microbial consumers. For example, Hünninghaus et al. (2019) pointed out that bacterial taxa with the highest abundance in the root of *Zea mays L.* were not necessarily those showing the highest enrichment of ¹³C from rhizodeposition, indicating substantial differences in consumption of exudates. Active and passive exudation of low molecular weight carbon compounds, e.g., sugars and organic acids, during root expansion and root hair zones (Canarini et al., 2019) constitutes microbial community modulation (Hu et al., 2018). These locations also modulate enzymatic activities (Zhang et al., 2020) and affect PTEs in soils and plant accessibility.

Arsenic reduction, methylation, and demethylation depend on the type of microbes in the soil. Under anaerobic conditions,

TABLE 3 Effects of rhizosphere microbes on plant hyperaccumulators/tolerant of Potentially toxic elements (PTE).

Hyperaccumulator/Tolerant plants	Rhizosphere microbes	PTE	Effects on plant	References
<i>Pteris vittata</i>	<i>Pseudomonas sp.</i> , <i>Delftia sp.</i> , <i>Bacillus sp.</i> , <i>Variovorax sp.</i> , and <i>Pseudoxanthomonas sp.</i>	As	Increased plant biomass, solubilization, and As removal efficiency in the soils	Yang et al. (2012)
<i>Pteris multifida</i>	<i>Bacillus sp.</i> , <i>Massilia sp.</i> , <i>Curtobacterium</i>	As	Increased tolerance	Zhu et al. (2014)
<i>Brassica napus</i>	<i>Enterobacter sp.</i> , <i>Klebsiella sp.</i>	Cd	Increased uptake	Jing et al. (2014)
<i>Arabidopsis thaliana</i> (non-hyperaccumulator)	<i>Bacillus megaterium</i>	Cd and Pb	Enhanced tolerance and accumulation	Hsieh et al. (2009)
<i>Dryobalanops fusca</i>	Siderophore-producing, phosphate-solubilizing, and acid-producing bacteria	Pb	Increase in metal ion uptake	Abou-Shanab et al. (2005)
<i>Brassica napus</i>	<i>Enterobacter sp.</i> , <i>Klebsiella sp.</i>	Pb	Increased uptake	Jing et al. (2014)
<i>Thlaspi praecox</i> Wulfen (Brassicaceae)	Arbuscular mycorrhizal fungal	Zn, Cd, and Pb		Vogel-Mikuš et al. (2006)
<i>Trifolium hybridum</i> , <i>Alopecurus pratensis</i> , <i>Poa pratensis</i> , <i>Hordeum violaceum</i> , <i>Ranunculus kotschyi</i> , <i>Cerastium sp</i>	<i>Bacillus megaterium</i> var. phosphaticum	Zn	Nutrient-solubilization; Pathogens control	Gullap et al. (2014)
<i>Nocceae caerulea</i> , <i>Alyssum bertolonii</i> , <i>A. murale</i> , and <i>B. juncea</i>	Rhizobacteria	Zn	Increased content of Zn	Delorme et al., 2001; Abou-Shanab et al., 2003; Whiting et al., 2001)
<i>Nicotiana tabacum</i>	<i>Neurospora crassa</i>	Zn	Enhanced Zn accumulation	Dixit et al. (2011)
<i>Trifolium hybridum</i> , <i>Alopecurus pratensis</i> , <i>Poa pratensis</i> , <i>Hordeum violaceum</i> , <i>Ranunculus kotschyi</i> , <i>Cerastium sp</i>	<i>Bacillus megaterium</i> var. phosphaticum	Zn	Nutrient-solubilization; Pathogens control	Gullap et al. (2014)
<i>Dryobalanops fusca</i>	Siderophore-producing, phosphate-solubilizing, and acid-producing bacteria	Zn	Increase in metal ion uptake	Abou-Shanab et al. (2005)

organoarsenicals reduce to volatile arsine, such as monomethylarsonous acid [MMA^(III)], dimethylarsinous acid [DMA^(III)], and trimethylarsine TMA^(III) (Zhang et al., 2021). Microbial As methylation is an effective method for As detoxification in microbes as a bioremediation approach.

6.2 Effects of PTEs on rhizosphere microbes during hyperaccumulation

Many rhizosphere microbiomes can tolerate high contents of Zn, As, Cd, and Pb (Abou-shanab et al., 2019), which contribute significantly to the mobility and immobilization of PTE in soils.

Rhizosphere microbes, such as bacterial siderophores, can increase PTE accumulation and induce tolerance during phytoremediation (Benizri and Kidd, 2018). For instance, rhizobacteria, endophytes,

siderophores, carboxylic acids, and phosphate solubilizers can contribute to the dissolution of As for plant uptake (He et al., 2013; Cabello-Conejo et al., 2014). Plant-associated microbes protect host plants by releasing phytohormones to combat biotic and abiotic elicitors that cause adverse effects on plants.

Moreover, the secretion of root exudates by hyperaccumulating plants and the attraction of rhizosphere microorganisms can significantly affect the availability of PTEs (Figure 4). For example, a Cd content of 7 mg kg⁻¹ in soil caused a reduction in rhizobium populations (Chaudri et al., 1992). Thus, high contents of some PTE can reduce microbial diversity and abundance (Abou-Shanab et al., 2005). For instance, the inoculation of *Bacillus sp.*, *Delftia sp.*, *Pseudomonas sp.*, *Pseudoxanthomonas sp.*, and *Variovorax sp.* on *P. vittata* plants under As stress resulted in increased plant biomass and As removal efficiency in soils (Yang et al., 2012).

Changes in pH affect microbial abundance and diversity, which are directly associated with the solubility of PTEs. According to Delorme et al. (2001), a high alkaline pH by adding lime increased bacteria count reduced Zn toxicity and enabled the growth of *N. caerulea* and *Trifolium pratense* L. Meanwhile, increasing acidity promotes the high solubility of PTE for effective bioaccumulation (Becker and Skaar, 2014). Microbial counts also affect hyperaccumulators, probably because of the different secretions.

For example, *N. caerulea* recorded a higher microbial population in Zn-contaminated soil than *Trifolium pratense* L. (Delorme et al., 2001) via acidification by microbes, which improves Zn availability, uptake, and selection for metal-resistant bacteria. Bacterial strains with Hexa-, Penta-, Tetra-, and Trivalent-metal ions tolerant are often abundant in the rhizosphere zone, where they can resist high Cd and Pb contents (Abou-Shanab et al., 2005). A unified multi-microbial influence on PTEs may result in fast stabilization or dissolution. These multi-facet abilities of diversified microbes in the rhizosphere are helpful during high levels of PTEs, as this can affect the uptake (Gremion et al., 2004). Antibiotics, phosphate solubilizers, hydrocyanic and indoleacetic acids, and siderophores obtained from some rhizobacteria increase Cd availability and facilitate absorption in plant roots (Sharma and Archana, 2016; He et al., 2020). Microbial populations often establish some positive relationship with the host plant system. Soil contaminated with PTEs can lead to the appearance of resistant rhizobacteria (Henao and Ghneim-Herrera, 2021; Table 3). Hyperaccumulating plant species of PTEs can significantly shape the rhizosphere ecosystem and impact the microbial community to favor the reduction of As, Cd, Pb, Zn, and many other pollutants. For example, Actinobacteria, Bacteroidetes, and genus *Streptomyces* were well-detected as dominant traits in Cd-stressed hyperaccumulator *Sedum alfredii* compared to non-hyperaccumulating ecotypes (Hou et al., 2018). Thus, *S. alfredii* and Cd exposure select suitable microbes for hyperaccumulation. According to Lu et al. (2023), *Acidobacteria*, *Bacteroidetes*, *Deltaproteobacteria*, and *Gemmatimonadetes* regulate excess Cd uptake and accumulation in *Triticum aestivum* L. with microbes partly influenced by soils with high OM.

Studies have shown that a high proportion of Zn-resistant bacteria persist in the rhizosphere of the hyperaccumulator *N. caerulea* (Delorme et al., 2001; Whiting et al., 2001) and *Alyssum bertolonii* Desv (Sessitsch et al., 2013) or *Alyssum murale* M. Bieb (Abou-Shanab et al., 2003) grown in soil contaminated with Zn. The addition of bacteria increased the shoot Zn content in *N. caerulea* about two times and the rate of soluble Zn transport compared to axenic controls (Whiting et al., 2001). Enzymatic processes during detoxification and activation of chemicals in plants are similar to microbial biotransformation pathways in soils.

The comparison of biochemical isolates such as phosphate solubilizers, siderophore, and acids showed that phosphate solubilizers dissolve 82.2% Zn and 68.2% of Pb, siderophores (71.02% Zn and 61.6% Pb), and acids—53.3% Zn and 42.9% Pb (Abou-Shanab et al., 2005). Hence, several organic materials released by microbes in the root rhizospheres are responsible for the dissolution of PTEs for plants' availability. According to Singh et al. (2022), the presence of siderophores decreased the uptake of metals by plants. Siderophores produced by *Pseudomonas sp.*,

Serratia marcescens, and *Streptomyces sp.* had either no effect or negatively affected Zn uptake by *Salix capreastrum*. These effects indicate that the principles underlying metal uptake are also plant-dependent. The efficiency of siderophore producers in mobilizing or immobilizing soil PTEs depends on the binding form of metal/(loid)s, the charge of siderophores, soil pH, mineral composition, and organic content (Jing et al., 2007). Soil microbiome, particularly bacteria, containing enzymes, such as 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, limits secretion in stressed plants (Tiwari et al., 2018). Moreover, arbuscular mycorrhizal fungi contribute to plant PTE uptake (Kranter and Colville, 2011). Therefore, mycorrhizal fungi with high metal contents tolerance and biomass production can be applied for phytoextraction (Sagardoy et al., 2010). Thus, it is pertinent to co-inoculate PTE hyperaccumulators with desired microbes, e.g., *Arthrobacter* and other *Microbacterium*, that can improve uptake and translocation (Visioli et al., 2015).

7 Future perspectives

Microbes exhibit preference for specific PTE during hyperaccumulation. These attractions result from the secretion of exudates into the root rhizosphere region. Meanwhile, the entire microbial community may not necessarily benefit from the chelation or dissolution of PTEs for effective uptake by plants. Culturomics purposed on adapting beneficial microbes can improve the accessibility of PTEs.

Gene encoding involved in the uptake and translocation of Pb remains less published among crops such as *Oryza sativa* (Gong et al., 2022), while so far neglected in the hyperaccumulation of risk elements from contaminated sites. The induction of many of these transporter families and the use of suitable nano/microparticles remain the next level of concern for the remediation of PTE-contaminated sites. Mutation and ionome modifications of plant species with effective uptake and above-ground accumulation offer another innovative approach to PTE management in contaminated soils for sustainable use (Navarrete and De La Fuente, 2015).

8 Conclusion

Anthropogenic interferences contribute significantly to excess potentially toxic elements (PTEs; As, Cd, Pb, and Zn) above the threshold of agricultural soils. Hyperaccumulating plants (above-ground accumulators of PTEs) possess uptake ability and accumulate the accessible portion of PTEs associated with the exchange complexes and soluble forms in the soil solution.

Additionally, soil characteristics, including high organic matter, carbon, and clay content increases microbial biomass and functionality and induce changes that regulate soil microbial community. These properties affect microbial abundance and increase the chances of high PTE reworking to ease uptake.

Root exudations of hyperaccumulators contribute to microbes' selection. Microbial stimulation (chemotaxis and excretion), e.g., flavonoids, also provide an anchor to colonize the root surface to support the solubilization and uptake of PTEs. The production rate of root exudate by hyperaccumulators and

the attraction of rhizosphere microbes can significantly affect the bioavailability and bioaccumulation of PTEs, which enhances phytoextraction by hyperaccumulators. Changes in soil physicochemical properties (e.g., pH and redox potential) and root exudation affect microbial abundance and diversity, which also influence the solubility, mobility, and accessibility of PTEs. Multiple resistance of As, Cd, Pb, and Zn by microbes can assist many hyperaccumulators during PTE uptake. Diversified microbes in the root rhizosphere are vital during high levels of PTEs, as this can increase metal uptake while plants utilize them to avoid toxicity.

Meanwhile, different transporters, including Zinc-iron protein (ZIP), Metal Tolerance Protein (MTP), Heavy metal ATPases (HMA), Yellow Strip-like (YSL), and Natural resistance-associated macrophage proteins (NRAMPs) and their transcription genes are responsible for the influx/efflux of PTEs to plant compartments. Many hyperaccumulators show unique transcriptional transporters associated with fast uptake of high contents of PTEs and subsequent translocation to the aerial parts. Part of the bioavailable fractions of the PTEs is chelated with intracellular organs of hyperaccumulators as a means of detoxification, while exudation contributes to tolerance.

Thus, hyperaccumulation depends on the availability of mobilized metal ions in soils, enhanced activity of metal transporters, and metal chelates/solubilizers provided by plants or their associated microbes.

Incorporating different transporter genes into plants to improve the ability for PTEs hyperaccumulation needs attention. The microbial community in the root rhizosphere during PTE hyperaccumulation is not well-studied. The inoculation of suitable transporter genes and rhizosphere microbes for an effective hyperaccumulation of PTEs requires critical studies.

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Conceptualization: MA, JS, and PT, Data curation: MA and JS, Formal Analysis: MA, JS, and PT, Funding acquisition: JS and PT, Methodology: MA, JS, and PT, Project administration: JS and PT, Resources: JS and PT, Supervision: JS and PT, Validation: JS and PT Writing–original draft: MA and JS, Writing–review and editing: MA, JS, and PT.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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