



# Arbuscular mycorrhizal fungi-based bioremediation of mercury: insights from zinc and cadmium transporter studies

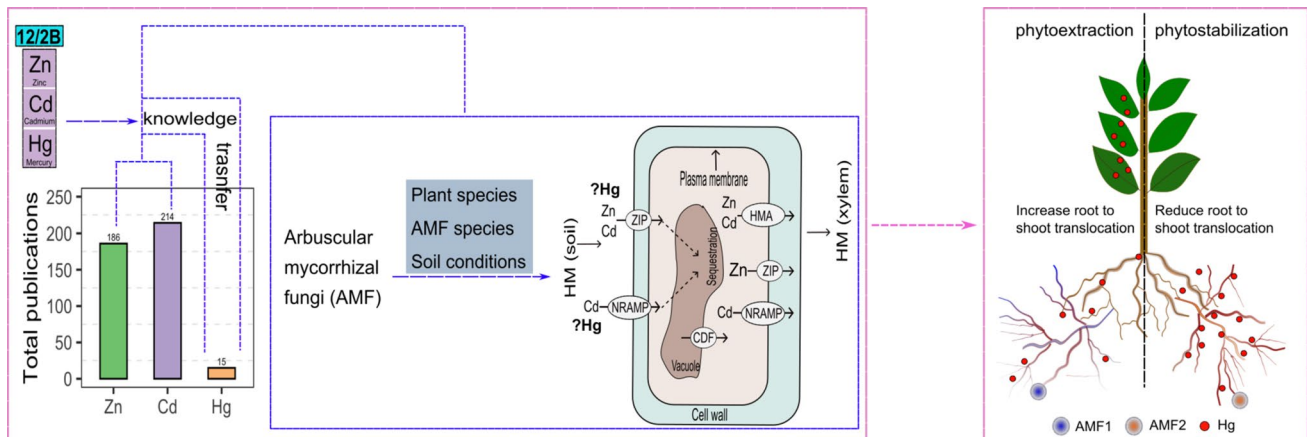
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## Abstract

Phytoremediation, a sustainable approach for rehabilitating mercury (Hg)-contaminated soils, can be enhanced by arbuscular mycorrhizal (AM) fungi, which promote plant growth and metal uptake, including Hg, in contaminated soils. Hg, despite lacking a biological function in plants, can be absorbed and translocated using Zn and/or Cd transporters, as these elements belong to the same group in the periodic table (12/2B). In fact, the specific transporters of Hg in plant roots remain unknown. This study is therefore to provide fundamental insights into the prospect to remediate Hg-contaminated soils, with a focus on the role of AM fungi. The hypothesis posits that Hg uptake in plants may be facilitated by transporters responsible for Zn/Cd, affected by AM fungi. The Scopus database was used to collect studies between 2000 and 2022 with a focus on the ecological role of AM fungi in environments contaminated with Zn and Cd. Particular emphasis was laid on the molecular mechanisms involved in metal uptake and partitioning. The study revealed that AM fungi indeed regulated Zn and/or Cd transporters, influencing Zn and/or Cd uptake in plants. However, these effects vary significantly based on environmental factors, such as plant and AM fungi species and soil conditions (e.g., pH, phosphorus levels). Given the limited understanding of Hg remediation, insights gained from Zn and Cd transporter systems can guide future Hg research. In conclusion, this study underscores the importance of considering environmental factors and provides fundamental insights into the potential of Hg phytoremediation with the assistance of AM fungi.

## Graphical abstract



**Keywords** Ecosystem restoration · Heavy metal · Mercury uptake · Molecular mechanisms · Phytoremediation · Soil contamination

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## Introduction

### Origin and consequence of mercury contamination

Environmental contamination by mercury (Hg) is a serious concern worldwide. Hg is a hazardous heavy metal (HM) that does not have any known biological function. It is toxic to both humans and other organisms, even at very low concentrations (Zahir et al. 2005). Studies have confirmed that soil contamination by Hg can lead to vegetation degradation, impact soil organisms and ultimately result in a reduction or even loss of ecosystem functions (Gworek et al. 2020). Exposure to Hg in humans can result in gene mutations, cancer induction and irreversible damage to the brain, lungs and other organs in the body (Mitra et al. 2022).

Hg exists in various forms (e.g.,  $\text{Hg}^0$ ,  $\text{Hg}^{2+}$ ,  $\text{CH}_3\text{Hg}^{+1}$ ) and has low melting and boiling points (He et al. 2015). These characteristics pose significant challenges for managing this chemical element effectively. Hg is known for its capacity to transform from one form to another, which enables it to cycle through the atmosphere as well as terrestrial and aquatic ecosystem. Global Hg pollution occurs, especially in the form of  $\text{Hg}^0$  which can be transported over long distances (Obrist et al. 2018; Pacyna 2020). The presence of Hg in the environment can be attributed to either natural deposition or anthropogenic dispersion resulting from various activities, such as manufacturing processes (e.g., production of sodium hydroxide), mining and smelting (Driscoll et al. 2013). In quantitative terms, artisanal and small-scale gold mining (ASGM) is the primary source of Hg pollution on a global scale (UNEP 2019). This is because Hg is an essential element for amalgamating gold during the extraction process (Bugmann et al. 2022). Unfortunately, there are no practical alternatives to Hg in ASGM at present, and as a result, the use of Hg in ASGM continues to be widespread (Yevugah et al. 2021; Bugmann et al. 2022).

Soil is known to be the ultimate sink for Hg (Ahmad et al. 2021; Rashid et al. 2022). However, it is also the foundation for sustaining essential ecosystem services (Banerjee and van der Heijden 2023). Therefore, remediating soil contaminated with Hg is an urgent and critical task. Initial physical and chemical methods for remediating Hg-contaminated soil include complete removal of the contaminated soil or on-site treatments such as ion exchange, chemical precipitation, soil vapor extraction and soil washing (He et al. 2015). Nevertheless, these techniques are frequently ineffective and costly, and may have detrimental effects on soil structure and productivity (Kuppusamy et al. 2017).

### Principles of phytoremediation

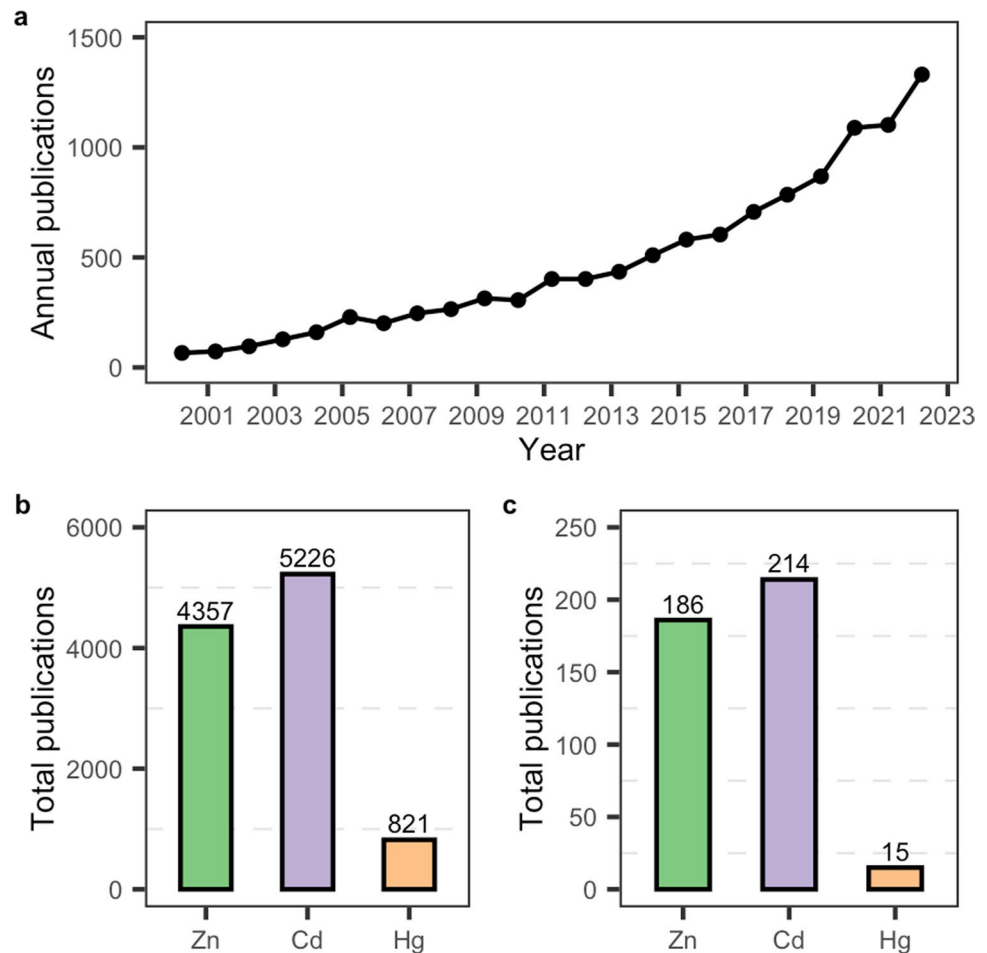
Alternatively, phytoremediation, which involves the application of plants to remove or stabilize contaminants, is emerging as a cost-effective and environmentally friendly technology (He et al. 2015; Bhat et al. 2022). As it originates from nature, minimizes soil disturbance and promotes ecosystem development, phytoremediation is becoming an increasingly studied approach (Fig. 1a). Three types of phytoremediation have been proposed for reclaiming Hg-contaminated soils: phytoextraction, phytostabilization and phytovolatilization (Tiodar et al. 2021). In phytoextraction, Hg is taken up and accumulated in the aboveground plant parts of Hg hyperaccumulator plants, which can then be harvested for disposal or recovery. Phytostabilization involves the immobilization of Hg in plant roots, reducing its bioavailability in the soil and preventing further migration into groundwater or entry into the food chain. Phytovolatilization refers to the use of plants or genetically modified plants to convert Hg into its volatile form ( $\text{Hg}^0$ ) and release it into the atmosphere. However, phytovolatilization may not be a sustainable solution, as the volatile form of Hg released into the atmosphere can be deposited back into the soil, resulting in a cycle of contamination (Vangronsveld et al. 2009; Kumar et al. 2017). Therefore, this method is not further considered in this discussion.

To date, no Hg hyperaccumulator plants have been identified, highlighting the need for complementary methods to improve the efficiency of Hg phytoremediation (Tiodar et al. 2021). In addition, the growth and survival of plants may be affected by Hg toxicity and nutrient depletion in contaminated areas, which can compromise the overall efficiency of phytoremediation. The use of plant-associated microorganisms is becoming increasingly popular to enhance plant performance under stress conditions, and thus improve the efficiency of phytoremediation. Among these microorganisms, arbuscular mycorrhizal (AM) fungi are of particular interest (Moura et al. 2022; Yang et al. 2022a, b).

### Role of arbuscular mycorrhizal (AM) fungi in phytoremediation

Under natural conditions, almost all vascular plants form intimate symbiosis with AM fungi, dated back to 450 million years ago (Martin et al. 2017). This coevolution between plants and AM fungi highlights the strategic importance of their interactions for environmental adaptation (Wang and Qiu 2006; Strullu-Derrien et al. 2018). Numerous studies have indicated that AM fungi

**Fig. 1** Overview of published studies. **(a)** The trend of the annual publications regarding phytoremediation from 2000 to 2022; **(b)** Total publications about phytoremediation concerning the three elements Zn (zinc), Cd (cadmium) and Hg (mercury); **(c)** Total publications emphasizing the three elements Zn, Cd and Hg, in which AM fungi are considered in phytoremediation



can facilitate the success of plant establishment in HM-polluted soils (Chen et al. 2007; Curaqueo et al. 2014; Zhan et al. 2018; Lu et al. 2020). In fact, some studies have suggested that the symbiosis between plants and AM fungi may be the most critical factor in achieving success in phytoremediation programs (Meier et al. 2011; Colombo et al. 2020; Moura et al. 2022). This is attributed to the well-known roles of AM fungi in nutrient uptake, such as phosphorus (P) and nitrogen (N), as well as water transfer beyond the root zone to plants. These functions help plants to develop resistance to various abiotic stresses, including drought, salinity and HM toxicity, as well as biotic stresses caused by pathogens (Bücking and Kafle 2015). Furthermore, AM fungi are known to enhance soil structure by producing external hyphae and glomalin (Rillig and Mummey 2006), which can also help in the sequestration of metals from soil (Gil-Cardesa et al. 2014; Chen et al. 2018). However, the application of AM fungi in Hg-contaminated soils is not yet practical and requires a better understanding of the underlying genetic

and physiological mechanisms. Nonetheless, the potential of AM fungi in phytoremediation of Hg makes it imperative to further explore and develop this approach.

Although there are several reviews available on the topic of Hg phytoremediation assisted with AM fungi (Solís-Ramos et al. 2021; Tiodar et al. 2021; Chen et al. 2022; Sharma et al. 2022; Yu et al. 2022), there is a lack of empirical data in Hg research (Fig. 1c). Existing reviews provide a broad understanding of the potential of AM fungi in phytoremediation, including their ability to increase plant biomass, improve plant nutrient uptake and enhance antioxidant activities (e.g., Tiodar et al. (2021)). However, there is a critical lack of information on the specific molecular mechanisms involved. Understanding these mechanisms is thus crucial for the practical implementation of this technology (Yang et al. 2022a, b).

## Knowledge gaps about Hg uptake mechanisms by plants and AM fungi

The first step of heavy metal (HM) uptake, such as Hg, involves plant membrane transporters, followed by translocation and detoxification (Shi et al. 2019). Therefore, exploring potential transporters and their functions would be the initial step to understand the molecular mechanisms of phytoremediation with AM fungi. Plants have evolved a vast array of genes involved in metal uptake and transport, ensuring an adequate supply of essential nutrients or metals required for vital biological processes (Tangahu et al. 2011). However, due to the structural similarity of HM with essential nutrients, they can enter the roots via similar nutrient transport pathways with the assistance of membrane transporter proteins (Manoj et al. 2020). Some examples of membrane transporters involved in metal uptake and transport include potassium ( $K^+$ ) transporters, which are also involved in cesium ( $Cs^+$ ) uptake (Boulois et al. 2006); silicon acid (Ma et al. 2008) and phosphate (Meharg and Hartley-Whitaker 2002) transporters facilitating arsenic ( $As^{3+}/As^{5+}$ ) uptake; Zn transporters (especially *ZIP* (zinc–iron permease) (Lin et al. 2016; Zhang et al. 2017; Liu et al. 2019)); or channels of divalent cations like iron ( $Fe^{2+}$ ), copper ( $Cu^{2+}$ ), calcium ( $Ca^{2+}$ ) and magnesium ( $Mg^{2+}$ ), facilitating cadmium ( $Cd^{2+}$ ) uptake (Nakanishi et al. 2006; Song et al. 2017).

However, the specific mechanisms of Hg uptake by plants remain largely unknown, highlighting a significant knowledge gap (Fig. 1b, c). Along with Cd, Hg belongs to the same group of elements in the periodic table (12/2B) as Zn and shares the same outer electronic configuration with Zn, suggesting the possibility of utilizing the same transporters for uptake. A recent study showed that root Hg concentration is negatively correlated with root Zn concentration (Guo et al. 2023). Tiodar et al. (2021) suggested that transporters that facilitate the influx of Cd may also facilitate the uptake of Hg. Therefore, studying the mechanisms of the uptake of chemically related elements, such as Zn and Cd, which are also the most studied elements in phytoremediation (Yang et al. 2022a, b), can provide important insights into Hg remediation mechanisms and facilitate the prospective application of Hg phytoremediation.

The main objective of this study is to provide essential insights into the possibility of remediation of Hg-contaminated soils, with a specific focus on the role of AM fungi. The hypothesis is that Hg uptake in plants may be facilitated by transporters that are involved in the uptake

of chemically similar elements such as Zn and Cd, which are regulated by mycorrhization. To test this hypothesis, a comprehensive analysis of recent studies, using the Scopus database between 2000 and 2022, on the ecological role of AM fungi in environments contaminated with Zn and Cd was conducted. A particular focus was given on the molecular mechanisms involved in metal uptake and partitioning. Specifically, the effects of different phosphorus (P) levels on metal uptake were considered, as P plays a critical role in HM detoxification (Sharma et al. 2016; Mehmood et al. 2022). It also confers a major factor for mycorrhizal colonization, influencing the functioning of AM fungi (Bedini et al. 2018). Furthermore, knowledge on Hg remediation with a particular focus on AM fungi-facilitated Hg uptake mechanisms was compiled. Finally, this study outlines future research directions of Hg remediation, which will contribute to the understanding of roles of AM fungi in Hg transporting to further facilitate management of Hg-contaminated sites in future.

This study was carried out at the University of Hohenheim from May 2022 to February 2023.

## Materials and methods

### Data collection

The data for this study were extracted from Scopus database which is considered as one of the most comprehensive databases of scientifically literature reviews globally (Zyoud et al. 2014; Sabour et al. 2023). A series of keywords were searched for different perspectives of view. Phytoremediation OR (plant AND remediation) OR (plant AND bioremediation) AND metal AND soil was used for the overview understanding related to this topic (Fig. 1a); Phytoremediation OR (plant AND remediation) OR (plant AND bioremediation) AND Zinc (OR Zn) OR Cadmium (OR Cd) OR Mercury (OR Hg) AND soil was used for specific three elements (Fig. 1b), and mycorrhiza was added to each search to obtain the studies related to mycorrhiza (Fig. 1c). The titles, abstracts and keywords of the detected publication were checked. The date was set from 2000 to 2022. It is supposed that AM fungi have been realized the potential in phytoremediation since 2000 and research related to explore this potential was gradually increased (Fig. 1a). Languages other than English were excluded to avoid misunderstanding.

### Data visualization

Data from Scopus database were exported to Microsoft Office Excel® and then imported to RStudio (version 4.0.3)

for visualization. Studies with specific focus on molecular understandings related to transporters were screened to arrange into the table.

## Results and discussion

### Molecular mechanisms of AM fungi in uptake and partitioning of zinc and cadmium

#### Zinc (Zn)

Zinc (Zn) is an essential cofactor for numerous enzymes and plays an important structural role in many proteins. Although Zn is a highly reactive element, it becomes toxic at high concentrations. Several studies have reported that AM fungi can play dual roles in Zn fluxes in the soil–plant ecosystem. On the one hand, AM fungi can improve Zn uptake under Zn-limited conditions, and on the other hand, they can prevent excessive Zn accumulation in Zn-contaminated soils (Watts-Williams et al. 2013, 2017; Sarkar et al. 2017). This phenomenon may be attributed to the regulation of transporters (Ruytinx et al. 2020). Two transporter families, *ZIP* (zinc–iron permease or *ZRT-IRT*-like protein) and *CDF* (cation diffusion facilitator), are related to Zn homeostasis in eukaryotes. Interestingly, these two Zn transporter families work in opposite direction. *ZIP* transports Zn and/or other metal ion substrates from the extracellular space or organellar lumen into the cytoplasm, while *CDF* transports Zn and/or other metal ions from the cytoplasm into the lumen of intracellular organelles or to the outside of the cell (Ruytinx et al. 2020). *GinZnT1*, a transporter belonging to the *CDF* family, was firstly identified in *Glomus intraradices* in relation to Zn toxicity (González-Guerrero et al. 2005). This is the only gene characterized to date in AM fungi, which encodes a Zn transporter. With the advent of advanced sequencing technologies, several putative Zn transporter genes have been identified in *Rhizophagus irregularis*, i.e., *ZRT1*, *YKE4*, *ZRT3.1* and *ZRT3.2* belonging to the *ZIP* family, and *ZnT1*, *ZnT2*, *MSC2* and *ZRG17* belonging to the *CDF* family (Tamayo et al. 2014). However, the functional characteristics of these genes have not been fully elucidated and require further research.

AM fungi are also known to regulate Zn transporters in plants. For instance, a previous study demonstrated that a mixed AM fungal inoculum can downregulate the expression of the *MtZIP2* gene to prevent excessive Zn uptake by plants under increasing Zn fertilization (Burleigh et al. 2003). Watts-Williams et al. (2017) provided further evidence that suggests the potential involvement of *MtZIP2*

genes in the detoxification of Zn stress with the help of *R. irregularis*. In the same study, it was demonstrated that *R. irregularis* upregulated the expression of *MtPT4*, a mycorrhizal-induced phosphate transporter, to maintain shoot P contents and biomass, resulting in reduced tissue Zn concentration and alleviated phytotoxicity under Zn stress. Another study reported that under Zn stress, *R. irregularis* increased the biomass of *Medicago truncatula*, resulting in the dilution of Zn concentration in the plant (Nguyen et al. 2019). However, this benefit was only observed when the levels of available P in the soil were low. Hence, the hypothesis of increased P uptake through the mycorrhizal pathway as a mechanism for plant tolerance to toxic soil Zn levels is proposed to be influenced by the availability of P in the soil.

#### Cadmium (Cd)

Cadmium (Cd) does not have any biological function in plants and is highly mobile and soluble in soil (Beesley et al. 2010). Studies have shown that Cd can be readily absorbed by plant roots through plasma membrane transporters of essential metals and transported to leaves through the xylem (Molina et al. 2020). Transporters, such as *ZIP* (*ZRT*, *IRT*-like protein), are crucial for the transport of Cd due to their structural similarity (Kaur and Garg 2018). Additionally, studies have shown that natural resistance-associated macrophage proteins (*NRAMP*), which are primarily expressed in endodermal plasma membranes, are involved in loading Cd into the xylem (Takahashi et al. 2011a, b). Furthermore, HM ATPase (*HMA*) plays a role in Cd translocation across the vacuolar membrane, which helps to mitigate Cd toxicity within plants (Sharma et al. 2016; Liu et al. 2017). As synergistic or antagonistic effects between Zn and Cd are possible, multiple studies have investigated the interplay between these two elements with respect to mycorrhizal colonization. Research has shown that *R. irregularis* induces divergent patterns of transport and partitioning of Cd and Zn in *Populus trichocarpa* (De Oliveira et al. 2020). When exposed to excessive Zn, *R. irregularis* exhibited restricted transport of Cd to the shoots, resulting in higher Cd accumulation in the roots (78%) compared to the control (14%). Conversely, the translocation of Zn was promoted, leading to greater Zn accumulation in the shoots (60%) than in the roots (8%). This resulted from upregulation of *PtHAM4* genes in roots and *PtZIP1* genes in leaves induced by *R. irregularis* (De Oliveira et al. 2020). Although recent studies confirmed that *R. irregularis* exerted different mechanisms for Zn and Cd toxicity of *Phragmites australis*, the colonization of *R. irregularis* resulted in reduced shoot Zn concentration (10–57%) under Zn stress and increased shoot Cd concentration (17–40%) under Cd stress (You et al. 2021). These



contrasting results suggest that both the plant species and the elements involved are crucial factors in determining the role of AM fungi in phytoremediation. In the same study, it was demonstrated that addition of Zn promoted the translocation of Cd to aboveground plant parts. These findings suggest that manipulating the Zn concentration in soil could enhance Cd translocation and lead to greater Cd accumulation in the shoots when colonized by AM fungi. This could be a crucial factor in the process of phytoextraction.

You et al. (2022) found that Cd uptake by *P. australis* is facilitated by different transporters, depending on the concentration of P in the substrate. Under low and medium P levels, *Funneliformis mosseae* upregulated the expression of ZIP genes, which facilitated Cd uptake. However, at high P levels, *F. mosseae* upregulated the expression of NRAMP genes, resulting in increased Cd uptake. These results underscore the interference of soil P in Cd uptake by plants. Furthermore, the regulation of Cd transporters via AM fungi is dependent on the specific fungal species. For instance, rice inoculated with *R. intraradices* exhibited reduced expression of NRAMP5 and HMA3 genes in roots, which prevented Cd uptake. Conversely, the expression of these genes in roots was increased when inoculated with *F. mosseae* (Chen et al. 2019). Similarly, in *Solanum nigrum* inoculated with *R. intraradices*, there was a reduction in Cd concentration in shoots. In contrast, Cd translocation was increased when inoculated with *F. mosseae* (Li et al. 2018). Motaharpoor et al. (2019) confirmed the downregulation of the NRAMP1 gene in *M. sativa* when inoculated with *R. intraradices*, resulting in reduced Cd concentration in shoots.

### AM fungi-facilitated Hg remediation: knowledge and perspectives

Remediation of Hg-contaminated soil is an urgent and challenging task, as the molecular mechanisms involved in the transport of this element are not well understood. However, plants associated with AM fungi are being proposed as a sustainable solution to address this issue (Riaz et al. 2021; Tiodar et al. 2021). In fact, several studies have reported that mycorrhizal inoculation can enhance the resistance of plant seedlings to Hg, such as *Lactuca sativa* (Vargas Aguirre et al. 2018; Escobar-Vargas et al. 2022) and *Nauclea orientalis* (Ekamawanti et al. 2014). However, the underlying mechanisms remain unexplored. In a greenhouse pot experiment, *L. sativa* plants associated with AM fungi (a commercial inoculum containing *R. irregularis* and *F. mosseae*) exhibited better Hg tolerance compared to the control group

(Cozzolino et al. 2016). The authors demonstrated that mycorrhizal inoculation improved the nutritional status of the plants, increased pigment content in plant leaves and inhibited both the uptake and translocation of Hg from roots to shoots. Another study reported that a mixture of AM fungi (*Glomus* sp., *Acaulospora* sp., *Entrophospora* sp. and *Giasporea* sp.) conferred Hg tolerance to plants (*Lolium perenne*) by upregulating the expression of glutathione-S-transferase (GST) genes, which encode detoxification enzymes (Leudo et al. 2020). Yu et al. (2010) demonstrated that the AM fungus *F. mosseae* increased Hg sorption by the soil and reduced Hg bio-availability, ultimately limiting the uptake of Hg by plant roots. In contrast, *Zea mays* inoculated with *Glomus* sp. can uptake and transport Hg from the soil into the plant roots more efficiently compared to non-inoculated plants (Kodre et al. 2017). The authors further demonstrated that the increase in Hg uptake was due to a change in the ligand structure from di-thiolate (2S) to tetra-thiolate (4S) caused by AM fungal inoculation. Kodre et al. (2017) also demonstrated that native AM fungal species from polluted environments outperformed commercial ones. Furthermore, the Hg accumulation of *Erato polymnioides*, a potential Hg hyperaccumulator plant, has been shown to be positively correlated with mycorrhizal colonization, emphasizing the importance of AM fungi in Hg remediation (Chamba et al. 2017). Recently, Li et al. (2023) investigated the coexistence of Hg and Cd, and demonstrated that the effects of Cd on Hg accumulation and transformation by *Arundo donax* followed the rule of 'low promotion and high inhibition'. However, AM fungi were not considered in this context. Another recent study demonstrated that AM fungi can enhance the accumulation of both Cd and Hg in *L. perenne* (Saldarriaga et al. 2023). These studies suggest a growing recognition of other metals such as Cd in Hg remediation.

Another mechanism that contributes to the increased uptake and accumulation of Hg is attributed to the improved nutrient status induced by AM fungi inoculation (Debeljak et al. 2018). It is widely recognized that the primary role of AM fungi on plants is to enhance mineral nutrient uptake, particularly phosphate (Karandashov and Bucher 2005). It has been demonstrated that phosphate is primarily transported in the form of polyphosphate via mycorrhizal hyphae (Wang et al. 2017). Coincidentally, transgenic tobacco plants engineered to express bacterial polyphosphate (polyP) exhibited higher Hg accumulation than wild-type tobacco (Nagata et al. 2006). This finding suggests that increasing the plant's polyphosphate content could be one way to enhance plant Hg accumulation, but it is unclear whether and to what extent this process

**Table 1** Key findings and regulations of transporters involved in the uptake of the three elements: Zn (zinc), Cd (cadmium) and Hg (mercury), as influenced by mycorrhizal colonization

Elements concentration	AM fungal species <sup>a</sup>	Plant species	Key results	Mechanisms <sup>b</sup>	Experimental conditions	References
<b>Zn</b>						
0, 75 and 7500 µM	<i>Rhizophagus irregularis</i> (WVAM10)	<i>Daucus carota</i>	Improved Zn stress	<i>GinZnT1</i> (CDF) ↑	In vitro	González-Guerrero et al. (2005)
100 mg kg <sup>-1</sup>	<i>Glomus versiforme</i> (BEG47), <i>Glomus intraradices</i> (BEG87), <i>Glomus caledonium</i> (BEG15), <i>Glomus claroideum</i> (BEG14), <i>Glomus mosseae</i> , <i>Scutellospora calospora</i> , <i>Gigaspora rosea</i> (BEG9)	<i>Medicago truncatula</i> cv. Jemalong A17	Improved Zn tolerance	<i>MiZIP2</i> ↓	Growth chamber	Burleigh et al. (2003)
5, 20,40 mg kg <sup>-1</sup>	<i>Rhizophagus irregularis</i> (WVAM10)	<i>Medicago truncatula</i> cv. Jemalong A17	Improved Zn tolerance	<i>MiZIP2</i> (ZIP) ↓ <i>MiPT4</i> ↑	Glasshouse	Watts-Williams et al. (2017)
2, 100, 300, 500, 700 mg L <sup>-1</sup>	<i>Rhizophagus irregularis</i> (FR17169)	<i>Phragmites australis</i>	Reduced Zn concentration (10–57%) Alleviates Zn toxic effects	Plant biomass ↑	Greenhouse	You et al. (2021)
0.3, 4.0, 5.8, 15.0 mg kg <sup>-1</sup>	<i>Rhizophagus irregularis</i> WFVAM10	<i>Medicago truncatula</i> cv. Jemalong A17	A 'protective' role of mycorrhizal fungi at high levels of soil Zn	<i>MiZIP5</i> expression was induced both by AMF and soil Zn deficiency, <i>MiZIP2</i> was downregulated in mycorrhizal plants and upregulated with increasing soil Zn concentration	Glasshouse	Nguyen et al. (2019)
<b>Cd</b>						
0.01, 1, 5, 10, 20 mg L <sup>-1</sup>	<i>Rhizophagus irregularis</i> (FR17169)	<i>Phragmites australis</i>	increased Cd concentration (17–40%) Alleviates Cd toxic effects	Plant biomass ↑	Greenhouse	You et al. (2021)
10 mg L <sup>-1</sup>	<i>Rhizophagus irregularis</i> (FR17169)	<i>Phragmites australis</i>	Increased Cd uptake and retained Cd in stems	<i>ZnT2</i> (ZIP) ↑ <i>Nramp2</i> , <i>Nramp5</i> ↑	Greenhouse	You et al. (2022)
0, 10 µM	<i>Funneliformis mosseae</i>	<i>Oryza sativa</i>	Higher root Cd content	<i>Nramp5</i> ↑ <i>HMA3</i> ↑	Greenhouse	Chen et al. (2019)
14.8 mg kg <sup>-1</sup>	<i>Rhizophagus intraradices</i>		Lower root Cd content	<i>Nramp5</i> ↓ <i>HMA3</i> ↓		
	<i>Funneliformis mosseae</i>	<i>Solanum nigrum</i>	Increased Cd translocation		Greenhouse	Li et al. (2018)
	<i>Rhizophagus intraradices</i>		Reduced Cd translocation			

Table 1 (continued)

Elements concentration	AM fungal species <sup>a</sup>	Plant species	Key results	Mechanisms <sup>b</sup>	Experimental conditions	References
100 mg kg <sup>-1</sup>	<i>Rhizophagus irregularis</i>	<i>Medicago sativa</i>	Increased plant biomass Reduced shoot Cd concentration	<i>MtRTI</i> (ZIP) ↓ <i>MtNRAMP1</i> ↓	Greenhouse	Motaharpoor et al. (2019)
3.06 (±0.12) mg kg <sup>-1</sup>	a mixture of spores of the genera <i>Glomus</i> sp., <i>Acaulospora</i> sp., <i>Entrophospora</i> sp. and <i>Giaspora</i> sp.	<i>Lolium perenne</i>	Increased accumulation of Cd		Rhizobox	Saldarriaga et al. (2023)
Hg						
1, 2, 4 mg kg <sup>-1</sup>	<i>Glomus mosseae</i>	<i>Zea mays</i>	Increased Hg soil sorption; Reduction of bioavailability and root uptake		Glasshouse	Yu et al. (2010)
0, 375, 750 μM	Mycorrhizal inoculum	<i>Naucllea orientalis</i>	Improved Hg tolerance		Greenhouse	Ekamawanti et al. (2014)
10 mg kg <sup>-1</sup>	A commercial arbuscular mycorrhizal formula, containing <i>Rhizophagus irregularis</i> and <i>Funneliformis mosseae</i> propagules	<i>Lactuca sativa</i>	Reduced Hg root uptake and translocation	plant growth ↑ P uptake ↑	Greenhouse	Cozzolino et al. (2016)
0, 100 mg kg <sup>-1</sup>	Soil mycorrhiza	<i>Lactuca sativa</i>	Improved Hg tolerance	Enhanced root elongation and seedling development	Greenhouse	Vargas Aguirre et al. (2018)
1, 10, 100, 1000 mg kg <sup>-1</sup>	Commercial mycorrhiza	<i>Lactuca sativa</i>	Improved Hg tolerance	Improved plant establishment	Greenhouse	Escobar-Vargas et al. (2022)
50 mg kg <sup>-1</sup>	<i>Glomus</i> sp.	<i>Zea mays</i>	Increased root Hg concentration and content	Change ligand from 2 to 4S complexes	Greenhouse	Kodre et al. (2017)
50 mg kg <sup>-1</sup>	<i>Glomus</i> sp.	<i>Zea mays</i>	Increased Hg uptake into the roots Increased Hg transfer to shoots	Imporve nutrient status	Greenhouse	Debeljak et al. (2018)
3.12 (±0.09) mg kg <sup>-1</sup>	A mixture of spores of the genera <i>Glomus</i> sp., <i>Acaulospora</i> sp., <i>Entrophospora</i> sp. and <i>Giaspora</i> sp.	<i>Lolium perenne</i>	increase the accumulation of Hg	Improve rhizosphere microbiome	Rhizobox	Saldarriaga et al. (2023)



**Table 1** (continued)

Elements concentration	AM fungal species <sup>a</sup>	Plant species	Key results	Mechanisms <sup>b</sup>	Experimental conditions	References
25 mg kg <sup>-1</sup>	<i>Rhizophagus irregularis</i> (QS81)	<i>Medicago truncatula</i> cv. Jemalong A17	Reduced the Hg translocation to shoots		Greenhouse	Guo et al. (2023)
50 mg kg <sup>-1</sup>			Increased the Hg translocation to shoots Reduced the Hg uptake into root		Greenhouse	

<sup>a</sup>The column 'AM fungal species' shows the current name, not the one at the time of publication

<sup>b</sup>↑ denotes increased or upregulated; ↓ means decreased or downregulated; and blank stands for not mentioned in the article

is facilitated by AM fungi. Interestingly, Hg transformation and uptake can be enhanced by microorganisms under P-limiting conditions, as demonstrated in a study by (Živković et al. 2019). Given the primary role of AM fungi in facilitating phosphate transport as polyphosphates, harnessing this function could be a crucial aspect of Hg bioaugmented phytoremediation.

The bioavailability of Hg for plants is relatively low, which has led to the introduction of many chemical amendments aimed at improving the efficiency of Hg uptake (Liu et al. 2020). Thiol-containing ligands, such as ammonium thiosulphate ((NH<sub>4</sub>)<sub>2</sub>S<sub>2</sub>O<sub>3</sub>) and sodium thiosulphate (Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub>), are a common choice among the many chemical amendments introduced to improve the efficiency of Hg uptake by plants (Moreno et al. 2005a, b; Wang et al. 2011; Makarova et al. 2021). This is because Hg has a strong affinity for thiol-containing ligands (Moreno et al. 2005a, b). However, the application of such amendments in natural environments can pose a significant risk of transferring Hg to local ecosystems through enhanced leaching (Smolińska and Król 2012; Smolińska 2020). Moreover, thiosulfate has been shown to cause physiological damage to the cell membranes of roots, leading to increased plasma membrane permeability and enhanced Hg uptake (Wang et al. 2018). Consequently, this process may induce the leakage of other ions (e.g., K), which might threaten plant performance or even plant survival. Thus, more sustainable strategies, namely the ability of AM fungi to facilitate the ligand environment for Hg uptake, should be targeted.

## Conclusion

The observed benefits of AM fungi in Hg remediation, including enhanced plant Hg tolerance, improved Hg ligand environment and the role of polyphosphate transfer, highlight the importance of further research into the plant–AM fungi symbiosis as a promising area of study for Hg-bioaugmented phytoremediation. As observed with Zn and Cd, AM fungi can modulate the expression of transporters, thereby enhancing or inhibiting metal uptake and translocation (Table 1). Consequently, understanding the underlying mechanisms of the corresponding transporters is crucial for optimizing the use of AM fungi in phytoremediation (Yang et al. 2022a, b). Further studies should focus on identifying the relevant membrane transporters that are responsible for facilitating Hg uptake by plant roots. However, the precise transporters involved in root Hg uptake have not yet been identified. It is plausible



that Zn and/or Cd transporters could play a role in Hg uptake due to their chemical similarities. Accordingly, insights from the knowledge of Zn and Cd transporters could provide a foundation for understanding Hg uptake. Additionally, other factors such as plant species, soil conditions (e.g., pH), other elements (e.g., P) and AM fungal species can also influence metal uptake and transport. Thus, future research should investigate the optimal environmental conditions under which AM fungi are effective in Hg remediation for their appropriate application.

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**Data availability** All data used in this discussion are included in this article.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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