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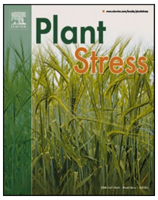

The current view on heavy metal remediation: The relevance of the plant interaction with arbuscular mycorrhizal fungi

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ABSTRACT

In the last years, heavy metal (HM) pollution has spread across natural and anthropic ecosystems posing inevitable, serious health risks. Commitments to resolve this issue resulted in tightening regulations and calls to action. The use of plants and their symbionts for remediation enjoys support. Nonetheless, keystones between mycorrhizal research and their application have still to be identified. The aim of this work was to provide an updated outlook on the current HM remediation contexts, with particular focus on the relevance of arbuscular mycorrhizal (AM) symbiosis as part of the plant-soil system. The AM potential implication in enhancing plant survival and performance in presence of HM stress could translate into efficient mitigation of environmental and health risks associated with increasing contamination of natural and human-managed ecosystems. Dust lift-up and leaching of HMs are the main routes of exposure and spread of pollution. The plant-soil system can reduce these risks. Moreover, the plants growing on HM-contaminated lands display decreased chlorophyll level as common toxicity symptom. Therefore, changes occurring in the chlorophyll content and/or in chlorophyll-associated parameters can be used as indicators revealing plant survival and physiological performance in phytoremediation contexts. Available scientific information suggests that plant inoculation with arbuscular mycorrhizal fungi (AMF) increases chlorophyll levels in most cases. Such response most likely occurs as the burden of HM stress is sustained by the symbiotic partners together, so that each partner has a role in mitigating the HM negative effects. Contaminated agricultural land and urban land come with their particular challenges. Feasibility in decontaminating them strictly relies on the achievement of long-term desired outcomes. Hence, perennial energy crops that establish successful AM symbiosis represent the best candidate plant species for further research on phytoremediation approaches.

1. Introduction

Soil pollution continues to be a world-wide problem (FAO and UNEP, 2021). Contaminated land sites number over millions across the planet (Kumar et al., 2019) including Europe ("European Environment Agency," 2023). Among the different types of pollutants, elevated levels of heavy metals (HMs) in top soil due to anthropogenic enrichment have been evidenced by surveys (Tóth et al., 2016a). These are of immediate concern due to the health and environmental threats they pose (Alengebawy et al., 2021). HMs interfere with plant growth and development and, *via* food chain, also endanger animals and humans (Feng et al., 2021). HMs are one of the concurrent environmental stressors contributing to a reduction of soil ecosystem services on global scale (Rillig et al., 2023). Therefore, these issues require urgent solutions. Worldwide, the most common HMs contaminants are As, Hg and Pb (FAO and UNEP, 2021). In Europe, some of the most abundant HMs in agricultural soil are As, Cu and Ni (Tóth et al., 2016b). The urban soil most often presents elevated levels of Cu, Cr, Ni, Pb and Zn (Binner et al., 2023). Green approaches to this problem enjoy the highest public acceptance (Riaz et al., 2022).

HMs in the widest sense include metals and metalloids of high elemental density and associated with toxicity for living systems. More restrictive definitions have been proposed (Ali and Khan, 2018), or replacement of the syntagma with "potentially toxic elements"

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(Pourret and Hursthouse, 2019). Therefore, the acceptations used by authors can vary across research literature. National legislations worldwide give their own definition and delimit thresholds (Kabata-Pendias and Pendias, 2001). In the European Union there are strategic plans, guidelines, policies and regulations in place aiming to limit their presence in soil (Kraemer et al., 2004), water (Zlati et al., 2023), air (Europe European Environment Agency, 2023), food products (The European Food Safety Authority, 2023) and various non-food goods (Restriction of Hazardous Substances in Electrical and Electronic Equipment, 2022). Tightening regulatory measures and health concerns inevitably requires the gap between science and applications to be reduced.

Phytoremediation is an attractive green technology that uses plants to mitigate negative consequences of HMs through stabilization, immobilization or removal of HMs from contaminated substrates (Yadav et al., 2023; Yan et al., 2020). Plant survival in phytoremediation settings is the most essential aspect (Shrestha et al., 2019). Natural or artificial enhancers might be required to ensure plant performance (Kafle et al., 2022). Commonly, the HMs excess in the growth environment causes chlorosis in plants, which understandably impends all other vital processes (Yaashikaa et al., 2022). How chlorosis might be reduced thereby represents a highly relevant objective. Without plant survival the pursuit of any other indicator and outcome becomes pointless in any phytoremediation initiative, not to mention the investment loss if the plants die. Plants are the primary producers and the backbone of natural ecosystems, agro-ecosystems and green urban spaces alike. An ancestral partnership between plant roots and some fungi, called arbuscular mycorrhizae, has been shown to be responsible for positive outcomes for host plants under various stressors (Diagne et al., 2020). AMF can establish mutual relationship with about 72 % of land plants by colonizing their roots (Brundrett and Tedersoo, 2018). Hence, many of the plant species suitable for phytoremediation might benefit from this relationship in the remediation contexts (Ma et al., 2022).

There is high potential interest in this concept. Hence, available information on arbuscular mycorrhizae – plant associations and their interaction with heavy metals requires to be examined in depth from the perspective of current remediation contexts. The aim of this work was to provide an overview on the major aspects that can move the needle in closing the gap between mycorrhizal research and application. To reach this aim two objectives were defined: to identify the keystone aspects that should be considered based on available literature, and to highlight the most relevant findings and novel approaches.

2. Sources of essential and non-essential heavy metals for plants

HMs are naturally present in the Earth crust (Kabata-Pendias and Pendias, 2001; Pais and Benton, 1997), but resulting from pedogenic processes, these are mostly remaining as trace elements (Wuana and Okieimen, 2011). Environmental enrichment with HMs following anthropogenic activity is posing the greatest issues. HMs have entered in massive amounts in the environment following the burning of fossil fuels, former or current industrial and manufacturing activities (Ali et al., 2021). Direct applications of pesticides containing HMs (such as Cu or As), sewage sludge, fertilizers with HM traces, livestock manures, food wastes and composts, have caused many land sites to become contaminated with HMs. Additionally, technogenic materials ranging from construction materials, ashes, demolition rubbles and mine wastes can leach HMs (Alengebawy et al., 2021; Alloway, 2013). Proximity to industrial, agricultural centers and municipal landfills can represent sources of HMs by particulate atmospheric deposition and rain runoff (Alengebawy et al., 2021). In cities, traffic exhaust, home heating systems, paints and electronic wastes are further sources of HM pollution (Binner et al., 2023). In this context, plants across all ecosystems (natural as well as human-managed ones) are due to encounter some levels of HM stress. Beyond their normal ranges HMs represent unfavorable environmental factors for plants and therefore qualify as plant stressors in the broad biological sense (Gaspar et al., 2002). The HMs can be present in various forms in soil such as exchangeable ions, dissolved ions, as part of the solid mineral component of soil, adsorbed on soil particles, as precipitated matter or in organic complexes (Rehman et al., 2023). The phyto-availability of metals of anthropogenic source is significantly higher than that of metals of pedogenic origin (Kabata-Pendias and Pendias, 2001), thereby explaining why these accumulate faster across food chain with concerning environmental and health consequences (Kumar et al., 2019).

Out of the large number of chemical elements that can potentially be present in the plant growth environment (Kabata-Pendias and Pendias, 2001; Utermann et al., 2006) including over 50 HMs (Ali and Khan, 2018), during their evolution higher plants selected only 19 for their basic metabolism, with some required in higher amounts (C, H, O, Ca, K, Mg, N, P and S) than others (B, Cl, Co, Cu, Fe, Mn, Mo, Na, Ni and Zn) (Wilfried, 2006). Therefore, based on their role, some HMs were classified as essential (Co, Cu, Mn, Mo, Ni, Zn), as directly involved in plant metabolism (Arif et al., 2016), while others as non-essential (*e.g.* As, Cd, Cr, Hg, Pb) because they possess no metabolic role in the plant, and are usually toxic to living systems even in small amounts (Furini, 2012; Kabata-Pendias and Pendias, 2001). The essential HMs are involved in oxidation or reduction processes and needed by the plant in small quantities, such as ferritin located in plastids that store Fe, Mn involved in photosystem II as well as some enzymatic processes, Cu in plastocyanin and cytochrome *c* oxidase, Zn in some enzymes, to name a few. These essential HMs are toxic to plants in higher amounts (Page and Feller, 2015). With the exception of metal hyperaccumulator plant species, plants do not accumulate trace elements in excess of their short term metabolic requirements (Tangahu et al., 2011).

The major sink for HMs released into the environment are the soils, where they remain for a long time ranging from decades to thousands of years (Kabata-Pendias and Pendias, 2001), therefore the plant rhizosphere is the first living system that deals with them. Most of HMs do not undergo microbial or chemical degradation, with only some changes in their chemical forms (speciation) and bioavailability occurring (Wuana and Okieimen, 2011). Therefore, once accumulated in soil, these elements are there to stay for a long time.

3. Plant interaction with heavy metals: effects at the cell-level

The HM active interaction with plants starts with the first contact *via* cell wall, which concomitantly represents a target and barrier. Plant cell wall components can take part to reactions *via* their functional groups with HMs leading to either damage by impaired synthesis or binding them and thus sequestrating the polluting agents (Parrotta et al., 2015). Among the cell wall components shown to play a role in HM resistance, are the pectin moieties able to chelate HMs or lignin, which exhibits increased biosynthesis upon HM stress (Kosakivska et al., 2021). HM uptake by plants can take place passively through underground or above-ground organs, or actively with the help of various ion channels and transporters. Once within the plant, HMs can be further systemically translocated *via* xylem and phloem to various plant parts (Ghuge et al., 2023). It was estimated that plants can produce over 200,000 kinds of metabolites, which metabolic pathways are typically altered during HM stress. Subtle changes observed under stress gradients are important in deciphering the biological mechanisms at play (Feng et al., 2021). Particularly, phytohormones and related signaling cascades were shown to be essential in regulating the plant's ability to cope with the HM toxicity effects (Nguyen et al., 2021; Saini et al., 2021).

At the whole plant level, early changes following exposure to HMs are difficult to detect. At the cell level, early plant responses are oxidative stress, transcriptomic and proteomic changes, accumulation of specific metabolites, sometimes mirroring the response to other types of abiotic stressors (Singh et al., 2016).

There have been named several processes involved in HM interference with the plant biological system: competition for absorption at the root level due to similarities (*e.g.* As and Cd, P and Zn), functionality collapse, resulting from the displacement of essential cations from their binding sites, disruption and inactivation of protein integrity by impinging with their sulfhydryl group (-SH), impairment of macromolecules by the release of reactive oxygen species (ROS) (Singh et al., 2016).

Prominent roles in HM homeostasis in plants are played by transport proteins, such as ATPases (CPx-type), cation diffusion facilitator (CDF), natural resistance-associated macrophage protein family (NRAMP) and zinc-regulated - iron-regulated transporter-like proteins (ZIP), with mechanisms and functional roles analyzed in detail (Ghori et al., 2019). Moreover, there are molecules, including organic acids, such as citrate, histidine, malate nicotinamide, which are involved in metal translocation, as it is the case for Zn, Cu and Cd (Kosakivska et al., 2021).

Besides physiological, anatomical and biochemical adjustments, the plant's resistance to toxic HMs is controlled at the molecular level by a wide consortium of genes. This includes stress responsive protein-coding as well as non-coding regulatory genes, involved in several biological pathways, from signal transduction and hormone metabolism to biosynthesis of osmoprotectant solutes and antioxidant compounds (Singh et al., 2016). Functional characterization of those genes is important for plant genetic improvement programs (Jamla et al., 2021). For instance, mounting experimental evidence has pointed to small noncoding RNAs as key effectors in the regulation of molecular signals activated in different crop species upon HM stress (Ding et al., 2018; Qiu et al., 2016; Silva et al., 2019), hence proposing miRNAs as target for genetically improving the plant's endurance to HM exposure. In addition to small non-coding RNAs, transcriptional reprogramming processes in response to HM-derived toxic damages can be controlled by epigenetic modifications, such as alterations in the chromatin structure and DNA methylation, which enable to maintain the plant genome stability under genotoxic stress, ultimately supporting the establishment of adaptive mechanisms on the long term (Dutta et al., 2018).

4. Understanding the main symptom of HM stress in plants: decreased chlorophyll content

HM toxicity effects in plants can occur at all stages of the plant's life and affect all plant tissues, with pronounced influence on incipient developmental stages such as germination and root growth. Particularly, decreased root elongation and increased lateral root formation are among the first consequences of decreased photosynthate flow towards roots under HM stress (Riyazuddin et al., 2022). Once symptoms start to set in, stunted growth, reduced biomass, chlorosis and eventually wilting can be observed (Ali and Gill, 2022). Some leaf anatomical changes also occur (Pandey et al., 2022). In *Rhus chinensis* the gradual increase of Mn caused progressive reduction of the leaf epidermis thickness and of leaf tissue compactness, and palisade tissue thinning (Pan et al., 2023a).

Based on the impact on growth and development of the most common crop plants, critical levels of HMs in plant tissues have been identified, with quantity per dry matter ranging between 7 and 520 mg/kg for Zn, 120–1000 mg/kg for Mn, 5–35 mg/kg for Cu, 14–26 mg/kg for Ni, 1–20 mg/kg for As, 1–8 mg/kg for Hg, 5–150 mg/kg Cd, 35 mg/kg for Pb, 1–18 mg/kg for Cr. At those levels, the toxicity symptoms occur, with chlorosis as the most common sign among others (Thakur et al., 2022).

Since it was univocally proven that integrity of chlorophyll, and therefore efficiency of the photosynthetic activity, is affected by HM stress (Küpper et al., 1996), chlorophyll measurements were reliably adopted to detect HM ion toxicity and damage in plants (Chen et al., 2019; Joshi and Mohanty, 2004). Because the green tissues of the land plants are the sites where organic substances are synthesized to sustain plant growth and development (Lawson and Milliken, 2023), the metabolism of chlorophyll has to be well-balanced during the plant's lifecycle, and hence the high relevance of the associated parameters. By impairing all other vital processes, overexcited photosynthetic apparatus, chlorophyll degradation or inhibited biosynthesis, all have devastating consequences for plants (Hörtensteiner and Kräutler, 2011). Therefore, chlorophyll integrity affects plant survival, growth and development under HM stress. The experimental evidence of the bio-protective and bio-alleviation role of AM in relation with maintenance of the photosynthetic process requires an in-depth examination. In the current scenario of increasing HM pollution worldwide, a more comprehensive knowledge on this subject is necessary due to the resulting practical implications on the future progress of green remediation technologies.

Plants are biological solar panels that absorb light within 400–700 nm range for their photo-processes, with the help of photosynthetic pigments (McDonald, 2003). The molecules of chlorophyll are bound to proteins located in the thylakoid membrane of the chloroplast (Rantala et al., 2020). They present a hydrophilic porphyrin head and a hydrophobic phytol tail. The pyrrole rings chelate a Mg^{2+} atom. In plants, the chlorophyll *a, b* and accessory pigments (carotenoids) complement each other to increase the range of light that can be absorbed. The chlorophyll *a* is 2–3 times more abundant than *b* (McDonald, 2003) and is the pigment instrumental to the photochemistry reactions (Björn et al., 2009), while chlorophyll *b* is important for light acclimation of plants (Tanaka and Tanaka, 2011; Voitsekhovskaja and Tyutereva, 2015).

The chloroplast envelope is a double membrane system with transporters localized on both of them and involved in maintaining the metal homeostasis of this organelle that is rich in transition metals. Its intermembrane space plays a role in detoxifying metals. Over 3000 proteins are found at the level of this organelle, with around 90 transporters being associated with its membranes and the exchanges taking place here (Schmidt et al., 2020). Transition metals are involved in the processes of photosynthesis and photolysis of the water molecule. The HM transporters localized on the envelope and thylakoid membrane are important for enabling the supply of Cu and Zn. The CMT1 (*CHLOROPLAST MANGANESE TRANSPORTER 1*) located on the inner chloroplast membrane, ensures Mn homeostasis. Different Fe transporters are involved in Fe homeostasis. ABC transporters with wide range of metal affinity are also crucial for chloroplast biogenesis and proper functioning, as well as for Co and Ni transport outside the chloroplast (Jogawat et al., 2021). The impact of HMs on photosynthesis mechanisms depends on the reactivity and concentration of HMs. Replacement of $Mg^{2+}$from the molecule of chlorophyll with a HM is one of the most important causes of metal-induced damage in plants (Küpper et al., 2006). Further negative effects deal with the inactivation of photosynthetic enzymes (such as RuBisCO) and ROS-induced damage in chloroplasts – all those responses lead to reduced chlorophyll concentration, destabilization of the chloroplast membranes and decreased photosynthetic rates (Riyazuddin et al., 2022).

The types of structural damages to the chloroplast found in plants under HM stress include shape-alteration, reduced size and number, decreased grana number as well as thylakoids per granum, disorganization of thylakoid ultrastructure, higher number and size of plastoglobuli. Besides substitution, the decreased chlorophyll concentration observed in HM-stressed plants is mainly due to inhibition of the pigment biosynthesis. To date, the effects of HM stress on carotenoids, the accessory pigments to photosynthesis, remain poorly studied (Souri et al., 2019). Deeper insights into this subject were provided through the analysis of the chloroplast genome (cpDNA) harboring about 120 genes that play a specific role in the functioning of this organelle. Furthermore, due to the prokaryotic evolutionary origin, chloroplast is highly suitable for genetic engineering: it presents the advantage of an operon system organization enabling poly-cistronic mRNA, thus transgenes inserted therein are not at risk of undesired gene silencing or position variation (Zhang et al., 2023a). Therefore, it has been proposed that plastid transformation could represent a successful approach for obtaining plant genotypes displaying improved physiological responses during stress exposure, including individuals with enhanced potential for phytoremediation (Singhal et al., 2023).

5. Phytoremediation: how it works

Plants display a great phenotypic plasticity because as sessile organisms are unable to escape the conditions of their substrate, and therefore have to evolve strategies to survive by adapting (Parrotta et al., 2015). It has long been established that the important soil properties that affect uptake of HMs by the plant cover are: soil pH, soil cation exchange capacity, soil texture, clay mineralogy and soil structure (Stevens et al., 2002). In turn, root exudates secreted by the plants modulate the physical-chemical parameters of the soil environment, due to the ability to change the forms and bioavailability of HMs, while also stimulating the coexisting rhizosphere microbiota activity – all contributors to reducing the environmental danger posed by HMs (Agarwal et al., 2023). The HM exogenous binding relies on the ability of organic anions released by roots to establish bonds by metal chelation with carboxylate groups, which can reduce the HM influx into the plant (Kosakivska et al., 2021).

Plants that are able to grow in environments rich in HMs can display two main divergent strategies: tolerance or avoidance (Parrotta et al., 2015), based on the fate of HMs in the interaction with the plant. The avoidant plant species will make use of mechanisms to prevent HMs from entering the protoplast, while the tolerant ones make use of strategies to either neutralize or remove the HMs from the most metabolically-sensitive areas (De Caroli et al., 2020).

In phytoremediation, tolerant species are mostly sought. Depending on the species and the identity of the HMs, different methods, namely rhizofiltration, phytostabilization, phytoextraction and phytovolatilization, can be employed. The first two are merely an immobilization of pollutants, but the latter two can actually reduce the HM levels in soil (Shen et al., 2022; Yadav et al., 2023, 2022). As a measure of phytoremediation potential, indicators such as bioconcentration factor (BCF) and translocation factor (TF), which should be $>$ 1, have been commonly used to evaluate whether a plant qualifies as hyperaccumulator (Sharma et al., 2020). Diminishing the exposure risk for humans, animals and spread of pollution is an important goal of phytoremediation.

Physiological regulation in response to metal influx in tolerant plants involves: guarding the most active sites of the cell by fast delivery of excess metal from cytosol across tonoplast into the vacuole, reallocation of metals to tissues that are less metabolically active like epidermis, preferential accumulation of metals in deciduous organs like leaves, and to lesser degree into generative organs like seeds. The metal-tolerance in plants is energy costly. Thus, reallocation of HMs across cell compartments requires ATP, the synthesis of complexing compounds requires energy from the primary metabolism as well as N, S (*e.g.*, synthesis of phytochelatins to detoxifying As and Cd, or synthesis of metallothionein to detoxify Cu) (Wilfried, 2006).

To date, the specific mechanisms caused by HMs that induce endomembrane remodeling remain mostly uncharacterized, although the vacuolar system extension in tolerant plants has enjoyed some attention (De Caroli et al., 2020).

Phytoremediation by phytoextraction of HMs was shown to be feasible for slightly contaminated soils, whereas more “invasive” procedures, such as soil washing, are more cost-effective in cases of severe pollution. This is due to several reasons: a given plant species can be used to target 1–2 HMs, the process is slow and takes several years to bring any HM to acceptable levels. That also means that respective land is not suitable for other use during that time (Chen and Li, 2018). There are novel interventions, which have been shown successful in mitigating HMs in soils. The results of such novel methods might turn the soil environment more suitable to sustain plant growth and development as well, and therefore could co-join the phytoremediation process. These novel practices concern application of conditioners such as charcoal, biochar and activated carbon (Golia et al., 2022) or various ameliorants, such as synthetic chelating agents, green or biosynthetic nano-particles (Awasthi et al., 2022).

6. Choosing the suitable plant species candidates for phytoremediation

The capacity of plants to survive and grow in metal rich soils and substrates is found across species from unrelated orders, families and genera, as well as within species through microevolution. The proposed explanation was that evolution of metal tolerance took place due to specific conditions occurring across geological ages, and therefore spatial distribution of metals might explain this particular plant adaptation (Wilfried, 2006).

Metal hyperaccumulator plants, which account only for 0.2 % of the vascular plants, grow naturally on either or both metal-rich soil/normal soil, and are distinguished by the ability to survive with metal concentrations per dry leaves exceeding 100 μg/g for Cd, Se and Tl, over 1000 μg/g for As, Ni, Pb, over 3000 μg/g for Zn and 10,000 μg/g for Mn (Pollard et al., 2014). Out of the 700 plant taxa listed as hyperaccumulators of metals, more than 100 species are from *Brassicaceae* (Zeremski et al., 2021), a botanic family in which most of the members are non-mycorrhizal plants (Anthony et al., 2020). Likely, this condition relies on the aims during early age of this green technology. Back then, it was sought to screen for HM tolerance in plants with the sole purpose to identify the best individuals suitable to accumulate certain HMs. The symbiotic potential of those plant species or suitability for large-scale phytoremediation settings were not among the criteria. Other metal-accumulator plant species are found in the botanic families *Asteraceae, Euphorbiaceae, Fabaceae, Rubiaceae* and *Scrophulariaceae* (Suman et al., 2018) to name a few of the AM hosts.

The AM plant host categories that can potentially be exposed to HM stress are virtually getting larger, as HMs accumulate across ecosystems. Today, one can recognize that there is stringent need for a congruence between data bases recoding phytoremediation capacity of plant species (McIntyre, 2003; Nelson et al., 2012) and those reporting their mycorrhizal status (Soudzilovskaia et al., 2020) in order to identify the best plant species candidates. This is particularly necessary, considering that often the front line of action is not represented by specialists on AM topics, but rather by landscaping specialists (Răcușan et al., 2023), who select plant species based on landscaping purposes mainly. For this reason, sources should be made available, to easily identify the best candidate species.

The databases that allow the choice of the suitable plant candidates for HM detoxification (McIntyre, 2003; Nelson et al., 2012) currently identify a limited number of species. This somewhat diminishes the options in phytoremediation. Furthermore, the plant species – AMF specificity in the context of phytoremediation remains less explored. Yet, the identification of the most suitable combination is determining the efficiency of the phytoremediation processes (Bentrad and Bouhired, 2022).

The plants growing on contaminated soil and substrates can often exceed the permissible limits of HM content, and the resulting biomass, if harvested, poses further environmental concerns (Raklami et al., 2022). Biomass and growth rate of a plant species are deciding criteria for suitability of a given species for phytoremediation programs (DalCorso et al., 2019). Considering these aspects, the utility criterion must have greater weight in selecting the candidate plant species. Studies on crop plants are relevant for low polluted soils, particularly in relation to methods aiming at reducing the risk and levels of HM uptake in the aboveground plant parts, to ensure these are not a danger in food and feed chain (Rai et al., 2019). However, for more severely polluted soils, which pose serious concern for metal uptake and accumulation in the plant biomass, one has to strongly consider two categories of plants: those of the highest attractiveness for biomass up-cycling possibilities (Khan et al., 2023; Prabha et al., 2021) or the ornamental plants (Deepika and Haritash, 2023; Khan et al., 2021).

Studies addressing those plant species that are highly attractive in phytoremediation programs such as energy crops or fiber plants, are among the most relevant, as the resulting biomass could be used for biofuel and energy production or as plant-based construction materials (Quarshie et al., 2021; Suman et al., 2018). Candidates from this category can be found among herbaceous and woody species alike. The annual crops: *Sorghum bicolor* and fiber crop plants such as *Cannabis sativa* and *Linum usitatissimum* are common examples. To these can be added several perennial energy crops such as *Agropyron elongatum, Arundo donax, Fallopia japonicum* × *bohemica* (*Reynoutria japonica*), *Helianthus tuberosus, Miscanthus* × *giganteus, Panicum virgatum, Phalaris arundinacea* and *Silphium perfoliatum*, as well as short rotation coppice crops like *Salix* spp., *Populus* spp. and *Paulownia tomentosa* (Abreu et al., 2022; Ruf et al., 2019; Suman et al., 2018).

Medicinal and aromatic plants (MAPs) grown on HM-enriched soils can be used for essential oil production, which is free of HMs. There is evidence for elicitation of secondary metabolites in MAPs by various HMs on contaminated soils in some economically valuable species, such as *Artemisia annua* (As)*, Hypericum perforatum* (Cr)*, Matricaria chamomilla* (Ni), *Mentha crispa* (Pb), *Mentha pulegium* (Cu, Zn). While not all MAPs species are actually able to phytoremediate effectively, these do represent an alternative use for contaminated land (Asgari et al., 2017).

Ornamental plants represent a highly diverse category that includes an array of short-habit herbaceous species, either hyperaccumulators or accumulators of HMs (*e.g. Calendula officinalis, Cosmos bipinnatus, Elsholtzia splendens, Euphorbia marginata, Gazania rigens, Impatiens balsamina* and *Tagetes erecta*), shrubs (*e.g. Lavandula angustifolia, Ulex europaeus*) and trees (*e.g. Morus alba, Populus deltoides*) (Khan et al., 2021). This broad group is suitable to mitigate HMs *in situ* pollution of urban and peri-urban spaces by inclusion in landscaping schemes, thereby representing a preferred approach, particularly for urban environment (Răcușan et al., 2023; Vidican et al., 2022).

It could be easily built arguments in favor of perennial plants over annual plants, based on an applicative rationale. The frequency of the investment in the planting material is one argument. The plant root system can reduce the HMs risks by immobilizing the HMs in the symbiotic network from the soil explored area. However, the annual crops cover the soil only for a limited number of months in a year. When the plant life cycle ends, the root no longer represents a living system actively interacting with HMs in soil. Perhaps any HM stored inside roots and in rhizosphere can once more be released and leach into the soil solution. In addition, annual crops require yearly soil works, which involves the soil mobilization, a cause of contaminated dust to lift-up. Further mobilization with air masses and deposition in non-target areas might increase the pollution threat.

Ecological compensation of pollution is in theory based on the "polluter pays principle", which guides the policies on dealing with pollution impact management on the environment (including soil) (European Court of Auditors, 2021). To ensure these objectives are addressed and not avoided or postponed, the offered solutions cannot be disconnected from feasibility aspects, as implementation strictly depends on costs (Rehman et al., 2023; Wan et al., 2016). Choosing the suitable plant species for phytoremediation can help cover some operational costs, by monetizing opportunities existing for harvested biomass grown on contaminated lands (Quarshie et al., 2021). The adopted methods can also rely on combined approaches (Rehman et al., 2023).

7. AM fungi and phytobionts under HMs

AMF comprise over 200 described species and estimated 300–1600 species of biotrophs classified in the Glomeromycota clade (van der Heijden et al., 2015). AMF improve many soil characteristics in ways that are beneficial for plants, and colonize their roots for mutual exchange (Fall et al., 2022). In the AM relationship, the host plant shares the carbon fixed by photosynthesis with its fungal partner. From 4 to 20 % of the assimilates are transferred to fungi in exchange for improved P, N and micronutrients acquisition. The cost-benefits are context-dependent and have been explored for only a limited number of traits. Outcomes for the partners depend either on the fungal strain or on the plant species involved in this partnership (Bennett and Groten, 2022). The failure to ensure mutual benefits can shift the relationship towards negative, and this can occur in specific conditions. Functional compatibility is important between the plant and AMF (Kaur et al., 2022). Conflict of interests between symbionts over C allocation could play an important role in the outcome of phytoremediation, considering that plants might experience reduced C fixation under metal stress. Detailed knowledge on the ability of the plant to sustain its symbiont in presence of reduced photosynthetic ability caused by HM stress could be highly relevant for the feasibility of inoculation.

When it comes to a contaminated substrate, the first organ exposed to HMs from the soil solution is the root, and its mycobiont (Ma et al., 2022). Fungi have higher metal tolerance than plants. AM was proposed as a candidate for co-remediation in association with plants (Bhantana et al., 2021; Wilfried, 2006). It has been suggested that metal hyperaccumulator plant species, hosting beneficial rhizosphere microbial communities, could provide attractive low-cost cleaning approaches for the remediation of metals from a large number of contaminated sites. This result is a consequence of the ability of AMF in mitigating phytotoxicity and HM stress in their hosts (Riaz et al., 2021).

Understanding of the AMF communities that colonize different plant groups is necessary to better connecting the symbiosis to ecosystem processes. Investigations showed that a large number of AMF taxa were significant indicators of certain plant functional groups, with grasses harboring higher AM abundance compared to forbs and woody species (Davison et al., 2020). Most commonly available inoculants are based on two generalist species *Rhizoglomus irregulare* and *Funneliformis mosseae* with worldwide distribution. Strain performance was so far evaluated based on the fungal colonization ability and efficiency in inducing beneficial plant response, particularly to be used in agroecosystems (Giovannini et al., 2020).

AMF are found in many ecosystems, including polluted ones. It was determined that although spore germination and hyphal growth are inhibited by HMs in these fungi, strains isolated from polluted environment display naturally-acquired resistance and could be used with presumably higher success (Göhre and Paszkowski, 2006). A recent study has shown that AMF strains acclimated to Pb for 1–2 years had an enhanced colonization capacity in *Bidens parviflora* under Pb stress (Yang et al., 2022). Investigation on the identity of AMF from HM-polluted sites can also provide important practical information, particularly related to formulations of efficient inoculants. Roots sampled from two sites in Ecuador, polluted by HMs (mainly Pb, Zn, Hg, Cd and Cu) due to gold mining activities, showed AM colonization between 40 and 80 %, with AMF generalists predominant over specialists (Suárez et al., 2023). Copper-based preparations are commonly used as fungicides applied to crop plants, making this HM one of the common pollutants in the European agroecosystems, with topping elevated Cu levels in vineyards, followed by olive plantations and orchards (Fuente et al., 2021). Experiments conducted in greenhouse on grapevine plantlets of the 1103 Paulsen rootstock (*Vitis berlandieri* × *Vitis rupestris*), subject to progressive Cu doses (from 50 to 150 mg/kg) and to a native AMF species mix (with *Glomus ambisporum* as the dominant species), revealed that AMF species richness and root colonization capacity decreased along with increasing Cu concentrations in the soil (Betancur-Agudelo et al., 2023).

Based on reviewing relevant studies on AMF and crop plants, a recent work highlighted that plants under various HM stresses are protected due to several "repairing" mechanisms of AMF, with frequent ones across HMs studies represented by: *Claroideoglomus etunicatum, Funneliformis mosseae* and *Rhizophagus irregularis* (Liu et al., 2023). AMF in association with various host plant species were shown to contribute to phytostabilization as well as to phytoextraction (Riaz et al., 2021). A recent meta-analysis revealed that both the bioavailability and the plant uptake of As and Cd (two common non-essential HM pollutants) decreased in presence of AMF. However, there was a variation across

Table 1
Influence of AMF inoculation on chlorophyll parameters in plants under single HM stress.

HM substrate content	Plant species	AMF inoculant	Main findings	Source
As (30 mg/kg)	*Vigna radiata* cv. BARI mung genotypes	AMF mix (unspecified)	AMF-inoculated plants had higher chlorophyll *a, b* and total chlorophyll content than control	Alam et al. (2019)
Cd (10–20 mg/kg)	*Triticum aestivum* cv. Bainong 207	*Glomus mosseae*	AM restored the chlorophyll content to 70–94 % relative to the normal levels, under Cd stress	Li et al., 2023a
Cd (4.5 mg/kg)	*Robinia pseudoacacia*	*Glomus mosseae* BGC NM04A	Total chlorophyll and carotenoids decreased in inoculated plants compared with non-inoculated Cd stressed plants, both under normal and elevated CO_2	Zhang et al. (2023b)
Cd (30–270 mg/kg)	*Broussonetia papyrifera*	*Rhizophagus irregularis* BGC BJ09	Chlorophyll *a* content was higher at 30–90 mg/kg Cd stress (but not significantly), chlorophyll *b* content was higher at 30–270 mg/kg Cd stress (significant only for 30 mg/kg Cd stress) with respect to non-inoculated plants exposed to same stress level	Liang et al. (2023)
Cd (10–50 mg/kg)	*Hibiscus cannabinus* cv. Zhe 367	*Rhizophagus aggreratus*	AM increased chlorophyll content (*a, b*, total) at two tested HM levels compared to control	Pan et al. (2023b)
Cd (80 mg/kg)	*Cannabis sativa*	*Rhizophagus irregularis*	AM promoted plant growth by regulating chlorophyll fluorescence parameters in stressed plants	Sun et al. (2022)
Cd (60 mg/kg)	*Lolium perenne* cv. Taya	*Glomus etunicatum, Glomus mosseae*	In presence of AM, total chlorophyll concentrations in Cd stressed plants increased, returning to control levels	Han et al. (2021)
Cd (10–50 mg/kg)	*Trifolium repens*	*Glomus aggregatum, G. etunicatum, G. intraradices, G. tortuosum, G. versiforme.*	AM significantly increased chlorophyll content (CCI, SPAD) at 10–20 mg/kg Cd stress level, compared to control	Xiao et al. (2021)
Cd (15–120 mg/kg)	*Solanum nigrum*	*Rhizophagus irregularis*	Cd detoxification by earthworm-AM-*S. nigrum* association was manifested by increased chlorophyll content (17–63 %) and improved photosynthetic capacity	Wang et al. (2021)
Cd (50 mg/kg)	*Zea mays*	*Funneliformis mosseae* BGC YN0	AMF inoculation and AMF + DSE co-inoculation, significantly increased the chlorophyll content in maize leaves, resulting in stronger photosynthetic activity	He et al. (2020)
Cd (10–100 mg/kg)	*Acroptilon repens*	mix of *Glomus* spp. (*G. intraradices, G. mosseae*, and *G. fasciculatum*)	Chlorophyll *a* and *b* content was higher in AMF-inoculated plants compared to control under Cd stress	Rasouli-Sadaghiani et al. (2019)
Cd (2.25–6.25 mM)	*Trigonella foenum-graecum* var. Giza	*Glomus monosporum, Glomus clarum, Gigaspora nigra, Acaulospora laevis*	The decrease of chlorophyll content index (CCI) was lower for inoculated plants with respect to non-inoculated plants under the same Cd stress	Abdelhameed and Metwally (2019)
Cd (150 μM)	*Bassia indica*	*Funneliformis mosseae, Rhizophagus intraradices, Claroideoglomus etunicatum*	AM inoculated plants had reduced chlorophyll *a* and *b* concentration at same Cd stress level	Hashem et al. (2019)
Cd (200–1000 ppm)	*Pistacia vera* cv. Ahmad Aghaei	*Glomus mosseae*	Total chlorophyll content was higher in the AMF inoculated plants than non-inoculated plants at same Cd levels	Rohani et al. (2019)
Cr (50–200 mg/kg)	*Iris tectorum*	*Rhizophagus intraradices*	Inoculated plants presented increased levels of chlorophyll *a*, total chlorophyll and carotenoids compared to non-inoculated plants under the same stress level	Zhao et al. (2023)
Cr (5–25 mg/kg)	*Iris wilsonii*	*Rhizophagus irregularis* BEG 140	Chlorophyll content increased with 4.7–37.7 % compared to the non-inoculated plants under the same stress level	Hu et al. (2020)
Cr (32,562 ppm)	*Solanum lycopersicum* var. Navodaya	mixed culture of four AMF and *Aspergillus terreus*	Treatment with soil compost amendment along with AMF and *A. terreus* inoculation enhanced the accumulation of photosynthetic pigments up to 214 %	Akhtar et al. (2020)
Hg (0.1–2 mg/kg)	*Oryza sativa* cv. Zhennuo 20	*Glomus etunicatum, Glomus mosseae*	Inoculation significantly improved chlorophyll content (CCI, SPAD) compared to non-inoculated plants exposed to the same stress level	Li et al. (2023b)
Mn (1–15 mM)	*Rhus chinensis*	*Funneliformis mosseae*	Chlorophyll *a* and *b* and carotenoid contents maintained consistently higher in inoculated plants compared to non-inoculated plants exposed to same stress	Pan et al. (2023a)
Mo (1000–4000 mg/kg)	*Zea mays*	*Claroideoglomus etunicatum* BEG 168	In inoculated plants chlorophyll *a* and *b* content significantly increased at 2000–4000 mg/kg Mo compared to non-inoculated plants at the same stress level	Shi et al. (2018)
Ni (450 mg/kg)	*Helianthus annuus*	*Claroideoglomus claroideum* BEG 210	AMF inoculation improved chlorophyll *b* content; *Pseudomonas libanensis* + AM improved chlorophyll *a* and *b* in plants under saline + HM stress, compared to their respective non-inoculated controls	Ma et al. (2019)
Pb (500–2000 mg/kg)	*Platycladus orientalis*	*Rhizophagus irregularis, Funneliformis mosseae*	Total chlorophyll content increased following AMF inoculation	Zhou et al. (2023)
Pb (500–2000 mg/kg)	*Bidens parviflora*	*Funneliformis mosseae* (Domesticated 6, 12, 24 months)	Domesticated AMF strains caused higher chlorophyll *b* concentration than non-domesticated strains in plants under the same Pb stress	Yang et al. (2022)
Pb (500–1500 ppm)	*Coriandrum sativum*	*Glomus mosseae*	Chlorophyll *a*, total chlorophyll and carotenoid contents increased following AMF inoculation compared to non-inoculated plants at the same Pb stress level	Fatemi et al. (2020)
Pb (100–1000 mg/kg)	*Miscanthus sacchariflorus*	*Gigaspora margarita*	AMF inoculation increased chlorophyll content of plants under Pb stress, though non-significantly	Sarkar et al. (2018)
Sb (300–1200 mg/kg)	*Oryza sativa* cv. Xiangwanxian No. 12	*Glomus mosseae*, BGC NM01A	Chlorophyll content (CCI, SPAD) was lower in AM plants than non-inoculated plants at the same Sb stress level, but data were significant only for Sb concentration of 1200 mg/kg	Zhou et al. (2022)

Table 2
Influence of AMF inoculation on chlorophyll parameters in plants under mixture of HMs.

HMs substrate content	Plant tested	AMF inoculant	AM effect on pigments	Source
mine soil (30.45 Cd + 5818.58 Pb + 13,120.71 Zn mg/kg)	*Zea mays* (23 different genotypes: 22 commercial cultivars and an inbred line)	*Funneliformis mosseae* (BGC YN05, 1511C0001BGCAM0013)	In the 21.74 % of cultivars chlorophyll content increased in presence of AM, but in 73.9 % of the cultivars AM had no significant difference	Yin et al. (2021)
dry tannery sludge (14,855 mg/kg Cr + Pb, Ni, Cd)	*Zea mays*	*Rhizophagus fasciculatus, Rhizophagus intraradices, Funneliformis mosseae, Glomus aggregatum*	Chlorophyll *a*, *b*, total chlorophyll and carotenoid contents increased in AMF inoculated plants under mixture of HMs; the highest chlorophyll contents were observed in *F. mosseae* treated plants (43–54 % higher than control)	Singh et al. (2019)
soil near smelter (1426.7 mg/kg Pb + 839.6 mg/kg Zn + 16.9 mg/kg Cd + 2.02 mg/kg As)	*Zea mays*	*Funneliformis mosseae* (BGC YN05, 1511C0001BGCAM0013); *Diversispora spurcum* (BGC SD03A, 1511C0001BGCAM0047)	Only *F. mosseae* inoculation significantly increased the chlorophyll *a* content in maize leaves	Zhan et al. (2018)
sewage water 25–70 % (31.3 μg/g Mn + 10.53 μg/g Zn + 5.6 μg/g Cu + 1.23 μg/g Co)	*Tagetes erecta* cv. Jubilee	*Glomus constrictum*	Chlorophyll content (CCI, SPAD) was higher for mycorrhizal plants than non-mycorrhizal plants at all tested levels	Elhindi et al. (2018)
soil from Zn deposit area (7200 mg/kg Zn + 1140 mg/kg Cu + 480 mg/kg Pb + 72 mg/kg Cd)	*Acacia mangium, Sorghum bicolor, Urochloa brizantha*	*Glomus macrocarpum, Paraglomus occultum, Glomus* sp.	Chlorophyll content (CCI, SPAD) of plants inoculated with AMF was significantly higher than those of non-inoculated ones, for the plant species: *A. mangium* and *U. brizantha*	de Fátima Pedroso et al. (2018)

botanic families. The prevalent inoculated species emerged from studies on As and Cd were: *Funneliformis mosseae, Funneliformis caledonium, Rhizophagus intraradices, Rhizophagus irregularis* and *Glomus versiforme* [*Diversispora versiformis*] (Tan et al., 2023). The compatibility of combined interventions, particularly the implications for the stability of AM-plant system or the outcome in the presence of novel soil conditioners and ameliorants, has not been addressed in depth yet. Recently, a mesocosm study has proven that AM increased HM translocation in barley plants grown on fly ash ameliorated soil, therefore amplifying food chain contamination risks (Goswami et al., 2023).

AM presence can favor the mobility of metals and their transfer to the plant (Cabral et al., 2015), although, under HM stress, the main ameliorative outcome of AM on plants is attributed to reduced adsorption of HMs, dilution of HMs, decreased oxidative stress and improved nutrient uptake (Fatemi et al., 2020). HMs can get immobilized at the level of extraradical fungal mycelium and in the vesicles and spores. Such defense strategies effectively limit the migration of HMs to the aerial plant tissues. Particularly, glomalin production and chelation of HMs with ligands with high metal affinity released by AMF contribute to HM stress relief in the host plant. In addition, it was observed that AM vesicle undergoes one-fold increase along with progressive HM accumulation in the soil, thereby playing a prominent role in the detoxification process (Dhalaria et al., 2020). *Eucalyptus grandis* under increasing Cd concentration in soil showed a decreased AM arbuscules colonization coupled with an increase of vesicle colonization (Kuang et al., 2023). At the level of the fungal cell wall, HMs ions find binding sites to functional groups such as imidazole carboxyl groups, amino groups and free hydroxyl groups (Dhalaria et al., 2020).

A survey performed on the endemic species *Metrosideros laurifolia* demonstrated that the co-inoculation with AMF of different families was more efficient under multiple-stress conditions (including various HMs), pointing to a possible functional complementarity of distantly related AMF species (Crossay et al., 2019). A diverse and reliable source of AM inoculants is necessary for phytoremediation. Nevertheless, this can often represent an issue due to the existing inconsistencies in declared composition of available commercial inoculants (Vahter et al., 2023).

The main advantage that AMF can bring to the mitigation of the negative effects of HMs in the environment is related to the retention of HMs in the soil volume explored by the extraradical mycelium. This prevents the pollutant leaching deeper into the soil and groundwater (Boorboori and Zhang, 2022). Consequently, the HM stabilization in the soil matrix promoted by AMF limits the spread of polluting agents. Notably, this stabilization can indirectly reduce the human exposure risk to HMs by supporting the survival of plant cover, which in turn decreases the dust lift-up that could be inhaled from air. A reduced uptake of HMs by plants due to AM mycelium-mediated immobilization can also break/lower HM accumulation across the food chain.

Although AMF take on great importance for regulating the metal balance in their host plants, the metal transporters identified in these organisms are still waiting to be fully characterized. Deeper insight into this subject has been provided by studies on the model species *Rhizophagus irregularis*, in which three components of the reductive Fe uptake pathway (Tamayo et al., 2018), two Cu transporters belonging to the CRT family (Gómez-Gallego et al., 2019), and four members of the NRAMP transporter family (López-Lorca et al., 2022) have been described so far.

A recent review article, reporting the outcome of the plant-AM interaction under As and Cd stress, indicated that the majority of experiments (>90 %) have been conducted in greenhouse conditions and only very few in open field environment (Tan et al., 2023). This is the case in most of the studies on AM fungi-plant interaction under various HM stressors, not just HMs. Understandably, this is due to the need to accurately study the effects of inoculation. However, if inoculation has to be conducted in field conditions on a polluted substrate, then the introduced AMF strains will encounter an edaphic background (including a community of microorganisms). For instance, in *Zea mays*, co-inoculation with dark septate endophytes (DSE) was shown to decrease AM colonization in the experimental HM stress assay. Furthermore, a highly significant interaction was found between AMF and DSE in terms of positive impact on chlorophyll content, photosynthetic and transpiration rates and intracellular CO_2 concentration (He et al., 2020). The fate of inoculants in field conditions is one of the least studied processes, and therefore there are persisting obstacles for using AMF in an ecological context.

8. Plant outcomes under AMF inoculation and HM stress

8.1. *Chlorophyll content*

Across the studies that investigated the effect of AMF inoculation on chlorophyll content of plants under HM stress, overall, the findings report improved chlorophyll measurements associated with AM inoculation either under single HM stress (Table 1) or multiple (Table 2) HM stresses. Thus, the physiological performance of plants is expected to be improved under HM stress in presence of AM.

In AMF-inoculated plants, the improvement of chlorophyll parameters was associated with decreased HM accumulation in leaves of wheat (Li et al., 2023a) and kenaf (Pan et al., 2023b), as well as in the shoot of maize (He et al., 2020) and rice plants (Li et al., 2023b).

Comparative analysis of the influence of AM on the chlorophyll parameters of plants under HM suggests the existence of different efficiency levels according to the type of HM stressor, plant genotype and tissue (Yin et al., 2021). Experimental trials carried out on *Cajanus cajan* PUSA 2002 and PUSA 991 genotypes indicated that AMF-inoculation was successful in preventing the degradation of chlorophyll pigments. Nonetheless, this beneficial effect was more evident under Zn (100–600 mg/kg) than Cd stress exposure (25–50 mg/kg) (Garg and Singh, 2018). Moreover, in *Solanum melongena* subject to comparative HM stress of 50 mg/kg Pb, 25 mg/kg Cd and 50 mg/kg As, the AMF inoculation (with unspecified strains) significantly increased chlorophyll content only when plants were exposed to Pb stress at 30 and 90 days after treatment (Chaturvedi et al., 2018).

The studies on multiple HM stresses (summarized in Table 2) are particularly insightful for the remediation of heavily contaminated soils.

8.2. Phytoremediation

Besides the ameliorative effect of AM on HM-stressed plants, the outcome and significance of the phytoremediation process have not been extensively and explicitly defined yet. Perhaps the current body of literature is not sufficient to draw a comprehensive conclusion, as many aspects related to AMF interaction with plants are still to be uncovered.

Experimental observations on model plants reported a reduced HM uptake following AMF inoculation/colonization. A study on *Zea mays* showed that the Cd transfer coefficient (TC) decreased in the AM maize plants. Particularly, AM colonization prompted Cd retaining in the maize root, thereby restricting its migration to the shoot (He et al., 2020). In *Zea mays* under multiple HM stresses the translocation factor (TF; *i.e.* the ratio of the HM concentration in the shoots to the HM concentration in the roots) was significantly lower in AM treatments with respect to control for Cd, Cr, Pb, Ni, and Fe. At the same time, the bioaccumulation factor (BCF; *i.e.* the ratio of the concentration of HMs in plants and in soils, used to estimate the capacity of a plant in metal uptake) significantly improved with inoculation of AMF spp. (Singh et al., 2019). Similar results concerning TF were previously reported in *Zea mays* (Zhan et al., 2018), hence supporting the AM-assisted cultivation of maize as a valuable strategy for the phytoremediation of HM polluted soils. Further experimental evidence was provided by studying *Trifolium repens* plants exposed to Cd stress and inoculation with various AMF strains. Results showed TF values lower than 1 at all treatment levels (Xiao et al., 2021). A study performed on *Cajanus cajan* indicated that, although AM root colonization decreased with increased HM stress levels, TF values remained below 1. Another worth-noting aspect relies on the fact that the ability of plants to establish effective AM symbiosis declined with introduction of Cd and Zn in the soil. This phenomenon occurred in a concentration and plant genotype-dependent manner (Garg and Singh, 2018). In *Solanum melongena* under As, Cd and Pb stress and AM inoculation, the results displayed a TF below 1 for Pb. However, at the same time, for Cd and As the TF was above 1, suggesting a phytoremediation potential by phytoextraction of Cd and As (Chaturvedi et al., 2018). Moreover, AM inoculation of hemp increased the plant tolerance index (TI) under Cd stress. Compared with control, AM-treated hemp plants showed ameliorated physiological performance in terms of gas exchange rates and chlorophyll fluorescence parameters. These responses led to a higher photosynthetic efficiency that in turn supported the improved growth of inoculated plants during stress occurrence (Sun et al., 2022). In presence of multiple HM stresses and AM association, *Tagetes erecta* plants were able to significantly reduce the metal accumulation (Zn, Co, Mn, Cu) in tissues (Elhindi et al., 2018).

The barrier of naturally-tolerant species is not necessarily fix, as the plant capacity for phytoremediation can be enhanced by genetic engineering (Nedjimi, 2021). In addition, the enhancement of AMF strain tolerance to HMs was shown to be achievable in 1–2 years (Yang et al., 2022). Since AMF strain tolerance can presumably be obtained in a shorter timespan than acquisition of plant-tolerance, the integration of AMF in phytoremediation procedures may represent a very promising and highly feasible strategy.

A decade ago, Furini (2012) remarked that the general methodological approach in HM literature had been to test acute stress by applying high doses of one single HM under experimental controlled conditions. However, the cited author further noticed that those concentrations could have been not always representative of the natural environmental conditions that plants most likely meet in the *in situ* contexts. This is a relevant aspect, considering that plants in natural environments usually have to cope with multiple stresses. The plant-microorganism interactions are the result of an evolutionary route established to aid exactly the need of plant-environment adjustment (Balestrini et al., 2022). Nonetheless, multiple plant stresses under temporal dynamics remain poorly documented. In addition, the majority of the studies on common HMs have been conducted in controlled conditions (Tan et al., 2023). Furthermore, studies often concerned HM stress effects at incipient stages of plant growth, thereby leaving a gap of knowledge on those responses occurring in the late developmental phases. Research trials addressing the entire plant life cycle can be particularly insightful, based on the notion that once plants are transitioned to the field, they experience HM stress all year round and it is still little known how their phenology gets impacted. AM is also expected to be modulated by the host metabolism across the plant's life cycle.

Long-term strategies aimed at stabilizing the plant-soil system under HM stress by leveraging natural mechanisms (such as AM) have to be devised. Environmental return benefit of the investment in this green technology can be ensured by sustained research efforts to better understanding the dynamics of the AM-plant-HM interplay.

The use of AM-symbiotic plants in phytoremediation should continue to be in focus, as most phytoremediation programs could be treated as ecosystem restorations. In light of the recent Nature Restoration Law proposal by the European Commission (Nature Restoration Law, 2024), the potential role of AM-plant interaction in sustaining the plant cover under anthropogenic-induced land degradation and stressors (such as HM elevated levels across ecosystems) gains great importance. This starts for the first time to exceed the prevalent agronomic perspective considered in the past. In this regard, interventions and therefore guiding points for AMF use on HM affected lands could be inspired by those proposed by Markovchick and colleagues in relation with AM use in ecosystem restoration (Markovchick et al., 2023). These authors underlined the importance of placing emphasis on ecological relevance and its ramifications, without limiting the perspective purely to the land agricultural exploitation potential.

9. The concluding overview

The HM pollution is a worldwide challenge to be addressed carefully. In this sense, tightening regulatory measures aim at solving this issue in foreseeable timelines. Phytoremediation is favored as cost-effective green solution relying on plants to reduce the human exposure to HMs. Plant species tolerant to HMs are the preferred ones in phytoremediation programs. AM symbiotic plants might be even better at reducing pollutant migration risk, as the burden of HMs is supported by the plant host and AMF together. In order to be resolved by this approach, the gap between mycorrhizal science and applications has to be diminished in accordance with the challenges posed by the current context of pollution. This work provides an overview on the state of play with emphasis on relevant aspects serving this purpose.

Dust lift-up and leaching of HMs in bare soil conditions are the main routes of spreading pollution. This also increases the exposure risk for humans and animals. Therefore, plant-soil system can reduce this primary risk compared to leaving the contaminated land bare. AM-plant system is able to further decrease the risks associated with HM-

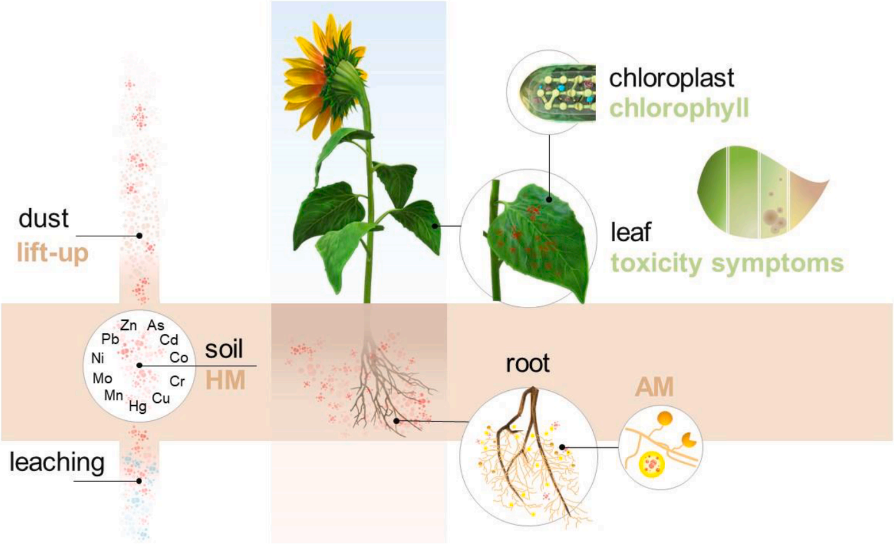

Fig. 1. The fate of HMs in bare soil *versus* plant-soil system (created with Microsoft Paint 3D and PowerPoint).

contaminated substrates, by the capacity to reduce their vertical and horizontal migration. Extraradical AM mycelium acts as an extension of the root, hence constituting with the plant's root a living network exploring the soil volume and enclosing the pollutant by various means. AM structures can immobilize some HMs in soil, reducing leaching and lift-up while consequently diminishing the exposure of plants to the stressor.

Plants are living systems, and they experience HM stress symptoms, with chlorosis as the main one. This is threatening the survival and sustainability of vegetation on HM-contaminated substrates. As such, chlorophyll is the most important and revealing indicator of plant fitness. If plants can live (survive and thrive) on HM-enriched substrates, it will be feasible to rely on potential outcomes of phytoremediation. Recent evidence examined in this work suggests that AM inoculation can increase chlorophyll content under presence of both single and multiple HMs. Nevertheless, further research efforts are needed to reach a complete understanding of these processes.

The significance of plant-soil system in reducing the risks posed by HM lift-up and leaching is displayed in Fig. 1. The image illustrates the core principle of the phytoremediation process. In turn, AM can further aid the plant in achieving this purpose. Chlorophyll degradation and inhibited synthesis are the main reasons for decreased chlorophyll level following HM exposure. Effect of chlorosis can then progress to plant wilting and ultimately death.

Plant survival and performance in the current remediation scenarios are important both for the financial investment in planting those areas and for reaching the long-term desired outcomes. Because of this, we presented arguments that perennial energy crops able to establish successful AM symbiosis are the best phytoremediation candidates for further research. However, different requirements for different contexts do exist: agricultural *versus* urban land.

The professionals from the first line of action that could implement phytoremediation actions are in need for an up-to-date database, which merges the symbiotic potential and remediation potential of plants. Implementation of such database will indeed allow easily selecting the candidates for planting schemes, based on the specific environmental context.

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Ioana Crișan: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Raffaella Balestrini:** Writing – review & editing, Supervision, Conceptualization. **Chiara Pagliarani:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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