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Review article

Mycorrhizae in mine wasteland reclamation

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ABSTRACT

Mycorrhizae are found on about 70–80 % of the roots of all plant species; ectomycorrhizae (ECM) are mostly found on woody plants and gymnosperms, whereas arbuscular mycorrhizal fungi (AMF) are found on 80–90 % of all plant species. In abandoned mining sites, woody plants dominate, while non-woody species remain scarce. However, this pattern depends on the specific mine site and its ecological context. This review article explores the potential of using mycorrhizae-plant associations to enhance and facilitate the remediation of mine wastelands and metal-polluted sites. In this review, we employed reputable databases to collect articles and relevant information on mycorrhizae and their role in plant growth and soil fertility spanning from the 1990s up to 2024. Our review found that the abilities of plants selected for mine-wasteland reclamation can be harnessed effectively if their mycorrhizae utilization is known and considered. Our findings indicate that AMF facilitates plant cohabitation by influencing species richness, feedback effects, shared mycelial networks, and plant-AMF specificity. Several types of mycorrhizae have been isolated from mine wastelands, including *Glomus mosseae*, which reduces heavy metal accumulation in plants, and *Rhizophagus irregularis*, which enhances plant growth and survival in revegetated mine sites. Additionally, studies on ECM in surface mine spoil restoration stands highlight their role in enhancing fungal biodiversity and providing habitats for rare and specialized fungal species. Recent research shows that ECM and AMF fungi can interact synergistically to enhance plant growth, with ECM improving plant nitrogen absorption and AMF increasing nitrogen use efficiency. Our review also found that despite their critical role in improving plant growth and resilience, there remains limited knowledge about the specific mechanisms by which mycorrhizae communicate with each other and other microorganisms, such as bacteria, root-associated fungi, soil protozoa, actinomycetes, nematodes, and endophytes, within the soil matrix. This article highlights the connection between mycorrhizae and plants and other microorganisms in mine wastelands, their role in improving soil structure and nutrient cycling, and how mycorrhizae can help restore soil fertility and promote plant growth, thus improving the overall environmental quality of mine wasteland sites.

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1. Introduction

Mining activities result in various environmental issues, including land degradation, soil erosion, and the removal of topsoil [1]. One of the consequences of mining is the accumulation of large amounts of mine waste on the surrounding land. This waste material, also known as mine spoil, is deposited in layers, forming overburden dumps [2]. These deposits lack the necessary nutrients and capacity to support vegetation growth due to minimal concentrations of organic matter and essential nutrients, unfavorable soil chemistry, and a dense structure [3]. As a result, abandoned mining sites often struggle to support the establishment of biomass and vegetation.

Mining activities and abandoned mining sites have caused severe ecological degradation worldwide, with numerous case studies illustrating the profound impact on ecosystems and human health [4–7]. In the town of Kabwe, Zambia, for instance, decades of lead mining have left behind significant environmental contamination, posing severe health risks to local communities [8,9]. The soil and water in Kabwe contain dangerously high levels of lead, causing widespread cases of lead poisoning, particularly among children, who exhibit high blood lead levels that far exceed safe limits [10]. This has led to severe health issues, including cognitive impairments and other developmental disorders.

Similarly, the aftermath of coal mining in the Appalachian region of the United States showcases another stark example of ecological degradation [11]. Mountaintop removal mining has decimated the landscape and polluted waterways with toxic heavy metals and mining byproducts, drastically affecting aquatic ecosystems and reducing biodiversity [12]. This form of mining has led to significant deforestation and habitat destruction, further exacerbating the loss of flora and fauna in the region. Moreover, abandoned mines across the Appalachian Mountains continue to leach hazardous substances into the environment, creating persistent ecological and health challenges for the surrounding communities.

Abandoned mining sites are notorious for the ecological and environmental degradation caused by overburden. The overburden, which lacks soil characteristics and has poor levels of nutrients, is filled with stones, boulders, and other debris [13]. The mining activity results in significant changes to the soil layers and configuration, which leads to soil erosion, water and air pollution, and disturbance in the ecosystem. These environmental impacts progressively modify the nutrient dynamics of the area [14]. The diminished growth of plants in abandoned mining sites is attributed to various environmental concerns, including steep slopes on overburden dumps, instability, wind erosion, sheet and gully erosion, elevated levels of toxic elements, depleted nutrient status, and minimal presence of soil fauna and microorganisms [3]. Additional constraining factors include salinity, nutrient deficiencies, acidity, and land degradation [15]. Successful restoration efforts of such an environment involve phytoremediation, soil amendments, and careful species selection. Notably, rejuvenating high-sulfur coal mine overburden dumping sites in India has led to primary and secondary succession within 3–5 years [16].

In abandoned mining sites, woody plants usually dominate, while non-woody plants make up only a tiny fraction. However, this trend depends on the particular mine site and its ecological context. For example, the mine site may show similar vegetation characteristics if the surrounding area is rich in shrubs or trees. This leads to an interesting question: How can we effectively use this specific vegetation type for remediation?

The specific vegetation types present at abandoned mining sites can be leveraged for bioremediation by utilizing their natural abilities to stabilize soil, absorb contaminants, and restore ecological balance. For instance, woody hyperaccumulator plants such as Jatropha with deep root systems can help stabilize soil and reduce erosion. At the same time, certain species may also be able to uptake heavy metals from contaminated soils, thus aiding in the remediation process [17]. Additionally, some plant species, such as grasses, low-growing shrubs, and groundcover plants, are commonly used to cover the soil and prevent dust from spreading, thereby improving degraded mine site restoration [18]. This is the case of a coal mine in the US, where it was discovered that *Poa compressa* and a blend of *P. compressa, Panicum virgatum*, and *Trifolium repens* offered sufficient ground cover while simultaneously supporting the highest diversity of species and the survival of woody plants [19].

In Val-d'Or, Québec, the Sigma-Lamaque gold mine has operated since 1935. White spruce (*Picea glauca*) is a commercially valuable boreal tree known for its ability to colonize deglaciated rock tailings. Over the last decade, there has been an increasing interest in using this species for the revegetation and successful restoration of abandoned mine spoils. Recent research indicates that mine-adapted mycorrhizal fungi and rhizobacteria can significantly improve the health and growth of white spruce when used for mine site reclamation [20]. These mine-adapted symbionts have been found to significantly enhance the health and growth of white spruce seedlings growing directly on waste rocks (WRs) or fine tailings (FTs) from the Sigma-Lamaque gold mine in the Canadian Abitibi region.

Similar findings have been shown in a 15-week greenhouse experiment where researchers investigated the effects of a dark septate endophyte (DSE), specifically *Phialocephala fortinii*, and two Helotiales strains, *Rhizoscyphus ericae* and *Meliniomyces* sp, on the growth of *Salix planifolia* cuttings planted on sterilized and unsterilized iron ore waste rock. The results revealed that *Rhizoscyphus ericae* enhanced shoot biomass in cuttings grown on sterilized waste rock, while *Meliniomyces* sp positively impacted cuttings grown on unsterilized waste rock. However, the DSE strain (*P. fortinii*) did not significantly affect the survival rate, shoot production, or biomass production of *S. planifolia* cuttings [21]. These symbiotic microorganisms are crucial in enhancing seedling health and growth, with mycorrhizae promoting belowground development and rhizobacteria enhancing aboveground plant biomass.

It has been shown that restoring degraded land to its natural form is sophisticated, particularly in under-researched areas affected by heavy mining activities. To address this problem, it is suggested that vegetation cover on mine spoil overburden dump be restored using microorganisms-vegetation relationships, particularly mycorrhizae-plant interactions [22]. According to Emam's findings, it is estimated that 92 % of plant families are mycorrhizal, which means that the plants in these families interact with mycorrhizal fungi to thrive [23]. These microorganisms play a vital role in initiating plant growth and contribute to soil fertility restoration by facilitating nutrient uptake. By restoring vegetation cover on the dump, threats to human beings can be removed, and the ecosystem's natural balance can be restored. Therefore, using microorganisms, such as mycorrhizae, is critical to restoring degraded land to its natural form.

Mycorrhizae represent a category of soil fungi that establish mutualistic associations with the roots of plants [24–27]. These symbiotic relationships benefit both the fungi and the plant, with the fungi providing nutrients, water, and protection from pathogens and the plant providing the fungi with carbohydrates produced through photosynthesis [28]. The mycorrhizal network is crucial for soil fertility and substantially influences plant growth and productivity [29]. However, there are conflicting results regarding classifying specific mycorrhizal genera as beneficial or non-beneficial for plants. This complexity is compounded by the considerable variation observed across previous studies [30–32]. The effects of AMF and ECM can vary depending on factors such as soil conditions, plant species, stress, and even the specific AMF species being considered [31,32]. In the past few years, there has been an increasing focus on the use of mycorrhizae for the remediation of abandoned mine land. However, according to several decades of research, it has been noted that new factors have not been taken into account when choosing plants that will produce yields on depleted soils and under low fertilization conditions, such as their receptivity to mycorrhizal fungi, which was never strategically considered during plant selection, especially in developing countries where there is still minimal research on the subject (Fig. 2). Mycorrhizae in mine site reclamation can help restore soil fertility and promote plant growth, improving the overall environmental quality of these sites [33]. This literature review aims to provide a comprehensive examination of the potential of mycorrhizae for improving soil fertility and their interactions with plants in mine wastelands. It will summarize various mycorrhizal types, their roles in soil fertility, potential for commercialization, and applications in mine wasteland reclamation. Additionally, the review will identify research gaps and prospects, and explore practical applications of mycorrhizae in other sectors, such as industrial agriculture and ecosystems, highlighting benefits beyond mine wastelands. This review is justified by the need to better understand and strategically utilize mycorrhizae in plant selection for mine wasteland reclamation, particularly in regions where this approach has not been thoroughly researched or implemented.

2. Methodology

2.1. Identification of relevant articles

To explore the databases and extract relevant research articles based on relevance, methodological rigor, and quality of evidence, we employed a keyword-based search. Keywords such as mycorrhizal association, ECM, AMF, rhizospheric soil microflora, plant-fungal symbiosis, bioremediation, mine wasteland, reclamation, abiotic stress, and soil rehabilitation were used in the search.

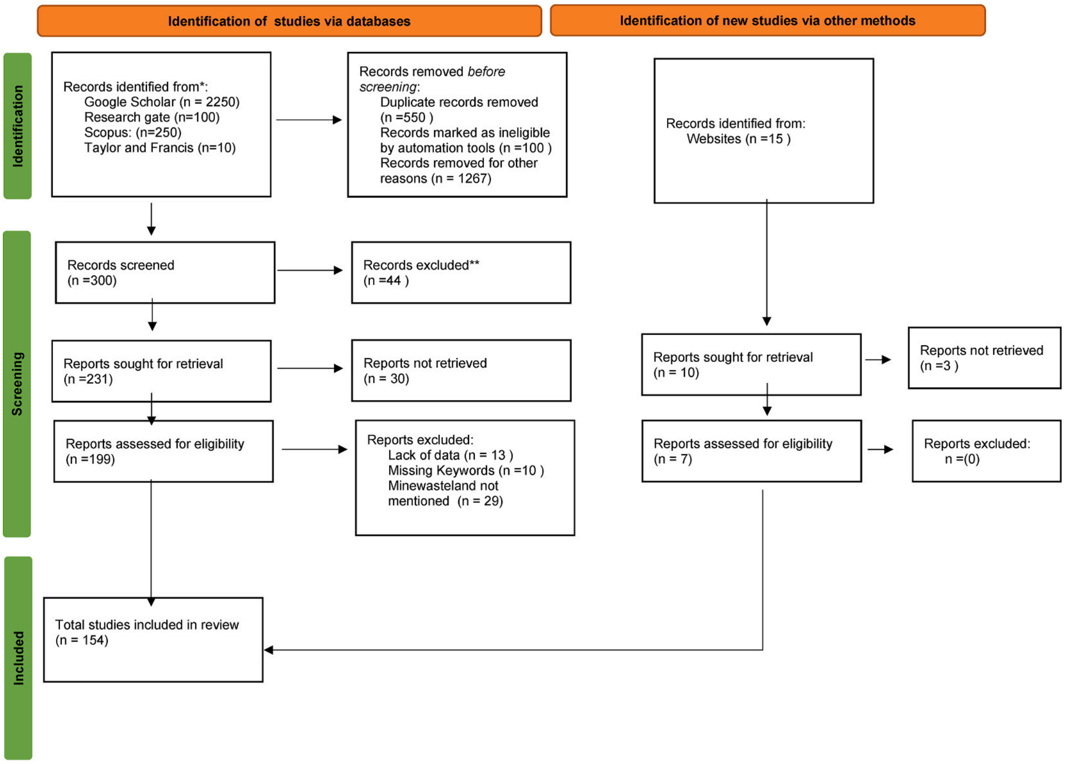


Fig. 1. The PRISMA method identifies, screens, and selects literature for review.

Articles outside ECM and AMF studies, those lacking connection to soil fertility and plant growth, and those unrelated to mine wasteland were excluded. Manual removal ensured that only relevant and complete articles were included (Fig. 1). The review aimed to identify gaps, challenges, and future opportunities in using mycorrhizae.

Constructing this review involved examining 174 research articles from peer-reviewed journals, carefully selecting the most appropriate ones to analyze the progress made in mycorrhizae research and their use in diverse experimental setups. The analysis showed their use in field experiments is still limited (Fig. 2). The findings from this review were used to inform the discussion and conclusions of the study.

2.2. Mine wasteland data

The articles for the review on mycorrhizae research in mine wasteland were selected based on their relevance to the topic and their contribution to understanding the role of AMF and ECM in nutrient exchange and their influence on plant growth. These studies investigated various experimental setups, including field, lab, and greenhouse experiments. Additionally, they have explored different types of mine wastelands, such as coal mines, gypsum mines, and areas with ultramafic soil (Fig. 2).

2.3. Bibliometric analysis and article handling

A bibliometric analysis was conducted on references related to the potential of mycorrhizae in mine wasteland reclamation.

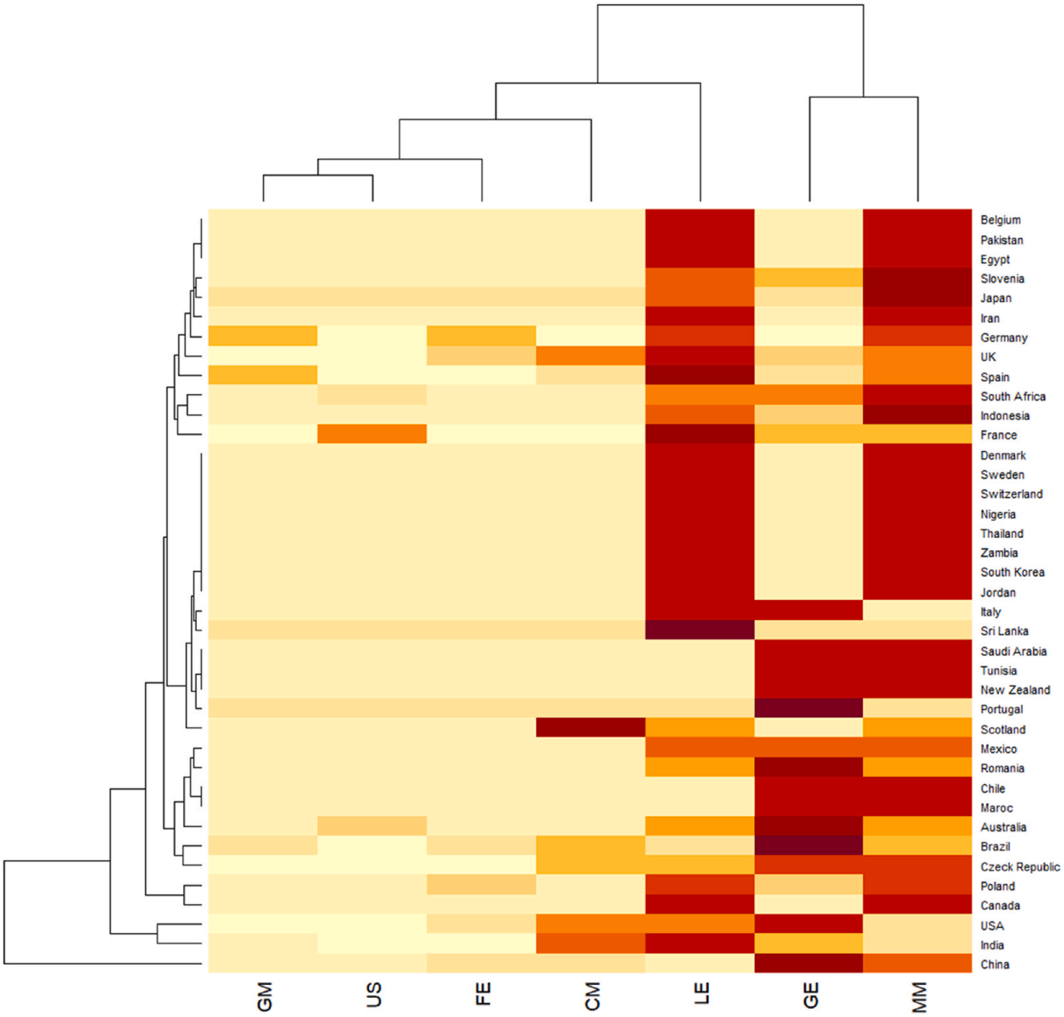


Fig. 2. Heatmap displaying progress in mycorrhizae research in diverse experimental setup: FE (Field Experiment), LE (Lab experiment), GE (Greenhouse experiment), CM (Coal mine), GM (Gypsum mine), US (Ultramafic soil), MM (Metallic mine): Metallic mines include ferrous metals (typically iron) and nonferrous metals (such as gold (Au), silver (Ag), copper (Cu), nickel (Ni), lead (Pb), and zinc(Zn)). Data source [33]: and other references in this article.

Initially, a total of 174 articles were extracted and imported into Mendeley reference management software. The data underwent cleaning, during which keywords were extracted for analysis. Co-citation and keyword co-occurrence analyses were performed to identify major research themes and the structure of the research field. Authorship and publication trends were also examined to identify prolific authors and significant periods of activity. Influential works and authors were identified. The database results were imported into Mendeley reference software for article handling. Metadata, including authors, title, publication year, volume, pages, abstract, keywords, and DOI, was checked and updated as needed. Articles missing critical metadata, such as author, title, or publication year, were excluded. A total of 154 articles were cited in accordance with the PRISMA protocol. Additionally, trends in publications were analyzed using R Version 4.1.0 on R Studio version 1.4.1717 (Rstudio Inc., Boston, MA, USA), and a trend analysis graph was plotted to show the number of publications over time on mycorrhizal research (Fig. 3). The findings provide insights into future research directions and practical applications in the field of environmental biotechnology.

3. Types of mycorrhizae

There are two primary categories of mycorrhizae: ECM and endomycorrhizae, also referred to as arbuscular mycorrhizae fungi (AMF) widely spread, taxonomically and geographically (Fig. 4). AMF are the most common and widespread type of mycorrhizae and are found in the roots of most land plants such as clubmosses, horsetails, ferns, gymnosperms, and angiosperms [34]; they are divided into three families namely, Acaulosporaceae (*Acaulospora* and *Entrophospora*), Gigasporaceae (*Gigaspora* and *Scutellospora*) and Glomaceae (*Glomus* and *Sclerocystis*) [35]. They form arbuscules, intricate structures with extensive branching that penetrate the root cells of the host plant. AMF are obligatory symbionts, requiring a host plant to survive [32]. ECM are found in the roots of trees and other woody plants, forming a sheath around the root cells rather than penetrating them. ECM are facultative symbionts, meaning they can survive without a host plant but form mutualistic associations with them. Both mycorrhizal types play crucial roles in maintaining soil fertility, and employing them in the reclamation of mine sites has demonstrated favorable impacts on soil quality and plant growth. However, their potential remains unexplored in large-scale mine wasteland reclamation [24].

4. Role of mycorrhizae in soil fertility and their contribution to tolerance against excess metals

Mycorrhizae are symbiotic associations between fungi and plant roots that benefit both partners and the environment [37]. Mycorrhizae are very ancient and widespread, they are thought to have helped plants colonize land and evolve. They create a web of fungal filaments that link plants together, enabling them to share resources and signals. Through this relationship, the fungi receive organic carbon from the plant, while the plant gets better access to water and nutrients, such as phosphorus (P) and nitrogen (N) [39]. Mycorrhizae and plants have a mutualistic association that is essential for plant development, especially in soils with low nutrients, where mycorrhizae can supply most of the plant's P requirements [40]. For example, a study by Janos (2007) provided empirical evidence supporting the existence of two phenomena related to the interaction between plants and mycorrhizal fungi in relation to soil phosphorus levels [41]. The first thing is how plants react to mycorrhizas, which means how much plants with and without

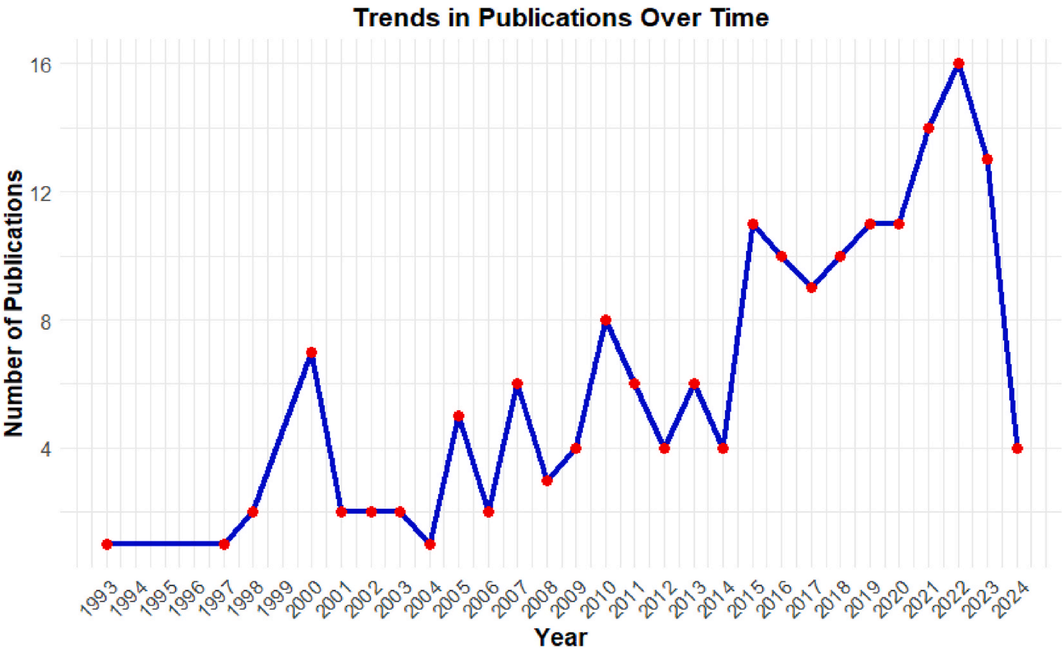


Fig. 3. Trends in publications on mycorrhizal research.

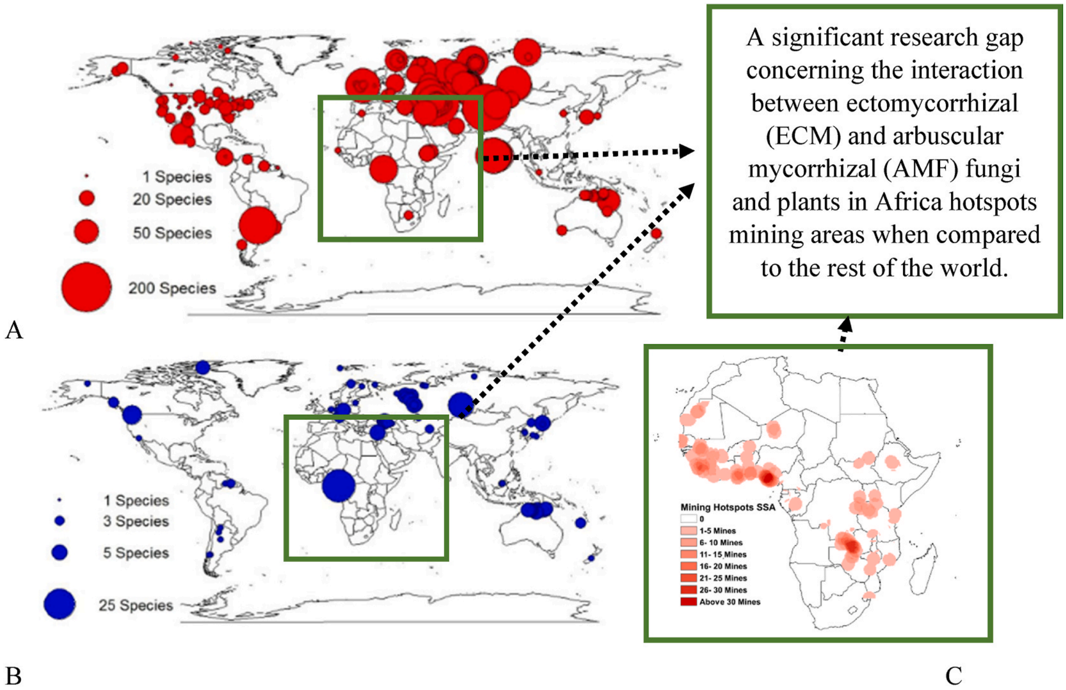

A significant research gap concerning the interaction between ectomycorrhizal (ECM) and arbuscular mycorrhizal (AMF) fungi and plants in Africa hotspots mining areas when compared to the rest of the world.

Fig. 4. Worldwide distribution of sites for (A) arbuscular mycorrhizal (AM) (Red) and (B) ectomycorrhizal (ECM) (Blue) colonization of vascular plant roots and (C) a graph showing summarized distribution of mine in Sub Saharan Africa. The size of the symbols is equal to the square root of the plant species total number at each site, which ranges between 1, 204 per site for AM, 1, and 26 per site for ECM. To improve readability, the plant species number is divided by 2 in the case of AM colonization. This figure was adopted from the article by Soudzilovskaia et al. (2015) [36] and Ahmed et al. (2021) [38] with permission.

mycorrhizas grow differently at a certain level of phosphorus in the soil, showing how well the fungi work. The second is the minimum phosphorus level at which plants can grow in absence of mycorrhizas, known as dependence upon mycorrhizas, a concept distinct from conventional usage. In a study by Neagoe et al. (2014), the applicability of sigmoid curves in assessing responsiveness, effectiveness, and dependence was confirmed. The researchers found that when evaluating the inherent abilities of various host plant species to utilize phosphorus, it is essential to assess their relative position along the phosphorus response curves for different host combinations [14]. Dependence, considered a constitutive property of plant species, serves as a criterion for categorizing them as facultatively or obligatorily mycotrophic. Unlike responsiveness and effectiveness, which can vary, dependence is an inherent attribute subject to natural selection.

Mycorrhizal fungi can stimulate plant growth not only by improving the plant's ability to absorb critical nutrients such as P, N, and other micronutrients like Zn, Cu, and Fe, but also by increasing tolerance to various biotic and abiotic stresses [28]. They also increase water uptake, reducing the risk of drought stress. Mycorrhizae increase soil structure through the formation of glomalin, a protein that binds soil particles together. This renders the soil more stable and less prone to erosion [42]. Mycorrhizae are also involved in the nutrient cycling in the soil. They breakdown organic matter and release nutrients, making them available to plants. Mycorrhizae acquire nutrients from the soil and deposit them in their mycelium, making them available to plants when they are needed. In addition, mycorrhizae can also enhance soil microbial diversity, which can further improve soil fertility and stability [31]. Moreover, ECM has also been found to play an important role in carbon sequestration. The carbon compounds supplied by host plants are stored in the soil as organic matter. This process can contribute to addressing climate change by sequestering carbon dioxide from the atmosphere [43].

Erik J Joner (2000) studied how *Glomus* spp. mycelium, with varying histories of exposure to heavy metals, binds to cadmium (Cd) and zinc (Zn). The research indicated that arbuscular mycorrhizal (AM) mycelium has a substantial capacity for metal sorption and a cation exchange capacity (CEC) equivalent to that of other fungi. The metal sorption occurred faster and was primarily attributed to passive adsorption. The metal-tolerant *G. mosseae* isolate showed the highest adsorption capacity, up to 0.5 mg Cd per mg dry biomass, which was three times higher than non-tolerant fungi and over 10 times higher than *Rhizopus arrhizus* [44]. This study demonstrated that AMF could play a significant role in protecting plants against excess heavy metal uptake. Similarly, a study by Sun et al. (2022) showed that the AMF *Rhizophagus irregularis* affected the plant's photosynthetic gas exchange and chlorophyll fluorescence, making the maize plants grow better and tolerate more metal in the soil with cadmium contamination [45].

5. The connection between mycorrhizae and commonly used plants in mine wastelands

The relationship between mycorrhizae and plants in mine wastelands has been a topic of research for several years due to the

Table 1
Different types of mycorrhizae from plants and soil in degraded or disturbed areas, including mining sites.

Mycorrhizal type	Host plants	Location	Reference
Tree Species			
AMF: *Glomus, paraglomus, ambispora, Claroideoglomus,Diversispora, Archaeospora, Funneliformis, Acaulospora, Geosiphon, Rhizoglomus, Scutellospora, Septoglomus*	Various	Coal mining sites in China	[70]
AMF: *Glomus* sp1 and *Acaulospora mellea*	Various	Iron mining areas in Brazil	[71]
ECM: *Scleroderma citrinum, Scleroderma* sp.*01, Rhizopogon* sp.*01, Russula decolorans, and Russula depallens*	*Betula pendula Roth* and *Pinus Sylvestris* L.	Mining-affected site-Non-ferrous metal smelters in Southern Poland	[72]
ECM	*Pinus halepensis*	The abandoned mine site of "Jebel Ressas" in North Tunisia	[73]
Root Fungal Endophytes	*Clethra barbinervis*	Mine sites	[74]
AMF:, (*Bacillus cereus,* and *Candida parapsilosis)*	Various	Multicontaminated soi	[75]
AMF: *Glomeraceae, Claroideoglomeraceae, Diversisporaceae, Acaulosporaceae, Pacisporaceae, and Gigasporaceae.*	*Robinia pseudoacacia*	Qiandongshan lead and zinc re-gion, Feng County, northwest part of China	[76]
Funneliformis and *Funneliformis monosporum*	*Hippophae rhamnoides* Linn., *Juniperus communis* L., *Populus cathayana* Rehd., *Robinia pseudoacacia* L., and *Salix matsudana* Koidz.	–	[62]
AMF (*Glomus etunicatum and Paraglomus occultum. Acaulospora tuberculata, Glomus aff. brotryoides, Glomus mosseae, Glomus clarum, Gl. rubiforme, Glomus taiwanense,* and *Kuklospora colombiana occurred only in one area and in a single sample. Glomus invermaium, Glomus tortuosum* and *Scutellospora aurigloba*)	Various plants	Mine Dune areas-Brazil	[77]
AMF: *G. intraradices*	*Populus generosa* and *Salix viminalis*	Cd, Cu, Pb and Zn	[78]
AMF	*Anona reticulata, Dendrocalamus strictus, Emblica officinalis,* and *Tectona grandis*, among others	Cd, Cr, Cu, Mn, Ni, Pb, and Zn	[79]
ECM	Leaves and Roots of Silver Birch (*Betula pendula* Roth.)	Mine tailings	[55]
ECM (Amphinema sp.)	Forest trees	Farmland	[80]
AMF and four isolates of the ectomycorrhizal fungus *Pisolithus tinctorius* (Pers.) Coker and Couch	*Acacia mangium* Willd.		[56]
Ectomycorrhizal basidiomycete *Suillus luteus*	Even-aged pine stands	An area polluted with high levels of Zn, Cd, and Cu	[81]
Shrub species			
AMF: *Glomus, Paraglomus*	*Ephedra fragilis, Rhamnus lycioides, Pistacia lentiscus,* and *Retama sphaerocarpa*	degraded, semiarid land in Spain	[43]
Ericoid mycorrhizae: *Oidiodendron maius*	*Vaccinium myrtillus*	Zinc contaminated environment	[82]
Ericoid mycorrhizae: *Oidiodendron maius*	*Vaccinium myrtillus*	Serpentine	[83]
AMF *Rhizophagus irregularis*	*Cajanus cajan* L.	Cadmium and zinc stress	[84]
AMF *Funneliformis mosseae* (F. m), *Rhizophagus intradices* (R. i), *F. mosseae* and *R. intraradices* (F. m + R. i), *Pantoea* sp. (CA), *F. mosseae and Pantoea* sp. (F. m + CA),	*Amorpha fruticose*	Coal mining areas, located in the arid/ semi-arid regions of Western China	[85]
AMF	*Acer ginnala*	Cu	[86]
AMF	*(Searsia lancea, S. pendulina,* and *Tamarix usneoides*)	Cr, Ni, Zn, and Pb	[87]
Herbaceous species			
AMF	*Eichhornia crassipes* (Mart.)	Pot experiment- the cadmium phytoremediation	[88]
AMF(*Glomus aggregatum, Glomus etunicatum, Glomus tortuosum, Glomus intraradices,* and *Glomus versiformewas*)	*Trifolium pratense*	Pot experiment- multi-contaminated soil.	[89]
AMF: *G. intraradices*, *G. albidum*, *G. diaphanum*, *G. claroideum*	*Helianthus annuus* L. and *Hordeum vulgare* L	Pot-experiment	[90]
AMF *Glomus mosseae*	Leguminous plants (*Sesbania rostrata*, *Sesbania cannabina, Medicago sativa*)	multi-metal tolerance-Pot Experiment	[91]
AMF	*Trigonella foenum- graecum* L.	Cadmium stress	[92]
AMF *(Glomus mosseae)*	Crops viz. soybean (Glycine max (L.) Merrill) and lentil (Lens culinaris Medic)		[93]
AMF	Chinese brake fern (*Pteris vittata* L.)	The abandoned copper–chromium–arsenic (CCA) wood treatment site in north-central Florida	[94]
AMF	*Elsholtzia splendens*	Cd, Cu, Pb and Zn	[95]

(*continued on next page*)

Table 1 (*continued*)

Mycorrhizal type	Host plants	Location	Reference
AMF	There are 22 distinct pioneer plant species from 11 distinct families. The most frequent families were *Fabaceae, Asteraceae*, and *Poaceae*.	Cd	[29]
AMF	21 herbaceous species from dry calcareous pastures	As, Cd, Pb, and Zn	[96]
AMF	*Thlaspi praecox* South	Cd, Pb, and Zn	[2]
AMF(*Glomus etunicatum*)	Tomato	Copper Toxicity	[97]
AMF *Claroideoglomus, Diversispora, Glomus, Acaulospora* and *Sclerocystis*	The trees, *Tamarix usneoides, Searsia lancea,* and *Searsia pendulina*	Gold, Uranium, Zinc, and Platinum mining wastes in South Africa	[2]
Grass and Sedge Species			
AMF (*Glomus mosseae*)	*Lolium perenne*	Cadmium Contaminated Soil	[98]
AMF *(Glomus mosseae, Glomus macrocarpum.Glomus fasciculatum, Glomus aggregatum*	Grasses of the genus Festuca *(Festuca brachyphylla Schult. & Schult., Festuca baffinensis Polunin, and Festuca hyperborea Holmen ex Frederiksen*)	–	[89]
AMF (*Funneliformis caledonium*)	Ryegrass (*Lolium perenne* L.)	Pot experiment (polychlorinated biphenyls (PCBs)	[99]
AMF	Grass species *(F. microstachys, Hordeum brachyantherum,* and *Stipa pulchra, (Avena species, Festuca perennis,* and *Bromus species; the most common non-native forb was Cen- taurea solstitialis*	Greenhouse experiment	[23]
AMF	*Chrysopogon zizanioides*	Pb and Zn	[100]
AMF	*Agrostis capillaris*	As, Cu, Pb, and Zn	[14]
AMF	Maize	Lead–Zinc Mining Area	[64]
AMF: (*Acaulospora delicata, Acaulospora mellea, Acaulospora scrobicu- lata, Acaulospora spinosa, Gigaspora decipiens, Glomus geosporum, Glomus* sp2*,* and *Glomus* sp5)	Maize and other crops	Disturbed Land	[101]

growing need to remediate polluted soils and improve plant growth in these areas Table 1 [33,37,46,47]. Mycorrhizae are present on approximately 70–80 % of the roots of all plant species. ECM are primarily found on woody plants and gymnosperms, while AMF are found on 90-80 % of all plant species [48,49]. Mycorrhizae have been proven in research to improve soil quality, nutrient cycling, plant growth and biomass [23]. Mycorrhizal relationships may additionally increase plant tolerance to heavy metal stress by lowering damaging metal uptake and sequestering them in fungal tissues, thereby preventing these contaminants from entering the plant [50].

Several types of mycorrhizae have been isolated from mine wastelands. One of the most commonly studied mycorrhizal fungi in mine wastelands is *Glomus mosseae* [51]. [Miransari et al. (2010) [32] found that *G. mosseae* was able to reduce the heavy metal accumulation in plants grown in a contaminated mine tailings by increasing the plant's nitrogen absorption and minimizing metal transfer to the shoot [32]. Another mycorrhizal fungus that has been isolated from mine wastelands is *Rhizophagus irregularis* [52]. Calonne-Salmon et al. (2018) found that *R. irregularis* was able to colonize the roots of several plant species in a revegetated mine site, thus enhancing their growth and survival [52]. In addition, a research by Kałucka et al. (2016) focused on 71 species of ECM, including 16 species that were recorded for the first time in surface mine spoil restoration stands in Poland, 23 species that were red-listed, and 32 species that are known from only a few localities. The research found that restoration tree stands established on reclaimed mine spoils provide a particular habitat for uncommon and attractive fungal taxa, such as pioneer species, species that are mostly found in steep or Northern European regions, and highly specialized and narrow-niche taxa [53]. Fungal biodiversity is greatly enhanced by the afforested mining wastes, both locally and globally.

The role that AMF play in facilitating plant cohabitation has been reviewed by Hart et al. (2003). Fine-scale research explore into interactions that happen once AMF has more fully evolved within ecosystems, while coarse-scale studies have compared the impact of AMF presence versus absence on plant coexistence. AMF species richness, plant-AMF feedback effects, shared mycelial networks, and AMF-plant specificity are a few examples of the variables that influence plant species cohabitation and biodiversity maintenance in plant communities [54]. To further understand these aspects, more research in these areas is required.

5.1. Trees species

Betula pendula seedlings' growth and chemical composition were studied in connection to the impacts of high concentrations of copper (Cu) and lead (Pb) in soil from a copper foundry in Poland [55]. According to the study, soil dehydrogenase activity, ectomycorrhizal colonization, and seedling growth were all negatively influenced by heavy metals. Ectomycorrhizal density and heavy metal accumulation in birch leaves, however, showed a reverse association, suggesting that mycorrhizas may be able to provide protection to immature silver birch seedlings' aboveground portions from high ambient Cu and Pb concentrations.

The effectiveness of mycorrhizae in promoting plant growth in mine sites may depend on the type of mycorrhizal fungi used [43]. For example, the beneficial effect of AMF and ECM in supporting the growth of *Acacia mangium* Willd. seedlings under glasshouse conditions was compared. The isolates *Pisolithus tinctorius* (Pers.) Coker and Couch (Pt) and several AM inoculants were utilized.

The findings revealed that the growth of *A. mangium* in height and diameter was more improved by ECM fungi than by AM inoculants. Some Korean Pisolithus isolates (PtKACC particulary) and 2 a.m. fungi (AMKFRI and AMM6) were identified as potential mycorrhizal inoculants for *A. mangium*. Research findings indicate that mycorrhizal inoculation can enhance *A. mangium* crops in Asia that have low soil fertility and a scarcity of suitable mycorrhizal fungi. More research is required to determine their beneficial effects and permanence on degraded soils in tropical countries where *A. mangium* is planted for restoration [56]. However, it has been confirmed that AMF inoculation can improve plant growth, nutrient uptake, and heavy metal tolerance in contaminated soils [50,57]. The findings highlight the potential of mycorrhizas as an effective strategy for remediating polluted soils and improving plant growth in mine wastelands. However, further research should be conducted to better understand the specific mechanisms underlying mycorrhizae's participation in mine site reclamation and to select optimal species for different soil types and environmental situations.

5.2. *Shrubs species*

A study was done in semi-arid north-western China on mining subsidence sites, where AMF inoculum was used to revegetate the land. The inoculum improved soil qualities such as glomalin-related soil protein (GRSP), soil organic carbon (SOC), enzyme activities and soil nutrients. The inoculum also increased the mycorrhizal colonization of *Artemisia ordosica*, *Hedysarum scoparium*, *Stipa grandis*, and *Salix psammophila*. The inoculated soil had much higher levels of total GRSR and readily extracted GRSP than the control soil. The soil also had more soil total nitrogen, Olsen phosphorus, and available potassium after 1–7 years of reclamation. The study concluded that AMF inoculum can help restore soil fertility and vegetation communities in harsh environments with low soil nutrients and water [58].

5.3. *Grass and sedge species*

AMF are beneficial to grasslands because they aid in the absorption of nutrients from the soil. However, the function of AMF connections varies, and no metric exists to link AMF functioning with fungal colonization of roots. According to the functional equilibrium concept, the assignment of AMF to different structures can signal shifts in mycorrhizal function. Nitrogen enrichment was found to decrease or increase AMF structures depending on the site's soil N: P ratio. The findings show that changes in mycorrhizal function caused by N enrichment might have an impact on plant community diversity and the functioning of ecosystems [59].

A number of studies have shown that mycorrhizal inoculation can accelerate seedling establishment, biomass production, and species richness in mine site reclamation [60,61]. For example, a study by He et al. (2019) found that the inoculation of mycorrhizal fungi such as *Glomus mosseae* and *Rhizobium* sp. NWYC129 enhances the worn soft rock soils of the Plateau and encourages the establishment of *R. pseudoacacia* seedlings [62]. A beneficial addition to plant roots improved soil structure, nutrient uptake, and plant growth in a mine site reclamation project. Furthermore, mycorrhizae can also help to accelerate microbial degradation of metals and organic compounds in mine soils, thereby reducing their toxicity [42].

Furthermore, Ingrid et al. (2016) showed that AMF-colonized wheat plants increased alkane and polycyclic aromatic hydrocarbon (PAHs) dissipation in aged polluted soils. Several processes contributed to this, including adsorption on roots, bioaccumulation in roots, transfer in shoots, and biodegradation. Mycorrhizal inoculation increased the growth of Gram-positive and Gram-negative bacteria as well as peroxidase activity in mycorrhizal roots, resulting in improved hydrocarbon biodegradation in polluted-contaminated soil [63]. This implies that AMF could also aid in the bioremediation of contaminated mining wastelands.

Another study by Chen et al. (2022) investigated effects of AMF on maize growth, root morphology, low-molecular-weight organic acid (LMWOA) concentrations, and cadmium (Cd) uptake in heavy metal-polluted soil in Yunnan Province, Southwest China. AMF promoted maize growth, root length, surface area, volume, and branch number, as well as malic and succinic acid secretion and Cd uptake, according to the findings. The impacts varied depending on the quantity of Cd pollution and were stronger in agriculture soils than in wasteland and slope land soils. According to this study, AMF-induced enhanced Cd absorption was directly related to their effect on root shape and LMWOA secretion [64].

5.4. *Bamboo species*

A recent study aimed to assess the impact of moso bamboo (*Phyllostachys pubescens*), a fast-growing bamboo used for forest expansion, on AMF ecosystems and soil carbon sequestration. The researchers found that extending bamboo forests promoted soil AMF biomass, which helped to improve soil aggregation and carbon storage. AMF communities were significantly different and structured by forest type, and their influence on soil carbon sequestration was mostly due to their indirect effect on AMF biomass [65].

5.5. *Herbaceous species*

According to Zhao and Naeth (2022) a combination of AMF and a humic material known as nano humus could substantially enhance soil chemical characteristics, reduce heavy metal concentrations, and promote plant biomass in coal mine areas with sandy soils. In year two, the combined application had the largest impact and delivered more advantages than the matching individual applications. The rate of mycorrhizal colonization was negatively linked with soil heavy metal concentrations, indicating that metals impede colonization. Alfalfa responded fastest to AMF and nano humus combinations, whereas barley responded best to AMF, nano humus, and fertilizers combinations [66].

According to Al-Karaki and Hammad (2001), AMF inoculation improved the yield and mineral content of salt-tolerant and saltsensitive tomato cultivars grown under various levels of salt stress. This implies that AMF inoculation is capable of enhancing plant resistance to environmental stress, which could be advantageous for mining wastelands [67].

Meng et al. (2015) investigated how nitrogen uptake and transfer in maize/soybean intercropping systems were affected by inoculating both plants with AMF and rhizobium. The findings showed that nitrogen uptake by soybean and maize was highest when both inoculants were used, and that nitrogen was transferred from soybean to maize more efficiently. This resulted in higher yield benefits than intercropping legume and non-legume plants [68]. This shows that AMF inoculation might facilitate plant nutrient absorption in mine wastelands, where nutrients are frequently scarce.

In a study on the capacity of several AMF species to improve phosphorus (P) absorption and lead (Pb) tolerance in soybean plants growing in Pb-contaminated soil. The results demonstrated that AMF inoculation increased plant growth, P absorption, and Pb accumulation in the roots, with decreased Pb transfer from roots to shoots. R. intraradices was the most effective AMF species for increasing soybean growth and Pb tolerance. According to this study, AMF may be significant for plant development, P nutrition, and metal resistance in heavy metal-polluted soils [69].

Matakala et al. (2023) reported that the diversity and abundance of native tree species on 7 mine wastelands in the Zambian Copperbelt and their ability for phytoremediation. They found 32 native tree species belonging to 13 different families, with Fabaceae (34 % of the total) and Combretaceae (19 % of the total) being the most common. They also found that most of the tree species were able to exclude Cu, Co, Cr, Ni, and Mo from their tissues. The most prevalent tree species on the tailing dams (TDs) that they examined were *Rhus longipes* (Anacardiaceae), *Syzygium guineense* (Myrtaceae), *Senegalia polyacantha* (Fabaceae), and *Ficus craterostoma* (Moraceae), which suggested that they were good candidates for phytostabilization of metal-contaminated soils. However, most of the tree species were not effective for phytostabilization of Mn, Zn, B, and Ba. On the contrary, *Annona senegalensis*, *Parinari curatellifolia*, and *Dombeya rotundilifolia* showed high translocation factors (TF > 1) for these metals in their leaves, indicating their ability for phytoextraction of Cu, Co, Cr, Ni, and Mo. The study provided valuable information on the suitability of Zambian native tree and shrub species for phytoremediation. However, according to our assessment and literature search, there has been little investigation on the interaction between these specific native tree species present on the Copperbelt and AMF. More research is needed to determine the impact of AMF on the phytoremediation capabilities of the identified tree species and their potential in improving the remediation of mining waste in Zambia [102].

Furthermore, our research has identified *Acacia sieberiana, Acacia polyacantha, Bauhinia petersiana, Dichrostachys cinerea, Ficus capensis, Ficus craterostoma, Gmelina arborea, Rhus longipes, Syzygium guineense*, and *Terminalia mollis* as the main plants that aid in facilitation mechanisms for mine waste reclamation at TD10 on the Copperbelt of Zambia (unpublished data). Facilitation is a crucial process that accelerates the recovery of degraded areas by improving environmental conditions, thereby aiding in the restructuring of plant communities. However, there is a notable lack of understanding regarding the mycorrhizal associations of these plants and their role in supporting the growth of native tree species, grasses, and shrubs in mine wastelands. Hence, forthcoming research should concentrate on investigating the involvement of mycorrhizae derived from these tree species in promoting the establishment of indigenous vegetation in mine wastelands.

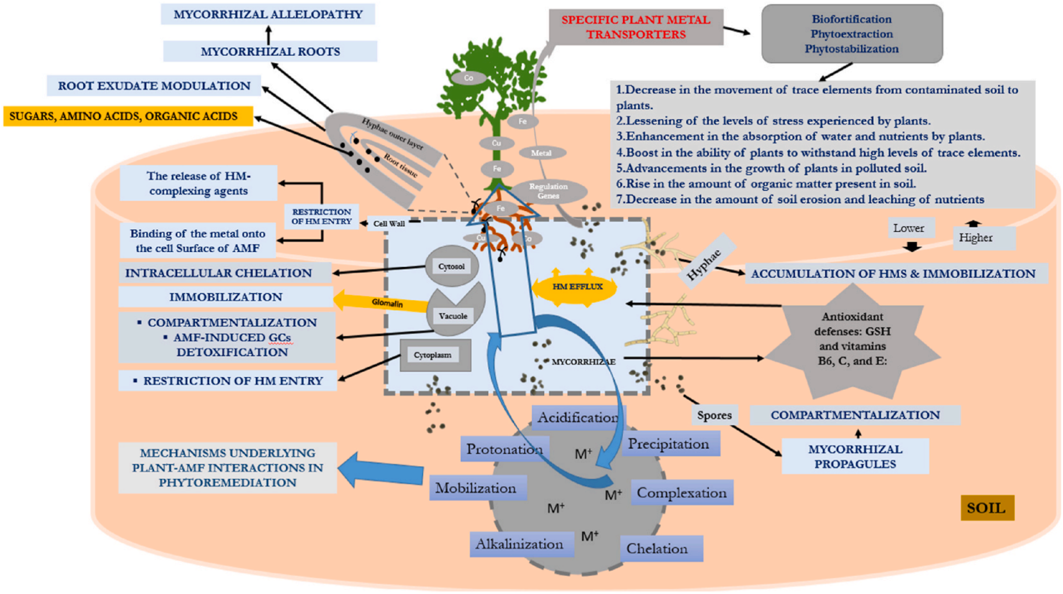


Fig. 5. A diagrammatic illustration depicting the mechanisms involved in the tolerance of metals by mycorrhizae, as well as its symbiotic relationship with plants, highlighting their role in phytoremediation.

6. The facilitation mechanism of mycorrhizae to aid in plant establishment and growth

Mycorrhizae are mutualistic interactions formed by plant roots and fungi that colonize the root systems of plants [46]. These fungi form a network of hyphae that extend beyond the root zone, which allows the plant to access soil resources beyond its root zone, including nutrients, water, and organic matter. There are several mechanisms underlying plant-AMF associations that enhance plant establishment and growth (Fig. 5).

6.1. Metal immobilization and detoxification

The accumulation of heavy metals, particularly geogenic contaminants (GCs), in plants is a serious environmental issue that can harm human health through the food chain, particularly when mine wastelands or their surroundings are used to grow food crops [103]. Mycorrhizal fungi, on the other hand, have been discovered to immobilize excess metals and GCs in plants by maintaining them in the cytoplasm or vacuole, cell wall by chelation, lowering metal toxicity in plants [46]. AMF can also enhance plant biomass and uptake of immovable nutrients while restricting the uptake of metals such as Cu, Co, Pb, Zn, and Cd in the cell wall of hyphae and cortical cells [104]. Mycorrhizae can also affect how plants take up metal from the soil around their roots and their translocation from the root zone to the aboveground parts [105]. The molecular regulation of genes is critical in the accumulation of excess metals and fungal cell detoxification, resulting in the avoidance of excess metal translocation toward the host plant [106]. AMF employs an efflux method protecting plants from metal toxicity [107].

6.2. Metal mobilization

Metal mobilization is a critical factor in the efficiency of phytoextraction, the process of making metals more available for plant uptake [108]. Mycorrhizae in the rhizosphere can mobilize metals, affecting metal element speciation and mobility in soils through biogeochemical cycling processes such as protonation, chelation, acidification, and immobilization [46]. Acidification of the environment, production of natural organic chelators, and immobilization of excess metals such as GCs in plant roots are some of the mechanisms involved in metal mobilization [109]. Other factors that can influence metal mobility in soils include soil pH, microbial and plant actions, and the association with AMF [110]. Understanding these processes is crucial for optimizing phytoextraction efficiency and reducing metal contamination in the environment.

6.3. Nutrient uptake

Mycorrhizae can help plants develop and establish by aiding nutrient intake. Mycorrhizal fungi’s hyphae can extend into nutrient-depleted soils, scavenging nutrients like phosphate and nitrogen and delivering them back to the plant. Mycorrhizae, in particular, are extremely excellent at facilitating phosphorus uptake, which is sometimes a limiting factor in plant growth. For example, research has shown that AMF can enhance plant phosphorus content by up to tenfold when compared to non-mycorrhizal plants [111,112].

6.4. Water relations

Mycorrhizae can also aid in plant establishment and growth by improving water relations. The extensive network of mycorrhizal hyphae can increase the surface area of the plant root system, allowing the plant to access water in a larger soil volume. Additionally, mycorrhizal hyphae can form a water channel, known as a "water bridge", between the plant and the soil, facilitating water uptake and transport [2]. Furthermore, mycorrhizal fungi may enhance plant tolerance to severe drought and increase plant water-use efficiency [62,85].

6.5. Disease resistance

Mycorrhizae can also help with disease resistance. Some mycorrhizal fungi can create mutualistic interactions with plant roots, resulting in better soil-borne disease resistance. The mycorrhizal fungi can either directly attack the pathogen, produce compounds that inhibit pathogen growth, or enhance plant defense responses [113]. In addition, mycorrhizae can also improve the health of plants by promoting nutrient uptake, which can increase plant resistance to disease [114].

6.6. Improved soil structure

Mycorrhizal fungi can also aid in soil structure by generating glomalin, a glycoprotein that aids in the binding of soil particles together [115]. The use of mycorrhizae in mine site reclamation can provide several significant environmental and economic benefits. Mycorrhizae may minimize the demand for artificial fertilizers, lowering the environmental impact of mining. The use of mycorrhizae can also help reduce erosion by improving soil stability and increasing the density of vegetation. Lastly, the use of mycorrhizae can be cost-effective over the long term, reducing the need for chemical fertilizers and other inputs while leading to faster and more successful reclamation efforts, thereby promoting sustainable land use practices and helping to restore degraded landscapes.

6.7. Availability of plant nutrients

The chemical processes arising from Mycorrhizae action can breakdown complex compounds leading to the availability of nutrients [58]. A recent study established, for example, that mycorrhizae could increase the activity of enzymes that contribute to the breakdown of complex organic compounds, such as beta-glucosidase and acid phosphatase, resulting in the release of nutrients such as phosphorus and glucose [116]. Another study showed that mycorrhizae can break down lignocellulosic biomass, such as crop residues and plant litter, releasing nutrients and improving soil quality [117].

6.8. Allelopathy and root exudate modulation

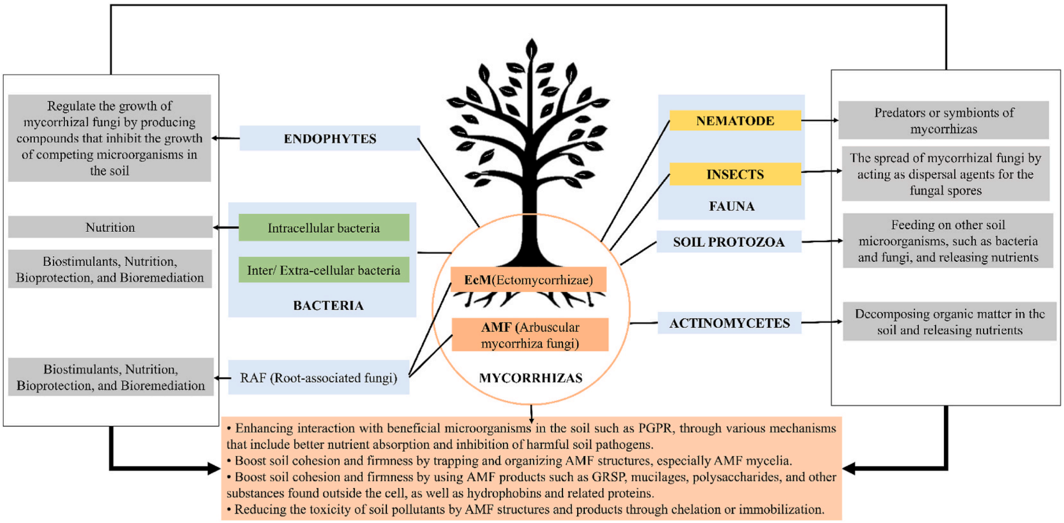
Mycorrhizal fungi enhance plant establishment and growth through the modulation of allelopathy and root exudates [118,119]. Allelopathy involves the biochemical interactions between plants, where certain plants release chemicals that can affect the growth and survival of other plants. Mycorrhizal fungi can boost the production and release of these allelochemicals, helping manage plant competition and promoting the growth of desired vegetation [120]. In the challenging environment of mine wastelands, this can prevent invasive species from outcompeting beneficial plants. Additionally, mycorrhizal fungi can modify the composition and quantity of root exudates—compounds secreted by plant roots, such as sugars, amino acids, and organic acids [121]. These exudates influence the microbial community in the rhizosphere, enhancing nutrient availability and protecting plants against pathogens.

These interactions lead to several benefits for plant growth and survival. Enhanced allelopathic effects suppress competing plant species, allowing desired vegetation to thrive. Improved root exudate profiles promote beneficial microbial communities that aid in nutrient cycling and disease suppression [122]. Increased nutrient availability through the chelation of essential nutrients by root exudates, facilitated by mycorrhizal fungi, results in better nutrient uptake and improved plant growth. Additionally, some root exudates can inhibit soil-borne pathogens, with mycorrhizal fungi enhancing this protective effect [123]. For instance, in the degraded soils of the Sudbury Basin in Canada, mycorrhizal associations have been shown to significantly alter root exudate profiles, promoting beneficial microbes and suppressing pathogens, which contributes to successful revegetation efforts [124].

7. Mycorrhiza as pollution stress indicators

Mycorrhiza's importance in forest ecosystems, as well as how ECM variety can be used to detect pollution stress in forest and mining waste soils. Previous research has investigated the effects of pollution on trees and forest soils by quantifying the diversity of ECM types, determining pollution-sensitive or -insensitive ECM types, monitoring root development and growth of ECM on non-mycorrhizal spruce seedlings, and infecting seedlings in an experimental setting. The study indicated that pollution reduced ECM species richness in Norway spruce trees, but not in European beech trees. *Hydnum rufescens* was identified as a pollution-sensitive ECM species, and *Paxillus involutus* as an insensitive species. The researchers also proposed using mycorrhizal potential in Norway spruce seedlings as a bioassay for soil pollution, which might be employed as a standardized and broadly applicable approach in soil pollution bioindication [125].

The susceptibility of plant-fungal connections to long-term changes in land use was studied in a recent study by comparing soil properties and fungal communities in primary and secondary forests and active farmlands in Wuying, China. The findings revealed that overall fungal diversity was higher in agriculture soils than in wooded soils, probably due to periodic disturbances. However,



- Enhancing interaction with beneficial microorganisms in the soil such as PGPR, through various mechanisms that include better nutrient absorption and inhibition of harmful soil pathogens.
- Boost soil cohesion and firmness by trapping and organizing AMF structures, especially AMF mycelia.
- Boost soil cohesion and firmness by using AMF products such as GRSP, mucilages, polysaccharides, and other substances found outside the cell, as well as hydrophobins and related proteins.
- Reducing the toxicity of soil pollutants by AMF structures and products through chelation or immobilization.

Fig. 6. The primary ways in which Mycorrhizas facilitate the ecological restoration of mining-impacted sites are through their interactions with other microorganisms, both biotic and abiotic, and at various levels.

reforestation mainly restored transitional fungal populations, as their composition in secondary forests differed from that in primary forests. Although primary forests had slightly higher ectomycorrhizal fungal diversity and richness than secondary forests, the latter nonetheless had a fairly diverse and available ectomycorrhizal fungal community. The research emphasizes the potential of fungi growing on previously intensively treated agricultural land to respond rapidly to rehabilitation and support forest trees [80].

Another study discussed how AMF communities respond to invasive plant species. The study used molecular methods to investigated AMF community structure in sites dominated by an invasive mycorrhizal forb, *Centaurea maculosa* Lam. The results showed significant alteration in the AMF community following the invasion, including a reduction in diversity and extraradical hyphal lengths. Changes in AMF community composition and abundance suggest possible effects on AMF-mediated ecosystem processes, which may have consequences for site restoration following weed invasion [111]. Even though the above study shows that AMF have the potential as bio-indicators for a healthy soil ecosystem due to their ability to influence the transport of heavy metals and other plant nutrients, their use as bio-indicators for heavy metal pollution is still under debate, as some studies have shown contradictory results [126,127]. For example, the study by Dietterich et al. (2017) argued that the colonization of AMF has minimal impact on the absorption of heavy metals by plants growing in soils contaminated with heavy metals while others have demonstrated that the presence of heavy metals in soil can reduce the expansion and activity of AMF [128].

8. Mycorrhizal fungi and other microorganisms' mutualistic associations for plant growth

Besides mycorrhizal fungi, other microorganisms such as bacteria, root-associated fungi, soil protozoa, actinomycetes, nematodes, and endophytes play important roles in mine site reclamation [129]. These microorganisms can facilitate nutrient cycling, organic matter decomposition, soil aggregation, and other necessary functions to promote plant growth (Fig. 6). Soil microbes not only inhabit the rhizosphere and rhizoplane, but they also invade and establish colonies within the cortical tissues. It is important to note that these fungi, bacteria, and actinomycetes microhabitats should be considered as a unified microbiological system without clear boundaries between them [130].

8.1. Bacteria and actinomycetes

Bacteria are capable of infiltrating multiple layers of cells, with potential routes of infiltration being preexisting pits in the cell walls of the cortex and endodermis, as well as perforations and channels in the epidermal and cortical cell walls of dune grasses and other plants [131]. The presence of these perforations suggested that bacteria had created holes in the cell wall through lysis. This phenomenon may indicate either a higher vulnerability of this region to bacterial lysis or an increased supply of nutrients in these intercellular junctions. Actinomycetes are a group of gram-positive bacteria that share some characteristics with both fungi and bacteria. Like other soil microorganisms, actinomycetes can penetrate and colonize various plant tissues, including roots, stems, and leaves. They have been found to colonize the rhizosphere and rhizoplane, as well as penetrate the cortical tissues of plants [132]. One study found that actinomycetes can penetrate plant tissues through preexisting wounds, including stomata and hydathodes [133]. In addition, actinomycetes have been shown to form hyphal networks in the rhizosphere, which may facilitate their penetration into plant tissues [134]. Actinomycetes have also been shown to produce a variety of secondary metabolites that can have beneficial effects on plant growth, including the production of phytohormones and antibiotics [135].

In the mantle of mycorrhizas, which are connected with the roots of eucalypts, different populations of bacteria and/or actinomycetes were discovered [136]. Variations in hyphal exudates produced by different symbionts, together with host root exudates, may have impacted the formation of these populations. In comparison to the rhizosphere, the mycorrhizosphere had four to five times more bacteria and/or actinomycetes present [137].

Noceto et al. (2021), revealed that the presence of distinct symbionts connected with the roots of olive trees resulted in unique populations of bacteria and/or actinomycetes in the mycorrhizas. The researchers suggested that variations in exudates produced by the different symbionts, in combination with root exudates, could potentially influence the development of these populations. Additionally, they found that the mycorrhizosphere of olive trees had a higher abundance of bacteria and/or actinomycetes compared to the rhizosphere. The authors stressed the importance of understanding the regulatory mechanisms involved in interactions between plants and symbionts, as well as symbiont-symbiont interactions. This knowledge is crucial for advancing agricultural practices and studying these interactions to improve symbiotic outcomes [138].

A similar study by Yu et al. (2020) also designed two systems with or without ECM inoculation, and bacterial community structure was analyzed in the rhizosphere and non-rhizosphere soil. The results show that ECM enhanced soil moisture, total carbon/total nitrogen, and nutrient absorption while decreasing soil bulk density and heavy metal content. With ECM, heavy metals accumulated more in the roots and less in the shoots. The bacterial community structure in soil seeded with or without ECM and bulk soil could be distinguished, however there was no distinction between rhizosphere and non-rhizosphere. The primary phyla that influenced the difference in treatments include *Acidobacteria, Actinobacteria,* and *Proteobacteria*.

A previous study Mohamedin (2000) examined how a fungal strain (*Glomus intraradices* no. LAP8) and a bacterial strain (*Streptomyces coelicolor* strain no. 2389) interacted symbiotically to affect the growth and metabolic activities of sorghum plants grown in non-sterilized soil with chitin waste added. The study found that chitin waste increased the population and activity of microbes and chitinase in soils. Sorghum plants inoculated with mycorrhizae had higher growth, photosynthetic pigments, total soluble protein, and nutrient contents. Inoculation with *S. coelicolor* 2389 also enhanced the mycorrhizal root colonization and arbuscular formation in sorghum plants, but the mycorrhizal infection and its benefits decreased when chitin waste was added. The rhizosphere microflora was greatly influenced by mycorrhizal inoculation [140].

There is little understanding of how fungal and bacterial plant growth-promoting organisms (PGPRs) interact in the soil and on the root surface [141]. Long-distance connections via chemical signals and soluble components have been studied, but direct cell-to-cell interactions may also be important in the soil. Some studies have shown that rhizobia and pseudomonads can attach to AM fungal structures, with varying degrees of bacterial colonization depending on the bacterial strain used [127,142]. Bacterial attachment and colonization on the cell walls of mycorrhizal fungi have also been observed. These bacterial-fungal interactions may result in either synergistic or antagonistic effects on the growth of AMF. Recent studies have begun to shed light on the complex interactions between these different soil microorganisms [143,144].

8.2. Fauna

The interaction of AMF with nematodes and insects is a complex and poorly understood topic. Although various interactions have been observed, no generalizations can be made. However, it is widely recognized that mycorrhizae can reduce the severity of plant nematode diseases. *Collembola Folsomia candida* has been observed feeding on the external hyphae of AMF, potentially reducing the efficacy of mycorrhiza on plants. Soil microfauna feeding on the locally enhanced productivity of the microflora in the rhizosphere provides food resources for grazers such as nematodes and protozoa, leading to increased nutrient availability and plant growth. Soil animal grazing of mycorrhizal fungi may limit their development, detach them from the internal or connected mycelium, or even encourage fungal growth, with either beneficial or detrimental effects on the host plant. The ecological importance of mycorrhiza-fauna relationship under field conditions remains uncertain, and more research is needed. Recent studies have suggested that AMF can indirectly affect above-ground herbivores via changes in the host plant's nutritional quality [47,145].

8.3. Interaction among mycorrhizae (ECM and AMF) for plant growth

ECM and AMF are two types of mycorrhizal fungi that form mutualistic associations with plant roots, enhancing plant growth and health. While these fungi have distinct ecological roles, recent research has shown that they can also interact and work together to promote plant growth.

Previous research by Kohout and Janoušková (2022) has shown that the relationship between a herbaceous plant that hosts AMF and a woody plant that hosts EcMF has an asymmetrical effect on their respective mycorrhizal symbionts and the colonization rates of seedlings [146]. Specifically, it was reported that when *H. caespitosum* and its associated AMF were present, there was a reduction in the abundance of soil EcMF and a decrease in mycorrhizal colonization of *B. pendula* seedlings. However, the presence of the ECM host did not have a similar effect on AMF plants and their associated AMF. These findings suggest that this interaction may favor *H. caespitosum* over *B. pendula* in competition, potentially slowing the transition of vegetation from AM-dominated to ECM-dominated in the early stages of succession in the spoil banks studied. The research supports the idea that the relationship between ECM and AMF should not be viewed as simple alternatives that promote host coexistence, as they can have both positive and negative effects on plant competition, ultimately shaping plant community shifts in succession [47].

A recent review study has shown that ECM and AMF fungi can interact and work together to enhance plant growth. Soudzilovskaia et al. (2015) that combining ECM and AMF fungi can improve plant nitrogen utilization efficiency. The global review discovered that the presence of ECM fungi can enhance the amount of nitrogen absorbed by the plant, whilst the presence of AMF fungi may enhance the plant's efficiency in using that nitrogen. ECM and AMF fungi relationship can improve plant growth and health by enhancing nutrient uptake, water absorption, and resistance to diseases and environmental stresses. These findings emphasize the significance of comprehending the complex interactions between various types of mycorrhizal fungi and their function in improving sustainable agriculture and forestry.

A recent review article by Wahab et al. (2023) has also explored the fascinating interactions between AMF and plants. It was found that these fungi form symbiotic relationships with the roots of nearly all land-dwelling plants. During abiotic stress, such as drought, salt, and heavy metal toxicity, AMF plays a crucial role in enhancing plant growth and productivity. How does it achieve this? By improving nutrient acquisition, including phosphorus, water, and minerals. The arbuscular mycorrhizal interface allows the exchange of nutrients, signaling molecules, and protective compounds between the fungal and plant partners. Additionally, AMF influences antioxidant defense systems, osmotic adjustment, and hormone regulation, all of which contribute to better plant performance, increased photosynthetic efficiency, and greater biomass production. Moreover, AMF positively impacts soil structure, nutrient cycling, and carbon sequestration, thereby contributing to the resilience of ecosystems. Despite their critical role in enhancing plant growth and resilience, there remains limited knowledge about the specific mechanisms by which AMF communicate with each other within the soil matrix. Investigating these inter-fungal interactions could provide valuable insights into optimizing AMF-based strategies for mine wasteland reclamation and other challenging environments [147].

9. Status and perspectives of commercialization of mycorrhizal inoculum

Using mycorrhizal inoculum instead of relying on the existing mycorrhizal populations in disturbed soil with low or impaired diversity may be necessary to mitigate plant stress or enhance biomass production [32]. The application of mycorrhizal inoculum can potentially improve plant nutrient uptake and offer protection against plant pathogens or drought stress [74]. Nevertheless, there are several challenges that must be addressed before this technology can be widely adopted. For microbial inoculation to be commercially viable, it needs to be mass-produced at an affordable cost and formulated into an easily applicable product [42]. The mycorrhizal and/or bacterial inoculum must also be adaptable to a range of plant species and soil types, and its effectiveness must be assessable through standardized evaluation methods [139]. The inoculum's efficacy should be straightforward to assess on a standardized scale.

Rhizophagus irregularis, formerly known as *Glomus intraradices*, is a type of arbuscular mycorrhizal fungus (AMF) that has been widely used as a soil inoculant in agriculture and horticulture [52]. It forms symbiotic relationships with plant roots, enhancing nutrient uptake and improving plant growth, stress tolerance, and disease resistance. The commercial production and distribution of *R. irregularis* inoculants have been largely successful, but there are still some research gaps and challenges that need to be addressed.

The production of *R. irregularis* inoculants typically involves growing the fungus in sterile culture and then mixing it with a carrier material such as vermiculite or peat [148]. The resulting product is then packaged and distributed to farmers and gardeners. The commercial production of *R. irregularis* inoculants has been successful due to several factors. First, the benefits of using AMF inoculants are well established, and there is a growing demand for sustainable and eco-friendly agricultural practices. Second, the technology for mass production and distribution of AMF inoculants has been developed and refined over several decades, with many companies specializing in this area. Finally, the cost of producing and distributing AMF inoculants has decreased over time, making them more accessible to farmers and gardeners [149].

Despite the success of *R. irregularis* inoculants in agriculture and horticulture, there are still some research gaps and challenges that need to be addressed. One challenge is the lack of standardization in the production and quality control of inoculants [150]. There is currently no standardized method for measuring the concentration and viability of AMF spores in inoculants, which can affect their effectiveness. Another challenge is the variability in the effectiveness of *R. irregularis* inoculants under different environmental conditions [151]. The efficacy of AMF inoculants can be affected by factors such as soil pH, nutrient availability, and plant species, among others. More research is needed to identify the optimal conditions for the use of *R. irregularis* inoculants in different cropping systems and environments.

Another research gap is the need to develop more cost-effective and sustainable production methods for Mycorrhizae inoculants. The use of sterile culture to produce AMF inoculants is expensive and requires specialized facilities and equipment. There is a need to explore alternative methods for producing AMF inoculants, such as using non-sterile culture or natural substrates, which could reduce production costs and improve sustainability [151].

Mycorrhizae inoculum commercialization in developing countries is still in its early stages, but it is gaining attention as a potential tool for sustainable agriculture. While mycorrhizae have been used in traditional farming practices in many developing countries, their commercialization and large-scale adoption have been slow due to several challenges. These challenges include limited awareness and understanding of the benefits of mycorrhizae among farmers, lack of access to affordable and high-quality inoculum, and inadequate regulatory frameworks to support the commercialization of mycorrhizae products [152]. However, some efforts are being made to address these challenges, such as research and development initiatives, public-private partnerships, and capacity-building programs for farmers and other stakeholders. As such, the future of mycorrhizae inoculum commercialization in developing countries looks promising, but much work remains to be done to realize its full potential.

10. Conclusion

Mycorrhizal fungi, along with other microorganisms like bacteria, actinomycetes, and nematodes, form complex mutualistic associations crucial for plant growth. These microorganisms facilitate nutrient cycling, organic matter decomposition, and soil aggregation while colonizing the rhizosphere and plant tissues. For instance, bacteria and actinomycetes penetrate plant roots, stems, and leaves, producing beneficial metabolites like phytohormones and antibiotics. Such interactions enhance soil fertility and plant growth, with symbiont exudates influencing microbial populations in the mycorrhizosphere. Additionally, interactions between AMF and ECM can synergistically improve plant nutrient uptake and resilience to environmental stressors, underscoring the importance of these symbiotic relationships in sustainable agriculture and forestry.

Mycorrhizal fungi serve as valuable indicators of pollution stress in forest and mining waste soils, with ECM diversity reflecting pollution impacts on these ecosystems. Studies comparing fungal communities in primary and secondary forests, as well as agricultural lands, have highlighted fungal resilience to reforestation, emphasizing their role in forest recovery. Furthermore, aAMF communities can be altered by invasive plant species, affecting ecosystem processes. While AMF have potential as bio-indicators for healthy soil ecosystems due to their role in nutrient and heavy metal transport, their efficacy in indicating heavy metal pollution is debated, with varying studies on metal absorption and AMF activity in contaminated soils.

Mycorrhizae form mutualistic associations with plant roots, extending a network of hyphae beyond the root zone to access nutrients, water, and organic matter. These fungi enhance plant establishment and growth by immobilizing excess heavy metals and geogenic contaminants within plant cells, reducing metal toxicity, and restricting metal uptake in hyphae and cortical cell walls. This regulation is essential for optimizing phytoextraction and reducing environmental metal contamination. Mycorrhizae aid nutrient uptake, particularly phosphorus, and significantly improve plant phosphorus content. They enhance water relations by increasing root surface area and forming water channels, improving drought tolerance and water-use efficiency. Additionally, mycorrhizal fungi contribute to disease resistance by attacking pathogens, producing inhibitory compounds, and promoting plant defense responses. They improve soil structure by producing glomalin, which binds soil particles, reducing erosion and enhancing stability. Mycorrhizae also contribute to nutrient availability by breaking down complex organic compounds, releasing essential nutrients, and improving soil quality, supporting sustainable land use and reclamation of degraded landscapes.

The relationship between mycorrhizae and plants in mine wastelands has been extensively studied for soil remediation and plant growth enhancement. Mycorrhizae, present on 70–80 % of plant species' roots, improve soil quality, nutrient cycling, plant growth, and biomass, while enhancing plant tolerance to heavy metal stress by sequestering metals in fungal tissues. Key mycorrhizal fungi like *Glomus mosseae* and *Rhizophagus irregularis* have shown significant benefits in reducing heavy metal accumulation and boosting plant growth in contaminated soils. Studies on various plant species, including *Betula pendula*, *Acacia mangium*, and *moso bamboo*, demonstrate mycorrhizae's role in improving soil properties, nutrient uptake, and vegetation restoration. Mycorrhizal inoculation accelerates seedling establishment, biomass production, and species richness in mine site reclamation while aiding nutrient absorption in grasslands and enhancing soil carbon sequestration in bamboo forests. Combining mycorrhizae with nano humus or inoculating with AMF and rhizobium further improves soil chemical properties, reduces heavy metal concentrations, and enhances plant resistance to environmental stress, making mycorrhizae a promising strategy for remediating polluted soils and promoting sustainable land use practices in mine wastelands.

Mycorrhizae hold immense promise for rehabilitating abandoned mining sites. By enhancing soil fertility, promoting plant growth, and aiding in metal detoxification, these fungal partners play a crucial role in restoring ecosystems devastated by mining activities. However, further research and practical applications are needed to fully harness their potential.

11. Gaps in mycorrhizal research and suggestions for future research

It is critical to understand the complex soil processes involved in the uptake, storage, and cycling of nutrients and water by reintroduced plant species in order to restore mining-disturbed areas to functioning ecosystems. The use of tree species for degraded site restoration provides a problem in identifying and reintroducing populations of soil microorganisms that are essential for ecosystem functioning.

Despite the promising results of these studies showing that mycorrhizal fungi play a critical role in the restoration of ecosystems affected by mining activities, there are still several gaps in our knowledge regarding the ecology, diversity, and dynamics of mycorrhizal fungi in many ecosystems, posing challenges for restoring degraded sites with tree species, particularly in developing countries such as Zambia. Moreover, there is a need to investigate the mechanisms by which mycorrhizae improve plant growth and survival in contaminated soils. This is particularly true because it has been previously shown that the impact of mycorrhizae on plant development can vary depending on the fungal strain, even if they belong to the same species. It has been reported, for example, that arctic AMF fungal strains have developed physiological characteristics that renders them more adaptable to a short growing season. Early season emergence, aggressive infective hyphal structures, and a quick sporulation process that permits them to survive and propagate in unfavorable soil conditions could all be examples of this. Evaluating their low-temperature ability to develop may reveal such specialized adaptations and their impact on plant survival and development in Arctic tundra [153]. Therefore, more investigation is required to understand the factors that affect the effectiveness of mycorrhizae in various types of contaminated soils.

Furthermore, the use of mycorrhizae in phytoremediation is still limited by several challenges. One challenge is the variability in the effectiveness of mycorrhizae in different plant species and different types of contaminants. Another challenge is the high cost and labor-intensive process of producing and applying mycorrhizae in contaminated soils. In conclusion, mycorrhizae isolated from abandoned mine land have shown promising applications in improving plant growth and survival in contaminated soils and enhancing the phytoremediation potential of plants. However, more research is needed to understand the mechanisms and factors affecting the effectiveness of mycorrhizae in different types of contaminated soils. Furthermore, the use of mycorrhizae in phytoremediation is still limited by several challenges that need to be addressed in future research.

The diversity of AMF in Sub-Saharan Africa has not been extensively studied. While some studies have indicated the existence of 29 % of the world's reported species, our understanding of their functional diversity remains limited [154]. For the successful research conducted on mycorrhizae fungi, further research is needed to optimize inoculation techniques and to understand the long-term effects of mycorrhizal inoculation on ecosystem function and resilience.

Some of the principal research gaps that need to be addressed include.

1. Insufficient knowledge of the interactions between mycorrhizal fungi and particular plant taxa: Mycorrhizal fungi have been demonstrated to improve the development and viability of plants on mining sites, but there is a dearth of data on which plant taxa are most compatible with various kinds of mycorrhizal fungi
2. Lack of standardized methods for inoculating mycorrhizal fungi: There is currently no standardized method for inoculating mycorrhizal fungi on mine sites, which can make it difficult to compare the efficacy of different methods and strains of fungi.
3. Limited research on the long-term impacts of mycorrhizal fungi on mine site reclamation: While mycorrhizal fungi have been shown to promote plant growth in the short term, there is limited research on their long-term impacts on soil fertility and plant communities.
4. Limited knowledge of the impacts of mine site characteristics on mycorrhizal fungi: Different mine sites characteristics, such as soil pH and nutrient availability, may impact the effectiveness of mycorrhizal fungi. Further research is needed to understand how these characteristics affect the relationships between mycorrhizal fungi and plants.
5. Limited research on the use of native mycorrhizal fungi for mine site reclamation: While there has been some research on the use of non-native mycorrhizal fungi for mine site reclamation, there is limited information on the potential benefits and drawbacks of using native mycorrhizal fungi.
6. Limited understanding exists on how mycorrhizae communicate with each other and other soil microorganisms, despite their crucial role in enhancing plant growth and resilience.

In summary, addressing these research gaps will be critical in developing effective strategies for using mycorrhizal fungi in mine site reclamation. Future research is expected to address these gaps in the coming years.

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Data availability statement

The datasets disclosed in this study can be obtained by contacting the corresponding author.

CRediT authorship contribution statement

Arthur A. Owiny: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Leonce Dusengemungu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

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