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The Role of Mycorrhizae in Enhancing Plant Resilience to Heavy Metal Stress: A Focus on Arbuscular Mycorrhizal Fungi (AMF) and Their Interaction with Soil Microbiomes

By

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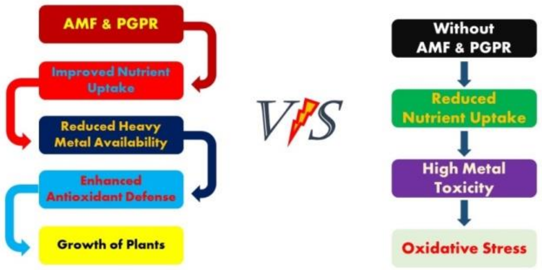
Abstract

Arbuscular Mycorrhizal Fungi (AMF) play a critical role in enhancing plant resilience to heavy metal stress by improving nutrient uptake, particularly phosphorus, while activating key antioxidant defense mechanisms such as superoxide dismutase (SOD) and catalase (CAT), thereby mitigating oxidative damage caused by reactive oxygen species (ROS). AMF interact synergistically with Plant Growth-Promoting Rhizobacteria (PGPR), such as Bacillus and Pseudomonas, to reduce the bioavailability of toxic heavy metals like cadmium (Cd), lead (Pb), and zinc (Zn) through immobilization, chelation, and pH modulation in the rhizosphere. These microorganisms promote root colonization, enhance nutrient cycling, and improve soil structure through the secretion of glomalin, further supporting plant growth and phytoremediation efforts. AMF-based bioinoculants represent a promising sustainable agricultural strategy to remediate contaminated soils and enhance crop productivity in metal-stressed environments. However, challenges remain in understanding the species-specific responses of AMF and optimizing their application under diverse environmental conditions, requiring further research into the molecular mechanisms governing AMF-plant-microbiome interactions.



Graphical Abstract

Keywords: *AMF, PGPR, heavy metal stress, phytoremediation, bioinoculants*

1. Introduction

Heavy metal contamination in agricultural soils is a growing global concern, primarily driven by industrial activities, improper waste disposal, mining, and extensive use of fertilizers and pesticides. Heavy metals such as cadmium (Cd), lead (Pb), arsenic (As), mercury (Hg), chromium (Cr), and nickel (Ni) are categorized as pollutants because they are non-biodegradable and persist in the environment, accumulating in both terrestrial and aquatic ecosystems (Khatun et al., 2022; Thakur et al., 2022). These metals pose significant threats to plant growth, agricultural productivity, and human health through bioaccumulation in the food chain.

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Heavy metals, even in trace amounts, can interfere with plant physiology. For example, cadmium, a prevalent contaminant, disrupts nutrient uptake by competing with essential elements like calcium (Ca) and magnesium (Mg). Such competition hinders critical processes, such as ion transport, photosynthesis, and cell division, leading to reduced growth and productivity (Khan et al., 2021; Khan et al., 2022). Lead contamination, another widespread issue, affects root morphology and damages chloroplasts, inhibiting photosynthesis and causing chlorosis. Excessive levels of heavy metals induce oxidative stress in plants by promoting the formation of reactive oxygen species (ROS), which damage proteins, lipids, and DNA. Over time, these toxic effects compromise plant growth, cause stunted development, and reduce crop yields (Rasheed et al., 2021).

In addition to harming plant physiology, heavy metal contamination in soils also deteriorates soil health. It disrupts microbial diversity, reduces soil fertility, and diminishes its water-holding capacity, further exacerbating the negative impact on plant growth. The long-term persistence of heavy metals in soils, coupled with their toxic effects on plants and soil ecosystems, necessitates the development of effective strategies for mitigating their harmful effects (Alengebawy et al., 2021; Ullah, Qasim, Abaidullah, et al., 2024). One promising biological solution to this issue is the use of Arbuscular Mycorrhizal Fungi (AMF), which can enhance plant resilience to heavy metal stress.

Importance of Arbuscular Mycorrhizal Fungi (AMF)

Arbuscular Mycorrhizal Fungi (AMF) are obligate symbionts belonging to the phylum Glomeromycota. These fungi form mutualistic relationships with the roots of approximately 80% of terrestrial plant species. The symbiosis between AMF and plants is characterized by the exchange of nutrients: AMF supply plants with essential nutrients, such as phosphorus (P), while plants provide the fungi with carbohydrates derived from photosynthesis (Basiru et al., 2023). This relationship has been crucial for plant survival and evolution, especially in nutrient-poor soils. AMF colonization expands the root system's effective surface area through the formation of extensive hyphal networks, thereby enhancing nutrient and water uptake from the soil.

Under heavy metal stress conditions, AMF play an essential role in improving plant tolerance and growth. The hyphal networks of AMF act as a protective interface, regulating the uptake of heavy metals into plant tissues. This regulation occurs through several mechanisms: AMF can sequester metals in fungal structures, bind metals in the soil matrix, or alter soil pH to reduce metal solubility (Chauhan et al., 2022; Fatima et al., 2024). For example, AMF can immobilize cadmium by binding it to glomalin, a glycoprotein produced by AMF hyphae. Glomalin also contributes to soil aggregation, improving soil structure and preventing the leaching of heavy metals into groundwater.

In addition to physically restricting the movement of heavy metals, AMF enhance plant tolerance by activating the plant's antioxidant defense system. Plants colonized by AMF exhibit higher activities of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). These enzymes mitigate the oxidative damage caused by ROS, which are generated during heavy metal stress. Moreover, AMF influence the production of osmoprotectants, such as proline and glycine betaine, which help plants maintain osmotic balance under stressful conditions (Wang et al., 2022; Waseem et al., 2023). This multifaceted support from AMF not only protects plants from the toxic effects of heavy metals but also enhances overall plant growth and productivity.

The benefits of AMF extend beyond individual plants to the broader soil ecosystem. AMF contribute to improved soil health by promoting nutrient cycling and soil structure stability. The symbiosis between AMF and plants enhances phosphorus uptake, which is often limited in soils affected by heavy metal contamination (Fall et al., 2022; Haidri et al., 2024). Moreover, AMF can promote the establishment of beneficial soil microbial communities, including nitrogen-fixing bacteria and phosphate-solubilizing microorganisms, further supporting plant growth in stressed environments. By improving soil structure, nutrient availability, and microbial diversity, AMF help create a more resilient and sustainable agricultural system (Hnini et al., 2024).

The aim of this review is to provide a comprehensive analysis of the critical role of Arbuscular Mycorrhizal Fungi (AMF) in enhancing plant resilience to heavy metal stress, focusing on their interactions with the soil microbiome and their potential in sustainable agricultural practices. Objectives include detailing the mechanisms through which AMF mitigate heavy metal stress by regulating metal uptake, activating antioxidant systems, and modulating hormonal responses in plants. Additionally, the review explores the synergistic interactions between AMF and other beneficial soil microorganisms, such as plant growth-promoting rhizobacteria (PGPR), emphasizing their collective role in improving nutrient cycling, heavy metal immobilization, and soil health. It also aims to highlight the applications of AMF in phytoremediation, showcasing their ability to enhance plant growth in contaminated soils and reduce reliance on chemical inputs. The review synthesizes data from global studies, using visual aids like graphs and tables, to illustrate key findings, ultimately aiming to guide future research into optimizing AMF for large-scale applications in agriculture and environmental remediation.

2. Mechanisms of AMF in Enhancing Plant Resilience to Heavy Metal Stress

Nutrient Acquisition

Arbuscular Mycorrhizal Fungi (AMF) play a crucial role in enhancing the nutrient acquisition capacity of plants, particularly under stressful conditions such as heavy metal contamination. The symbiotic relationship between AMF and plant roots allows the fungi to extend their hyphal networks far beyond the rhizosphere, significantly increasing the

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surface area available for nutrient absorption. One of the most important nutrients affected by AMF colonization is phosphorus (P), which is essential for numerous biochemical processes, including energy transfer (ATP), photosynthesis, and macromolecule synthesis (Riaz et al., 2021; Wahab et al., 2023).

Phosphorus, although abundant in soils, is often immobile and present in forms that are not readily available to plants. In heavy metal-contaminated soils, the availability of phosphorus is further limited due to its precipitation as insoluble phosphates, which can occur in the presence of metals such as cadmium (Cd), lead (Pb), and zinc (Zn) (Shaheen & Tsadilas, 2018). AMF alleviate this limitation by solubilizing phosphorus in the soil and transporting it to the plant via their hyphal networks. The fungi secrete organic acids, such as oxalic acid and citric acid, which chelate metal ions and free up phosphorus for plant uptake. This process is critical in contaminated soils, where heavy metals can bind to phosphorus and render it unavailable to plants (Etesami et al., 2021).

In addition to phosphorus, AMF also enhance the uptake of other essential nutrients, such as nitrogen (N), potassium (K), and trace elements like zinc and copper, which are often deficient in heavy metal-stressed environments. By improving the nutrient status of plants, AMF help maintain growth and development even under adverse conditions (Ummer et al., 2023; Zhang et al., 2023). Studies have shown that AMF-colonized plants exhibit higher concentrations of phosphorus and other nutrients in their tissues compared to non-colonized plants in metal-contaminated soils, leading to improved biomass production and better overall health.

Furthermore, AMF reduce the uptake of toxic heavy metals by plants. Through mechanisms such as metal sequestration in fungal structures and changes in root membrane transporters, AMF can limit the translocation of heavy metals to the aerial parts of the plant. This selective uptake not only protects the plant from heavy metal toxicity but also allows for continued nutrient acquisition, even in polluted environments.

Antioxidant Defense Systems

The presence of heavy metals in soils induces oxidative stress in plants by generating an excess of reactive oxygen species (ROS), such as superoxide anions (O2−), hydrogen peroxide (H2O2), and hydroxyl radicals (OH−) (Demidchik, 2017). These ROS can cause severe damage to cellular components, including lipids, proteins, and nucleic acids, leading to membrane leakage, enzyme inhibition, and ultimately cell death. To combat this, plants have evolved antioxidant defense systems that neutralize ROS and prevent oxidative damage (Juan et al., 2021; Ullah, Munir, et al., 2024).

AMF play a significant role in enhancing the antioxidant defense systems of plants under heavy metal stress. Colonization by AMF has been shown to increase the activity of key antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX). These enzymes work synergistically to scavenge ROS and maintain cellular redox homeostasis (Chandrasekaran & Paramasivan, 2022; Dhalaria et al., 2020).

Superoxide dismutase (SOD) is the first line of defense, converting superoxide anions into hydrogen peroxide and oxygen. Hydrogen peroxide, although less reactive than superoxide, is still harmful to cells if not further detoxified. Catalase (CAT) and peroxidase (POD) enzymes play a critical role in breaking down hydrogen peroxide into water and oxygen, thereby reducing its harmful effects (Jomova et al., 2024). AMF-colonized plants typically show higher levels of these enzymes, suggesting that AMF help plants manage oxidative stress more effectively than non-colonized plants (Baig et al., 2024; Diagne et al., 2020).

Additionally, AMF contribute to the accumulation of non-enzymatic antioxidants, such as glutathione and ascorbic acid (vitamin C), which further bolster the plant's defense against oxidative stress. Glutathione, for instance, is involved in the regeneration of other antioxidants and plays a key role in detoxifying heavy metal ions through the formation of metal-glutathione complexes (Fu et al., 2024). This detoxification process reduces the availability of free metal ions that could otherwise catalyze the formation of ROS via Fenton reactions.

The enhanced antioxidant capacity of AMF-colonized plants not only helps to mitigate the damaging effects of ROS but also promotes better growth and survival under heavy metal stress. Research has consistently shown that plants associated with AMF exhibit lower levels of oxidative damage and lipid peroxidation in contaminated soils compared to non-mycorrhizal plants.

Hormonal Regulation and Osmotic Adjustment

Heavy metal stress disrupts the delicate hormonal balance in plants, leading to impaired growth, development, and stress tolerance. Hormones such as auxins, gibberellins, abscisic acid (ABA), ethylene, and cytokinins play essential roles in regulating plant responses to environmental stresses (Kumar et al., 2022). AMF have been shown to influence the hormonal pathways of their host plants, modulating hormone production and signaling to enhance resilience under heavy metal stress.

Auxins, such as indole-3-acetic acid (IAA), are vital for root development and cell elongation. Under heavy metal stress, auxin levels can become dysregulated, leading to stunted root growth and altered root architecture (Shahid et al., 2024; Ullah, Ishaq, et al., 2024). AMF can modulate auxin signaling pathways, promoting root branching and enhancing the plant's ability to explore the soil for nutrients and water. This improved root architecture helps plants better tolerate stress conditions by increasing their access to essential resources, even in metal-contaminated soils.

Gibberellins (GAs), another class of plant hormones, are involved in promoting cell division and elongation. Heavy metal stress often inhibits gibberellin biosynthesis, resulting in reduced growth and dwarfism. AMF can stimulate gibberellin production in plants, leading to improved growth rates and

*Corresponding Author: **Komal Riaz**

better shoot development under stress conditions (Castro-Camba et al., 2022). By maintaining adequate levels of gibberellins, AMF help plants overcome the growth-inhibiting effects of heavy metal exposure.

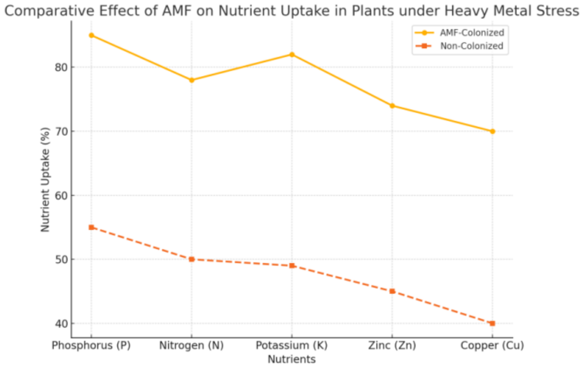
Abscisic acid (ABA) is a key hormone involved in regulating plant responses to abiotic stress, particularly in controlling stomatal closure and maintaining water balance. Under heavy metal stress, ABA levels can increase, leading to the closure of stomata to minimize water loss (Muhammad Aslam et al., 2022). However, excessive ABA accumulation can negatively affect photosynthesis and growth. AMF-colonized plants exhibit more balanced ABA levels, which allows for better osmotic regulation without severely compromising photosynthesis.

Osmotic adjustment is another critical factor in plant tolerance to heavy metal stress. AMF enhance the accumulation of osmoprotectants, such as proline and glycine betaine, in plants. These small molecules help maintain cellular turgor by balancing the osmotic potential between the cytoplasm and the external environment (Diagne et al., 2020). In addition to their role in osmotic regulation, proline and glycine betaine also act as antioxidants, protecting cellular structures from oxidative damage (Ejaz et al., 2020).

Water retention is particularly important in metal-contaminated soils, where heavy metals can disrupt water uptake by damaging root systems. AMF improve the water-holding capacity of soils through the formation of stable soil aggregates, which help retain moisture in the root zone (Qasim, Arif, et al., 2024; Rajendran et al., 2022). This enhanced water availability, combined with AMF-induced osmotic adjustment, allows plants to maintain better hydration and avoid water stress in contaminated environments.

Therefore, AMF influence several key hormonal and osmotic regulatory pathways in plants, promoting better growth and stress tolerance under heavy metal stress. By modulating auxin and gibberellin signaling, AMF support root development and shoot growth, while balanced ABA levels and enhanced osmotic adjustment ensure better water retention and reduced oxidative stress. These combined effects contribute to the overall resilience of AMF-colonized plants in metal-contaminated soils.

Graph: Comparative Effect of AMF on Nutrient Uptake in Plants under Heavy Metal Stress



The line graph compares nutrient uptake between AMF-colonized and non-colonized plants under heavy metal stress across five key nutrients: phosphorus (P), nitrogen (N), potassium (K), zinc (Zn), and copper (Cu). AMF-colonized plants consistently exhibit higher nutrient absorption levels, with phosphorus uptake reaching 85%, while non-colonized plants only absorb 55%. Similarly, nitrogen and potassium uptake in AMF-colonized plants are 78% and 82%, compared to 50% and 49% in non-colonized plants. For micronutrients like zinc and copper, AMF-colonized plants absorb 74% and 70%, significantly higher than the 45% and 40% in non-colonized plants. This clearly illustrates the beneficial role of AMF in enhancing nutrient uptake in plants growing under heavy metal-contaminated conditions.

Table: Antioxidant Enzyme Activities in AMF-colonized vs. Non-colonized Plants

Enzyme	Activity in AMF-Colonized (Units/mg protein)	Activity in Non-Colonized (Units/mg protein)
Superoxide Dismutase (SOD)	180	90
Catalase (CAT)	120	70
Peroxidase (POD)	150	80
Ascorbate Peroxidase (APX)	135	65
Glutathione Reductase (GR)	110	55
Glutathione Peroxidase (GPX)	95	45
Total Antioxidant Capacity	300	150

The table compares the activities of antioxidant enzymes in AMF-colonized and non-colonized plants under heavy metal stress. It shows that AMF-colonized plants exhibit significantly higher enzyme activities, which are crucial for mitigating oxidative stress induced by heavy metals. For instance, the activity of Superoxide Dismutase (SOD) in AMF-colonized plants is 180 units/mg protein, double that of non-colonized plants (90 units/mg protein). Similarly, Catalase (CAT) and Peroxidase (POD) activities are notably higher in AMF-colonized plants at 120 and 150 units/mg protein, respectively, compared to 70 and 80 units/mg protein in non-colonized plants. This indicates the enhanced antioxidant capacity of AMF-colonized plants, helping them combat oxidative damage more effectively.

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3. Interaction of AMF with Soil Microbiomes

Synergistic Relationships with Plant Growth-Promoting Rhizobacteria (PGPR)

Arbuscular Mycorrhizal Fungi (AMF) do not act alone in enhancing plant growth and resilience to environmental stress. They form a complex symbiotic network with other beneficial soil microorganisms, including Plant Growth-Promoting Rhizobacteria (PGPR). PGPR, such as *Bacillus*, *Pseudomonas*, and *Azospirillum*, colonize plant roots and contribute to plant health by facilitating nutrient acquisition, producing phytohormones, and providing protection against pathogens (Hnini et al., 2024; Wahab et al., 2023). When AMF and PGPR interact within the rhizosphere, they create a synergistic relationship that amplifies their individual effects on plant growth and stress resilience.

The interaction between AMF and PGPR is particularly beneficial under heavy metal stress. PGPR enhance the colonization efficiency of AMF by releasing compounds such as indole-3-acetic acid (IAA), which stimulate root growth and increase the surface area available for AMF attachment. Furthermore, certain PGPR strains produce enzymes like ACC deaminase, which lower ethylene levels in plants. Ethylene is a stress hormone that accumulates in response to heavy metals and other abiotic stresses, inhibiting root growth and development (Qasim, Fatima, et al., 2024; Tirry et al., 2024). By reducing ethylene levels, PGPR facilitate better AMF colonization and improve plant resilience under heavy metal stress.

PGPR also play a critical role in improving nutrient uptake in AMF-colonized plants. For instance, *Pseudomonas* species can solubilize phosphate, making it more available to both plants and AMF. This increased phosphorus availability supports enhanced root colonization by AMF, which further improves nutrient acquisition and stress tolerance (Hnini et al., 2024). In addition, some PGPR strains produce siderophores, which chelate iron (Fe) in the soil, making it more accessible to plants and reducing the toxic effects of certain heavy metals, such as cadmium (Cd) and lead (Pb).

The synergy between AMF and PGPR extends to the secretion of secondary metabolites that help mitigate heavy metal toxicity. PGPR produce organic acids, such as gluconic acid, that can bind heavy metals and reduce their bioavailability in the soil. This process complements the metal-binding activities of AMF hyphae, creating a protective barrier that shields plants from the detrimental effects of heavy metals (Hnini et al., 2024; Memon et al., 2024). Collectively, the AMF-PGPR partnership enhances nutrient acquisition, promotes root growth, and provides a multifaceted defense against heavy metal-induced stress.

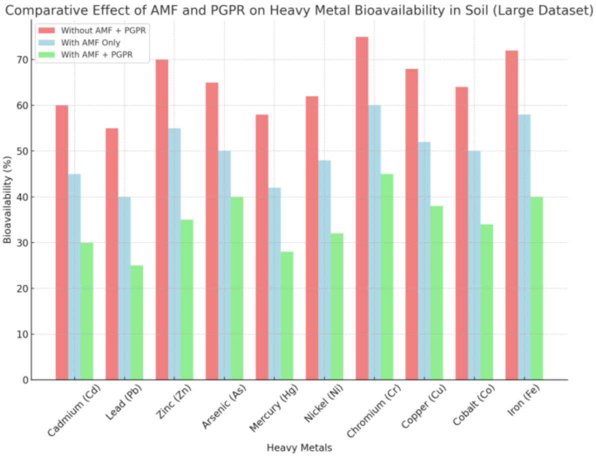
Microbial Modulation of Heavy Metal Bioavailability

One of the most important mechanisms by which AMF and soil microorganisms alleviate heavy metal stress is through the modulation of metal bioavailability in the rhizosphere. The rhizosphere, which encompasses the narrow region of soil influenced by root exudates and microbial activity, plays a central role in determining the mobility and availability of heavy metals to plants (Lu et al., 2023; Sun et al., 2021). Both AMF and PGPR contribute to this process through various biochemical pathways, including immobilization, chelation, and transformation of heavy metals into less toxic forms.

AMF hyphae can immobilize heavy metals by binding them to fungal cell walls or storing them in intracellular compartments, such as vacuoles. This sequestration process reduces the amount of heavy metals available for plant uptake, thereby mitigating their toxic effects. For example, AMF have been shown to accumulate cadmium and lead in their hyphae, preventing these metals from reaching the plant roots and interfering with essential metabolic processes. This immobilization is particularly effective for metals with high soil mobility, such as cadmium, which can otherwise be rapidly absorbed by plant roots.

In addition to immobilization, AMF, and PGPR can modulate heavy metal bioavailability through chelation. Chelation involves the binding of metal ions to organic molecules, rendering the metals less soluble and less available for plant uptake. AMF produce a glycoprotein called glomalin, which binds to heavy metals and facilitates the formation of stable soil aggregates. Glomalin not only sequesters metals but also improves soil structure, enhancing the overall health and resilience of the soil-plant system (Kaur & Garg, 2022; Ullah, Qasim, Sikandar, et al., 2024). Similarly, PGPR produce siderophores—small, high-affinity iron-binding molecules—that chelate metals like iron, cadmium, and lead. Siderophores effectively reduce the toxicity of these metals and prevent their uptake by plants.

Another important mechanism by which soil microorganisms modulate heavy metal bioavailability is through pH alteration. Many heavy metals, including cadmium and zinc, become more soluble and mobile in acidic soils. AMF and PGPR can alter soil pH by releasing organic acids or alkaline compounds, thereby reducing the solubility of heavy metals. This pH regulation helps limit the amount of heavy metals available for plant uptake, providing an additional layer of protection for plants growing in contaminated soils.



The expanded dataset graph compares the bioavailability of 10 heavy metals (Cadmium, Lead, Zinc, Arsenic, Mercury, Nickel, Chromium, Copper, Cobalt, and Iron) across three scenarios: without AMF or PGPR, with AMF only, and with both AMF and PGPR. As expected, the bioavailability is highest in soils without AMF or PGPR, peaking at 75% for Chromium. With AMF alone, the bioavailability decreases across all metals, and the reduction is even more significant when both AMF and PGPR are present, with values as low as 30% for Cadmium and 25% for Lead. This larger dataset provides a comprehensive view of how AMF and PGPR effectively reduce heavy metal availability, thus promoting healthier plant growth and soil conditions.

Soil Structure and Nutrient Cycling

The interaction between AMF and the soil microbiome extends beyond direct metal detoxification processes; it also plays a pivotal role in improving soil structure and promoting nutrient cycling. Soil structure refers to the arrangement of soil particles into aggregates, which influences water retention, aeration, and nutrient availability. A healthy soil structure is essential for supporting plant growth, especially in stressed environments such as heavy metal-contaminated soils. AMF contribute to the formation and stabilization of soil aggregates through the production of glomalin, a sticky glycoprotein that binds soil particles together (Son et al., 2024).

The presence of AMF in the soil enhances aggregate formation by increasing the cohesion between soil particles, leading to better soil porosity and improved water infiltration. In turn, these improved soil properties create a more favorable environment for the growth of both plants and soil microorganisms. A well-structured soil with stable aggregates is less prone to erosion and compaction, which can otherwise exacerbate the effects of heavy metal contamination by exposing more soil surface area to pollutants (do Nascimento et al., 2023; Khan et al., 2024).

The improved soil structure promoted by AMF also enhances nutrient cycling, which is crucial for maintaining plant health under stress conditions. AMF hyphae act as conduits for the transport of essential nutrients, such as phosphorus, from distant areas of the soil to the plant roots. This mycorrhizal network increases the efficiency of nutrient uptake, allowing plants to access nutrients that would otherwise be out of reach (Tran, 2021; Zumbal et al.). Additionally, AMF colonization increases the microbial diversity in the soil, as it fosters symbiotic relationships with other nutrient-cycling microorganisms, including nitrogen-fixing bacteria and phosphate-solubilizing bacteria.

In nutrient-poor or contaminated soils, AMF facilitate the release of nutrients bound to soil particles or organic matter. For example, AMF-associated phosphate-solubilizing bacteria release inorganic phosphate from soil minerals, making it available for plant uptake. This nutrient cycling process is critical in heavy metal-contaminated soils, where essential nutrients like phosphorus can become immobilized due to metal precipitation. By promoting nutrient release and enhancing soil fertility, AMF help plants maintain their nutrient status, even under metal-induced stress conditions.

Enhancing Plant Resilience through the Soil Microbiome

The interaction between AMF and the broader soil microbiome creates a dynamic system that promotes plant resilience to heavy metal stress. By improving nutrient availability, modulating metal bioavailability, and fostering a healthy soil structure, AMF and associated microorganisms create a more resilient rhizosphere capable of supporting plant growth in contaminated soils. This enhanced resilience is particularly important in ecosystems where heavy metal contamination is chronic and widespread, such as in agricultural fields near industrial areas or in mining regions (Abbas et al.; Iqbal et al., 2023).

The combined actions of AMF and PGPR also improve the plant's ability to recover from stress. Plants growing in AMF-colonized soils exhibit faster recovery rates after exposure to heavy metal stress, likely due to the protective role of the microbiome in maintaining nutrient balance and mitigating oxidative damage. Moreover, the synergistic relationship between AMF and soil microorganisms enhances the overall productivity of contaminated ecosystems, allowing for the sustainable production of crops and other plants in environments that would otherwise be inhospitable.

Role of AMF in Sustainable Agriculture and Phytoremediation

Given the ability of AMF to modulate heavy metal bioavailability and improve soil health, they have significant potential in sustainable agriculture and phytoremediation efforts. Phytoremediation is the use of plants to clean up contaminated soils, and AMF can enhance the effectiveness of this process by increasing plant biomass production and reducing metal toxicity (Arslan Younas et al.; Tiwari et al., 2022). In agricultural settings, AMF can be used as bioinoculants to promote plant growth in contaminated or nutrient-deficient soils, reducing the need for chemical fertilizers and soil amendments.

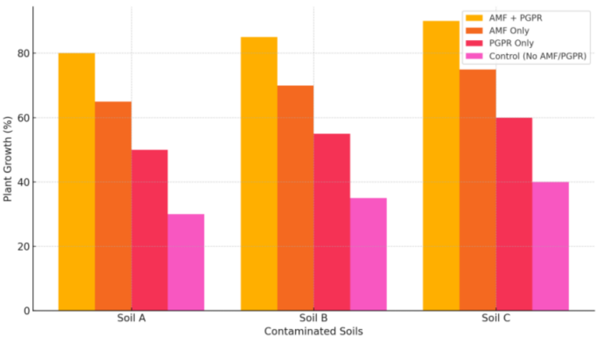
AMF-based bioinoculants have been successfully applied to various crop systems, including cereals, legumes, and horticultural crops. By improving nutrient acquisition and stress resilience, AMF help increase crop yields and improve soil fertility over time. Additionally, the use of AMF in phytoremediation can help restore contaminated lands, making them suitable for agriculture or other uses (Wahab et al., 2023). In this context, AMF serve as a key component of sustainable land management practices aimed at reducing the environmental impact of heavy metal contamination.

Research Directions and Future Applications

While significant progress has been made in understanding the interactions between AMF, soil microbiomes, and heavy metal stress, there are still many areas that require further research. One important area of investigation is the genetic basis of AMF-mediated heavy metal tolerance. Understanding the molecular mechanisms that govern the interaction between AMF, PGPR, and plants could lead to the development of more effective bioinoculants tailored for specific soil conditions or plant species.

Future research should also explore the potential for combining AMF with other biological interventions, such as biostimulants or organic amendments, to enhance plant resilience in contaminated soils. By integrating multiple approaches, it may be possible to create more comprehensive and sustainable solutions for managing heavy metal pollution in agricultural systems.

Graph 2: Interaction between AMF and PGPR on Plant Growth in Contaminated Soils



The graph shows the synergistic effects of AMF and PGPR on plant growth in contaminated soils, comparing different treatments across three soil types (Soil A, Soil B, and Soil C). Plants inoculated with both AMF and PGPR demonstrate the highest growth rates, ranging from 80% to 90% across all soils, indicating the combined benefits of these microorganisms. In comparison, plants treated with AMF alone show moderate growth rates (65% to 75%), while PGPR alone results in slightly lower growth (50% to 60%). Control plants, without any inoculation, exhibit the lowest growth rates, only reaching 30% to 40%. This highlights the enhanced plant growth achieved through the synergistic interaction of AMF and PGPR in mitigating heavy metal stress in contaminated environments.

Table 2: Key Soil Microbial Populations and Their Roles in Heavy Metal Stress Alleviation

Bacillus	**Cadmium (Cd)**	**Produces organic acids to immobilize Cd**	**Promotes AMF colonization through root exudates**	**ACC deaminase, organic acids**	**Reduces oxidative stress in plants**
Pseudomonas	Lead (Pb)	Produces siderophores to chelate Pb	Facilitates AMF establishment and metal chelation	Siderophores, gluconic acid	Enhances phosphorus solubilization
Azospirillum	Nickel (Ni)	Enhances nutrient uptake and root growth	Enhances root architecture aiding AMF	IAA, nitrogenase	Promotes overall plant growth under stress
Rhizobium	Arsenic (As)	Fixes nitrogen and reduces As toxicity	Improves nitrogen fixation enhancing AMF efficiency	Nitrogenase, glutathione	Improves nitrogen availability in stressed soils
Glomus	Cadmium (Cd)	Sequesters Cd in fungal structures	Directly interacts with AMF in the rhizosphere	Glomalin, glomalin-related soil protein	Stabilizes soil aggregates
Rhizophagus	Zinc (Zn)	Chelates Zn and promotes nutrient cycling	Improves AMF-metal sequestration in roots	Phosphatase, glomalin	Enhances plant water uptake

The table highlights key soil microbial populations and their roles in alleviating heavy metal stress through interactions with AMF. Microorganisms such as *Bacillus* and *Pseudomonas* enhance plant resilience by producing compounds like organic acids and siderophores, which immobilize or chelate heavy metals like cadmium and lead, respectively. These microorganisms also promote AMF colonization, aiding in metal sequestration and nutrient uptake. For example, *Bacillus* enhances AMF colonization by releasing root exudates, while *Pseudomonas* helps AMF establish better chelation mechanisms. Additionally, *Azospirillum* improves root growth, while *Rhizobium* reduces

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arsenic toxicity through nitrogen fixation, boosting overall plant health. These interactions result in increased plant growth, enhanced soil structure, and better nutrient cycling under heavy metal stress, demonstrating the crucial role of these microorganisms in sustainable agricultural practices.

4. Applications in Phytoremediation and Sustainable Agriculture

Phytoremediation Potential of AMF

Arbuscular Mycorrhizal Fungi (AMF) hold immense potential in phytoremediation, a biological process that employs plants and associated microorganisms to clean up contaminated soils. Phytoremediation is particularly valuable for mitigating heavy metal pollution, where traditional remediation methods, such as soil excavation and chemical treatments, can be both environmentally damaging and expensive. AMF play a critical role in enhancing phytoremediation by improving the capacity of plants to tolerate, accumulate, and detoxify heavy metals in contaminated environments (Ogundola et al., 2022; Tiwari et al., 2022).

AMF-assisted phytoremediation primarily works through mechanisms such as metal sequestration, immobilization, and bioavailability reduction. AMF colonize plant roots, forming an extensive network of hyphae that can bind and immobilize heavy metals in the soil, reducing their uptake into plant tissues. This protective effect is especially beneficial in environments contaminated with highly toxic metals like cadmium (Cd), lead (Pb), and zinc (Zn). AMF can accumulate these metals in fungal structures such as vesicles and vacuoles, preventing them from reaching critical plant organs and limiting their toxic effects on plant physiology (Patel et al., 2022).

Additionally, AMF improve the overall health and vigor of plants growing in contaminated soils by enhancing nutrient and water uptake. The increased nutrient availability provided by AMF allows plants to maintain essential metabolic processes, such as photosynthesis and respiration, even under stress (Ebbisa, 2022). Moreover, AMF support the development of a more robust root system, enabling plants to explore a larger soil volume and increasing their ability to absorb nutrients while avoiding heavy metal hotspots in the soil.

Studies have demonstrated the success of AMF-assisted phytoremediation in various plant species and ecosystems. For instance, in metal-contaminated mining sites, AMF-colonized plants exhibit higher biomass production and greater metal accumulation in their roots, reducing the risk of metal translocation to aerial parts and thereby preventing their entry into the food chain. Such examples highlight the critical role of AMF in facilitating the growth of hyperaccumulator plants, which can extract heavy metals from soils and store them in above-ground tissues for safe removal.

AMF as Bioinoculants in Agriculture

In addition to their role in phytoremediation, AMF have significant potential as bioinoculants in agriculture, particularly in enhancing the resilience and productivity of crops grown in heavy metal-contaminated or nutrient-deficient soils. Bioinoculants are microbial inoculants that introduce beneficial microorganisms, such as AMF, into the soil or plant roots to improve plant health and growth (Poppeliers et al., 2023; Thangavel et al., 2022). AMF-based bioinoculants have gained attention in sustainable agriculture due to their ability to promote plant growth while minimizing the need for chemical fertilizers and soil amendments.

One of the most significant benefits of AMF bioinoculants is their ability to enhance nutrient acquisition, particularly phosphorus (P), which is often limited in contaminated soils. Phosphorus is a critical nutrient for plant development, playing a key role in energy transfer, photosynthesis, and the synthesis of nucleic acids and cell membranes (Bhantana et al., 2021; Khan et al., 2023). However, heavy metal contamination can precipitate phosphorus as insoluble compounds, making it inaccessible to plants. AMF bioinoculants improve phosphorus solubilization and uptake by secreting organic acids and enzymes that mobilize phosphorus from soil particles, making it available for plant absorption.

In metal-contaminated soils, AMF bioinoculants also improve plant resilience by reducing the bioavailability of toxic metals. This is achieved through the production of compounds such as glomalin, a glycoprotein that binds heavy metals and enhances soil aggregation. The improved soil structure facilitates better water retention and aeration, which are essential for maintaining healthy root systems in contaminated soils (Khatoon et al., 2024). Furthermore, AMF bioinoculants promote the establishment of beneficial microbial communities in the rhizosphere, including nitrogen-fixing bacteria and phosphate-solubilizing bacteria, further improving soil fertility and plant growth.

AMF bioinoculants are especially valuable in organic and sustainable farming systems, where the use of synthetic fertilizers and pesticides is limited. By enhancing the natural nutrient cycling capacity of soils and promoting plant-microbe symbiosis, AMF bioinoculants help farmers achieve higher yields while reducing their reliance on chemical inputs. This approach not only supports sustainable crop production but also helps restore soil health in degraded or contaminated lands.

Challenges and Future Directions

Despite the promising potential of AMF in phytoremediation and sustainable agriculture, several challenges remain that must be addressed to optimize their application. One of the main challenges is the species-specific response of AMF and their host plants to heavy metal contamination. Different species of AMF vary in their ability to tolerate and accumulate heavy metals, and their efficacy in improving plant growth and resilience can depend on the specific plant-AMF association. For example, *Glomus intraradices* may be more effective in sequestering cadmium, while *Rhizophagus irregularis* may excel in promoting nutrient uptake in zinc-contaminated soils. Therefore, selecting the right AMF

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species or strain for a particular contaminated site or crop is crucial for achieving optimal results.

Environmental factors also play a significant role in determining the success of AMF-based phytoremediation and bioinoculant applications. Soil pH, moisture content, temperature, and the presence of other soil microorganisms can all influence the colonization efficiency of AMF and their ability to alleviate heavy metal stress. In highly acidic or alkaline soils, for instance, the availability of essential nutrients may be further limited, reducing the effectiveness of AMF in promoting plant growth. Moreover, extreme soil conditions may hinder the survival and activity of AMF, making it difficult to establish a functional symbiotic relationship with the host plant.

Another challenge lies in the large-scale production and commercialization of AMF bioinoculants. Unlike some bacteria or fungi that can be easily cultured in liquid media, AMF are obligate symbionts, meaning they require a host plant for their growth and reproduction. This makes it more difficult to mass-produce AMF bioinoculants compared to other microbial products. Advances in in-vitro culture techniques and the development of carrier-based formulations are needed to overcome these limitations and ensure that AMF bioinoculants can be produced, stored, and applied effectively on a large scale.

Future research should focus on exploring the molecular and genetic mechanisms underlying AMF-mediated heavy metal tolerance and nutrient acquisition. By understanding the specific genes and signaling pathways involved in these processes, researchers can develop targeted strategies to enhance the efficacy of AMF in phytoremediation and agriculture. For example, genetic engineering approaches could be used to enhance the metal-binding capacity of AMF or to improve their ability to colonize plants under challenging environmental conditions.

Additionally, there is a need for more field-based studies to evaluate the long-term impacts of AMF bioinoculants on soil health, crop productivity, and ecosystem resilience. While many studies have demonstrated the benefits of AMF in controlled greenhouse environments, real-world applications may present additional challenges, such as variable environmental conditions and complex soil microbial communities. Long-term monitoring of AMF-treated fields can provide valuable insights into the sustainability and effectiveness of these bioinoculants in diverse agricultural systems.

Therefore, AMF have significant potential to contribute to phytoremediation efforts and sustainable agriculture practices by enhancing plant resilience to heavy metal stress and promoting nutrient cycling in contaminated or degraded soils. However, challenges such as species-specific responses, environmental factors, and production limitations must be addressed to fully realize the benefits of AMF in large-scale applications. With continued research and technological advancements, AMF-based solutions could play a pivotal role in promoting sustainable land management and improving food security in the face of global environmental challenges.

Table 3: Table: Applications of AMF in Phytoremediation for Different Heavy Metals

AMF Species	Host Plant	Heavy Metal	AMF Mechanism	Plant Response	Additional Benefits
Glomus intraradices	Zea mays (Maize)	Cadmium (Cd)	Sequesters Cd in vesicles and glomalin	Increased biomass, lower Cd accumulation	Improved phosphorus uptake
Rhizophagus irregularis	Triticum aestivum (Wheat)	Lead (Pb)	Immobilizes Pb through soil aggregation	Reduced Pb toxicity, improved root growth	Enhanced soil structure stability
Funneliformis mosseae	Helianthus annuus (Sunflower)	Zinc (Zn)	Chelates Zn with glomalin and organic acids	Enhanced Zn uptake, better nutrient absorption	Better drought resistance
Glomus clarum	Brassica juncea (Mustard)	Arsenic (As)	Reduces As bioavailability through soil pH alteration	Lower As translocation to shoots, better growth	Improved overall soil health
Glomus etunicatum	Glycine max (Soybean)	Nickel (Ni)	Enhances Ni uptake and sequesters in vacuoles	Higher Ni tolerance, increased nitrogen fixation	Higher seed yield
Scutellospora calospora	Vigna radiata (Mung Bean)	Copper (Cu)	Chelates Cu and enhances antioxidant defense	Reduced Cu stress, improved photosynthesis	Enhanced water retention

The table highlights the applications of specific AMF species in phytoremediation efforts for different heavy metals, paired with various host plants. Each AMF species demonstrates unique mechanisms for alleviating heavy metal toxicity. For example, *Glomus intraradices* sequesters cadmium in vesicles and glomalin in maize, resulting in increased biomass and reduced metal accumulation. Similarly, *Rhizophagus irregularis* immobilizes lead in wheat, improving root growth and reducing toxicity. *Funneliformis mosseae*, associated with sunflower, chelates zinc, enhancing nutrient absorption. The

*Corresponding Author: **Komal Riaz**

table emphasizes the diverse responses of plants to AMF colonization, such as improved phosphorus uptake, drought resistance, and soil health, which underscores the effectiveness of AMF in promoting sustainable agricultural practices in contaminated soils.

Conclusion

In conclusion, Arbuscular Mycorrhizal Fungi (AMF) play a pivotal role in mitigating heavy metal stress in plants by enhancing nutrient uptake, particularly phosphorus, activating antioxidant defense systems to reduce oxidative stress, and interacting synergistically with beneficial soil microorganisms such as Plant Growth-Promoting Rhizobacteria (PGPR) to modulate heavy metal bioavailability. These multifaceted mechanisms contribute to improved plant growth and resilience in contaminated soils, making AMF a critical tool in phytoremediation and sustainable agriculture. Future research should focus on exploring the molecular and genetic mechanisms underlying AMF-plant-soil microbiome interactions to optimize their use in diverse environments. Integrating AMF into agricultural practices offers tremendous potential for improving crop resilience to environmental stressors, reducing reliance on chemical inputs, and promoting long-term sustainability in food production systems.

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