Research & Reviews in Biotechnology & Biosciences **ISSN No: 2321-8681**
Website: www.biotechjournal.in **Research Paper**
Volume: 12, Issue: 2, Year: 2025 **PP: 1-24**
DOI: https://doi.org/10.5281/zenodo.16681038 **Peer Reviewed Refereed Journal**

ADVANCES IN UNDERSTANDING THE ROLE OF MYCORRHIZAL FUNGI IN PLANT NUTRITION AND STRESS TOLERANCE

Aditya Sheershwal[1], Vani Sharma[2]

[1,2,] Faculty of Science, Motherhood University, Roorkee 247661-India

Article History

Received: 23/07/2025

Accepted: 01/08/2025

Article ID: RRBB/01_2025

Corresponding Author:

E-Mail: asheershwal@gmail.com, vanisharma1988@gmail.com

ABSTRACT

Mycorrhizal fungi play a pivotal role in plant nutrition and stress tolerance, forming intricate mutualistic relationships with approximately 80% of terrestrial plant species. Recent advances in molecular and imaging techniques have shed new light on the dynamic role of these fungi in facilitating nutrient acquisition, particularly for immobile elements like phosphorus and micronutrients. Transcriptomic analyses have revealed the upregulation of specific phosphate transporter genes in plants colonized by arbuscular mycorrhizal fungi (AMF), while isotopic labelling studies have quantified the bidirectional transfer of nutrients and carbon in mycorrhizal systems. Beyond their role in nutrition, mycorrhizal fungi have been empirically shown to enhance plant tolerance to various abiotic stresses, including drought, salinity, and metal toxicity, by employing physiological mechanisms that enhance water absorption, facilitate osmotic adjustment, and regulate antioxidant systems. The production of glomalin by AMF also contributes to soil aggregate formation and long-term carbon storage, improving soil health and fertility. The incorporation of mycorrhizal fungi into agricultural production systems presents a viable alternative to chemical-intensive practices, as meta-analyses have demonstrated their ability to enhance nutrient use efficiency, reduce dependency on synthetic fertilizers, and increase yield across diverse cropping systems. This review provides a critical analysis of the multifaceted contributions of mycorrhizal fungi to plant nutrient dynamics, drawing on recent empirical evidence and contextualizing these insights within the broader framework of current environmental and agronomic challenges. The review aims to underscore the pivotal role of mycorrhizal fungi as integral components of the plant-soil interface and their potential to promote sustainable agricultural practices.

Keywords: Mycorrhizal Fungi, Nutrient Acquisition, Plant Nutrition, Arbuscular Mycorrhizal Fungi, Soil Fertility, Sustainable Agriculture

1. INTRODUCTION

Efficient acquisition and utilization of nutrients are essential for plant growth, physiological performance, and yield potential. Key macronutrients, such as nitrogen, phosphorus, and potassium, as well as critical micronutrients like zinc, iron, and manganese, are fundamental for enzyme activity, photosynthesis, and overall metabolic functioning (Hawkesford et al., 2011). However, the bioavailability of numerous essential nutrients in natural and agricultural soils is often restricted due to their sequestration in non-bioavailable forms, limited solubility, or competition with other ions. For instance, phosphorus frequently forms insoluble complexes with calcium, iron, or aluminum in soils, thereby diminishing its accessibility to plants despite its abundant presence in the environment (Prasad & Shivay, 2021).

To address these limitations, plants have established intricate mutualistic relationships with a diverse array of soil microorganisms. Among these, mycorrhizal fungi constitute one of the most ecologically and evolutionarily successful mutualistic associations. Arbuscular mycorrhizal fungi (AMF), belonging to the phylum *Glomeromycota*, form associations with approximately 80% of terrestrial plant species, including most agriculturally important crops (Aryal & Xu, 2001). Mycorrhizal fungi permeate the rhizosphere and invasively colonize the root cortical cells, whereupon they develop specialized structures known as arbuscules that facilitate nutrient exchange. In return for photosynthetically derived carbon from the host, mycorrhizal hyphae permeate the surrounding soil, greatly enhancing the absorptive surface area accessible for nutrient uptake, particularly for immobile elements like phosphorus and micronutrients (Garg et al., 2006).

Recent advances in molecular and imaging techniques have shed new light on the dynamic role of mycorrhizal fungi in plant nutrition. For example, transcriptomic analyses have revealed the upregulation of specific phosphate transporter genes in plants colonized by AMF, indicating a direct genetic and physiological response to symbiosis (Facelli et al., 2009). Isotopic labeling studies have also confirmed the bidirectional transfer of nutrients and carbon in mycorrhizal systems, quantifying the extent to which these fungi can mobilize soil-bound P and Zn and deliver them to host plants under both field and controlled conditions (Shi et al., 2023).

Beyond their role in facilitating nutrient acquisition, mycorrhizal fungi have been empirically shown to serve a pivotal role in enhancing plant health and resilience. Extensive research has substantiated their capacity to improve plant tolerance to various abiotic stresses, including drought, salinity, and metal toxicity (Kumar et al., 2014; Lanfranco et al., 2016). By employing physiological mechanisms that enhance water absorption, facilitate osmotic adjustment, and regulate antioxidant systems, arbuscular mycorrhizal fungi can mitigate the deleterious effects of stress and maintain plant productivity under suboptimal growing environments (Malhi et al., 2020; Mitra et al., 2021). Furthermore, the production and release of glomalin, a glycoprotein synthesized by arbuscular mycorrhizal fungi, enhances soil aggregate formation and promotes long-term carbon storage, thereby improving soil health and fertility in a sustained manner (Nautiyal et al., 2019).

The incorporation of mycorrhizal fungi into agricultural production systems presents a viable alternative to chemical-intensive practices, as global agriculture strives to achieve greater sustainability and reduced environmental impact. Notably, several recent meta-analyses have demonstrated that AMF inoculation can significantly enhance nutrient use efficiency, reduce dependency on synthetic fertilizers, and increase yield across diverse cropping systems and agroecological zones (Schaefer et al., 2021; Sun & Shahrajabian, 2023). These findings align with the principles of regenerative agriculture and agroecology, where fostering beneficial soil-plant-microbe interactions is central to achieving productivity, resilience, and ecological balance (Jayasinghe et al., 2023).

This review provides a critical analysis of the multifaceted contributions of mycorrhizal fungi to plant nutrient dynamics, drawing on recent empirical evidence from diverse research settings. Particular emphasis is placed on elucidating the physiological mechanisms underlying nutrient acquisition, symbiotic signaling, and the potential of mycorrhizal technologies to promote sustainable agricultural practices (Wahab et al., 2024). By contextualizing these insights within the broader framework of current environmental and agronomic challenges, the review aims to underscore the pivotal role of mycorrhizal fungi as integral components of the plant-soil interface (Chaudhary et al., 2025).

2. TYPES OF MYCORRHIZAL ASSOCIATIONS

Mycorrhizal fungi are broadly categorized based on their morphological features and the nature of their association with plant roots. These symbiotic relationships, though universally centered around nutrient exchange, differ significantly in terms of host range, structural adaptations, and ecological distribution. The four principal types are arbuscular mycorrhizae, ectomycorrhizae, ericoid mycorrhizae, and orchid mycorrhizae (Powell & Rillig, 2018) .

Arbuscular mycorrhizal fungi (AMF), belonging to the phylum *Glomeromycota*, represent the most widespread and ancient form of mycorrhizal association. They colonize the root cortex of a vast majority of terrestrial plants, particularly herbaceous crops, cereals, and legumes. Within the root tissue, AMF develop extensively branched structures within the host plant's root cortical cells, known as arbuscules, which serve as the principal sites for the exchange of nutrients between the fungus and the plant. In some cases, vesicles are also formed, serving as storage organs (Willis et al., 2013). The extraradical mycelium of AMF significantly increases the overall absorptive capacity of the root system, thereby enhancing the uptake of immobile nutrients, especially phosphorus, and various micronutrients from the surrounding soil matrix . Despite their ubiquity, AMF exhibit relatively low host specificity, allowing them to form functional associations with a broad spectrum of plant species across diverse ecosystems (Alrajhi et al., 2024).

Ectomycorrhizal fungi (EMF), in contrast, are predominantly associated with woody plants such as conifers, oaks, and eucalypts. Unlike AMF, EMF do not penetrate root cortical cells. Instead, they form a dense hyphal sheath, or mantle, around the root tip, from which hyphae extend into the surrounding soil and between cortical cells to form a structure known as the Hartig net. This interface enables the transfer of nutrients without breaching cell membranes, a key difference from the intracellular arbuscules of AMF (Cahanovitc et al., 2022). Ectomycorrhizal associations are typically more specialized, with certain fungal taxa forming partnerships with specific host genera or families. These fungi play a critical role in nutrient cycling within forest ecosystems, particularly in facilitating the acquisition of nitrogen and organic-bound phosphorus under nutrient-limited conditions (Van Der Heijden et al., 2015).

Ericoid mycorrhizae, primarily found in members of the Ericaceae family such as heathers and blueberries, are adapted to highly acidic and nutrient-poor soils (Smith & Read, 2008). The fungal partners in this association, typically ascomycetes, form loose coils within the epidermal cells of fine hair roots. Unlike AMF and EMF, ericoid mycorrhizal fungi possess saprotrophic capabilities, allowing them to decompose complex organic matter and liberate nutrients otherwise inaccessible to the host plant (Mitchell & Gibson, 2006; Wei et al., 2022). This functional trait is particularly important in environments where mineral nutrients are tightly bound in organic forms.

Orchid mycorrhizae are a distinct and highly specialized type of association observed exclusively in *Orchidaceae*. Orchids rely on these fungi, often from the *Rhizoctonia* complex, for seed germination and early seedling development, as orchid seeds lack sufficient nutrient reserves for autonomous growth. The fungal hyphae invade the cells of the developing protocorms and form pelotons, coiled hyphal structures that are periodically digested by the host to derive nutrients (Van Der Heijden et al., 2015) . While many orchids transition to photosynthesis as they mature, some remain fully or partially mycoheterotrophic throughout their life cycle, relying entirely on fungal partners for carbon and nutrients (Hossain, 2022).

Comparative studies of these mycorrhizal types reveal distinct structural and functional adaptations that reflect the evolutionary trajectories and ecological niches of their host plants. These distinctions are summarized in Table 1, which outlines key features of the major mycorrhizal associations relevant to both natural and agricultural systems. While AMF and EMF dominate agronomic and forest ecosystems respectively, ericoid and orchid mycorrhizae illustrate the specialization required for survival in nutrient-deficient or physiologically extreme habitats. Understanding the diversity of these associations is crucial for harnessing their potential in ecological restoration, conservation biology, and sustainable agriculture (Verbruggen & Toby Kiers, 2010).

Table 1. Comparison of Major Types of Mycorrhizal Associations

Type of Mycorrhiza	Fungal Taxa	Host Range	Structure	Nutrient Uptake	Ecological Role	Reference
Arbuscular Mycorrhiza (AMF)	Glomeromycota (*Rhizophagus*, *Funneliformis*)	Broad (80% of vascular plants, mainly herbaceous)	Arbuscules, vesicles, extra-radical hyphae	Enhanced P, Zn, Cu uptake; drought tolerance	Common in croplands; essential for nutrient efficiency	(Lewis, 2016)
Ectomycorrhiza (ECM)	Basidiomycota, Ascomycota (*Laccaria*, *Pisolithus*)	Woody trees (e.g., pine, oak)	Mantle, Hartig net	N, P, organic nutrient uptake	Dominant in forest ecosystems	(Lehmann et al., 2016)
Ericoid Mycorrhiza	Ascomycota (*Hymenoscyphus*)	Ericaceae (e.g., blueberry)	Hyphal coils in root epidermis	Organic N, P from acidic soils	Found in heathlands and peatlands	(Ward et al., 2022)
Orchid Mycorrhiza	Basidiomycota (*Tulasnella*)	Orchidaceae	Intracellular pelotons	Carbon for germination	Critical for orchid establishment	(Hossain, 2022)

3. MECHANISMS OF NUTRIENT UPTAKE

Mycorrhizal fungi significantly enhance plant nutrient uptake through a variety of direct and indirect mechanisms that extend beyond the physical root-soil interface. By establishing an expansive hyphal network within the rhizosphere, these fungi access nutrient pools otherwise unavailable to plant roots alone (Wahab et al., 2023). This network acts not only as an extension of the root system but also as a dynamic biochemical interface that modifies the soil environment, solubilizes nutrients, and facilitates their translocation to the host plant (Saeed et al., 2021).

The enhancement of phosphorus (P) uptake remains the most widely recognized benefit of mycorrhizal symbiosis, particularly in the case of AMF. Phosphorus is a relatively immobile nutrient in soils due to its tendency to form insoluble complexes with calcium, iron, and aluminum. The extraradical hyphae of AMF scavenge phosphorus from beyond the root depletion zone and transport it to the plant via specialized phosphate transporters induced during colonization (Miyasaka & Habte, 2001). Molecular studies have identified the upregulation of *PT4* and *PT11* transporters in AMF-colonized plants, underscoring the integration of fungal and plant nutrient pathways(Banasiak et al., 2021; Chiu & Paszkowski, 2019) . Moreover, recent isotopic tracing experiments have quantified the proportion of phosphorus acquired via the mycorrhizal pathway, often exceeding 60% of total plant P uptake under low-P conditions (Watts-Williams, 2022).

Beyond phosphorus, AMF also enhance the acquisition of essential micronutrients such as zinc (Zn), copper (Cu), and manganese (Mn), which are critical cofactors in enzymatic processes and redox reactions. These elements, though required in trace amounts, often exist in unavailable forms under alkaline or heavily weathered soil conditions. The acidification of the rhizosphere by AMF hyphae, coupled with the secretion of low-molecular-weight organic acids and siderophores, plays a central role in mobilizing these micronutrients (Mishra et al., 2023). Empirical studies have shown substantial enhancements in Zn and Cu concentrations in the tissues of mycorrhizal plants, especially in calcareous and degraded soils (Lehmann et al., 2014).

The contribution of mycorrhizal fungi to nitrogen (N) acquisition is more complex and often context-dependent. While AMF do not possess nitrogen-fixing capabilities, they enhance nitrogen uptake by accessing organic and inorganic N forms from microenvironments beyond the root's immediate influence. In legume systems, a synergistic interaction is often observed between AMF and rhizobia, whereby the mycorrhizal symbiosis supports more efficient biological nitrogen fixation by improving phosphorus nutrition, which is essential for the energetically demanding process of nitrogenase activity (Reynolds et al., 2005). Several studies have also reported the involvement of ectomycorrhizal fungi in the direct uptake and mineralization of organic nitrogen compounds in forest soils, further highlighting the diversity of nitrogen acquisition strategies across mycorrhizal types (Zhang et al., 2023).

In addition to nutrient uptake, mycorrhizal fungi play a pivotal role in enhancing plant water relations, thereby indirectly supporting nutrient transport and overall plant vigor under drought conditions. The extensive hyphal network functions as a hydraulic bridge, facilitating water uptake from micropores in the soil matrix that are otherwise inaccessible to roots (Aragon et al., 2025). Furthermore, AMF colonization has been associated with increased root hydraulic conductivity, enhanced accumulation of osmoprotectants, and modulation of aquaporin expression—mechanisms that collectively improve plant drought tolerance. These adaptations collectively contribute to improved

Research & Reviews in Biotechnology & Biosciences **ISSN No: 2321-8681**
Website: www.biotechjournal.in **Research Paper**
Volume: 12, Issue: 2, Year: 2025 **PP: 1-24**
DOI: https://doi.org/10.5281/zenodo.16681038 **Peer Reviewed Refereed Journal**

drought resilience and nutrient transport efficiency under water-limited conditions, as illustrated in Figure 1. These physiological benefits are particularly valuable in arid and semi-arid agricultural systems where water availability is a primary constraint to productivity (Cheng et al., 2021).

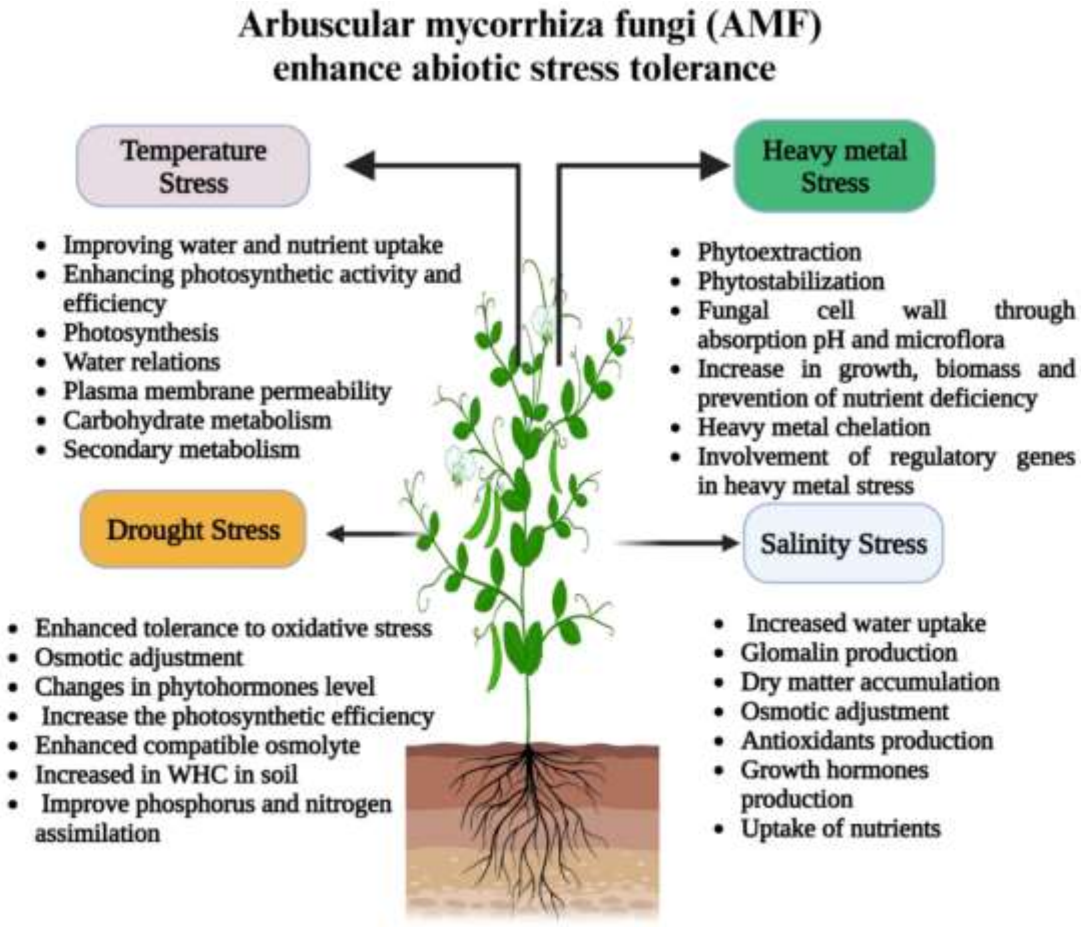

Figure 1: Schematic overview of how arbuscular mycorrhizal fungi (AMF) improve plant resistance to abiotic stress.

Collectively, these mechanisms underscorethe pivotal function of mycorrhizal fungi in facilitating plant-soil nutrient interactions. Their ability to improve the acquisition of both macro- and micronutrients, along with their indirect influence on nitrogen fixation and water stress mitigation, makes them indispensable partners in nutrient-efficient and climate-resilient agricultural systems (Tang et al., 2022). A comparative overview of these nutrient acquisition pathways is presented in Table 2, summarizing the direct and indirect mechanisms through which mycorrhizal fungi enhance plant nutrition.

Table 2. Mycorrhizal Contributions to Plant Nutrient and Water Uptake

Nutrient/Element	Mycorrhizal Role	Mechanism of Uptake	Notable Findings	Reference
Phosphorus (P)	Primary uptake via AMF	Hyphal transport	Up to 80% of P from AMF in low-P soils	(Etesami et al., 2021)
Nitrogen (N)	Indirect enhancement with N-fixing bacteria	AMF-assisted organic N mineralization	Improved N assimilation in cereals and legumes	(Soumaré et al., 2020)
Zinc (Zn)	Increased root and shoot Zn	Chelation and transport by fungal hyphae	Higher Zn uptake in wheat and maize	(Saboor et al., 2021)
Copper (Cu)	Enhanced bioavailability in low-Cu soils	Absorption via hyphal surfaces	Elevated Cu uptake in citrus, vineyards	(Betancur-Agudelo et al., 2023)
Manganese (Mn)	Facilitated absorption in deficient soils	Improved root-soil interface	Mn uptake enhanced in legumes	(Khoshru et al., 2023)
Water	Improved drought resistance	Hyphal penetration into micropores	Greater water use efficiency under stress	(Tang et al., 2022)

4. INFLUENCE ON PLANT GROWTH AND YIELD

The contribution of mycorrhizal fungi to plant growth extends far beyond nutrient acquisition, manifesting in tangible improvements in biomass accumulation, physiological performance, and crop productivity (Begum et al., 2019). Numerous researches have provided substantial evidence for the positive effects of mycorrhizal colonization on plant growth metrics across a diverse array of agricultural and horticultural species. These effects are particularly pronounced under suboptimal nutrient conditions, where mycorrhizal associations compensate for limited resource availability and reduce the dependency on external inputs (Bortolot et al., 2024).

Controlled experiments and field trials have consistently demonstrated that mycorrhizal inoculation leads to significant increases in shoot and root biomass, leaf area, and total chlorophyll content (Jabborova et al., 2021). For instance, in phosphorus-deficient soils, inoculated maize (*Zea mays*) plants have shown biomass increases ranging from 20% to 80%, depending on fungal species, soil type, and climatic conditions. Similarly, in wheat (*Triticum aestivum*), AMF colonization has been linked to enhanced tillering, spike formation, and grain yield, even in high-input systems (Bouzeriba et al., 2021). In legume crops such as soybean (*Glycine max*) and chickpea (*Cicer arietinum*), dual inoculation with AMF and rhizobia has been found to significantly improve both nodulation and nitrogen fixation, translating into increased pod number, seed weight, and overall yield (Meng et al., 2015).

The synergistic association between mycorrhizal fungi and other beneficial soil microbes further amplifies their growth-promoting effects. In particular, co-inoculation with plant growth-promoting rhizobacteria (PGPR) has shown promise in enhancing nutrient use efficiency and stimulating phytohormone production (Ramasamy et al., 2011). Certain PGPR strains, such as *Pseudomonas fluorescens* and *Bacillus subtilis*, produce indole-3-acetic acid (IAA), siderophores, and enzymes that modulate root. architecture, thereby improving the root's capacity to engage in mycorrhizal colonization. Figure 2 illustrates a diagrammatic representation of the various mycorrhizal functions in regulating ecosystem processes and promoting plant growth, especially under abiotic stress conditions. Studies have shown that combined AMF–PGPR inoculation in crops like tomato and cucumber can result in a synergistic increase in nutrient uptake, antioxidant enzyme activity, and resistance to pathogens and abiotic stress (Khoso et al., 2024).

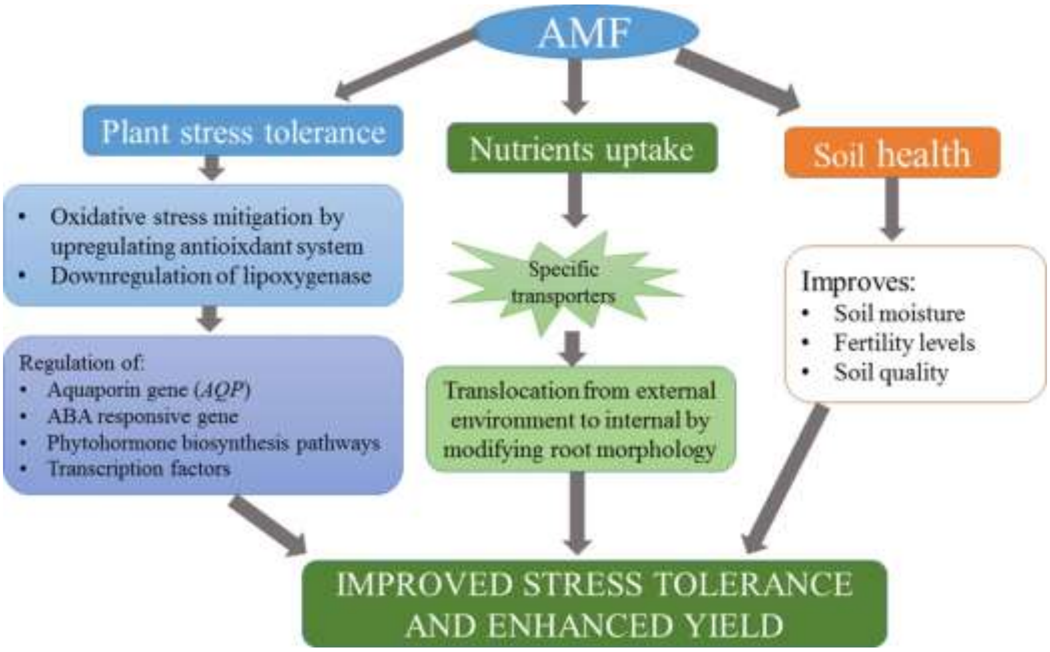

Figure 2: **A diagrammatic illustration of multifaceted roles of mycorrhizal fungi in regulating diverse processes in the ecosystem and plant growth promotion under abiotic stress**

Recent field-level meta-analyses have further confirmed the yield-enhancing potential of AMF under diverse agroecological conditions. A global synthesis of over 100 peer-reviewed studies reported an average increase of 23% in crop yield due to AMF inoculation, with the greatest responses observed in legumes and cereals cultivated in nutrient-poor or drought-prone soils (Wu et al., 2022). Moreover, the benefits of mycorrhizal associations are increasingly being recognized in conservation agriculture and organic farming systems, where reliance on biological inputs is paramount. In long-term cropping trials, continuous AMF presence has been correlated with cumulative gains in soil organic matter, microbial biomass, and yield stability across seasons (Kozjek et al., 2021).

In maize-based intercropping systems, AMF have been shown to facilitate resource partitioning and improve nitrogen and phosphorus uptake efficiency, especially when combined with low levels of organic or mineral fertilizers (Xue et al., 2024). Similar findings have been observed in rice-wheat rotation systems, where AMF colonization of residual roots during the off-season supports early establishment and nutrient uptake in the succeeding crop (Kuila & Ghosh, 2022).

Collectively, these findings highlight the capacity of mycorrhizal fungi not only to enhance plant nutrient status but also to translate these improvements into measurable gains in growth and yield. Their interactions with other soil microbiota further reinforce their ecological importance and underscore the value of integrating mycorrhizal technologies into holistic crop management strategies (Khaliq et al., 2022). Table 3 summarizes representative studies documenting the effects of mycorrhizal inoculation on growth and yield parameters in major crops, illustrating both the magnitude and variability of responses under different environmental and management conditions.

Table 3. Impact of Mycorrhizal Inoculation on Agronomic Performance and Yield Components in Crops

Crop	Observed Benefits	Study Highlights	Reference
Wheat	Increased grain yield and nutrient efficiency	Yield gains under water stress with AMF	(Abdelaal et al., 2024)
Maize	Better root development and P uptake	20–25% yield increase in field trials	(Koech et al., 2024)
Soybean	Improved nodulation and protein content	Synergism with rhizobia enhances N2 fixation	(Meng et al., 2015)
Tomato	Improved fruit quality and lycopene levels	Enhanced antioxidant profile with AMF	(Ganugi et al., 2023)
Rice	Higher tillering and water-use efficiency	Reduced lodging and drought impact	(Chareesri et al., 2020)

5. SOIL HEALTH AND ECOSYSTEM BENEFITS

Beyond their role in plant nutrition, mycorrhizal fungi contribute significantly to the maintenance and enhancement of soil health and ecosystem stability. Their presence and activity influence the physical, chemical, and biological properties of soil, thereby supporting agroecosystem resilience and sustainability. As concerns about soil degradation, nutrient runoff, and declining biodiversity intensify, the ecological functions of mycorrhizal fungi have gained renewed scientific and agronomic interest (Fall et al., 2022).

One of the most distinctive contributions of arbuscular mycorrhizal fungi (AMF) to soil structure is through the production of glomalin-related soil proteins (GRSPs). Glomalin is a hydrophobic glycoprotein secreted by AMF hyphae that acts as a binding agent, stabilizing soil aggregates and improving porosity and water retention (Yang et al., 2024). Research has shown that glomalin content is positively correlated with soil aggregate stability, organic carbon levels, and reduced erosion potential. For instance, in long-term cropping systems, AMF-colonized soils exhibited 30–40% greater aggregate stability and 20% higher water infiltration rates compared to non-mycorrhizal controls (Nautiyal et al., 2019).

In addition to physical improvements, mycorrhizal fungi shape the soil microbial community structure by influencing rhizosphere interactions and resource availability. The hyphosphere—a niche surrounding mycorrhizal hyphae—serves as a hotspot of microbial activity and diversity. AMF interactions with free-living nitrogen-fixers, phosphate-solubilizing bacteria, and other beneficial microorganisms have been documented to enhance nutrient cycling and suppress soil-borne pathogens (Vieira et al., 2025). Metagenomic analyses have revealed that AMF colonization alters the expression of microbial genes involved in nitrogen metabolism, organic matter decomposition, and plant hormone synthesis, suggesting a broader ecosystem engineering role. Such microbial shifts are especially beneficial in degraded or marginal soils, where microbial diversity is typically low and nutrient turnover is inefficient (Samantaray et al., 2024).

The cumulative impact of mycorrhizal fungi on soil health has profound implications for reducing dependence on chemical fertilizers. Excessive fertilizer use not only disrupts native microbial communities but also contributes to nutrient leaching, greenhouse gas emissions, and water eutrophication. Mycorrhizal symbioses offer a biologically mediated nutrient delivery system that enhances plant access to existing soil reserves and reduces the need for exogenous inputs (Sosa-Hernández et al., 2019). Numerous studies have demonstrated that crops inoculated with AMF can achieve comparable or superior yields with significantly lower phosphorus and nitrogen application rates. In wheat and maize, for example, AMF inoculation allowed for a 30–50% reduction in phosphorus fertilizer use without compromising yield or grain quality (Beslemes et al., 2023).

Moreover, the long-term integration of mycorrhizal inoculants into cropping systems contributes to carbon sequestration and climate regulation. Glomalin production, combined with increased root biomass and microbial turnover, enhances soil carbon inputs and stabilization. Field studies across multiple agroclimatic zones have shown that AMF-rich soils exhibit higher microbial biomass carbon and reduced CO_2 fluxes, especially under conservation tillage and organic farming practices (Pelosi et al., 2024).

In sum, mycorrhizal fungi serve as keystone organisms in the soil ecosystem, providing multifunctional benefits that align with the goals of ecological intensification and regenerative agriculture. Their ability to enhance soil structure, foster beneficial microbial consortia, and reduce agrochemical dependency positions them as essential components in building resilient and sustainable agroecosystems (Kalamulla et al., 2022). A synthesized overview of these ecological contributions is presented in Table 4, highlighting key soil functions supported by mycorrhizal activity alongside relevant empirical evidence.

Table 4. Ecosystem Functions of Mycorrhizal Fungi

Function	Mechanism	Ecological Benefit	Reference
Glomalin production	Secreted glycoproteins from AMF hyphae	Promotes soil aggregation and C sequestration	(Zhou et al., 2023)
Microbial diversity	Modulates rhizosphere via exudates	Suppresses pathogens; supports beneficial taxa	(Pantigoso et al., 2022)
Nutrient cycling	Enhances mineralization and nutrient fluxes	Improves soil fertility, reduces nutrient loss	(Gou et al., 2022)
Fertilizer reduction	Increases nutrient-use efficiency	Lowers reliance on synthetic inputs	(Wahab et al., 2023)

6. APPLICATIONS IN SUSTAINABLE AGRICULTURE

The integration of mycorrhizal fungi into sustainable agriculture practices has emerged as a promising strategy to reconcile productivity with environmental stewardship. Their capacity to enhance nutrient uptake, promote soil health, and improve crop resilience positions them as powerful allies in the transition away from high-input conventional systems. In this context, mycorrhizal fungi are increasingly employed in the development of biofertilizers, used in organic farming, and incorporated into broader agroecological frameworks (Herath et al., 2024).

6.1. Use in Biofertilizers and Organic Farming

Mycorrhizal biofertilizers, composed of viable fungal propagules—spores, hyphal fragments, and colonized root pieces—are now widely used to augment soil fertility in both certified organic and low-input conventional systems. These bio-inoculants serve as a sustainable alternative to synthetic fertilizers, promoting nutrient availability while reducing environmental externalities (Berruti et al., 2016). Numerous field studies have shown that AMF inoculation significantly improves nutrient-use efficiency and crop yield under organic farming conditions, where synthetic inputs are restricted. In organic tomato and carrot production systems, AMF application has led to enhanced root development, increased phosphorus uptake, and greater marketable yields, even under reduced fertility regimes (Keller-Pearson et al., 2020).

Recent meta-analyses support these findings. A global review reported that AMF-based inoculation under organic systems increased plant biomass by an average of 28%, with concurrent improvements in phosphorus use efficiency and plant nutrient status (Burak et al., 2024). The ability of mycorrhizae to stabilize yields in organically managed soils is especially valuable under conditions of environmental stress, where nutrient delivery from mineralization processes may be asynchronous with plant demand (Khan et al., 2024).

6.2. Commercial Inoculants – Current Products and Challenges

A growing number of commercial mycorrhizal inoculants are now available in global markets, targeted at a wide range of crops and soil types. These products vary widely in formulation—ranging from granular and liquid suspensions to seed coatings and root dips—and are produced by both small-scale biotechnological firms and major agro-input corporations. Key genera commonly used in these products include *Rhizophagus*, *Funneliformis*, and *Claroideoglomus* for AMF, and *Pisolithus* and *Laccaria* for ectomycorrhizal applications (Basiru et al., 2020).

However, challenges remain in ensuring the efficacy, consistency, and scalability of commercial inoculants. Field performance is often influenced by multiple factors, including soil physicochemical conditions, native microbial communities, crop genotype, and farming practices. Moreover, the establishment of introduced mycorrhizal strains can be inhibited by competition with indigenous fungi or disrupted by fungicide residues in the soil (Ghorui et al., 2025). Recent studies emphasize the importance of site-specific strain selection and the use of multi-species consortia to improve inoculant adaptability and ecological function.

To address regulatory and quality control concerns, several international agencies have called for standardized protocols for inoculant testing, viability assessment, and labeling accuracy. Advances in microbial encapsulation technology and shelf-life stabilization are also being explored to enhance product effectiveness and farmer adoption (Berninger et al., 2018).

6.3. Integration into Agroecological Practices and Crop Rotation

Mycorrhizal fungi are well-suited for incorporation into agroecological farming models, where biodiversity, ecosystem services, and soil health are central tenets. In such systems, AMF can be integrated with conservation tillage, cover cropping, intercropping, and diversified crop rotations to sustain their populations and maximize ecological function. For instance, studies have shown that cover crops such as clover and vetch maintain AMF propagule density during fallow periods, thereby supporting early colonization and nutrient uptake in subsequent cash crops (Trinchera et al., 2021).

Rotational designs that include mycotrophic crops—such as maize, sorghum, and legumes—can enhance the continuity of the mycorrhizal network, improving both crop performance and soil biological activity over time (Bakhshandeh et al., 2017). In contrast, continuous monoculture or the frequent cultivation of non-mycorrhizal crops like brassicas has been shown to reduce AMF abundance and diversity, underscoring the importance of strategic crop sequencing (Jansa et al., 2006).

Moreover, the integration of AMF with other biological inputs such as composts, vermicast, and microbial consortia is being explored as part of regenerative soil management frameworks. These combinations have demonstrated synergistic effects on nutrient cycling, disease suppression, and soil carbon stabilization under both tropical and temperate farming conditions (Cavagnaro, 2014).

In conclusion, the application of mycorrhizal fungi in sustainable agriculture represents a viable path toward reduced chemical dependency, improved soil fertility, and resilient crop production. However, realizing their full potential requires a systems-level approach that incorporates ecological principles, localized knowledge, and innovations in microbial technology (Helena Devi et al., 2021).

7. CHALLENGES AND RESEARCH GAPS

Despite the well-documented benefits of mycorrhizal fungi in agriculture and ecology, several challenges continue to hinder their widespread and effective utilization, particularly in field-scale applications. Among the most significant limitations is the inherent variability in plant response to mycorrhizal colonization, which can be influenced by host specificity, fungal strain compatibility, and environmental conditions. Not all plant species exhibit the same degree of responsiveness to mycorrhizal inoculation, and even within a single crop, genotypic differences can result in variable symbiotic efficiency and nutrient acquisition outcomes (Owiny & Dusengemungu, 2024).

Host specificity remains a critical determinant of the success of mycorrhizal associations. Some fungal strains exhibit a narrow host range and may form effective symbioses only with select plant species or cultivars (d'Entremont & Kivlin, 2023). This specificity complicates the development of broad-spectrum inoculants and necessitates a more tailored approach to inoculum selection. Recent studies using high-throughput sequencing and isotopic tracing have shown that differential colonization patterns can significantly affect nutrient flow dynamics and yield outcomes in crops such as maize, soybean, and rice. Moreover, indigenous soil fungi often compete with or outcompete introduced strains, affecting the establishment and persistence of commercial inoculants (Kaminsky et al., 2019).

Environmental and edaphic factors also play a critical role in modulating mycorrhizal colonization and function. Soil pH, temperature, moisture, and organic matter content all influence the density and activity of both fungal propagules and host roots. Acidic or alkaline soils may inhibit spore germination or root penetration, while extreme temperatures can suppress hyphal extension and nutrient exchange efficiency (Jansa et al., 2009). Additionally, tillage practices, pesticide use, and synthetic fertilizer application can disrupt mycorrhizal networks or inhibit their formation altogether, undermining the potential benefits of inoculation (Barber et al., 2013).

Another challenge lies in the scalability and consistency of field-level applications. While promising results are often reported under controlled greenhouse conditions, translating these benefits to heterogeneous field environments has proven more complex (Guan et al., 2023). Factors such as inconsistent inoculum quality, suboptimal application techniques, and lack of farmer awareness contribute to the variable success of mycorrhizal technologies in real-world contexts. The interaction of mycorrhizal fungi with other components of the soil microbiome adds another layer of complexity, as these relationships are dynamic and context-dependent (Madawala, 2021).

Furthermore, a considerable gap persists in the availability of region-specific and crop-specific studies. Much of the existing research has been concentrated in temperate regions, with a focus on a limited number of economically important crops (Kumar et al., 2022). There is a pressing need for more studies that evaluate native mycorrhizal biodiversity and functional potential in tropical, arid, and high-altitude ecosystems, where these symbioses may play an even more critical role in plant survival and productivity. Likewise, more research is needed to optimize inoculation protocols for underutilized and indigenous crops that form the backbone of smallholder and subsistence farming systems (Madouh & Quoreshi, 2023).

In summary, while the promise of mycorrhizal fungi in sustainable agriculture is substantial, addressing these multifaceted challenges requires a coordinated research agenda. Advances in molecular biology, microbial ecology, and precision agriculture offer new tools to better understand and manage mycorrhizal interactions, but their practical implementation must be grounded in site-specific realities and informed by local ecological knowledge (Martin & Van Der Heijden, 2024).

8. CONCLUSION AND FUTURE PERSPECTIVES

Mycorrhizal fungi represent a foundational component of terrestrial plant ecosystems and a pivotal tool in advancing sustainable agriculture. Their symbiotic association with plant roots not only facilitates enhanced uptake of essential nutrients—most notably phosphorus and micronutrients—but also contributes to improved plant health, increased yield stability, and reduced dependence on chemical fertilizers. In doing so, these fungi align with global goals to reduce environmental degradation, mitigate climate change, and ensure food security through more resilient and regenerative farming systems (Dhiman et al., 2022).

Beyond their agronomic benefits, mycorrhizal fungi also perform vital ecosystem services. Through the secretion of glomalin, they improve soil structure and water retention; through interactions with other microbial communities, they foster biodiversity and suppress soil-borne pathogens (Ghorui et al., 2024). Their role in enhancing nutrient cycling and carbon sequestration places them at the intersection of soil biology and climate resilience, underscoring their relevance in both scientific research and agricultural policy. Especially in the face of increasing climate variability, mycorrhizae offer a biological means to buffer crops against abiotic stresses such as drought, nutrient scarcity, and soil degradation (Raihan, 2023).

However, to fully harness the potential of mycorrhizal fungi, a comprehensive and interdisciplinary approach is essential. This includes advancing our understanding of fungal ecology, host specificity, and strain compatibility through modern molecular and ecological tools (Garg et al., 2025). Likewise, addressing challenges related to large-scale inoculant production, field consistency, and farmer adoption requires collaboration between microbiologists, agronomists, extension services, and policymakers. The integration of mycorrhizal technologies into national and international agricultural strategies—particularly those aimed at low-input and smallholder systems—should be prioritized to promote equitable access to sustainable innovations (Díaz-Rodríguez et al., 2025).

Future research must also be regionally contextualized, accounting for local soil types, climate conditions, cropping systems, and indigenous mycorrhizal diversity. Participatory approaches involving farmers, researchers, and community stakeholders will be key in tailoring interventions that are both scientifically robust and socioeconomically viable(Chave et al., 2019; Rillig et al., 2016). Furthermore, the development of regulatory frameworks and quality standards for mycorrhizal inoculants will play a crucial role in ensuring their efficacy and reliability in diverse agroecological contexts.(Salomon et al., 2022; Tiwari & Park, 2024)

In conclusion, the integration of mycorrhizal fungi into modern agricultural paradigms offers a scientifically grounded and ecologically sound strategy for enhancing crop productivity, safeguarding soil health, and fostering climate resilience. Their multifunctional benefits underscore the urgent need for sustained investment in research, education, and policy support to unlock their full potential in meeting the agricultural challenges of the twenty-first century (Ahmad et al., 2024).

REFERENCES

1. Abdelaal, K., Al–Askar, A. A., & Hafez, Y. (2024). Effect of arbuscular mycorrhizal fungi on physiological, bio-chemical and yield characters of wheat plants (Triticum aestivum L.) under drought stress conditions. BMC Plant Biology, 24(1). https://doi.org/10.1186/s12870-024-05824-9
2. Ahmad, Z., Niyazi, S., Firdoos, A., Wang, C., Manzoor, M. A., Ramakrishnan, M., Upadhyay, A., & Ding, Y. (2024). Enhancing plant resilience: Nanotech solutions for sustainable agriculture. *Heliyon*, *10*(23), e40735. https://doi.org/10.1016/j.heliyon.2024.e40735
3. Alrajhi, K., Bibi, S., & Abu-Dieyeh, M. (2024). Diversity, Distribution, and applications of arbuscular mycorrhizal fungi in the Arabian Peninsula. *Saudi Journal of Biological Sciences*, *31*(2), 103911. https://doi.org/10.1016/j.sjbs.2023.103911
4. Aragon, B. V., Cardinale, M., Rolli, E., Rustioni, L., & Francioli, D. (2025). The role of Arbuscular Mycorrhizal Fungi in abiotic stress management in viticulture under climatic shifts. *Plant Stress*, 100863. https://doi.org/10.1016/j.stress.2025.100863
5. Aryal, U. K., & Xu, H. (2001). Mycorrhizal Associations and Their Manipulation for Long-Term Agricultural Stability and Productivity. Journal of Crop Production, 3(1), 285. https://doi.org/10.1300/j144v03n01_24
6. Bakhshandeh, S., Corneo, P. E., Mariotte, P., Kertesz, M. A., & Dijkstra, F. A. (2017). Effect of crop rotation on mycorrhizal colonization and wheat yield under different fertilizer treatments. *Agriculture, Ecosystems & Environment*, *247*, 130–136. https://doi.org/10.1016/j.agee.2017.06.027
7. Banasiak, J., Jamruszka, T., Murray, J. D., & Jasiński, M. (2021). A roadmap of

plant membrane transporters in arbuscular mycorrhizal and legume–rhizobium symbioses. PLANT PHYSIOLOGY, 187(4), 2071. https://doi.org/10.1093/plphys/kiab280

8. Barber, N. A., Kiers, E. T., Theis, N., Hazzard, R. V., & Adler, L. S. (2013). Linking agricultural practices, mycorrhizal fungi, and traits mediating plant–insect interactions. *Ecological Applications*, *23*(7), 1519–1530. https://doi.org/10.1890/13-0156.1
9. Basiru, S., Mwanza, H. P., & Hijri, M. (2020). Analysis of Arbuscular Mycorrhizal Fungal Inoculant Benchmarks. *Microorganisms*, *9*(1), 81. https://doi.org/10.3390/microorganisms9010081
10. Begum, N., Qin, C., Ahanger, M. A., Raza, S., Khan, M. I., Ashraf, M., Ahmed, N., & Zhang, L. (2019). Role of Arbuscular Mycorrhizal Fungi in Plant Growth Regulation: Implications in Abiotic Stress Tolerance. *Frontiers in Plant Science*, *10*, 1068. https://doi.org/10.3389/fpls.2019.01068
11. Berninger, T., González López, Ó., Bejarano, A., Preininger, C., & Sessitsch, A. (2018). Maintenance and assessment of cell viability in formulation of non-sporulating bacterial inoculants. *Microbial Biotechnology*, *11*(2), 277–301. https://doi.org/10.1111/1751-7915.12880
12. Berruti, A., Lumini, E., Balestrini, R., & Bianciotto, V. (2016). Arbuscular Mycorrhizal Fungi as Natural Biofertilizers: Let's Benefit from Past Successes. *Frontiers in Microbiology*, *6*. https://doi.org/10.3389/fmicb.2015.01559
13. Beslemes, D., Tigka, E., Roussis, I., Kakabouki, I., Mavroeidis, A., & Vlachostergios, D. (2023). Effect of Arbuscular Mycorrhizal Fungi on Nitrogen and Phosphorus Uptake Efficiency and Crop Productivity of Two-Rowed Barley under Different Crop Production Systems. *Plants*, *12*(9), 1908. https://doi.org/10.3390/plants12091908
14. Betancur-Agudelo, M., Meyer, E., & Lovato, P. E. (2023). Increased copper concentrations in soil affect indigenous arbuscular mycorrhizal fungi and physiology of grapevine plantlets. Rhizosphere, 27, 100711. https://doi.org/10.1016/j.rhisph.2023.100711
15. Bortolot, M., Buffoni, B., Mazzarino, S., Hoff, G., Martino, E., Fiorilli, V., & Salvioli Di Fossalunga, A. (2024). The Importance of Mycorrhizal Fungi and Their Associated Bacteria in Promoting Crops' Performance: An Applicative Perspective. *Horticulturae*, *10*(12), 1326. https://doi.org/10.3390/horticulturae10121326
16. Bouzeriba, T. B. A., Mehjin, A. M. A.-A., Mikaeel, Y. F., Dennis, S. A., Ahmed, A. A., & Peter, D. S. (2021). Effects of arbuscular mycorrhizal fungi on growth and phosphorus uptake of maize (Zea mays L.) at different levels of soil phosphorus and soil moisture. *Journal of Dryland Agriculture*, *7*(3), 22–33. https://doi.org/10.5897/JODA2020.0063
17. Burak, K., Yanardağ, İ. H., Gómez-López, M. D., Faz, Á., Yalçin, H., Sakin, E., Ramazanoğlu, E., Orak, A. B., & Yanardağ, A. (2024). The effect of arbuscular mycorrhizal fungi on biological activity and biochemical properties of soil under vetch growing conditions in calcareous soils. *Heliyon*, *10*(3), e24820. https://doi.org/10.1016/j.heliyon.2024.e24820

18. Cahanovitc, R., Livne-Luzon, S., Angel, R., & Klein, T. (2022). Ectomycorrhizal fungi mediate belowground carbon transfer between pines and oaks. *The ISME Journal*, *16*(5), 1420–1429. https://doi.org/10.1038/s41396-022-01193-z
19. Cavagnaro, T. R. (2014). Impacts of compost application on the formation and functioning of arbuscular mycorrhizas. *Soil Biology and Biochemistry*, *78*, 38–44. https://doi.org/10.1016/j.soilbio.2014.07.007
20. Chareesri, A., Deyn, G. B. D., Sergeeva, L. I., Polthanee, A., & Kuyper, T. W. (2020). Increased arbuscular mycorrhizal fungal colonization reduces yield loss of rice (Oryza sativa L.) under drought. Mycorrhiza, 30, 315. https://doi.org/10.1007/s00572-020-00953-z
21. Chaudhary, A., Poudyal, S., & Kaundal, A. (2025). Role of Arbuscular Mycorrhizal Fungi in Maintaining Sustainable Agroecosystems. *Applied Microbiology*, *5*(1), 6. https://doi.org/10.3390/applmicrobiol5010006
22. Chave, M., Angeon, V., Paut, R., Collombet, R., & Tchamitchian, M. (2019). Codesigning biodiversity-based agrosystems promotes alternatives to mycorrhizal inoculants. Agronomy for Sustainable Development, 39(6). https://doi.org/10.1007/s13593-019-0594-y
23. Cheng, S., Zou, Y.-N., Kuča, K., Hashem, A., Abd_Allah, E. F., & Wu, Q.-S. (2021). Elucidating the Mechanisms Underlying Enhanced Drought Tolerance in Plants Mediated by Arbuscular Mycorrhizal Fungi. *Frontiers in Microbiology*, *12*, 809473. https://doi.org/10.3389/fmicb.2021.809473
24. Chiu, C. H., & Paszkowski, U. (2019). Mechanisms and Impact of Symbiotic Phosphate Acquisition. Cold Spring Harbor Perspectives in Biology, 11(6). https://doi.org/10.1101/cshperspect.a034603
25. d'Entremont, T. W., & Kivlin, S. N. (2023). Specificity in plant-mycorrhizal fungal relationships: Prevalence, parameterization, and prospects. *Frontiers in Plant Science*, *14*, 1260286. https://doi.org/10.3389/fpls.2023.1260286
26. Dhiman, M., Sharma, L., Kaushik, P., Singh, A., & Sharma, M. (2022). Mycorrhiza: An Ecofriendly Bio-Tool for Better Survival of Plants in Nature. *Sustainability*, *14*(16), 10220. https://doi.org/10.3390/su141610220
27. Díaz-Rodríguez, A. M., Parra Cota, F. I., Cira Chávez, L. A., García Ortega, L. F., Estrada Alvarado, M. I., Santoyo, G., & De Los Santos-Villalobos, S. (2025). Microbial Inoculants in Sustainable Agriculture: Advancements, Challenges, and Future Directions. *Plants*, *14*(2), 191. https://doi.org/10.3390/plants14020191
28. Etesami, H., Jeong, B. R., & Glick, B. R. (2021). Contribution of Arbuscular Mycorrhizal Fungi, Phosphate–Solubilizing Bacteria, and Silicon to P Uptake by Plant. *Frontiers in Plant Science*, *12*, 699618. https://doi.org/10.3389/fpls.2021.699618
29. Facelli, E., Smith, S. E., & Smith, F. A. (2009). Mycorrhizal symbiosis – overview and new insights into roles of arbuscular mycorrhizas in agro- and natural ecosystems. Australasian Plant Pathology, 38(4), 338. https://doi.org/10.1071/ap09033

30. Fall, A. F., Nakabonge, G., Ssekandi, J., Founoune-Mboup, H., Apori, S. O., Ndiaye, A., Badji, A., & Ngom, K. (2022). Roles of Arbuscular Mycorrhizal Fungi on Soil Fertility: Contribution in the Improvement of Physical, Chemical, and Biological Properties of the Soil. *Frontiers in Fungal Biology*, *3*, 723892. https://doi.org/10.3389/ffunb.2022.723892
31. Ganugi, P., Fiorini, A., Tabaglio, V., Capra, F., Zengin, G., Bonini, P., Caffi, T., Puglisi, E., Trevisan, M., & Lucini, L. (2023). The Functional Profile and Antioxidant Capacity of Tomato Fruits Are Modulated by the Interaction between Microbial Biostimulants, Soil Properties, and Soil Nitrogen Status. Antioxidants, 12(2), 520. https://doi.org/10.3390/antiox12020520
32. Garg, N., Geetanjali, G., & Kaur, A. (2006). Arbuscular mycorrhiza: Nutritional aspects. Archives of Agronomy and Soil Science, 52(6), 593. https://doi.org/10.1080/03650340601037127
33. Garg, S., Kim, M., & Romero-Suarez, D. (2025). Current advancements in fungal engineering technologies for Sustainable Development Goals. *Trends in Microbiology*, *33*(3), 285–301. https://doi.org/10.1016/j.tim.2024.11.001
34. Ghorui, M., Chowdhury, S., & Burla, S. (2025). Recent advances in the commercial formulation of arbuscular mycorrhizal inoculants. *Frontiers in Industrial Microbiology*, *3*, 1553472. https://doi.org/10.3389/finmi.2025.1553472
35. Ghorui, M., Chowdhury, S., Balu, P., & Burla, S. (2024). Arbuscular Mycorrhizal inoculants and its regulatory landscape. *Heliyon*, *10*(9), e30359. https://doi.org/10.1016/j.heliyon.2024.e30359
36. Gou, X., Ni, H., Sadowsky, M. J., Chang, X., Liu, W., & Wei, X. (2022). Arbuscular mycorrhizal fungi alleviate erosion-induced soil nutrient losses in experimental agro-ecosystems. CATENA, 220, 106687. https://doi.org/10.1016/j.catena.2022.106687
37. Guan, K., Jin, Z., Peng, B., Tang, J., DeLucia, E. H., West, P. C., Jiang, C., Wang, S., Kim, T., Zhou, W., Griffis, T., Liu, L., Yang, W. H., Qin, Z., Yang, Q., Margenot, A., Stuchiner, E. R., Kumar, V., Bernacchi, C., … Yang, S.-J. (2023). A scalable framework for quantifying field-level agricultural carbon outcomes. *Earth-Science Reviews*, *243*, 104462. https://doi.org/10.1016/j.earscirev.2023.104462
38. Hawkesford, M. J., Horst, W. J., Kichey, T., Lambers, H., Schjøerring, J. K., Møller, I. S., & White, P. R. (2011). Functions of Macronutrients. In Elsevier eBooks (p. 135). Elsevier BV. https://doi.org/10.1016/b978-0-12-384905-2.00006-6
39. Helena Devi, S., Bhupenchandra, I., Sinyorita, S., Chongtham, S. K., & Lamalakshmi Devi, E. (2021). Mycorrhizal Fungi and Sustainable Agriculture. In *Nitrogen in Agriculture—Physiological, Agricultural and Ecological Aspects [Working Title]*. IntechOpen. https://doi.org/10.5772/intechopen.99262
40. Herath, B. M., Kalamulla, K. W. Y. R., Mayadunna, T. A. N., Perera, M. A. E. G., Jayamanna, I. K., & Yapa, P. N. (2024). Applications of Arbuscular Mycorrhizal Fungi for Sustainable Agricultural Systems. In G. J. Ahammed & R. Hajiboland (Eds.), *Arbuscular*

Mycorrhizal Fungi and Higher Plants (pp. 319–340). Springer Nature Singapore. https://doi.org/10.1007/978-981-99-8220-2_14

41. Hossain, M. M. (2022). Orchid mycorrhiza: Isolation, culture, characterization and application. *South African Journal of Botany*, *151*, 365–384. https://doi.org/10.1016/j.sajb.2022.10.003
42. Jabborova, D., Annapurna, K., Al-Sadi, A. M., Alharbi, S. A., Datta, R., & Zuan, A. T. K. (2021). Biochar and Arbuscular mycorrhizal fungi mediated enhanced drought tolerance in Okra (Abelmoschus esculentus) plant growth, root morphological traits and physiological properties. *Saudi Journal of Biological Sciences*, *28*(10), 5490–5499. https://doi.org/10.1016/j.sjbs.2021.08.016
43. Jansa, J., Oberholzer, H.-R., & Egli, S. (2009). Environmental determinants of the arbuscular mycorrhizal fungal infectivity of Swiss agricultural soils. *European Journal of Soil Biology*, *45*(5–6), 400–408. https://doi.org/10.1016/j.ejsobi.2009.07.004
44. Jansa, J., Wiemken, A., & Frossard, E. (2006). The effects of agricultural practices on arbuscular mycorrhizal fungi. *Geological Society, London, Special Publications*, *266*(1), 89–115. https://doi.org/10.1144/GSL.SP.2006.266.01.08
45. Jayasinghe, S., Thomas, D., Anderson, J. P., Chen, C., & Macdonald, B. (2023). Global Application of Regenerative Agriculture: A Review of Definitions and Assessment Approaches. Sustainability, 15(22), 15941. https://doi.org/10.3390/su152215941
46. Kalamulla, R., Karunarathna, S. C., Tibpromma, S., Galappaththi, M. C. A., Suwannarach, N., Stephenson, S. L., Asad, S., Salem, Z. S., & Yapa, N. (2022). Arbuscular Mycorrhizal Fungi in Sustainable Agriculture. *Sustainability*, *14*(19), 12250. https://doi.org/10.3390/su141912250
47. Kaminsky, L. M., Trexler, R. V., Malik, R. J., Hockett, K. L., & Bell, T. H. (2019). The Inherent Conflicts in Developing Soil Microbial Inoculants. *Trends in Biotechnology*, *37*(2), 140–151. https://doi.org/10.1016/j.tibtech.2018.11.011
48. Keller-Pearson, M., Liu, Y., Peterson, A., Pederson, K., Willems, L., Ané, J.-M., & Silva, E. M. (2020). Inoculation with arbuscular mycorrhizal fungi has a more significant positive impact on the growth of open-pollinated heirloom varieties of carrots than on hybrid cultivars under organic management conditions. *Agriculture, Ecosystems & Environment*, *289*, 106712. https://doi.org/10.1016/j.agee.2019.106712
49. Khaliq, A., Perveen, S., Alamer, K. H., Zia Ul Haq, M., Rafique, Z., Alsudays, I. M., Althobaiti, A. T., Saleh, M. A., Hussain, S., & Attia, H. (2022). Arbuscular Mycorrhizal Fungi Symbiosis to Enhance Plant–Soil Interaction. *Sustainability*, *14*(13), 7840. https://doi.org/10.3390/su14137840
50. Khan, W., Zhu, Y., Khan, A., Zhao, L., Yang, Y.-M., Wang, N., Hao, M., Ma, Y., Nepal, J., Ullah, F., Rehman, M. M. U., Abrar, M., & Xiong, Y.-C. (2024). Above-and below-ground feedback loop of maize is jointly enhanced by plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi in drier

soil. *Science of The Total Environment*, *917*, 170417. https://doi.org/10.1016/j.scitotenv.2024.170417

51. Khoshru, B., Mitra, D., Nosratabad, A. F., Reyhanitabar, A., Mandal, L., Farda, B., Djebaili, R., Pellegrini, M., Sierra, B. E. G., Senapati, A., Panneerselvam, P., & Mohapatra, P. K. D. (2023). Enhancing Manganese Availability for Plants through Microbial Potential: A Sustainable Approach for Improving Soil Health and Food Security. Bacteria, 2(3), 129. https://doi.org/10.3390/bacteria2030010
52. Khoso, M. A., Wagan, S., Alam, I., Hussain, A., Ali, Q., Saha, S., Poudel, T. R., Manghwar, H., & Liu, F. (2024). Impact of plant growth-promoting rhizobacteria (PGPR) on plant nutrition and root characteristics: Current perspective. *Plant Stress*, *11*, 100341. https://doi.org/10.1016/j.stress.2023.100341
53. Koech, K., Koskey, G., Njeru, E. M., & Maingi, J. M. (2024). Leveraging the complex interplay between arbuscular mycorrhizal fungi, seasonal dynamics, and genotypic diversity to optimize maize productivity in semi-arid agroecosystems. Heliyon, 10(18). https://doi.org/10.1016/j.heliyon.2024.e37659
54. Kozjek, K., Kundel, D., Kushwaha, S. K., Olsson, P. A., Ahrén, D., Fliessbach, A., Birkhofer, K., & Hedlund, K. (2021). Long-term agricultural management impacts arbuscular mycorrhizal fungi more than short-term experimental drought. *Applied Soil Ecology*, *168*, 104140. https://doi.org/10.1016/j.apsoil.2021.104140
55. Kuila, D., & Ghosh, S. (2022). Aspects, problems and utilization of Arbuscular Mycorrhizal (AM) application as bio-fertilizer in sustainable agriculture. *Current Research in Microbial Sciences*, *3*, 100107. https://doi.org/10.1016/j.crmicr.2022.100107
56. Kumar, A., Dames, J. F., Gupta, A., Sharma, S., Gilbert, J. A., & Ahmad, P. (2014). Current developments in arbuscular mycorrhizal fungi research and its role in salinity stress alleviation: a biotechnological perspective [Review of Current developments in arbuscular mycorrhizal fungi research and its role in salinity stress alleviation: a biotechnological perspective]. Critical Reviews in Biotechnology, 35(4), 461. Taylor & Francis. https://doi.org/10.3109/07388551.2014.899964
57. Kumar, L., Chhogyel, N., Gopalakrishnan, T., Hasan, M. K., Jayasinghe, S. L., Kariyawasam, C. S., Kogo, B. K., & Ratnayake, S. (2022). Climate change and future of agri-food production. In *Future Foods* (pp. 49–79). Elsevier. https://doi.org/10.1016/B978-0-323-91001-9.00009-8
58. Lanfranco, L., Bonfante, P., & Genre, A. (2016). The Mutualistic Interaction between Plants and Arbuscular Mycorrhizal Fungi [Review of The Mutualistic Interaction between Plants and Arbuscular Mycorrhizal Fungi]. Microbiology Spectrum, 4(6). American Society for Microbiology. https://doi.org/10.1128/microbiolspec.funk-0012-2016
59. Lehmann, A., Leifheit, E. F., & Rillig, M. C. (2016). Mycorrhizas and Soil Aggregation. Elsevier eBooks, 241.

https://doi.org/10.1016/b978-0-12-804312-7.00014-0

60. Lehmann, A., Veresoglou, S. D., Leifheit, E. F., & Rillig, M. C. (2014). Arbuscular mycorrhizal influence on zinc nutrition in crop plants – A meta-analysis. *Soil Biology and Biochemistry*, *69*, 123–131. https://doi.org/10.1016/j.soilbio.2013.11.001
61. Lewis, J. D. (2016). Mycorrhizal Fungi, Evolution and Diversification of. Elsevier eBooks, 94. https://doi.org/10.1016/b978-0-12-800049-6.00251-1
62. Madawala, H. M. S. P. (2021). Arbuscular mycorrhizal fungi as biofertilizers: Current trends, challenges, and future prospects. In *Biofertilizers* (pp. 83–93). Elsevier. https://doi.org/10.1016/B978-0-12-821667-5.00029-4
63. Madouh, T. A., & Quoreshi, A. M. (2023). The Function of Arbuscular Mycorrhizal Fungi Associated with Drought Stress Resistance in Native Plants of Arid Desert Ecosystems: A Review. *Diversity*, *15*(3), 391. https://doi.org/10.3390/d15030391
64. Malhi, G. S., Kaur, M., Kaushik, P., Alyemeni, M. N., Alsahli, A. A., & Ahmad, P. (2020). Arbuscular mycorrhiza in combating abiotic stresses in vegetables: An eco-friendly approach [Review of Arbuscular mycorrhiza in combating abiotic stresses in vegetables: An eco-friendly approach]. Saudi Journal of Biological Sciences, 28(2), 1465. Elsevier BV. https://doi.org/10.1016/j.sjbs.2020.12.001
65. Martin, F. M., & Van Der Heijden, M. G. A. (2024). The mycorrhizal symbiosis: Research frontiers in genomics, ecology, and agricultural application. *New Phytologist*, *242*(4), 1486–1506. https://doi.org/10.1111/nph.19541
66. Meng, L., Zhang, A., Wang, F., Han, X., Wang, D., & Li, S. (2015). Arbuscular mycorrhizal fungi and rhizobium facilitate nitrogen uptake and transfer in soybean/maize intercropping system. *Frontiers in Plant Science*, *6*. https://doi.org/10.3389/fpls.2015.00339
67. Meng, L., Zhang, A., Wang, F., Han, X., Wang, D., & Li, S. (2015). Arbuscular mycorrhizal fungi and rhizobium facilitate nitrogen uptake and transfer in soybean/maize intercropping system. Frontiers in Plant Science, 6. https://doi.org/10.3389/fpls.2015.00339
68. Mishra, P., Mishra, J., & Arora, N. K. (2023). Biofortification revisited: Addressing the role of beneficial soil microbes for enhancing trace elements concentration in staple crops. *Microbiological Research*, *275*, 127442. https://doi.org/10.1016/j.micres.2023.127442
69. Mitchell, D. T., & Gibson, B. (2006). Ericoid mycorrhizal association: ability to adapt to a broad range of habitats. Mycologist, 20(1), 2. https://doi.org/10.1016/j.mycol.2005.11.015
70. Mitra, D., Djebaili, R., Pellegrini, M., Mahakur, B., Sarker, A., Chaudhary, P., Khoshru, B., Gallo, M. D., Kitouni, M., Barık, D. P., Panneerselvam, P., & Mohapatra, P. K. D. (2021). Arbuscular mycorrhizal symbiosis: plant growth improvement and induction of resistance under stressful conditions. Journal of Plant Nutrition, 44(13), 1993. https://doi.org/10.1080/01904167.2021.1881552
71. Miyasaka, S. C., & Habte, M. (2001). PLANT MECHANISMS AND

MYCORRHIZAL SYMBIOSES TO INCREASE PHOSPHORUS UPTAKE EFFICIENCY*. *Communications in Soil Science and Plant Analysis*, *32*(7–8), 1101–1147. https://doi.org/10.1081/CSS-100104105

72. Nautiyal, P., Rajput, R., Pandey, D., Arunachalam, K., & Arunachalam, A. (2019). Role of glomalin in soil carbon storage and its variation across land uses in temperate Himalayan regime. *Biocatalysis and Agricultural Biotechnology*, *21*, 101311. https://doi.org/10.1016/j.bcab.2019.101311
73. Owiny, A. A., & Dusengemungu, L. (2024). Mycorrhizae in mine wasteland reclamation. *Heliyon*, *10*(13), e33141. https://doi.org/10.1016/j.heliyon.2024.e33141
74. Pantigoso, H. A., Newberger, D. R., & Vivanco, J. M. (2022). The rhizosphere microbiome: Plant–microbial interactions for resource acquisition. Journal of Applied Microbiology, 133(5), 2864. https://doi.org/10.1111/jam.15686
75. Pelosi, C., Taschen, E., Redecker, D., & Blouin, M. (2024). Earthworms as conveyors of mycorrhizal fungi in soils. *Soil Biology and Biochemistry*, *189*, 109283. https://doi.org/10.1016/j.soilbio.2023.109283
76. Powell, J. R., & Rillig, M. C. (2018). Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist*, *220*(4), 1059–1075. https://doi.org/10.1111/nph.15119
77. Prasad, R., & Shivay, Y. S. (2021). Phosphorus × Other Plant Nutrient Interactions, Reaction Products, Anion Exchange and Phosphate Fixation in Soil and Strategies to Increase Availability of the Native and Applied P to Crop Plants-A Mini Review and Critique. Agricultural Reviews. https://doi.org/10.18805/ag.r-2028
78. Raihan, A. (2023). A review of climate change mitigation and agriculture sustainability through soil carbon sequestration. *Journal of Agriculture Sustainability and Environment*, *2*(2), 23–56. https://doi.org/10.56556/jase.v2i2.783
79. Ramasamy, K., Joe, M. M., Kim, K.-Y., Lee, S.-M., Shagol, C., Rangasamy, A., Chung, J.-B., Islam, Md. R., & Sa, T.-M. (2011). Synergistic Effects of Arbuscular Mycorrhizal Fungi and Plant Growth Promoting Rhizobacteria for Sustainable Agricultural Production. *Korean Journal of Soil Science and Fertilizer*, *44*(4), 637–649. https://doi.org/10.7745/KJSSF.2011.44.4.637
80. Reynolds, H. L., Hartley, A. E., Vogelsang, K. M., Bever, J. D., & Schultz, P. A. (2005). Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytologist*, *167*(3), 869–880. https://doi.org/10.1111/j.1469-8137.2005.01455.x
81. Rillig, M. C., Sosa-Hernández, M. A., Roy, J., Aguilar-Trigueros, C. A., Vályi, K., & Lehmann, A. (2016). Towards an Integrated Mycorrhizal Technology: Harnessing Mycorrhiza for Sustainable Intensification in Agriculture. Frontiers in Plant Science, 7. https://doi.org/10.3389/fpls.2016.01625
82. Saboor, A., Ali, M. A., Hussain, S., Enshasy, H. A. E., Hussain, S., Ahmed, N., Gafur, A., Sayyed, R. Z., Fahad, S., Danish, S., & Datta, R. (2021). Zinc nutrition and arbuscular mycorrhizal

symbiosis effects on maize (Zea mays L.) growth and productivity. Saudi Journal of Biological Sciences, 28(11), 6339. https://doi.org/10.1016/j.sjbs.2021.06.096

83. Saeed, Q., Xiukang, W., Haider, F. U., Kučerik, J., Mumtaz, M. Z., Holatko, J., Naseem, M., Kintl, A., Ejaz, M., Naveed, M., Brtnicky, M., & Mustafa, A. (2021). Rhizosphere Bacteria in Plant Growth Promotion, Biocontrol, and Bioremediation of Contaminated Sites: A Comprehensive Review of Effects and Mechanisms. *International Journal of Molecular Sciences*, *22*(19), 10529. https://doi.org/10.3390/ijms221910529
84. Salomon, M. J., Watts-Williams, S. J., McLaughlin, M. J., Bücking, H., Singh, B. K., Hutter, I., Schneider, C., Martin, F., Vosátka, M., Guo, L., Ezawa, T., Saito, M., Declerck, S., Zhu, Y., Bowles, T. M., Abbott, L. K., Smith, F., Cavagnaro, T. R., & Heijden, M. G. A. van der. (2022). Establishing a quality management framework for commercial inoculants containing arbuscular mycorrhizal fungi [Review of Establishing a quality management framework for commercial inoculants containing arbuscular mycorrhizal fungi]. iScience, 25(7), 104636. Cell Press. https://doi.org/10.1016/j.isci.2022.104636
85. Samantaray, A., Chattaraj, S., Mitra, D., Ganguly, A., Kumar, R., Gaur, A., Mohapatra, P. K. D., Santos-Villalobos, S. D. L., Rani, A., & Thatoi, H. (2024). Advances in microbial based bio-inoculum for amelioration of soil health and sustainable crop production. *Current Research in Microbial Sciences*, *7*, 100251. https://doi.org/10.1016/j.crmicr.2024.100251
86. Schaefer, D., Gui, H., Mortimer, P. E., & Xu, J. (2021). Arbuscular Mycorrhiza and Sustainable Agriculture. Circular Agricultural Systems, 1(1), 1. https://doi.org/10.48130/cas-2021-0006
87. Shi, J., Wang, X., & Wang, E. (2023). Mycorrhizal Symbiosis in Plant Growth and Stress Adaptation: From Genes to Ecosystems [Review of Mycorrhizal Symbiosis in Plant Growth and Stress Adaptation: From Genes to Ecosystems]. Annual Review of Plant Biology, 74(1), 569. Annual Reviews. https://doi.org/10.1146/annurev-arplant-061722-090342
88. Smith, S. E., & Read, D. J. (2008). Ericoid mycorrhizas. In Elsevier eBooks (p. 389). Elsevier BV. https://doi.org/10.1016/b978-012370526-6.50013-1
89. Sosa-Hernández, M. A., Leifheit, E. F., Ingraffia, R., & Rillig, M. C. (2019). Subsoil Arbuscular Mycorrhizal Fungi for Sustainability and Climate-Smart Agriculture: A Solution Right Under Our Feet? *Frontiers in Microbiology*, *10*, 744. https://doi.org/10.3389/fmicb.2019.00744
90. Soumaré, A., Diédhiou, A. G., Thuita, M., Hafidi, M., Ouhdouch, Y., Gopalakrishnan, S., & Kouisni, L. (2020). Exploiting Biological Nitrogen Fixation: A Route Towards a Sustainable Agriculture. Plants, 9(8), 1011. https://doi.org/10.3390/plants9081011
91. Sun, W., & Shahrajabian, M. H. (2023). The Application of Arbuscular Mycorrhizal Fungi as Microbial Biostimulant, Sustainable Approaches in Modern Agriculture [Review of The Application of Arbuscular Mycorrhizal

Fungi as Microbial Biostimulant, Sustainable Approaches in Modern Agriculture]. Plants, 12(17), 3101. Multidisciplinary Digital Publishing Institute. https://doi.org/10.3390/plants12173101

92. Tang, H., Hassan, M. U., Feng, L., Nawaz, M., Shah, A. N., Qari, S. H., Liu, Y., & Miao, J. (2022). The Critical Role of Arbuscular Mycorrhizal Fungi to Improve Drought Tolerance and Nitrogen Use Efficiency in Crops. *Frontiers in Plant Science*, *13*, 919166. https://doi.org/10.3389/fpls.2022.919166
93. Trinchera, A., Testani, E., Roccuzzo, G., Campanelli, G., & Ciaccia, C. (2021). Agroecological Service Crops Drive Plant Mycorrhization in Organic Horticultural Systems. *Microorganisms*, *9*(2), 410. https://doi.org/10.3390/microorganisms9020410
94. Van Der Heijden, M. G. A., Martin, F. M., Selosse, M., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytologist*, *205*(4), 1406–1423. https://doi.org/10.1111/nph.13288
95. Verbruggen, E., & Toby Kiers, E. (2010). Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evolutionary Applications*, *3*(5–6), 547–560. https://doi.org/10.1111/j.1752-4571.2010.00145.x
96. Vieira, C. K., Marascalchi, M. N., Rozmoš, M., Benada, O., Belova, V., & Jansa, J. (2025). Arbuscular mycorrhizal fungal highways – What, how and why? *Soil Biology and Biochemistry*, *202*, 109702. https://doi.org/10.1016/j.soilbio.2024.109702
97. Wahab, A., Batool, F., Muhammad, M., Zaman, W., Mikhlef, R. M., Qaddoori, S. M., Ullah, S., Abdi, G., & Saqib, S. (2024). Unveiling the complex molecular dynamics of arbuscular mycorrhizae: A comprehensive exploration and future perspectives in harnessing phosphate-solubilizing microorganisms for sustainable progress. *Environmental and Experimental Botany*, *219*, 105633. https://doi.org/10.1016/j.envexpbot.2023.105633
98. Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A., Khizar, C., & Reddy, S. P. P. (2023). Role of Arbuscular Mycorrhizal Fungi in Regulating Growth, Enhancing Productivity, and Potentially Influencing Ecosystems under Abiotic and Biotic Stresses. *Plants*, *12*(17), 3102. https://doi.org/10.3390/plants12173102
99. Ward, E. B., Duguid, M. C., Kuebbing, S. E., Lendemer, J. C., & Bradford, M. A. (2022). The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. New Phytologist, 235(5), 1701. https://doi.org/10.1111/nph.18307
100. Watts-Williams, S. J. (2022). Track and trace: How soil labelling techniques have revealed the secrets of resource transport in the arbuscular mycorrhizal symbiosis. *Mycorrhiza*, *32*(3–4), 257–267. https://doi.org/10.1007/s00572-022-01080-7
101. Wei, X., Zhang, W., Zulfiqar, F., Zhang, C., & Chen, J. (2022). Ericoid mycorrhizal fungi as biostimulants for improving propagation and production of ericaceous plants [Review of Ericoid mycorrhizal fungi as biostimulants for improving propagation and production of ericaceous plants]. Frontiers in Plant

Science, 13. Frontiers Media. https://doi.org/10.3389/fpls.2022.1027390

102. Willis, A., Rodrigues, B. F., & Harris, P. J. C. (2013). The Ecology of Arbuscular Mycorrhizal Fungi. *Critical Reviews in Plant Sciences*, *32*(1), 1–20. https://doi.org/10.1080/07352689.2012.683375

103. Wu, S., Shi, Z., Chen, X., Gao, J., & Wang, X. (2022). Arbuscular mycorrhizal fungi increase crop yields by improving biomass under rainfed condition: A meta-analysis. *PeerJ*, *10*, e12861. https://doi.org/10.7717/peerj.12861

104. Xue, J., Guo, L., Li, L., Zhang, Z., Huang, M., Cai, J., Wang, X., Zhong, Y., Dai, T., Jiang, D., & Zhou, Q. (2024). Effects of arbuscular mycorrhizal fungi on uptake, partitioning and use efficiency of nitrogen in wheat. *Field Crops Research*, *306*, 109244. https://doi.org/10.1016/j.fcr.2023.109244

105. Yang, H., Xiao, Q., Huang, Y., Cai, Z., Li, D., Wu, L., Meersmans, J., Colinet, G., & Zhang, W. (2024). Long-term manuring facilitates glomalin-related soil proteins accumulation by chemical composition shifts and macro-aggregation formation. *Soil and Tillage Research*, *235*, 105904. https://doi.org/10.1016/j.still.2023.105904

106. Zhang, M., Liu, S., Cao, X., Chen, M., Chen, J., Xu, G., & Shi, Z. (2023). The effects of ectomycorrhizal and saprotropic fungi on soil nitrogen mineralization differ from those of arbuscular and ericoid mycorrhizal fungi on the eastern Qinghai-Tibetan Plateau. *Frontiers in Plant Science*, *13*, 1069730. https://doi.org/10.3389/fpls.2022.1069730

107. Zhou, X., Wang, T., Wang, J., Chen, S., & Ling, W. (2023). Research progress and prospect of glomalin-related soil protein in the remediation of slightly contaminated soil. Chemosphere, 344, 140394. https://doi.org/10.1016/j.chemosphere.2023.140394