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Mycorrhizal Fungi: An Important Tool for Rhizosphere Engineering

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Abstract: *Mycorrhizal fungi are a component of rhizosphere microbiome, facilitating symbiotic relationships with plant roots that enhance nutrient uptake, bolster stress tolerance and modulate plant immune responses. Emphasis is placed on the intricate interactions within the rhizosphere an ecologically dynamic interface between roots and soil biota which significantly influence plant growth, development, and productivity. The concept of rhizosphere engineering is introduced as an innovative, sustainable strategy to manipulate and optimize soil microbial consortia for enhanced plant performance. Within this framework, mycorrhizal fungi emerge as biofunctional agents capable of modifying rhizospheric nutrient fluxes, altering root exudate composition, and reinforcing beneficial plant-microbe interactions. Particular focus is given to arbuscular mycorrhizal fungi (AMF) due to their widespread occurrence and proven roles in phosphorus solubilization, water-use efficiency, and abiotic stress mitigation. The review synthesizes current research findings to illustrate how strategic incorporation of mycorrhizal inoculants into conventional and conservation-based agricultural systems can engineer a functionally resilient rhizosphere. The synergistic application of mycorrhizae in rhizosphere engineering is proposed as a viable tool for promoting agroecosystem sustainability, optimizing nutrient cycling, and supporting long-term soil health. This chapter offers a comprehensive overview and updated classification of mycorrhizal fungi, delineating their taxonomic diversity and ecological functionality.*

Keywords*:* Rhizosphere, Mycorrhizae Fungi, Rhizodeposits, Rhizosphere Engineering

I. INTRODUCTION

The rhizosphere, the region surrounding the plant roots, harbors a diverse range of microorganisms. These include pathogens, saprophytes that decompose organic matter and symbiotic organisms such as mycorrhizae, which form mutualistic associations with the plant. Mycorrhizae are fungi that refer to the beneficial symbiotic relationships between the arbuscular mycorrhizal fungi (AMF) and the roots of numerous plants widespread in the soil. The interaction between the plant and the fungus is mutualistic, with both benefiting from the association. Many of these fungi are obligate symbionts, meaning they cannot survive for long periods without their plant host. More than 80% of land plants, including over 250,000 species, form symbiotic relationships with mycorrhizal fungi (Tedersoo *et al*., 2014; van der Heijden *et al*., 2015). As it involves different species, this interaction is termed interspecific and since it benefits all participants, it is considered a harmonious relationship. Mycorrhizal associations are widely recognized as typical in nearly all terrestrial ecosystems, from deserts and tropical forests to savannahs and agriculture (Tedersoo *et al.*, 2014; van der Heijden *et al*., 2015).The hyphae of the mycorrhizal fungi are thinner than the plant's roots, allowing them to contact a larger volume of soil. The fungi have a root-like structure and a network of mycelium that extends beyond the plant roots into the soil. This mycelium absorbs nutrients and transports them back to the host plants, resulting in an increased area for nutrient absorption.

Mycorrhizae are primarily classified into three main types: endomycorrhizae (mycorrhiza living within a plant), ectomycorrhizae (mycorrhiza living on the outside of a plant) and ectendomycorrhiza (act as both ectomycorrhiza and arbuscular mycorrhiza). Endomycorrhizae are further classified into five main types of mycorrhizal symbioses that have been identified based on their structure and function: arbuscular mycorrhiza (AM), ectomycorrhiza (ECM) and ericoid mycorrhiza (ERM) and orchid mycorrhiza. These fungi inhibit the root cortex and rhizodermis with their extended hyphae into the near soil to acquire important nutrients for plant growth, such as phosphorus (P), nitrogen (N) and various micronutrients (e.g., Cu, Fe, Zn and Mn). Some mycorrhizal fungi, such as ERM and ECM also obtain phosphorus and nitrogen in organically bound forms. In exchange for these nutrients and other benefits, the fungi receive carbon (C) compounds and vitamins from their host plants (van der Heijden *et al*., 2015; Martin *et al*., 2017). In return for these nutrients and other benefits, the fungi receive carbon (C) assimilated by the plant, these symbiotic relationships help in water and nutrient uptake, reduce plant abiotic stress (Li *et al*., 2013; Chandrasekaran *et al*., 2014; Pozo *et al.,* 2015), influence plant interactions and community structures (Klironomos *et al*., 2011), enhance pathogen resistance (Jung *et al.,* 2012) and contribute to ecosystem and restoration.

Ectomycorrhizal Fungi (ECM)

Ectomycorrhizae (ECM), also known as sheathing mycorrhizae, are typically found on various evergreen trees and shrubs, as well as on deciduous trees such as Betula, Tilia, Salix, Quercus, Populus, Fagus and Castanea. These fungi belong to the Basidiomycetes class, which is known for producing mushrooms as their fruiting bodies. ECM fungi do not penetrate the plant or its roots but instead grow around the plant and along the surface of the roots, forming a structure known as the “mantle” and a network called the Hartig net. The mantle not only aids in nutrient absorption but also protects against certain pathogens. These fungi cover the tips of young roots and penetrate only the cell walls of the cortex, without further cellular invasion. In addition, to absorbing phosphate, ECM fungi play a vital role in the uptake of ammonium and zinc from the soil. They are dispersed through airborne spores or infected plant tissue. This type of ectomycorrhizae association primarily occurs in forest species (Hartmann *et al*., 2009).

Endomyorrhizal fungi

Endomycorrhiza fungi penetrate and develop entirely within the plant’s root tissues. The fungal component is primarily internal to the root structure, with the hyphae penetrating the host’s cortical cell walls. This penetration increases the contact surface area, enhancing and facilitating a more efficient exchange of carbon and other macronutrients. Endomycorrhizais further classified into five types: arbuscular mycorrhiza (AM), ectomycorrhiza (ECM) and ericoid mycorrhiza (ERM) and orchid mycorrhiza.

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) are among the most widespread types of mycorrhizal fungi, forming mutualistic associations with approximately 80% of terrestrial plant species (Smith & Read, 2008) and are present in nearly all ecosystems (Van der Heijiden *et al*., 2015). AMF is a mycorrhizal association formed by fungi from the phylum Glomeromycota with various vascular plants, including grasses, herbs and trees. The fungal hyphae penetrate the plant’s roots cortical cells, pushing against the cell membranes and branching into tree-like arbuscular structures. The hyphae grow both inter and intracellularly within the root,increasing the contact surface area between the fungus and host cells. Some fungi also produce storage structures known as vesicles within the root tissues. As a result, this type of mycorrhiza is also referred to as Arbuscular Mycorrhiza/ Vesicular- Arbuscular Mycorrhiza.This fungus belongs to the Phycomycetes class, also known as water molds. Other fungi in this class include *Phytophthora*, which causes root and crown rot and *Pythium*, responsible for damping off in seedlings. This fungus forms specialized absorptive structures called haustoria, which aid in the uptake of zinc and phosphate. The spores of the fungus germinate in the rhizosphere, the area of soil directly surrounding the root and are dispersed through infected plant material in the soil. Interaction between Arbuscular Mycorrhizae Fungi (AMF) and soil microorganisms are discussed in table 1.

Orchidoid Mycorrhizae

Orchidoid mycorrhizal association occurs in orchid roots, where an extensive intracellular mycelium is formed. These fungi belong to the Basidiomycetes family and include genera such as *Thanatephorus*, *Rhizoctonia*, *Ceratobasidium*, *Tulasnella*, *Fomes*, *Sebacina*, *Armillaria*, *etc*.

Some orchids cannot photosynthesize during their seedling stage, and others are completelynonphotosynthetic. These fungi play a crucial role in seed development and nutrient uptake during their orchids' early stages. This delicate symbiosis is further characterized by theorchid producing an antifungal chemical that disrupts the fungal hyphal coils inside the cells, preventing fungal invasion.

Arbutoid Mycorrhizae

Arbutoid mycorrhiza refers to the symbiotic relationship between fungi and plants in the Ericaceae family, including genera like*Pyrola, Arctostaphylos* and *Arbutus*. This association involves Basidiomycetes fungi that form ectomycorrhizal relationships between arbutoid plants and nearby trees, facilitating the exchange of essential nutrients and photosynthates. A thin fungal sheath surrounds the plant roots, while fungal hyphae penetrate between the epidermal and outer cortical cell layers, forming a paraepidermal Hartig net.

Ericoid Mycorrhizae

This association includes a specific group of fungi, such as Ascomycota and Deuteromycota which form relationships with plants from the *Empetraceae, Ericaceae* and *Epacridaceae* families. Like, Arbutoid Mycorrhiza, these fungi penetrate cortical cells, forming hyphal coils within the epidermal cells. They secrete proteinases that help break down nitrogen sources in the soil, providing the plants with essential nitrogen. Mycorrhizal fungi establish endomycorrhizal relationships with plants belonging to the Ericales genus and serve an important ecological function, especially as effective decomposers of soil organic matter (SOM). Nonetheless, they are predominantly found in health and environments (Read & Perez-Moreno, 2003).

Monotropoid Mycorrhizae

This relationship occurs between non-chlorophyllousplants like *Monotropa* and Basidiomycetes fungi, particularly *Boletes*. These fungi usually form ectomycorrhizal associations with other plants, such as conifers, and provide essential nutrients to *Monotropa*. Like Orchid Mycorrhiza, *Monotropa* cannot perform photosynthesis and relies on the fungi for sustenance. The fungal hyphae penetrate the plant's cells but remain confined to the outer cells, forming peg-like structures within the epidermal cells where nutrient exchange occurs.

EctenomycorrhizalFungi

This mycorrhizal association exhibits traits of both Ectomycorrhiza and Arbuscular Mycorrhiza. Initially, the fungi were difficult to identify due to the absence of fruiting structures. However, subsequent analysis has classified these fungi as E-strain fungi, belonging to the genus *Wilcoxina* within the Ascomycota phylum and Peizizales order. They fungi are structurally and developmentally similar to Ectomycorrhiza and differ in their ability to penetrate plant cells with intracellular hyphae.

Table 1.| Interaction between Arbuscular Mycorrhizae Fungi (AMF) and soil microorganisms

Interaction Arbuscular Mycorrhizae Fungi and microorganisms	Methods	Impacts	Reference
Arbuscular Mycorrhizae Fungi and *Pseudomonas fluorescens*	*Glomus intraradice and* AMF enhance the production of 2,4 diacetylphloroglucinol antibiotic by *Pseudomonas fluorescens.*	Protects the host plants from *Gaeumannomyces graminis.*	Ma *et al*., 2019
Arbuscular Mycorrhizae Fungi and saprotrophic fungi	Enhance saprotrophic fungi biomass	Soil organic matter dissolved into mineral matter	Carteron *et al*., 2021

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Arbuscular Mycorrhizae Fungi and Gram positive/negative bacteria	Gram-positive/negative bacteria have deletion effect	Effects the organic matter decomposition and bioactive metabolites	Welc *et al*., 2010
Arbuscular Mycorrhizae Fungi and *Rhizobia*	*Rhizobia* and Arbuscular Mycorrhizae Fungi synergy	Provide crop legumes and Faba bean	Xavier and Germida, 2002
Arbuscular Mycorrhizae Fungi, Phosphorus Solubilizing Microorganisms and *Rhizobia*	Solubilize Phosphate by mineralization, low soil pH, chelation and production of organic acid, proton and phosphatase	Enhance Phosphorus uptake by host plant	Nacoon *et al*., 2020
Arbuscular Mycorrhizae Fungi and Mycorrhization Helper Bacteria (MHB)	Alteration of the rhizospheric soil to enhance the germination of AMF propagules.	Increase soil fertility and nutrients uptake by the host plants	Rigamonte et al., 2010
Arbuscular Mycorrhizae Fungi and Plant Growth Promoting Rhizobacteria (PGPR)	Enhance solubilization of mineral phosphate, N fixation, Ammonia production and other vital nutrients, plant hormones production. Accumulate glutathione peroxidase and ascorbate peroxidase. Produce organic acid for inorganic P solubilisation and phosphorus phytate mineralization. Produce indol acetic acid and siderophore.	Increase the plant growth, abundance of soil parasite antagonists and diversity. Enhance tolerance of water stress	Moreira et al., 2020
Arbuscular Mycorrhizae Fungi and *Frankia*	Synergistic interaction between *Frankia* and Arbuscular Mycorrhizae Fungi	Improve numbers, height of actinorhizal plants	Oliveira et al., 2005
Arbuscular Mycorrhizae Fungi and *Bacillus subtilis*	Enhance the production of nitrite, nitrate reductase and nitrogenase activities. Also osmoprotectants such as betaine, proline and glycine by *Bacillus subtilis*.	Increase root and shoot dry weight,leghemoglobin content and nodule number	Hashem et al., 2017

Rhizosphere and Its Impact on Plant Growth

Soil is a fundamental area of study in science, with the rhizosphere being its most dynamic region, where various biogeochemical processes occur that influence numerous environmental and global systems (McNear 2013; Haldar and Sengupta 2015). The rhizosphere is the narrow soil region directly impacted by root secretions, rhizodeposits and the associated soil microorganisms. This region differs from the bulk soil in factors like water potential, redox conditions and availability of carbon compounds which shape the distribution and activity of diverse microbial populations within the rhizosphere (Cardon and Whitbeck 2007). The rhizosphere hosts roughly 10^11 microbial cells per gram of root (Egamberdieva *et al.,* 2008) and is home around 30,000 parkaryotic species, all of which significantly impact plant productivity (Mendes *et al*., 2013). It functions as a hub for interaction, where symbionts organisms and nearby root

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engage with the plant. Additionally, the rhizosphere functions as a protective microbial interface, safeguarding the plant against pathogenic threats (Baetz and Martinoia 2014).

The rhizosphere refers to three different zones, each defined by their proximity and effects from the root of plants (Morgan *et al.*, 2005). The endorhizosphere includes portions of endodermis and cortex where cations and microbes occupy the apoplastic space, the intercellular region between cells (Reinhold-Hurek *et al.,* 2015). The root surface or rhizoplane is the middle zone, comprising the mucilage root and epidermis (Nihorembere *et al*., 2011; Bulgarelli *et al.,* 2012). The ectorhizosphere, the outermost zone, extends from the rhizoplane into the bulk soil surrounding the root.

The rhizosphere effect encompasses the range of processes that take place at the root-soil interface of plants, such as microbial activity, root exudation, genetic exchange, gradient diffusion and nutrient transformation. Around 1/3 to more than half of the total carbon absorbed by plants is directed to the roots, with 15-25% of that carbon being released into the soil, leading to rapid carbon turnover. Elevated microbial activity in the rhizosphere, driven by increased carbon availability, leads to intensified antagonism among microorganisms for essential nutrients (Hartmann *et al*., 2009; Haldar and Sengupta 2015). In contrast, root- free bulk soil contains an abundance of all nutrients except carbon. Consequently, the rhizosphere exhibits distinct physical, chemical and biological properties compared to root- free zones (Hartmann *et al*., 2009).

Plants are affected by the soil and also by the microbial population and the gradients of microbial communities within the rhizosphere. These microorganisms, along with the exchange of substances like root exudates, water, other volatile compounds nutrients and gases play a crucial role in shaping the rhizosphere environment. The rhizosphere zone is distinctly different from root-free zones in its physical, chemical and biological characteristics (Hartmann *et al.,* 2009).

Rhizodeposits

Rhizodeposits are the substances secreted by plant roots and their associated microorganisms into the rhizosphere. These substances are categorized based on their function or chemical composition, method of discharge. The rhizodeposits substances comprise: (1) Low-molecular mass compounds, such as amino acids, monosaccharides, water-soluble ions and organic acids which are passively released along a concentration gradient; (2) High-molecular mass compounds, including proteins, carbohydrates that act as lipids and signal molecules which are actively transported along an electrochemical gradient; (3) Insoluble mucilage, made up of polysaccharides and polygalacturonic acid; (4) Secondary metabolites like flavonoids, and nematicides antimicrobial compounds; and (5) Remnants from lysed or dead root border and caps cells (Weston *et al.,* 2013; Zhang *et al.,* 2014). Interaction and Communication within the rhizosphere are initiated when recipient organisms detect the signaling properties of these rhizodeposits. The nature and composition of root exudates can affect the microorganism's diversity and activity in the soil, encouraging the growth of beneficial microbes that enhance productivity and plant health, while also inhibiting harmful microbes in some cases (Chaparro *et al.,* 2012; Dutta *et al.,* 2013; Li *et al.,* 2013).

Rhizosphere Engineering: as an Innovative Tool

The concept of "rhizosphere engineering" was first introduced by O'Connell *et al*. (1996), who suggested manipulating plant exudate production comprising nutrients like amino acids, sugars, organic acids, flavonoids, mucilage, and proteins to attract a beneficial microbiome that can impact the plant's phenotype. Furthermore, it has been proposed that genetically engineered plants could release specific microbial gene inducers, which not only stimulate plant growth but also improve plant health and soil conditions, including through the remediation of pollutants. Rhizosphere engineering can also be achieved by altering the resident microbiota, thereby influencing the plant's metabolism (Roohi *et al*., 2020). The modified rhizobiome has the potential to enhance plant growth or improve tolerance to various environmental and biotic stresses, including pathogen infestations.

This strategy is increasingly recognized as a critical tool for addressing pressing global challenges. These challenges encompass: (i) enhancing the sustainability and productivity of agroecosystems; (ii) mitigating climate change, such as through the enhancement of soil carbon sequestration; (iii) overcoming abiotic and biotic stresses, including extreme pH, salinity, and drought conditions, in crop production; (iv) enhancing soil health and fertility; and (v) enhancing the efficiency of fertilizer and natural resource utilization. While optimizing rhizosphere management for plant productivity

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is important, other aspects of rhizosphere management are equally vital, especially in the context of sustainable ecosystem management and climate change mitigation (Ryan *et al*., 2009; Dubey *et al*., 2022; Zhang *et al*., 2023).

Rhizosphere engineering elicits targeted modifications in the physical, chemical, and biological dynamics of soil (Vetterlein *et al.,* 2020).Among these domains, rhizodeposition—the release of organic and inorganic substances by plant roots—exerts a pivotal influence on microbial activity and the cycling of carbon within the soil matrix.

Microorganisms are essential in the transformation of organic matter, facilitating its stabilization and full mineralization. Mycorrhization is a unique rhizosphere engineering approach that enhances soil carbon sequestration by increasing the transfer of photosynthates belowground (Corrêa *et al.,* 2018), promoting the production and accumulation of mycorrhizal biomass and necromass in the soil, and stimulating plant growth and productivity through nutrient delivery and the formation of soil aggregates. Mycorrhizal fungi support plant growth through various mechanisms, include improved nutrient attainment, alleviation of abiotic and biotic stresses, and the detoxification of heavy metals, which in turn increases root-derived carbon inputs into the soil.

Microbial Interactions within the Rhizosphere

The bacterial community in the rhizosphere plays a crucial role in stimulating the production and germination of spores, as well as the growth of hyphae in arbuscular mycorrhizal (AM) fungi. Both AM fungal spores and plant roots (Bharadwaj *et al.,* 2008; Cruz and Ishii 2011), along with extraradical mycelium (Mansfeld-Giese *et al*., 2002), form primary associations with bacteria in the mycosphere. These bacteria interact with both extraradical mycelium and AMF spores. The nature of this interaction is influenced by factors such as the surface and texture size of the spore wall (Bharadwaj *et al*., 2008). Several bacterial species are found entirely with certain mycorrhizal isolates, while others are more broadly distributed across various AM fungal species (Rillig *et al*., 2005). The interaction between bacteria and AM fungal spores can promote establishment of mycorrhizal associations and spore germination, particularly under suboptimal conditions (Xavier and Germida 2003; Hildebrandt *et al*., 2006). This process is often facilitated by nutrient acquisition, spore wall rupture and bacterial secretion of volatile compounds (Ruiz-Lozano and Bonfante 2000). While bacteria can support AM fungal activities, some studies have indicated that bacteria may inhibit AM fungal growth possibly due to specific interactions between AMF and bacterial species. AMF serve as a link between soil and plant roots and in doing so; they impacts the composition of bacterial communities in the rhizosphere. Furthermore, both bacteria and fungi in the rhizosphere contribute to plant resistance against various environmental stresses. The bacterial diversity in the rhizosphere is primarily composed of beneficial nitrogen-fixing bacteria.

Mycorrhizosphere

The concept of the rhizosphere has been expanded to encompass the fungal component of the symbiosis, leading to the term "mycorrhizosphere". It is shaped by both myceliums of the AMF and plant roots. Consequently, the term "mycorrhizosphere" also includes the particular term "hyphosphere," which refers to the soil zone adjoining individual fungal hyphae, extending outside the rhizosphere into the bulk soil (Johansson *et al*. 2004).

The mycorrhizosphere encompasses the soil region effects by mycorrhizal roots and is composed of two primary mechanisms: (1) the rhizosphere, layer of soil directly adjacent the root system, effects by the root hairs and roots, and (2) the hyphosphere, where interactions between the the surrounding soil and mycorrhizal fungal hyphae occur. Both the hyphosphere and rhizosphere influence a variety of organisms, including bacteria and saprotrophic fungi (Meier *et al.,* 2015). These microbes interact within mycorrhizosphere, impacting both abiotic and biotic factors (Rillig and Mummey 2006).

Significance of Mycorrhizosphere

The mycorrhizosphere plays a pivotal role in sustainable agriculture (Johansson et al. 2004), plant health, nutrient cycling and soil quality (Azcon-Aguilar and Barea 2015). They effectively vital for ecosystem restoration, biological control of root pathogens, soil quality improvement, alleviating osmotic stress and phytoremediation of heavy metals in polluted soils (Barea *et al.*, 2013). Additionally, it is crucial for various applications, including cost-effective

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phytoremediation, carbon sequestration, the development of bioenergy crops (Philippot *et al.,* 2013), the breakdown of pyrene in soil (Li *et al.,* 2008) and mineral weathering (Koele *et al*., 2014).

II. CONCLUSION AND FUTURE PROSPECTIVE

This review emphasizes the substantial role of arbuscular mycorrhizal fungi in supporting agricultural sustainability and improving plant-microbe interactions. AMF contribute to plant growth by facilitating nutrient uptake, particularly phosphorus (P), and improving resilience to environmental stresses such as salinity, pathogen attacks and drought. Additionally, AMF enhance the soil health by improving nutrient mineralization, soil structure, organic matter decomposition and aggregation which not only decerase the requirement for fertilizers but also mitigates nutrient runoff and environmental contamination. Furthermore, arbuscular mycorrhizal fungi role in stress alleviation can improve crop resilience against diseases and pests, decrease dependence on chemical pesticides and maintain ecological balance. Integrating AMF into agricultural practices offers promising solutions to global challenges related to food sustainability and security. By harnessing the beneficial interactions between AMF and plants, we can reduce resource consumption, advance sustainable agricultural methods and enhance crop productivity.

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