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Shalini Devi
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Ashima Choudhary
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Monalisa Mathan
Project Associate-I, Agrotechnology Division, Council of Scientific Research-Institute of Himalayan Bioresource Technology, Palampur, Himachal Pradesh, India

Shivani Dhiman
Department of Genetics and Plant Breeding, Eternal University, Baru Sahib, Himachal Pradesh, India

Pradeepti Sharma
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Aditi Sharma
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Robin Kumar
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Nikhil Thakur
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Kunal Lakhanpal
Division of Fruit Science, SKUAST, Jammu, Jammu and Kashmir, India

Corresponding Author:
Monalisa Mathan
Project Associate-I, Agrotechnology Division, Council of Scientific Research-Institute of Himalayan Bioresource Technology, Palampur, Himachal Pradesh, India

Mycorrhizal symbiosis: Evolution, ecology, and functional dynamics in plant-fungal interactions

Shalini Devi, Ashima Choudhary, Monalisa Mathan, Shivani Dhiman, Pradeepti Sharma, Aditi Sharma, Robin Kumar, Nikhil Thakur and Kunal Lakhanpal

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Abstract
Mycorrhiza refers to the mutually beneficial relationship between fungi and plant roots, which plays a crucial role in nutrient cycling, plant growth, and maintaining ecosystem balance. This review explores different types of mycorrhizas: arbuscular, ectomycorrhiza, orchidaceous, and ericoid—along with their diverse structures and functions. Mycorrhizal fungi enhance the absorption of phosphorus and micronutrients, increase plant tolerance to various biotic and abiotic stresses, and contribute to overall plant health through interactions with beneficial microorganisms such as nitrogen-fixing and phosphate-solubilizing bacteria. Beyond supporting plant growth, these fungi are vital for soil aggregation, carbon sequestration, and the remediation of heavy metal-contaminated soils. Future studies should prioritize selecting efficient strains, improving inoculum quality, and applying molecular tools to gain deeper insights into symbiotic effectiveness. Overall, mycorrhizal technology holds great promise for advancing sustainable agriculture and ecological restoration efforts.

Keywords: Mycorrhiza, arbuscular mycorrhiza, ectomycorrhiza, symbiosis, phosphorus uptake, bioremediation, sustainable agriculture.

Introduction
Mycorrhiza, which derives from the Greek words "mykes" (fungi) and "rhiza" (root), refers to a mutually beneficial relationship between certain soil fungi and a plant's roots. Coined by Frank in 1885 [10], mycorrhizal associations are prevalent in various ecosystems and play a crucial role in plant growth and ecosystem functioning (Brundrett, 2009) [6]. The four types of mycorrhizal associations are arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), orchidaceous mycorrhiza (OrM), and ericoid mycorrhiza (ErM). At least one type of mycorrhizal association present in most plants (Heijden *et al.*, 2015) [28]. Evidence suggests that mycorrhizal associations have been present since the early stages of land plant evolution, dating back to the Ordovician and Devonian periods (Brundrett, 2002) [5]. Mycorrhizal fungi provide various benefits to plants, including enhanced nutrient uptake, particularly of phosphorus and other essential nutrients like nitrogen and micronutrients. They also help in maintaining water balance, reducing oxidative stress, and providing resistance to biotic and abiotic stresses (Bennett *et al.*, 2009) [4].
The symbiotic association between mycorrhizal fungi and plants influences the structure of plant communities in ecosystems and the composition of soil microbial communities in the rhizosphere (Heijden *et al.*, 2008; Toljander *et al.*, 2007) [27, 26]. It is estimated that around 50,000 fungal species form mycorrhizal associations with approximately 250,000 plant species globally, highlighting the widespread importance of these interactions (Heijden *et al.*, 2015) [28]. Mycorrhizal associations play a critical role in plant nutrient acquisition, stress tolerance, and ecosystem functioning, making them an essential component of terrestrial ecosystems. The root colonization process by AM fungi shows in Figure 2.

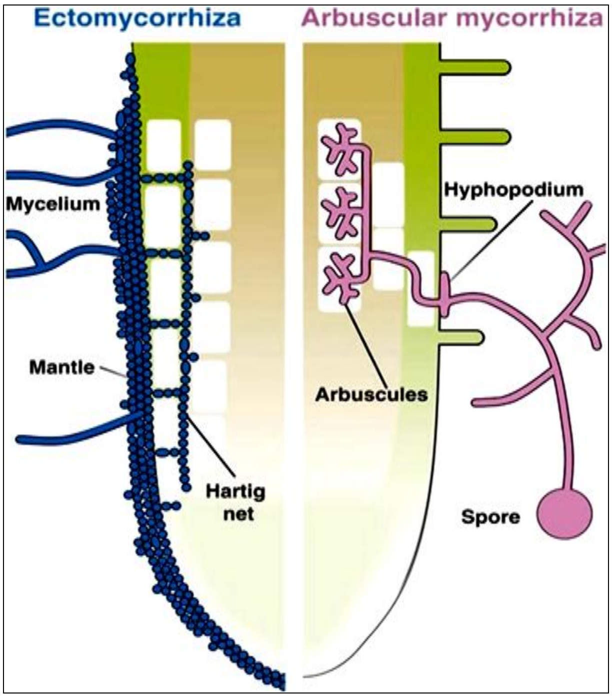


Fig 1: Image of root colony structures under the influence of ectomycorrhiza (blue) and arbuscular mycorrhiza (pink) (Source: Bonfante and Genre (2010).

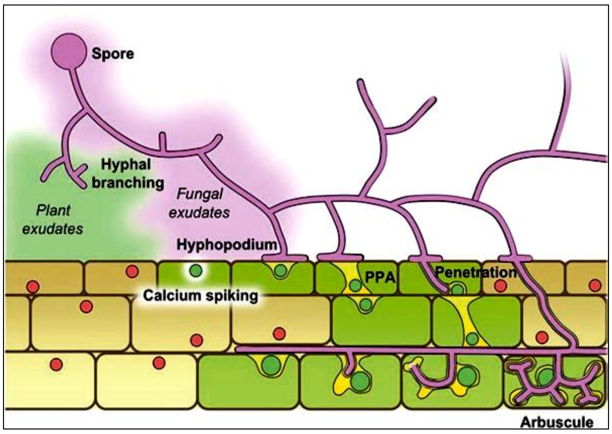


Fig 2: Root colonization process by AM fungi (Source: Bonfante and Genre 2010).

Types of Mycorrhizae

Mycorrhizal fungi are classified into two major types based on their hyphal penetration into the host plant's epidermis and subsequent development: endomycorrhiza and ectomycorrhiza (Fig.1). Endomycorrhiza form structures such as arbuscules, vesicles and spores inside the host cell and includes types such as AM (arbuscular mycorrhiza), ErM (ericoid mycorrhiza), and OrM (orchidaceous mycorrhiza). On the other hand, ectomycorrhiza forms a Hartig net and a thick mantle around the roots. Some mycorrhizal fungi are capable of forming both types of structures, known as ecto-endomycorrhizae, which occur in certain plant species such as the subfamily Ericaceae and Arbutoideae (Heijden *et al.,* 2015) [28]. The mycorrhizal association in plants involves either intracellular (endomycorrhiza) or extracellular (ectomycorrhiza) colonization, where the fungi penetrate the epidermis and enter cells to the exchange of nutrients such as carbon, nitrogen and phosphorus.

Arbuscular Mycorrhiza

Arbuscular mycorrhiza (AM) fungi were previously referred to as vesicular arbuscular mycorrhizal (VAM) fungi, but this term is no longer used because not all AM fungi produce vesicles. More than 80% of vascular terrestial plants and 74% of all plant species can now associate with AM fungi, making them widespread in terrestrial ecosystems, including aquatic plants and agroecosystems, and in metal-polluted soils (Brundrett 2009) [6]. However, certain plant families such as Brassicaceae, Chenopodiaceae, Polygonaceae, Juncaceae, Caryophyllaceae and Proteaceae, do not exhibit mycorrhization.

Studies by Kivlin *et al.* (2011) [14] estimated that there are between 300-1600 species of AM fungi belonging to the phylum Glomeromycota. These fungi were reported to form symbiotic relationships with Devonian gametophytes of early land plants. In the symbiotic association, AM fungi form hyphae, arbuscules, vesicles and spores inside the root cortex of the host plant, as well as hyphae, vesicles, and spores outside the roots. However, members of the Gigasporaceae family produce auxiliary cells instead of vesicles. (Fig.3).

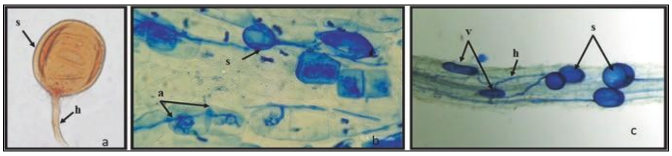


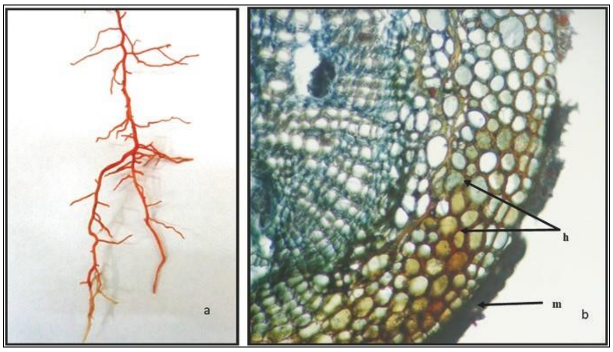
Fig 3: Arbuscular mycorrhizal fungi are shown: (a) AM fungi spore, (b and c) AM colonization in Sorghum plant roots with different structures, where h hyphae, a arbuscules, v vesicles and s spores (Source- Pandey *et al.*,2019) [16].

The mycorrhizal formation that results from intraradical hyphal modification is typically classified as either Paris type and the Arum type. The Paris type is present in 41 angiosperm families and present exclusively intracellular and forming coils within cortical cells. In contrast, the Arum type present intercellular and form arbuscules within cortical cells and occurring in 30 angiosperm families. Both types are found in 21 families (Dickson, 2004) [9].

Furthermore, indigenous AM fungal isolates that are adapted to specific native soil types have been shown to promote plant growth. AM fungi play a crucial role in mitigating the negative effects of stress on plants and act as a barrier to filter out heavy metals, preventing their transfer from roots to plant shoots. These fungi are obligate biotrophs, meaning that they depend entirely on living host roots to grow and complete their life cycle. As a result, no synthetic medium is currently available for the *in vitro* proliferation of AM fungi. However, researchers have made several attempts to create artificial culture media that can support the growth of these fungi (Hildebrandt *et al.*, 2007) [13]. The obligate biotrophic nature of AM fungi is still a major limitation in their artificial cultivation.

Ectomycorrhiza

Ectomycorrhiza (EcM), an essential symbiotic relationship between certain fungi and plant roots, manifests crucial anatomical structures recognized as the Hartig net and mantle in gymnosperms, angiosperms (specifically shrubs and trees), and a select few liverworts dwelling in temperate zones. Predominantly comprising fungal species from the Basidiomycota and Ascomycota phyla, estimated at around 20,000, this association also involves some representatives of the Zygomycota. Extending its influence over a diverse spectrum, the EcM symbiosis spans over 6,000 plant species, as documented by Brundrett (2009) [6]. Tracing back to the Jurassic era, the earliest fossil indications of EcM suggest a probable initiation with Pinaceae, potentially marking them as pioneers in forming this intricate bond. Molecular analyses and phylogenetic studies lend support to the notion that EcM arose from ancestors within woody saprophytic fungal lineages, as proposed by Tedersoo *et al.* (2010) [25]. The evolutionary trajectory of EcM appears intricately intertwined with the exigencies of nutrient limitation in temperate soils, particularly conspicuous in boreal forest ecosystems, possibly precipitating the development of this symbiotic association. Ectomycorrhizal (EcM) symbiosis engenders the creation of diverse anatomical formations, notably the Hartig net, which intricately extends within the confines of the root, and the mantle, characterized by a dense, intricate woven configuration enveloping the root structure, as depicted in Figure 4.



Illustrated in Figure 4 are images depicting the symbiotic relationship between ectomycorrhizal fungi and their host, exemplified by (a) a root of Pinus sp. visibly colonized by such fungi and (b) a cross-sectional view (T.S.) of a Pinus root, revealing the intricate structures of the Hartig net (h) and mantle (m). This information is sourced from Pandey *et al*. (2019) [16].

Importance of mycorrhiza: Mycorrhizal associations play a crucial role in various aspects of plant health and soil ecology:

Root disease suppression: Beneficial microorganisms, including mycorrhizal fungi such as AMF (Arbuscular mycorrhizal fungi), compete with plant pathogens for nutrients and space, thereby suppressing root diseases. These microorganisms produce antibiotics, parasitize pathogens, or induce resistance in host plants, leading to a reduction in pathogen populations.

Enhancing plant nutrition uptake: Mycorrhizal fungi improve plant growth by enhancing the mineral nutrient status of plants, particularly phosphorus uptake (Sharma *et al.*, 2007) [21]. After colonizing the roots, mycorrhizal hyphae spread inter- and/or intra-cellularly in the root cortex without damaging the integrity of the cells, facilitating nutrient uptake (Strack *et al*., 2003) [23].

Damage compensation: Mycorrhizal fungi possess the capacity for damage compensation wherein they enhance the host's resilience against pathogenic assaults originating from the soil. This is achieved by mitigating the adverse effects inflicted upon the host, such as the impairment of root function and reduction in biomass, resulting from the activities of soilborne pathogens.

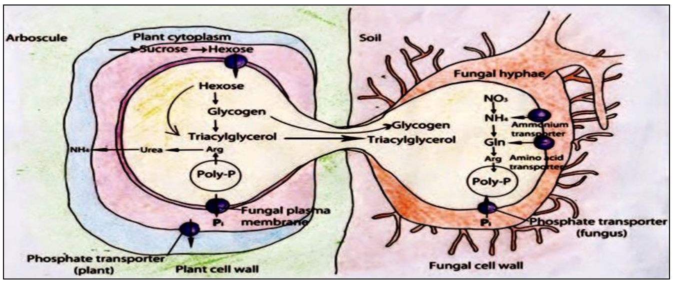
Soil microbial population interactions: Mycorrhizal fungi interact with other soil biota, improving plant nutrition and overall soil health.

Nutrient transportation across the plant and fungus: Mycorrhizal associations facilitate the transportation of nutrients between the plant and the fungus, enhancing nutrient uptake and utilization efficiency.

Enhanced tolerance to heavy metals (bioremediation): Mycorrhizal plants have been shown to enhance tolerance to heavy metals, such as copper and zinc, by increasing their uptake and accumulation in plant tissues. This can contribute to bioremediation efforts in contaminated soils (Clark and Zeto, 2000; Raju *et al.*, 1990) [7, 18].

Plants provide carbon to their fungal partners: Plants assume a pivotal role in sustaining their fungal counterparts within mycorrhizal associations through the provision of carbon. This intricate process involves the transportation of photosynthetically derived hexose to the arbuscular regions of fungal cytoplasm, where it undergoes conversion into glycogen and triacylglycerol (TAG) (Figure 4). These metabolites, adept at traversing long distances within the fungal network, serve as vital energy sources, nurturing fungal growth and metabolic activities, thus fostering mutualistic relationships. Furthermore, mycorrhizal associations confer reciprocal benefits upon plants by amplifying root surface area, thereby augmenting the absorption of water and nutrients. This enhancement is particularly pronounced in nutrient-depleted tropical regions experiencing abundant rainfall, where essential elements such as nitrogen, phosphorus, potassium, and calcium are prone to leaching from soil surfaces. In response, mycorrhizal fungi extend their external hyphae beyond the impoverished zones, effectively expanding the soil volume accessible to plant roots. Consequently, plants engaged in mycorrhizal associations exhibit heightened efficiency in nutrient uptake, underscoring the symbiotic synergy between plants and fungi in optimizing ecological resource utilization.

Nutrient transportation across the plant: The interface established by fungi assumes paramount importance, particularly concerning the acquisition of immobile soil elements such as phosphorus. Vascular-arbuscular (VA) fungi play a pivotal role in this context by facilitating the delivery of phosphorus to plant roots via phosphate transporters embedded within their hyphal membrane. The filamentous extraradical hyphae of arbuscular mycorrhizal (AM) fungi further contribute by aiding in the uptake of readily available phosphates from the soil, while also exhibiting the capacity to enzymatically hydrolyze organic phosphates, thus rendering them soluble for absorption by the host plant. Moreover, phosphate transporters belonging to the PhT_1 family within fungi facilitate the internalization of inorganic phosphate into the cytosol, where it undergoes polymerization, forming polyphosphate chains (poly-P). These polyphosphates are subsequently translocated to the intraradical hyphae, where their hydrolysis liberates free phosphate molecules for transfer to the interfacial apoplast of the AM fungi. The fungi, thus, serve as conduits for the provision of phosphorus to plants in the form of a polyphosphate reservoir, thereby facilitating nutrient acquisition. Notably, in phosphate-deficient soil environments, mycorrhizae extend their beneficial influence by also aiding in the absorption of other essential elements such as copper and zinc through analogous mechanisms, as illustrated in Figure 4.



In Figure 4, delineating the intricate process of nutrient translocation between the plant and fungus, critical elements like phosphate and nitrogen are acquired. Phosphate, sourced by the fungal symbiont, is conveyed to the plant via the phosphate transporter PhT_1. Likewise, nitrogen is transported through the nitrogen transporter AMT_1 to the plant counterpart. In reciprocity, the plant furnishes carbonaceous substrates to its mycorrhizal fungal associates, thereby fostering their nutritional requirements.
(Adapted from M. Parniske, Nature Reviews Microbiology, Vol. 6, pp. 763-775, 2008) [15].

Interaction Between AM Fungi and Other Beneficial Organisms

Interaction of AM Fungi with Symbiotic Nitrogen Fixers

The interaction between arbuscular mycorrhizal (AM) fungi and symbiotic nitrogen-fixing organisms, such as the legume bacterium Rhizobium species, has been widely studied. These investigations indicate a synergistic relationship, wherein AM fungi improve both nodulation and AM fungal colonization, resulting in enhanced plant growth. Leguminous plants, in particular, have exhibited a pronounced need for elevated levels of phosphate to facilitate effective nodulation and robust growth, given the substantial phosphate demand inherent in nitrogen fixation processes (Gibson, 1976) [11]. While the principal impact of mycorrhizal symbiosis on nodulation predominantly operates through phosphate mediation, ancillary effects also come into play. These secondary effects encompass the provision of photosynthates, trace elements, and plant hormones, all of which exert significant influence on nodulation and nitrogen fixation processes. Notably, colonization by arbuscular mycorrhizal (AM) fungi has been observed to elevate the levels of phytoalexins, specifically iso-flavanoid substances, within certain legume root systems. These compounds are acknowledged for their capacity to stimulate the expression of nod genes, thus enhancing the nodulation process.This discovery has opened up new avenues of research into the role of AM fungi in regulating the expression of nodulation genes in rhizobia (Suresh and Bagyaraj, 2002) [24].
Spanish researchers have observed that cell-free extracts of Rhizobium can enhance the colonization of the host by AM fungi. This phenomenon was later attributed to the presence of extracellular polysaccharides produced by Rhizobium, which increase the number of entry points of AM fungi per unit length of root (Reverkar *et al.*, 2005) [19]. The interaction between arbuscular mycorrhizal (AM) fungi and asymbiotic nitrogen fixers has been studied extensively. Bagyaraj and Menge (1978) delved into the intricate interplay between *Azotobacter chroococcum* and the arbuscular mycorrhizal (AM) fungus *Glomus fasciculatum* within tomato plants, unveiling a synergistic effect that significantly bolstered plant growth. Their investigation revealed that mycorrhizal infection elicited a notable surge in the population of *A. chroococcum* within the rhizosphere, sustaining it at elevated levels for prolonged durations. Moreover, *A. chroococcum* augmented both colonization and spore production by the mycorrhizal fungus. Analogous synergistic interactions were documented between *A. paspali* and AM fungi in paspalum, as well as between *A. chroococcum* and *G. fasciculatum* in tall fescue.
Furthermore, explorations into the interplay of AM fungi with phosphate-solubilizing bacteria shed light on intriguing dynamics. Phosphate-solubilizing bacteria, exemplified by strains like *Agrobacterium sp*. and *Pseudomonas sp*., when inoculated onto seeds and/or seedlings, demonstrated a propensity for maintaining heightened populations over extended periods within the rhizosphere of mycorrhizal roots, surpassing those observed in non-mycorrhizal root environments of lavender and maize plants (Dar, 2010) [8]. The co-inoculation of AM fungi alongside phosphate-solubilizing bacteria yielded notable enhancements in plant dry matter and phosphorus uptake from the soil. Furthermore, these bacteria exhibited the capacity to produce plant growth hormones, thus further amplifying the overall growth potential of the plants.
Raj *et al*. (1981) [17] undertook a comprehensive examination into the impact of *Glomus fasciculatum*, alongside a phosphate-solubilizing bacterium strain of *Bacillus circulans* devoid of phytohormone production, on phosphate solubilization dynamics, finger millet growth and phosphorus uptake derived from labeled tricalcium phosphate and superphosphate. Their findings unveiled that while arbuscular mycorrhizal (AM) fungi did not directly engage in the solubilization of unavailable phosphorus forms, they nonetheless facilitated heightened phosphorus uptake, presumably attributable to their adeptness in enhancing soil exploration capabilities.

Synergistic Dynamics Between Arbuscular Mycorrhizal Fungi and Mycorrhiza Helper Organisms: The co-inoculation strategy involving arbuscular mycorrhizal (AM) fungi alongside Mycorrhiza Helper Organisms (MHO) has demonstrated efficacy in augmenting mycorrhizal colonization, consequently fostering enhanced plant growth and yield outcomes. Within the realm of high-tech agriculture, characterized by practices often entailing cultivation in sterilized soil or controlled nursery environments, the application of disinfection treatments poses a potential challenge. These treatments, while intended to eliminate indigenous AM fungi and root pathogens, inadvertently jeopardize the presence of beneficial MHO. Consequently, this disruption in microbial balance can lead to suboptimal colonization by AM fungi and diminished plant benefits.
To circumvent this predicament, a proposed solution entails the development of milder disinfection protocols capable of selectively targeting indigenous AM fungi and root pathogens, while concurrently preserving the beneficial MHO. This nuanced approach aims to mitigate the unintended consequences associated with conventional disinfection practices, thereby facilitating the maintenance of symbiotic relationships crucial for optimal plant health and productivity.
Looking ahead, there exists a promising prospect for the integration of MHO within commercial mycorrhizal inoculum formulations. By incorporating MHO into these inoculants, the efficiency of inoculation can be significantly enhanced across diverse environmental conditions, thereby reducing the requisite quantity of inoculum needed while concurrently broadening the scope of application scenarios. This forward-looking approach holds considerable potential in bolstering agricultural sustainability and productivity through the judicious harnessing of symbiotic microbial interactions.

Interactions Between Arbuscular Mycorrhizal Fungi and Plant Pathogens

Numerous studies have demonstrated that AM fungi can reduce or mitigate the severity of diseases caused by various plant pathogens. AM fungi have been shown to consistently reduce disease symptoms caused by fungal pathogens such as *Phytophthora species, Fusarium species, Rhizoctonia solani*, and *Botrytis species*, as well as bacterial pathogens like *Pseudomonas syringae* and *Ralstonia solanacearum* and nematodes including *Meloidogyne* and *Pratylenchus* species (Bagyaraj, 2006; Bagyaraj & Chawla, 2012) [2, 3]. Mycorrhizal plants exhibit a propensity to host elevated populations of microorganisms within the rhizosphere, presenting a formidable challenge for pathogens seeking to establish root access and compete for resources. Furthermore, the rhizosphere of mycorrhizal plants is enriched with microorganisms capable of producing siderophores, specialized chelating agents known to impede the growth of various pathogens. Notably, the abundance of these siderophore-producing microorganisms is notably higher in mycorrhizal plant rhizospheres. Additionally, mycorrhizal plants demonstrate a heightened presence of actinomycetes, known for their antagonistic properties against root pathogens (Azcon-Aguilar & Barea, 1996) [1].

An example of the beneficial interaction between AM fungi and plant pathogens is observed in the wilt disease of the medicinal plant *Coleus forskohlii* caused by *Fusarium chlamydosporum*. Inoculation with both AM fungi and Trichoderma viride was found to increase root yield and root forskolin concentration while significantly reducing the severity of the disease under field conditions (Singh *et al.***,** 2012) [22].

Ecological Significance

The evolutionary trajectory of mycorrhizal associations within plants is characterized by a stable process, wherein fungal partners demonstrate adeptness in efficiently exchanging resources. Nonetheless, the efficacy of this resource exchange mechanism exhibits variability across different plant species (Walter *et al.*, 2002) [29]. Within the vast majority of ecosystems, mycorrhizal fungi assume a pivotal role in facilitating essential transfers, encompassing nutrients, water, and occasionally carbon. For instance, in tropical ecosystems, prevalent species such as *Rizophagus irregularis* and *Funeliformis mosseae* typify arbuscular mycorrhizal (AM) fungi.

The ecological significance of mycorrhizal associations is profound, extending to various facets of ecosystem functioning. They contribute significantly to seedling establishment (Heijden and Horton, 2009), aid in litter decomposition, promote soil formation, facilitate soil aggregation, and play a fundamental role in shaping and sustaining plant communities. Additionally, mycorrhizal associations support plant invasion in new communities. By binding nutrients in the soil, mycorrhizal associations reduce leaching and promote nutrient efficiency, thereby contributing to ecosystem stability (Fig. 5).

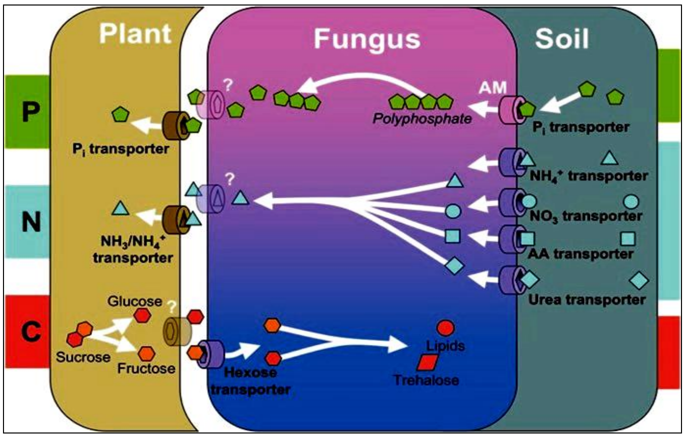


Fig 5: illustrates a schematic representation summarizing the principal nutrient exchange mechanisms observed within ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) symbiotic associations (Source: Bonfante and Genre (2010)

Conclusion and Future Prospects

In conclusion, the evolution of mycorrhizal associations has occurred in tandem with changing climatic conditions, leading to coevolution with different host plants across various habitats. These associations play a crucial role in helping host plants adapt to stressful environments, including those contaminated with heavy metals and toxic chemicals, as well as polluted water sources. In modern agricultural practices, mycorrhizal associations, particularly arbuscular mycorrhiza (AM), are widely utilized to enhance crop production and soil health. The ongoing decline in plant diversity and persistent agricultural practices present formidable obstacles to the diversification of mycorrhizal symbioses. To advance, concerted research endeavors are imperative to delve deeper into the genetic underpinnings, intricacies of interaction biology, and mechanisms of tolerance exhibited by mycorrhizal associations. Field assessments hold paramount importance in corroborating findings gleaned from controlled pot culture trials, while screening initiatives should prioritize the identification of crop plants that exhibit a pronounced dependency on mycorrhizal symbiosis for subsequent inoculation.

Furthermore, endeavors should strive to ascertain the optimal arbuscular mycorrhizal (AM) fungi strains tailored to specific crop plants, alongside probing agricultural methodologies conducive to enhancing the activity of indigenous AM fungi. Moreover, comprehensive investigations should explore the interplay between mycorrhizal associations and other beneficial soil microorganisms, in addition to evaluating the biocontrol potential of AM fungi against soil-borne plant pathogens. Screening efforts targeting potential mycorrhiza helper organisms warrant intensified focus, alongside heightened research endeavors dedicated to understanding parasites and predators within the AM fungal ecosystem.

Furthermore, efforts should be directed towards improving the quality of commercial mycorrhizal products and establishing labs to test quality control norms. Lastly, experiments utilizing molecular techniques are needed to track the competitive ability of introduced AM fungi with indigenous counterparts. Overall, further research and development efforts are crucial for maximizing the potential of mycorrhizal associations in sustainable agriculture and environmental remediation.

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