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Mycorrhiza: The Importance of This Hidden Network

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ABSTRACT

Mycorrhizal symbiosis represents a mutualistic association between fungi and plant roots which significantly impacts terrestrial ecosystems. Mycorrhizal fungi enhance plant nutrient acquisition, especially phosphorus (P) and nitrogen (N). In contrast, plants hand over carbon (C) from photosynthesis, making mycorrhizal fungi relevant in P, N and C cycling in forest ecosystems. Furthermore, they can improve soil health, water absorption, and plant defense against environmental stress. Besides nutrient exchange, mycorrhizal symbiosis facilitates plant communication, creating a hidden underground mycorrhizal network, known as common mycorrhizal network (CMN). Arbuscular mycorrhizae and ectomycorrhizae, together with ericoid mycorrhizae, are the most geographically widespread mycorrhizal types, colonizing over 85% of vascular plants in terrestrial ecosystems. Understanding mycorrhizal dynamics can be useful for improving forestry, agriculture and climate change mitigation activities. This review paper analyzes the mechanisms and benefits of mycorrhiza.

Keywords: black truffles; mycorrhizal fungi; plant nutrition; root fungi; seedling inoculation; soil health

INTRODUCTION

Fungi are irreplaceable in numerous microbiological and ecological processes in terrestrial ecosystems. They influence soil fertility, organic matter decomposition, mineral cycling and they can contribute to plant health and nutrition. As heterotrophic organisms, fungi have evolved three distinct trophic strategies. They function as mycorrhizal symbionts, saprophytes, and pathogens (Finlay 2008, Egli 2011, Adnan et al. 2022), while the ratio of these trophic groups can be a reliable indicator of health status (Brinkmann et al. 2019).

Fungi are most abundant in forest ecosystems (Adnan et al. 2022), where many of them form mycorrhizal relationships with woody plants (Laanisto et al. 2025). Mycorrhizae are mutualistic relationships between plants and fungi in which fungi provide nitrogen (N) and phosphorus (P) to plants. In return, plants provide photosynthetically fixed carbon (C) and nutrients (vitamins) to fungi (Kumar and Atri 2018, Soudzilovskaia et al. 2019). Thus, both partners are nutritionally dependent on each other (Martin and Van Der Heijden 2024). Professor A. B. Frank (1885) is considered one of the first to recognize this ubiquity of the partnership between plants and fungi (Trappe 2005). He was the first to use the term "mycorrhiza" (from the Greek *mykês* for fungus and *rhiza* for root), which means "fungal root" or "fungus-infected root" (Egli and Brunner 2011). Today, mycorrhizal associations occur in almost all ecosystems, from deserts and tropical forests to cultivated farmland. In mycorrhizal symbiosis, plants give 5–40% of the sugars they produce during photosynthesis to the fungi and, in return, receive vital nutrients from the soil that would not be available to them without the fungi (Tedersoo et al. 2014, Van Der Heijden et al. 2015). Hence, in natural ecosystems mycorrhizal fungi play a crucial role in facilitating the acquisition of nutrients by plants. Up to 80% of their N needs and as much as 90% of P requirements are sourced through intricate hyphal networks adapted to explore and extract soil nutrients (Van Der Heijden and Horton 2009). Mycorrhizae can be understood as an interface between plant and fungus where a mutual exchange of resources takes place, providing a much-needed link between roots, fungus and soil (Futai et al. 2008, Anthony et al. 2022).

The wide-ranging nature of mycorrhizal symbiosis is reflected in its far-reaching effects on plant and microbial communities, ecosystem processes, and various interactions between organisms. These include mobilization of P and N from organic polymers, release of nutrients through mineral weathering, C cycling, interactions with myco-heterotrophic plants (plants entirely supported by a fungus) (Brundrett 2004) and regulation of plant responses to stressors such as drought, soil acidification, toxic metals, and pathogens (Finlay 2008).

This review aims to provide a summary of the basic knowledge on mycorrhiza, with a particular emphasis on arbuscular mycorrhizae and ectomycorrhizae, which are the most common mycorrhizal fungi forming symbiotic relationships with plant species in forest ecosystems.

MYCORRHIZAL TYPES IN FOREST ECOSYSTEMS

Considering the structure and physiology of the plant host, there are two main types of mycorrhizae: ectomycorrhiza and endomycorrhiza (arbuscular mycorrhiza) (Mohammadi et al. 2011, Huey et al. 2020, Chen et al. 2024). They differ in the contact area between plant and fungus because, in ectomycorrhiza, septate hyphae surround the root cells, while in endomycorrhiza, the non-septate hyphae penetrate the root cells. Morphological classifications of mycorrhizae in the second half of the 20th century divided them into ectomycorrhiza, endomycorrhiza, and ectendomycorrhiza (Brundrett 2004b).

More precisely, seven or more types of mycorrhiza have been described based on morphological and anatomical characteristics and taxonomy of plant hosts or fungi. These seven types are ectomycorrhiza (ECM), arbuscular or vesicular-arbuscular mycorrhiza (AM/VAM), ericoid mycorrhiza, arbutoid mycorrhiza, monotropoid mycorrhiza, ectoendomycorrhiza, and orchid mycorrhiza (Brundrett 2004, Sangeetha et al. 2023). Of these, four representative types are shown in Figure 1 to illustrate key structural differences. AM, ECM, and ericoid mycorrhiza are the most geographically widespread mycorrhizal types, colonizing over 85% of vascular plants in terrestrial biomes, as Soudzilovskaia et al. (2019) reported. Most AM plants are facultative mycorrhizal plants, while ECM plants are mainly obligatory mycotrophic (Tedersoo and Brundrett 2017). This article describes the crucial role of AM and ECM in forest ecosystems, especially the role of ECM in temperate forests.

Arbuscular Mycorrhiza (AM)

Arbuscular mycorrhizal symbiosis is a very ancient and vital reciprocal relationship between plants and fungi. This symbiotic association dates back to about 450 million years ago, long before the development of what are considered "true" roots in plants (Kuyper and Jansa 2023). The partnership between plants and arbuscular mycorrhizal fungi (AMF) of the Glomeromycota allowed early plants to improve their ability to absorb nutrients, such as P and N (Finlay 2008), which allowed land colonization by plants (Bucking et al. 2012). AM symbiosis is characterized by intricately branched fungal-type structures known as arbuscules and globular structures vesicles, which grow within plant cells (intracellularly), but do not penetrate the host's plasmalemma (Finlay 2008, Van Der Heijden et al. 2015). Involving primitive, non-septate fungi, AM supports predominantly 80–90% of phototrophic plants (Courty et al. 2010). AM symbioses can evolve with a wide range of plant species, possibly up to 200,000–250,000 different plant species. While traditional morphological approaches have identified only 150–200 different AMF species, modern DNA-based studies suggest that the actual diversity may far exceed these numbers. It is estimated that 300–1,600 fungal taxa from the Glomeromycota group form AM with most herbs, grasses, many trees, hornworts, and liverworts. These fungal taxa are associated with about 200,000 plant species, indicating low host specificity. Although host preferences and selectivity have been widely reported, there is no compelling evidence that AMF exhibit strict host specificity. The richness of AM fungal communities is very high compared to global species richness, and the composition of AM fungal communities depends on factors such as host plant characteristics, climate, and soil conditions. In addition, intensive land use has been observed to disrupt AM fungal communities, as AM symbiosis is highly sensitive to soil disturbances and chemical interaction (Van Der Heijden et al. 2015, Wilkes 2021).

Ectomycorrhiza (ECM)

Most tree species form symbiotic relationships with ectomycorrhizal fungi (EMF) (Satomura et al. 2006) to facilitate their access to growth-limiting soil resources. ECM symbiosis has repeatedly occurred in plants and fungi, and the earliest ECM communities involved Pinaceae (Tedersoo and Brundrett 2017). Although it is difficult to determine the exact timing of the origin of EMF, it probably began about 150–220 million years ago. This transition from AM to ECM supported colonizing regions with organic matter, such as the temperate and boreal zones (Courty et al. 2010). EMF form symbiotic relationships with about 60% of the world's trees and are an essential component of the forest soil microbiome (Suz et al. 2014, Anthony et al. 2022). They take a central ecological place in temperate, boreal, and Mediterranean forests and tropical regions, predominantly comprising trees and woody shrubs (Kumar and Atri 2018).

Within the ECM, the fungi envelop the root and form a so-called mantle or sheath. The shapes and colors of mantles vary extensively, primarily influenced by the EMF species responsible for their formation and, to a much lesser extent, by the plant partner involved (Janowski and Leski 2023). They spread into the root cortex, forming an intercellular fungal mycelium network known as a Hartig's network (Courty et al. 2010, Tyub et al. 2015), which serves as a central zone for nutrient exchange (Brundrett 2004). EMF have undergone a reduction in their capacity to break down polysaccharides found in plant cell walls, such as cellulose, pectins and pectates. Consequently, this limitation impedes their ability to infiltrate the root and access intercellular spaces (Bucking et al. 2012). Furthermore, ECM develops mainly on short and fine feeder roots (generally, fine roots are less than 2 mm in diameter) (Kubisch et al. 2016, Williams et al. 2023) rather than long lateral roots (Molina et al. 2003, Tyub et al. 2015).

The estimated number of plants entering ECM relationships is 6,000, with approximately 20,000 fungal species, which is more than 250 genera from the Basidiomycota, Ascomycota and very few from the Zygomycota (Van Der Heijden et al. 2015, Kumar and Atri 2018, Janowski and Leski 2023). Sexual reproduction occurs in sporocarps formed by the soil mycelium, and many EMF form aboveground (epigeous) or belowground (hypogeous) fruiting bodies (Molina et al. 2003). The characterization and identification of fungal species in classical mycology rely on the morphology of sporocarps and the spores they produce (Huey et al. 2020, Janowski and Leski 2023).

The numerous EMF species include those from the genera *Amanita, Tuber, Boletus, Cortinarius, Suillus, Russula, Gomphidius, Hebeloma, Tricholoma, Laccaria,* and *Lactarius*

(Molina et al. 2003, Tyub et al. 2015), which have a significant part in the survival and growth of trees (Ważny 2014). Most ECM studies were conducted in temperate and boreal coniferous forests and have concluded that the dominant members of ECM fungal communities associated with conifer roots include *Cenococcum geophilum*, as well as species within Clavulinaceae, Russulaceae, and Thelephoraceae families (Kumar and Atri 2018). Woody plant species that form ECM belong to Pinaceae, Abietaceae, Fagaceae, Tiliaceae, Betulaceae, and Myrtaceae families. In the family Betulaceae, the genus *Alnus* forms a dual symbiosis with EMF and AMF, the same as the Salicaceae and part of the Rosaceae (Courty et al. 2010). Although these species make up only a relatively small proportion of the total land plant population, they often dominate forest ecosystems and occupy remarkably large areas (Finlay 2008). Furthermore, plant hosts of EMF are economically and ecologically important forest tree species from the genera *Pinus*, *Picea*, *Abies*, *Populus*, *Salix*, *Fagus*, *Betula*, and *Quercus* (Satomura et al. 2006), and southern hemisphere trees such as *Eucalyptus* (Vellinga et al. 2009, Tyub et al. 2015). While the diversity of ECM plants remains limited, the variety of fungal species involved in ECM associations far surpasses that found in other mycorrhizal types (Janowski and Leski 2023).

Most EMF form complex mycelial networks or rhizomorphs that extensively traverse the surrounding soil with a vital role in transporting and storing nutrients and water. Mycorrhizal fungi have a central function in the nutrient cycling of various vegetation types. They help break down organic and inorganic compounds, release and assimilate minerals, and transport nutrients to host plants along with numerous organisms (Tyub et al. 2015). Since mycorrhizal fungi require C from plants, and in return increase P and N uptake by plants, they are relevant in C, P and N cycling in natural ecosystems, but also for other trace elements such as potassium (K),sulfur (S), iron (Fe), copper (Cu), zinc (Zn) and manganese (Mn) (Jha and Songachan 2023, Shi et al. 2023, Martin and Van Der Heijden 2024).

NUTRIENT ACQUISITION AND NUTRIENT CYCLE

While P is essential for plant productivity, yield, and survival, its availability to plants is often limited in most soils, since P in the soil exists in forms such as organic and inorganic phosphates. Apart from P, which represents the primary advantage gained by the host plant through AM associations, the impact of AMF on plant N nutrition is comparatively modest. In contrast, EMF plays a more significant role in N cycling (Soudzilovskaia et al. 2019, Shi et al. 2023). ECM plants are typically known to colonise soils containing nutrients bound in organic compounds. This could explain why ECM tree species tend to dominate cool-temperate and boreal forests, while AM species are more present in tropical and subtropical forests (Kubisch et al. 2016).

Phosphorus and Nitrogen Uptake by Mycorrhizae

Mycorrhizal plants have two pathways for nutrient uptake (Huey et al. 2020). Firstly, the plant pathway involves direct absorption of nutrients by the non-mycorrhizal roots from the soil. Then, in contrast, the mycorrhizal pathway involves nutrient absorption through the extraradical mycelium (ERM) of the fungus. In ECM associations, nutrients are

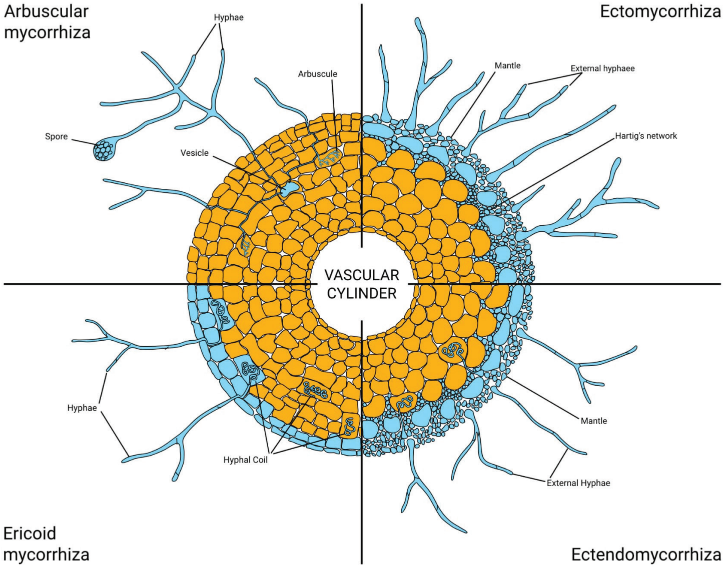

Figure 1. Structural comparison of four different mycorrhizal types associated with plant roots. Arbuscular mycorrhiza: non-septate hyphae enter root cells and form arbuscules and vesicles; the dominant type of mycorrhiza in agricultural lands. Ectomycorrhiza*:* septate hyphae surround root cells, forming Hartig's network and mantle; important in forest ecosystems because most ectomycorrhizal plants are trees. Ericoid mycorrhiza: septate hyphae enter root cells; includes most plant species from the Ericaceae family (Ward et al. 2022). Ectendomycorrhiza: mycorrhiza with characteristics of both ecto- and endomycorrhiza; the plant hosts are primarily *Pinus* and *Larix* species (Yu et al. 2001). Illustrated by Anamarija Zegnal.

transported to Hartig's network, while in AM associations they are transported to the intraradical mycelium. The fungal hyphae extending within mycorrhizal roots are referred to as intraradical mycelium, whereas the portion of hyphae present in the soil is known as ERM (Futai et al. 2008, Shi et al. 2023). Nutrient uptake through the plant pathway is frequently constrained by the limited mobility of nutrients in the soil. The low mobility of elements, like P, can quickly establish depletion zones around the roots, restricting further P absorption through the plant pathway, and in such scenarios, plants derive significant advantages from utilising the mycorrhizal pathway (Shi et al. 2023).

The selection of plant or mycorrhizal pathway by mycorrhizal plants depends on the levels of nutrient availability in the soil (Shi et al. 2023). The expansive system of extraradical hyphae originating from mycorrhizal root tips enhances the root's absorptive surface area, enabling efficient exploration of the surrounding soil (Zhang et al. 2023). The root hairs extend about 1–2 mm, while the AM hyphae extend 8 cm or more beyond the root, significantly increasing the area where P is available to the plant (Mohammadi et al. 2011).

The mycelium of EMF facilitates the liberation of complexed nutrients by secreting extracellular enzymes and acids (Kumari and Atri 2018). These enzymes play a role in releasing inorganic phosphate from organic sources like phospholipids, nucleic acids, and proteins. Moreover, mycorrhizal fungi synergise with phosphate-solubilising bacteria (PSB) that convert organic phosphate into inorganic phosphate, which the mycorrhizal fungi can then absorb and transport to their host plant (Shi et al. 2023).

ECM plant communities usually prevail in ecosystems characterized by low availability of N in the soil and where N supply is often a limiting factor for plant growth. The possibility of a dual lifestyle makes EMF facultative saprotrophs. They are highly competitive in soil conditions for nutrient uptake and also release various hydrolytic enzymes to break down litter polymers and exploit organic sources of nutrients. Most N in forest soils is present in organic form, so it can be formed through litter, decay, root decomposition and decomposition by soil organisms (Shi et al. 2023). Hence, approximately 95% of the N in the soil is contained in the soil organic matter (SOM) (Pellitier and Zak 2018, Laganière et al. 2022). While EMF efficiently take up inorganic N from the soil, their ability to utilize organic N sources is crucial for the N supply of their plant symbionts (Bucking et al. 2012). In particular, the importance of N uptake by mycorrhizae appears to differ between AM and ECM forests. Inorganic forms of N are significant in AM forests, while organic forms are significant in ECM forests (Rotter et al. 2020). The ERM of mycorrhizal fungi serves to absorb both inorganic forms of N, ammonium (NH_4^+) or nitrate (NO_3^-), and organic N in the form of amino acids from the soil, thus facilitating the transfer of N. In this context, it is noteworthy that AMF generally prefer NH_4^+ over NO_3^-. This preference arises from the fact that NO_3^- must be converted to NH_4^+ before incorporation into organic compounds, which requires additional energy (Shi et al. 2023). Therefore, NH_4^+ is often referred to as the preferred N source for mycorrhizal fungi, as it can be taken up more efficiently in terms of energy compared to NO_3^- (Bucking et al. 2012).

Although there are differences in the mechanisms by which EMF and AMF facilitate the uptake of nutrients (Liese et al. 2018), mycorrhizal fungi greatly facilitate the uptake of nutrients, especially in hard-to-reach soil zones. Further evidence and detailed description of these mechanisms have been reviewed by Shi et al. (2023).

Carbon Stocks

EMF dependent of their hosts' ability to produce organic C and up to 50% of plants photo-assimilates can be transferred to EMF (Niego et al. 2023). Plant nutrient acquisition and large fungal biomass associated with various mycorrhizal types suggests that mycorrhizal associations can influence global distribution of soil carbon stocks (Soudzilovskaia et al. 2019). ECM fungi assist in the transportation of nutrients to the host plants and photosyntetically produced C from the host plant into the soil, pathogens contribute to the death of plants, and saprotrophic fungi decompose dead plants releasing the accumulated nutrients back into the ecosystem (Niego et al. 2023). Despite the highly debated differences between ECM and AM mechanisms of C acquisiton, recent findings provide evidence that ECM symbionts may be the key driver for soil C accumulation. This finding can be explained through greater mycelial biomass EMF development compared to AMF, and through the ability of EMF to immobilise most of N in their biomass suppressing the saprtotrophic decomposition processes (Soudzilovskaia et al. 2019). Furthermore, the same authors predict that on a global scale, ectomycorrhizal, arbuscular and ericoid plants combined can store 12 times more carbon than non-mycorrhizal plants.

IMPACT ON PLANT GROWTH AND HEALTH

Improved Water Absorption and Drought Tolerance

The main benefit of mycorrhizal fungi lies in the improved uptake of nutrients and water from the soil by plants, which is made possible by the considerable increase in root surface area due to the mycelium. The mycorrhizal hyphae act as extensions of the roots, and can reach length of over 100 cm. These mycorrhizal hyphae also act as a direct conduit for water movement in dry soils (Zhang et al. 2018) since extraradical hyphae closely engage with soil particles (Dietz et al. 2010). Furthermore, some EMF develop rhizomorphs, consisting of central hyphae encircled by smaller living hyphae. Rhizomorphs function as a powerful pathway for the translocation of resources, transporting bulk water over long distances from the hyphae growing in the soil towards ECM and the plant root. Radial water transport in roots can go through apoplastic and cell-to-cell pathways (Marjanović and Nehls 2008, Guerrero-Galán et al. 2018). The apoplastic pathway is governed by Casparian bands at the exodermis and endodermis (Marjanović et al. 2005), while the cell-to-cell pathway is controlled by membrane intrinsic proteins (MIPs) called aquaporins (Guerrero-Galán et al. 2018). These proteins act as gradient-driven water channels (Dietz et al. 2011). Aquaporins respond to changes in water availability, regulating water permeability where the apoplastic pathway is constrained by Casparian bands (Xu and Zwiazek 2020).

Drought and salt stress are the most considerable challenges for plant growth (Shi et al. 2023). When it is dry, trees struggle as the lack of soil moisture affects their physiology, harms growth and increases the mortality. Nutrient availability decreases during drought, affecting the plant's overall function. For example, the biomass of beech trees can decrease due to a lower concentration of P and K (Marušić et al. 2023). Mycorrhizal plants have a higher photosynthesis rate, greater mass, higher nutrient content and better water use efficiency than non-mycorrhizal plants. Mycorrhizal formation is particularly beneficial for plants under drought conditions, possibly because mycorrhizal roots have a higher water transport capacity, which is reflected in the increased hydraulic conductivity of the roots (Marjanović et al. 2005). Zhang et al. (2018) showed that water uptake by mycorrhizal hyphae is utilised more in dry soils than in saturated soils by investigating the water uptake of ERM in citrus plants under drought stress and in well-watered soil conditions. Studies indicate that the water absorbed by the ERM can be pivotal, determining the survival or death of a young tree seedling (Lehto and Zwiazek 2011, Zhang et al. 2018).

On the other hand, the impact of mycorrhizae on enhancing the plant's water supply can vary, even showing neutral or adverse effects. This variability may depend on the quantity of nutrients accessible to the plant. If mycorrhizal seedlings are adjusted to a nutrient status similar to non-mycorrhizal ones, the symbiosis no longer enhances growth, but is influenced by the available nutrient quantity. Ultimately, the usefulness of ECM for the plant during drought conditions relies on the EMF's capacity to absorb nutrients and effectively deliver them to the plant (Marjanović and Nehls 2008).

Defense Against Some Biotic Stresses

Mycorrhizal fungal mycelium can connect plants into a below-ground community, creating a common mycorrhizal network (CMN) (Simard et al. 2012, Karst et al. 2023, Frew et al. 2025), also known as the wood-wide web (Gilbert and Johnson 2017), hypothetically illustrated in Figure 2. This means that extensively and densely growing hyphae form a network with the length of 10–100 m of hyphae per gram of soil. CMN involves not only direct physical link between plants, but also the possibility of multiple simultaneous interactions between neighboring fungi that colonize neighboring plants (Frew et al. 2025, Rillig et al 2025). Further, because CMN can connect multiple species of plants and mycorrhizal fungi, it creates a medium for nutrient exchange and defense signal transfer between plants (Kadam et al. 2020). Through CMN, one attacked plant can warn other related plants about the impending attack of pests and pathogens (Gilbert and Johnson 2017). The study conducted by Babikova et al. (2013) demonstrated that insect herbivory induces changes in plant volatiles, leading to bean plants (*Vicia faba* L.) becoming repellent to aphids while simultaneously attracting aphid predators such as parasitoids. Moreover, the research revealed that these effects extend to aphid-free plants if they are connected to aphid-infested plants through a shared CMN (Babikova et al. 2013).

CMN is usually defined as a set of direct, continuous hyphal connections that connect plants via mycorrhizal fungi. However, this narrow definition overlooks broader forms of fungal interconnections among plant roots. There is a more comprehensive definition of CMN as a network formed by mycorrhizal fungi among different plants, regardless of the type of connection. To distinguish the specific example of direct hyphal continuity, which is CMN, Rillig et al. (2025) proposed the term CMN-HC (CMN with hyphal continuity). In addition, they introduced the broader concept of common fungal networks (CFN), which encompasses all fungi-driven plant networks (including non-mycorrhizal fungi). This hierarchical structure (CMN-HC, CMN, CFN) can provide a basis for advancing research on fungal networks.

Mycorrhizal colonization contributes to plant fitness and protects against various biotic stresses. This resistance to harmful organisms is called mycorrhizal-induced resistance (MIR) (Jung et al. 2012, Kadam et al. 2020). One of the plant's defense mechanisms is "priming", which is probably the leading mechanism working in MIR. Priming is the process of preparing plants for potential enemy attacks and warning of the same future attack, and it is a way of supporting the plants' immune memory (Kadam et al. 2020, Alves Cardoso Filho 2023). MIR is characteristic of AM symbiosis because one of the defense hormones, jasmonic acid (JA), is expressed in the arbuscules, which is proceeded by salicylic acid (SA) (Kadam et al. 2020).

Barea et al. (2002) suggest several mechanisms that can enhance plant resistance/tolerance to pathogens. One of those is the shift of microbial communities connected with mycorrhizal growth and the achievement of microbial equilibria that can affect the growth and health of the plants. Changes in the population of soil microorganisms can lead to stimulation of microbiota antagonistic to root pathogens. For instance, widely used mycorrhiza helper bacteria (MHB) that promote the symbiosis by stimulating mycelial extension can have detoxification properties against antagonistic substances (Frey-Klett et al. 2007).

ECOSYSTEM SERVICES PROVIDED BY MYCORRHIZAE

Climate change is a global challenge with intense consequences for different ecosystems worldwide. In forest ecosystems, part of the impact is expressed through temperature changes, water quality and availability, in the changed distribution of precipitation (Bennett and Classen 2020) and the frequency of extreme weather events (floods, long-term drought, salinity), which can lead to disturbances in the forest vegetation (Usman et al. 2021). Carbon storage in the forest soil is one of the most important ecosystem services forests provide, and mycorrhizal symbiosis helps greatly in this process. Mycorrhizal symbiosis also helps plants cope with heat stress. In such situations, trees affected by extreme temperatures will signal danger to neighboring trees through CMN. Also, dying mature trees will pass their ECM inoculum to surrounding younger seedlings, which will then begin to adopt fresh resources (Usman et al. 2021), thus keeping the population alive.

In temperate and boreal forests, trees rely on mycorrhizal fungi to extend their root exploration beyond the rhizosphere, enhancing the acquisition of nutrients and water, which is vital for tree adaptation to climate change and abiotic stressors. There is a possibility that mycorrhizal colonization will help plants adapt to these new and ongoing changes in the future (Field et al. 2020, Usman et al. 2021).

Soil Health Improvement

Soil supports the diversity of ecosystems and maintains the ecological balance. Soil quality is one of the most critical components of managed and natural ecosystems

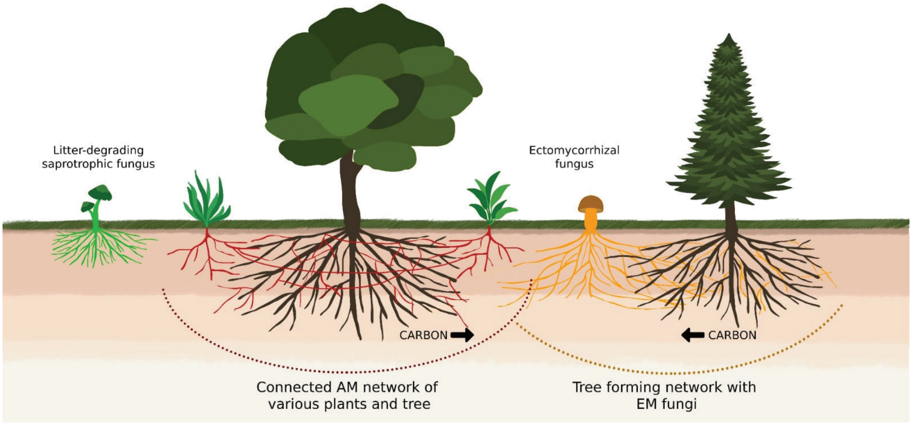

Figure 2. Hypothetical illustration showing the diversity of plant-mycorrhizal associations within a plant community, as an example of a common mycorrhizal network (CMN). Different plant species can form different associations with different types of mycorrhizal fungi (AM – arbuscular mycorrhiza, EM – ectomycorrhizal fungi), highlighting the complexity and ecological importance of these symbioses in supporting nutrient uptake, plant growth, and overall ecosystem resilience (Ullah et al. 2024, Frew et al. 2025). Illustrated by Anamarija Zegnal.

(Williams et al. 2023), and its protection and preservation are decisive for water quality and the health of plants and animals throughout entire ecosystems (Lehmann et al. 2020). Soil biodiversity manifests in the biodiversity of the microorganism community (like microalgae, bacteria, and fungi) (Williams et al. 2023), known as the soil microbiome, which is crucial for soil health. Bacteria-fungal interactions (BFIs) take a significant place in this complex soil microbiome according to host plant conditions, e.g., an increase in growth and resistance to stress. BFIs occur in different soil zones, like rhizosphere (soil zone around and influenced by plant roots) and bulk soil (without plant roots). The rhizosphere is the zone of the soil where the biology and chemistry of the soil are affected by chemicals released from the plant roots, respectively (Barea et al. 2002, Williams et al. 2023).

Moreover, mycorrhizal fungi can engage bacteria, forming the mycorrhizosphere (Barea et al. 2002, Williams et al. 2023). Consequently, the mycorrhizosphere represents the rhizosphere, additionally influenced by mycorrhizal fungi, where microbial populations are altered both quantitatively and qualitatively by mycorrhiza initiation. These interactions contribute to soil biodiversity, resilience, and resistance, which are critical for sustainable agriculture and ecosystem health, fostering nutrient cycling, water retention, and overall stability in diverse environments (Williams et al. 2023).

Mycorrhizae can have particular importance in soil structure, influencing soil aggregation, which contributes to agroecosystems' land and recuperation of the disturbed land and eroded soil. Different plant species within the same plant community have different effects on soil aggregation, and AMF has been shown to be an essential factor in the productivity of plant communities (Rillig and Mummey 2006). It is important to mention glomalin, a fungal soil-related protein (glycoprotein) produced by AM fungal cell walls. One of its roles is assumed to be active excretion to improve soil aggregation stability, acting as a soil-glue. (Hayes et al. 2017, Usman et al. 2021, Wilkes 2021).

Direct and Indirect Contributions

Within the group of mycorrhizal fungi, EMF are considered the only ones that produce visible fruiting bodies. They belong to macrofungi, and certain species are edible. Macrofungi in forest ecosystems are a source of food for both animals and humans. One such example are truffles from the genus *Tuber*, which are hypogeous ascomycetes growing in a ectomycorrhizal symbiosis with the roots of host plants such as *Quercus*, *Corylus*, *Populus*, *Fagus*, and *Cistus.* Truffles create sporocarps whose spores are dispersed and transported by mycophagous mammals. Foremost, black truffles are precious and delicious fungi in sophisticated gastronomy, which is why they are also known as "black diamonds" (Tang et al. 2015, Niego et al. 2023, García-Montero et al. 2024). Among the most expensive truffles are *Tuber magnatum* Picco, *T. melanosporum* Vittadini and *T. aestivum* Vittadini (Özderin 2018). For that reason, collecting and marketing truffles from natural habitats is a source of income for people in rural areas (Reyna and Garcia-Barreda 2014). Additionally, mushrooms, including truffles, are Europe's most important non-wood forest products. Their use is recorded in 15 out of 27 European countries (Mosquera-Losada et al. 2008). Therefore, food sources and improvement of income sources represent direct contributions of mycorrhizal fungi in relation to human activities (Niego et al. 2023).

One example of indirect contributions provided by mycorrhizal fungi is bioremediation. Bioremediation refers to the application of biological systems for detoxification of the environment contaminated with metals and persistent organic pollutants (POPs) (Meharg and Cairney 2000). When fungi are involved in the bioremediation process, this is called mycoremediation. Fungal mycelium tolerates heavy metals and can adjust its growth to available nutrients and extreme pH and temperature conditions. In remediation, fungi have an advantage over bacteria because of the hyphal network quality, biomass and long-term lifecycle (Akpasi et al. 2023). For effective mycoremediation by mycorrhizal fungi, it is necessary to select pioneer tree species that can grow in severely contaminated conditions. For example, birch (*Betula* spp.) is a pioneer ECM tree that effortlessly inhabits contaminated areas, and its mycorrhiza tolerates such conditions well (Meharg and Cairney 2000).

PRACTICAL APPLICATION OF MYCORRHIZAL FUNGI

Intensive agricultural systems face major challenges, including soil degradation, nutrient imbalances, and the need to reduce chemical inputs, all of which have significantly disrupted mycorrhizal community structures. Mycorrhizal fungi have great potential to improve anthropogenic land systems through the practical applications of AMF in agriculture and most natural ecosystems and ECM in forestry and wasteland regeneration. As mentioned in the previous section, the most important aspect of these symbiotic fungi is the enhancement of plant growth and yield through improved P absorption (Sharma et al. 1997, Jha and Songachan 2023, Frew et al. 2025). AMF can positively influence the maintenance of photosynthetic efficiency and physiological activities of plants, leading to improved fruit quality and yield. Like other microbial biostimulants, AMF can increase the sustainability of agricultural and horticultural production systems, and ensure better quality and greater quantities of food (Sun and Shahrajabian 2023).

On the other hand, EMF show benefits in plant establishment and in nursery production, for example by controlled inoculation of seedlings with a specific EMF. One specific example is the cultivation of seedlings inoculated with black truffles to produce truffle fruiting bodies in a new land, that is, in the form of orchards or plantations (Guerin-Laguette 2021). Productive truffle orchards represent an agricultural alternative in rural areas, encourage the restoration of forest habitats, and recover abandoned lands under cereals with relatively low agricultural investments (Bonet et al. 2006). Modern truffle cultivation is based on planting nursery-inoculated seedlings on suitable soils of appropriate ecological conditions to complete the life cycle of the fungus (Olivera et al. 2011, Garcia-Barreda et al. 2017). Inoculation of seedlings with black truffles refers to the controlled process of colonizing the roots of host tree seedlings, such as oaks (*Quercus ilex* L.) or hazel (*Corylus avellana* L.), with the mycorrhizal fungi like *T. melanosporum* or *T. aestivum.* In general, the inoculation process typically involves introducing truffle spores or mycelium into the seedling roots zone, so when the spores germinate, mycelium is formed (as schematically depicted in Figure 3). This symbiotic relationship between the fungus and the tree roots is essential and among the first steps for successful truffle cultivation (Gómez-Molina et al. 2023). This natural partnership, formed by mycorrhizal colonization in nurseries, reduces the need for chemical fertilizers and pesticides, thereby reducing the ecological footprint of agricultural and forestry practices (Qian et al. 2024).

Managing mycorrhizal fungi effectively requires a deeper understanding of plant–fungal selectivity and its implications for symbiotic functions such as nutrient uptake, soil biodiversity, and plant vitality (Frew et al. 2025). Overall, the use of mycorrhizal fungi as inoculum in forestry and agriculture represents a natural way of improving plant growth and survival, and contributes to the preservation of soil biodiversity.

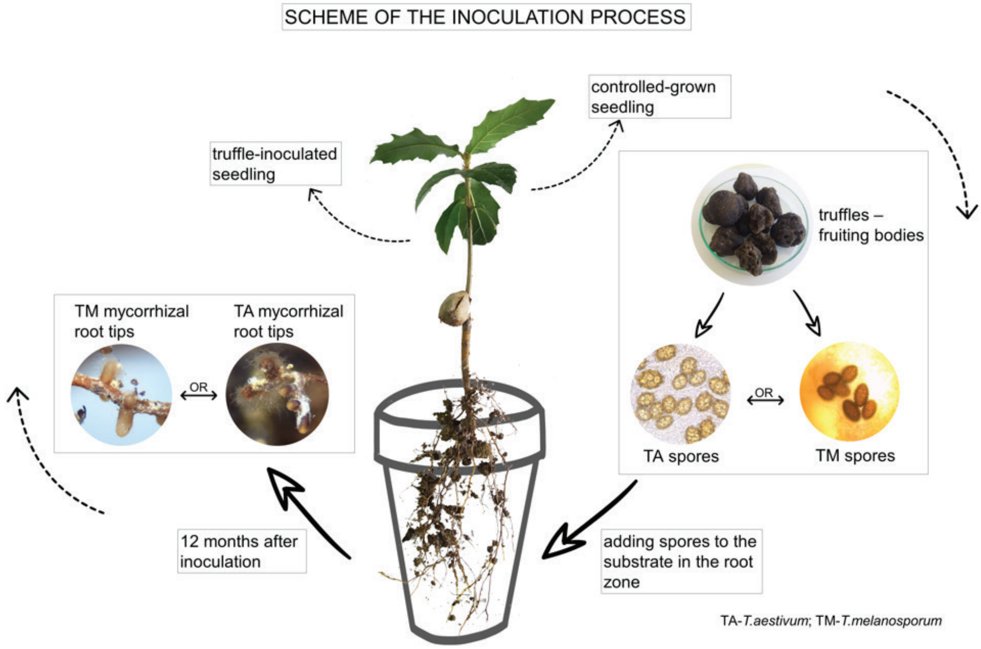

Figure 3. The seedling inoculation process involves putting the truffle spores into the root zone of a controlled-grown seedling for the establishment of a mycorrhizal association. Fresh truffle fruiting bodies provide spores, either from *Tuber melanosporum* (TM) or *Tuber aestivum* (TA), which are added to the substrate in which seedlings are transplanted. Over approximately 12 months, mycorrhizal root tips are present, resulting in a truffle-inoculated seedling that should be capable of supporting future truffle production. Illustrated by IZ.

CONCLUSIONS

Whether mycorrhizal fungi are hidden underground or produce visible fruiting bodies, they are significant to terrestrial ecosystems. Mycorrhizae are necessary for the health and functioning of forest ecosystems because they improve the trees' absorption of nutrients and water by increasing their root surface and resistance to stressful conditions such as drought and soil disturbance. This symbiotic relationship between fungi and tree roots also promotes nutrient cycling, maintains soil structure, and supports forest biodiversity. Mycorrhizal fungi also play an important role in the adaptation of forests to climate change and contribute to the sustainability of the ecosystem. Some of the mycorrhizal fungi are edible (e.g., truffles and porcini mushrooms) and represent important non-timber forest products, as well as being an additional income source.

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IZ, JM, and AB, contributed equally to the writing of this review paper, IZ conducted the literature selection.

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Conflicts of Interest

The authors declare no conflict of interest.

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