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# Understanding the Mycorrhizal Network's Ecological Symphony: A Review

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## ABSTRACT

Mycorrhizal fungi, notably arbuscular mycorrhizal fungi, are essential components of plant ecosystems as they promote nutrient exchange, stress tolerance and communication. They are in mutual symbiosis with 80% of terrestrial plant species, assisting with growth and communication. The complex symbiosis, mediated by fungal hyphae networks, enables plants to photosynthesize carbon for crucial nutrients such as nitrogen. Furthermore, they participate in plant communication, defense and resource distribution, thereby influencing plant community structure and efficiency. Mycorrhizal networks are connected to biological markets and source-sink relationships, furthering the beneficial trade interaction between plants and fungi. However, it is due to the fungemia that the resource distribution and transfer processes remain controversial.


**Key words:** Arbuscular mycorrhizal fungus, Biological markets, Common mycorrhiza network, Mutualistic relationships, Resource allocation.

Mycorrhiza fungi, which fall into categories like arbuscular, arbutoid, ecto orchid, ericoid and monoptropoid, are commonly found in the rhizosphere. 25,000 terrestrial plant species share a relationship with these fungi, with arbuscular mycorrhizal fungi being the most significant. It is notable that Chenopodiaceae and Brassicaceae plant species typically do not coexist with mycorrhizal fungi. Among them, arbuscular mycorrhizal fungi play a role in soil fertility and plant growth (Gosling *et al*., 2006; Smith *et al*., 2011). By aiding in the exchange of carbohydrates and minerals in plant roots and facilitating the movement of carbon and nitrogen, arbuscular mycorrhizal fungi boost host plant resistance to diseases and drought. For the plants to gain access to and movement of nitrogen, they give arbuscular mycorrhizal fungus their photosynthetic carbon (Liu *et al*., 2013). It has been suggested by Requena *et al.* (1996) and Smith *et al.* (2011) that this symbiosis between host plants and arbuscular mycorrhizal fungi begins with hyphae as well as asexual spores colonizing roots. Plant uptake of nitrogen, phosphorus, potassium, manganese, copper and zinc is facilitated by nutrient transfer occurring in the arbuscules (Smith and Read, 2008; Peterson *et al.,* 2004). According to Smith and Read (2008); Smith *et al.* (2011) and Seleiman *et al.* (2013), plant nutrition is improved through such nutrient transfers. Up to 20% of the organic carbon required for growth and development of the fungal hyphae of arbuscular mycorrhizae come from plant organic matter (Smith and Read, 2008; Smith and Smith, 2011).

As per the research conducted by Atakli *et al.* (2022), the AMF is important in nutrient uptake under optimal and stress conditions. They explored that increased plant height stem fresh weight and stem dry weight due to AMF treatment which also induced dry matter accumulation in all parts while enhancing the leaf nitrogen phosphorus and potassium content of seedlings. Such results are similar to earlier experiments (Etesami *et al*., 2021). Generally, it is believed that increasing nutrients supply to plants particularly through ions that have low mobility is the main role played by AMF, including ammonium, phosphate, copper and zinc (Barea *et al*., 2005). This review describes how these AMFs play roles in regulating plant growth, including stress-tolerant environments, through bio-fertilizers, which will also be described together with notable advances in relevant research towards their application in agriculture. The objective of this paper is to summarize, evaluate and give current information regarding the impact of mycorrhizal relationships on crop resilience as well as productivity parameters.

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## The role of arbuscular mycorrhizal fungi in stress tolerance and symbiotic exchange

Arbuscular fungi are important in regulating plant responses to abiotic stresses. These responses occur at various physiologic, morphological and molecular stages. These processes serve to protect plants from damaging effects caused by abiotic stresses. Agriculture all over the world has been significantly affected by drought stress as stated by Hu *et al.* (2022). In order to solve this problem, the microbiological theory of microbe symbiosis has proven to

be a useful strategy. This method is less expensive, non-destructive and more efficient than other physical, chemical or biological approaches. AMF was previously regarded as beneficial for soil nutrient uptake but recent studies have indicated its ability to successfully withstand different types of environmental stressors such as salinity, rainfall scarcity, increased demand for nutrients, alkaline stress, cold temperatures and extreme heat restoring substantial crop yield in different types of crops and vegetables. The symbiotic relationship that arbuscular fungi and plants improves water and nutrient uptake, facilitating plant development. Thus, it increases the abiotic stress tolerance. For the plants to gain access to and movement of nitrogen, they give arbuscular mycorrhizal fungus their photosynthetic carbon (Liu *et al.,* 2013). It has been suggested by Requena *et al.* (1996) and Smith *et al.* (2011) that this symbiosis between host plants and arbuscular mycorrhizal fungi begins with hyphae as well as asexual spores colonizing roots. Plant uptake of nitrogen, phosphorus, potassium, manganese, copper and zinc is facilitated by nutrient transfer occurring in the arbuscules (Smith and Read, 2008; Peterson *et al.,* 2004). According to Smith and Read (2008); Smith *et al.* (2011) and Seleiman *et al.* (2013), plant nutrition is improved through such nutrient transfers. Up to 20% of the organic carbon required for growth and development of the fungal hyphae of arbuscular mycorrhizae come from plant organic matter (Smith and Read, 2008; Smith and Smith, 2011). This review describes how these AMFs play roles in regulating plant growth, including stress-tolerant environments, through bio-fertilizers, which will also be described together with notable advances in relevant research towards their application in agriculture. The objective of this paper is to summarize, evaluate and give current information regarding the impact of mycorrhizal relationships on crop resilience as well as productivity parameters. A comprehensive bibliometric study about legume mycorrhiza can be obtained (Xu, 2021) by doing a bibliographic analysis of the characteristics and trends in research on legume mycorrhizas. There have been 837 papers in the topic of legume mycorrhiza over the past 16 years. The number of articles significantly increased from 2009 to 2020, which means that the legume mycorrhiza research remains popular. Meanwhile, tight international collaboration was noted between other countries and research institutions. On the other hand, co-cited references analysis gave higher priority scores to works in the domain of nitrogen fixation. They further noted that in the near future, the interaction between legume plants and mycorrhizal fungi would seem to be a hotspot and trend of study for improving nutrition absorption and N-fixation, stress resistance and their mechanisms, which was most strongly supported by citation bursts analysis.

## Understanding mutualistic relationships: Exploring the diversity and impact of mycorrhizal fungi on plant systems

Arbuscular mycorrhizae, a common and widely distributed type of fungus found in the phylum Glomeromycota (Schüßler and Walker, 2011), is associated with 80% of terrestrial plant species, especially in hot areas and different habitats such as tropical forests. The ectomycorrhizal (EM) fungi are the second most prevalent sort of parasite in nature, with many hosts being dominant even though fewer plant species form symbiosis with them, as per Brundrett (2009) and Teste *et al.* (2020). Unlike AM fungi, which are found in warmer environments that have fewer host plants (Gorzelak *et al.,* 2015), EM fungi occur in colder climates and ecosystems (Brundrett, 2009; Gorzelak *et al.,* 2015). For instance, AM fungi occur in warm regions with few host plant species, whereas EM fungi present in cooler regions or ecosystems. Different fungal species of AM and EM often occur together in the same ecosystem, where some plants may support both types of these organisms within their roots, subject to stage development.

## Complex dynamics of plants interaction: Unraveling the role of mycorhizal network

Every species appears to have its individual trade-offs and both benefit-cost analyses can be complex and compounded by the fact that different fungal species coexist with plants in real environments, some of them showing commensalistic interactions whereas others show antagonism (Kiers *et al.,* 2011). It is hard to differentiate the interactions among connected plant communities arising from common ancestry in nature because multiple forms of symbiosis with mutually beneficial associations exist between host plants, like networks of mycorrhizal root systems. In this case, it is possible for some plant species to gain greater benefits than others through commensalistic or antagonistic interactions occurring among interconnected mycorrhizal plants or fungi (Toju *et al.,* 2013). There are various reasons why some plant families may gain an advantage over others. However, AM fungi constitute a single type of mycorrhiza, even though there are variations in functional characteristics and temporal patterns among different strains (Kiers *et al.,* 2011). Nonetheless, predicting the ecological dynamics within these interconnected plants can be challenging due to the varied effects CMN has on natural ecosystems, as noted by Wagg *et al.* (2015). Few studies on the impact of CMN on connected plants have been conducted in controlled environments and microcosms, which has significantly influenced the findings. The physiological state of the host, the kinds of plants and fungus involved and the surrounding conditions, among other factors, may influence how beneficial connected plants are, therefore results could still differ significantly even in these circumstances (Wagg *et al.*, 2011). To identify unanswered questions from existing literature, future research looking into CMN's potential plant-to-plant interactions and their implications for plant communities should be concentrated on resource exchange amongst plants in biological markets. The balance between plants and arbuscular mycorrhizal fungi is a biological market where more carbohydrates are provided by plants to fungal partners, whereas more soil

nutrients are provided by fungi. Merrild *et al*. (2013); Weremijewicz *et al*. (2016). Moreover, Merrild *et al.* (2013) study showed that unequal resource distribution would increase competition between closely related species. Pruning large plants' shoots decreased the growth suppression of smaller ones, allowing them to uptake P at a higher rate. According to this study, only when seedlings are associated with the extra-radical mycelium of the larger plant does suppression happen. The research indicates that the characteristics of different plant species, such as their growth rate and size, can impact how they absorb nutrients. Certain types of fungi that are more beneficial have a greater amount of carbon enrichment, showing a preference for allocating carbon in smaller areas. It was also observed that there was a counterbalancing exchange, where the fungi provided more phosphorus to the host while the host provided more carbon to the fungi. Fellbaum *et al*. (2014) showed that fungi can adjust their nutrient allocation by increasing nitrogen supply to the host when there is more carbon available. Bigger plants receive essential nutrients from fungal networks more effectively, serving as a barrier to prevent smaller species from outcompeting them.

## Understanding interactive concept of mycorrhiza with plants and soil

In the study of ecological systems, theories such as the biological market and cost-benefit analysis have been put forward to explain how different species coexist and interact with each other. The biological market theory proposes that fungi can adjust their nutrient allocation depending on the amount of carbon plants are able to produce, while the source-sink theory suggests a fairer distribution of resources among organisms. In the upcoming sections, we will delve deeper into these concepts to gain a better understanding of their implications.

## Concept of biological market

In biological markets, two groups of traders, arbuscular mycorrhizal fungi and plants, exchange items to benefit each other. Plants provide more carbohydrates, while fungal partners supply nutrients for the soil (Merrild *et al.,* 2013; Weremijewicz *et al.,* 2016). Merrild *et al*. (2013) found that pruning back the shoots of large plants decreased the growth suppression of nearby small plants, allowing them to absorb P at a rate 6.5 times higher. The study also included treatments with solitary and networked seedlings to eliminate the possibility of suppression due to a general unfavorable growth response. Different characteristics of plant species, such as how fast they grow and the ratio of roots to shoots, play a role in how they absorb nutrients. Some types of helpful fungi have a higher level of carbon enrichment, indicating that they are preferentially given resources by the host in specific locations. Research by Fellbaum *et al.* (2014) showed that fungi can differentiate between different nutrients, providing more phosphorus to the host while receiving more carbon in return, creating a counterbalancing flow. By trading resources, mycorrhizal fungi and plant hosts allow larger plants to get more nutrients and carbon, giving them an advantage over smaller species and reducing competition.

## Concept of source and sink

Heaton *et al*. (2012) studied the concept of how source and sink are interrelated in the ecosystem. According to them, the sources provide more resources than whatever they consume, while sinks may demand more resources. Better plant survival and growth affect better resource flow in the micorrhizal network, as already shown by Lekberg *et al.* (2010) and Philip *et al.* (2010). Montesinos-Navarro *et al*. (2017) and Munteer *et al*. (2020) have observed the pattern of nitrogen (N) movement in a source-sink relationship. Teste and collaborators (2009) suggested that this process could help rejuvenate forest ecosystems by regulating the carbon flow among different regions (Deslippe and Simard, 2011) and among plants connected *via* mycorrhizal networks.

## Exploring the underground dynamic of plant communication through the mycorrhizal network

Plants talk to each other in several ways, one of which is through the Common Mycorrhizal Network (CMN), also referred to as the "wood wide web". This network connects plants and fungi, allowing them to share nutrients and information. It is essential for the health of trees and the carbon supply of fungi in land ecosystems. Around 30% of the sugar produced by connected trees is kept by the network, using it as energy. This communication system is efficient in many plants and is important for the balance of land ecosystems (Simard and Durall, 2004; Simard *et al.,* 2012; Hoeksema, 2015). Several species of arbuscular mycorrhizal (AM) fungi have been shown to effectively coexist with their host plants. Research conducted by Giovannetti *et al*. (2001) revealed the presence of genetically compatible hyphae capable of merging, sharing cytoplasm and nuclei and breaking down hyphal barriers (Barreto de Novais *et al.,* 2017). These findings indicate the presence of widespread CMNs, although more evidence from field studies is required to confirm this hypothesis. Despite these discoveries, further concrete proof from field studies is still necessary. Plants from different species can sometimes share the same fungus species or gene in various habitats, as suggested by Simard *et al*. (2012) and Beiler *et al*. (2015). According to Beiler *et al.* (2010) and Diédhiou *et al.* (2010), plants with micorrhizal networks connecting to them are more similar to one another. Bever *et al*. (2010) investigated the impact of fungal species in the genet dispersal among Douglas fir roots and found that larger trees have a scale-free design, are important suppliers of nutrients for understory regeneration and exhibit a scale-free architecture. The studies highlight the complex relationship between organisms, such as those involving Collembolas that eat fungal hyphae and the common mycorrhizal network (CMN) (Ekblad *et al*., 2013; Ngosong *et al.,* 2014). As per

Wu *et al*. (2005) and Beiler *et al*. (2015), the disruption of common mycorrhizal networks (CMN) in soil can pose a detection challenge. The technical complexities involved in proving hyphal connections between plants hinder the assessment of whether the effects reported are inherent to a mycelial network. There is a limited availability of non-invasive methods for observing mycelium networks, especially for the arbuscular mycorrhizal (AM) fungus. Some common techniques include in vitro dual systems (Kiers *et al.,* 2011; Van't Padje *et al.,* 2021) and root observation chambers (Mikkelsen *et al.,* 2008; Gyuricza *et al.,* 2010). Research has found that there is a close connection between plants through mycelium, but the actual importance of this phenomenon is still a matter of debate because of complications in forest experiments and the effects of interactions with plant-soil feedback, soil microbiota, biogeochemical cycles and root exudates (Hu *et al.,* 2018). The study of mycorrhizae encounters difficulties in ensuring the accuracy of data due to uncertainties surrounding causality.

## Unveiling the dual roles of common mycorrhizal networks; facilitation and competition among plants

There is a debate about how plants benefit from and interact with each other in a common mycorrhizal network (CMN) experience. Some theories suggest that established mycorrhizal plants act as a source of inoculation and carbon supply, helping nearby seedlings establish mycorrhizal associations. By boosting competitiveness, resource distribution can be encouraged by this method. But whereas plants might transmit resources directly in one situation, they might also distribute resources unfairly in another. Seedlings can acquire fungal inoculums very quickly with the help of CMN, thus utilizing soil resources.

This can be important in challenging environmental conditions when plants are just starting to grow, where many plants may die because of a lack of water and interactions with other living things. Research from Simard *et al.* (2012) and Teste *et al*. (2015) has shown this. Varga and Kytöviita (2016) have also discovered a strong link between young plants being taken over by certain fungi and where the fungi came from. Field studies by McGuire (2007) and Grove *et al.* (2019) have also found a positive connection between how close a young plant is to an older tree and how likely it is to survive.

As per Nara (2006) and Pec *et al.* (2020), disturbing the soil can lead to higher seedling death rates by disrupting their ability to connect with a network of fungal symbioses. Being part of a Common Mycorrhizal Network (CMN) with older trees can help reduce the costs associated with maintaining the fungi (Smith and Read, 2010; Keymer *et al.,* 2017; Rezá¡cová *et al.,* 2017). Sugars and lipids play a crucial role in providing carbon for the fungi's growth and nutrient uptake (Bravo *et al.,* 2017; Bezrutczyk *et al.,* 2018). Seedlings can benefit from mycorrhizal connections without using their own carbon resources if larger trees support the growth and upkeep of the CMN (Diédhiou *et al.,* 2010; Walder *et al.,* 2012*;* Weremijewicz *et al.,* 2016). Högberg *et al.* (1999) conducted a study that revealed that symbyiotic fungi that link lower understory plants with upper pine trees get a substantial amount of carbon from minimum understory trees (87-100%). Further, Walder *et al.* (2012) discovered that unequal carbon allocation in some plant species does not always disadvantage others, especially when basic carbon sources are inexpensive.

## Understanding the intricacies of mycorrhizal networks: conduit for resource transfer among plants

Micorrhizal networks not only support better plant growth but also reduce dependence on chemical fertilizers (Pena *et al*., 2013; Jansa *et al*., 2019). However, it is still debatable whether there is a direct exchange of photosynthates and plant nutrients. Mycoheterotrophic plants derive nutrients indirectly by parasitizing green plants through CMN and utilizing carbon from neighboring plants. This research emphasizes the intricacies of interactions below the ground and the potential importance of CMN in influencing plant communities and the dynamics of ecosystems. Parasitic plants that do not rely on photosynthesis attach themselves to fungi in the roots, obtaining carbon and nutrients. Researchers have found evidence of this relationship in studies by Bidartondo *et al.* (2002); Girlanda *et al.* (2006) and Selosse and Roy (2009). Tedersoo *et al.* (2018); Brundrett (2013) and Waterman *et al.* (2013) have conducted research in this area and opined that plant relationships are influenced by mycorrhizal fungi, which are essential for the movement of carbon and nutrients between plants. Gorzelak *et al.* (2015) and Prescott *et al.* (2020) focused on the importance of these networks and reported that extra carbon is known to be absorbed for their own advantage and then allocated to other plants, thus supporting the survival of the host plant and also serving as a source of carbon (Bücking *et al.,* 2016). Studies have shown that high-quality hosts release more carbon compared to low-quality hosts (Kiers *et al.,* 2011; Fellbaum *et al.,* 2014; Bücking *et al.,* 2016). Fungi thrive on high-quality hosts and maintain high colonization rates. There is a two-way transfer of carbon between Douglas-fir and paper birch plants, which helps fungi survive in changing environments (Perry *et al.,* 1989; Wilkinson, 1998). One plant species did receive carbon in the second year, according to a study by Simard *et al*. (1997); however, methodological problems cast doubt on the overall benefits of carbon transfer to plants (Robinson and Fitter, 1999). By tracking carbon exchange in plants using electromagnetic fields and double tagging, Simard *et al.* (1997) demonstrated that carbon can travel through many channels. According to Robinson and Fitter's (1999) theory, fungi facilitate the transfer of carbon from photosynthetic plants to roots. The significance of low net carbon transfer in Douglas fir seedlings compared to their photosynthesis for the health of the ecosystem and plants has been

discussed by Teste *et al.* (2010). Findings have repercussions on plant fitness and ecosystem dynamics, as suggested by Robinson and Fitter (1999) and Lekberg *et al.* (2010). They further suggested that carbon is mostly stored in micorrhizal roots; however, some believe that under stress conditions, carbon may contribute to reducing the plant's nutrients and moisture gain. Studies have suggested that mycorrhizal networks take part in the underground movement of nitrogen. Studies on the movement of C-nitrogen have generated consistent results. Recent investigations have indicated that the transfer of nitrogen can occur bidirectionally, contrary to earlier suggestions of one-way transfer. Plant physiology or plant size is among the various factors influencing the direction of transport, with nitrogen making up less than 5% of the total as usual. Although the origin of this theory is not known, multiple studies by Bever *et al.* (2010); Teste *et al.* (2015); He *et al.* (2009); Pirhofer-Walzl *et al.* (2012); Meding and Zasoski (2008); Wermijewicz *et al.* (2018) and Simard *et al.* (2015) have concluded that carbon and nitrogen move together as amino acids. Thus, studies explore how the mycorrhizal network facilitates resource exchange, particularly carbon, among plants and generate a debatable issue over the impact of these networks on the dynamics of ecosystems. The fungi known to develop mycorrhizae associations with mycoheterotrophic plants and green orchids are typically part of a wide fungal taxonomic group that also forms these associations with the roots of phototrophic trees (Brundrett and Tedersoo, 2018). Theories about the potential C allocation between phototrophic trees have also been proposed as C transfer between mycoheterotrophic and green plants was demonstrated and the same fungi species that connected those plants can also colonize many phototrophic trees.

## Exploring resource transfer mechanisms in mycorrhizal networks: Direct hyphal pathways vs. indirect channels

Fungi underground networks enable plants to share nutrients directly, bypassing usual barriers (Høgh-Jensen, 2006; Meng *et al.,* 2015; He *et al.,* 2019). Hyphae, often called 'pipelines,' can act as indirect routes for substances. Klein *et al.* (2016) and Van Der Heijden (2016), Studies by Jansa *et al.* (2019); Fernandez *et al.* (2020) and Fang *et al.* (2021), proposed that direct mycorrhizal pathways could offer a more efficient way of resource sharing among plants without the usual interruptions or losses. According to Philip *et al.* (2010); Simard *et al.* (2012); Merrild *et al.* (2013) and Song *et al.* (2014), there are technical challenges in understanding transport channels, which creates uncertainty about transfer preferences. Advanced technologies and fungal gene manipulation could improve research on resource allocation and plant responses. Plants share resources indirectly, but neighboring plants can still help each other, showing interactions among plants (Høgh-Jensen, 2006; Alaux *et al.,* 2021).

## Quantifying carbon and nitrogen transfer in mycorrhizal networks: Challenges and perspectives

Kytöviita *et al.* (2003) and Bücking *et al.* (2016) argued that the interchange of compounds does not benefit plant health as most research lacks specific data on carbon flow. Wu *et al.* (2001) and Klein *et al.* (2016) suggested that even a minute amount of carbon traveling via the carbon-mitigating network (CMN) is essential for plant development and survival, particularly for early seedlings (Burke *et al.,* 2018; Liang *et al.,* 2021). Research indicates that the transfer of carbon between different plant species ranges from 0% to 10% (Teste *et al.,* 2010; Lin *et al.,* 2020). The initial research by Simard *et al.* (1997b) did not show any clear transfer of resources between different species. However, this finding was met with some controversy because it was difficult to apply the results from young plants to fully grown trees and understand how the carbon-mitigating network functions (Robinson and Fitter, 1999; Simard *et al.,* 2012; Tedersoo *et al.,* 2020). A new method to investigate how carbon is shared among trees within a forest has been proposed by Klein *et al.* (2016). However, according to them, the movement of carbon within plants is a debatable issue. Some studies reported that carbon is absorbed by receiving plants to promote growth, while others suggested it is primarily stored in the roots. Fitter *et al.* (1998) and Waters and Borowicz (1994) estimated that transferred carbon makes up 4% of total primary productivity. However, Song *et al.* (2015) discovered that the shoots of the receiving plant contained 13C and defoliation in Ponderosa pine led to an increase in transferred carbon. Furthermore, under an agroforestry system, a range of nitrogen transfer from 0% to 16% has been mentioned in the literature (Chapagain and Riseman, 2014; Zhang *et al.,* 2020). They further stated that besides weather conditions, numerous other factors like tress, plant/fungal interactions, experimental settings and soil nutrient availability are responsible for this diversity. As a result, there is a need for new technologies to accurately measure nitrogen transfer in both agroforestry and grassland ecosystems (Montesinos-Navarro *et al.,* 2016; Fang *et al.,* 2021). Research is being done to understand how carbon monoxide affects interactions between plants, but it is difficult to measure these exchanges because of their complexity. Knowing how they work is important for understanding how plants interact with each other.

## CONCLUSION

To wrap it up, complex connections between mycorrhizal fungi and plants shape ecosystem dynamics, an area needing further research in farming practices and environmental management. Common mycorrhizal networks have been known to exchange nutrients among plants, but underground interactions are still debated. Further research would be needed in understanding their impact on plant communities and ecosystem dynamics.

**Conflict of interest**

On behalf of all authors of this manuscript, I declare that there are no potential conflicts of interest with respect to the research, authorship and/or publication of this article.

All authors have contributed significantly to the work and agree with its content. We affirm that there are no financial, personal, or professional conflicts that could be perceived as influencing the research outcomes or interpretations presented in the manuscript.

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