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Mutualistic Relationships between Plants and Mycorrhizal Fungi Impacts on Ecosystem Functioning: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

ABSTRACT

Mycorrhizal fungi form mutualistic relationships with the majority of terrestrial plants, influencing nutrient uptake, soil structure, plant growth, and ecosystem functioning. The diverse types of mycorrhizal associations, including arbuscular mycorrhizae (AM), ectomycorrhizae (ECM), ericoid

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mycorrhizae (ERM), and orchid mycorrhizae (ORM), each contributing uniquely to plant health and soil ecosystems. Mechanisms of interaction, such as fungal colonization, nutrient exchange, signaling pathways, and carbon allocation, underscore the complexity and significance of these symbioses. Mycorrhizal fungi enhance ecosystem functioning by improving nutrient cycling-particularly the carbon, nitrogen, and phosphorus cycles-stabilizing soils, and increasing plant stress tolerance. Case studies in agricultural systems demonstrate how mycorrhizal inoculation can improve crop yields and soil health, while natural ecosystems illustrate their role in supporting biodiversity and resilience. In restoration ecology, mycorrhizal fungi aid in the recovery of degraded lands, enhancing plant establishment and soil stability. Urban and industrial landscapes also benefit from mycorrhizal associations, which support vegetation in challenging environments. Despite advancements, significant knowledge gaps and technological limitations persist, particularly regarding the ecological specificity of mycorrhizal fungi and their interactions within the soil microbiome. Addressing these challenges requires interdisciplinary approaches and integrating mycorrhizal research into policy and management practices. Such integration can enhance sustainable agricultural practices, promote biodiversity conservation, and mitigate climate change impacts. Future research should focus on advancing molecular techniques, improving in situ study methods, and fostering collaboration across scientific disciplines to fully harness the ecological and agricultural potential of mycorrhizal fungi. This comprehensive understanding of plant-mycorrhizal interactions is crucial for developing strategies to sustain healthy ecosystems and improve agricultural productivity in the face of environmental challenges.

Keywords: Mycorrhizae; symbiosis; nutrient-cycling; biodiversity; carbon-sequestration.

1. INTRODUCTION

Mutualistic relationships are a fascinating and crucial aspect of ecological interactions, where two different species engage in a mutually beneficial association. These interactions are fundamental to the stability and productivity of ecosystems. One of the most notable and widespread examples of mutualism is the relationship between plants and mycorrhizal fungi. This introduction delves into the definition of mutualism, provides an overview of mycorrhizal fungi, emphasizes the importance of studying plant-mycorrhizal relationships, and outlines the objectives of this review. Mutualism refers to an interaction between two different species where both parties derive benefits that enhance their survival, growth, or reproduction [1]. This type of relationship is one of the fundamental interactions in nature, alongside competition, predation, and parasitism. Mutualistic relationships can occur in various forms, including resource exchange, protection, and reproduction assistance. These interactions often result in co-evolution, where the involved species adapt traits that further reinforce their mutual benefits [2]. Mycorrhizal fungi are a diverse group of fungi that form symbiotic associations with the roots of most terrestrial plants [3]. These fungi are broadly categorized into several types, including arbuscular mycorrhizae (AM), ectomycorrhizae (ECM), ericoid mycorrhizae (ERM), and orchid mycorrhizae (ORM), each with distinct structural and functional characteristics [4]. Arbuscular mycorrhizal fungi penetrate plant root cells to form arbuscules, which are sites of nutrient exchange. Ectomycorrhizal fungi, on the other hand, form a sheath around plant roots and extend their hyphae into the surrounding soil, enhancing nutrient and water absorption [5]. The mutualistic relationship between plants and mycorrhizal fungi is ancient, with fossil evidence suggesting that such associations existed over 400 million years ago [6]. These fungi play a pivotal role in plant nutrient acquisition, particularly for phosphorus and nitrogen, and improve soil structure, thereby enhancing plant growth and ecosystem productivity [7].

1.1 Importance of Studying Plant-Mycorrhizal Relationships

Plant-mycorrhizal relationships is critical for several reasons. First, these interactions are fundamental to plant health and nutrition. Mycorrhizal fungi enhance plant nutrient uptake, particularly in nutrient-poor soils, by extending the root system's reach through their hyphal networks [8]. This is particularly important for phosphorus, a nutrient that is often limiting in soils but is essential for plant growth and development [9]. Mycorrhizal associations contribute to soil health and structure. The hyphae of mycorrhizal fungi bind soil particles together, improving soil aggregation and stability, which reduces erosion and enhances water infiltration and retention [10]. Additionally, mycorrhizal fungi play a role in organic matter decomposition and nutrient cycling, contributing to the overall fertility and sustainability of ecosystems [11]. These relationships have significant implications for plant community dynamics and biodiversity. Mycorrhizal fungi can influence plant competition, successional patterns, and the ability of plants to colonize new areas [12]. They also play a crucial role in the resistance and resilience of plant communities to environmental stressors such as drought, pathogens, and climate change [13].

1.2 Objectives of the Review

The primary objective of this review is to provide a comprehensive synthesis of the current understanding of mutualistic relationships between plants and mycorrhizal fungi and their impacts on ecosystem functioning. Specifically, this review aims to: Examine the different types of mycorrhizal associations and their distinct characteristics. Explore the mechanisms underlying plant-mycorrhizal interactions and nutrient exchange processes. Highlight the ecological functions and benefits of these mutualistic relationships, including their roles in nutrient cycling, soil health, and plant stress tolerance. Discuss the impacts of plant-mycorrhizal associations on plant communities and ecosystem functioning, including biodiversity, productivity, and resilience. Identify the methodologies used to study these interactions and review significant case studies and examples from various ecosystems. Address the challenges and future directions in the research of plant-mycorrhizal relationships, emphasizing the need for interdisciplinary approaches and the implications for ecosystem management and conservation.

2. TYPES OF MYCORRHIZAL ASSOCIATIONS

Mycorrhizal associations are critical symbiotic relationships between fungi and plant roots, facilitating nutrient exchange and enhancing plant growth and soil health (Table 1). These associations are diverse and can be broadly categorized into several types, each with unique characteristics and ecological roles. The main types of mycorrhizal associations include arbuscular mycorrhizae (AM), ectomycorrhizae (ECM), ericoid mycorrhizae (ERM), and orchid mycorrhizae (ORM).

2.1 Arbuscular Mycorrhizae (AM)

Arbuscular mycorrhizae (AM) are the most widespread and ancient form of mycorrhizal associations, found in approximately 80% of vascular plant species [14]. These fungi belong to the phylum Glomeromycota and form intricate networks within the root cortex of plants. The hallmark of AM is the formation of arbuscules-branched, tree-like structures inside root cells where nutrient exchange occurs [15]. In addition to arbuscules, AM fungi also produce vesicles, which serve as storage organs. AM fungi significantly enhance the uptake of phosphorus, an essential but often limiting nutrient in soils [16]. They also aid in the absorption of other nutrients such as nitrogen, potassium, and trace elements. The extensive hyphal networks of AM fungi increase the surface area for nutrient and water absorption, improving plant drought tolerance and soil structure [17]. These fungi also contribute to soil aggregation and stability by producing glomalin, a glycoprotein that binds soil particles together [18].

2.2 Ectomycorrhizae (ECM)

Ectomycorrhizae (ECM) are primarily associated with trees and shrubs in temperate and boreal forests, involving around 2% of plant species but playing a crucial role in forest ecosystems [19]. ECM fungi belong to various taxonomic groups, including Basidiomycota, Ascomycota, and some members of the Zygomycota. Unlike AM fungi, ECM fungi form a dense hyphal sheath around the root tips, known as a mantle, and extend hyphae into the surrounding soil and between root cells, creating a Hartig net [20]. ECM associations are particularly effective in nutrient-poor, acidic soils where they facilitate the uptake of nitrogen and phosphorus. They can decompose organic matter and mobilize nutrients bound in complex organic molecules, making them available to the host plant [21]. ECM fungi also enhance the resilience of forest ecosystems to environmental stresses, such as soil acidity and heavy metal contamination [22].

2.3 Ericoid Mycorrhizae (ERM)

Ericoid mycorrhizae (ERM) are specialized associations primarily found in plants of the Ericaceae family, such as heaths and heathers, which typically inhabit acidic, nutrient-poor soils [23]. ERM fungi are mostly Ascomycetes, including species like Oidiodendron and Hymenoscyphus [24]. These fungi form simple intracellular coils within the epidermal cells of fine hair roots. ERM fungi play a vital role in the decomposition of organic matter, enabling plants to access nutrients from complex organic compounds [25]. This ability is particularly important in the nutrient-poor, acidic environments where ERM plants are commonly found. By breaking down organic matter, ERM fungi release nitrogen, phosphorus, and other essential nutrients, supporting the growth and survival of their host plants [26].

2.4 Orchid Mycorrhizae (ORM)

Orchid mycorrhizae (ORM) are unique symbiotic associations essential for the germination and growth of orchids, which have tiny seeds with limited nutrient reserves [27]. ORM fungi belong primarily to the Rhizoctonia complex, which includes members of the Basidiomycota and some Ascomycota [28]. These fungi colonize orchid seeds and young seedlings, forming pelotons-coiled hyphal structures within root cells where nutrient exchange occurs. Orchids rely on ORM fungi not only for nutrient acquisition but also for successful seed germination and establishment [29]. The fungi provide the necessary carbohydrates and other nutrients to support the early growth stages of orchids. This symbiotic relationship is crucial for the survival of orchids in their native habitats, often characterized by low nutrient availability and specific ecological conditions [30].

2.5 Comparison of Different Mycorrhizal Types

While all mycorrhizal associations facilitate nutrient exchange and enhance plant growth, they differ in their structural characteristics, ecological roles, and specific benefits to host plants. AM fungi, with their extensive hyphal networks and arbuscules, are particularly effective in enhancing phosphorus uptake and improving soil structure [31]. ECM fungi, forming a dense mantle and Hartig net, excel in mobilizing nutrients from organic matter and are vital in forest ecosystems [32]. ERM fungi, with their ability to decompose organic matter in acidic soils, support the growth of ericaceous plants in challenging environments [33]. ORM fungi, crucial for orchid seed germination, highlight the diversity of mycorrhizal associations and their specialized adaptations [34]. Each type of mycorrhizal association represents a unique adaptation to specific ecological niches, contributing to the diversity and functioning of ecosystems. Understanding these differences is essential for managing ecosystems and harnessing the benefits of mycorrhizal fungi in agriculture, forestry, and conservation.

Table 1. Types of Mycorrhizal Associations (Source: [15,19,24,32])

Type	Fungi Involved	Plant Partners	Key Characteristics
Arbuscular Mycorrhizae	Glomeromycota	Most land plants	Forms arbuscules inside root cells, increases nutrient absorption (especially phosphorus).
Ectomycorrhizae	Basidiomycota, Ascomycota	Trees (pines, oaks, willows)	Forms a dense network around root tips, helps in nutrient and water absorption.
Ericoid Mycorrhizae	Ascomycota	Ericaceae family plants (heathers)	Forms coils inside root cells, assists in nutrient uptake in acidic and nutrient-poor soils.
Orchid Mycorrhizae	Basidiomycota	Orchid family plants	Forms coils and pelotons inside root cells, essential for seed germination and nutrient uptake.
Arbutoid Mycorrhizae	Basidiomycota	Arbutoideae subfamily (madrone)	Forms structures similar to both ecto- and endomycorrhizae, aids in nutrient absorption.
Monotropoid Mycorrhizae	Basidiomycota, Ascomycota	Non-photosynthetic plants (Monotropes)	Forms highly specialized associations, supports plants that obtain nutrients through mycoheterotrophy.

3. MECHANISMS OF PLANT-MYCORRHIZAL INTERACTIONS

Understanding the mechanisms of plant-mycorrhizal interactions is fundamental to comprehending how these symbiotic relationships enhance plant growth, soil health, and overall ecosystem functioning. The mechanisms involve complex processes including fungal colonization and root penetration, nutrient exchange, signaling pathways, molecular interactions, and carbon allocation within mycorrhizal networks.

3.1 Fungal Colonization and Root Penetration

The initial stage of the plant-mycorrhizal symbiosis involves the colonization of plant roots by mycorrhizal fungi (Fig. 1). This process begins when fungal spores germinate in the soil and hyphae grow towards plant roots, attracted by root exudates containing signaling molecules such as strigolactones [35]. Upon contact with the root surface, the fungi penetrate the root epidermis and cortex cells. In arbuscular mycorrhizae (AM), hyphae penetrate the root cells to form highly branched structures known as arbuscules, which are the primary sites for nutrient exchange [36]. The formation of arbuscules involves the reorganization of plant cell membranes and cytoskeleton to accommodate the fungal structures without causing cell death. In ectomycorrhizae (ECM), the fungi do not penetrate root cells; instead, they form a dense hyphal sheath around the root tip and a Hartig net between root cortical cells, facilitating nutrient exchange without intracellular colonization [37].

3.2 Nutrient Exchange Processes

One of the primary benefits of mycorrhizal associations is the enhanced uptake and exchange of nutrients between the fungus and the host plant. Mycorrhizal fungi improve the plant's access to essential nutrients, particularly phosphorus and nitrogen, which are often limiting in soils [38]. In AM symbiosis, the arbuscules act as interfaces for nutrient exchange, where the fungi deliver inorganic phosphorus (Pi) and other nutrients absorbed from the soil to the plant, in exchange for carbon compounds from the host plant [39]. Phosphate transporters in the plant cell membrane facilitate the transfer of phosphorus from the arbuscules to the plant [40]. ECM fungi, which are particularly efficient in nutrient-poor and acidic soils, utilize enzymes to decompose organic matter, releasing nutrients such as nitrogen and phosphorus from organic compounds [41]. The Hartig net formed by ECM fungi is the site of nutrient exchange, where nutrients absorbed from the soil are transferred to the plant roots, and carbohydrates from the plant are supplied to the fungi.

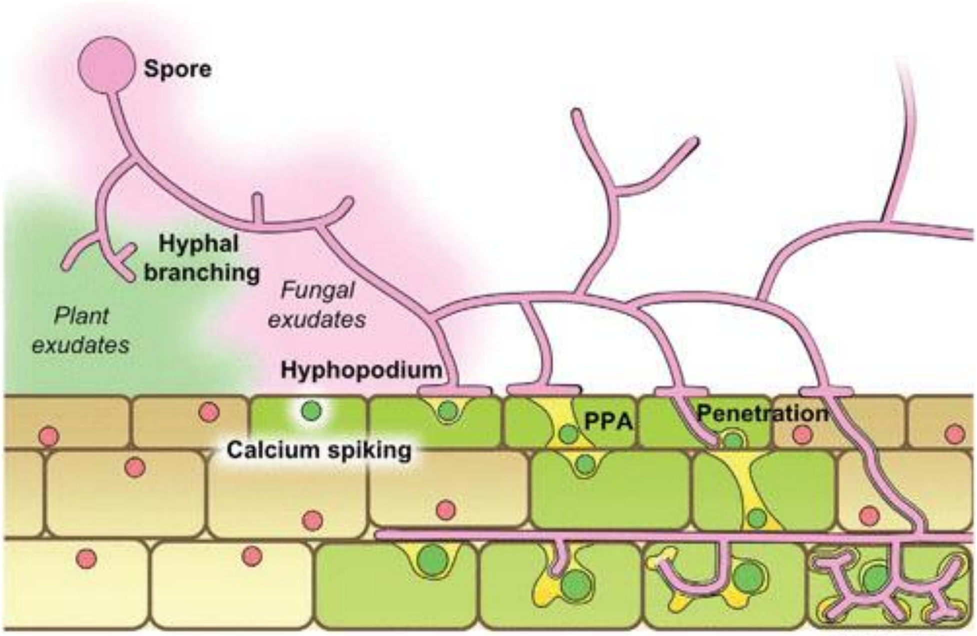

Fig. 1. Root colonization by AM fungi (Source-ASM Journals)

3.3 Signaling Pathways and Molecular Interactions

The establishment and functioning of mycorrhizal symbiosis are regulated by intricate signaling pathways and molecular interactions between the plant and the fungi. Initial recognition involves signaling molecules such as strigolactones released by plant roots, which stimulate fungal spore germination and hyphal growth [42]. In AM associations, the common symbiosis signaling pathway (CSSP) is crucial for the formation of arbuscules. This pathway involves several key components, including receptor-like kinases (RLKs), calcium/calmodulin-dependent protein kinases (CCaMK), and transcription factors that regulate gene expression necessary for symbiosis [43]. Similarly, in ECM associations, signaling molecules such as flavonoids and other phenolic compounds play roles in the mutual recognition and development of the symbiosis [44]. The exchange of nutrients also involves specific transporters and channels. For example, the AM-specific phosphate transporter PT4 is essential for the uptake of phosphorus from arbuscules into plant cells [45]. In ECM symbiosis, ammonium transporters and amino acid transporters are involved in nitrogen transfer from fungi to plants [46].

3.4 Carbon Allocation and Mycorrhizal Networks

Carbon allocation is a critical aspect of the plant-mycorrhizal symbiosis, as the fungi depend on the host plant for their carbon supply. Plants allocate a significant portion of their photosynthetically fixed carbon to mycorrhizal fungi, which use this carbon for their growth and metabolism [47]. In AM associations, the carbon is primarily transferred in the form of hexoses, which are metabolized by the fungi to produce energy and other compounds necessary for their growth and function [48]. In ECM associations, the carbon is supplied to the fungi as monosaccharides and polyols, supporting the extensive hyphal networks that explore the soil for nutrients [49]. Mycorrhizal networks, also known as common mycorrhizal networks (CMNs), extend beyond individual plant roots, connecting multiple plants within an ecosystem. These networks facilitate the transfer of nutrients, water, and signaling compounds between interconnected plants, enhancing resource distribution and community stability [50]. CMNs can also play roles in plant-plant communication, helping plants respond to environmental stresses and improving overall ecosystem resilience [51].

4. ECOLOGICAL FUNCTIONS AND BENEFITS

The mutualistic relationships between plants and mycorrhizal fungi confer numerous ecological functions and benefits, significantly enhancing plant health, soil structure, and overall ecosystem functioning.

4.1 Enhanced Nutrient Uptake

One of the primary ecological benefits of mycorrhizal associations is the enhanced uptake of essential nutrients, which is crucial for plant growth and development. Mycorrhizal fungi extend the effective root surface area through their hyphal networks, allowing plants to access nutrients that would otherwise be unavailable. Phosphorus is a vital nutrient for plants, playing a critical role in energy transfer, photosynthesis, and macromolecule biosynthesis. However, phosphorus is often limited in soils due to its low solubility and tendency to form insoluble complexes. Arbuscular mycorrhizal (AM) fungi are particularly effective in enhancing phosphorus uptake. The extensive hyphal networks of AM fungi can explore soil volumes beyond the depletion zones of root hairs, accessing phosphorus that is otherwise out of reach for plants [52]. The fungi transport phosphorus to the arbuscules, where it is exchanged for plant-derived carbon compounds [53]. Nitrogen is another essential nutrient that is often limited in availability. Both arbuscular mycorrhizal and ectomycorrhizal (ECM) fungi contribute to nitrogen acquisition. ECM fungi, in particular, are adept at mobilizing nitrogen from organic matter through the production of extracellular enzymes that break down complex organic compounds [54]. The nitrogen is then absorbed by the fungal hyphae and transferred to the host plant through the Hartig net. AM fungi also play a role in nitrogen uptake, particularly in agricultural systems where they can enhance nitrogen use efficiency [55]. In addition to macronutrients like phosphorus and nitrogen, mycorrhizal fungi aid in the uptake of micronutrients such as zinc, copper, and iron, which are essential for various plant metabolic processes. Mycorrhizal fungi can solubilize these nutrients from soil minerals and organic matter, making them available to plants [56]. This ability is particularly important in micronutrient-deficient soils, where mycorrhizal associations can significantly improve plant nutrition and health.

4.2 Improved Soil Structure and Health

Mycorrhizal fungi play a pivotal role in enhancing soil structure and health through various mechanisms, including soil aggregation, organic matter decomposition, and soil erosion prevention. Soil aggregation is crucial for maintaining soil structure, porosity, and water infiltration. Mycorrhizal fungi contribute to soil aggregation by producing hyphae that physically bind soil particles together. Additionally, AM fungi produce a glycoprotein called glomalin, which acts as a glue, stabilizing soil aggregates and improving soil structure [57]. Enhanced soil aggregation reduces soil compaction, promotes root growth, and improves water retention and drainage. Mycorrhizal fungi, particularly ECM fungi, are involved in the decomposition of organic matter, facilitating nutrient cycling and soil fertility. ECM fungi produce a range of extracellular enzymes that break down complex organic molecules, releasing nutrients such as nitrogen and phosphorus [58]. This decomposition process contributes to the formation of humus, a stable organic matter fraction that enhances soil health and nutrient availability. Healthy soil structure, supported by mycorrhizal fungi, plays a crucial role in preventing soil erosion. The hyphal networks of mycorrhizal fungi stabilize soil aggregates and improve soil cohesion, reducing the susceptibility of soil to erosion by wind and water [59]. This stabilization effect is particularly important in protecting topsoil, which contains the highest concentration of organic matter and nutrients essential for plant growth.

4.3 Plant Stress Tolerance

Mycorrhizal associations enhance plant resilience to various abiotic and biotic stresses, including drought, pathogens, and heavy metal contamination. Mycorrhizal fungi improve plant drought resistance by enhancing water uptake through their extensive hyphal networks. The hyphae can access water from micropores in the soil that roots cannot reach, increasing the plant's water supply during periods of drought [60]. Additionally, mycorrhizal fungi can induce physiological changes in the host plant, such as increased root biomass and altered root architecture, which further improve water acquisition and retention. Mycorrhizal fungi contribute to plant defense against soil-borne pathogens through several mechanisms. They can compete with pathogenic fungi and bacteria for space and resources, reducing pathogen establishment and proliferation [61]. Mycorrhizal colonization also induces systemic resistance in the host plant, enhancing its defense mechanisms against a range of pathogens [62]. This induced resistance involves the activation of plant defense genes and the production of antimicrobial compounds. In environments contaminated with heavy metals, mycorrhizal fungi can aid in plant survival and growth by sequestering and detoxifying heavy metals. The fungi can immobilize heavy metals in the soil, reducing their bioavailability and toxicity to the host plant [63]. Mycorrhizal fungi also enhance the production of metal-chelating compounds and antioxidant enzymes in plants, further mitigating heavy metal stress [64].

5. IMPACTS ON PLANT COMMUNITIES

The mutualistic relationships between plants and mycorrhizal fungi significantly influence plant communities, affecting biodiversity, species richness, plant growth and productivity, successional dynamics, and the control of invasive species.

5.1 Biodiversity and Species Richness

Mycorrhizal fungi contribute to plant community biodiversity and species richness by facilitating the coexistence of diverse plant species. These fungi enhance nutrient uptake and stress tolerance, allowing a wider range of plants to thrive in various environments [65]. The hyphal networks of mycorrhizal fungi connect multiple plants, creating common mycorrhizal networks (CMNs) that facilitate resource sharing and communication among plants, further promoting biodiversity [66]. Research has shown that the presence of diverse mycorrhizal fungi can increase plant species richness in grasslands and other ecosystems [67]. For instance, AM fungi have been found to enhance plant diversity by reducing the dominance of highly competitive species and allowing less competitive species to establish and persist [68]. Similarly, ECM fungi play a crucial role in maintaining forest biodiversity by supporting the coexistence of tree species with varying nutrient acquisition strategies [69].

5.2 Plant Growth and Productivity

Mycorrhizal associations significantly enhance plant growth and productivity by improving nutrient acquisition, particularly in nutrient-poor soils. AM fungi, for example, enhance phosphorus uptake, which is critical for plant growth and development [70]. This increased nutrient availability leads to enhanced biomass production and higher yields in agricultural and natural ecosystems [71].

ECM fungi also contribute to plant productivity by mobilizing nitrogen and phosphorus from organic matter, making these nutrients available to trees and other plants in forest ecosystems [72]. The enhanced nutrient uptake provided by ECM fungi supports greater plant growth and increases the overall productivity of forest ecosystems [73]. The positive effects of mycorrhizal associations on plant growth and productivity are not limited to individual plants but extend to entire plant communities. By enhancing the nutrient status of plants, mycorrhizal fungi contribute to higher community biomass and productivity, which are essential for the sustainability and resilience of ecosystems [74].

5.3 Successional Dynamics

Mycorrhizal fungi play a vital role in successional dynamics, influencing the establishment, growth, and survival of plant species during different stages of ecological succession. In early successional stages, pioneer species often rely on mycorrhizal fungi to establish and thrive in nutrient-poor and disturbed soils [75]. The fungi enhance the nutrient acquisition and stress tolerance of these pioneer species, facilitating their establishment and growth [76]. As succession progresses, mycorrhizal associations continue to influence plant community dynamics by affecting competition and coexistence among plant species. Mycorrhizal fungi can mediate competitive interactions by enhancing the nutrient uptake of less competitive species, allowing them to coexist with dominant species [77]. In later successional stages, the diversity and abundance of mycorrhizal fungi often increase, supporting the coexistence of a wider range of plant species and contributing to the stability and resilience of mature ecosystems [78].

5.4 Invasive Species Control

Mycorrhizal fungi can also influence the success of invasive species, playing a role in the control of plant invasions. Invasive species often disrupt native plant communities and alter ecosystem processes, but mycorrhizal associations can mitigate these impacts by enhancing the competitive ability of native species [79]. In some cases, invasive species may form associations with native mycorrhizal fungi, gaining a competitive advantage over native plants. However, native plants that are strongly mycorrhizal can resist invasion by outcompeting invasive species for nutrients and space [80]. Additionally, mycorrhizal fungi can enhance the resistance of native plant communities to invasion by improving soil health and nutrient cycling, creating unfavourable conditions for invasive species [81]. The effectiveness of mycorrhizal fungi in controlling invasive species depends on various factors, including the compatibility of invasive species with native mycorrhizal fungi and the diversity and abundance of mycorrhizal fungi in the ecosystem [82]. Managing mycorrhizal associations through conservation and restoration practices can therefore be a valuable strategy for controlling invasive species and preserving native plant communities.

6. IMPACTS ON ECOSYSTEM FUNCTIONING

Mycorrhizal associations profoundly influence ecosystem functioning through their roles in biogeochemical cycles, ecosystem stability and resilience, primary productivity and biomass accumulation, and climate change mitigation. These impacts are mediated through the extensive interactions between mycorrhizal fungi and plants, as well as their influence on soil processes and nutrient dynamics.

7. BIOGEOCHEMICAL CYCLES

Mycorrhizal fungi play crucial roles in regulating biogeochemical cycles by facilitating nutrient and carbon fluxes within ecosystems. Their extensive hyphal networks enhance the movement and transformation of key elements, including carbon, nitrogen, and phosphorus. Mycorrhizal fungi significantly impact the carbon cycle through their symbiotic relationships with plants. Plants allocate a substantial portion of their photosynthetically fixed carbon to mycorrhizal fungi, which use this carbon for growth and metabolic processes [83]. This carbon transfer supports the formation of extensive hyphal networks that enhance soil carbon storage. Mycorrhizal fungi also contribute to soil organic matter formation by decomposing organic substrates and incorporating plant-derived carbon into soil aggregates [84]. In forest ecosystems, ectomycorrhizal (ECM) fungi play a vital role in carbon sequestration by stabilizing soil organic matter and promoting the formation of stable carbon compounds [85]. Mycorrhizal fungi influence the nitrogen cycle by enhancing nitrogen uptake and mobilization from organic matter. ECM fungi, in particular, produce extracellular enzymes that decompose complex organic compounds, releasing nitrogen in forms accessible to plants [86]. This process not only supports plant nutrition but also contributes to nitrogen cycling within ecosystems. Arbuscular mycorrhizal (AM) fungi can also improve nitrogen use efficiency in plants by facilitating the uptake of inorganic nitrogen forms [87]. By enhancing nitrogen availability and uptake, mycorrhizal fungi help maintain soil nitrogen balance and support ecosystem productivity. The phosphorus cycle is significantly influenced by mycorrhizal fungi, especially AM fungi, which enhance phosphorus uptake from soil. Phosphorus is often present in insoluble forms that are not readily available to plants. AM fungi solubilize these phosphorus compounds and transport them to plant roots, thus facilitating efficient phosphorus acquisition [88]. This enhanced phosphorus uptake supports plant growth and productivity, contributing to the overall nutrient cycling within ecosystems. Additionally, mycorrhizal fungi can access phosphorus from organic matter and mineral sources, further integrating phosphorus into biogeochemical cycles [89].

7.1 Ecosystem Stability and Resilience

Mycorrhizal associations contribute to ecosystem stability and resilience by enhancing plant health and soil structure, which buffer ecosystems against environmental stresses. The extensive hyphal networks of mycorrhizal fungi improve soil aggregation and structure, reducing soil erosion and enhancing water retention [90]. These improvements in soil physical properties support plant growth and help maintain ecosystem stability during adverse conditions, such as drought or heavy rainfall. Mycorrhizal fungi enhance plant stress tolerance by improving nutrient and water uptake, increasing plant resistance to pathogens, and aiding in the detoxification of heavy metals [91]. These benefits contribute to the overall resilience of plant communities, enabling them to recover more quickly from disturbances and maintain ecosystem functioning. The presence of diverse mycorrhizal fungi can also enhance ecosystem resilience by supporting a variety of plant species with different stress tolerance mechanisms, thus promoting biodiversity and ecosystem stability [92].

7.2 Primary Productivity and Biomass Accumulation

Mycorrhizal associations play a crucial role in enhancing primary productivity and biomass accumulation in ecosystems. By improving nutrient acquisition, particularly phosphorus and nitrogen, mycorrhizal fungi support higher rates of photosynthesis and plant growth [93]. This increased nutrient availability leads to greater biomass production, which is essential for the sustainability and productivity of both natural and managed ecosystems. In agricultural systems, mycorrhizal inoculation has been shown to increase crop yields and improve soil fertility, contributing to sustainable agricultural practices [94]. In natural ecosystems, the presence of mycorrhizal fungi supports the growth of dominant plant species, leading to higher primary productivity and biomass accumulation [95]. This enhanced productivity is crucial for ecosystem services such as carbon sequestration, soil stabilization, and nutrient cycling.

7.3 Climate Change Mitigation

Mycorrhizal fungi have significant implications for climate change mitigation through their roles in carbon sequestration and ecosystem resilience. By enhancing carbon storage in soils, mycorrhizal fungi contribute to reducing atmospheric carbon dioxide levels, a key factor in mitigating climate change [96]. The stabilization of soil organic matter by mycorrhizal fungi, particularly ECM fungi, supports long-term carbon sequestration in forest ecosystems [97]. The ability of mycorrhizal fungi to improve plant stress tolerance and support diverse plant communities enhances ecosystem resilience to climate change impacts, such as increased temperature variability, altered precipitation patterns, and extreme weather events [98]. By maintaining ecosystem stability and productivity under changing climatic conditions, mycorrhizal associations play a critical role in mitigating the adverse effects of climate change on ecosystems.

8. METHODOLOGIES FOR STUDYING PLANT-MYCORRHIZAL INTERACTIONS

The study of plant-mycorrhizal interactions encompasses a wide range of methodologies, each contributing unique insights into the complex symbiosis between plants and fungi. These methodologies include experimental approaches, molecular techniques, imaging and microscopy, and modeling and simulation. Together, these techniques provide a comprehensive understanding of the mechanisms, functions, and ecological impacts of mycorrhizal associations.

8.1 Experimental Approaches

Field studies are essential for understanding plant-mycorrhizal interactions in their natural ecological context. These studies involve observing and experimenting with plants and their mycorrhizal partners in situ, providing valuable information on the ecological roles and benefits of mycorrhizal associations under real-world conditions. Field experiments often involve manipulating variables such as soil nutrient levels, moisture, and the presence of mycorrhizal fungi to assess their impacts on plant growth, nutrient uptake, and community dynamics [99]. One common field study method is the use of exclusion techniques, where certain plots are treated to prevent mycorrhizal colonization, allowing researchers to compare the growth and health of mycorrhizal and non-mycorrhizal plants. These studies can reveal the direct benefits of mycorrhizal associations for plant fitness and ecosystem functioning [100]. Greenhouse experiments provide a controlled environment to study plant-mycorrhizal interactions, allowing precise manipulation of environmental variables and conditions. These experiments often involve growing plants in pots or containers with different soil treatments, such as varying levels of nutrients, water, and mycorrhizal inoculation. Greenhouse studies are valuable for isolating specific factors and their effects on mycorrhizal symbiosis, providing detailed insights into the mechanisms of nutrient exchange, stress tolerance, and plant growth responses [101]. In greenhouse experiments, researchers can use sterilized soil to eliminate native mycorrhizal fungi and then introduce specific mycorrhizal species to assess their effects on plant growth and nutrient uptake. This approach allows for the controlled study of individual mycorrhizal species and their interactions with different plant species [102].

8.2 Molecular Techniques

DNA sequencing is a powerful molecular technique used to identify and characterize the genetic diversity of mycorrhizal fungi and their plant hosts. High-throughput sequencing technologies, such as next-generation sequencing (NGS), have revolutionized the study of mycorrhizal communities by enabling the comprehensive analysis of fungal DNA from soil and root samples [103]. These techniques allow researchers to identify mycorrhizal species, assess their abundance and distribution, and study their genetic relationships. Metabarcoding, a method that combines DNA sequencing with barcoding, is commonly used to analyze complex mycorrhizal communities. By amplifying and sequencing specific DNA regions, such as the internal transcribed spacer (ITS) region, researchers can identify multiple mycorrhizal species within a single sample, providing insights into fungal diversity and community composition [104]. RNA analysis, including transcriptomics, is used to study gene expression patterns in mycorrhizal fungi and their plant hosts. This technique involves extracting RNA from plant and fungal tissues and sequencing the RNA molecules to identify actively expressed genes. RNA analysis provides insights into the molecular mechanisms underlying mycorrhizal symbiosis, including nutrient exchange, signaling pathways, and stress responses [105]. RNA-Seq, a high-throughput sequencing method for analyzing RNA, enables researchers to compare gene expression profiles between mycorrhizal and non-mycorrhizal plants, as well as between different stages of mycorrhizal colonization. This information helps identify key genes and regulatory networks involved in establishing and maintaining mycorrhizal associations [106]. Metabolomics involves the comprehensive analysis of metabolites, the small molecules produced during metabolic processes. This technique is used to study the biochemical interactions between plants and mycorrhizal fungi, providing insights into the metabolic changes associated with mycorrhizal symbiosis. Metabolomic analyses can reveal how mycorrhizal fungi influence plant metabolism, including nutrient uptake, stress responses, and secondary metabolite production [107]. By comparing the metabolite profiles of mycorrhizal and non-mycorrhizal plants, researchers can identify specific metabolites that play roles in the symbiosis, such as signaling compounds, defensive chemicals, and nutrient transport molecules. These insights contribute to a deeper understanding of the functional aspects of mycorrhizal associations [108].

8.3 Imaging and Microscopy

Electron microscopy provides high-resolution images of the ultrastructure of mycorrhizal fungi and their interactions with plant roots. Scanning electron microscopy (SEM) and transmission electron microscopy (TEM) are commonly used to visualize the detailed morphology of fungal hyphae, arbuscules, vesicles, and Hartig nets within root tissues [109]. SEM allows researchers to observe the surface structures of mycorrhizal roots and fungal hyphae, revealing the intricate networks formed during colonization. TEM, on the other hand, provides detailed images of the internal structures of fungal and plant cells, allowing for the study of intracellular interactions and nutrient exchange processes. These imaging techniques are crucial for understanding the physical and functional aspects of mycorrhizal symbiosis at the cellular level [110]. Confocal microscopy is a powerful tool for studying mycorrhizal interactions in living tissues. This technique uses laser light to generate high-resolution, three-dimensional images of fluorescently labeled structures within plant and fungal cells. Confocal microscopy is particularly useful for visualizing the spatial distribution of mycorrhizal fungi within root tissues and tracking the dynamics of colonization [111]. Fluorescent dyes and genetically encoded fluorescent proteins can be used to label specific components of the mycorrhizal symbiosis, such as fungal hyphae, plant cell membranes, and nutrient transporters. These labels allow researchers to observe the real-time interactions between plants and mycorrhizal fungi, providing insights into the processes of nutrient exchange, signaling, and colonization [112]. Modeling and simulation are essential for understanding the complex dynamics of plant-mycorrhizal interactions and predicting their impacts on ecosystem processes. Mathematical and computational models can integrate data from experimental studies to simulate the behavior of mycorrhizal networks, nutrient cycling, and plant growth under various environmental conditions [113]. Models can be used to explore how mycorrhizal associations influence nutrient uptake, carbon allocation, and plant community dynamics. For example, ecological models can simulate the effects of mycorrhizal fungi on plant competition, succession, and ecosystem productivity [114]. These models help researchers and land managers predict the outcomes of different management practices and environmental changes on mycorrhizal symbiosis and ecosystem health. Simulation tools, such as agent-based models and process-based models, can also be used to study the interactions between mycorrhizal fungi and other soil organisms, such as bacteria and pathogens. These simulations provide insights into the complex web of interactions within the soil microbiome and their effects on plant health and ecosystem functioning [115].

9. CASE STUDIES AND EXAMPLES

Understanding the diverse roles and impacts of mycorrhizal fungi across different environments is crucial for both theoretical knowledge and practical applications.

9.1 Agricultural Systems

Mycorrhizal fungi play a vital role in enhancing crop productivity and soil health in agricultural systems. Their ability to improve nutrient uptake, particularly phosphorus and nitrogen, can significantly increase crop yields and reduce the need for chemical fertilizers. One notable example is the use of arbuscular mycorrhizal (AM) fungi in maize cultivation. Studies have shown that inoculating maize with AM fungi can enhance phosphorus uptake, leading to increased plant growth and higher grain yields [116]. In maize fields with low phosphorus availability, mycorrhizal inoculation has been particularly beneficial, demonstrating the potential of mycorrhizal symbiosis to improve crop performance in nutrient-poor soils. In organic farming systems, where synthetic fertilizers and pesticides are minimized, mycorrhizal fungi contribute to soil fertility and plant health. For instance, in organic tomato production, AM fungi have been shown to enhance nutrient uptake, improve plant growth, and increase resistance to soil-borne pathogens [117]. The use of mycorrhizal inoculants in organic farming aligns with sustainable agricultural practices, promoting soil health and reducing environmental impacts.

9.2 Natural Ecosystems

In natural ecosystems, mycorrhizal fungi are integral to plant community dynamics, nutrient cycling, and ecosystem stability. They facilitate plant coexistence, enhance biodiversity, and contribute to ecosystem resilience. A well-documented example is the role of ectomycorrhizal (ECM) fungi in boreal and temperate forests. ECM fungi form symbiotic associations with dominant tree species, such as pines, oaks, and birches, enhancing their nutrient uptake and stress tolerance [118]. These fungi are crucial for the decomposition of organic matter and the mobilization of nutrients, supporting forest productivity and sustainability [119]. The extensive hyphal networks of ECM fungi also stabilize soil structure, reducing erosion and maintaining soil health. In tropical rainforests, AM fungi are prevalent and play a significant role in supporting the diversity and productivity of plant communities. For example, research in Amazonian forests has shown that AM fungi contribute to the nutrient acquisition and growth of diverse plant species, promoting biodiversity and ecosystem functioning [120]. The symbiotic relationships between tropical plants and AM fungi are critical for the maintenance of these complex and highly productive ecosystems.

9.3 Restoration Ecology

Mycorrhizal fungi are increasingly recognized for their potential in ecological restoration, particularly in degraded landscapes where soil health and plant diversity have been compromised. By enhancing plant establishment, nutrient cycling, and soil structure, mycorrhizal fungi can facilitate the recovery of degraded ecosystems. One example is the use of mycorrhizal fungi in the restoration of mining sites. Inoculating plants with mycorrhizal fungi has been shown to improve plant survival and growth in soils contaminated with heavy metals [121]. For instance, in the restoration of copper mine tailings, AM fungi have been used to enhance the growth of pioneer plant species, stabilize soil, and reduce heavy metal bioavailability [122]. These mycorrhizal-assisted restoration efforts contribute to the establishment of vegetation cover and the recovery of ecosystem functions in contaminated sites. In prairie restoration, the reintroduction of native mycorrhizal fungi has been shown to enhance the establishment and growth of native plant species, promoting biodiversity and ecosystem resilience [123]. By restoring mycorrhizal associations, these projects aim to recreate the natural symbiotic relationships that support healthy and diverse prairie ecosystems.

9.4 Urban and Industrial Landscapes

Urban and industrial landscapes present unique challenges for plant growth and soil health due to pollution, soil compaction, and limited nutrient availability. Mycorrhizal fungi can play a crucial role in mitigating these challenges and enhancing the sustainability of urban green spaces and industrial sites. In urban forestry, mycorrhizal fungi have been used to improve the health and growth of street trees and urban forests. For example, inoculating urban trees with AM fungi has been shown to enhance their nutrient uptake, drought tolerance, and resistance to pollutants [124]. These benefits are essential for maintaining the health and longevity of urban trees, which provide critical ecosystem services such as air quality improvement, temperature regulation, and aesthetic value. In industrial landscapes, such as brownfields and landfill sites, mycorrhizal fungi have been used to support vegetation establishment and soil remediation. For instance, research has demonstrated that inoculating plants with AM fungi can enhance their growth and survival in soils contaminated with hydrocarbons and heavy metals, facilitating the phytoremediation process [125]. By improving plant health and soil structure, mycorrhizal fungi contribute to the ecological restoration and stabilization of these challenging environments.

10. CHALLENGES AND FUTURE DIRECTIONS

The study of plant-mycorrhizal interactions has advanced significantly in recent decades, yet numerous challenges and opportunities for future research remain. Addressing these challenges requires a multifaceted approach, integrating advancements in technology, interdisciplinary research, and policy development to fully harness the potential of mycorrhizal fungi for ecological and agricultural sustainability.

10.1 Knowledge Gaps and Research Needs

Despite considerable progress, significant knowledge gaps persist in understanding the complexities of plant-mycorrhizal interactions. One of the primary areas requiring further research is the ecological specificity and functional diversity of mycorrhizal fungi. While many studies have focused on the general benefits of mycorrhizal associations, the specific roles of different mycorrhizal species in diverse ecological contexts remain poorly understood [126]. Future research should aim to elucidate the functional traits of various mycorrhizal fungi and their contributions to ecosystem processes under different environmental conditions [127]. Another critical area is the interaction of mycorrhizal fungi with other soil microorganisms and their collective impact on plant health and soil fertility. The soil microbiome is a complex network of organisms, and understanding how mycorrhizal fungi interact with bacteria, other fungi, and soil fauna is essential for a holistic view of soil ecology [128]. Research should focus on the synergistic and antagonistic relationships within the soil microbiome and their implications for nutrient cycling and plant growth.

10.2 Technological and Methodological Limitations

Technological and methodological limitations pose significant challenges in the study of mycorrhizal associations. Traditional methods of studying mycorrhizal fungi, such as root staining and spore identification, are time-consuming and may not capture the full diversity and functional capabilities of these fungi [129]. Advances in molecular techniques, such as high-throughput sequencing and metagenomics, have revolutionized the field, but these technologies also come with challenges, including high costs, complex data analysis, and the need for standardized protocols [130]. Another limitation is the difficulty in studying mycorrhizal fungi in situ. Many studies rely on controlled greenhouse experiments, which may not fully replicate the complex interactions and environmental conditions of natural ecosystems [131]. Developing methods to study mycorrhizal associations in their natural habitats, using non-invasive imaging and real-time monitoring techniques, is crucial for obtaining accurate and comprehensive data.

10.3 Interdisciplinary Approaches

Addressing the challenges and knowledge gaps in mycorrhizal research requires interdisciplinary approaches that integrate insights from ecology, microbiology, plant science, soil science, and environmental science. Collaborative efforts between researchers from different disciplines can lead to a more comprehensive understanding of mycorrhizal functions and their applications [132]. For example, combining ecological and molecular approaches can help elucidate the genetic and environmental factors that influence mycorrhizal symbiosis. Integrating soil science and plant physiology can enhance our understanding of how mycorrhizal fungi affect soil properties and plant health under various environmental conditions. Moreover, collaboration with agronomists and land managers can facilitate the translation of research findings into practical applications for sustainable agriculture and ecosystem management [133].

10.4 Policy and Management Implications

The ecological and agricultural benefits of mycorrhizal fungi have significant policy and management implications. Developing policies that promote the conservation and utilization of mycorrhizal fungi can enhance ecosystem resilience and agricultural sustainability. For instance, policies encouraging the use of mycorrhizal inoculants in agriculture can reduce the dependence on chemical fertilizers and improve soil health [134]. Conservation policies should also prioritize the protection of mycorrhizal diversity, particularly in habitats threatened by land-use change, pollution, and climate change. Protecting natural habitats and promoting sustainable land management practices can help preserve the ecological functions of mycorrhizal fungi and the plant communities they support [135]. Integrating mycorrhizal research into environmental education and public awareness campaigns can highlight the importance of soil health and microbial diversity in maintaining ecosystem services. Engaging policymakers, land managers, farmers, and the public in mycorrhizal conservation efforts can foster a more sustainable relationship with the environment [136].

11. CONCLUSION

The study of plant-mycorrhizal interactions reveals their profound impact on nutrient uptake, soil health, plant growth, and ecosystem resilience, highlighting their essential role in both natural and agricultural systems. Despite significant advances, knowledge gaps remain, particularly regarding the specific functions of diverse mycorrhizal species and their interactions within the soil microbiome. Technological and methodological limitations, such as the need for more accurate in situ studies and cost-effective molecular techniques, must be addressed. Embracing interdisciplinary approaches and integrating mycorrhizal research into policy and management practices can enhance sustainable agriculture and ecosystem conservation. Future research and collaboration across scientific disciplines will be crucial in unlocking the full potential of mycorrhizal fungi for ecological and agricultural sustainability, ultimately fostering healthier and more resilient ecosystems.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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