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Mycorrhizal symbioses and plant interactions

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Keywords

Plants interaction; Symbiotic microorganisms; Microbial biodiversity; Rhizosphere

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REVIEW ARTICLE

Mycorrhizal Symbioses and Plant Interactions

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Abstract

The growing interest in mycorrhizal fungi in agriculture is related to their symbiotic relationships with cultivated plants. Thanks to functional genomics approaches, mycorrhizae and symbioses with host plants have emerged for their features. Besides improving nutritional supply, plant–fungal interactions increase plants' tolerance to abiotic stresses such as drought, salinity and cold, as well as their resistance to diseases. Recent studies have investigated the interactions between plants and mycorrhizae, however the mechanisms often remain unclear. Indeed, plants in the field are affected by various stresses and results often appear contradictory. This review is aimed at presenting the most relevant studies in this field in order to highlight the possible benefits of mycorrhizal interactions and their application in agriculture.

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1. Introduction

Towards the end of the 19th century, symbiosis was understood as a long-lasting association established by different species [1]. Symbiosis encompasses a broad spectrum of relationships involving benefits for both partners, antagonistic relationships and relationships from which one organism benefits [2,3]. The type of association often depends on the type of environment and the developmental stage of the partners. The basis of symbiosis is undoubtedly the possibility of an organism acquiring new metabolic capabilities from the relationship established with its new partner. Symbioses represent a solid evolutionary and innovative significance in the development of new organs, tissues and cells [4]. In the interaction that can take place between nitrogen-fixing microorganisms and leguminous plants, a series of events occur that ensure the relationship between the two organisms: the presence of signal molecules, a signal uptake system, the activation of transcription factors and target genes [5]. Plants has an underdeveloped root system, which makes arbuscular mycorrhizae a crucial factor in plant evolution and territory conquest [6]. The ability of symbiont micro-organisms to enhance the mineral uptake of plants, especially in nutrient-poor environments, certainly favoured symbiotic relationships [7]. Unlike arbuscular mycorrhizae, ectomycorrhizae seem to have appeared much later. These fungi and their symbiotic relationships have adapted to environments rich in organic matter, so it can be outlined that the type of nutrient exchange certainly depends on the type of mycorrhiza and reflects the different ecological specialisations of these associations [8]. Mycorrhizae are not obligatory relationships with plants, as the latter can also grow without the fungus, especially in nutrient- and water-rich soils, such as those fertilised by agriculture. Nervetheless, the mycorrhizal arbuscules can develop symbiotic relationships with their host plants that determine their dependence. Mycorrhizae play a crucial role in the establishment and stability of plant communities [9–11]. The role of mycorrhizal symbiosis in plant communities and ecosystems has received more attention in recent research. In fact, it has become increasingly important to study the extraradical mycelial phase of the symbiosis and to use realistic substrates in answering pertinent ecological questions [12,13]. Many authors have highlighted the multifunctional nature of mycorrhizal effects [14,15], including

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interactions with bacteria [16], weathering of minerals [17−19], carbon cycling [20], effects on plant communities [21], tripartite syntheses with mycoheterotrophs [22,23], and mediation of plant responses to stress [24]. Through symbiosis, the plant improves its mineral nutrition, having a positive effect on its growth, in exchange for carbon compounds that are given to the fungus [25,26]. The success of mycorrhizal fungi, in time and space, is mainly related to the nutritional benefits they confer on their host plants: through the extraradical mycelium they absorb phosphate and other macronutrients, as well as trace elements and water from the soil, and release them to the plant [27]. Specifically, nutrients are exchanged through the symbiotic interface between the plant and the fungus, which is created within the roots [25,27−30]. Moreover, using the symbiosis, the plant becomes more resistant to biotic stresses [31] and increases tolerance to abiotic stresses, such as lack of water or the presence of pollutants [28,29]. In recent years, it has also been highlighted that the effects of symbiosis on plant response may be different and may be related to the genotypes of the two symbiotic organisms, environmental conditions as well as the availability of resources [32].

The aim of this review is to highlight the mechanisms and effects that underlie the symbiosis between plants and mycorrhizae, in order to gain a better understanding of these fundamental relationships in plant life and for soil biodiversity and fertility. There is still little understanding of the detailed functioning and regulation of these mycorrhizosphere processes, but recent progress has been reviewed, as well as the potential benefits of an improved understanding of mycorrhizosphere interactions.

2. The various mycorrhizal symbioses

Generally, mycorrhizal symbioses can occur for several reasons: anatomical characteristics, the type of nutrients exchanged, and the taxonomic position of the organisms involved [33]. In order to determine the type of mycorrhizal symbiosis, it is generally observed how the symbiont fungus affects the host plant cells. By contrast, ectomycorrhizal fungi remain outside plant cells, while endomycorrhizal fungi colonize root cells. In the ectomycorrhizal symbiosis, the fungus produces a layer of hyphae called mycoclena around the root, from which organized hyphae branch off to explore the soil and transport water and nutrients. At the same time, a hyphal network develops on the root, which surrounds the plant cells without penetrating them (Hartig's network) [34,35]. A similar process occurs in endomycorrhiza, where extraradical hyphae explore the soil and absorb nutrients, however the process is not comparable to ectomycorrhiza [36]. Arbuscular mycorrhizae take their name from the arbuscule, a structure generated by branching the hypha within cortical cells. There are also other types of symbiosis, in which fungi generate hyphal galls, as in the case in orchids and ericoid mycorrhizae (Table 1) [37]. Ectoendomycorrhizae present characters intermediate between ectomycorrhizae and endomycorrhizae and are specialized in a limited number of plant species, on which they generally develop a mycoclena or Hartig reticulum associated with the root penetration of the fungus [38,39]. Ectomycorrhizae are found in deciduous and coniferous woodland environments in temperate and cold climates. The soil of temperate forests generally has a thick layer of organic material from leaf litter, rich in compounds that are difficult to degrade [40]. In these soils, nitrogen is in organic form, easily absorbed by ectomycorrhizal fungi and transferred to the host plant. In contrast, arbuscular mycorrhizae are present in temperate and warm climates. In these areas, microbial activity quickly degrades organic matter, and phosphorous is the limiting element for plant growth [41,42]. Therefore, arbuscular mycorrhizal fungi mainly specialize in the transfer of phosphates in inorganic form. Three different forms of mycorrhiza can be identified in the Ericaceae. These plants are characterized by having excellent roots, and generally, the epidermis is the cell layer colonized by the fungi. Erycoid mycorrhizae are mainly found in tundra and heathland environments both in Mediterranean and cold regions. In heaths strongly characterized by acidic soils, mineralization processes are mainly slowed down, and the availability of heavy metals can be high [43]. Under these conditions, the plants' resistance is significantly increased by their association with symbiotic fungi, which enable the breakdown of complex molecules and transfer of nutrients in organic form to the plants [44,45]. Plants in the soil exhibit mycorrhiza consistently

Table 1. List of certain ectomycorrhizal fungi [37].

Ectomycorrhizal symbionts	Family
Suillus luteus (L.) Roussel	*Suillaceae*
Suillus granulatus (L.) Roussel	*Suillaceae*
Boletus edulis Bull.	*Boletaceae*
Amanita muscaria (L.) Lam.	*Amanitaceae*
Clitopilus prunulus (Scop.) P. Kumm.	*Entolomataceae*
Lactarius delicious (L.) Gray	*Russuluceae*
Craterellus lutescens (Pers.) Fr.	*Cantharellaceae*

regardless of the ecological area in which they grow, whether they are epiphytes or terrestrials [46]. Orchids are characterized by a complex life cycle. Plants in the heterotrophic phase cannot photosynthesize since photosynthetic pigments are absent and rely on mycorrhizal fungi for carbon acquisition. For this reason, mycorrhizae represent a standard and, in many cases, a fundamental element in the life of terrestrial species. Their first appearance coincided with the evolution of host plants [47,48]. In addition to mycorrhizal fungi's crucial nutritional role, they defend the host plant from numerous abiotic and biotic stresses [49].

3. Determining mechanisms in biological biodiversity

Mycorrhizal biodiversity at the root level closely reflects the specificity of the particular fungus−plant association [50]. In the different mycorrhizal types, very different situations are observed regarding the diversity of fungal symbionts. In ectomycorrhizae, an impressive richness of fungal symbionts species is observed, requiring the host plant to complete its life cycle and produce a fruiting body [51,52]. Measuring the number of fruiting bodies produced by each species within the plant community has long been used to assess the diversity and relative abundance of different ectomycorrhizal species. The first study on symbionts showed a massive discrepancy in the production of fruiting bodies, as species frequently found as symbionts produced significantly few fruiting bodies [53,54]. In contrast, other species found as fruiting bodies were rarely associated with root apices [55]. Studies have thus shown that a small number of ectomycorrhizal fungal species colonize up to 70% of root apices, while many species appear more rarely [56]. The composition of these fungal communities varies depending on numerous biotic and abiotic factors [57]. The plant benefits obtained from symbioses with ectomycorrhizal fungi are attributable to access to otherwise inaccessible nutrients [58,59]. They produce a wide range of extracellular enzymes capable of decomposing complex organic molecules. The fungus can recover nitrogen and phosphorous in an organic form that can be partly given to the plant in exchange for sugars [60]. Since each fungus strain produces its spectrum of enzymes with different biochemical characteristics, the advantage of associating with a variety of fungal symbionts is quite evident for a plant growing in nutrient-poor ecosystems rich in organic compounds of a varied and complex nature [61−63]. Compared to ectomycorrhizae, where fungal species are numerous and belong to different taxa, arbuscular mycorrhizae have around a hundred species of symbionts. Several recent studies have demonstrated that plants and arbuscular mycorrhizae' biodiversity is closely related [64]. Microcosm studies have shown that the species composition of the plant community correlates with the type of fungi present. The plants most favoured by establishing an affluent fungal population depend on mycorrhiza for mineral nutrition and growth (Fig. 1) [65]. The increase in diversity observed in plant communities following the increase in fungal species primarily reflects an increased presence of these mycorrhiza-dependent species. Concerning the diversity of fungal symbionts, very different conclusions have been reached by identifying mycelia isolated from mycorrhized roots or by molecular analysis [66]. Regarding the diversity of fungal symbionts, very different conclusions have been reached by identifying mycelia isolated from mycorrhized roots or by molecular analysis [67]. In the heterotrophic phase of the life cycle, the plant acquires organic carbon compounds by exploiting its symbionts' strong degradative ability to degrade organic matter in the environment [68]. These methods have been used to identify the mechanism of acquiring organic carbon compounds. In mycorrhizal symbiosis, filamentous structures are composed of symbiont fungi. On the one hand, they interact with plant roots and explore the soil extensively, even over considerable distances. This unique cellular organization makes mycorrhizal symbiosis a fascinating phenomenon [69]. Alternatively, in this exploration phase in the soil, fungal hyphae can make contact with the roots of other potential hosts, forming hyphal connections between the roots of distinct plant individuals [70]. Depending on the specificity of the plant-fungus interaction, these hyphal connections may involve individuals of the same or different species. Different types of mycorrhizal fungi transport different nutrients: arbuscular mycorrhizal fungi transport mainly phosphorous and inorganic nitrogen. As opposed to this, ectomycorrhizal fungi transfer organic carbon compounds [30,71]. Studies concerning these interconnections have revealed

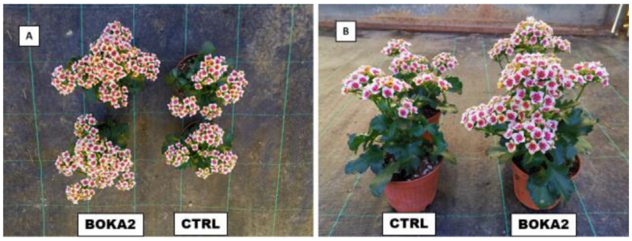

Fig. 1. Improving plant nutrition through mycorrhizal symbioses can increase flowering in Kalanchoe blossfeldiana. Boka2 (TREATED) vs CTRL (CONTROL).

some consequences of the distribution of organic carbon resources [72], for example, in transferring sugars between photosynthetic adult plants and young seedlings, which would otherwise die. In *Crocus sativus* plants, the different types of mycorrhizae (ectomycorrhizae and endomycorrhizae) have a different effect on the vegetative and root development of the plants (Fig. 2). Most heterotrophic plants have evolved this sophisticated exchange mechanism through the fungi's network of hyphal interconnections to obtain the needed sugars. Moreover, several species have evolved a similar mechanism, indicating evolutionary convergence [73].

4. The different interactions between plant and symbiont fungus

Despite the genetic and functional multiplicity, there is a unifying factor in that the host plant must accommodate the fungus in the root, giving rise to micromorphogenesis events that can only be appreciated microscopically. It can be observed that the modification of the root is the result of coordinated colonization processes.

1) development of the fungus in the rhizosphere and the exchange of signals with the plant;
2) contact with the root surface and the development of adhesion structures (Fig. 3)
3) development of fungal structures associated with the root surface and intraradical.

The mycorrhizal symbiosis phase represents a stage in a very complex life cycle comprising.

i) a saprotrophic phase where mycelia originating from spores of the sexual origin or vegetative propagules grow even in the absence of the host plant and proliferate in the soil;
ii) a symbiotic association phase;
iii) a reproductive phase culminating in the production of an ascocarp or basidiocarp.

Fig. 2. Effect of different types of mycorrhiza Laccaria bicolor (LB) ectomycorrhiza and Glomus deserticola (GD) endomycorrhiza, on root and vegetative growth of Crocus sativus.

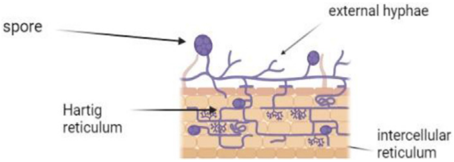

Fig. 3. Process of colonisation of the root by mycorrhizae with description of their structures.

In the molecular interaction between the two partners, the fungus contacts the root surface, and the hyphae increase in diameter and branch out, cleaving the median lamella between the epidermal cells and insinuating themselves, forming the first elements of the Hartig reticulum [74]. As a result of this morphological organization, functions are compartmentalized: extraradical hyphae function as nutrient uptake structures; the mantle serves as a reserve structure for nutrients; the Hartig reticulum serves as a site for exchange between both hosts due to its increased contact surface. In some fungal genotypes, defence reactions can also occur, with an accumulation of callose. It is clear, therefore, that there are essential processes that change the morphology of the root and the shape of the epidermal cells in the type of growth regulated by genes and signal exchanges in the rhizosphere [75]. The genetic determinants that control the process of mycorrhizal symbiosis in plants are beginning to be known through the study of mutants, which have enabled the identification of a good number of genes that perform similar functions in different plants have highly conserved sequences. In controlling the colonization process, the secondary metabolism of host plants may be of great importance [76]. It has long been known that flavonoids released from roots can enhance the growth process of hyphae from germinated spores, but the role of these compounds is still unclear. Recently, however, it has been shown that the release of metabolites into the soil stimulates hyphal branching, simultaneously the respiratory process, and other related oxidative metabolisms [77].

5. Molecular mechanisms determining the establishment of symbioses

Knowledge of the molecular mechanisms that enable the establishment of symbioses has leapt forward thanks to the development of molecular biology technologies [78]. Through them, it has been possible to identify genes of interest, analyze their functions and assess gene expression under different environmental conditions [79]. Various scientific tests have shown that mycorrhized plants grow better than non-mycorrhized ones [30]. This is generally related to the improved uptake of nutrients mediated by the symbiont fungi, which is particularly important for poorly mobile ions such as phosphate and ammonium [80]. These ions are known to be growth-limiting for plants, as they become deficient in the rhizosphere, where a depletion zone forms, following uptake by the root hairs [81]. The hyphae of the symbiont fungi can efficiently counterbalance cuttings depletion area, as nutrients through the fungal hyphae pass to the root cells acting as sinks faster than they diffuse into the soil. This faster translocation activity explains the increased uptake rate of mycorrhized roots [82]. The improved vegetative development of mycorrhized plants is primarily due to the improved availability of phosphorus (Fig. 4). The symbiont fungi can take up the free phosphorus in the soil beyond the depletion zone and transfer it to the plant [83]. Mycorrhizal fungi can solubilize forms of phosphorous that the plant cannot solubilize, such as calcium and aluminium phosphates, thanks to the controlled secretion of extracellular phosphatases [84]. A gene coding for a high-affinity transporter for phosphate, especially active in outer hyphae, is present in *Glomus* spp. [85]. Even in the same ecosystem, mycorrhizal fungi can explore different niches and exploit mineral element sources differently. It is especially true for nitrogen: significant changes are influenced by the concentration, form, and availability of plants, all of which correlate with soil microorganism degradation cycles (Fig. 5) [86]. At low temperatures and acid pH, nitrogen mineralization is so slow that organic sources become essential. In addition to having high-affinity ammonium transporters similar to yeast ammonium permeases MEP2, ectomycorrhizal fungi possess very active ammonium uptake agents [87]. Activated transporters occur during nitrogen deficiency, are repressed by glutamine, and are active during the symbiotic phase. It is still being determined how glutamine synthetase is transferred to plants [88]. Several studies have indicated glutamine synthetase to be highly expressed in some symbionts during nitrogen deficiency and fruiting body formation [89]. A gene expression study has shown that gene determinants are only activated when the fungus emerges on a sugar–poor medium and is low in glucose and ammonia. Therefore, assimilation pathways differ significantly depending on how closely the plant is associated with the host [90]. The molecular approach was used to identify nitrate reductase genes expressed by mycorrhizal maize roots and distinguish between symbiont genes and host genes [91].

Fig. 4. Increased plant height and leaf growth in Plectranthus amboinicus plants treated with Glomus intraradices under phosphorus deficient conditions. The growth is evident in treated plants (AM), compared to control plants (CTRL).

Fig. 5. Stimulating effect of Glomus mossae on Kalanchoe daigremontiana plants in the presence of nitrogen. Increased vegetative and root growth and number of new shoots in the treated thesis (TREATED) compared to the control (CTRL) under conditions of reduced nitrogen content in the growing medium.

6. Synergistic activity of soil microorganisms

Several analyses have recently been conducted on the relationship between soil microorganisms and symbiotic fungi, demonstrating that they can significantly impact plant health because of the synergy between various populations in the rhizosphere [92]. In order to explain these interactions, many mechanisms have been proposed, including phytohormone production, enzyme release, vitamin release, and growth stimulation. Mycorrhizae and rhizobacteria may be able to form biofilms on the surface of hyphae, preventing their leaching and, ultimately, their loss of the inoculum. In light of this, increased bacteria numbers and concentrations locally may explain the beneficial effects [93]. Recent studies have shown that certain *Pseudomonas* strains can adhere to fungal hyphae due to the presence of specific molecules such as mucopolysaccharides [94]. Some mycorrhizae also harbour several bacteria in their cytoplasm, which, though unculturable with small genome size, are transmitted vertically to future generations. As a result of this symbiosis within symbiosis, the fungal genome is more complex due to the resident genomes [95]. Symbioses between microorganisms are fascinating because of their peculiar cellular organization, which has structures capable of interacting with the roots of host plants and exploring the soil around them. Depending on the specificity of the microorganism—plant interaction, these connections may involve individuals of the same or different species [94]. Depending on the environment, these lattices can move organic and inorganic nutrients from one plant to another (Table 2). According to these relationships in the subsoil, the concept of plant communities as distinct individuals competing with one another is profoundly altered. Rather than acting antagonistically, these individuals symbiosis to provide nutrients as part of their resources [96].

7. Importance of exploiting soil interactions between stimulating microorganisms

In response to the adverse effects of plant protection products and synthetic fertilizers on agrosystems, strategies have been developed to promote beneficial soil microorganisms [97]. Consequently, microbial inoculation is of utmost importance because the soil microbiota can play an essential role in plant growth. As a result of microbiota's beneficial effects on plant health under biotic and abiotic stress conditions, biotechnology applications are relevant. In recent years, mycorrhizal growth and health have been highlighted, as well as the nutritional value of edible parts of various crops [98]. Mycorrhizae are not only a simple substitute for chemical fertilizers or pesticides but also can be used in food products of organoleptic and nutraceutical quality despite a lack of comprehensive research on their systemic effects on edible plants. Various vegetables were shown to yield more and be healthier with mixed inoculations of mycorrhizae and growth-promoting bacteria. Similar results were obtained for strawberries and perennials, including olives and vines [99]. Mycorrhizal fungi have been studied on some ornamental plants, especially *Camellia japonica*, with significant effects on growth and protection [100]. The development of large-scale sequencing approaches has led to the identification and selection of isolates forming symbiotic relationships with plants in different environments or soils subjected to different cultivation techniques, allowing researchers to identify and select symbiotic fungi. Identifying isolates for a specific crop or already adapted to certain conditions and, thus, potentially more efficient depends on data on the composition of mycorrhizal fungi communities [101,102].

8. Benefits of introducing mycorrhizal fungi into the soil

The enhancement of P uptake is generally considered to be the most important benefit that mycorrhizae provide to the host plant, and the P status of the plant is often the main controlling factor in the plant—fungus relationship [103]. In some cases, mycorrhizae can increase P uptake and increase the performance efficiency of P nutrition of crops [104]. Increased yield and growth can be associated with this phenomenon [104]. It is common for several nutrients to be absorbed by the host simultaneously by mycorrhizal fungi, though different nutrients may be affected differently [105,106]. The mycorrhizal association has been extensively studied, but there is also evidence that mycorrhizae play a role in the suppression of crop pests and diseases, particularly soil-borne fungal diseases (Table 3) [107,108]. As a result of improved nutrition, plants may appear resistant to pests and diseases [109], although multiple mechanisms of resistance may be at work simultaneously [110]. Exclusion appears to be one of the most important factors here, as it seems to be merely a matter of competing for space [111]. Mycorrhizae have been

Table 2. Nutritional exchanges between different types of mycorrhizae.

Mycorrhizal typology	Symbiont > host nutritional interaction	Host > symbiont nutritional interaction
Arbuscular mycorrhizae	Mineral nutrients (P)	Carbohydrates
Ectomycorrhizae	Mineral nutrients (N)	Carbohydrates
Hericoids	Mineral nutrients (N)	Carbohydrates
Arbutoids	Mineral nutrients	Carbohydrates
Monotropoids	Carbohydrates and mineral nutrients	–
Orchid mycorrhizae	Carbohydrates and mineral nutrients during the young phase; minerals during the adult phase	–

Table 3. Mycorrhizae control some soil fungal diseases.

Pathogen	Disease	Crop
Sclerotium cepivorum	White rot	Onions (*Allium cepa*)
Fusarium oxysporum	Fusarium root rot	Asparagus (*Asparagus officinalis*)
Verticillium dahlie	Verticillium wilt	Tomatoes (*Lycopersicon esculentum*)
Helicobasidium mompa	Violet root rot	Asparagus
Rhizoctonia solani	Root and stem rots	Mung bean (*Vigna radiate*)
Aphanomyces euteiches	Root rot	Pea (*Pisium sativum*)

shown to increase the host plant's tolerance to water stresses [112], including those caused by high salinity [106,113,114]. Several mechanisms have been proposed to explain why water is extracted from smaller pores [112]: increased hydraulic conductivity of the roots, improved stomatal regulation, osmotic regulation of the host and better contact with soil particles due to the binding effect of hyphae). Many studies have focused on how mycorrhizae directly influence the growth of the host plant. They also have a direct effect on soil structure, which is particularly relevant in agricultural environments, in which cultivation, traffic and low levels of organic matter tend to damage soil structure. According to Jakobsen and Rosendahl [115], host plants can transfer up to 20% of fixed carbon to their fungal partners and mycorrhizae can produce significant biomass in agricultural soils [116].

9. Conclusions

The molecular mechanisms underlying the exchange of nutrients between two symbiont organisms are rapidly emerging and a nutritional advantage for the host plant has been established. Thanks to the development of large-scale sequencing approaches, several researches have been focused on the characterisation of mycorrhizae in different environments or in subsoils characterized by different cultivation techniques. In recent years, mycorrhizal symbiotic interactions have been studied in greater depth, and it appears that nutritional exchanges and physiological responses of plants may depend on the environment and the partners involved in the symbiotic relationship, at least in mycorrhizal symbioses. In addition, mycorrhizal fungi could regulate the process of signal transfer between plants above ground, as well as the transfer of signalling molecules between plants. In order to optimize the use of these fungi in application programmes, all of these aspects will have to be investigated in the future. Many of these studies have also been carried out in roots sampled in natural soils, making it possible to identify isolates that form symbioses with the plants under consideration and making it possible to observe that not all fungi associated with roots form a functional symbiosis. Despite much research, on the whole, the beneficial properties of mycorrhizal symbioses are still not widely exploited in sustainable agriculture. This is because many factors must be considered in order to achieve successful application. In order to be used for agricultural purposes, mycorrhizae must also be evaluated nutritionally and physiologically in fields with different soil microbiota communities, with which both symbiont fungi and plant roots interact, as well as multiple stress factors affecting plants. Although we are beginning to understand the association of microorganisms and plants, there are significant gaps, including the role of species diversity of bacteria and fungi in producing plant benefits, as well as how agronomic practices can affect the ecology and function and development of beneficial microorganisms in the soil. It is crucial to improve our understanding of the physiology and function of mycorrhiza, as well as their interactions with crops and environmental conditions, to achieve long-term agricultural stability and productivity.

The study of the specific plant–fungus–environment combination is an important prerequisite, as well as the implementation of less impactful agricultural practices so that the biodiversity of this group of fungi is maintained in the soil.

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