Review

The Importance of Mycorrhizal Fungi and Their Associated Bacteria in Promoting Crops' Performance: An Applicative Perspective

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Abstract: Agricultural systems are particularly impacted by global climate change (CC), responsible for the introduction of multiple environmental stressors negatively affecting plant growth. Soil microbial communities are crucial in agricultural practices, influencing crop performance and soil health. Human activities and CC threaten soil microbial biodiversity, leading to soil quality degradation and decreasing plant health and productivity. Among plant-beneficial microorganisms, mycorrhizal fungi are widespread in terrestrial ecosystems, including agroecosystems, and they play a key role by enhancing plants' fitness and resilience to both abiotic and biotic stresses. Therefore, exploring the role of mycorrhizal symbiosis in sustainable agriculture has become increasingly critical. Moreover, the application of mycorrhizal bioinoculants could reduce dependence on inorganic fertilizers, enhance crop yield, and support plants in overcoming environmental stresses. This review, after briefly introducing taxonomy, morphology and mechanisms supporting the symbiosis establishment, reports the roles of mycorrhizal fungi and their associated bacteria in improving plant nutrition and mitigating CC-induced abiotic stresses such as drought and salinity, also giving specific examples. The focus is on arbuscular mycorrhizal fungi (AMF), but ericoid mycorrhizal (ErM) fungi are also considered as promising microorganisms for a sustainable agricultural model. New emerging concepts are illustrated, such as the role of AMF hyphosphere in acting as a preferential niche to host plant growth-promoting bacteria and the potential of ErM fungi to improve plant performance on Ericaceae plants but also on non-host plants, behaving as endophytes. Finally, the potential and limitations of mycorrhizal-based bioinoculants are discussed as possible alternatives to chemical-based products. To this aim, possible ways to overcome problems and limitations to their use are discussed such as proper formulations, the systematic check of AMF propagule viability and the application of suitable agronomical practices in the field.

Keywords: arbuscular mycorrhiza; ericoid mycorrhiza; bacterial–fungal interactions; mycorrhiza helper bacteria (MHB); mycorrhizal bioinoculants

1. Introduction

Global climate change (CC) significantly impacts natural ecosystems, introducing a range of environmental abiotic stressors that negatively affect plant growth and development. Agriculture is particularly sensitive to climate variability due to its reliance on climate-dependent resources such as land and water. Moreover, soil microbial communities are also crucial in agricultural practices, functioning as natural capital, influencing crops'

performance, and as indicators of soil health. However, human activities and CC threaten soil microbial biodiversity, leading to declines in soil quality that can affect plant health and productivity. The environmental changes imposed by CC can have a major effect on soil microbiota communities. For example, an increase in the activity of organic matter decomposers is predicted to occur as a consequence of a rise in average temperatures, which will eventually lead to an unbalance of nutrients available for plant growth [1]. Recently, Fu and colleagues applied a high-throughput sequencing approach to the soil bacterial and fungal communities of different soil layers in an Abies forest, finding relevant alterations as a result of both cooling and heating [2]. Again, the microbiota community from montane grassland soils has been proved highly sensitive to artificially imposed drought events as only 4% of the overall community was able to thrive under these harsh conditions [3].

To mitigate these effects, urgent actions are necessary to conserve and promote soil- and plant-beneficial microorganisms. This approach is in line with the World Health Organization's One Health vision that recognizes the strict link connecting the health of all the living beings and the whole environment and recommends addressing questions relevant for the ecosystems with holistic and systemic approaches [4].

Among plant-beneficial microorganisms living in the soil, mycorrhizal fungi are prevalent across almost all terrestrial ecosystems, including agricultural systems [5,6]. Mycorrhizal symbioses are of great importance due to their profound effects on plant growth, fitness, and productivity [7]. Indeed, over 80% of land plants, including most crop species, form symbiotic relationships with mycorrhizal fungi [5,8]. Four main types of mycorrhizal symbioses have been identified based on their structure and function: arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), orchid mycorrhiza (ORM), and ericoid mycorrhiza (ErM). The iconic feature of the mycorrhizal symbiosis is the enhancement by the fungal partner of the plant nutrient acquisition by the active exploration of the soil and capture of nutrients vital for plant growth, such as nitrogen (N), phosphorus (P), and various micro-elements [9]. Beyond improved mineral nutrition, mycorrhizal associations also boost plants' resilience to both abiotic and biotic stresses.

With the ongoing global CC, exploring the role of mycorrhizal associations in sustainable agriculture is increasingly critical [10]. Indeed, mycorrhizas are crucial for belowground C stocks, with one-third of the forest soil living biomass being represented by ectomycorrhizas and with arbuscular mycorrhizal fungi constituting one half of the microbial biomass in agricultural systems. Mycorrhiza perturbation can therefore largely influence the global C balance, while enhancing mycorrhizal benefits in agriculture, horticulture, and forestry may greatly reduce the growing impact of food and textile production at a global scale [11]. The application of mycorrhizal-based bioinoculants in agriculture aims to reduce dependence on inorganic fertilizers, enhance crop yield, and support plants in overcoming (a)biotic stressors. Although the bioinoculants market is expanding globally, assessing the efficacy of commercial mycorrhizal-based products, which are often marketed for their growth-promoting properties, remains challenging.

This review investigates the roles of mycorrhizal fungi and their associated bacteria in improving plant nutrition and mitigating CC-induced abiotic stresses such as drought and salinity. The focus will be on those associations that, for the identity of the plant partners involved, are of particular interest in an agronomical (and especially horticultural) perspective. We firstly describe the most widespread, studied and exploited plant root symbiosis, i.e., the one that involves arbuscular mycorrhizal fungi, to discuss how horticultural crops can benefit from such association. Then, we move to consider how the Ericoid Mycorrhiza, though historically less regarded, can be considered promising to be exploited under a sustainable agriculture perspective. Finally, we also analyze the potential and the limitations of mycorrhizal-based bioinoculants, which show promise for advancing sustainable crop production systems.

2. Arbuscular Mycorrhizal Fungi: How They Interact with Plants and Why Are They Considered Crucial in Agroecosystems

Arbuscular mycorrhizal (AM) symbiosis represents one of the most ancient symbioses, since its origin dates back to the Ordovician period, around 460 million years ago, as testified by fossil records and phylogeny studies [12]. This association involves 80% of land plants, among which are horticultural crops, cereals, hornworts and liverworts [13], and soil fungi belonging to the sub-phylum Glomeromycotina, within the phylum Mucoromycota [14]. To date, around 355 AM fungal species across 44 genera have been described ([15] last update April 2024). AM fungi (AMF) are obligate biotrophs (Box 1) and in this mutualistic interaction they increase plant nutrition, especially phosphorus (P), nitrogen (N), and water uptake, improve photosynthetic capacity, and promote plant yield and growth [16]. In return, the host plant allows the growth and development of the fungus, providing up to 20% of carbon photo-assimilates to the AMF [17] in the form of sugars and lipids [18,19].

Box 1. Glossary of the most used terms in this review.

Bioprotection
The use of beneficial organisms to reduce the presence of pathogens, relying on their natural competition
Biostimulant
Substances or microorganisms applied to plants to enhance nutrient efficiency, abiotic stress tolerance and/or crop quality traits regardless of its nutrient content
Biotroph
Organism able to live and multiply only on another living organism
Dark Septate Endophytes (DSE)
Group of fungi that inhabit the root tissues of a wide variety of host plants without causing visible symptoms of disease. They are distinct from other types of mycorrhizal fungi by their dark pigmentation and the presence of septate hyphae. DSE fungi can be found not only in the roots but also in the stem and leaf tissue.
Hyphosphere
Area around the hyphae influenced by their exudates
Microbiome
Microorganisms, such as bacteria, fungi and viruses, that live in a defined habitat (microbiota), including their genomes, their activities and functions
Mycorrhizosphere
The area of intersection between the hyphosphere and the rhizosphere, where fungal hyphae interact with plant root
Mutualism
Relationship between two or more organisms in which each of them benefits from the interaction
Rhizosphere
The area around the root of a plant influenced by root exudates
Saprotrophism
Nutrition strategy where organisms obtain their nutrients by decomposing soil organic matter

The establishment of the AM symbiosis is the consequence of a cascade of molecular and cellular events that begin with mutual recognition between the two partners and includes the perception by the fungus of plant-derived molecules called strigolactones [20,21]. Strigolactones are plant hormones constitutively released by roots, but their concentration is higher in the exudates of plants that can form arbuscular mycorrhizas compared to those that cannot establish such symbiosis. Furthermore, strigolactone biosynthesis and secretion were found to be induced under low-phosphate conditions [21,22]. Their perception by the fungus increases its metabolism and hyphal branching, leading to a higher colonization, but it is not strictly required for mycorrhiza establishment. On its side, the AM fungus releases pre-signal molecules, such as short-chain chitooligosaccharides (COs) and lipo-chito-oligosaccharides (LCOs) [23,24], that can be targeted by plant receptors and that remain only partially characterized. Such recognition initiates a signal transduction called common symbiosis signaling pathway (CSSP) that includes sharp oscillations in the nuclear and perinuclear calcium ion concentrations that promote the mycorrhiza

establishment. This conserved signaling pathway is involved in both mycorrhiza and legume nodule formation [25]. In mycorrhizal plants, the CSSP is not only involved in partner recognition and fungal accommodation, but it also regulates the expression of downstream genes involved in nutrient exchange [26]. Interestingly, the LCO recognition in plants is influenced by N and P availability in the region surrounding the roots, with the low nutrient condition maximizing the perception of the signal by CSSP components [27]. Consistent with this, high N and P availability has been shown to reduce the establishment and functioning of the AM symbiosis [28,29]. Subsequently, the fungus can penetrate the plant root cortex through the formation of hyphopodia on the surface. After crossing the outer root cell layers, it finally reaches the inner cortical cells, in which it is able to form branched intracellular structures, called arbuscules (Figure 1). Arbuscules are the key structure of the symbiosis, hosting the mutual exchange of nutrients between partners. This fungal structure is not directly in contact with plant cytoplasm since it is surrounded by the peri-arbuscular membrane (PAM), which is in continuity with the plant plasma membrane [30]. After having formed the mycorrhiza, AMF develop an extensive net of extraradical mycelium spreading in the surrounding soil. AM hyphae diameter is one or two orders of magnitude lower than roots, ranging from 2–20 μm [31]. Hyphae are therefore able to penetrate wider, overcoming depletion zones and reaching nutrients and water that would not be accessible to the roots [32].

Considering their ability to access soil resources, it is not surprising that nutrient transfer from the fungus to the plant has been considered the iconic benefit that AMF provide to their host from an applicative perspective. Several reports have documented that AMF inocula increase plant growth, enhancing their shoot and root biomass on different horticultural crops, such as eggplant, spinach, courgette and apple [33–36]. In wheat, a meta-analysis revealed that AMF inoculation increases plant dry weight, P, N, and Zinc content [37]. AMF application can also enhance nutritional crop quality levels or keep them high under stressful conditions, as it has been reported on lettuce plants inoculated with *Funneliformis mosseae* under low P conditions [38].

Several studies have reported that AMF application not only improves crop yield and quality, but it also enhances tolerance to abiotic stress, such as drought, salinity, extreme temperatures, and heavy metal toxicity, representing a valuable tool for mitigating the effects of climate change (Table 1) [32].

Water limitation is a serious concern that increasingly affects cultivated lands. The AMF symbiosis influences plant–water relation following multiple mechanisms: (i) increasing water absorption by extraradical hyphae or by altering root architecture, (ii) enhancing water and nutrient use efficiency, (iii) improving the capacity of the host plant to detoxify reactive oxygen species produced under water stress, (iv) regulating hormone balance (auxin, abscisic acid and cytokinin) and regulating stomatal conductance, (v) upregulating photosynthetic rate [16,39], and (vi) modulating the expression of plant aquaporins [40–42]. Despite this plethora of multiple, often overlapping mechanisms, the general outcome of the AM symbiosis is an improved plant tolerance to water-limiting conditions, with much recent data supporting this view. The application of *Rhizophagus irregularis* on tomato and maize plants under drought stress conditions has led to an increase in stomatal conductance and water absorption [43,44]. A meta-analysis published in 2015 showed that AM colonization generally has little effect on plant stomatal conductance under well watering and mild drought stress, while under severe drying, the AM effect becomes more important [45]. Under water deficit, a higher fruit growth and yield has been detected on mycorrhizal tomato and strawberry plants compared to non-inoculated controls [46,47]. Mycorrhizal coffee and soybean plants showed an increase in the photosynthesis and transpiration rate under a low water regime, suggesting an improvement in the physiological tolerance to drought stress [48,49]. Interestingly, how AMF influences the overall plant–water relation seems to be highly dependent on the water status of the plant.

Under high salinity conditions, AMF deploy several mechanisms to increase the host plant's tolerance, some of which are shared with drought stress: (i) alteration of root

architecture to reach non-saline areas; (ii) improvement of nutrient and water uptake; (iii) maintenance of ionic homeostasis in host plants, in particular a low Na+:K+ ratio; (iv) osmoregulation through the accumulation of osmolytes (e.g., proline, betaine, sugars, organic acids); (v) reduction in oxidative stress through an increase in ROS scavenging system; and (vi) enhancement of photosynthetic efficiency [50]. Zhang et al., 2019 [51] reported that the application of *R. irregularis* under salinity conditions increased *Asparagus* biomass and enhanced its antioxidant activity. AMF inocula under saline stress resulted in photoprotection mechanisms and a higher photosynthetic capacity on several crops such as rice, hemp, and cucumber [52–54]. *Glomus* sp. application has been reported to increase nutrient availability and uptake on maize and sweet basil plants under salinity [55,56]. A recent work applied a Funneliformis mosseae-based inoculum to maize fields located in sandy and saline soils; the authors recorded an improvement in root growth and grain yield and quality upon AMF application [57]. Similar beneficial effects have also been observed in tomato plants under field conditions, both in optimal and drought-stressed environments [58].

The current CC scenario is characterized by extreme heat waves and drought; soil salinization is also predicted to become prominent, due to salty water intrusion into fertile lands as a consequence of the sea level rise [59]. In this context, and on the basis of the aforementioned mechanisms, the mycorrhizal symbiosis could play a pivotal role in mitigating the effect of CC on plant health and performance by inducing a better tolerance to such stressful conditions. More generally, the fact that the AMF external mycelium can scavenge and capture water from the soil in a very efficient way could provide an indirect benefit to the soil itself, contributing to reduced water losses and percolation.

As shown above, AMF-based biostimulants (Box 1) represent a sustainable strategy to enhance crops' yield, productivity, and resistance to abiotic stresses, reducing the input of mineral inorganic fertilizer and eventually increasing the quantity of food for the growing world population [60].

Table 1. AMF inoculation effects on different crop species under abiotic stress conditions. Articles published within the last 10 years.

Abiotic Stress	Crop Species	AM Fungal Species	AMF Inocula Effects (Compared to the Untreated Condition)	Source
Drought	*Solanum lycopersicum* L.	*Rhizophagus irregularis*	Improve water use efficiency of the plant and enhance soil-root hydraulic conductance in drying soil, reducing the drop in matric potential in the rhizosphere.	[43]
	Solanum lycopersicum L.	*Rhizophagus irregularis* and/or compost	Improve growth traits and fruit weight, number and quality. Increase in hydraulic conductance. Improve photosynthetic efficiency and photoprotection mechanisms. Reduction in oxidative stress.	[46]
	Oryza sativa L.	*Funneliformis mosseae, Funneliformis geosporus, Claroideoglomus claroideum, Glomus microaggregatum, Rhizophagus irregularis*	Higher rice grain yields, higher stomatal conductance and photosynthetic activity. Higher IAA levels.	[61]
	Fragaria x ananassa	*Funneliformis mosseae, Funneliformis geosporus*	Increase in fruit growth and yield. Increase in water use efficiency. Increase in P uptake.	[47]
	Glycine max L.	*Rhizophagus clarus*	Increase in water absorption and stomatal conductance. Higher photosynthetic and transpiration activity.	[48]

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Table 1. *Cont.*

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| Abiotic Stress	Crop Species	AM Fungal Species	AMF Inocula Effects (Compared to the Untreated Condition)	Source
Drought	*Coffea arabica* L.	*Rhizophagus clarus, Acaulospora colombiana*	Increase in photosynthetic rates, stomatal conductance, transpiration and water use efficiency.	[49]
	Glycine max L.	*Rhizophagus irregularis*	Increase in plant biomass. Enhance of photosynthetic capacity and hydraulic conductivity. Increase in antioxidant enzyme activity.	[62]
	Malus hupehensis	*Rhizophagus irregularis*	Increase in antioxidant enzyme activity. Improve plant water use efficiency. Increase in photosynthetic activity and photoprotection mechanisms.	[63]
Salinity	*Oryza sativa* L.	*Funneliformis mosseae, Aucaulospora laevis, Gigaspora margarita*	Higher total chlorophyll in AMF plants at all salinity levels. Regulation of plant ionic homeostasis. Increase in root dry matter, grain yield and spikelet fertility.	[64]
	Cucumis sativus L.	*Claroideoglomus etunicatum, Rhizophagus intraradices* and *Funneliformis mosseae*	Increase in growth promotion. Enhance total chlorophyll concentration. Improve antioxidant system. Stimulation of endogenous JA and SA, reduction in ABA. Regulation of plant ionic homeostasis.	[54]
	Cannabis sativa L.	*Funneliformis mosseae*	Mitigation of negative effect of the stress on plant growth. Reduction in oxidative stress. Increase in photosynthetic capacity and photoprotection mechanisms. Regulation of plant ionic homeostasis.	[53]
	Asparagus officinalis L.	*Rhizophagus irregularis*	Higher plant biomass. Increase in antioxidant activity. Regulation of plant ionic homeostasis. Photoprotection mechanism.	[51]
	Lactuca sativa L.	*Funneliformis mosseae, Claroiedeoglomus lamellosum*	Higher biomass production. Enhance gas exchange and photosynthetic efficiency. Regulation of plant ionic homeostasis. Increase in leaf relative water content and in photosynthetic activity.	[65]
	Citrullus lanatus L.	*Glomus mosseae, Gigaspora gigantea* and/or silicon addition	Higher leaf area, fruit size and yield. Increase in pigment (chlorophyll and carotenoid) and mineral content. Enhance antioxidant enzyme activity.	[66]
	Zea mays L.	*Glomus mosseae* and/or biochar	Increase plant nutrient uptake. Increase in antioxidant activities. Increase concentration of unsaturated fatty acid, improving maize growth.	[55]
	Ocimum basilicum L.	*Glomus deserticola*	Improve fresh and dry weight. Higher chlorophyll content. Higher root hydraulic conductance and higher water use efficiency.	[56]
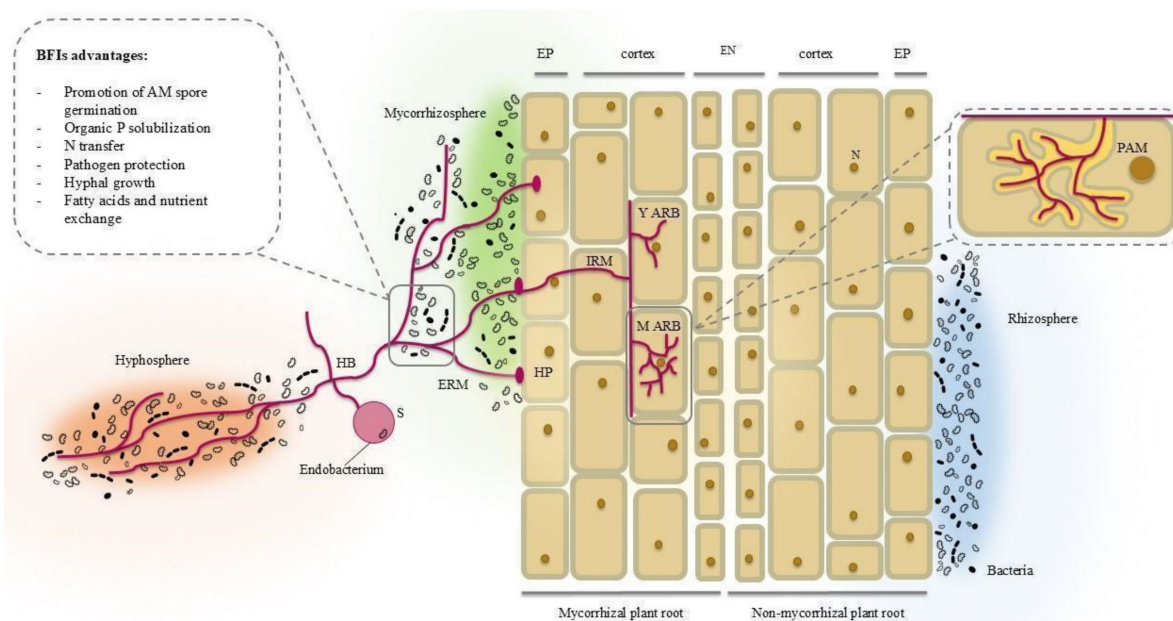
Figure 1. Schematic presentation of the AM colonization process and the rhizosphere and hyphosphere microbiome. AM fungal spores (S) germinate after a molecular dialog between partners (i.e., SLs and COs). Fungal hyphae reach the root epidermis (EP) and develop a swollen structure called hyphopodia (HP). After this contact, the fungal hyphae penetrate the root and progress until the cortex cells, where AM fungi form arbuscules (ARB); in these structures, the nutrient exchange occurs bidirectionally. The arbuscule is surrounded by a plant-derived membrane (PAM, peri-arbuscular membrane in gray) and between the PAM and fungal cell wall there is an apoplastic space called the peri-arbuscular space (in yellow). Outside the root, bacteria live in association with the plant in a narrow space called rhizosphere (in non-mycorrhizal root plants, area in blue), mycorrhizosphere (in mycorrhizal root plants, area in green), and in association with the hyphae (hyphosphere area in orange). Bacteria that live inside the spore are called endobacteria [67]. ARB = arbuscule (Y, young, or M, mature), ERM = extraradical mycelium, HB = hyphal branching, IRM = intraradical mycelium, N = nucleus, EN = endodermis.

3. The Interaction Between Soil Bacteria and AMF an Its Emerging Role in Promoting Plant Performance

Bacteria can establish different associations with other living organisms, which can range from pathogenic, causing harm to the host, to neutral, or mutualistic; in these structures, both organisms gain benefits from the interaction [68].

Within soil microbial communities, bacteria and fungi are considered cornerstone members, driving biogeochemical cycles and playing a crucial role in maintaining plant health [69,70]. Beyond their individual interactions with plants, fungi and bacteria also interact with each other, mutually influencing their behavior and fitness, often leading to not easily predictable outcomes and/or affecting plant host activity.

However, several works have reported that bacterial–fungal interactions (BFIs) perform different ecological functions in agriculture, horticulture, and forestry [71–73]. Regarding the agricultural context, BFIs play a crucial role in enhancing soil fertility, improving microbial community performance and plant growth and health [68]. However, over the last decades, numerous studies and reviews have analyzed the impact of co-inoculating fungi with various plant growth-promoting bacteria (PGPB), revealing that the outcome of the interaction strictly depends on the bacterial, fungal, and plant species involved (Table 2) [74]. In this context, Vannini and colleagues [75] demonstrated that co-inoculation with *Azospirillum brasilense* and *Paraburkholderia graminis*, either individually or in combination with AMF, elicited distinct phenotypic and proteomic responses in wheat, depending on the composition of the inoculum.

Furthermore, BFIs are intrinsically modulated by various levels and degrees of specificity. On one hand, BFIs can involve a wide range of species, such as *Pseudomonas* spp., *Streptomyces* spp., and *Rahnella aquatilis*, interacting with various fungi such as *Funneliformis mosseae* and *Trichoderma* spp. [76]. On the other hand, cases of more intimate associations have been reported such as those involving bacteria thriving inside living fungal cells and hyphae [77]. Endofungal bacteria have been reported in taxonomical diverse fungi, including Basidiomycota and Ascomycota, and involve fungal hosts with different lifestyles, from pathogenic to endophytic and even ectomycorrhizal fungi [78,79]. In particular, fungi belonging to the Mucoromycota phylum seem to be particularly prone to stably hosting endobacteria in their cytoplasm [80]. This is the case of the endosymbiont *Mycetohabitans rhizoxinica*, detected in the plant pathogen *Rhizopus microsporus* and responsible for the production of its toxin rhizoxin [81] and of *Mycoavidus cysteinexigens*, reported in the cytoplasm of some Mortierellomycotina [82]. Another well-known example in the Mucoromycota clade is represented by the endobacteria hosted by AMF. Two different types of endohyphal bacteria of AMF are described in the literature: (i) rod-shaped, Gram-negative bacteria associated with the Gigaspoaceae family [83,84]; and (ii) coccoid cells, belonging to the class Mollicutes, which typically lack a cell wall and live inside hyphae and spores, whose presence is more widely distributed among AMF families [84].

The establishment of BFIs entails different mechanisms to allow the recognition and the selection of the partners; bacteria and fungi may interact by secreting proteins, employing chemotaxis, or engaging in antibiosis [68]. Moreover, they can also communicate via *quorum* sensing or by altering the pH of their environment, which can influence the growth and survival of the other organism [68,85]. Once recognized, bacteria can colonize fungal structures, mainly hyphae, by adhering to their surface or, in some specific cases, penetrating the cell wall, establishing an endohyphal symbiosis. However, most of the BFIs take place at the surface of fungal hyphae, known as the hyphosphere (Box 1). This is a dynamic region where numerous interactions with microbial communities occur, including the exchange of metabolites and mutual responses through the release of signaling molecules [68,86]. In this environment, bacteria can exist as exohyphal symbionts or form biofilms [85,87].

Over the past decades, an increased interest in the interplay between bacteria and fungi has been seen, with a specific focus on the associations between bacteria and AM fungi (Figure 2). These bacteria, previously known as mycorrhiza helper bacteria (MHB), were first introduced by Mosse (1962) and further discussed by Garbaye (1994). It has been demonstrated that MHB can support the fungus during (i) the pre-symbolic stage, promoting spore germination by producing hydrolytic enzymes involved in the erosion of the spore wall and facilitating hyphal growth [88,89], or (ii) during the symbiotic phase, enhancing the rate of mycorrhizal colonization, contributing to host plant growth and soil fertility [89–91]. Studies have shown that MHB can be categorized based on their natural niches, as they can be isolated from various AM fungal environments such as the hyphosphere, the mycorrhizosphere (Box 1), and the spore surface [92] (Figure 1).

Studies showed that the dominant bacterial phyla interacting with AM fungi primarily included *Proteobacteria*, *Actinobacteria*, and *Firmicutes* [93]. This finding suggests that, in analogy with the plant rhizosphere (Box 1), the AMF hyphosphere represents a specific ecological niche, different from the bulk soil, where the fungus possibly exerts a selective pressure on its associated bacterial community. Notably, several works indicated that plant species have a minimal impact on bacterial recruitment in these interactions; instead, the assembly of the bacterial community is primarily driven by the species of AM fungi involved [74,93–95].

The interaction between soil bacteria and fungal hyphae plays a crucial role in establishing AM fungi as key ecosystem players. Given their limited capacity to utilize organic nutrients, AMF necessitate reliance on bacterial partners thriving in the hyphosphere for nutrient acquisition [96–98]. This relationship not only enhances the fungal nutrient uptake but also promotes bacterial activities, such as the solubilization of organic phosphorus (P),

facilitated by the fungal excretion of compounds that act as nutrients or signaling molecules on the hyphal surface [99]. Consequently, the hyphosphere operates as a significant biological marketplace for carbon (received by the host plant) and mineral nutrients, especially P, characterized by trade-offs between AM fungi and bacteria [100,101]. Additionally, compounds released by AM fungal hyphae can influence soil pH and aggregation, thereby altering microbial composition, nutrient availability, and water distribution [102]. An illustrative example is the association between the phosphate-solubilizing bacterium (PSB) *Rahnella aquatilis* and the AM fungus *R. irregularis*. In this symbiotic relationship, the fungus exchanges fructose for solubilized phosphorus, with these nutrient exchanges occurring within the hyphosphere [103]. In analogy, nitrogen availability also benefits from hyphosphere bacteria capable of altering the amount of N available in the soil [84,93]. MHB can also stimulate hyphal growth under unfavorable conditions, such as in soil with high ammonium concentrations, by consuming it as a N source [104]. Under certain experimental conditions, AMF-associated bacteria have been proven so crucial for fungal nutrition to the point of overcoming their obligate biotrophy; a strain of *Paenibacillus validus* isolated from the surface of *R. irregularis* spores has been shown to promote the fungal growth and the production of vital spores [105]. This evidence has important implications for the use of MHB in sustainable agriculture; due to their mycorrhiza-promoting activity, they are predicted to boost plant symbiotic associations and to also possibly exert a direct PGP activity. This makes MHB a valuable component for effective bioinoculants, to be exploited alone or in consortia with AMF.

Another interesting service exerted by BFIs is bioprotection against pathogens (Box 1), an important service for advancing sustainable agricultural practices [106,107]. This protective function is also facilitated by the capacity of MHB to promote and accelerate the establishment of mycorrhization, thereby increasing the plant's resilience to biotic stress [108]. MHB also contributes to biocontrol through various mechanisms such as antibiosis, competitive exclusion for ecological niches, and the synthesis of volatile organic compounds with antibiotic properties [71]. Recently, it has been shown that *B. velezensis*, a plant-beneficial bacterium known for its strong ability to produce antimicrobial compounds, migrates and forms biofilms along *R. irregularis* hyphae. During this hyphospheric colonization, AM fungi modulate bacterial secondary metabolites and therefore ensure a stable tripartite relationship by warding off mycoparasitic and plant-pathogenic microbes [109].

While fungal partners in MHB interactions derive numerous benefits, the bacteria participating in these associations also experience benefits, such as a predator-free environment within the hyphosphere, which can facilitate bacterial transport [68]. AM fungi can selectively enrich or reduce specific bacterial groups at their hyphal surface [110], suggesting that the selected bacteria may represent keystone taxa within the microbial communities of the hyphosphere. For instance, the soluble exudates of *R. irregularis* can have either antagonistic or stimulatory effects on individual fungal and bacterial isolates [100]. However, it remains unclear whether these bacterial taxa influence the composition of hyphosphere communities and affect the fitness of AM fungi. Notably, there is a distinct symbiotic footprint in the plant microbiome (Box 1), as the rhizosphere of plants hosting AM fungi (mycorrhizosphere) harbors a different microbiome compared to non-mycorrhizal plants (rhizosphere) [96,97,111].

The application of deep sequencing techniques to the study of AMF-associated bacteria represents an emerging study field. Nonetheless, recent results have already provided interesting functional clues. The comparison of bacterial communities associated with AMF hyphae revealed a core microbiota conserved across sites that showed a good degree of taxonomical and functional convergence, since members supporting phosphatase activity and P mineralization were constantly significantly enriched [95]. Accordingly, the inoculation of *R. irregularis* on two different host plants was shown to impact the composition of the rhizosphere bacterial community, increasing the presence of phosphate-mobilizing bacteria more than in the sole hyphosphere [112]. Taken together, this evidence suggest that the AMF core microbiota can provide crucial functions that the fungus itself lacks

(e.g., P solubilization), and that might complement the iconic benefits provided by mycorrhiza establishment to the host plant in terms of improved nutrition and resilience to climate change induced stress.
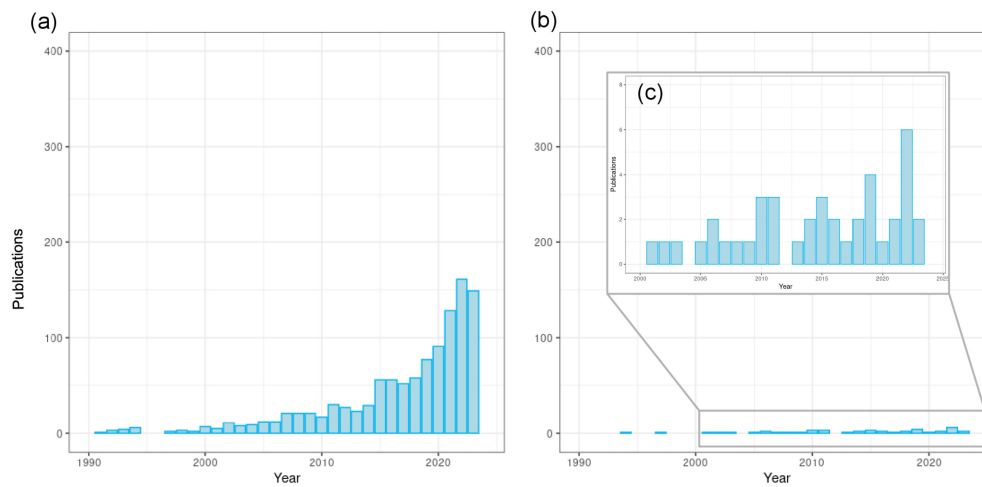

Figure 2. Publications per year related to: (**a**) bacterial–fungal interaction in crop plants and soil (keywords used in PUBMED: interaction, crop, plant, soil, fungi, fungal, mycorrhizal, bacteria), and (**b**) mycorrhiza helper bacteria in crop plants and soil (keywords used in PUBMED: crop, plant, soil, mycorrhiza helper bacteria). In figure (**c**), we have a focus on mycorrhiza helper bacteria publications in the last 20 years.

Table 2. Examples of co-inoculation of bacteria and fungi on horticultural species.

Crop Species	Fungal sp.	Bacterial sp.	Effects	Source
Solanum lycopersicum L.	*Glomus fasciculatum*	*Azotobacter chroococcum*	Higher cytokinins production. Increased water adsorption, nutrients and physiological—metabolic activity. Increased total soluble carbohydrates (TSS) content in fruits. Increased vitamin C content	[113]
Solanum melongena	*Rhizophagus irregularis*	*Azotobacter* sp.	Increased plant height, leaf length, leaf width, and TSS	[114]
Helianthus tuberosus L.	*Glomus multisubtensum, Rhizophagus intraradices*	*Klebsiella variicola*	Increased plant growth. Higher tuber inulin content	[115]
Medicago Sativa L.	*Glomus mosseae, Glomus intraradices*	*Sinorhizobium meliloti*	Competitive inhibition. Increased root system	[116]
Abelmoschus esculentus	*Glomus* spp.	*Azospirillum brasilense, Azotobacter vinelandii, and Beijerinckia mobilis*	Increased plant growth, fruit yield, and photosynthesis rate	[117]
Lotus corniculatus L.	*Claroideoglomus etunicatum*	*Novosphingobium resinovorum*	Increased plant biomass, plant height, fungal colonization rate. Higher total root length, number of forks, and number of tips	[111]
Vaccinium corymbosum	*Oidiodendron maius*	*Klebsiella* sp.	Increased water use efficiency. Enhanced leaf area	[118]
Vaccinium uliginosum	*Oidiodendron maius*	*Paenarthrobacter nicotinovorans, Bacillus circulans*	Increased growth of blueberry seedlings	[119]
Spinacia oleracea	*Glomus mossae* and *Glomus fasciculatum*	*Azotobacter chroococcum, Bacillus megaterium* and *Bacillus mucilaginous*	Increased phenolic and flavonoids content, and antioxidant activity content of leaves	[120]

Table 2. *Cont.*

Crop Species	Fungal sp.	Bacterial sp.	Effects	Source
Solanum lycopersicum L.	*Trichoderma lixii*	*Streptomyces atrovirens*	Promoted the production of enzymes and phenolic compounds	[121]
Solanum lycopersicum L.	*Rhizophagus intraradices*, *Glomus aggregatum*, *Glomus viscosum*, *Claroideoglomus etunicatum* and *Claroideoglomus claroideum*	*Pseudomonas fluorescens*, *Pseudomonas* sp.	Enhanced plant performance leading to increased flowering, fruit weight and size, dry biomass, and elevated concentrations of sugars and organic acids	[122]

4. Ericoid Mycorrhizal Fungi Are Poorly Acknowledged Though Promising Plant Symbionts

While AM plants are widespread at lower latitude, in lowland agroecosystems where soil organic matter (SOM) decomposition rate is quite fast, other mycorrhizal associations, i.e., ectomycorrhizae (ECM) and ericoid mycorrhizae (ErM), are found at higher latitude, in upland/boreal forest ecosystems characterized by slow SOM decomposition rate [123]. Ericoid endomycorrhizal fungi are still poorly investigated for their potential use in crop performance improvement. These fungi include Ascomycota and Basidiomycota lineages which have a positive effect on host plant nutrition, growth, and abiotic stress resistance [124,125]. ErM fungi can grow as endophytes in the roots of nonhost plants [126] or form intracellular mycorrhizal coils in the epidermal cells of ericaceous host plants [125].

Within Ascomycota, ErM fungi are grouped in the Hyaloscyphoid clade of the order Helotiales, in the class Leotiomycetes, which include fungi that play an important role in plant nutrient acquisition. These fungi establish mycorrhizal interactions with ericaceous plants, but they can also form ectomycorrhizae and some isolates can transfer nutrients to plants in a non-symbiotic way (i.e., they may transfer P or N to the plant without forming specific intraradical structures, and a reciprocal exchange of nutrients with the plant has not been demonstrated) [127]. The *Hyaloscypha hepaticicola* aggregate, previously known as *Rhizoscyphus ericae* aggregate or *Hymenoscyphus ericae* aggregate, includes *H. hepaticicola*, the first fungal species to be isolated from ErM roots and experimentally proved to form ericoid mycorrhiza [124,128–130]. This aggregate also includes the recently described ErM fungal species *H. gryndleri* [131], *H. finlandica* (formerly *Cadophora finlandica*), a species reported to form ectomycorrhizae with conifers and ErM with ericaceous plants [132], and also a species in the genus *Meliniomyces*, now reclassified as *Hyaloscypha variabilis* and *H. bicolor*, and confirmed to be ericoid fungi. ErM fungi also include *Oidiodendron maius* and *Leohumicola* spp. [129], which were later attributed to this group of symbiotic fungi, and some other ascomycetes which are considered as putative ErM fungi, as they can form hyphal coils (Figure 3d,e) in the roots of ericaceous plants *in vitro* (e.g., *Acremonium strictum*, *Geomyces pannorum*). Also, some Dark Septate Endophytes (DSE) (Box 1) of the *Phialocephala fortinii* s. l.—*Acephala applanata* species complex [133] can form loose intracellular hyphal loops similar to ericoid coils. In a *Rhododendron* cultivar, *P. fortinii* s. s. was able to form ericoid mycorrhizae-like structures [134]. Some Basidiomycota species in the Serendipitaceae family also commonly colonize ericaceous roots, forming the typical hyphal coils [135–137].

ErM associations are quite peculiar when compared to AM and ECM symbioses. Firstly, their recent evolutionary history may be responsible for a dual saprotrophic and biotrophic lifestyle of the fungal partner [125,138], assuming an unfinished switchover from saprotrophy to symbiosis or a multifaceted life strategy recalling fungal endophyte habit. Moreover, ErM fungi can live as endophytes in non-ErM plants [139,140]. This versatility may render ErM fungi more resilient to adverse and changing environmental

conditions, compared to the other groups of mycorrhizal fungi [123,141]; in this view, they could assume an important role for agronomic practices.

ErM host plants belong to the Ericaceae family (e.g., the genera *Calluna*, *Erica*, *Rhododendron*, *Vaccinium*) which comprises dwarf shrubs, shrubs or trees, distributed worldwide in specific ecosystems such as tundra, heathland, or boreal forests [142,143]. ErM symbiosis habitats are characterized by acidic soils, low nutrient availability, a high amount of recalcitrant compounds and a slow rate of SOM decomposition [144]. The ability of ErM plants to adapt and survive in these harsh environments is mostly attributed to the presence of ericoid mycorrhizal fungi. These fungi have retained a rich repertoire of gene encoding for hydrolytic enzymes (CAZymes, lipases proteases), enabling them to decompose complex SOM [138,145,146]. This enzymatic action is essential for SOM mineralization, thus providing simple P and N forms to the ERM host plant. Moreover, in the ErM symbiosis habitats, due to the low pH soil conditions, heavy metal ions can be highly available [147]. ErM fungi have been shown to protect their host plants from the adverse effects of heavy metals [148,149]. Some mechanisms allowing the ErM fungal partner to withstand heavy metal stress have been reported for the metal-tolerant ErM strain *O. maius* Zn, isolated from a metal contaminated plot [150]. Among these mechanisms, antioxidant enzymes, metal transporters, enzymes involved in nitrogen metabolism, organic acids, DNA damage repair proteins, molecular chaperons, and polyamines biosynthesis were shown to be involved in the response of this isolate to metal toxicity [150]. The molecular and cellular mechanisms extending metal tolerance to the host plant were rarely investigated. Casarrubia et al., 2020 showed that mycorrhizal roots of *V. myrtillus* exposed to Cd had a reduced metal content when compared with non-mycorrhizal plants. Metal transporters known to transport Cd were downregulated in symbiosis and may be responsible for the reduced Cd content measured in mycorrhizal roots [151].

ErM symbioses therefore play a key ecological role in heathland habitats; moreover, some ericaceous plant genera are commercially important as agronomic cultures in the flower (e.g., Azaleas and common heats and heathers), fruit (blueberry, cranberry, bilberry, huckleberry), and horticultural industry, both for food and nutraceutical production and also because of the high content in secondary metabolites [152,153], with many species belonging to the *Vaccinium* genus. Over the last few years, berry production and commercialization have greatly expanded, with barriers gaining a lot of importance due to their high nutritional and healthy values. For example, blueberries and cranberries are considered super fruits due to their important nutraceutical and pharmaceutical values [152], attributable to the high anthocyanin and antioxidant content, with anti-inflammatory and antitumoral properties [116,154].

Despite this growing commercial importance of ericaceous plants and notwithstanding the crucial ecological role played by ErM fungi, these fungal symbionts have so far received little attention in relation to their possible use as biostimulants, although some studies have shown their potential ability to act as plant growth-promoting (PGP) fungi (Table 3).

Some authors reported higher biomass and vitality for *Vaccinium corymbosum* (highbush blueberry) and *Rhododendron* plants after inoculation with ErM strains [155–157]. Different ErM strains have been tested, *O. maius* being the most commonly used but with *H. variabilis*, *P. fortinii*, and *H. hepaticicola* strains having shown PGP abilities too [156,158,159], also improving flowering and productive plant traits [160,161]. Low pH soil conditions could impair nitrate absorption by ericaceous plants. Kosola et al., 2007 [162] showed that cranberry plants inoculated with *H. hepaticicola* displayed an eightfold increase in their ability to absorb nitrate under low pH conditions. Wei et al., 2016 [163] showed that the expression of genes related to N uptake and metabolism (ammonium transporter (AMT), nitrate transporters (NRT1-1 and NRT1-2), glutamate synthase (GOGAT), and glutamine synthetase (GS)) were upregulated two- to ninefold in *Rhododendron* plants inoculated with *O. maius*. ErM fungi have also been shown to significantly improve seed germination, root initiation and root growth, the rooting of microcuttings or stem cuttings, and the overall growth of blueberry plants [152,164–166] (Figure 3). Wei et al. (2020) [167] investigated

R. fortunei adventitious root (AR) formation and they showed that ARs rapidly appeared from microcuttings after *O. maius* inoculation and that the nutrient acquisition and growth of *O. maius*-inoculated plants significantly increased compared to the uninoculated ones (Figure 3f–h). They were also able to show that *O. maius* can synthesize key phytohormones and precursors such as the indole-3-acetic acid (IAA), tryptophan (Trp), indole-3-pyruvate (IPA), brassinolides (BRs), jasmonic acid (JA), and salicylic acid (SA). ErM fungi also produce other bioactive compounds, which can increase soil mineral elements' bioavailability (e.g., siderophores; [168]), or which have antimicrobial (e.g., harzianic acid, [169]) or antioxidant properties (e.g., rutin; [159]).

Beyond growth promotion, ErM fungi can also substantially enhance host plant tolerance to abiotic [152] and biotic [170] stresses. Some authors reported improved drought tolerance and alleviation of salt stress for ericaceous plant species belonging to the *Vaccinium* and *Rhododendron* genera inoculated with ErM fungi [171–173]. Grunewaldt-Stöcker et al., 2013 [170] reported that ErM fungi were able to reduce root pathogen infections of *C. vulgaris* and *R. hirsutum* plants.

As reported in the previous sections, MHB play crucial roles in promoting mycorrhizal establishment and plant growth [89], specifically interacting with mycorrhizal fungi and increasing mycelial growth and root colonization rate. Reports of dual inoculation of ericaceous plants with both ErM fungi and plant growth-promoting bacteria are very scant so far. In a recent work, blueberry plants were inoculated with *O. maius* and *Klebsiella pneumoniae*. ErM fungi inoculation promoted stomatal opening and increased overall plant biomass, while *K. pneumoniae* inoculation resulted in an increased photosynthetic rate. The combined inoculation of the two microbes gave contrasting results, suggesting that more research is needed to clarify the possible exploitation of ericoid fungi in mixed consortia [118]. Clearer results were obtained by Yang and colleagues (2023) [119], who showed that two MHB strains and one *O. maius* strain promote the growth of each other and that the co-inoculation of these three microorganisms can promote blueberry seedling growth. Increased root growth contributes to nutrient uptake, also inducing enzyme activities in blueberry leaves and leading to a higher photosynthetic rate, thus finally prompting blueberry growth. This result could represent a good starting point for the development of blueberry biofertilizers based on mixed bacterial–fungal bioformulations which could prompt plant growth, avoiding the use of chemical fertilizers [119].

In conclusion, future research directions could start to consider ErM fungi as valuable biostimulants thanks to their ability to promote plant growth by increasing nutrient bioavailability, to synthesize hormones and other bioactive compounds, thus promoting seed germination and rooting, and to improve plant tolerance to biotic and abiotic stress [152].

Table 3. Examples of reported beneficial effects on ericaceous plant growth, health, and development after inoculation with ERM fungi.

Host Plants	Fungal sp.	Effects	Source
Vaccinium corymbosum	*Oidiodendron maius*	Improved plant growth and vitality increasing treated plants biomass	[155]
Rhododendron fortunei	*Oidiodendron maius*	Enhanced microcutting rooting and plant growth	[167]
Vaccinium corymbosum	*Oidiodendron maius*, *Phialocephala fortinii*	Increased plant biomass and vitality	[156]
Vaccinium vitis idaea (ligonberry)	*Oidiodendron maius*	Increased growth and biomass of roots and stem. Alleviation of drought stress	[171]
Vaccinium corymbosum	*Hyaloscypha hepaticicola*, *Oidiodendron griseum*	Enhanced plant investment on flowering and reproductive success	[160]

Table 3. *Cont.*

| Host Plants	Fungal sp.	Effects	Source
Vaccinium myrtilloides	*Meliniomyces variabilis, Oidiodendron maius, Hymenoscyphus ericae*	Significant improvement on drought tolerance	[172]
Vaccinium myrtilloides, Rhododendron groenlandicus, Vaccinium vitis idaea	*Oidiodendron maius, Meliniomyces variabilis*	Increased plant tolerance to salt stress	[173]
Rhododendron cv. Azuro	*Oidiodendron maius*	Increased root biomass	[157]
Vaccinium corymbosum	*Hymenoscyphus ericae, Oidiodendron griseum*	Larger amount of plants flowers and fruits compare to the controls condition	[161]
Rhododendron pseudochrysanthum	*Phialocephala fortinii, Hyaloscypha complex*	Improved seedlings growth	[159]
Vaccinium virgatum 'Rabbiteye blueberry Ait.	*Meliniomyces variabilis, Oidiodendron maius, Rhizoscyphus ericae*	Enhanced rooting and vegetative growth	[158]
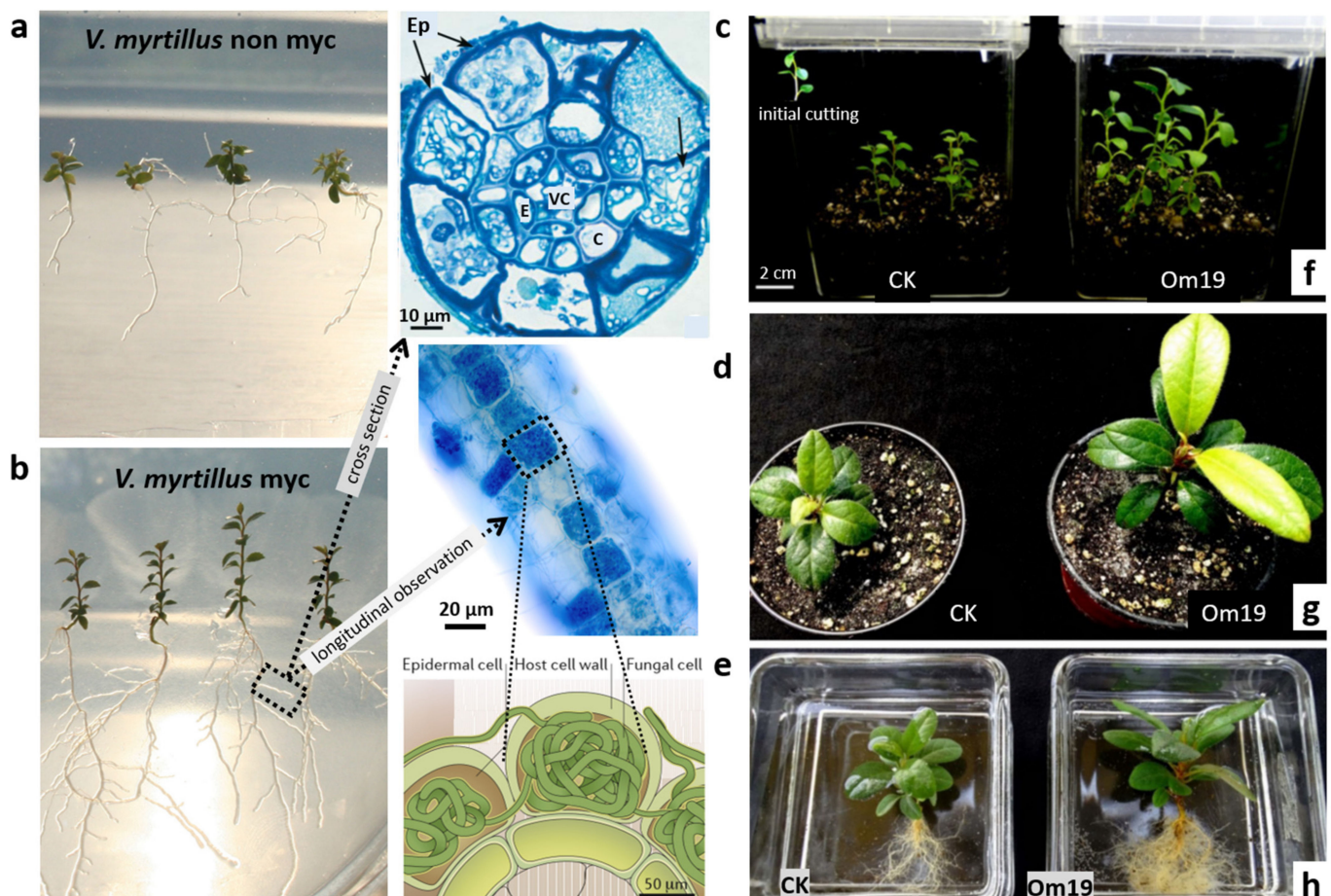
Figure 3. (**a**–**e**) ErM symbiosis morphology. (**a**) *In vitro V. myrtillus* non-inoculated seedlings. (**b**) *In vitro V. myrtillus* seedlings inoculated with *O. maius*. (**c**) Transverse section of a *V. oxycoccos* hair root characterized by very large epidermal cells (Ep) colonized by an ericoid fungus (arrow), a single layer of cortical cells (C), the endodermis (E), the vascular cylinder (VC). (**d**) Light microscope observation of a *V. myrtillus* hair root colonized by *O. maius*; the typical coils formed by the fungus inside the root epidermal cells can be seen (cotton blue staining). (**e**) Morphology of a densely intertwined intracellular fungal coil; the outer tangential wall of the epidermal cells is very thick. The intracellular hyphae are separated from the cytoplasm of the epidermal root cell by the plant cell

membrane that surrounds the fungal coil (perisymbiotic membrane) and by an interface matrix (modified with permission from [138] (**a,b,d**); [174] (**c**); [175] (**e**)). (**f**) Microcuttings (the insertion on the upper left corner) derived from *in vitro* cultured *R. fortunei* grown on a sterilized peat-based substrate non-inoculated (CK) and inoculated with an *O. maius* strain. (**g**) Ex vitro rooting of *R. fortunei* microcuttings non-inoculated (CK) and inoculated with an *O. maius* strain three months after being transplanted to 10-centimeter diameter containers. (**h**) Plant hair roots after washing away the substrate ((**f**–**h**): modified with permission from [167]).

5. New Challenges and Perspectives for the Application of Mycorrhizal Fungi as Bioinoculants: Lessons from the Case of AMF-Based Products

To meet the challenges of population growth and globalization, and to face the environmental constraints inherent to climate change, the agri-food sector needs to embark on a major transformation to offer farmers innovative and sustainable solutions for crops. To that end, microbial inoculants containing symbiotic fungi, alone or in consortia with PGP bacteria, are seen as a promising tool for sustainable agriculture and have received an increasing interest in the past few years. In this context, AMF-based inocula surely takes the lion's share, having their use being proposed and implemented in agriculture for over a decade. If their potential as biostimulants no longer needs to be demonstrated, the application of commercial inoculants on fields or in greenhouses leads, however, to contrasting results. Recently, several studies have evaluated the effectiveness of commercial AMF inoculants and revealed, in most cases, an absence of benefits for the plants or, even more concerningly, an overestimation of viable propagules leading to poor mycorrhizal root colonization [176,177]. Based on this observation, there is an urgent need to improve our comprehension of AMF propagules' resistance over time, to better understand how these AMF inocula will behave in their new environment and interact with the plant and the already existing microbial community that it hosts.

A recent AMF inoculants benchmark analysis performed on 68 marketed products across Europe, America, and Asia revealed that (i) one third of the products contain only one single species, (ii) 100% of the products contain species from the *Glomeraceae* family, and (iii) only six species are found in the marketed products, with 60% of them containing at least one *Rhizophagus irregularis* or *Funneliformis mosseae* strain [178]. This observation reveals the poor AMF diversity among marketed products and raises questions about how this lack of diversity may influence product efficiency across different agrosystems. AMF species can either be categorized as "generalist" or "specialist", meaning that they can respectively establish many interactions with low fidelity, or few interactions with high fidelity [179]. Considering the ubiquitous repartition of AMF species like *R. irregularis* and *F. mosseae* across the planet and the high number of plant species with whom they associate [180], these species can certainly be categorized as "generalist". However, does this "generalist" status assure in any cases a successful symbiosis with the target plant? How does the fungus/plant genotype affect the outcome of the symbiosis? How does the environmental stimuli impact the success of the symbiosis? The reality seems to be far more complex for different reasons:

- Variation in mycorrhizal function is linked to phylogeny. AMF from the *Glomeraceae* family have been shown to be more effective at limiting infection by pathogenic fungi like *Fusarium oxysporum* in *Plantago lanceolata*, whereas AMF belonging to the *Gigasporaceae* family were more efficient at increasing P uptake [181]. As another example, co-inoculation of *F. mosseae* and *Rhizophagus intraradices* on tomato has brought an increase in NPK content in fruits, which proved to be higher compared to the values obtained with single species inocula [182]. This suggests complementary roles of both isolates that could not be underlined with single species inoculum.

- Not only AMF influence the outcome of symbiosis, but the plant's genotype also plays a significant role [183]. Plants' responses to AMF are described as responsiveness, contrasting with dependence, which refers to genetically determined limitations in nutrient-use efficiency that AMF can help to offset [184–186]. Responsiveness can vary,

even among cultivars of the same species, and is further influenced by soil nutrient levels, highlighting a complex interaction between genotype and environment [187,188].

- Environmental and abiotic factors contribute to AMF community shaping and persistence since some plant species carry different AMF communities in different habitats [189]. This statement is well illustrated by a large-scale study performed on over 300 soil samples to evaluate the distribution and relative abundance of AM fungal taxa in relation to a range of abiotic environmental factors [190]. This study reveals that temperature and pH are the most important abiotic drivers of AMF taxa-relative abundance and distribution. As an example, *Acaulosporaceae* generally had niche optima in low pH and low temperature conditions [190].
- Soil microbiome has an influence on inoculum efficiency. A recent large-scale field inoculation trial on maize with *Rhizoglomus irregulare* SAF22, performed in 54 fields in Switzerland, showed a large variation in mycorrhizal growth responses ranging from −12 to +40%. Among the different factors that could explain successful inoculation or not, the authors showed that some specific microbial taxa present in the targeted soil, including soil pathogens like *Fusarium*, could successfully predict the variation in plant growth response to inoculation [191].

To improve the efficiency of AMF-based products, companies will face several challenges in the next coming years including reaching a better comprehension on how environmental factors shape AMF diversity and the role that the different taxa can play in interaction with the plant. This involves large-scale metagenomic studies to be able to correlate environmental factors to the AMF taxa but also functional experiments targeting specific AMF strains. For AMF isolates with agronomic interest, there is an urgent need to improve access to genome information. The full genome can be very informative and helps to better track strains in the environment. First, the AMF genome from *Rhizophagus irregularis* was sequenced not more than 10 years ago [192] and since then only few species have had at least one sequenced genome [193–197]. Even at a single-species level, AMF diversity is predicted to be huge since different *R. irregularis* isolates from a similar geographic area harbor striking genome variations with some strain specific genes [198]. Digging into AMF genomes can bring to light important information on fungal physiology and ecology. For example, the *Gigaspora margarita* genome revealed a high content of phosphate-metabolism-related genes [196], suggesting that this species may be particularly efficient in P uptake.

Another critical point for AMF biostimulants' success will reside in the optimization of the AMF inoculum life chain, going from propagules amplification to inoculation. For amplification, many of the commercially available AMF inocula rely on *in vitro* systems, since they are mass produced with transformed root cultures (TRC). If this system is very convenient for industrialization, it presents several clear limits. Indeed, TRC is an artificial growing environment with specific nutritive conditions (consistent and continuous carbon flow), a lack of abiotic stimuli, an absence of interaction with other microbes, and reliance on a single host plant [199]. Due to these constraints, only a few species may be adapted, and a potential mid-term domestication may affect AMF functionality in a natural ecosystem [199]. It therefore raises questions was to whether the use of this amplification process for tailored AMF solutions and an in vivo production system, mimicking natural environmental constraints and preserving the whole microbial diversity from the hyphosphere, may be preferable to provide successful products. Mastering AMF products' conservation also remains one of the main challenges for industrials. To date, only a few studies have focused on the long-term survival and infectivity of AMF propagules. If it appears obvious that propagules' infectivity significantly decreases with time, this phenomenon can therefore be reduced with adapted storage temperature. Conservation at room temperature or at −20 °C severely affects mycorrhizal inoculation potential whereas conservation at 4 °C helps to maintain propagules' infectivity on maize for at least one year [200]. Direct exposure to sunlight also accelerates degradation of propagules. More generally, to better control mycorrhiza infectivity potential, it becomes vital to redefine

what exactly a propagule is. For many years, it has been thought that spores are the sole active AMF propagules. However, it is now accepted that vesicles and even extraradical mycelium (ERM) can be used to initiate the symbiotic partnership. Although ERM can last for at least 5 months in the absence of active plant roots [201], their structure makes them more fragile than spores and should lead industrialists to rethink the way they store their products to maximize propagule infectivity.

To guarantee a good microbial inoculum establishment in the rhizosphere in spite of the pressure of environmental factors, it is vital to develop AMF products that are compatible with the physico-chemicals and climatic parameters of the targeted fields. In the past years, several studies have shown that inoculation of native AMF species had a better effect on plant growth and stress resistance. Examples of this include plants like *Salvia miltiorrhiza*, cassava, or maize [202]. To answer the market needs, the development of native inoculum may not be adapted to large-scale production considering the technological and economic constraints related to AM fungi isolation and amplification. A good compromise could be represented by the development of databases like GlobalAMFungi [180], which will help to illustrate how environmental factors shape the worldwide distribution of AMF species across different ecosystems, and to propose adapted AMF solutions to farmers.

Finally, at the end of the product life chain, there is a compulsory need to understand the farmers' concerns and to increase their awareness on the agronomical practices that maximize the inocula effectiveness. Indeed, AMF performance is strongly affected by cultural practices. The impact of chemicals like fertilizers and fungicides appears to be substance- and dose-dependent [203], and it is vital to apprehend their detrimental effects on symbiosis development prior to inoculation. To optimize the chance of success, it is also important to produce the product in a formulation adapted to the target culture that could help to increase symbiosis establishment and reduce the necessary number of propagules. To that end, seed coating with AMF became one important technical challenge in the past decade and has been successfully implemented on wheat and chickpea seeds [204,205], suggesting that AMF spore size may not be a technical limitation for this approach. Independently of the way inoculant is brought to the field, future formulations studies must focus on the right combination of co-formulants to increase the product efficiency. AMF inoculum can be coupled with biologically active matrices, such as compost, humic acids, algae extracts or inorganic micronutrients (e.g., silicon) [206]. Another emerging practice consists of applying exogenous COs, the signal molecules produced by AMF, alone or mixed into the mycorrhizal inoculum to improve the development of the symbiosis under field conditions [207]. Co-formulants can also include some other microbes like plant beneficial bacteria that could act in synergy with AMF. As an example, plant-growth-promoting rhizobacteria or the biocontrol fungus *Trichoderma* can be successfully coupled with AMF spores in alginate beads to efficiently colonize plant roots [208,209].

6. Conclusions

Microorganisms perform several processes that are fundamental for plant growth and health. Microbial function investigation represents a key step to reach productive and sustainable food production. The intensive agricultural practices performed over the last 50 years have significantly increased crop yield, but they have also possibly suppressed the interactions between plants and microorganisms, with chemical products substituting microbial functions and increasing land pollution and degradation and resistant pathogen dispersal. More sustainable and green strategies to support food production are therefore urgently needed. Beneficial soil microorganisms, including mycorrhizal fungi and their associated bacteria, may be a key answer for increasing crop yield with environmentally friendly procedures [210]. Turning these concepts into practice, there is an urgent need to include the attitude of crops to associate efficiently with beneficial members of the root microbiota among the plant traits that are positively selected in breeding programs [211].

To maximize plant-growth promotion and crop yield, a promising scenario considers multiple microbe–microbe and microbe–plant interactions by exploiting beneficial synergistic relationships.

Considering this wide scenario, the promising results obtained by applying AM fungi based biostimulants could drive ErM fungi bioformulations. Considering the current emerging relevance of ericoid plants' cultivation, such as blueberry [212], there is room for the development of new mycorrhizal inocula based on ErM fungi, also taking into account complex fungal/bacteria interactions. In fact, a complex interplay supports plant development, with plant-associated fungi interacting with other microorganisms such as bacteria that can, in turn, promote plant fitness in many ways, both directly and indirectly [213].

In conclusion, boosting the health and the biodiversity of the soil microbiota represents a winning strategy to help our environment and our society to cope with the challenges posed by global CC, both from an ecosystem and agricultural perspective.

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