



Mycorrhizae Helper Bacteria: Unlocking Their Potential as Bioenhancers of Plant–Arbuscular Mycorrhizal Fungal Associations

Seema Sangwan¹ · Radha Prasanna¹

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Abstract

The dynamic interactions of plants and arbuscular mycorrhizal fungi (AMF) that facilitate the efficient uptake of minerals from soil and provide protection from various environmental stresses (biotic and abiotic) are now also attributed to a third component of the symbiosis. These are the less investigated mycorrhizae helper bacteria (MHB), which constitute a dense, active bacterial community, tightly associated with AMF, and involved in the development and functioning of AMF. Although AMF spores are known to host several bacteria in their spore walls and cytoplasm, their role in promoting the ecological fitness and establishment of AMF symbiosis by influencing spore germination, mycelial growth, root colonization, metabolic diversity, and biocontrol of soil borne diseases is now being deciphered. MHB also promote the functioning of arbuscular mycorrhizal symbiosis by triggering various plant growth factors, leading to better availability of nutrients in the soil and uptake by plants. In order to develop strategies to promote mycorrhization by AMF, and particularly to stimulate the ability to utilize phosphorus from the soil, there is a need to decipher crucial metabolic signalling pathways of MHB and elucidate their functional significance as mycorrhiza helper bacteria. MHB, also referred to as AMF bioenhancers, also improve agronomic efficiency and formulations using AMF along with enriched population of MHB are a promising option. This review covers the aspects related to the specificity and mechanisms of action of MHB, which positively impact the formation and functioning of AMF in mycorrhizal symbiosis, and the need to advocate MHB as AMF bioenhancers towards their inclusion in integrated nutrient management practices in sustainable agriculture.

Keywords Bacteria · Fungi · Growth Stimulation · Rhizosphere · Symbiosis

Introduction

Access to vital nutrients, particularly minerals, is often limited for plant roots, and mycorrhiza (plural mycorrhizas or mycorrhizae), also known as “root-fungus,” is a type of biological adaptation used by a number of plants to thrive in oligotrophic environments. Mycorrhizae represent a non-disease producing association in which the fungus colonize the roots of plants, leading to a symbiotic relationship, which can be mutualistic or parasitic depending on the ecological conditions in different environments [1]. This obligate symbiotic relationship promotes the adaptability and survival of plants in an integrated manner by inducing morphological and physiological changes in the roots [2]. The fungals

partner takes organic molecules such as sugars, which are produced by the plant through photosynthesis, and in turn supplies water and mineral nutrients, especially phosphorus, to the plant from the soil. Colonization by mycorrhiza can be either inside the plant roots, as arbuscular mycorrhizal fungi (AMF), or on the surface of roots, as ectomycorrhizal fungi. Fossil evidence of primitive plants lacking roots shows the presence of arbuscular mycorrhizal associations, which supports their ancient origin [3]. Among angiosperms, 92% of families and 80% of species host a mycorrhizal symbiosis, with only Brassicaceae and Chenopodiaceae being the exceptions [4, 5].

Arbuscular mycorrhizal fungi (AMF) belonging to the phylum *Glomeromycota* [6] are ubiquitous in their distribution across different ecosystems around the world and represent one of the most widespread beneficial interactions of plants with microorganisms. Their distribution in plant hosts is the primary defining criterion, and on that basis, AMF have been categorized into three classes (Glomeromycetes,

✉ Seema Sangwan
cmasangwan123@gmail.com

¹ Division of Microbiology, ICAR Indian Agricultural Research Institute, New Delhi 110012, India

Archaeosporomycetes, and Paraglomeromycetes), with almost 250 species distributed across 11 families and 25 genera [7, 8]. AMF associations have been recorded from the Arctic [9], to the high Himalayan regions [10], to tropical forests and deserts in the Arabian Peninsula [11, 12], i.e., virtually ubiquitous in all major ecosystems [13]. AMF play critical roles in alleviating the limitation of inadequate nutrient supply, improving tolerance to salinity/drought stress and building disease resistance [14].

For a long time, the mycorrhizal symbiotic relationship was believed to be a bipartite interaction. However, under natural conditions, it is now known that several communities of bacteria and fungi interact with this symbiotic association, and influence at the metabolic level. With the major mode of reproduction of AMF being spores, the significance of AMF spores hosting several bacteria, within or on their spore walls or in the cytoplasm, is being explored. These mycorrhiza helper bacteria (MHB), which belong to diverse genera, are considered as the third partner in the AMF–plant symbiosis and can be used to improve agronomic efficiency in sustainable agriculture by formulating inocula containing the fungus and MHB, referred to as AMF bioenhancers [15, 16]. This review covers the specificity and mechanism of action of MHB, through which they positively impact the functioning of AMF as bioenhancers and play key roles in mycorrhizal symbiosis.

AMF and Plant Responsiveness

Through their beneficial effects, arbuscular mycorrhizal fungi (AMF) help the host plants to manage various environmental stresses. A number of studies have revealed the significant influence of AMF on the acquisition of plant nutrients from the soil, especially under various abiotic and biotic stresses, which resembles a typical genotype \times environment ($G \times E$) interaction. This involves a series of complex signalling communication events, leading to enhanced gaseous exchange and photosynthate assimilation. Host plants benefit in the presence of AMF, as result of higher water uptake, leading to vigorous growth [17]. The domain of access to a larger surface area of soil for the roots is facilitated by AMF, through the formation of a network of hyphae with the plant roots, which improves plant development and growth [18]. Many reports have provided evidence of the underlying processes leading to the enhanced ability of the host plant to resist water stress, unfavourable temperature changes, and the presence of excess salts, pollutants, and pathogen attack, due to this symbiotic association [19–21]. The network formed by AMF comprises its infective propagules, lipid storage structures in the form of vesicles, arbuscules resembling tree-like structures, and filamentous hyphae associated with roots; this structural and functional diversity improves

the nutrient availability in the rhizosphere and facilitates its transport from the soil to plants [22]. The texture, structure, and fertility of soil are also improved by AMF, as they expedite the formation of soil organic matter [23, 24]. Furthermore, AMF also improves the sink effect by increased fixation of atmospheric CO_2 and assimilation of photosynthates from the aerial parts to the roots of the plant. A recent study revealed the role of AMF in promoting the production of secondary metabolites, especially phytochemicals in food plants, e.g., lettuce, tomato, strawberry, and maize thereby improving the health of the plants. *Funneliformis mosseae*, *Rhizophagus intraradices*, and *Rhizophagus irregularis* and associated bacteria were reported to increase the production of polyphenols and carotenoids with enhanced activity of antioxidant enzymes, leading to stimulated plant growth and health benefits [25].

AMF act as natural biofertilizers and play a significant role in enhancing plant growth in climate regimes under stress [14]. AMF responsiveness also relies on the abiotic and biotic environment for their widespread use in agriculture. Several reports have documented that the specificity of the fungi–host plant relationship and related genetic factors influence the level of root colonization. Huang et al. [26] investigated the polymorphism in chitin elicitor receptor kinase 1 (OsCERK1), which is a LysM receptor-like kinase (RLK) and plays an important role in promoting root colonization by AMF. It is the first polymorphic gene identified whose major function is related to its involvement in the perception of chitin oligomer release and chitin-triggered immune responses. It plays a significant role in the responsiveness in terms of root colonization and yield of the host plant.

Mycorrhiza Helper Bacteria

The symbiotic association of AMF with plant roots is affected by the third partner in this complex association, i.e., a group of bacteria called mycorrhiza helper bacteria (MHB), which can promote the functioning of AMF symbiosis, hyphal growth, spore germination, root colonization, and the metabolic fitness of AMF. The first experimental evidence of the so-called helper bacteria was identified as *Pseudomonas fluorescens* Bbcb and led to the coining of the generic term, i.e., mycorrhiza helper bacteria (MHB) [27, 28]. Frey-Klett et al. [29] later categorized two groups of MHB, based on their mode of function: mycorrhiza helper bacteria which affect the functioning of an already established AMF symbiosis; and mycorrhization helper bacteria, which stimulate the formation of the symbiotic association of AMF with host plant roots. Both categories are represented under the general term MHB and can be differentiated based on their natural niches: MHB can be isolated from different AMF environments, i.e., hyphosphere, mycorrhizosphere,

and sporocarps. AMF-associated MHB were first reported in the endomycorrhizal fungus *Rhizophagus (Glomus)* [30, 31], and since then, many bacteria stimulating AMF symbioses have been documented (Table 1). Being inhabitants of the mycorrhizosphere, MHB are not specified by the plant host, but they possess a gradation of specificity with respect to the fungus [32]. The MHB identified to date can be categorized into Gram-negative Proteobacteria (*Agrobacterium*, *Azospirillum*, *Azotobacter*, *Burkholderia*, *Bradyrhizobium*, *Enterobacter*, *Pseudomonas*, *Klebsiella*, and *Rhizobium*), Gram-positive Actinobacteria (*Rhodococcus*, *Streptomyces*, and *Arthrobacter*), and Firmicutes (*Bacillus*, *Brevibacillus*, and *Paenibacillus*). Some MHB use quite specific mechanisms of interaction that have co-evolved with their fungal partners in contrast to other groups of MHB that stimulate mycorrhiza formation less specifically. However, various reports have also documented the plant growth promoting (PGP) activities of MHB [30]; therefore, the beneficial effects of MHB may not always be limited to the formation

and functioning of mycorrhizal associations. The details of various MHB with their origin and their beneficial effects on AMF are listed in Table 1.

Ecological Niche and Specificity of Interaction of MHB with AMF Symbiosis

In natural ecosystems, MHB include diverse and active bacterial communities that positively impact the functioning of AMF. Their occurrence has been documented mainly in the mycorrhizosphere, the region surrounding the mycorrhizal fungi, colonized roots, spores, and associated mycelium present in the soil [40, 41], including the associated biofilm-like structures [42]. Spores of different AMF taxa harbor numerous strictly associated bacteria that have been identified by both culture-dependent and culture-independent methods as belonging to specific genera such as *Pseudomonas*, *Flexibacter*, *Cellvibrio*, *Chondromyces*, and *Lysobacter* [43], or phyla such as α -, β -, and γ -Proteobacteria, Actinobacteria,

Table 1 Details of MHB, their origin and beneficial effects on the AMF association

S. no	MHB identified	Associated AMF	Host plant	Beneficial effect on AMF	References
1	<i>Rhizobium tropici</i>	<i>Rhizophagus irregularis</i>	Bean (<i>Phaseolus vulgaris</i> L.)	Improvement in growth of hyphae; Increase in number of infective propagules, i.e., vesicles, arbuscules	[33]
2	<i>Paenibacillus validus</i>	<i>Rhizophagus irregularis</i>	Carrot (<i>Daucus carota</i>)	Enhancement in fungal mycelia, upto the formation of fertile spores	[16]
3	<i>Bacillus megaterium</i>	<i>Gigaspora margarita</i>	Neem (<i>Azadirachta indica</i>)	Enhance the mycorrhization efficiency	[18]
4	<i>Bacillus pabuli</i>	<i>Glomus clarum</i>	Pea (<i>Pisum sativum</i>)	Increases spore germination, hyphal growth and root colonization	[34]
5	<i>Pseudomonas fluorescens</i>	<i>Funneliformis mosseae</i>	Barrelclover (<i>Medicago truncatula</i>)	Promotes root colonization by AMF	[35]
	<i>Pseudomonas</i>	<i>Rhizophagus irregularis</i> , <i>Funneliformis mosseae</i>	Potato (<i>Solanum tuberosum</i> L.)	Increases upto sevenfold, in terms of AMF root colonization	[36]
6	<i>Burkholderia anthina</i>	<i>Rhizoglomus irregulare</i>	Chicory (<i>Cichorium intybus</i>)	Improves Phosphate solubilization	[7]
7	<i>Ralstonia eutropha</i>	<i>Glomus claroideum</i>	Common velvetgrass (<i>Holcus lanatus</i> L.)	Help AMF in copper sequestration	[28]
8	<i>Burkholderia cepacia</i>	<i>Gigaspora spp.</i>	In vitro study	Help in mycorrhization	[37]
9	<i>Methylobacterium</i>	<i>Gigaspora margarita</i>	In vitro study	Production of ethylene, a volatile stimulator of mycorrhizal fungal growth	[38]
10	<i>Cellvibrio</i> , <i>Chondromyces</i> , <i>Flexibacter</i> , <i>Lysobacter</i> , <i>Pseudomonas</i>	<i>Glomus geosporum</i> , <i>Glomus constrictum</i>	Ribwort (<i>Plantago lanceolata</i>)	Maturation and eventual germination of AMF spores	[4]
11	<i>Bacillus pabuli</i>	<i>Glomus clarum</i>	Pea (<i>Pisum sativum</i>)	Enhance AMF-colonization and nutrient uptake	[5]
12	<i>Pseudomonas fluorescens</i>	<i>Funneliformis mosseae</i>	Tomato (<i>Lycopersicon esculentum</i>)	Improve hyphal growth and colonization of the roots by AMF	[39]

more specifically *Bacillales*, *Burkholderiales*, *Actinomycetales*, *Rhizobiales*, and *Pseudomonadales*. Other researchers have documented the presence of genera such as *Bacillus*, *Paenibacillus*, *Rhizobium*, *Sinorhizobium*, *Arthrobacter*, *Streptomyces*, *Pseudomonas*, *Herbaspirillum*, and *Massilia* [44–46]. Electron microscopy studies revealed that the cytoplasm of a single spore of *Gigaspora margarita* can be a haven to thousands of bacterial cells [37]. *Gigaspora margarita* spores were reported to host *Burkholderia* in their cytoplasm as endobacteria, which were renamed as the endobacterium *Candidatus Glomeribacter gigasporarum* [47, 48]. MHB were also found to be integrated in the layers of the spore cell wall of *Glomus clarum* NT4, *Glomus versiforme*, [49, 50], *Gigaspora margarita* [51], *Funneliformis mosseae*, and *Rhizophagus intraradices* [40, 52]. Other MHB have been reported in the intraradical hyphae, propagules, and extraradical mycelia of AMF, e.g., in the microniche formed by the interlacing of peridial hyphae around the spores in sporocarps [53]. There is a gradation of specificity between AMF and MHB depending upon the species and strains that are interacting [54, 55] and various other factors, e.g., exudates from mycelium of AM fungi present freely in soil, plant roots, soil structure, and nutrient competition [52]. The MHB exhibit their stimulatory effects mainly through the production of volatile compounds which stimulate spore germination, or produce hydrolytic enzymes involved in the erosion of spore walls or facilitate acquiring phosphorus; this showcases their importance in the development and adaptation of AM fungi [53, 56]. It has been suggested that

some MHB can be obligate biotrophs and require AMF as their host to grow [57]. The survival of the MHB strain *Pseudomonas fluorescens* 92rk in the rhizosphere of tomato plants over long periods of time was reported to be improved by *Funneliformis mosseae* earlier known as *Glomus mosseae* [39]. This illustrates the complexity and diversity in this tripartite association of plant, AMF and MHB, which needs in-depth investigation.

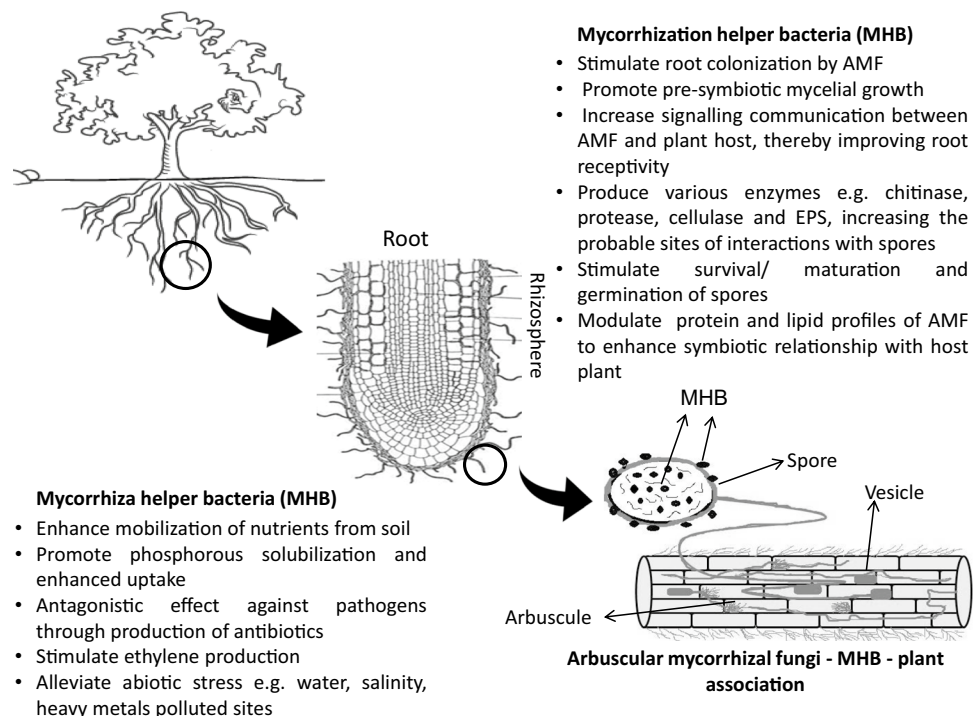
Functional Aspects of MHB in AMF Symbiosis

The functional role and mechanism of MHB as bioenhancers of AMF can be divided into two categories: (1) MHB promoting establishment of AMF symbiosis, i.e., mycorrhization helper bacteria; (2) MHB promoting mycorrhizal functions in already established AMF symbiosis, i.e., mycorrhiza helper bacteria. Figure 1 illustrates the functional roles of MHB under these two categories.

Role of MHB as Mycorrhization Helper Bacteria

In the surveyed literature, several examples of MHB associated with AMF spores illustrate that they have an important role in establishing the symbiotic relationship of AMF with its host by promoting spore germination, growth of AMF hyphae, and root colonization, besides broadening the metabolic profile of the association [15, 28, 58]. This is accomplished because of the different attributes of the MHB e.g., production of growth factors, improving availability of

Fig. 1 Diversity of niche of MHB and their functions, as mycorrhiza helper bacteria and mycorrhization helper bacteria



nutrients, and antagonistic properties against competitors or pathogens.

Stimulating Spore Germination

Mosse [31] was the first to report that the fungal spore germination of *Funneliformis mosseae* was stimulated by MHB and their culture filtrates. The effects of MHB associated with *Glomus clarum* and *Rhizophagus irregularis* spores earlier known by the name *Glomus intraradices* were studied in relation to spore germination in pea–AMF symbiosis, which illustrated that MHB produce several volatile and non-volatile compounds, e.g., CO₂ and 2-methylisoborneol, through which they regulate the germination of spores (88). It was also documented that stimulation of spore germination occurred only when MHB were in contact with spores, which showed the importance of the direct physical interaction between AMF and MHB [50, 59]. *Pseudomonas montellii* strain HR13 produces certain phenolic compounds such as hypaphorine that stimulates root colonization by *Rhizophagus irregularis* in Australian *Acacia* species [15]. Different species of *Streptomyces* were documented to produce certain volatile compounds that stimulate the germination of *Funneliformis mosseae* spores [60]. Hildebrandt et al. [38] detected a specific sugar, i.e., raffinose, as a carbon source produced by *Paenibacillus validus* that accelerates the germination of fertile spores of *Rhizophagus irregularis*, even if the host plant is not in the vicinity. Cruz et al. [51] demonstrated through an in vitro study that the growth, development, and early sporulation of *Rhizophagus irregularis* were supported by a bacterium *Paenibacillus validus*, isolated from the surface of AMF spores. The main functions of this bacterium were nitrogen fixation and P solubilization. Bacterial endophytes (*Burkholderia cepacia* UMPB3 and *Pseudomonas aeruginosa* UPMP3) with antagonistic activity against the white wood rot fungal pathogen were found to significantly increase spore germination and hyphal growth when paired with the AMF *Glomus clarum* BR152B and *Rhizophagus irregularis* UT126 [59].

Selvakumar et al. [61] utilized BOX-PCR fingerprinting to illustrate the diversity of bacterial communities embedded in the walls of spores belonging to *Funneliformis caldonium*, *Racocetra alborosea*, and *Funneliformis mosseae* and identified the MHB as belonging to the phyla *Proteobacteria*, *Bacteriodes*, *Firmicutes*, and *Actinobacteria*. These bacteria were found to possess the ability to produce cell-wall degrading enzymes including cellulase, chitinase, protease, and capable of breaking down exopolysaccharides (EPS); further insights into their associations would be gained through molecular analyses. The role of chitinase in degrading the main component of the fungal spore cell wall has previously been documented, in which *Actinobacteria* were the producers [62]. Scanning electron microscopy

and PCR-DGGE (denaturing gradient gel electrophoresis) showed that MHB associated with spores of *Glomus constrictum* and *Glomus geosporum* received nourishment from the outer hyaline spore layer, which may accelerate the maturation and germination of AMF spores [56].

Invigorating Hyphal Growth, Root Receptivity, and Root Colonization

The fungus–MHB association has been studied in various experiments, which illustrated a significant role of MHB in promoting the establishment of the mycorrhiza. Bharadwaj et al. [36] showed experimentally that the *Funneliformis mosseae* spore-associated bacteria, belonging to the genus *Pseudomonas* sp. were responsible for stimulating its early colonization of potato roots. As discussed earlier regarding the plant's responsiveness to AMF colonization, the effect of MHB on stimulating root receptivity to AMF may be linked to an increase in the probable sites where plants and fungi interact. Several reports have described signal molecules produced by MHB, which regulate the fungal gene networks underlying the AMF symbiosis [63].

Bradyrhizobium japonicum is known to produce several nod factors that stimulate the *Funneliformis mosseae*–soybean endomycorrhizal symbiosis [50]. The growth rate of hyphae of *Glomus fistulosum* was significantly elevated when coinoculated with MHB *Pseudomonas putida* or its culture supernatant [34]. MHB contribute to AMF hyphal growth through their ability to solubilize phosphorus [64], produce ethylene [65] and their antipathogenic efficacy [66]. The mycorrhizospheric MHB *Paenibacillus* sp. strain B2 was found to stimulate root colonization of *Funneliformis mosseae* in *Sorghum bicolor*, and suppress soil-borne pathogens, e.g., *Phytophthora parasitica*, *Fusarium oxysporum*, *Fusarium culmorum*, *Aphanomyces euteiches*, *Chalara elegans*, *Pythium* spp., and *Rhizoctonia solani* [67]. Characterization of plant root exudates led to the identification of molecules called strigolactones, which stimulate the multiplication of endobacteria in the pre-symbiotic stage in germinating spores of AMF *Gigaspora margarita*. These compounds also indirectly improve hyphal growth and branching in the presence of the host root and influence the metabolic profiles of the fungal spores with/without bacteria [47, 68]. This was validated by the increased expression of *ftsZ*, a marker gene for bacterial division in the presence of plant signals. *Bacillus megaterium* isolated from surface-sterilized AMF spores of *Gigaspora margarita* enhanced mycorrhizal root colonization by 58.3%, when coinoculated, in comparison to the uninoculated control [69]. Functional analysis of *Bacillus* and *Streptomyces* associated with *Gigaspora margarita*, both of which are involved in stimulating hyphal growth and spore germination, revealed that this attribute can be ascribed to their ability to solubilize phosphorus, chitin

degradation, and disease suppression [70]. A *Bacillus* sp. strain identified as an MHB from *Rhizophagus irregularis* had a stronger stimulatory effect on AMF colonization in the root cortex and the formation of tree-like structures, i.e., arbuscules, under drought stress conditions than in well-watered soil [71]. MHB inoculation leads to a surge in the growth of mycelia and root colonization and lessens the damage to *Funneliformis mosseae* [72].

Modulating Metabolic Profiles

MHB also influence AMF symbiosis at the molecular level by modulating the nutrient use efficiency of AMF and regulating the fungal cell cycle. Lumini et al. [68] analyzed the cured spores (devoid of bacteria) of *Glomus margarita* in terms of fatty acid and proteome profiles and demonstrated that the endobacteria significantly modulate the presymbiotic growth of AMF by improving mycelial elongation, proliferation in response to root exudates, and through stimulation of stress-responsive proteins. Salvioli et al. [6] investigated the changes induced in the lipid and protein profiles of AMF by *Candidatus Glomeribacter gigasporarum* living as an endobacterium, and provided a metabolic snapshot illustrating the balance existing between the partners. MHB influenced the metabolic profile of the host AMF *Gigaspora margarita* by modulating the fungal protein expression and fatty acid profiles. MHB cured spores showed a lower abundance of fatty acids (such as palmitic acid), and their absence led to the host AMF perceiving it as a stimulus, eliciting increased synthesis of stress proteins, particularly heat shock proteins.

Role of MHB as Mycorrhiza Helper Bacteria in Promoting Mycorrhizal Functioning

Enhanced Nutrient Acquisition

Mycorrhiza helper bacteria interacting with arbuscular mycorrhizal fungi also enhance the functioning of already established mycorrhizal symbioses, ultimately leading to better plant growth [32]. This was mediated by their involvement in escalating acquisition of nutrients from the soil, antipathogenic influence and providing relief from abiotic stresses (water, salinity, and heavy metal), when co-inoculation of AMF and MHB rather than either AMF or MHB alone was undertaken [73]. In an onion crop, the MHB strains *Enterobacter* sp. and *Bacillus subtilis* expedited the uptake of phosphorus from rock phosphate when inoculated with *Rhizophagus irregularis* [74]. This characteristic of MHB was also demonstrated by Jayasinghearachchi and Seneviratne [57], who found that mixed biofilms of phosphate-solubilizing fungi and *Bradyrhizobium elkanii* accelerated the process of rock phosphate solubilization. These findings highlight

the role of AMF-associated bacteria in the mobilization of nutrients from the soil.

Activity Against Plant Pathogens

Mycorrhization helper bacteria promote mycorrhizal development and reduce the impact of antagonistic AMF pathogens [33] and promote the establishment of symbiosis. Many AMF-associated bacteria described as MHB show antagonistic activity against soil-borne pathogens [75]. AMF-associated actinobacteria, e.g., *Streptomyces* spp. were found to produce several antibiotics with a suppressive effect on certain pathogens, thus shielding their host. P solubilization and a suppressive effect on pathogenic fungi were also found with other bacterial groups isolated from *Gigaspora margarita* spores [51]. Budi et al. [69] reported a few fungal-regulated genes in *Pseudomonas aeruginosa* during an investigation of its pathogenic effects on the fungus *Candida albicans*. The extraradical mycelium of AMF has been reported to have both a promoting [19] and suppressing effect on its surrounding microbiome [76], with differential effects on Gram-negative and Gram-positive bacteria [40, 77]. Li et al. [78] hypothesized that the hyphosphere, comprising microbes associated with AM mycelia, plays a vital role in their beneficial interactions with plants. Several strains of actinobacteria associated with AMF spores have been investigated for their crucial role as promoters of plant growth and agents of biocontrol [40, 45, 66].

MHB as Natural Biofilms

In the tripartite interaction of plant roots with fungi and associated bacteria, MHB also survive as biofilms embedded within a self-produced exopolysaccharide matrix associated with AMF spores and play significant roles in the functioning of this tripartite association [35]. MHB biofilms attached to the surface of AMF not only provide benefit in terms of their metabolic activities but also help towards the maintenance of ecological health. Many MHB colonize the surface of filamentous hyphae form biofilms, because the hyphosphere is a rich nutrient feeding zone, and a preferred niche for microbes [79]. Such biofilms represent channels, facilitating long-distance migration and the acquisition of nutrients from distant locations [80]. These biofilms possess an inherent advantage, as they represent a safe niche for the associated bacteria, shielded from various biotic and abiotic stresses, along with access to nutrients from AMF. Many endobacteria associated with AMF spores have also been reported for their potential to enhance nutrient availability and the uptake of phosphorus, nitrogen, or the production and secretion of phytohormones, such as indole acetic acid and siderophores, as well as the suppression of fungal pathogens [44]. *Pseudomonas fluorescens* WCS365

associated with the AMF *Gigaspora margarita* was more efficient at forming a biofilm on the hyphae, compared to another strain of *Pseudomonas* sp. MI14 [81]. Iffis et al. [82] reported a wide variety of bacterial OTUs belonging to *Sphingomonas* sp., *Massilia* sp., *Pseudomonas* sp., and *Methylobacterium* sp. with the infective propagules of AMF, i.e., spores and vesicles. In carrot roots, biofilm was formed by *Pseudomonas fluorescens* on the extraradical mycelia of *Rhizophagus irregularis* [81]. In the mycorrhizosphere of maize, *Bacillus* spp. form biofilms on the surface of *Gigaspora margarita* spores; these bacteria exhibit phosphorus solubilization, ethylene production, nitrogenase activity, and anti-pathogenicity [42]. Phosphate-solubilizing strains of MHB, such as *Rhizobium miluonense* and *Burkholderia anthina*, were observed to become strongly attached to the surface of *Rhizoglossum irregulare* [83].

Further exploration is needed to map the diversity of unculturable bacteria, and obtain a complete picture of the novel bacteriome/microbiome directly associated with AMF, because to date, most of the MHB reported in the literature are the culturable representatives. The molecular interactions between such associations, their pathways and genes involved in the process of biofilm formation have not yet been explored. A better insight into the bacterial–biofilm interactions and biofilm–root biology can be obtained by in-depth studies of selected bacterial and AMF species with their plant hosts. A combination of traditional culture-dependent approaches and metagenomic analyses will help to understand the functional roles of such biofilms. This will be valuable in attempts to improve the ecological health or restoration of denuded habitats or in the bioremediation of polluted habitats, wherein mycorrhiza–bacteria–plant symbioses can serve as useful and promising interventions.

Recent studies have shown that the functional compatibility between the AMF genotype and host plant species along with their influence on the surrounding microbiota needs to be scrutinized. Analyses of the defence response and gene expression in AMF-colonized plants after *Botrytis fabae* infection in the leaves of *Vicia faba* illustrated a corresponding induction of the defence response in neighbouring plants. Investigations on the changes in microbial communities and metabolism in the hyphosphere highlighted the linked induction of plant defence in neighbouring plants [84]. Such networks need to be investigated in depth, using modern omics tools.

Challenges and Future Prospects

The stationary nature of roots and limited access to nutrients and moisture makes the AMF association a significant and integral part of diverse ecosystems. The responsiveness of AMF is influenced by the type of interacting plant and fungal genotypes, as well as the environmental

conditions, and in recent times, also, by the third partner, MHB, which represents an interesting facet of these associations. It is well known that the diverse aspects of plant physiology, particularly the root structure and composition of root exudates, are affected by colonization with mycorrhiza. Modulation of these associations is visible in both quantitative and qualitative terms with changes not only in the nature of the interaction per se, but as also demonstrated in the metabolic profiles of lipids, carbohydrates, the proteome and transcriptome. This, in turn, also influences the composition and structure of the microbiome, and its functionality in the rhizosphere. In addition, the structure, texture, hydrological properties, etc., of the surrounding soil and interactions with soil microorganisms influence the functioning of the AMF association. Over time, research is increasingly focusing on mycorrhiza-induced interactions in the mycorrhizosphere that can be tailored to benefit soil quality, plant growth, and health. Some specific areas that need attention are the following:

- One of the main problems that have been faced is the taxonomy of AMF as it has been amended repeatedly in the last few years [85–87]; this makes it an uphill task to link a taxon with the specific properties of AMF or the associated diverse MHB communities [41].
- Limited information is available regarding the changes in gene expression in the AMF association, particularly due to the associated MHB, except for scanty information on expression studies related to transcripts modulated by beneficial bacteria associated with AMF [88].
- Underlying mechanisms involved at the molecular level in these interactions and the relative contribution of the various microbial partners needs to be investigated further.
- More concerted efforts on plant–AMF association-related interactions at the root level are needed to identify additional polymorphic genes determining AM responsiveness in plants; this can improve our understanding of the mechanistic basis as well as signaling mechanisms involved.
- There is a need to strengthen translational research and functional genomics studies towards the identification and selection of the best performing MHB strains and consortia.

The diverse community of MHB associated with AMF may represent an opportunity for selection towards developing consortia that can serve as bioenhancers, resulting in mutualistic advantages for the three partners in this tripartite relationship. Deciphering the intricate signalling processes and molecules involved in the MHB–AMF associations would provide a firm foundation for developing MHB as promising options for sustainable agriculture.

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Declarations

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