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Mycorrhizae helper bacteria for managing the mycorrhizal soil infectivity

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Arbuscular mycorrhizal fungi are major components of soil microbiota and mainly interact with other microorganisms in the rhizosphere. Mycorrhiza establishment impacts the plant physiology and some nutritional and physical properties of the rhizospheric soil. These effects alter the development of the root or mycorrhizas resulting from the activity of soil microorganisms. The rhizosphere of mycorrhizal plants (mycorrhizosphere), is inhabited by large microbial activities responsible for several key ecosystem processes. This review is focused on the microbial interactions between mycorrhizal fungi and components of rhizosphere microbiota and highlight the agronomic potentialities of the Mycorrhiza Helper Bacteria on mycorrhiza formation. The main conclusion is that this MHB effect in the rhizosphere of mycorrhizal plants, enhance plant fitness and soil quality and are of great interest to ensure sustainable agricultural development and ecosystem functioning.

KEYWORDS

biostimulant, biofertilizer, mycorrhizal symbiosis, mycorrhiza helper bacteria, sustainable agriculture

Introduction

By 2050, and in order to cope with the increase in the number of the world's population which will reach 9 billion people according to the FAO, agricultural production needs to be doubled in developing countries and increased by 70% in the rest of the word (1). The major challenge is to occur a world food security but in the last decades, agricultural lands have been severely impacted by human over-exploitation of the naturelle resources, and the abusive use of fields, resulting in land degradation and desertification (2). Soil erosion and desertification have reduced by 50% the productivity of some lands (3). In Africa, fertile yield decrease is estimated from 2 to 40%, with a mean loss of 8.2% for the continent. Both processes are commonly related to an alteration of the plant cover (species diversity, abundance) but they also affect the physical, chemical and biological characteristics of soils (soil structure, nutrient bioavailability, microbial activity, etc) (4, 5). In agriculture, the adoption of high-input farming practices is dependent to the use of resources such as, mineral nutrients, soil, or water, known to become limiting soon. Hence, the use of fertilizer application will decrease due to increasing costs of mineral fertilizer (6, 7), and the environmental damages (8, 9). This projection will be aggravated by the environmental conditions predicted by current climate change scenarios (10) allowing to a worsening of the impact of abiotic stress on agricultural productivity. At the same time, the demand for food from an over-increasing world population will also be greater, leading to a large imbalance between supply and demand, whose resolution will be a major challenge in defining the basis for an environmentally friendly and productive agriculture.

In order to deal with these increasing agricultural problems, it has been suggested to integrate key processes from natural ecosystems in agricultural practices (2, 3). In many cases, non-degraded ecosystems ensure a high plant and soil health (11). Among all these natural processes, the potentialities of arbuscular mycorrhiza (AM), associations between plant roots and fungi belonging to the phylum Glomeromycota (12) into three classes (Glomeromycetes, Archaeosporomycetes, and Paraglomeromycetes), with almost 250 species distributed across 11 families and 25 genera (13, 14), have been highlighted. They are of particular interest to promote the productivity, stability and resistance of agricultural systems. A recent study has reported that AMF accounted for about one-third of the maize grain production in a medium input field showing the great importance of this biological process in crop yield (15). Mycorrhizal symbiosis is the most common beneficial mutualistic association between fungal symbionts and plant roots (16, 17). This fun gal symbiosis can also be considered as an indicator of soil health (18). There are different forms of mycorrhizal symbiosis depending on the type of fungus and the mode of association: (i) arbuscular mycorrhizae; (ii) ectendomycorrhizae: and (iii) ectomycorrhizae.

It has been well demonstrated that these microorganisms play a main role in improving the water, trophic nutrition and enhance plant defenses against root pathogens and root browsing and can also impair the performance of their host plant by colonizing and exploiting a large surface of the soil invaded by roots alone (17).

There are more than 90% of terrestrial plants whose roots are colonized by mycorrhizal fungi. This association contributes to a succession of physiological and morphological changes in the roots of host plants, thus inducing healthy plant growth. Hence mycorrhizae could be used in agriculture, forestry to ensure better restoration to improve yield. Indeed, the ability of mycorrhizal fungi is not only reduced to their ability to improve the nutrition of plants or to strengthen their immune system, but also have an ability to accumulate metals making them potential candidates for the restoration and remediation of diseases. polluted environments (17, 19, 20). Many studies confirm the interest of the use of mycorrhizal fungi to assess soil and plant health. Gupta et al. (2020) (18) argue in their review that mycorrhizae are not only as indicators but also as determining organisms of soil health. The interaction between the plant species considered and the symbiotic fungus confers multiple advantages for the plant, including the improved of plant nutrition by allowing better uptake of water, P, Cu, Zn and nitrogen (21–23), release of carbonaceous compounds forming the mycorrhizosphere (24); stimulation of the production of phytohormones such as abscisic acid (25); improving plant resistance to (a)biotic stresses (26) and improving soil structure and stability (21). Tahat et al. (2020) (27) highlight that AMF (arbuscular mycorrhizal fungi) improve the functions of the rhizospheric part of the soil. Mahmoudi et al. (2021) (28) also showed that AMF are indicators of soil multifunctionality. Indeed, the multifunctionality of the soil is strongly dependent on the mycorrhizal traits and the mycorrhizal intensity is more correlated with the multifunctional character of the soil than the mycorrhizal frequency. These fungal symbionts are also involved in the biological processes that impact plant community productivity and plant-plant interactions (29).

Nutrient cycling and biological diversity are considered as the main differences between natural ecosystems and agrosystems resulting from the high-input of fertilizers to ensure the high crop productivity. Two different technical ways could be considered to integrate the AMF in agricultural practices: (i) the “reductionist” approach where specialized fungal inocula adapted to the given condition are mixed to the cultured soil (also named controlled mycorrhization) and (ii) the “holistic” approach where the main objective is to conserve, promote or restore native AMF diversity (Figure 1).

The potentialities of using single AMF strains to restore or conserve the whole range of ecosystem services resulting from the AM symbiosis could be challenging. Although numerous studies have been published on AMF symbiosis, data on the “reductionist” management of AMF in field conditions remain scarce (30).

Several scientifical studies conducted on the mycorrhizal symbiosis have been limited to the interactions between each biological component (host plant/AMF) resulting to bipartite interaction investigation. However, and in natural conditions, plants are in constant selection of their microbial host from different surrounding microbial reservoirs (11, 17). The “Plants/Microorganisms” associations are not randomly established.

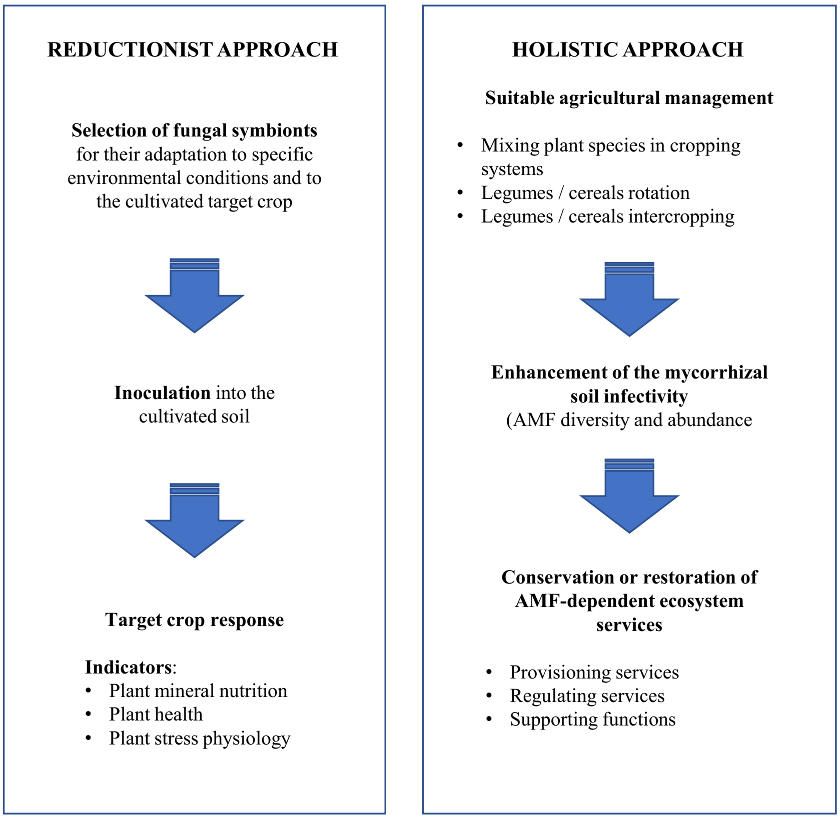


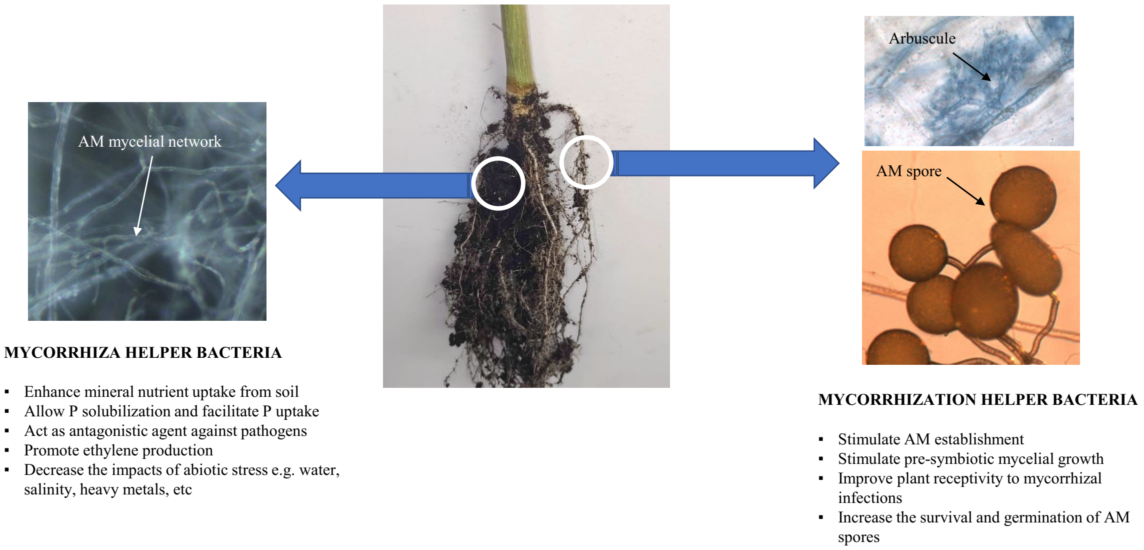
FIGURE 1
Technical approaches to ensure the AMF integration in agricultural practices (Adapted from Fester & Sawers (2011).

They are controlled by many conditions and multiple factors. Plant microbiota is in fact influenced by (i) soil type, (ii) plant immune system, (iii) stage of plant development, (iv) season and genotype and (v) the host specie (11). Furthermore, it is now well established that several communities of bacteria and fungi interact with the establishment and functioning at the metabolic level of the mycorrhizal association. For instance, it has been reported that AMF spores hosted some bacteria within or on their spore walls or in the cytoplasm (31). In order to optimize establishment and effectiveness of artificial fungal inocula under field conditions, a promising way of research could be envisaged by designing complex inoculants combining strains of mycorrhizal fungi and microbial biofertilizers (30). Hence, the associated microbial biofertilizers are generally selected for their agronomic features of interest (i.e. P solubilizers, N-fixers, etc) but their impacts the fungal symbionts and/or the AM establishment and functioning are generally not considered. One of the strategies would be to select bacterial strains capable to promote the establishment and functioning of the mycorrhizal symbiosis and thus optimize the performance of the AMF introduction on plant development (14, 15).

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.

Mycorrhizae helper bacteria: A tripartite symbiosis

The concept of “Mycorrhizae Helper Bacteria” refers to bacteria that have the ability to promote the establishment of the “Root-Mycorrhizal Fungus” interaction, or bacteria associated with roots and mycorrhizal fungi and which will selectively promote the development of this mycorrhizal symbiosis. Two groups of MHB have been distinguished according to their functional action (32): (i) mycorrhiza helper bacteria that impact the functions of an already established AMF symbiosis and (ii) mycorrhization helper bacteria that stimulate the establishment of the fungal symbionts on the host plants. Both groups are generally named MHB but they can be discriminated according to their natural location around the root systems such as hyphosphere, mycorrhizosphere and sporocarps (Figure 2). Some MHB have been first observed in



MYCORRHIZA HELPER BACTERIA

- Enhance mineral nutrient uptake from soil
- Allow P solubilization and facilitate P uptake
- Act as antagonistic agent against pathogens
- Promote ethylene production
- Decrease the impacts of abiotic stress e.g. water, salinity, heavy metals, etc

MYCORRHIZATION HELPER BACTERIA

- Stimulate AM establishment
- Stimulate pre-symbiotic mycelial growth
- Improve plant receptivity to mycorrhizal infections
- Increase the survival and germination of AM spores

FIGURE 2
Spatial distribution and functions of Mycorrhiza Helper Bacteria and Mycorrhization Helper Bacteria.

the AMF *Rhizophagus* (33, 34). Since this report, numerous examples of positive interactions between AMF and bacteria have been documented (Table 1). Bacteria with MHB-like properties are classified into two groups: 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*). It has been also suggested that this MHB effect could result from plant growth promoting (PGP) activities (39)

Microbe-microbe interaction

In order to facilitate co-habitation of different microbial species under the same habitat, many mechanisms are established to permit a healthy growth of different microbe profile. One of the most important aspects is the communication among several microbial species (40). The intraspecies an interspecies microbial communication is made possible by several chemical secretion that regulate microbial interactions in numerous ecological environment and that is also known as Quorum sensing (QS) (41).

Microbes have the ability to create and detect tiny molecule signals in QS, in response to this phenomena, the expression levels of several genes can change and be modified. Autoinducers, or QS signals, may gather surrounding the cell and convey information about ambient conditions, transport dynamics, and the quantity and identity of microbial neighbors (42).

These autoinducers can modify the transcription of multiple QS-regulated genes that take part in the biofilm formation and other factors (43).

In other hand, “Cross feeding” is an important mechanism in microbe–microbe interactions to stabilize cooperation and to reach a maximum growth under different environment conditions (44). For example, in a Pande et al. study in 2013 (45), the combining of two, non-amino acids producing, Escherichia coli mutants can complement each other by overproducing the amino acid. Also, they showed a higher fitness when grown together compared to E. coli wildtype alone.

Other studies, shown that this complementarity can also be seen in a bacteria-fungus combination and not only in a bacteria-bacteria coexisting (46).

These strategies permit to microbes to survive and persist in the most unfavorable environment (47).

MHB- microbe interaction

The MHB-microbes interaction, and as cited above, is no different from the microbes-microbes interaction.

For the MHB-microbes interaction, the communication is also due to chemical secretion (41).

As an example, Pseudomonas fluorescens BBc6R8 (Considered as an MHB) secrete a chemical component: Thiamine, that helps with the growth of mycorrhizal fungus: Laccaria bicolor S238. In the

TABLE 1 Examples of MHB effects on AMF establishment and on the impacts on plant development.

Fungal symbiont	MHB Isolates	Host Plant	MHB effect	Reference
Glomus intraradices	*Paenibacillus favisporus*	*Solanum lycopersicum*	Root promotion, Biomass increase, IAA production	(35)
Glomus intraradices	*Paenibacillus rhizosphaerae*	*Solanum lycopersicum*	Root promotion, Biomass increase, IAA production	(35)
Rhizophagus intraradices	*Azospirillum* sp.	–	germination and the mycelia formed from AM propagules; increased extraradical mycelial length, mycorrhization percentages and the number of newly formed spores	(36)
Rhizophagus intraradices	*Rhizobium elti*	–	germination and the mycelia formed from AM propagules; increased extraradical mycelial length, mycorrhization percentages and the number of newly formed spores	(36)
Rhizophagus intraradices	*Bacillus megaterium*	–	germination and the mycelia formed from AM propagules	(36)
Rhizophagus intraradices	*Bacillus* sp.	–	germination and the mycelia formed from AM propagules	(36)
Rhizophagus intraradices	*Paenibacillus rhizosphaerae*	–	germination and the mycelia formed from AM propagules; increased extraradical mycelial length, mycorrhization percentages and the number of newly formed spores	(36)
Glomus geosporum	*Cellvibrio, Chondromyces, Flexibacter* sp., *Lysobacter* sp., and *Pseudomonas* sp.	*Planteo lanceolata* *Hieracium pilosella*	Spore germination	(31)
Glomus constrictum	*Cellvibrio, Chondromyces, Flexibacter* sp., *Lysobacter* sp., and *Pseudomonas* sp.	*Planteo lanceolata* *Hieracium pilosella*	Spore germination	(31)
Gigaspora margarita	*Curtobacterium* sp.	*Medicago sativa, Sorghum bicolor, Zea mays*	Spore germination, improved the hyphal growth, solubilized degraded chitin, Leaf fresh and dry weight, Root fresh weight	(37)
Gigaspora margarita	*Ensifer* sp.	*Medicago sativa, Sorghum bicolor, Zea mays*	spore germination, improved the hyphal growth, solubilized degraded chitin, Leaf fresh and dry weight, Root fresh weight	(37)
Gigaspora margarita	*Bacillus* sp.	*Medicago sativa, Sorghum bicolor, Zea mays*	spore germination, improved the hyphal growth, solubilized degraded chitin, Leaf fresh and dry weight, Root fresh weight	(37)
Glomus sp.	*Pseudomonas diminuta* and *Bacillus subtilis*	*Coffea* sp.	Pratylenchus coffeae biocontrol	(38)

other hand, The mycorrhizal fungus releases trehalose that serve as chemoattractant for the Mycorrhiza Helper Bacteria (MHB) Pseudomonas fluorescens BBc6R8 (41).

The MHB and AMF interaction

Factors affecting MHB and AMF colonization

Mycorrhizal symbiosis is generally influenced by the presence of other microorganisms, and particularly bacteria in the rhizosphere. These bacteria develop mechanisms of selective interaction with the rhizospheric microbiome and exert neutral, negative, or positive effects on the development and establishment of mycorrhizal associations. Given the positive effect exerted by some bacteria on mycorrhization, the term 'mycorrhization helper bacteria' was first used by Duponnois & Garbaye in 1991 (48) describing bacteria that promote the establishment of the root–fungus symbiosis.

Numerous factors can affect the MHB/AMF colonization. The affinity between the AMF and the MHB is influenced by the specificity between the mycorrhizal and bacterial (i) species and strains, (ii) plant roots, (iii) soil structure, (iv) biotic and abiotic stresses, (v) nutrient competition and soil microbiome composition (49, 26).

A heat shock can also disturbed the MHB/AMF colonization due to the alteration of soil microbiomes that influence directly the tripartite association "Plant/AMF/MHB" (49)

It has also been reported in several studies, that MHB have also the ability to produce molecule signals that influence and regulate the fungal gene networks under the AMF symbiosis (50, 51). Some reports have highlighted the role of MHB associated with AMF spores in contracting the symbiotic relationship of AMF with its host plant by increasing spore germination, growth of AMF hyphae, and root colonization (36, 52).

Indeed, the complexity of this tripartite association needs to be more explored (53).

The mycorrhization helper bacteria and AMF spore germination

Some bacteria are strictly associated with AMF spores (54, 55). Using both culture-dependent and culture-independent methods, they have been identified as *Pseudomonas*, *Flexibacter*, *Cellvibrio*, *Chondromyces*, and *Lysobacter* (31) or Bacillales, Burkholderiales, Actinomycetales, Rhizobiales, and Pseudomonadales. It has also been reported the presence of several genera inside AMF spores such as *Bacillus*, *Paenibacillus*, *Rhizobium*, *Sinorhizobium*, *Arthrobacter*, *Streptomyces*, *Pseudomonas*, *Herbaspirillum* and *Massilia* (56, 57), MHB were also detected in the layers of the spore cell wall of *Glomus clarum* NT4, *Glomus versiforme* (58, 59), *Gigaspora margarita* (60), *Funneliformis mosseae*, and *Rhizophagus intraradices* (53, 55). One of the well-documented effect of MHB on mycorrhizal establishment is related to the stimulation of the spore germination. The first report on this mode of action showed that that the fungal spore germination of *Funneliformis mosseae* was stimulated by MHB and their culture filtrates (33). Other mechanisms have been then suggested such as:

- MHB production of several volatile and non-volatile compounds, e.g., CO_2 and 2-methylisoborneol regulating the germination of spores (54). This mechanism has been also described with different species of Streptomyces that increase the germination of *Funneliformis mosseae* spores.
- A specific sugar (raffinose) excreted by *Paenibacillus validus* could stimulate the germination of *Rhizophagus irregularis* spores (61).
- The growth, development, and early sporulation of *Rhizophagus irregularis* was also facilitated by a strain of *Paenibacillus validus* that exhibited nitrogen fixation and P solubilization (60).
- The importance of direct physical interaction. has been also emphasized in the MHB positive effect on spore germination (59, 62).
- MHB enzymatic production (i.e. cell-wall degrading enzymes including cellulase, chitinase,

protease) could also enhance spore germination (63). For instance, the main component of the fungal spore cell wall role of chitinase was degraded by chitinase produced by actinomycete strains (37).

Other mechanisms have been suggested to explain the MHB effects on mycorrhizal establishment such as the stimulation of root receptivity to AMF by increasing the infection sites where plants and fungi interact (64). Other reports have identified signal molecules produced by MHB, which regulate the fungal gene networks underlying the AMF symbiosis (65). It has been also well demonstrated that the co-culture of *Glomus fistulosum* and the MHB *Pseudomonas putida* or its culture supernatant resulted to a higher growth of the fungal symbiont (66).

MHB and impact on soil

The practice of intensive agriculture reducing the density of AMF in agricultural soils (67), the introducing af the MHB can promote the ecosystem services rendered by fungal symbiot by improving rhizospheric soil functions leading to better soil properties and increased yield (68).

MHB have an indirect effect on soil fertility due to the release of chemical substances necessary for communication between the different microbial communities present in the soil. These molecular exchanges induce a difference in soil properties (69)

Formulation of AMF inocula embedded with MHB strains in field conditions

Data showing the beneficial effects on plant growth resulting from the association of MHB and mycorrhizal fungi are scarce. Duponnois & Garbaye (1991) and Garbaye et al. (1992) (48, 70), showed that a MHB strain (Fluorescent pseudomonads) could reduce the amount of ectomycorrhizal inoculum (Laccaria bicolor) inoculated to the cultural soil with the same beneficial effect on Douglas-fir growth than that obtained with a higher rate of inoculation. Most of the available data have been recorded from glasshouse experiments. Hence it has been demonstrated that *Bradyrhizobium japonicum* was able to positively influence and establish symbiosis with *G.mosseae* and synergistically effectively act as “mycorrhiza helper bacteria” (MHB) when both were co-inoculated in Bambara plant. The use of Phosphate solubilizing bacteria as mycorrhiza helper bacteria promoted a higher colonization rate and spore number of AMF which increased the solubilization of a mineral phosphate and allowed a sustainable nutrient supply to *Sesamum indicum* L for higher yield (71).

In 2009, a study conducted by Gamalero and his team, proved that the interaction of the MHB strain Pseudomonas putida UW4 and the AMF strain Grigaspora rosea BEG9, affected positively the growth of cucumber under a sever soil salinity conditions (72).

On the same pattern, in 2016, the combined use of both AMF and it associated MHB isolated from a salt affected soil, has significantly improves the soil salinity tolerance of maize plants (73). In fact, the co-inoculation of AMf and it associated MHB strain, has improved the soil salinity tolerance of maize plants by impacting the plant root colonization and the efficiency of the nutrient use of the maize plants. A tripartite interaction between the AMF, the MHB isolated and the maize plants has been assessed.

Another example of the MHB/AMF field use; in a recent 2021 study, the beneficial effect of the co-inoculation using AMF and MHB strains was demonstrated (64). The use of this consortium has significantly improved the growth of plants and enhance their biomass. The co-inoculation has significantly improved both the nitrogen and phosphorus nutrition.

In a 2019 review, the interaction between AMF and Bacillus spp. Strains in order to promote field plant growth has been explained (74). The synergically acting between both the AMf and MHB strains was define as the key of yield field enhancement.

Mycorrhization helper bacteria could play the role of environmental probiotics or ecosystem catalysts by exerting a positive influence on the intensity of mycorrhization. Indeed, the practice of intensive agriculture reducing the density of AMF in agricultural soils, the use of these auxiliary bacteria could make it possible to promote the ecosystem services rendered by fungal symbionts such as improved rhizospheric soil functions (Figure 3).

Conclusion and further prospects

Mycorrhizal helper bacteria are currently used in some practices in agriculture and forestry. Indeed, these microorganisms would represent an opportunity to optimize the mycorrhizal effects within agrosystems for the benefit of agriculture. According to Garbaye (48), mycorrhizal helper bacteria are not plant-specific, but are selected according to the fungal species, and are therefore specific to the mycorrhizal fungus genus. MHB include a wide range of Gram-negative and Gram-positive species (49). Among the fungi described as interacting with MHB, we note the basidiomycetes belonging to the ectomycorrhizae and the arbuscular mycorrhizae (48).

According to several studies, these MHB would act (i) by improving the receptivity and recognition of the fungal partner by the root, (ii) by improving the growth of the mycorrhizal fungus, (iii) by bringing about certain modifications at the level of the rhizosphere or (iv) by improving the germination of fungal propagules (15, 48, 49).

With all these advantages in the service of the ecosystem, MHB have a large agro-industrial potential (49). These bacteria having the possibility to positively influence the abundance of mycorrhizal propagules, their introduction into the soil will allow obtaining a significant improvement of the physico-chemical properties of the soil and therefore of the agricultural yield (51).

However, as it has been well established that the potential practical application of MHB in agriculture and forestry was great, new screening criteria are needing that will facilitate a performant selection of efficient bacterial isolates (75). The screening strategies used so far are too time-consuming. Therefore, there is a need to identify fungal marker genes specific for the mycorrhiza helper effect. This knowledge will have major practical outputs, more particularly for the improvement of crop yields in degraded soils.

In addition, and from a practical point of view, more data have to be obtained from field experiment using innovative microbial inoculum formulations which allow

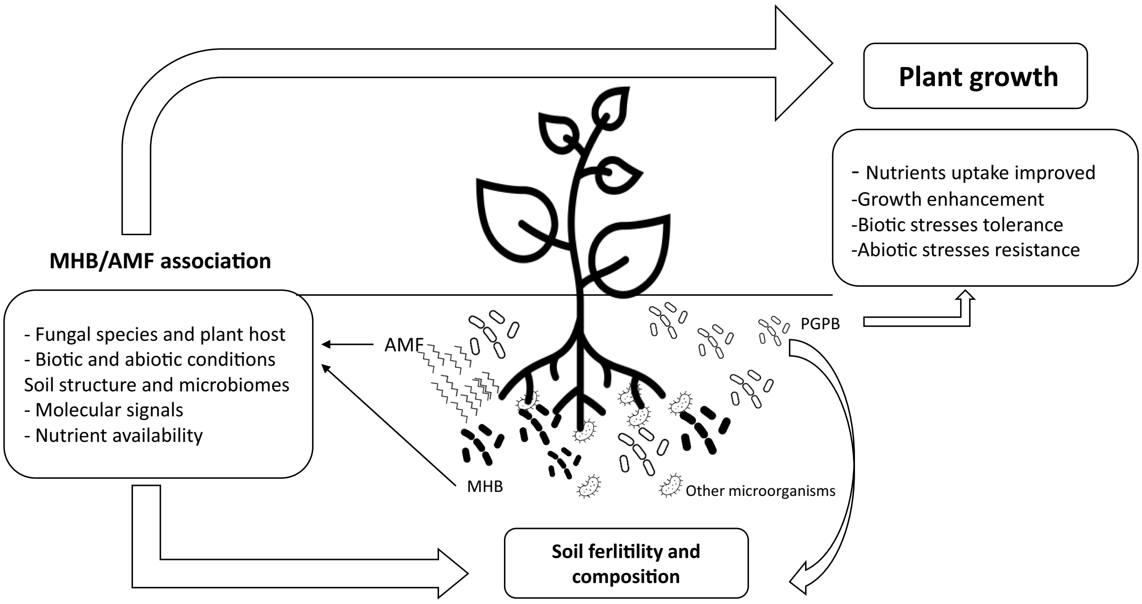


FIGURE 3
MHB mechanism to improve plant growth.

the expected impacts from the MHB/interaction on plant and soil health.

Author contributions

NB: realization of the experiments and manuscript redaction. DR: redaction and proof-reading of the manuscript FH: proof-reading of the manuscript. SA: proof-reading of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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