

Review Article

Regulatory Role of Arbuscular Mycorrhiza Fungi and Helper Bacteria Associations in P and N Dynamics in Agriculture

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Abstract

Interactions among microflora and plants represent a major pillar in rhizosphere biology for improving soil fertility and crop productivity. As the most important macronutrients in soil, the availability of Phosphorous (P) and Nitrogen (N) significantly affects plant growth and yield, across crops, and around the globe. In soil, bacteria and fungi constitute the major groups of microbes, existing, both as free-living and in symbiotic/ loose associations with other living forms, which find use as biofertilizers in integrated nutrient management. Among various types of fungi, Arbuscular Mycorrhiza Fungi (AMF) comprise symbiotic fungi which form an extensively dense network of mycelia around the plant roots, and improve the soil structure and increase the uptake of water, as well as nutrients such as P, N/ micronutrients by plants. Several bacteria capable of solubilizing phosphorous mainly via releasing a wide range of organic acids and chelating metabolites are also present in free living form and in association with AMF. Such bacteria associated with AMF hyphae and spores are called as Mycorrhiza Helper Bacteria (MHB) as they help in regulating the activity and functioning of AMF. Characterization of such bacteria and developing promising combinations of AMF and MHB, can be beneficial for improving the nutrient availability in soil and stimulating plant growth. This review summarises and discusses the current knowledge on the interactions among AMF and MHB towards

enhancing the availability of N and P availability, and its uptake by plants, thereby, highlighting the research gaps that need attention and in-depth research.

Key Words: Arbuscular Mycorrhiza Fungi; Mycorrhiza Helper Bacteria; Nitrogen; Phosphorous; Synergism

Introduction

Replenishing the soil biological properties through the tools of microbial inoculation and addition of requisite quantities of nutrient inputs is the hall mark for keeping agricultural revolution evergreen. For getting optimum yields in a sustainable manner without any dire consequences to environment, it becomes necessary to provide a regular supply of these macronutrients, through fertilization (chemicals or biofertilizers). Phosphorous (P) and Nitrogen (N) are the primary nutrients required for the growth, development of plants and are essential because they actively participate in various processes e.g., carbon metabolism, energy generation, energy transfer, enzyme activation, membrane fixation and nutrient cycling [1-4]. Phosphorous is involved in formation of ATP, nucleic acids and phospholipids [5]. P deficiency is known to cause approximately 50% losses in all agricultural lands around the world [6,7]. Like P, N is also a primary major nutrient required by plants as it forms a part of the structure and functioning of some important macro and micro building blocks in plants such as chlorophylls, proteins and amino acids [5,8]. For improving the availability of P and N to the plants, chemical fertilizers are often used in an unbalanced manner, without knowing its long-term consequences and its ill effects on the environment. To mitigate this, the use of biological options to make available N and P to the plants is the sustainable way forward. Arbuscular Mycorrhizal Fungi (AMF) and their intimate relationship with Mycorrhiza Helper Bacteria (MHB), are getting more attention among various types of biofertilizers, as they effectively increase P, N uptake and crop productivity [9,10].

AMF represent an obligate biotrophic association with plant roots that establishes mutualistic symbiosis with 80% of the terrestrial plants such as cereals, pulses, fruit trees, vegetable, medicinal plants and other commercial crops such as sunflower, cotton and sugarcane [11]. In exchange for plant photosynthates, AMF facilitate the uptake and transfer of mineral nutrients such as P, N, S, Ca, Cu and Zn from the soil to the host plant through their Extra Radical Mycelium (ERM) [12]. ERM function as an efficient absorbing system that enables the uptake of nutrients beyond the depletion zone [13-15]. Besides providing nutrition to the plants, AMF also facilitates the completion of several biochemical cycles, enhances tolerance to biotic and abiotic stress [16], sequesters carbon, improves soil aggregation [17] and plays an important role in synthesis of health promoting phytochemicals [18]. In the mycorrhizosphere, MHB which are associated with AMF spores and hyphae, thereby, playing an important role in nutrient uptake and overall growth of the plant, as they are potent bio-enhancers of plant-AMF associations [19]. They help in improving hyphal growth, spore germination and establishment of mycorrhizal symbiosis. MHB isolated and characterized till date are gram-positive Actinobacteria and Firmicutes (e.g., *Streptomyces*, *Brevibacillus*,

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Bacillus, *Rhodococcus*, *Arthrobacter*, *Paenibacillus*) and *Azospirillum*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Enterobacter*, *Agrobacterium*, *Azotobacter*, *Bradyrhizobium* and *Klebsiella* which come under the category of gram negative Proteobacteria. Species of *Streptomyces*, *Pseudomonas* and *Corynebacterium* have been shown to improve the germination of *F. mosseae*, *G. versiformae* and *G. margarita* spores [19,20]. Actinobacteria are a group of bacteria frequently associated with AMF spores able to hydrolyze chitin found in the spore wall [21,22]. Other MHB such as *Klebsiella pneumonia* and *Paenibacillus validus* have been reported to increase germling hyphae growth [23] and *Oxalobacteria* enhance both spore germination and germling growth along with root colonization. ERM development is promoted by *Penibacillus spp.*, *Azospirillum spp.* and *Pseudomonas spp.* [24]. Additionally, MHB:

- Promote mycorrhizal symbiosis by several direct and indirect means including- improvement in root receptiveness of fungi [25].
- Modulate plant-fungi recognition and symbiosis establishment.
- Accelerate EMF propagule germination as well as spore survival and mycelial growth.
- Modify soil chemical properties e.g., for a better connectivity with the soil fungus, protection against pathogen and promote defence mechanism [26].

MHB are also known to help breakdown molecules to a usable form as they can utilize both organic and inorganic nutrients in soil through a process called “mineral weathering” which aids in the recycling of nutrients in the rhizosphere environment. MHB help to make available, P from soil [27,28] and phosphorus solubilizing rhizobia are the most common MHB involved in P uptake. They release compounds in soil to break down organic inorganic P for further use by mycorrhizae. They are active even under P limited conditions, helping mycorrhiza to establish and grow [29]. Several MHB also have the capability to acquire nitrogen and fix N in the soil, without plant modification, as done by legumes to help in N fixation [28]. Researchers reported the significant contributions of *Bacillus spp.* to N fixation [30] (Table 1).

Ecological function	AMF	Crop	Reference
N, P, K, Fe and Zn	<i>Glomus mosseae</i>	Rice	[31]
C, N, P, K	<i>Glomus spp.</i>	Finger millet peanut, pigeon pea	[32]
N, P	<i>Rhizophagus intraradices</i> , <i>Glomus versiformae</i> , <i>Claroideoglomus uncatum</i> , <i>Claroideoglomus claroideum</i>	Tomato	[33]
C, N, P	<i>Funnelformismosseae</i> , <i>Rhizophagus irregularis</i>	Apple	[34]
N	<i>Funnelformismosseae</i> , <i>Diversisporaversiformis</i>	Chrysanthemum morifolium	[35]

Table 1: Ecological role of AMF to facilitate P and N uptake.

Plant Response to Deficiency of P and N in Soil: Plants exhibit several biochemical, physiological and morphological adaptations to deal with N and P deficiency, which work in a linked manner. To increase P and N acquisition capacity, plants show “P and N starvation

response” as shown in Figures 1&2. Recent scientific advances have helped to provide a better understanding of the signalling pathway of plant response to N limitation by microarray and sequencing-based transcription profiling, e.g. genome scale expression in many plants e.g., rice, corn [36-38]. Arabidopsis adapts itself to limited nitrogen through NLA gene (nitrogen limitation adaptation) by inducing the anthocyanin synthesis [39].

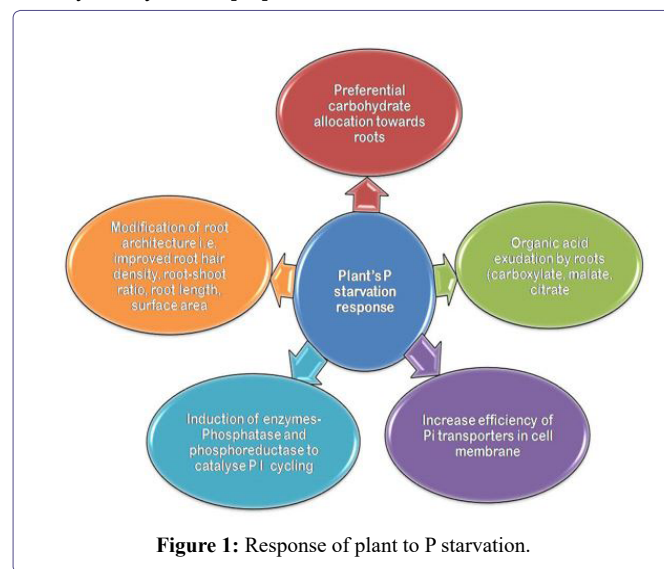


Figure 1: Response of plant to P starvation.

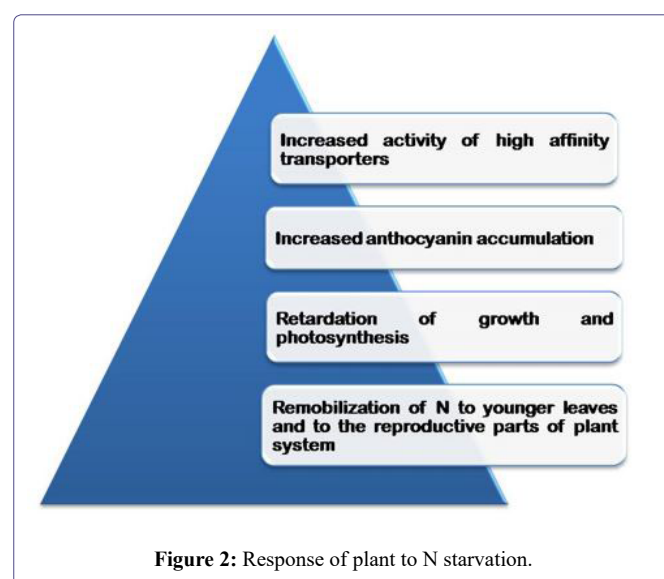
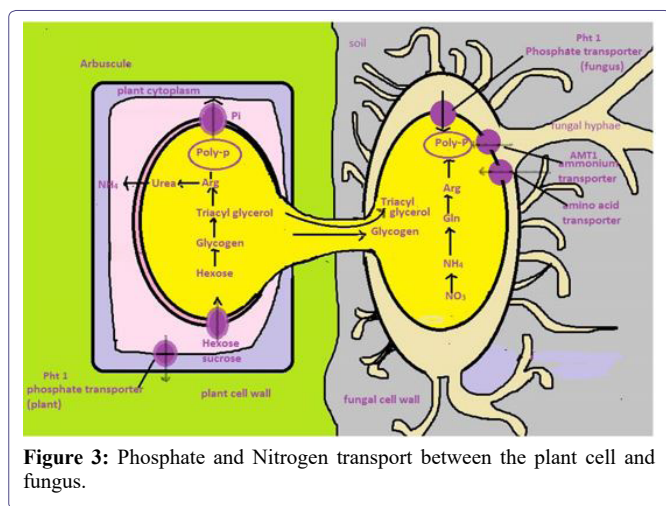


Figure 2: Response of plant to N starvation.

Mechanism of AMF for P Mobilisation and uptake: The benefits of AMF in various plants are documented and its significance in P uptake is the most noteworthy. AMF being obligate biotrophs, they form a symbiotic relationship with the roots of plant for their survival [11,40]. These fungi penetrate the root cortical cells, establish arbuscules, and mediate the exchange of nutrients such as P [41]. AMF expands the extent of the mycorrhizal hyphae network up to 25 cm around the root in the mycorrhizosphere and creates a niche for other microbes, to facilitate better availability of plant nutrients like P and N [11]. It has been established that 50% of P uptake in the mycorrhizal plants is supported by the AMF [42] and the P uptake mechanisms include-

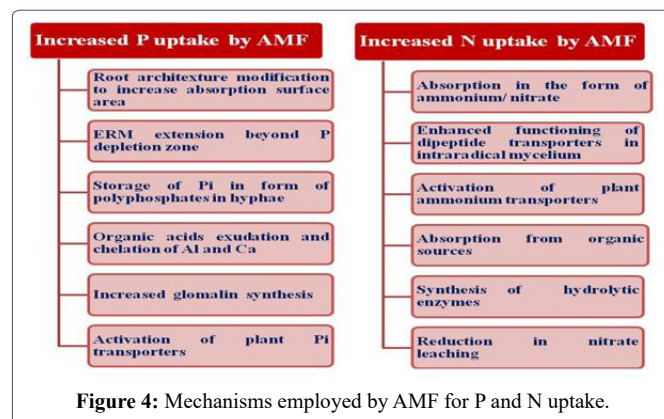
- i. P uptake rate (influx) per unit of arbuscular mycorrhizal root increases due to the greater absorption surface area of mycorrhizal roots compared to the cylindrical root surface of plant systems [43].
 - ii. AMF enhances the root zone absorption by 10-100% and improves the plant's ability to reach more soil resources due to ERM by increasing absorption area of root through ER hyphae which extend beyond the P depleted zone, leading to greater bioavailability of Pi [43].
 - iii. These hyphae with small diameter allow the ERM to access small cores to achieve greater P intake, improve P acquisition plant possess the ability have to overcome the depletion zone and improve root surface area [11].
 - iv. AMF store P in polyphosphate form so that they can keep their Pi level low to efficiently transfer Pi from the soil to extra radical hyphae and then to intra radical hyphae [28,44].
 - v. In addition, organic exudates (citrate, malate) which chelate Ca, Al ions and dissolve aluminum and calcium phosphate are secreted in soil [45].
 - vi. AMF also release some chemicals such as glomalin (a glycoprotein) which are reservoirs of C in soil and aid in uptake of Fe, and P [46,19].
 - vii. Improve the functioning of cell-specific Pi transporters (Figure 3) which transfer Pi to the host plant also known as plant Phosphate Transporters (PTs) [47,48]. They facilitate the acquisition of inorganic Phosphate (Pi) and maintain its homeostasis within the plant.
- i. Inorganic nitrogen in the form of ammonia and nitrate [52,53].
 - ii. Directly facilitate the uptake of glycine in *Glomus mosseae* through a mechanism, as depicted in Figure 3, in which AMF acquires organic N directly from the soil substrate. Researchers have provided evidence for the uptake of organic N by dipeptide transporters in the intraradical mycelium of *Rhizophagus irregularis* [54].
 - iii. In arid regions, where N mobility/nitrate mobility is low, AMF can be effective under such conditions to absorb inorganic N [55,56] indicating that even in such stress conditions, AMF can help to increase the uptake of N.
 - iv. Plant ammonium transporter activation in the presence of AMF has been reported similar to P [57]. Using labelled N, it has been demonstrated that the hyphae of AMF are able to utilise inorganic N efficiently and transfer it to 10-30 cm [58,59,25].
 - v. AMF utilise the inorganic N reused from organic source such as like amino acids [60,61].
 - vi. To mineralise N, it also produces hydrolytic enzymes such as pectinase, xyloglucanases, cellulases which are able to decompose SOM, under humid conditions. This also helps to reduce the leaching of nitrate in the soil [62].

Under low N availability, competition for N between AMF and plant has been documented resulting in non-mycorrhizal plants becoming more efficient than mycorrhizal plant [63]. AMF-mediated P uptake could also have a significant positive effect on BNF [64]. There are various modes of N uptake in the rhizosphere, so it is difficult to distinguish the most important process- biotrophic, nutrient cycling or transfer through root exudates [61,65]. There is limited evidence from experiments involving quantum dot technology that the organic N fragment could have been taken up by the AMF and uptake of N in the form of amino acid has also been reported to be as high as compared to non-mycorrhizal plants (Figure 4).



(Phosphate and nitrogen acquisition by fungus and transport to the plant cell through Pht1 i.e. phosphate transporters; nitrogen through AMT1 i.e. nitrogen transporters).

Mechanism of AMF for N Availability: It is also indicated that AMF fungi can influence the uptake of other nutrients e.g., nitrogen which is necessary for plant growth and yield [49]. Results from the root organ culture studies suggest that up to 50% of the root N is acquired through AMF route [50]. A “Trade balance model” was proposed to explain the apparent nitrogen paradox [51]. This model suggested that fertilization with N will be only beneficial, if plant is limited by P and will therefore benefit from providing C to the roots and mycorrhizal fungi. AMF can acquire N in various ways:-



Organic N uptake by AMF: AMF development favours the release of nutrients from soil through mineralisation (specifically NH_4^+ ions) [66]. AMF is found to possess a weak exoenzyme repertoire [67], such as exophosphatase activities. However, they are very unlikely to mineralise on their own. AMF rely on other saprophytic /hyper symbiotic microbes for the N mineralisation [68]. There are some microbial grazers who excrete a large amount of NH_4^+ ions in the soil when they digest other microbes in soil, thereby returning the N to soil-free ammonium pool. It can be easily utilised by AMF [61,66]. As of now, there is very scanty information regarding ERM to be able

to directly take organic N molecules such as amino acids, peptides and nucleosides from the soil solution [53].

Chitin as a Source of Organic N for AMF: Chitin is a polymer rich in N (>6%) by weight which is present abundantly in the soil micro and microfauna. It has been reported that the addition of crab shell chitin during plant cultivation as substrate can promote AMF species sporulation [69]. The genes responsible for the breakdown of NAG (N acetyl glucosamine); a subunit of chitin polymer, are present in the membrane in *Rhizophagus irregularis* [70]. The transporter genes have also been identified in intra-radical hyphae only. After the chitinolytic degradation of chitin by various fungi and microbes, it gets transported by the AMF and while the decomposers are eaten up by grazers and the N returns to the ammonium pool. But there is a chance of competition between AMF and ammonium oxidising bacteria in the soil solution [66].

Mechanism of MHB for P uptake: In order to develop strategies to promote mycorrhization of AMF and improve uptake of P from soil, there is a need to elucidate the aspects of metabolic signalling pathway of MHB and illustrate their functional significance. MHB are known to help break down molecules to a more usable form [28]. They obtain both organic and inorganic nutrients from the soil through a direct process called “mineral weathering” which aids in recycling the nutrients e.g., *Pseudomonas*, *Burkholderia*. Phosphate Solubilizing Rhizobacteria (PSRB) are the most common MHB which aid in the phosphate uptake. They release the phosphate degrading compounds to break down organic and inorganic phosphate, thus creates a phosphate pool that mycorrhiza can further use. PSB are also called as PGPR [28,71,72] as the improved availability of P improves plant growth. PSB solubilise P by producing phenolic compounds, organic acids, siderophores and hormones [73]. The acids destroy the P-bound structure, such as those of dicalcium phosphate, hydroxyl phosphate, tricalcium phosphate, rock phosphate, and make P available to plant in the form of dihydrogen phosphate or hydrogen phosphate [28]. As a result of all these mechanisms, it has been found that PSB can increase the growth of cereals, legumes, fibre crops, horticultural and oil seed crops [22]. The details of these mechanisms are given as:

Production of Organic Acids: The dissolution of P bearing compounds is pH dependent i.e., P uptake occurs at a pH of 6.5-7 so PSB produce organic and inorganic acids by mineralization [74,75]. Organic acids like malic, aspartic, tartaric, oxalic, gluconic are produced by bacterial metabolism, due to oxidative respiration. Organic acids can solubilize P from mineral surfaces by ligand exchange or ligand promoted dissociation. PSB indirectly reduce the pH and increase the P level by enhancing root exudates that increase the P availability by maintaining electro-neutrality in the soil [75]. Such organic acids sometimes also compete with phosphate at the fixation site but the siderophores (chelating agent) present in root exudates facilitate the soluble complex formation and improve Pi precipitation [76]. Root exudates attract the MHB and lead to the production of more organic acids and reduction in pH.

Production of Inorganic Acids: MHB also include Sulfur Oxidizing Bacteria (SOB) and Nitrifying Bacteria (NB) belonging to the genera *Thiobacillus* and *Nitrobacter* which participate in the production of inorganic acids (carbonic acid, hydrochloric acid, nitric acid, sulphuric acid) reported to solubilize P by reducing the pH and increasing the P availability in the soil [77,78]. SOB oxidizes sulphur compounds in the presence of oxygen to produce sulphuric acid and NB oxidizes inorganic nitrogen to produce nitric acid.

Siderophore Production: Plant and microbes both produce siderophores under low iron conditions. Siderophores are the organic compounds having iron chelating ability which makes iron available to both plants and microbes [79]. These siderophores also bind to various metals like Cd, Pb, Zn, Al, Ca, Mn, and Mo. Several PSB also reported to produce siderophore [80] and mediate solubilising / dissolution of the insoluble P bearing minerals [77].

IAA and ACC Deaminase Production: PGPB and PSB and other MHB can improve P uptake by plant, by promoting phytostimulation i.e., stimulating root growth through increased branching as a result of hormonal stimulation, or root hair development by the production of IAA and ACC deaminase [81-83]. The IAA and ACC deaminase promote effective root architecture, branching, increase root exudation to lower the rhizospheric pH and improve P solubilization [84,85]. Many PSB were reported to produce IAA and ACC deaminase, as also IAA producing PSB similarly solubilising Pi by increasing surface area and root exudates [82,86]. This synergy of IAA production and P solubilization being intricately linked is beneficial for plant growth [87].

P Hydrolyzing Enzymes: Organic P contributes 40-80% of soil total P. To hydrolyze organic P compounds, plant and microbes both produce enzymes. PSB mineralize organic P by secreting phosphatase enzymes [28,77] while microbes derive phosphatase mainly combine with phosphate and help in releasing orthophosphates from soil organic P [28,77,88]. Phytases are enzymes secreted by microbes which convert phytate into esters, followed by action of phosphatase to break down to Pi [5,89]. According to Le-Chateliers principle, lowering the concentration of Pi in soil solution promotes the production of Pi by indirect dissolution of K-apatite or calcium phosphate [90].

Mechanism of MHB for N uptake: MHB in the rhizosphere often have the capability to acquire nitrogen that the plant can use. Such MHB are able to fix N in the soil and create pools of available nitrogen [28,91]. However, MHB do not bring about any plant modification, as legumes do, to help with nitrogen fixation [61,91]. Nitrogen fixation is done in the surrounding soil in relation to mycorrhiza. A *Bacillus* functioning as MHB contributed to the nitrogen fixation and among other factors helped the plant grow when inoculated with fungus and tripartite interaction with AMF [92], host plant and soil microbes enhancing the nitrogen fixation capacity in *Rhizobium*. The P uptake pathway positively affects the rhizobium N fixation by influencing the energy-producing pathway. Inoculation of diazotrophic bacteria such as *Gluconacetobacter*, *Diazotrophicus*, *Burkholderia tropica*, *Azospirillum amazonense*, *Herbaspirillum rubisubalbicans*, and *Herbaspirillum seropeduca* has been shown to distinctly influence and promote N fixation in sugarcane [93]. Except for sugarcane, the use of non-rhizobial N fixing MHB in other non-leguminous crops has met with limited success [94] (Table 2).

Improving P and N Availability through Synergism between AMF and MHB

“MHB are known to influence AMF fitness” i.e., the synergistic relationship between MHB and AMF can be described as one in which MHB leads to increase in plant growth parameters by stimulating the native AMF association, spore germination, hyphal growth, rate of colonisation and effectively access soluble P and N sources [101-103]. The presence of MHB on the surface of the spores belonging to *Rhizophagus irregularis*, is illustrated using Scanning Electron Microscopy (SEM), wherein they are visible as members of the sheet

Crop	MHB	Nutrient uptake	Mechanism involved	Reference
Finger millet, Maize, Amaranth, Buckwheat, French bean	<i>Bacillus spp.</i>	P	P solubilisation	[95]
<i>Ficus benjamina</i>	<i>Bacillus coagulans</i> , <i>Trichoderma harizanum</i>	P	Positively affecting mycorrhizal fungi	[96]
Wheat	<i>Azotobacter chroococcum</i>	P	P solubilisation and hormone production	[97]
Wheat	<i>Bacillus circulans</i> , <i>Cladosporium herbarum</i>	P	P solubilisation and interact with AMF	[98]
Tomato	<i>Enterobacter agglomerans</i>	N, P	P solubilisation also positively affects mycorrhizal fungi	[99]
Maize and sunflower	<i>Pseudomonas alcaligenes</i> , <i>Bacillus polymyxa</i>	N, P, K	Hormonal effect on root growth	[100]
Chickpea	<i>Rhizobia</i>	N	N fixation	[10]

Table 2: MHB functions in P and N uptake.

forming biofilms, and shown to enhance growth in such associations (Figure 5). *Glomus mosseae* spores were reported to be stimulated in terms of mycelial growth by PGP rhizobacterium [104]. Such bacteria also help to enhance root colonization of indigenous and inoculated AMF [92,105]. Bacterial IAA is known to loosen plant cell walls to release root exudates for providing additional nutrition to support microbial growth. These exudates contain several enzymes such as amylase, urease, phosphatases and plant hormones like IAA, ABA, and gas [106], which help in mineralisation of P and N for AMF [107,108] and flavonoids to facilitate root colonization [109]. MHB sometimes release exudates and create a biofilm; this biofilm represents a means of long-distance migration and acquisition of nutrients from distant locations. In onion crop, MHB strains *Enterobacter spp.* and *Bacillus subtilis* were seen to enhance the uptake P from rock phosphate when inoculated alone with *Rhizophagus irregularis* [105]. A mixed biofilm was developed constituting the *Bradyrhizobium ekanii* along with phosphate solubilizing fungi that could solubilise the rock phosphate. AMF also establish extensive network creating a dedicated niche for bacteria and its hyphae are the C-rich source to MHBs [21,72]. PSB can grow alongside AMF hyphae in and out of root in sterile conditions as well as with an indigenous microbial community [110,111]. AMF release *myc* factors similar to nod factors of Rhizobium that activate nodulation factors inducible gene i.e., MtEnod 11 [61]. This gene enhances lateral root formation and mycorrhization leading to increased nodulation and symbiotic nitrogen fixation in mycorrhizal legumes [112]. It also lowers down the root zone pH by uptake of ammonium ions and release hydrogen ions into the soil solution which increase the solubility of P and also increases the nitrogen flow to the plant. PSB mobilise orthophosphate and also decomposes organic matter in turn to improve N and P availability for AMF and plants [113]. Co-inoculation of AMF-MHB by different formulations is efficient for P and N uptake and needs to be advocated across crop and ecologies.

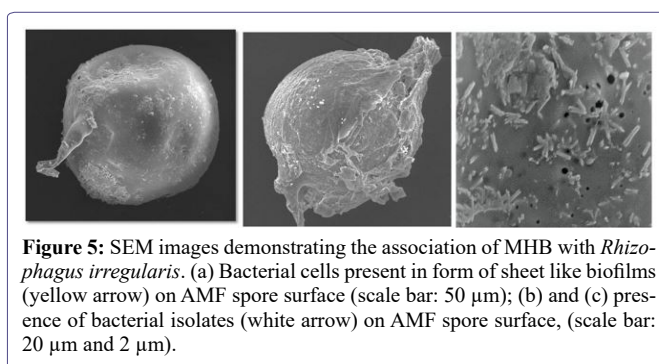


Figure 5: SEM images demonstrating the association of MHB with *Rhizophagus irregularis*.

Improvement in Product Quality and Yield by AMF and MHB: The quality of plant products and their derived foods and ingredients represent the main area of focus in sustainable agriculture, which is also in the best interests of farmers, consumers, and producers. Recently, the concept of food quality, traditionally based on nutritional and sensory properties, has acquired an additional meaning, referring to the health-promoting properties of plant foods, thereby representing an important societal issue, highly demanded by consumers. The potential of AMF in enhancing the crop yield and grain quality have been very widely studied since decades. Their inoculation causes improvement in plant nutrition, photosynthesis, and stress resistance which results in 25-30% increase in overall shoot and root biomass [114]. The potential effects of AMF alone and in synergism with beneficial microbes have been attested in some crops yield including wheat [115], barley [116], soybean [117], and chickpea [118-120]. AMF and associated bacteria enhance plant growth and health, and affect the production of polyphenols and carotenoids, and the activity of antioxidant enzymes. The diversity and content of phytochemicals in plant products are affected by different variables, such as plant genotype, agronomic factors, and Arbuscular Mycorrhizal Fungi (AMF), which establish mycorrhizal symbioses with most crops, including cereals, legumes, vegetables, fruit trees, sunflower, cotton, and sugarcane. The production of health-promoting phytochemicals was shown to be differentially modulated by different AMF isolates and bacterial strains, in several food plants, i.e., tomato, lettuce, strawberry, artichoke, maize, grapevine, sunflower. Here, we provide an overview of recent studies concerning the multiple roles played by AMF and associated bacteria in the modulation of the biosynthesis of plant secondary metabolites with health-promoting activity, and discuss the development of designed multifunctional consortia to be used in sustainable agriculture [121]. However, the beneficial effect of AMF whether alone or in synergism with MHB is always regulated by the functional group of crops, across agroecologies.

Future Perspectives

The multiple beneficial activities of AMF and their associated bacteria with complex networking in the mycorrhizosphere are functionally important for plant growth, nutrition and overall health. Very little is known about their phylogenetic interactions and intraspecific diversity of AMF and MHB. Recent studies confirmed the occurrence of diverse beneficial taxa in a commercial AMF inoculum in which 14 isolates showed the best combination of PGP traits, while 6 of them were able to solubilise P i.e., *Bacillus spp.*, *Enterobacter* and *Streptomyces* [21]. This highlights the need for more such studies using different AMF species and associated bacteria, both singly and in various combinations to identify the best performing inoculants. The areas requiring focussed attention include:

- In-depth studies on elucidating the mechanisms underlying the resilience to diverse environmental conditions such as drought, salt and metal stress, pesticides [122] and etc.
- Transcriptomic or genomic studies to reveal the expression level of P transporter genes and ammonium transporter genes in fungal hyphae. Molecular level studies are needed to understand the transporter mechanisms using tools such as Real Time PCR (RT-PCR), Phospholipid derived Fatty Acid (PLFA) / Neutral derived Fatty Acid (NLFA) ratio.
- Commercial production of newly designed multifunctional microbial consortia for use as a bioenhancer for a sustainable production system
- Rapid and automated methods for identification and screening criteria for quick and efficient selection of performing bacteria and fungi.
- Deciphering the signaling mechanism(s) involved in the interaction of AMF and the metabolites that benefit the microorganisms. Although previous research has suggested the significance of physical interaction of AMF leading to competition for nutrients [123,124], and AMF hyphal exudation directly or indirectly manipulating the communities.
- Targeted research to identify the combinations and PGP characters that are critically affecting fungal secretion and growth along with the synergistic interaction between AMF and PSB. It is not clear whether PSB is able to attach to extraradical AMF hyphal or not. Nitrogen Limitation Adaptation (NLA) genes and their function at molecular level in nitrogen deficiency conditions and the mineralization of organic N and their uptake mechanism need to be elucidated, which underpin their role as the future hope of organic farming.
- Efforts to characterize unculturable bacteria in the mycorrhizosphere and develop synthetic microbial-AMF as an option to enhance the AMF-PSB combinations efficacy.

It is difficult to distinguish the transfer of the N, as it is biotrophic and mediated through root exudates and nutrient cycling. This can be traced by monoxenic cultures or tissue culture-based experiments. By using isotopically labelled compounds, uptake of simple amino acids has been tested. There has been no specific information about the identity of any primary organic N decomposers associated with AMF. Also, an interesting question that needs to be explained in the future is - can AMF utilize N from exogenous chitin, without the contribution of any helper bacteria and if there is any significance of N uptake depending upon rate of N release. In addition to this, future experimentation should focus on complex N/C-rich compounds such as plant biomass or litter for deeper understanding of mechanism(s) underlying the utilisation of organic sources by AMF and the associated plant.

Conclusion

A number of macromolecules that support life on this earth contain Phosphorous (P) and Nitrogen (N) as integral components e.g., in polysaccharides, proteins, nucleic acids and many secondary metabolites. It is very important to think about the roles played by the omnipresent, yet still broadly under-appreciated Arbuscular Mycorrhizal Fungi (AMF) and associated helper bacteria which need to be

highlighted such that the tri-partite association between plant and microbes can be utilized for accelerating agricultural sustainability and promoting human welfare. To improve environmentally sustainable agricultural practices, basic findings about the efficiency of organic P and N recycling in soils using microbes can be translated in the form of applied research by improving our understanding the mechanism underlying the interactions of AMF with its microbiome. In order to ensure enough food on this planet for every human being, there is an urgent need to improve the efficient and sustainable production of agriculture, without any decrease in productivity, which is a challenge itself. To ensure sustained food availability on this planet for every human being now and in the future, it is vitally important to take up this challenge and come up with novel options, including broadening the scope of use of AMF and its multifunctional attributes which provide immense benefits to agriculture.

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