

Synergistic roles of arbuscular mycorrhizal fungi and plant growth-promoting bacteria in sustainable agriculture and abiotic and biotic stress mitigation

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Abstract. Arbuscular mycorrhizal (AM) fungi form mutualistic associations with plant roots and play a critical role in regulating nutrient cycling, soil structure, and plant physiological performance in agricultural ecosystems. This review summarizes the functional roles of AM fungi in improving phosphorus uptake, enhancing soil aggregation, promoting bioremediation processes, and strengthening plant defense responses. In addition, the contributions of plant growth-promoting bacteria (PGPB) are discussed, particularly their ability to enhance nutrient solubilization, produce phytohormones, fix atmospheric nitrogen, and induce systemic tolerance against environmental stresses. Recent studies indicate that the combined application of AM fungi and PGPB results in improved nutrient availability, higher crop productivity, enhanced stress tolerance, and better soil biological activity compared to their individual use. Furthermore, this microbial consortium shows strong potential in mitigating abiotic stresses such as drought, salinity, and heavy metal contamination, as well as suppressing soil-borne pathogens. Overall, the integration of AM fungi and PGPB offers a biologically driven approach for improving soil fertility and crop performance, highlighting their importance in sustainable and climate-resilient agricultural systems.

Keywords: environment, fertilizer, pathogen, pollution, population.

1. Introduction

The continuous rise in the global population is intensifying challenges related to health and food security (Salcedo Gastelum et al., 2020). The global population is expected to reach around 9 billion within the next one or two decades, placing increasing pressure on agricultural systems. A substantial segment of this population already suffers from food scarcity and malnutrition. Addressing food insecurity requires tackling interconnected issues such as fair food distribution, minimizing food waste, and mitigating climate change impacts (Prosekov & Ivanova, 2018). A major concern is the urgent need for more sustainable agricultural practices, particularly through the long-term and responsible management of soil health. This includes

reducing pollution caused by excessive agrochemical use and minimizing their adverse effects on human health and non-target organisms (Khatoon et al., 2020). Modern agricultural practices, which heavily rely on synthetic chemical inputs, are increasingly criticized for causing ecological degradation, environmental toxicity, pollution, and declining chemical efficiency. Moreover, these practices contribute to habitat degradation that disrupts natural biological control of invasive species, highlighting their limitations and raising serious environmental and societal concerns (Boedeker et al., 2020). Promoting sustainable agriculture, therefore, depends on reducing harmful agrochemical usage while simultaneously enhancing crop productivity.

Among the promising alternatives is the application of beneficial soil microbes, which improve soil fertility, suppress

plant diseases, and mitigate microclimatic stresses, thereby serving as environment-friendly substitutes for conventional agrochemicals. Their potential to enhance crop productivity and stress resilience provides valuable opportunities for advancing sustainable agriculture (Almuslimawi et al., 2024). Soil microbes play a vital role in maintaining soil health by recycling nutrients and facilitating their availability for plant uptake. Their involvement in biogeochemical cycles makes microbial inoculants an environmentally sustainable option (Mercado-Blanco et al., 2018). However, many agricultural soils worldwide are unsuitable for optimal plant growth due to multiple biotic and abiotic stress factors. Biotic stresses include pathogens such as fungi, bacteria, viruses, and insects, while abiotic stresses include drought, salinity, flooding, temperature extremes, heavy metal contamination, and chemical pollutants (Gamalero & Glick, 2020).

Interestingly, the soil ecosystem also supports beneficial microorganisms, particularly within the rhizosphere, the narrow zone surrounding plant roots. This region is enriched with root exudates, including metabolites, amino acids, and vitamins, which serve as nutrient sources for microbial growth (Vives-Peris et al., 2020). These rhizospheric microbes establish complex interactions with plants that are critical for improving plant growth, health, and tolerance to environmental stresses (Trivedi et al., 2020).

Among beneficial soil microorganisms, AM fungi play a prominent role in enhancing plant development and maintaining soil ecosystem functions (Phour et al., 2020). Their application supports environment-friendly agriculture by potentially reducing or replacing agrochemical inputs (Molina-Romero et al., 2021). Mycorrhiza refers to the symbiotic association between fungi and the roots of higher plants, extending into the rhizosphere and providing mutual benefits. These associations can range from mutualism to commensalism and parasitism, with AM fungi being particularly recognized for improving plant vegetative growth and nutrient acquisition (Paszkowski & Gutjahr, 2013). When AM fungi colonize plant roots, they modify various structural and physiological properties of the host plant. In addition, plant growth-promoting bacteria (PGPB) represent crucial components of the soil microbiome that contribute significantly to plant growth and development (Kumar et al., 2020; Wu et al., 2020). The synergistic interaction between PGPB and mycorrhizal fungi plays a pivotal role in establishing a beneficial plant microbiome and contributes to sustainable agriculture by enhancing plant resistance to both abiotic and biotic stresses (Massa et al., 2020). This review aims to highlight the synergistic interactions between AM fungi and PGPB and their roles in enhancing sustainable agriculture and crop stress resilience. While existing studies often examine AM fungi and PGPB as separate biological inputs, this review addresses a critical

gap by emphasizing their functional interdependence and coordinated activities within the rhizosphere. By integrating current findings, this study provides a comprehensive perspective on microbial consortia-based strategies for improving nutrient acquisition, plant growth, and stress tolerance, thereby contributing to the development of sustainable agricultural systems.

2. Overview of Arbuscular Mycorrhiza (AM)

Based on the morphological and anatomical features of mycorrhiza, as well as the species of mycorrhizal fungi and host plants, mycorrhiza is generally classified into seven groups (Singh et al., 2019) (Fig 1).

The term *mycorrhiza* originates from the Greek words *mykes* (fungus) and *rhiza* (root), reflecting the close association between fungal species and plant roots. These soil microbes are widely distributed and can colonize plant roots either internally, forming endomycorrhiza, or externally, as ectomycorrhiza. Typically, ectomycorrhiza associate with trees and shrubs, whereas endomycorrhizal types may interact with orchids, ericoid plants, or AM. Many terrestrial plants rely on these relationships to improve nutrient and water acquisition while gaining enhanced resistance to various plant pathogens (Yusuf et al., 2025). Mycorrhizal symbioses are vital in both natural and cultivated systems because they increase nutrient access, strengthen plant health, and bolster resilience to environmental stress (Turnau & Haselwandter, 2002). While AM fungi can establish associations with a broad diversity of plant species, orchid mycorrhiza are exclusive to the Orchidaceae, and ericoid mycorrhiza occur only in the Ericales order (Genre et al., 2020). AM fungi propagate through structures such as spores, and hyphae, ensuring their persistence and spread in the rhizosphere. Their symbiosis involves the development of arbuscules, specialized structures that enable nutrient exchange between the two partners (the fungus and the plant). This mechanism is remarkably consistent among different host species and AM fungi (Oldroyd, 2013). Ectomycorrhizal hyphae, in contrast, can penetrate between root epidermal cells to form a Hartig net, while some germinate and produce hyphae that envelop the root surface, creating an external fungal mantle. On the surface are extramatrical hyphae (or extraradical mycelium), which explore the soil, thereby improving water and nutrient absorption (Genre et al., 2020).

Before symbiosis becomes fully established between plant and AM, a pre-symbiotic phase takes place. Plant roots release chemical signals known as root exudates into the soil, with strigolactones playing a particularly important role in attracting AM fungi (Mayzlish-Gati et al., 2012). One of the earliest well-documented examples of such interactions

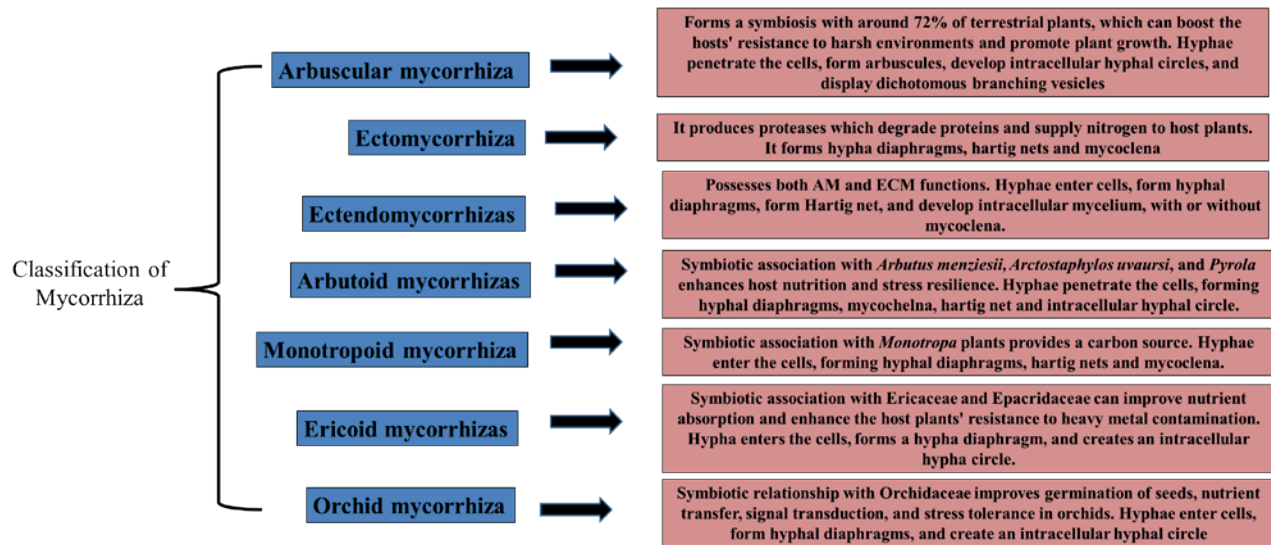


Figure 1. Classification of mycorrhiza (Created by the author)

involves *Gigaspora margarita* and *Lotus japonicus*, where strigolactones stimulate AM spore germination and growth (Besserer et al., 2006). Alterations in AM fungal metabolism during this stage such as changes in respiration, mitochondrial restructuring, and lipid degradation—drive the formation of a new primary mycelium (Tamasloukht et al., 2003). Without plant-derived cues, fungal growth halts, leading to vacuolation of apical hyphae, septation of hyphal segments, and retraction of cytoplasm and nuclei. Eventually, AM fungi release Myc factors—lipochitooligosaccharides that trigger the expression of symbiosis-related genes in plant roots (Maillet et al., 2011).

Several evidences suggest that mycorrhizal associations with plants date back nearly 400 million years, coinciding with the colonization of land by early terrestrial vegetation. In exchange for photosynthetically based carbon from their host, these fungi enhance plant growth primarily by improving nutrient acquisition (Bahadur et al., 2019; Begum et al., 2022). For example, in *Rhizophagus clarus*, aquaporin 3 (AQP3) facilitates the long-distance transfer of polyphosphate through fungal hyphae to the plant, supporting nutrient exchange between symbiotic partners (Kikuchi et al., 2016). Among the various types of mycorrhiza, the relationship between AM and their host plants has been more extensively investigated than other fungal–plant interactions (Bonfante & Anca, 2009).

Certain plant root exudates promote spore germination in mycorrhizal fungi, although this process typically depends on the host plant. Successful colonization happens when germinated hyphae make physical contact with the root. Volatile organic compounds (VOCs) and strigolactones secreted by roots are known to trigger hyphal growth, while carbon dioxide acts as a volatile signaling cue that enhances

AM fungal metabolism and growth (Gadkar et al., 2001). Entry into the root is facilitated by a prepenetration apparatus (PPA) (forms before fungal entry during arbuscular AM symbiosis), formed when root epidermal cells undergo structural rearrangements in response to fungal presence (Genre et al., 2008). From there, the fungus produces a hyphopodium, penetrates the epidermal layer, and develops intra-radical mycelium that spreads intercellularly within the cortical tissues (Genre et al., 2008).

In AM inside the root cortex cells, the fungus produces arbuscules—highly branched structures specialized for nutrient and signal exchange (Genre et al., 2008). Through these structures, plants allocate up to 20% of carbon mainly as carbohydrates and fatty acids in exchange for macro- and micronutrients absorbed by the fungal extraradical mycelium (Kakouridis et al., 2022). Arbuscules remain functional for around five days of their average 8.5 day lifespan before breaking down, restoring the plant cell to its original condition (Kobae & Hata, 2010). Intra-radical hyphae may also form vesicles or coiled structures, which serve as lipid storage sites when photosynthetic carbon is limited, ensuring fungal survival (Bach et al., 2018). The extraradical hyphae eventually produce new spores.

AM fungi can colonize either the roots of one host plant or multiple other host plants simultaneously. These interactions create common mycorrhizal networks that facilitate nutrient, water, and stress signal transfer across different plants and species. Such connectivity influences competition, fitness, behavior, and survival for all associated partners (Bücking et al., 2016). The genetic basis of mycorrhizal symbiosis includes genes linked to sugar and fatty acid metabolism (Fig. 2). Under low-phosphorus (P) conditions, expression of *carotenoid cleavage dioxygenases* (CCD7 and CCD8) is

upregulated, resulting in higher strigolactone production and secretion via the PDR transporter (PDR transporter refers to a specific ATP-binding cassette responsible for exporting strigolactones from plant root cells into the rhizosphere) (Kretschmar et al., 2012). Detection of these strigolactones by AM fungi enhances fungal metabolism, encouraging mycelial proliferation near potential host roots (Bessener et al., 2008). In rice and maize, the N-acetylglucosamine transporter (NOPE1) is essential for AM colonization, as mutants lacking this transporter fail to be infected, suggesting additional signaling molecules are involved in the pre-contact phase beyond strigolactones (Nadal et al., 2017).

Recent research shows that in rice, Arbuscule Development Kinase 1 (OsADK1) is critical for arbuscule formation (Guo et al., 2022). Furthermore, mutations in DIPI, NSP1, NSP2, MIG1, and other transcription factors impair intracellular fungal development, underlining their importance in AM symbiosis (Maillet et al., 2011; Yu et al., 2014; Heck et al., 2016). Fatty acid recruitment is another key step for AM colonization, as *Rhizophagus irregularis* cannot synthesize its own. Genes like RAM2 (*Required for Arbuscular Mycorrhization 2*) and ATP-binding cassette transporters play a central role in transferring fatty acids from plant to fungus (Jiang et al., 2017).

3. Application of AM in sustainable agriculture

A significant portion of the world's cultivable soils is deficient in essential nutrients, or the nutrients present are not readily available to plants. Modern agriculture methods, especially the overuse of chemical fertilizers, often worsen the situation leading to problems such as nutrient runoff, eutrophication, water contamination, ecological imbalances, and increased greenhouse gas emissions (Parihar et al., 2019). In fact, nearly 50% of nitrogen fertilizers applied in agriculture are not absorbed by crops, resulting in both resource wastage and environmental harm (Garnett et al., 2009). AM associations with plants offer a sustainable alternative, as these symbiotic fungi can enhance nutrient uptake and may reduce the dependence on chemical fertilizers. These fungi promote sustainable agriculture by enhancing nutrient acquisition, improving soil aggregation, supporting soil bioremediation, and strengthening plant defense (Fig 3).

3.1. Enhancing Nutrient acquisition

Mycorrhizal associations are pivotal for plant growth and development, primarily by enhancing the efficiency of nutrient acquisition (Shi et al., 2023). One of the most

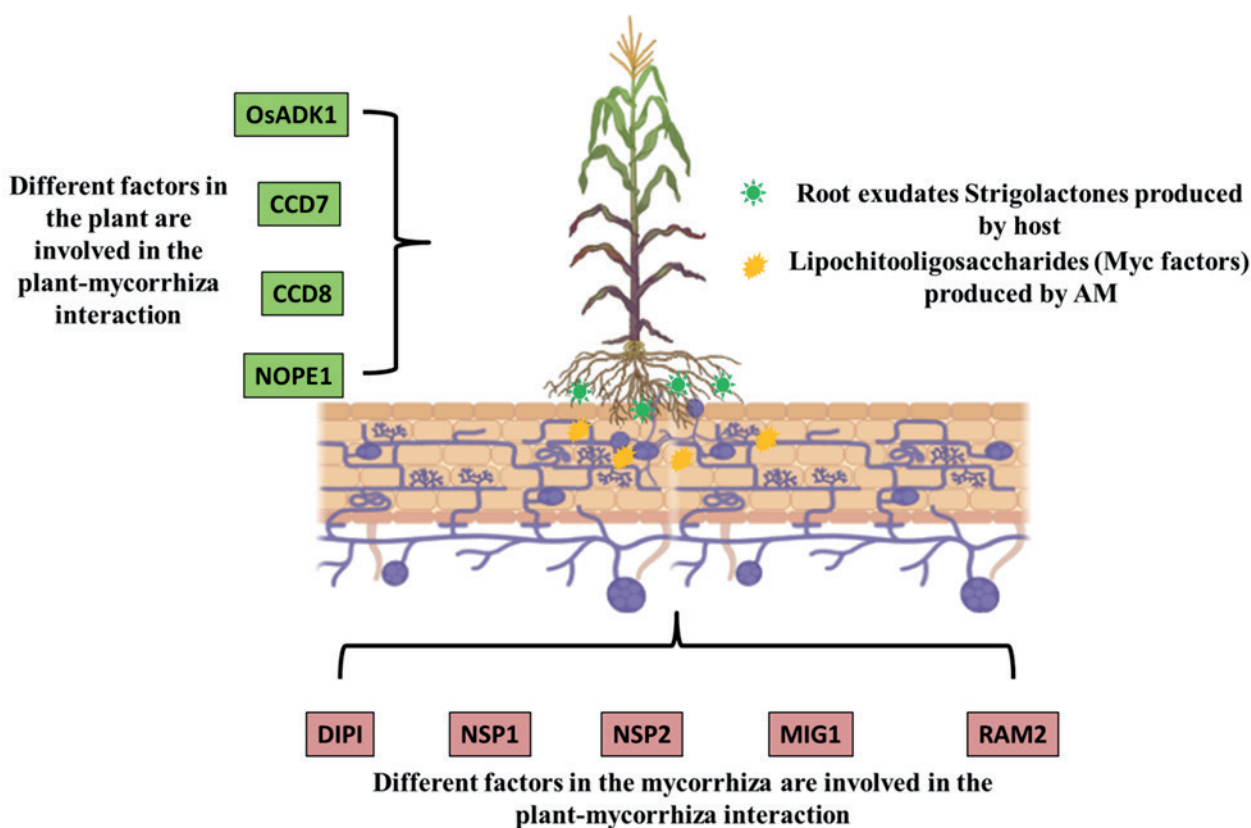


Figure 2. Different factors (gene or protein) involved in the plant-mycorrhiza interaction (Created by the author)

recognized contributions of AM is the improvement of phosphorus (P) uptake in host plants (Wang et al., 2024). However, this symbiotic relationship also plays a significant role in the absorption of other key nutrients such as nitrogen (N), sulfur (S), and zinc (Zn) (Hodge & Storer, 2014). The fungi obtain carbon from the host in returns for these nutrients. This mutualistic relationship can function as a carbon sink, storing carbon produced via photosynthesis (Hodge & Storer, 2014).

Phosphorus (P) is an essential nutrient involved in many physiological and developmental processes in plants. While many soils contain orthophosphate, it often exists in forms (HPO_4^{2-} , H_2PO_4^-) that are chemically available but become poorly bioavailable due to fixation and immobilization in soil matrices (Richardson et al., 2009). AM fungi improve P acquisition by storing it in polyphosphate granules within their hyphal vacuoles, later transferring it into intraradical structures and releasing it into plant cells (Bago et al., 2003). For example, Tawaraya et al. (2006) found that AM improved absorption in *Allium cepa* by increasing the solubility of inorganic phosphate. Similarly, Jakobsen et al. (2005) demonstrated that AM inoculation compensated for the absence of root hairs in barley grown under low P conditions, significantly improving P absorption. Field trials also highlight the benefits cotton inoculated with *R. irregularis* produced higher yields and better-quality fibers due to improved P status (Gao et al., 2020), while sorghum grown in P-deficient soils with AM showed enhanced grain nutrition, including higher P, Fe, and Zn content (Watts-Williams et al., 2022). *Glomus intraradices* increased the

Zn and P levels in maize shoots at 45 and 75 days after inoculation, respectively (Subramanian et al., 2009). During grain filling, inoculated plants showed significantly higher P contents in both roots and shoots, indicating that AM colonization enhances the translocation of P during this stage of the host's development (Azaizeh et al., 1995). *G. intraradices* improved rice's P levels and boosted grain yield and straw biomass by mitigating the negative impact of heavy metals under arsenic conditions (Li et al., 2009). This is attributed to the 'dilution effect,' which reduces arsenic levels in grains as a result of the higher growth rates in AM-inoculated plants. Radiotracer experiments have quantified the amount of P that a plant receives through the AM and directly via the root transport system. These studies have also shown that the fungus can transfer P to the plant even when no visible growth benefit is observed (Pearson & Jakobsen, 1993; Smith et al., 2003, 2004).

In addition to P, AM fungi also enhance nitrogen uptake and utilization. Their external hyphae can absorb nitrogen in multiple forms, including amino acids such as arginine, ammonium (NH_4^+), and nitrate (NO_3^-) (Govindarajulu et al., 2005). Mycorrhizal symbiosis enhances nitrogen acquisition by promoting the mineralization of organic nitrogen, facilitating microbially mediated nitrification, and synergizing with associative nitrogen-fixing bacteria in non-leguminous plant systems. (Hernaández-Esquivel et al., 2020). Mycorrhiza can also influence the rhizosphere microbiome, altering carbon and nitrogen availability for other soil organisms (Hodge & Storer, 2014). For instance, mycorrhizal rice plants show elevated nitrogen and carbon

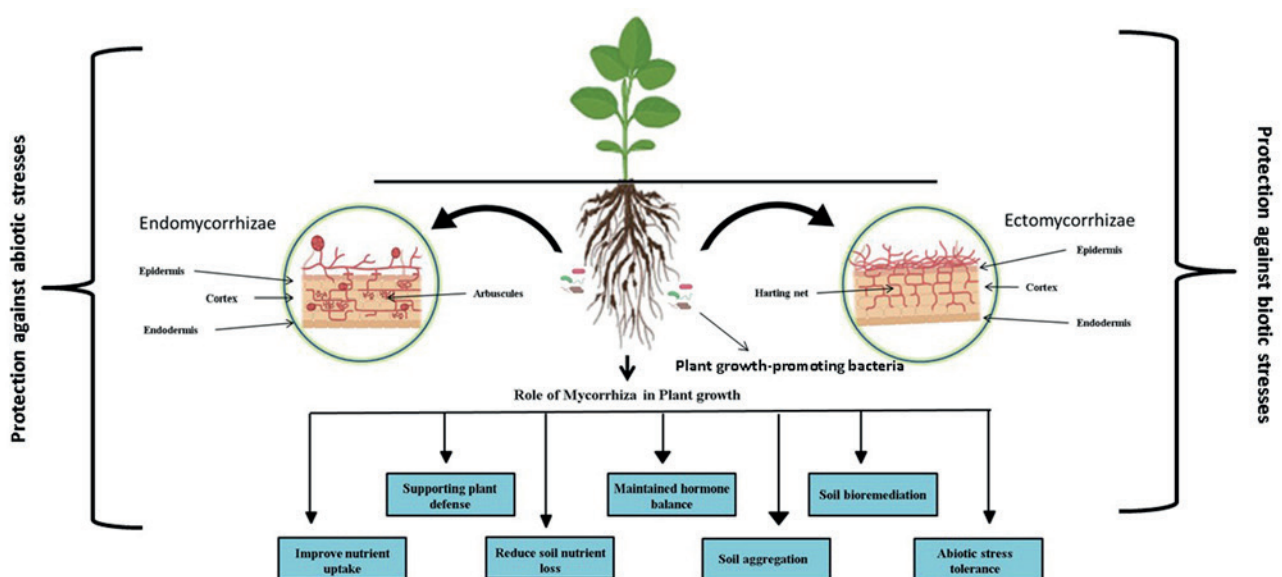


Figure 3. Beneficial role of mycorrhiza in sustainable agriculture (Created by the author)

content across all tissues, leading to improved yields and protein levels (Zhang et al., 2017). In rice, the AM fungi enhanced N uptake in the roots and increased P levels in the shoots, leading to improved growth and higher yield (Chareesri et al., 2020). Additionally, another study showed that rice inoculated with these fungi had a greater total ^{15}N uptake compared to non-inoculated control plants (Li et al., 2009). In sorghum, *G. versiforme* enhanced the uptake of N, P, and K, but it did not affect the C: N: P stoichiometry (Guo et al., 2013). In salinity conditions, *G. intraradices* enhanced the uptake of P, Fe, and Zn in barley plants, while it reduced the absorption of sodium in the host plants (Mohammad et al., 2003). In buckwheat (*Fagopyrum esculentum*), total N and P absorption improved with the presence of mixed AM fungi under both inorganic and organic P applications (Boglaienko et al., 2014).

The agricultural benefits extend beyond nutrient uptake. AM inoculation has been shown to increase yields in yams, maize, and potatoes and enhance the phytochemical content of crops (Lu et al., 2015; Hijri, 2016; Sabia et al., 2015). For example, *R. fasciculatus*, *R. irregularis*, and *Funneliformis mosseae* improve anthocyanin, carotenoid, and phenolic compound concentrations in lettuce (Baslam et al., 2011) and improve the synthesis of essential oils by enhancing the terpene and flavonoid profiles in aromatic and medicinal plants (Yuan et al., 2023).

Another important contribution of AM is reducing nutrient loss from soils. By producing the glycoprotein, they help stabilize soil aggregates, bind inorganic P, and retain it for future use by both fungi and plants (He et al., 2020; Vlcek & Pohanka, 2020). Species such as *Glomus intraradices*, *Rhizophagus irregularis*, *Funneliformis mosseae*, and *Claroideoglomus claroideum* have been found effective in minimizing nutrient leaching, thereby indirectly supporting plant growth (Van Der Heijden, 2010; Bender et al., 2015; Bowles et al., 2018).

3.2. Enhancing soil aggregation

Mycorrhiza offers multiple benefits to their host plants, both directly and indirectly, by improving soil conditions that promote plant development. One key contribution is the production of specific protein glomalin, a natural adhesive that binds soil particles into stable aggregates, enhancing soil structure. This improvement leads to better aeration, water retention, percolation, and overall moisture regulation (Syamsiyah et al., 2017). Additionally, AM fungi stabilize soils, making them more resilient to erosion by water and wind. Glomalin can persist in soils for roughly seven to forty-two years and may represent up to 27% of the total soil carbon. Both glomalin and glomalin-related soil proteins (GRSP) add significant value to AM-based bioinoculants

due to their unique physical and chemical characteristics. These proteins are highly stable, poorly soluble in water, and resistant to degradation, making them especially effective in protecting soil aggregates, particularly in erosion-prone areas (Vlcek & Pohanka, 2020). Research on GRSP from various AM species, including *Diversispora epigaea*, *Paraglomus occultum*, and *R. intraradices*, in association with *Citrus trifoliata* demonstrated that these proteins play a vital role in maintaining organic carbon in soils (He et al., 2020). By conserving both nutrients and water, GRSP reduce the stress on cropping systems and improve agricultural sustainability.

3.3. Supporting soil bioremediation

Agricultural soils are often exposed to various contaminants that can degrade soil quality, hinder plant growth, and lower crop productivity. However, rhizosphere microbiota plays a key role in alleviating such stress factors. For example, GRSP synthesized by *Glomus intraradices*, *Glomus versiforme*, and *Acaulospora laevis* can act as bioindicators of pollution in terrestrial and aquatic systems due to their capacity to interact and bind with pollutants in the soil (Wang et al., 2020). Research also indicates that GRSP, along with a wide range of mycorrhizal fungi such as members of the genera *Chaetomium*, *Gibberella*, *Pseudorhizoglyphus*, *Devriesia*, *Didymella*, *Plenodomus*, *Pyrenochaetopsis*, *Septoriella*, and *Hypholoma* can be deployed in polluted environments for bioremediation, particularly in soils contaminated with polycyclic aromatic hydrocarbons (Gałazka et al., 2020). AM fungi also possess natural enzymatic capabilities to degrade and transform pollutants (Aguilar et al., 2011). Moreover, some soil bacteria complement these fungi by working synergistically to restore contaminated soils efficiently. This is especially relevant in agricultural regions situated near industrial activities (Kim et al., 2020). Studies have further shown that AM associations enhance plant tolerance to soils contaminated with heavy metals such as copper, zinc, lead, and cadmium (Chen et al., 2007).

3.4. Strengthening plant defense

The presence of mycorrhiza in plant roots initiates a series of systemic defense responses across the plant, a phenomenon referred to as mycorrhiza-induced resistance (Cameron et al., 2013). This resistance strengthens the plant's defense against necrotrophic pathogens, chewing insects, and other pests through defense pathways regulated by jasmonic acid and ethylene (Pieterse et al., 2017). Research by Mustafa et al. (2016) reported that AM fungi such as *Funneliformis mosseae* and *Rhizophagus irregularis* offer varying levels of protection against wheat powdery mildew.

Although mycorrhizae generally do not possess direct antimicrobial activity like some other microbes (Santoyo et al., 2021), they can still mitigate the impact of soil-borne pathogens through several mechanisms. The type of pathogen, the particular mycorrhizal species, and the current soil and environmental circumstances all affect the degree of protection. Mycorrhiza can strengthen a plant's defense system by stimulating the synthesis of phenolic compounds and inducing the production of pathogenesis-related (PR) proteins, both of which contribute to disease resistance (Song et al., 2015). Indirectly, they may suppress pathogens for nutrients and space, while improving the plant's overall vigor. Structural changes in the root system such as increased lignification and altered root architecture can further reduce susceptibility to infection and enhance nutrient uptake efficiency (Berta et al., 2002). Additionally, mycorrhizal symbiosis can influence the rhizospheric microbial community, which in turn plays a role in plant defense. By modifying root exudation patterns, mycorrhiza can foster beneficial bacterial populations that suppress pathogens (Hodge & Storer, 2014). These bacteria may, in turn, support mycorrhizal growth and colonization (Garbaye, 1994).

4. Plant growth-promoting bacteria (PGPB)

Plant growth-promoting bacteria (PGPB) are primarily soil microbes that form beneficial interactions with plants, resulting in enhanced growth and development (Orozco-Mosqueda et al., 2020). The phyllosphere, which includes the plant's above-ground structure, can serve as a habitat for these beneficial microbes (Liu et al., 2020). Another key environment for such interactions is the rhizosphere, the soil zone directly influenced by root secretions and closely associated with mycorrhizal activity (Trivedi et al., 2020). In trees and shrubs with extensive root systems, this zone can extend from just a few centimeters to several meters. The rhizosphere hosts a rich variety of beneficial organisms, including a large population of PGPB (Kuzayakov & Razavi, 2019).

In the soil ecosystem, several types of biotic (pathogens) and abiotic (drought, pH, salt stress, etc.) factors affect the composition and diversity of beneficial microbes like PGPB (Santoyo et al., 2017). For instance, a study on maize at different growth stages found a shift in bacterial populations over time: *Burkholderia*, *Ralstonia*, *Dyella*, *Chitinophaga*, *Sphingobium*, *Bradyrhizobium*, and *Variovorax* dominated in later growth phases, whereas *Massilia*, and others microbes were more abundant early on (Li et al., 2014). Plants under stress can also recruit beneficial soil microbes to help mitigate adverse conditions. For example, drought-sensitive pepper plants (*Capsicum annuum* L.) cultivated in traditional

Egyptian farms attracted PGPB capable of enhancing photosynthetic efficiency and biomass, thereby improving drought tolerance (Marasco et al., 2012). PGPB are also found inside plant tissues (endosphere) and promote growth through mechanisms similar to those in the rhizosphere. However, genome analyses reveal that endophytic PGPB often carry unique genetic traits compared to rhizosphere-associated bacteria (Ali et al., 2014).

5. Importance of PGPB in promoting plant growth

Several studies have examined the direct and indirect mechanisms in plant growth employed by PGPB in the presence and absence of various abiotic and biotic stresses (Morales-Cedeño et al., 2021; Khatoon et al., 2020; Phour et al., 2020).

5.1. Direct mechanisms

One of the primary ways plant growth-promoting bacteria (PGPB) enhance plant development is by improving nutrient acquisition (Glick, 2012). For instance, species such as *Pseudomonas*, *Bacillus* and others facilitate the mineralization and solubilization of phosphates, making them more accessible to plants. Nitrogen-fixing PGPB, including *rhizobia*, can capture atmospheric nitrogen, convert it into plant-usable forms like ammonia, and supply it to the host plant—thereby not only promoting growth but also enriching the nutritional quality of crops (Peralta et al., 2004). Another significant contribution of PGPB is their ability to synthesize essential phytohormones—such as indole-3-acetic acid (IAA), cytokinins, gibberellins, and abscisic acid—which regulate plant growth and development (Munné-Bosch & Müller, 2013). Some PGPB species can produce multiple hormones, with their effects depending on the plant's endogenous hormone levels. Moreover, many PGPB harbor the enzyme ACC deaminase, which lowers plant ethylene concentrations—a stress-related hormone—while simultaneously aiding in hormone production (Glick, 2004). Whether under normal conditions or in response to biotic and abiotic stress, the interplay between plant hormones and those produced by PGPB can influence various stages of growth (Santoyo et al., 2017; Kumar et al., 2020; Wu et al., 2020). Additionally, siderophore production by PGPB allows them to sequester iron from the rhizosphere, improving plant iron availability.

5.2. Indirect mechanisms

Plant growth-promoting bacteria (PGPB) can enhance crop productivity indirectly by inhibiting pathogen activity or by boosting plant immune responses. Such actions help reduce reliance on toxic pesticides, which has led to increasing interest and large scale use of PGPB in agriculture (Khatoon et al., 2020). Many PGPB strains secrete lytic enzymes capable of degrading the structural components of pathogen cell walls. Since pathogen cell walls are vital for survival and virulence, targeting them is an effective disease control approach (Bowman & Free, 2006). These enzymes include glucanases, chitinases, cellulases, proteases, and lipases, which can break down fungal cell walls composed mainly of β -D-glucans, cellulose, proteins, and chitin (Inglis & Kawchuk, 2002). Pathogens of this kind cause significant crop damage, and the integration of beneficial PGPB into agricultural systems is a sustainable measure to curb such diseases (Morales-Cedeño et al., 2021). Furthermore, degradative enzymes produced by PGPB can break down the eggshell of the nematode (parasitic to plants), which is a mixture of chitin and protein. Given that nematodes contribute to over 12.3% of annual crop losses worldwide, particularly in developing nations, this property offers potential for developing novel biopesticides (Gamalero & Glick, 2020).

Indirect biocontrol also involves the production of antimicrobial compounds such as 2,4-diacetylphloroglucinol, phenazines, pyoluteorin, and pyrrolnitrin (Glick, 2012). Additionally, siderophores low molecular weight, iron-chelating compounds can restrict iron availability under deficient conditions, suppressing the growth of harmful microbes. Another key protective mechanism is the colonization of plant tissues vulnerable to phytopathogens (Dowling & O'Gara, 1994). Certain molecules, including chitin, pyoverdine, and β -glucans, can activate induced systemic resistance (ISR) in plants, a defense response observed in species such as *Arabidopsis*, tomato, bell pepper, muskmelon, watermelon, sugar beet, and cucumber (Choudhary & Johri, 2009).

Biotic stress often elevates ethylene production in plants, which can worsen disease outcomes by promoting senescence, chlorosis, and premature leaf or fruit drop (Etesami & Glick, 2020). Some PGPB counter this by producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that reduces ethylene synthesis. Research demonstrates that ACC deaminase-producing PGPB protect plants against pathogens and alleviate stress caused by drought, flooding, salinity, and heavy metal contamination (Paço et al., 2020).

6. AM and PGPB interaction

Research indicates that certain microbes in the rhizosphere, such as PGPB, can influence the symbiotic relationship between mycorrhizal fungi and host plants (Mitra et al., 2019). Beyond soil characteristics and nutrient levels, interactions between AM fungi including *Funneliformis* sp., *Rhizophagus* sp., *Gigaspora* sp., *Clarodeoglossum* sp., *Dentiscutata* sp., and *Paraglossum* sp. and PGPB such as *Bacillus* sp., *Pseudomonas* sp., and others play a pivotal role in shaping plant-associated microbial communities (Berendsen et al., 2012; Cameron et al., 2013). Some bacteria, often referred to as mycorrhiza helper bacteria, enhance fungal colonization by stimulating hyphal growth and spore germination, thereby indirectly supporting plant health (Panneerselvam et al., 2013; Ganeshamurthy et al., 2017). PGPB may also release phytohormones and growth-promoting metabolites that increase root surface area, making plants more receptive to AM fungal penetration and colonization. In turn, AM fungi can facilitate the uptake of nutrients that PGPB have solubilized, creating a synergistic nutrient exchange pathway. This cooperative relationship has been linked to improved nutrient efficiency, disease suppression, stronger plant immunity, and the promotion of sustainable agricultural systems (Table 1).

The spatial arrangement of these microbes varies, bacterial cells may occur freely in the mycorrhizosphere, form biofilms on fungal structures, or reside within hyphae (Frey-Klett et al., 2011). Historical evidence of such endosymbiotic relationships dates back to Mosse's observation in 1970, followed by reports of bacterial cells inside spores of *Gigaspora margarita*, *G. heterogama*, and *G. mosseae* (MacDonald et al., 1982). Initial studies on AM and PGPB interactions revealed that plant responses to dual inoculation were variable in field trials (Meyer & Linderman, 1986; Germida & Walley, 1996). While early research often focused on root growth, later work examined broader outcomes such as plant biomass and yield (Gamalero et al., 2009; Fadji & Babalola, 2020; Moreira et al., 2020). It has been demonstrated that when *Gigaspora rosea* was co-inoculated with *Pseudomonas* sp., it enhanced cucumber growth. (Gamalero et al., 2008; Duan et al., 2013). Tomato plants co-inoculated with *G. mosseae* BEG12 and *P. fluorescens* 92rk exhibited greater phosphate uptake, root biomass, and improved root architecture compared to single-inoculated plants (Gamalero et al., 2004).

The mechanisms behind bacterial facilitation of AM colonization remain under investigation, though phytohormone production and root cell wall-modifying compounds are suspected factors. Ethylene regulation appears important—high ethylene concentrations can suppress AM colonization in low-phosphorus conditions

(Zsögön et al., 2008), whereas lower ethylene levels promote symbiosis in phosphorus-rich soils (Torres de los Santos et al., 2016). PGPB that can produce ACC deaminase has been shown to regulate plant ethylene levels. Field studies on multi-microbe applications remain limited, but some promising results exist. For example, wheat and faba bean plants grown in open fields and treated with a microbial mix including two *Rhizobia* strains (*Ensifer meliloti* RhOF4 and RhOF155), PGPB strains (*Acinetobacter* sp. BS17 and *Rahnella aquatilis* PGP27), and an AM fungi (*Glomus* sp., *Sclerocystis* sp., and *Acaulospora* sp.) showed improved shoot and root biomass and higher leaf counts (Raklami et al., 2019). Dual inoculation of PGPB and AM fungi in modern agriculture aims to increase both biomass and the nutritional profile of edible plant parts (Bona et al., 2018). Plants treated with both microbial groups often produce larger, nutrient-rich fruits, with higher sugar and vitamin

contents than controls (Bona et al., 2017). Similar trends have been observed in maize, where AM fungi increased protein content especially zein, while PGPB boosted starch levels (Berta et al., 2014).

Tomato trials involving *Pseudomonas* sp. 19Fv1T or *P. fluorescens* C7 in combination with AM fungi yielded higher production, improved sugar content, and specifically from AM inoculation increased citric acid levels in fruits (Bona et al., 2017, 2018). While the interactions between *rhizobia* and AM fungi in enhancing crop yields are documented (Raklami et al., 2019), their effect on seed nutrient composition remains less explored. For instance, *Phaseolus vulgaris* plants co-inoculated with AM fungi and *Rhizobium leguminosarum* PhVyNOD3 produced seeds with distinct nutritional profiles under open-field conditions compared to uninoculated plants (Massa et al., 2020).

Table 1. Impact of AM and PGPB interaction on sustainable agriculture

AM fungi	Associated PGPB	Host plant	Impact on sustainable agriculture	References
<i>Glomus</i> sp., <i>Sclerocystis</i> sp., and <i>Acaulospora</i> sp.	<i>Ensifer meliloti</i> , <i>Acinetobacter</i> sp. BS17 and <i>Rahnella aquatilis</i>	Faba bean	Shoot and root dry weights, along with leaf count, increased to 130%, 200%, and 78% of control levels	Raklami et al., 2019
<i>Glomus</i> sp., <i>Sclerocystis</i> sp., and <i>Acaulospora</i> sp.	<i>Ensifer meliloti</i> , <i>Acinetobacter</i> sp. BS17 and <i>Rahnella aquatilis</i>	Wheat	Wheat's shoot and root dry weights and leaf numbers rose by 293%, 258%, and 87%.	Raklami et al., 2019
<i>Glomus</i> sp.	<i>Rhizobium leguminosarum</i> , and <i>Variovorax paradoxus</i>	Pea	Enhance cadmium accumulation and tolerance in cadmium-resistant plants	Belimov et al., 2020
<i>Glomus mosseae</i> and <i>G. etunicatum</i>	<i>Azotobacter chroococcum</i> , and <i>Azospirillum lipoferum</i>	Walnut	The microbial consortium lessened the adverse effects of drought stress on seedlings	Behrooz et al., 2019
<i>Claroideoglomus etunicatum</i>	<i>Micrococcus yunnanensis</i>	<i>Dracocephalum moldavica</i>	The growth of drought-sensitive plants can be enhanced	Ghanbarzadeh et al., 2020
<i>R. intraradices</i>	<i>Massilia</i> sp.	Maize	Enhanced salt stress resistance via combined action	Krishnamoorthy et al., 2016
<i>Rhizoglossum irregulare</i>	<i>Pseudomonas</i> sp. and <i>Pantoea</i> sp.	Maize	Enhance nutrient levels, such as N and Mg in plants, and provide effective protection from salt stress through a combination microbe	Moreira et al., 2020
<i>Glomus etunicatum</i>	<i>Methylobacterium oryzae</i>	Maize	Increased dry biomass and nutrient uptake in salt-stressed plants	Lee et al., 2015
<i>Glomus mosseae</i> and <i>G. fasciculatum</i>	<i>Alcaligenes</i> sp., <i>Lichtheimia</i> sp., and <i>Brevibacterium</i> sp.	Onion	Reduced the use of chemical fertilizers and controlled <i>Sclerotium rolfsii</i>	Nepomuceno et al., 2019
<i>Glomus fasciculatum</i>	<i>Pseudomonas monteilii</i>	<i>Coleus forskohlii</i>	Reduced wilt incidence and root rot, while also increasing plant height, tuber yield, and forskolin content	Singh et al., 2013
<i>R. irregularis</i>	<i>Pseudomonas jessenii</i> R62 and <i>Pseudomonas synxantha</i> R81	Tomato	Protection from the root-knot nematode <i>Meloidogyne incognita</i>	Sharma and Sharma, 2017
<i>Glomeromycota</i>	<i>Sphingomonas</i> sp., <i>Pseudomonas</i> sp., <i>Massilia</i> sp., and <i>Methylobacterium</i> sp.	<i>Solidago rugosa</i> Mill.	Potential enhancement of plant growth in soil polluted with aliphatic and aromatic petroleum hydrocarbons	Iffis et al., 2014
<i>Glomus</i> sp.	<i>Bacillus subtilis</i> and <i>Pseudomonas fluorescence</i>	Bean	Controlled stem rot infection, especially when soil phosphate levels are low	Mohamed et al., 2019

7. AM and PGPB interaction in the mitigation of abiotic stresses

AM and PGPB enhance plant resistance to a wide range of abiotic stressors, as reported in multiple studies (Table 2). The AM–host plant symbiosis improves physiological functions that help plants withstand stresses such as drought, extreme temperatures, salinity, pollution, osmotic stress, and oxidative damage (Zhu et al., 2010). Co-inoculation of AM fungi with PGPB further enhances soil fertility, nutrient uptake, growth, and yield, even under stress conditions (Raklami et al., 2019; Massa et al., 2020). For example, AM fungi paired with *Brevibacillus* sp. from lead-polluted soils enhanced *Trifolium pratense* L. growth (Vivas et al., 2003). Similarly, *Sphingomonas* sp., *Pseudomonas* sp., *Massilia* sp., and *Methylobacterium* sp., together with Glomeromycota AM fungi, promoted *Solidago rugosa* growth in petroleum hydrocarbon–polluted soils, where mycorrhiza-associated bacteria aided both mycorrhization and phytoremediation (Iffis et al., 2014; Guarino et al., 2020). In another example, *Oloptum miliaceum* and *Pennisetum setaceum* benefited from rhizobacteria with emulsification capabilities that degraded hydrocarbons, while AM fungi enhanced associated enzymatic activities (Liu et al., 2015). Microbial consortia can also improve heavy metal tolerance. A combination of *Glomus* sp. 1Fo, *Rhizobium leguminosarum* bv. *Viciae* RCAM1066, and *Variovorax paradoxus* 5C-2 enhanced cadmium accumulation and tolerance in pea plants, showing a tolerance pattern similar (Belimov et al., 2020). Water stress mitigation is another major benefit of AM and PGPB co-inoculation. In walnut seedlings, *G. mosseae* and *G. etunicatum* combined with *Azotobacter chroococcum* and *Azospirillum lipofrum* alleviated drought effects more effectively than single inoculations (Behrooz et al., 2019). Drought-sensitive *Dracocephalum moldavica* responded positively to *Claroideoglomus etunicatum* with *Micrococcus yunnanensis* (Ghanbarzadeh et al., 2020), and *Lavandula dentata* showed improved oxidative metabolism under water deficit when inoculated with *Bacillus* endophytes and AM fungi (Pereira et al., 2016).

Salt stress responses often mirror drought tolerance mechanisms (Forni et al., 2017). While both AM fungi and PGPB individually reduce salinity damage (Orozco-Mosqueda et al., 2020), co-inoculation frequently produces stronger effects (Santoyo et al., 2021). For example, *Massilia* sp., isolated from *Rhizoglosum intraradices*, improved maize salt tolerance through combined AM–bacteria interactions (Krishnamoorthya et al., 2016). In maize, *Rhizoglosum irregulare* with *Pseudomonas* sp. and *Pantoea* sp. enhanced nutrient status while reducing sodium ion (Na⁺) accumulation in saline soils (Moreira et al., 2020). Likewise, in the presence of salt stress, AM (*G. etunicatum*) and PGPB

(*Methylobacterium oryzae* CBMB20) improve plant growth by enhancing nutrient absorption, increasing dry biomass, and promoting AM root colonization (Lee et al., 2015).

8. AM and PGPB interactions in the mitigation of biotic stresses

Mycorrhizal fungi assist plants in coping with various biotic stresses through several key mechanisms (Table 2). These include competing with pathogens for space and resources as well as forming a protective barrier around roots (Hooker et al., 1994). Additionally, mycorrhiza can stimulate the production of antimicrobial compounds and promote the growth of antagonistic plant-associated bacteria (Edwards et al., 1998). They also enhance the synthesis of phenolic compounds and pathogenesis-related proteins, both of which act as plant defense tools (Al-Askar & Rashad, 2010; Song et al., 2015). Some studies indicate that the disease-suppressive effect of ectomycorrhizal and endomycorrhizal symbiosis may occur only under specific conditions, such as those involving nematode or fungal attacks (Wehner et al., 2010). Evidence strongly supports that both AM and PGPB can inhibit phytopathogens or improve plant defenses against diverse pathogens, including bacteria, fungi, and parasitic nematodes (Table 2). For example, when exposed to leafhopper vectors, a combined inoculation of AM (*F. mosseae* sp.) and PGPB (*Pseudomonas* sp.) improves the plant growth by changing root properties and features, decreasing infection rates and delaying symptom appearance. This treatment not only increased plant biomass but also reversed the growth inhibition caused by phytoplasma (D'Amelio et al., 2011). Similarly, *Pseudomonas jessenii* R62 and *Pseudomonas synxantha* R8, used alongside *Rhizophagus irregularis*, improved the growth of tomato plants infected with the nematode (*Meloidogyne incognita*). Plants treated with this AM and PGPB combination also displayed a 28% rise in phenolic compounds and enhanced activities of defense-related enzymes—peroxidase (1.26 fold), polyphenol oxidase (1.35 fold), and superoxide dismutase (1.09 fold)—all contributing to nematode resistance (Sharma & Sharma, 2017).

A study by Mohamed et al. (2019) showed that co-inoculation with mycorrhiza, *B. subtilis*, and *P. fluorescens* was more cost-effective in controlling *Sclerotium rolfsii* in common bean plants compared to single inoculations. In another case, *G. fasciculatum* and *G. mosseae* reduced complete use of chemical fertilizers. When paired with PGPB such as *Alcaligenes* sp., *Lichtheimia* sp., and *Brevibacterium* sp., these AM fungi effectively controlled *S. rolfsii* in onions (Nepomuceno et al., 2019). Interestingly, neither mycorrhiza nor PGPB alone significantly protected onions, but their combination reduced disease incidence by 20–40%.

The AM *Gigaspora margarita* together with the PGPB *Paenibacillus rhizospherae* has also been shown to protect Japanese apricot and other fruit seedlings (grape, fig, apple) from the white root rot pathogen (*Rosellinia necatrix*) (Freire Cruz & de Oliveira Soares, 2014). In a two-year field trial, *Coleus forskohlii*, a medicinal plant producing forskolin, was safeguarded from *Ralstonia solanacearum* and *Fusarium chlamydosporum* infections by the combined use

of *Pseudomonas monteilii* (PGPB) and *G. fasciculatum* (AM). Compared with uninoculated controls, the co-inoculated plants had lower incidences of wilt and root rot, greater plant height, higher tuber yields, and increased forskolin content. Moreover, the bacterial partner acted as a mycorrhiza-helper organism, enhancing the colonization efficiency of *G. fasciculatum* (Singh et al., 2013).

Table 2. Impact of AM and PGPB interactions on sustainable agriculture under abiotic and biotic stresses

S.No.	AM fungi	PGPB	Host	Abiotic/Biotic stress	Impact of AM and PGPB on stresses	Reference
1	AM Glomeromycota	<i>Sphingomonas</i> sp., <i>Pseudomonas</i> sp., <i>Massilia</i> sp., and <i>Methylobacterium</i> sp.	<i>Solidago rugosa</i>	Highly contaminated soil containing aliphatic and aromatic petroleum hydrocarbons	AM-PGPB coinoculation promoted plant growth, and AM-PGPB enhance mycorrhization and support phytoremediation	Iffis et al., 2014
2	<i>Glomus</i> sp. 1Fo	<i>Rhizobium leguminosarum</i> and <i>Variovorax paradoxus</i> 5C-2	<i>Pisum sativum</i> L.	Cadmium stress	Successfully improved cadmium accumulation and tolerance in plants resistant to cadmium	Belimov et al., 2020
3	<i>Glomus mosseae</i> and <i>G. etunicatum</i>	<i>Azotobacter chroococcum</i> , and <i>Azospirillum lipoferum</i>	Walnut	Drought stress	The negative effects of drought stress on walnut seedlings were reduced through co-inoculation with the microbial consortium	Behrooz et al., 2019
4	<i>Claroideoglossum etunicatum</i>	<i>Micrococcus yunnanensis</i>	<i>Dracocephalum moldavica</i>	Drought stress	Improved the growth by combined inoculations of AM and PGPB	Ghanbarzadeh et al., 2020
5	<i>R. intraradices</i>	<i>Massilia</i> sp.	Maize	Salt stress	Enhanced salt stress resistance through the synergistic effects of AM and bacteria.	Krishnamoorthya et al., 2016
6	<i>Rhizoglossum irregulare</i>	<i>Pseudomonas</i> sp. and <i>Pantoea</i> sp.	Maize	Salt stress	Enhanced nutrient levels like nitrogen and magnesium in plants, while decreasing ions such as Na ⁺ that accumulate in saline soils	Moreira et al., 2020
7	<i>Glomus etunicatum</i>	<i>Methylobacterium oryzae</i> CBMB20	Maize	Salt stress	Enhanced biomass and nutrient absorption in plants under salt stress	Lee et al., 2015
8	<i>F. mosseae</i> BEG12	<i>P. putida</i> S1Pf1Rif	<i>Chrysanthemum carinatum</i>	Candidatus Phytoplasma asteris infection	AM-PGPB led to fewer infected plants, delayed symptom development, changes in root morphology and increased plant biomass and mitigated the growth inhibition caused by the phytoplasma.	D'Amelio et al., 2011
9	<i>R. irregularis</i>	<i>Pseudomonas jessenii</i> R62 and <i>Pseudomonas synxantha</i> R8	Tomato	<i>Meloidogyne incognita</i>	Phenolics increased by 28%, along with defensive enzymes like peroxidase, polyphenol oxidase, and superoxide dismutase (resist nematodes)	Sharma and Sharma, 2017
10	<i>G. mosseae</i> and <i>G. fasciculatum</i>	<i>Alcaligenes</i> sp., <i>Lichtheimia</i> sp., and <i>Brevibacterium</i> sp.	Onion	<i>Sclerotium rolfsii</i>	Control <i>Sclerotium rolfsii</i> and protect crops and reduce the disease occurrence from 20% to 40%	Nepomuceno et al., 2019
11	<i>Gigaspora margarita</i>	<i>Paenibacillus rhizospherae</i>	Japanese apricot and other fruit seedlings	Root rot fungal pathogen <i>Rosellinia necatrix</i>	Protected fruit seedlings from pathogens	(Freire Cruz and de Oliveira Soares, 2014)
12	<i>G. fasciculatum</i>	<i>P. monteilii</i>	<i>Coleus forskohlii</i>	<i>Ralstonia solanacearum</i> and <i>Fusarium chlamydosporum</i>	Reduced wilt incidence and root rot, while increasing plant height, tuber yield, and forskolin content	Singh et al., 2013

8. Commercialization and global use of AM

Jakobsen et al. (1995) demonstrated that AM inoculation can replace up to 80% of conventional P fertilizers in agriculture. Since the 1990s, AM fungi have been applied as biostimulants to enhance crop productivity (Torres-Arias et al., 2017). Today, the global production and trade of AM-based products are expanding rapidly, with the market projected to reach around USD 620 million in the near future (Basiru et al., 2020). AgriLife (Hyderabad), Ambika Biotech (Mandsaur), and several others are the companies that produce AM inoculums, which are widely used in India to promote sustainable agriculture. Globally, companies such as Biofa (Graz), Agronutrition (Carbonne), Agritech Store SAS (Mori), Dudutech (Naivasha), and BioTabs Organic Fertilizers (Den Haag) are key suppliers, with most manufacturers concentrated in North America, Asia (especially India and China), and Europe. AM-based bio-products are mainly used in agriculture and various other sectors such as forestry, and horticulture (Chen et al., 2018). Commercial formulations often contain one or more AM species, predominantly *Rhizophagus irregularis* and *Funneliformis mosseae*, along with smaller proportions of other fungi such as *Claroideoglomus etunicatum*, *R. aggregatum*, *R. clarus*, *R. iranicus*, and *Septoglomus deserticola* (Basiru et al., 2020). These inoculums are commonly made from mycorrhizal root fragments, spores, hyphal filaments, and are provided in forms like granules, powders, liquids, or seed coatings. In some cases, ectomycorrhizal fungi and plant growth-promoting bacteria (PGPB) are also included (INRAE, 2017). Roughly 29% of products are liquid, produced *in vitro* and typically containing a single AM species, while about 60% are powders prepared *in vivo* with multiple species (Basiru et al., 2020).

Although considerable research progress has been made in understanding the roles of AM and PGPB, several key gaps in knowledge remain. The mechanisms by which AM and PGPB consortia establish stably and sustainably over long periods under various field conditions remain poorly understood. It is also unclear how different microbial combinations perform across various soil types, crop varieties, and climate zones. Furthermore, there are limited reports on the long-term ecological consequences of repeated microbial inoculations for native soil microbes and ecosystem health. The molecular signalling pathways and biochemical pathways involved in host-microbe recognition and in coordinating AM and PGPB under stress conditions need further study. Additionally, there are no standardized methods for selecting effective microbial strains and for optimizing their application timing and dosage. Addressing these issues is crucial to translating laboratory successes into

reliable, large-scale field applications and to enhancing the sustainability of microbial-based farming technologies.

10. Limitations, and practical challenges of AM products

AM fungi provide significant benefits for sustainable agriculture, and employing commercial AM inoculants helps address various limitations and operational challenges. Responses in the field vary significantly, influenced by various soil physicochemical characteristics, native microbial communities, plant species, climate, and crop management practices (Lekberg & Koide, 2005; Hart et al., 2015). High soil P levels are known to suppress mycorrhizal colonization and function, thereby reducing the efficiency of AM products under intensive fertilization. Furthermore, application of AM strains often struggle to survive and establish due to competition with local fungal populations, which can hinder successful root colonization (van der Heijden et al., 2015). AM fungi are obligate symbionts it means they cannot be grown in pure cultures outside of their host plants. This limitation makes large-scale production of AM inocula highly challenging and complex

The quality of commercial inocula is often a concern because of variations in spore density, propagule viability, formulation stability, and contamination, all of which can affect product performance. (Gianinazzi et al., 2010). The conditions of storage, shelf life, and transportation also affect inoculum viability and effectiveness in the field (Berruti et al., 2016). Additionally, scaling up use presents challenges such as high costs, inconsistent results in the field, less farmer awareness, and a lack of standardized application protocols. To overcome these issues, efforts should focus on improving strain selection, developing crop-specific formulations, establishing quality-control standards, and conducting long-term, multi-location field trials. These measures are crucial for enhancing the reliability and broader adoption of AM-based technologies in sustainable agriculture.

11. Conclusion

The synergistic relationship between AM and PGPB presents an environmentally friendly and efficient strategy to enhance crop productivity and soil health, representing a major advancement toward biologically driven, sustainable agriculture. AM contributes to sustainable agriculture by enhancing nutrient uptake, improving soil structure, facilitating bioremediation, and strengthening plant defence mechanisms. Likewise, PGPB support plant growth by facilitating nutrient solubilization, producing essential

phytohormones, and helping plants cope with environmental stress. When these two microbial partners work together, they amplify each other's benefits, resulting in better nutrient acquisition, greater tolerance to both abiotic and biotic stresses, and improved overall plant development compared to when they function individually. This integrated microbial partnership surpasses single-inoculant approaches, offering a scalable and eco-friendly framework for reducing chemical inputs while maintaining high productivity. This partnership offers a resilient and sustainable approach to agriculture. Future research should focus on successful application in field conditions, investigating various crop responses, and exploring their interactions within complex soil microbial communities to further strengthen their practical implementation in sustainable agriculture.

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