Review

Harnessing Green Helpers: Nitrogen-Fixing Bacteria and Other Beneficial Microorganisms in Plant–Microbe Interactions for Sustainable Agriculture

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Abstract: The health of soil is paramount for sustaining life, as it hosts diverse communities of microorganisms that interact with plants, influencing their growth, health, and resilience. Beneficial microorganisms, including fungi and bacteria, form symbiotic relationships with plants, providing essential nutrients, promoting growth, and enhancing stress tolerance. These microorganisms, such as mycorrhizal fungi and plant growth-promoting bacteria, play crucial roles in nutrient cycling, soil health, and plant productivity. Additionally, they help lessen reliance on chemical fertilizers, thereby mitigating the environmental risks associated with their use. Advances in agricultural practices harness the potential of these beneficial microorganisms to improve crop yields while minimizing the environmental impact. However, challenges such as competition with indigenous microbial strains and environmental factors limit the universal utilization of microbial inoculants. Despite these challenges, understanding and leveraging the interactions between plants and beneficial microorganisms hold promise for sustainable agriculture and enhanced food security.

Keywords: beneficial microorganisms; nitrogen-fixing bacteria; solubilizing microorganisms; arbuscular mycorrhiza

1. Introduction

Someone once said, "Soil is not just dirt, it's alive, and the health of soil is vital for the health of plants, animals, and people". And they were right, since soil harbors many communities of microorganisms. These microbial communities interact with plants, both externally and internally, and shape their behavior and health [1]. These interactions can range from pathogenic to mutualistic. Beneficial microorganisms are those that provide the host plant with different benefits, such as enhanced growth and stress resistance, while obtaining sources of nutrition, shelter, and ways of transmission besides air and soil. They are also used for entomological, medicinal, biotechnological, and other industrial purposes. Thus, beneficial microorganisms can represent an important tool for future sustainable agriculture as they can take part in plant nutrition, health, and product quality.

Under natural or agronomic conditions, plants are continuously exposed to ongoing disease pressures caused by pests and pathogens, leading to considerable crop losses. Furthermore, repeated cultivation practices exacerbate nutrient depletion within soil, consequently diminishing both crop yield and quality. Historically, chemical fertilizers and pesticides have been utilized as countermeasures against these challenges. However, prolonged reliance on these chemicals has led to severe health and environmental concerns,

including ecological harm and pest resistance. In an effort to mitigate chemical usage, biofertilizers and biopesticides offer a more environmentally sustainable approach to enhancing crop yields [2,3].

Beneficial microorganisms are part of the microbiome, a set of microorganisms that inhabit the interior or surroundings of a living organism and play crucial roles in the health and growth of plants across ecosystems (Figure 1). The importance of the interaction between the microbiome and the host at survival and evolutionary levels has been demonstrated in numerous scientific studies. Such importance suggests considering plant and microbiota as a whole, referred to as a holobiont [4]. Plant-associated microorganisms belong to groups such as archaea, bacteria, and fungi, forming symbiotic relationships aiding in nutrient uptake, disease resistance, and overall resilience [5].
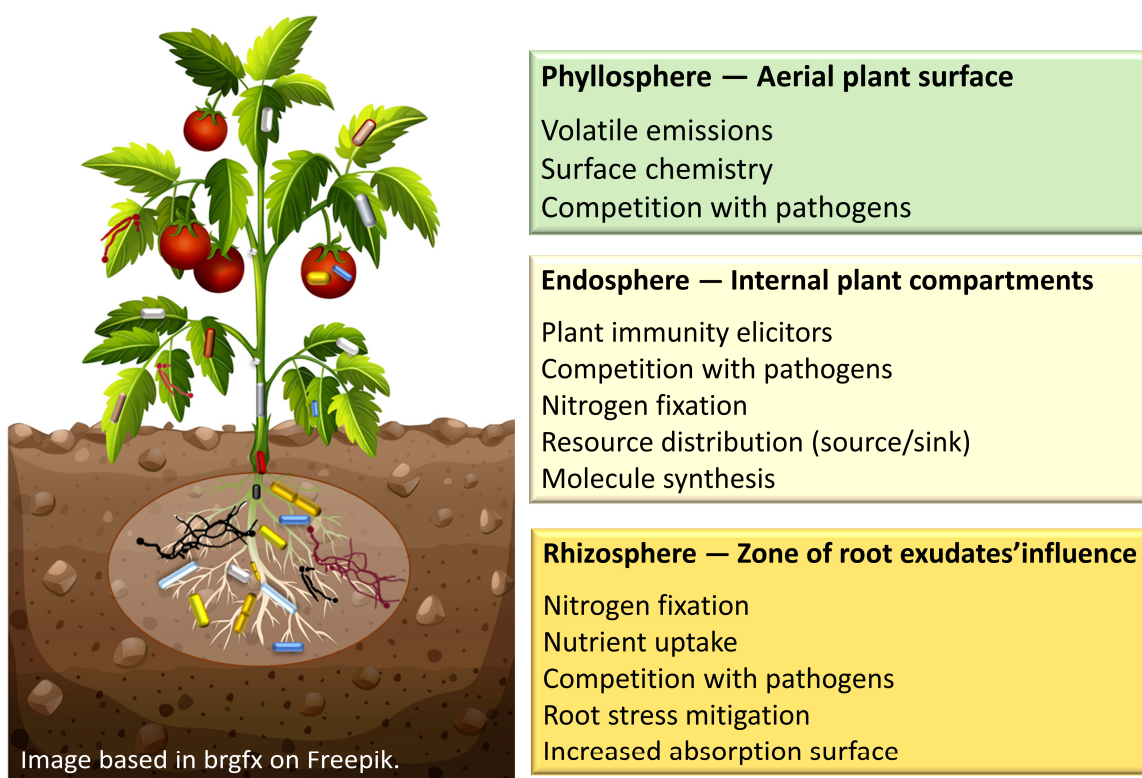

Phyllosphere — Aerial plant surface

Volatile emissions
Surface chemistry
Competition with pathogens

Endosphere — Internal plant compartments

Plant immunity elicitors
Competition with pathogens
Nitrogen fixation
Resource distribution (source/sink)
Molecule synthesis

Rhizosphere — Zone of root exudates'influence

Nitrogen fixation
Nutrient uptake
Competition with pathogens
Root stress mitigation
Increased absorption surface

Image based in brgfx on Freepik.

Figure 1. Location and role of the microbiome in different parts of the plant. Figure adapted from Johnston-Monje et al. [6] and Dhaliwal et al. [7].

The communities forming the microbial ecosystem will vary depending on the host species, as well as the host's age, health conditions, and environment. Similarly, we can differentiate as many ecosystems as there are parts of an individual plant. The most important ones are the rhizosphere, the phyllosphere, and the endosphere [8]. The rhizosphere is composed of communities of microorganisms that inhabit both the inner tissues of the root and its surroundings, contributing to soil nutrient acquisition, the conversion of molecules into more readily accessible forms for the plant, the modulation of root pH, and soil texture [5]. The phyllosphere comprises microorganisms capable of adapting to the changing conditions on the plant's aerial surface, and although they do not usually form communities as rich as those in the rhizosphere, some stable communities can contribute to the plant's development and defense [9]. Finally, the endosphere includes internal zones such as the plant's intercellular space or apoplast [10] and comprises microorganisms that reside within the tissues of plants without causing any apparent harm to the host plant [11]. These microorganisms may play an important role in synthesizing essential compounds like amino acids, enhancing leaf growth rates, or boosting photosynthetic efficiency and stomatal conductance [12,13]. They also actively participate in nitrogen fixation and enhance

plant defenses [14]. Furthermore, their influence extends to agricultural fields, impacting nutritional and sensory qualities, including flavors and odors [6].

Regarding plant health under abiotic stress, beneficial microorganisms could play an important role against drought, salinity, extreme temperatures, or low-nutrient regimes [15,16]. These functions are performed by several mechanisms, such as N_2 fixation and mineral solubilization (phosphorus, potassium, zinc), reducing reliance on chemically synthesized fertilizers while directly supplying plants with macro- and micronutrients, as well as plant growth-promoting hormones [17].

On the other hand, beneficial microorganisms have the ability to suppress diverse phytopathogens through several mechanisms. These include the production of antibiotics, lytic enzymes, and siderophores and competing with pathogens for nutrients and space [18]. Beneficial microorganisms can disrupt pathogens' quorum sensing (QS) by inhibiting the production of signal molecules through chitinases, pectinases, and lactonases [19]. Some beneficial microbes serve as natural enemies to diverse phytopathogens, exhibit antagonistic behaviors, and compete with pathogenic microorganisms, either inhibiting their growth or outright eliminating them.

Understanding and harnessing the potential of plant-beneficial microorganisms aligns directly with the European Green Deal since they can improve soil health (nutrient cycling and structure) and crop yields and reduce contamination caused by the abuse of chemical inputs. This will promote sustainable farming practices that support the Farm to Fork Strategy and several sustainable development goals (SDGs) by leading to more resilient crop production systems that can help ensure a stable food supply. As such, research into the interactions between plants and beneficial microorganisms is crucial for advancing agricultural resilience and productivity.

2. Beneficial Microorganisms

2.1. Bacteria

Bacteria proliferate in soil, where they form the most abundant and diverse communities. Plant-associated bacteria are primarily found in the rhizosphere, though some can penetrate and colonize plant roots and aerial tissues [20]. These endophytes were initially thought to be plant pathogens, but they were later found to confer several beneficial effects. Plant-associated bacteria exhibit diverse lifestyles and benefits, and classic reviews include [21]. In this review, we focus on the main plant growth-promoting bacteria (PGPB) from the perspective of plant nutrition and development.

2.1.1. Nitrogen-Fixing Bacteria

Nitrogen (N) is one of the main macronutrients needed for the correct growth and development of plants, and therefore is one of the most limiting nutritional factors. The uptake of N by the plant is entirely dependent on the amount present in the soil since plants are unable to assimilate atmospheric N_2. Atmospheric N_2 must be first reduced to ammonia (NH_3) to be assimilable by plants. Fortunately, certain prokaryotic microorganisms, known as diazotrophs, possess the ability to reduce the atmospheric N_2 to NH_3 in a process known as biological nitrogen fixation (BNF) via the enzymic complex nitrogenase. Considering their life strategies, diazotrophic bacteria can be classified as nodule-forming bacteria or as non-nodular bacteria [22].

The main examples of nodule-forming bacteria are those collectively called rhizobia, which associate with plants of the Leguminosae (=Fabaceae) family. In addition to rhizobia, actinobacteria of the *Frankia* genus can form nodules and establish symbioses with a diverse group of plants from 23 genera from eight different families belonging to the orders Fagales, Rosales, and Cucurbitales.

Non-nodular bacteria can be found as free-living in the rhizosphere, associated with roots (associative) or inside plant tissues (endophytic). The soil free-living group includes the genera *Azotobacter*, *Bacillus*, *Beijierinckia*, *Burkholderia*, *Clostridium*, *Desulfovibrio*, *Derxia*, *Enterobacter*, *Klebsiella*, *Paenibacillus*, and *Serratia* [23,24]. The free-living group also includes

cyanobacteria and phototrophic sulfur bacteria. In addition to those in the free-living group, cyanobacteria may live in symbiosis with fungi (forming lichens) or with plants (for example, *Nostoc* with bryophytes, a few gymnosperms and angiosperms, and *Anabaena* with the aquatic fern *Azolla*) [25]. Rhizospheric associative bacteria proliferate on the root surface and nourish on root exudates. The most studied genera of associative diazotrophic bacteria are *Acetobacter*, *Azoarcus*, *Azospirillum*, *Burkholderia*, and *Herbaspirillum* [23], but, without question, the genus *Azospirillum* (with an emphasis on *A. brasilense* and *A. lipoferum*) is the most important agronomically [23,26,27] and is marketed as inoculants in many countries. Endophytic bacteria invade and rapidly proliferate in inner plant parts during at least a part of their life cycle, without causing symptoms of plant disease [23]. It is considered that nitrogen-fixing endophytic bacteria have some advantages over rhizospheric associative bacteria since, being protected inside plant tissues, they have less competition and can make fixed nitrogen directly available to plants. Moreover, efficient biological nitrogen fixation requires low levels of oxygen, which are easily found inside plant tissue [28]. *Acetobacter diazotrophicus* (=*Gluconobacter diazotrophicus*) was one of the first endophytic diazotrophic bacteria to be studied with emphasis on sugarcane [29]. Moreover, *Herbaspirillum* is usually found as endophytic diazotrophic bacteria, particularly in grasses, such as sugarcane, rice and wheat, and pastures. *Herbaspirillum seropedicae* is considered to be a diazotrophic bacteria model for endophytic associations [30]. Until now, N_2-fixing endophytes have been mainly isolated from monocots, from a varied number of species such as kallar grass [31], sugarcane [32], rice [33], maize [34], wheat [33], *Sorghum halepense* [35], miscanthus [36], and elephant grass [37]. There are also some reports of endophytic diazotrophic bacteria in mosses [38] and in conifers [39,40]. However, little is known about their presence in dicots when compared with monocots. In dicots, N_2-fixing endophytes have been isolated from sweet potato [41] and coffee plants [42]. Moreover, Kandel et al. [43] isolated diatrotrophic endophytes from poplar and willow and tested them in rice, while Wozniak et al. [44] isolated diatrotrophic endophytes from *Arctium lappa* belonging to the Asteraceae family. A list of the endophytic diazotrophic bacteria isolated and the agricultural crops in which they were colonized into is provided in the work by Puri et al. [45] and Rana et al. [46].

All these bacteria hold the potential to improve plant performance by enhancing the availability of nutrients and to improve soil fertility, mainly through BNF and also through other features such as phosphate solubilization or iron sequestration by siderophores [27,47,48]. In addition, they produce plant growth regulators and are involved in the modulation of phytohormone and defense responses, the production of antioxidants, osmotic adjustment, and plant tolerance against biotic and abiotic stresses, as reviewed in detail by Thiebaut et al. [49].

2.1.2. Phosphate- and Potassium-Solubilizing Bacteria

Another essential macronutrient required for plant growth and metabolism is phosphorus (P), which is often unavailable for plant uptake [50]. Bacteria that convert insoluble organic and inorganic substances into soluble forms of phosphate that are easily absorbed by plants through various mechanisms are called phosphate-solubilizing bacteria (PSB) [51]. The involved mechanisms include the secretion of enzymes (phosphatase and phytolase), acids (both organic and inorganic), and chelation (siderophores and extracellular polysaccharides) (reviewed by Pan and Cai [52]). The most abundant PSB genera are *Bacillus*, *Burkholderia*, *Pseudomonas*, and *Pseudocystis*, and to a lesser extent, *Enterobacter*, *Salmonella*, *Flavobacterium*, *Micrococcus*, *Thiobacillus*, *Azotobacter*, *Pantoea*, *Serratia*, and *Baeyerlingia*, among others [52]. Several studies have investigated the effectiveness of PSB on P solubilization and crop performance. For example, plant-unavailable P can be dissolved in either inorganic (calcium phosphate) or organic (phytin) forms by different bacteria, such as *Pseudomonas pseudoalcaligenes* and *Bacillus thuringiensis* [53]. Moreover, Habibi et al. [54] isolated *Paenibacillus*, *Pseudomonas*, and *Enterobacter* from rice plants, which were able to dissolve tricalcium phosphate, one of the unavailable forms of P. PSB have the capacity

to modify phosphorus speciation on their own, but they can also work in concert with phosphate fertilizers to increase phosphorus use [55].

Potassium (K) is another of the essential nutrients, a deficiency of which in soil can impair plant growth, cause disruptions to plant activities, and lower the quality of fruit [56]. The rhizospheric bacteria responsible for converting insoluble potassium (K) into soluble forms that promote plant development and yield are known as potassium solubilizing bacteria (KSB) [57]. Furthermore, several authors highlighted the role of KSB in releasing K from mineral sources such as feldspar and aluminosilicate minerals through various mechanisms, including acidolysis, chelation, exchange reactions, and organic matter and crop residue decomposition [58]. Among others, *Bacillus mucilaginosus*, *Bacillus circulans*, *Bacillus cereus*, *Bacillus edaphicus*, and *Pseudomonas* sp. are considered KSB.

2.2. Fungi

Beneficial or symbiotic fungi exist in almost all plants [25] mainly involving mycorrhizal, epiphytic, or endophytic lifestyles. These fungi interact with plants and other organisms, establishing complex and dynamic systems where multipartite interactions often occur [59,60]. Mycorrhiza might be able to associate with bacterial communities to colonize the plant roots, converting into an endophytic lifestyle [61]. Other studies discuss if all fungi might have past endophytic behavior [62]. Although the complexity of these interactions may seem daunting, in this review, we will focus on the main categories studied for agronomic progress.

2.2.1. Mycorrhizal Fungi

The term mycorrhiza was introduced as early as 1885 by Frank [63], as a fungus–root symbiosis that occurs in the rhizosphere, a zone rich in microbial activity. This relationship enhances nutrient availability and influences plant health. The fungus provides water and nutrients like phosphate and nitrogen to the plant, while the plant supplies carbohydrates and other organic metabolites to the fungus [64–66].

Mycorrhizal fungi play important roles in soil biology and chemistry, and most terrestrial plants have associations with them, including many crop species [64,67]. On the other hand, some exceptions include several species of Brassicaceae [68]. In environments in which plants do not require assistance in obtaining water and nutrients, they do not form these associations, and in some conditions like excessive plant stress, mycorrhizal fungi can turn parasitic with plants [69]. Mycorrhizae can be classified based on how they colonize plant roots. These fungi have developed diverse strategies of colonization, as well as different degrees of plant dependence. These include facultative biotrophic ectomycorrhizal fungi (EMF) and the most common obligate biotrophic arbuscular mycorrhizal fungi (AMF), also known as endomycorrhizal fungi [64]. Arbuscular mycorrhiza is one of the oldest interactions on Earth and was considered crucial for plant evolution on land [70–72]. The main AMF species belong to the phylum Glomeromycota, order Glomerales [65], and have been reported to improve plant health and nutrition as well as resistance to stress [66,73]. However, AMF are complex organisms, and studying their biology and use in agriculture was challenging until recently thanks to the advances in computational tools and omics data [74].

Many AMF are known to boost plant growth and yield by forming extensive hyphal networks and producing substances like glomalin. These enhance water and nutrient uptake and improve soil structure [75]. AMF is also known to increase the activity of antioxidant enzymes to counteract the negative effects of reactive oxygen species generated by salinity stress [76]. Some examples include the improvement of drought tolerance [77–79], salinity tolerance by species of the *Glomus* genus [80], zinc-induced stress [81], weed management, or pathogen and nematode resistance [82]. In comparison, EMF are not as well characterized [83].

The interaction between a host plant and mycorrhizal fungi is regulated by signaling mechanisms. Some insightful reviews which delve into the details of mycorrhizal fungi

colonization and symbiosis accommodation can be found in [84–87]. In brief, plants secrete root exudates into the rhizosphere to alter the soil properties and shape the microbial community [88–90]. For instance, AMF spores detect the host plant through biochemical signals that include a class of plant hormones known as strigolactones. Then, AMF release signaling molecules that trigger root responses [65] and extend hyphae into the host's root cortical cells, forming highly branched arbuscules for nutrient exchange and vesicles for storage. Interestingly, the plant's responses to mycorrhizal colonization are similar to the molecular events in other interactions, including ones with pathogenic microorganisms [71].

2.2.2. Endophytic Fungi

Fungal endophytes have recently gained considerable interest [91]. Modern molecular and genomic techniques have facilitated significant progress in their discovery and characterization, and it is now believed that fungal endophytes may be as abundant as mycorrhizal fungi [92]. These fungi can establish symbiosis with their host plants, yet the relationship needs to be properly characterized to distinguish them from saprobes or latent plant pathogens [93].

Endophytic fungi have remarkable diversity in their lifestyles. They can be found in a wide range of plant species and can be found in any tissue (roots, stems, leaves, and seeds). They may colonize plant tissues locally or systemically, intra- or intercellularly [11]. Some valuable reviews which introduce fungal endophytes can be found in [93–95]. The modern study of fungal endophytes dates to the discovery of the *Epichloë* genus (family Clavicipitaceae), which extensively colonizes Poaceae grasses such as ryegrass (*Lolium* spp.) [96,97]. Similar to endophytic bacteria, they were initially thought to be detrimental since they produced mycotoxins (alkaloids) that affected grazing cattle [98]. However, these endophytes provided the plants higher resistance to pests and other stresses [99], and many studies were performed to find and use these endophytes for their benefits while reducing the potentially detrimental effects.

Most endophytes are ascomycetous fungi as they are the most ubiquitous in nature. Some well-known examples include species from genera such as *Fusarium* [100], *Cladosporium* [101], *Penicillium* [102], *Trichoderma* [103], or *Aspergillus* [104]. On the other hand, Basidiomycota and basal fungi are less studied due to their difficult identification and cultivation [66]. Some endophytes from these categories include the most outstanding *Serendipita indica* [105] or *Streptomyces* spp. [106]. Interestingly, some studies use the term Dark Septate Endophytes (DSEs) to describe a diverse group of ascomycetous endophytes with melanin hyphae that colonize root tissues [68], including some *Alternaria* spp. or *Penicillium* spp. Another commonly used term to categorize some beneficial fungal endophytes is plant growth-promoting fungi (PGPF) [107,108].

Endophytic fungi can establish contact with plants either through the soil or via airborne mechanisms (horizontal transmission). In addition, they can be transmitted through plant seeds to the next plant generations (vertical transmission) [109,110]. To colonize the plant tissues, the beneficial endophytic fungi may be able to evade the plant's immune system [110] and invade tissues using penetration structures or by producing enzymes for the degradation of the cell walls [11,111]. The specific molecular events that enable a beneficial interaction instead of a pathogenic one are still being elucidated [112–114]. Interestingly, some endophytic fungi form relationships that are similar to mycorrhizal fungi by exchanging nutrients and enhancing plant vigor. In this way, *Serendipita indica* is a species that has been reported to have different behaviors that range from endophytic to mycorrhizal [115] and is a model system due to its wide range of host plants and benefits [116].

Endophytic fungi interact with their host plants in several ways. They can promote plant growth by enhancing nutrient uptake, producing growth-promoting substances, and modulating plant hormone levels. Some fungal endophytes, such as *Metarhizium* and *Beauveria*, are also able to transfer nitrogen to their plant hosts [117]. Endophytic fungi may also modulate the plant's immune system, thereby improving its ability to withstand abiotic

and biotic stresses. For instance, they can protect from pathogens and herbivores [118] by serving as a physical barrier against pathogens or producing bioactive compounds.

Additionally, fungal endophytes are a rich source of secondary metabolites that might be of human interest. Fungal endophytes, especially those from medicinal plants, have been extensively explored as potential bioactive compounds for pharmaceutical, industrial, and agricultural applications [11,119–121]. Interestingly, many bioactive compounds that were previously thought to be plant metabolites have been recently discovered as endophyte ones [74,83].

3. Benefits of Microorganisms in Agriculture

3.1. Advances in Agriculture

Beneficial microorganisms are essential tools for sustainable agriculture due to their multifaceted roles in enhancing soil health, promoting plant growth, and ensuring crop productivity (Figure 2). In addition, they can help mitigate climate change through their roles in carbon sequestration, reductions in greenhouse gas emissions, and the bioremediation of contaminated soils. Nevertheless, in this review, we focus on agronomic ecosystems and how the synergistic interactions between soil microbes and plants contribute to improving soil fertility and crop productivity in several ways.
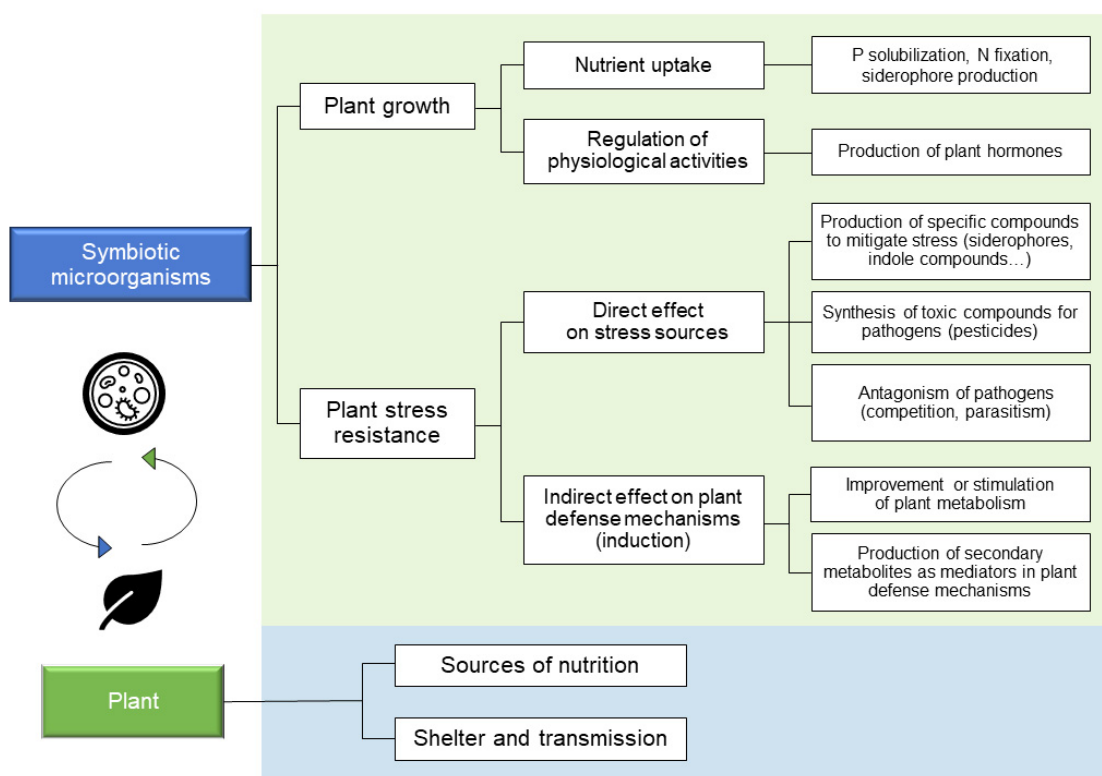

Figure 2. Potential benefits of interaction between symbiotic microorganisms and plants.

Many beneficial microorganisms have been shown to improve plant health in a wide range of plant species. Conversely, other microorganisms are restricted to a very narrow range of hosts, such as the genus *Epichloë*, whose different species can only colonize a small range of hosts [122]. Their significance extends beyond mere nutrient cycling to encompass a range of actions that contribute to the resilience and productivity of agricultural ecosystems. For example, experiments in Mexico using the enrichment of ^{15}N over five years revealed that atmospheric nitrogen fixation contributed significantly to maize's nitrogen nutrition, ranging from 29% to 82% [123]. Similarly, Rose et al. showed that a commercial biofertilizer could replace 23% to 52% of nitrogen chemical fertilizers without reducing rice yield in Southeast Asia. In sugarcane plants, Serna-Cock et al. [124]

demonstrated that the application of *Azospirillum brasilense*, *Azotobacter chroccocum*, and *Trichoderma lignorum* can effectively substitute 60% of the required nitrogen for this crop. Supporting these findings, Antunes et al. [125] demonstrated that the inoculation with *Herbaspirillum seropedicae*, *Pseudomonas* sp., and *Bacillus megaterium* led to a notable increase in sugarcane yield, ranging from 18% to 57.31%.

Regarding the solubilization of nutrients, the utilization of PSB as bioinoculants enhances P availability through various strategies [126–128]. Specifically, PSB has the ability to convert insoluble forms of P into soluble orthophosphate, effectively dissociating fixed P pools accumulated from indiscriminate P fertilizer use. Combining PSB with P fertilizers has shown synergistic effects, particularly enhancing the agronomic efficiency of P rock in soils with high P retention [129,130].

Recent studies have highlighted the benefits of PSB inoculation in various crop systems. Adnan et al. [110] demonstrated significant improvement in maize growth with PSB inoculation, especially when combined with different types of inorganic and organic P fertilizers. Similarly, Javeed et al. [131] observed enhanced maize growth parameters with PSB inoculation in conjunction with NPK fertilizer. Suleman et al. [132] reported increased P uptake and use efficiency in wheat plants inoculated with *Pseudomonas* sp. or *Enterobacter* sp. alongside diammonium phosphate fertilizer. Shirmohammadi et al. [133] found substantial increases in grain yield and plant growth parameters in rainfed wheat with the single or co-inoculation of *Pseudomonas baetica* and *Pseudomonas helmanticensis*, particularly when fertilized with triple superphosphate.

Furthermore, studies have shown that PSB consortia have a more pronounced effect on P uptake by plants. Duarah et al. [134] demonstrated higher rice plant growth with a mixture of PSB strains and NPK fertilizer, while Barra et al. [135] found enhanced ryegrass growth due to better P acquisition from Triple Super Phosphate fertilizer (TSP) with a PSB consortium. The co-inoculation of *Vicia faba* plants with specific bacterial strains significantly increased biomass and P content under different P supplies [48]. These findings underscore the agronomic potential of efficient PSB strains, especially when used in consortia, to enhance P use efficiency and plant growth across various cropping systems.

On the other hand, the ability of mycorrhizal fungi to improve P uptake is based on increasing absorption surface area and solubilizing soil P [136]. AMF enhanced phosphorus uptake during fast-growing stages in maize, contributing up to 19.4% of the total available soil P and significantly increasing yield [137]. Interestingly, Zhang et al. [138] have reported that AMF recruit bacteria that are able to solubilize P instead of directly affecting the P in the soil. Some soil fungi interact synergistically with rhizobacteria to enhance plant growth and nutrient acquisition. For instance, Bouhraoua et al. [139] demonstrated that inoculation with certain PSB strains, such as *Pseudomonas* sp., was correlated with AMF colonization, and this combination improved NPK uptake in peanut plants by up to 200%. AMF can also facilitate colonization by symbiotic bacteria, as seen in the work by Barreto de Novais et al. [140], who revealed how AMF *Glomus formosanum* facilitates the transfer of N-fixing *Bradyrhizobium diazoefficiens* in *Glycine max* roots. Furthermore, bacteria of the genus *Frankia* were studied as co-inoculants with several EMF in *Alnus viridis* under poor-nutrient soil by Chen et al. [141] and were proved to benefit both fungal and plant growth.

In addition to plant development, beneficial microorganisms can play a crucial role in protecting host plants from infections. The biocontrol bacteria *Bacillus* and *Pseudomonas* spp. along with the fungal genera *Trichoderma*, *Aspergillus*, and *Penicillium* are among the most popular biocontrol agents against both bacterial and fungal plant diseases in major crops [142]. For instance, inoculation with *Bacillus* strains such as *B. subtilis* or *B. amyloliquefaciens* have been proven to confer resistance against pathogens such as *Botrytis cinerea* in strawberry [143], *Ralstonia solani* in cowpea [144], and *Sclerotium rolfsii* in peanut [145].

Antibiotic compounds are known to be produced by bacteria such as Actinomycetes and fungi such as *Penicillium* [18,19]. These can include volatiles such as HCN, phenazines, pyrrolnitrin, siderophores, and more [146]. As an example, Kang et al. [147] found that

HCN production in *Pseudomonas chlororaphis* was key in the nematicidal activity against *Meloidogyne hapla* in tomato plants.

Alternatively, the arsenal of antibacterial compounds produced by fungal endophytes can range from broad-spectrum to more specific agents [148]. It has been reported that endophytes generate a plethora of secondary metabolites with broad antimicrobial activity, including terpenoids, alkaloids, phenylpropanoids, aliphatic compounds, polyketides, acetol, hexanoic acid, acetic acid, and peptides [149,150]. For instance, javanicin, a compound with potent antimicrobial properties, exhibits effectiveness against a wide range of microbes, with particular efficacy against *Bacillus* spp. and *Escherichia coli* [148]. Notably, terpenoids like Phomadecalin E and 8α-acetoxyphomadecalin C, synthesized by some *Microdiplodia* endophytes, demonstrate potent antibacterial effects against strains of *Pseudomonas aeruginosa* [149]. Extracts from *Trichoderma harzianum*, an endophyte isolated from *Salvia rosmarinus*, exhibit significant antimicrobial activity against *P. aeruginosa*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Bacillus subtilis*, and *Escherichia coli*, suggesting its potential as a biocontrol agent against phytopathogenic bacteria [151]. Additionally, *Diaporthe phaseolorum*, *Aspergillus fumigatus*, and *A. versicolor*, isolated as endophytes from healthy tomato (*Solanum lycopersicum*) plants, produce antibacterial metabolites like acetol, hexanoic acid, and acetic acid, which effectively combat bacterial spot disease caused by *Xanthomonas vesicatoria* [152]. These antimicrobial compounds may originate directly from the endophytic fungus or be induced by the host plant following endophyte inoculation [149]. However, our understanding of the secretion of these compounds and associated gene expression is still limited.

Endophytes contribute to host plant resistance against fungal pathogens through systemic responses, including strengthening cell walls and inducing defensive gene expression [153–156]. They also enhance photosynthesis rates, chlorophyll content, and the production of defensive compounds like phytoalexins [153,155,157]. Competitive exclusion, where endophytes outcompete pathogens for niche space, is another protective mechanism [154].

Certain fungal endophytes, such as those from the genus *Daldinia* and *Fusarium*, have demonstrated inhibitory effects on plant pathogens [136–138]. *Acremonium sclerotigenum*, isolated from an ancestral wheat species, is capable of inducing resistance in both wheat and tomato [158]. Moreover, species from genera like *Trichoderma*, *Aspergillus*, *Colletotrichum*, and *Diaporthe* show promising antifungal properties [159,160]. Overall, the exploration of fungal endophytes and their activities against fungal pathogens offers valuable insights into developing sustainable agricultural practices while minimizing environmental impacts. Further understanding of these interactions will facilitate the development of effective biocontrol strategies and the identification of novel antifungal compounds for agricultural applications.

3.2. Limiting Factors

Despite their potential to reduce fertilizer dependency and contribute to agricultural sustainability, microbial inoculants face several challenges that limit their universal utilization.

The efficacy of biofertilizers depends on various factors, including the targeted crop, soil conditions (such as pH, salinity, and type), competition with indigenous microbial strains, and climatic factors. Additionally, microbial strains used in commercial inoculants often do not fully represent the diversity of strains associated with plants under field conditions, leading to functional limitations; for example, while cereals derive significant benefits from diazotrophs, most microbes are unlikely to fix nitrogen in the presence of high rates of chemical fertilizers [161].

Phosphate-solubilizing microorganisms, for instance, play a particularly crucial role in soils facing extreme environmental conditions such as saline–alkaline or nutrient-deficient environments. However, reports vary regarding the optimal temperature for phosphate solubilization, ranging from 20–25 °C to 30 °C [162–164]. Some studies even demonstrate solubilization at extreme temperatures, from 45 °C in desert soil to as low as 10 °C [165].

Various factors influence microbial phosphate solubilization, including soil microbial interactions, plant growth stage, environmental conditions, soil types, and agronomic practices. Both aerobic and anaerobic bacteria contribute to phosphate solubilization, with different genera exhibiting varying preferences. Additionally, the presence of exogenous soluble phosphate affects the physiological activity of PSB. While low levels of soluble phosphate stimulate microbial growth and phosphorus nutrition of plants, high concentrations can suppress PSB activity, posing a barrier to their widespread use [166].

The application of microbial inoculants must also be carefully optimized. For seeds, proper seed coating is essential to ensure better contact and inoculation rates. For soil applications, combining the inoculants with soil amendments can enhance their efficacy [167]. Lastly, another current limitation is the lack of well-developed inoculant formulations, since they require extensive exploration before reaching the market. Moreover, compliance with constantly evolving regulations poses a challenge, hindering the utilization of existing beneficial microorganisms. However, as on-field experiments increasingly demonstrate the benefits of microorganisms, we anticipate the greater use of these sustainable alternatives in the near future.

4. Conclusions and Future Prospects

Plant–microorganism interactions represent a promising avenue for advancing agriculture and food security while minimizing the environmental impact caused by chemical fertilizers and pesticides. Beneficial microorganisms are essential in this quest, forming symbiotic relationships with plants to improve nutrient cycling, soil health, and plant resilience against various stresses. From mycorrhizal fungi extending the reach of plant roots for nutrient uptake to nitrogen-fixing bacteria enhancing nutrient availability, the multifaceted functions of these microorganisms offer many alternatives for addressing the challenges of modern agriculture. Integrating microbial inoculants into precision farming practices can optimize resource use and crop performance. Additionally, expanding these technologies to a broader range of crops and adapting them to diverse climates and soils will further their application and benefits.

Supportive regulatory frameworks and policies are crucial for widespread adoption, including developing standards and guidelines for microbial inoculants' production and application. Public awareness and education initiatives are essential to inform farmers and consumers about the benefits of these technologies for sustainable agriculture.

However, to fully harness the potential of beneficial microorganisms in agricultural systems, we must address key aspects of microbial ecology. Despite the significant strides that have been made in understanding their mechanisms of action and agronomic applications, challenges such as competition with indigenous microbial strains and environmental variability persist. To overcome these barriers, interdisciplinary approaches that integrate microbiology, agronomy, and environmental science are required to optimize the efficacy and sustainability of microbial inoculants.

In conclusion, by promoting the natural symbiotic relationships that have evolved over millennia, we expect to reduce the reliance on chemical inputs while we enhance soil health and crop yields in a way that is environmentally sound and economically viable. As we continue to unlock the secrets of plant–microbe interaction, we will strive towards future agriculture that is both resilient and sustainable.

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