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Harnessing endophytes: Advanced insights into nutrient acquisition and plant growth enhancement

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Abstract

The rapid growth of the global population and the rising demand for sustainable agriculture have intensified interest in eco-friendly alternatives to synthetic fertilizers. While synthetic fertilizers effectively boost crop yields, they seriously threaten soil health, human well-being and environmental stability. Researchers are increasingly exploring microbial solutions such as biofertilizers and biocontrol agents. Among these, endophytes-microorganisms that live within plant tissues without causing harm-show considerable promise. Recent studies underscore the critical role of endophytes, both rhizobial and non-rhizobial, in improving nutrient use efficiency, promoting plant growth and enhancing resistance to pests, diseases and environmental stresses. However, despite these advancements, significant knowledge gaps remain concerning the mechanisms through which endophytes facilitate macro- and micronutrient acquisition. This review seeks to clarify these mechanisms and highlights the need for more extensive research to fully understand the functional dynamics of endophytes in nutrient acquisition and their potential to support sustainable agricultural practices.

Keywords

rhizobial endophytes; non-rhizobial endophytes; symbiotic relationship; microbial fertilizers; nutrients sequestration; sustainable agriculture

Introduction

The global community faces numerous challenges that hinder sustainable and eco-friendly agricultural productivity. These restrictions encompass diminishing soil fertility and a range of biotic (pests and diseases) and abiotic (temperature extremes, drought, salt, UV radiation, and elevated light intensities) stresses (1). Such limitations stem from factors like the over-exploitation of agricultural land, urbanization, overuse of synthetic agrochemicals, land degradation, the challenges posed by destructive plant pathogens and pests and adverse abiotic conditions. Addressing these issues is essential to enhancing crop yield and productivity in a sustainable and effective manner (2).

The rapidly growing global population is a major factor exacerbating constraints on eco-friendly and sustainable agricultural productivity. With the human population projected to surpass 9 billion by 2050 (3), this increase places significant pressure on the agricultural sector to produce more food to meet rising demand. Addressing this challenge requires the implementation of sustainable agricultural practices that boost crop yield and productivity and ensure efficient resource management. This involves adopting technologies and techniques that enhance soil fertility and reduce reliance on synthetic agrochemicals. Furthermore, investing in research and development, promoting education and awareness and encouraging international collaborations can help drive innovative solutions to feed the expanding population while minimizing the environmental impact(4).

Modern agricultural practices have increasingly relied on the intensive use of pesticides and synthetic fertilizers to overcome these limitations and enhance agricultural productivity. These agrochemicals are applied extensively to provide essential nutrients to crops and protect them from diseases and pests. However, excessive use of agrochemicals can negatively affect the environment, human health, and the long-term fertility of soil (5). To improve crop output while addressing limitations in agricultural productivity and environmental health, it is essential to focus on maximizing productivity in a sustainable way that preserves ecological balance (6).

To address these challenges, scientists are exploring microbial-based alternatives to synthetic fertilizers. The application of microbial inoculants provides a cost-efficient, environmentally sustainable method for agricultural intensification, improving both productivity and ecological well-being. Microbial inoculants contain beneficial microorganisms that improve the availability and utilization of essential soil nutrients. When introduced into the soil, these inoculants can form symbiotic relationships with plants, promoting nutrient uptake and enhancing overall plant health (7). Additionally, microbial inoculants can help mitigate both abiotic stresses (such as drought, cold, heat, toxin, and salinity) and biotic stresses (including fungi, bacteria, nematodes and insects) in crops (8). They enable plants to tolerate adverse environmental conditions, including salinity, drought, and extreme temperatures.

Microbial inoculants, such as *Agrobacterium tumefaciens*, *Pythium oligandrum*, *Beauvaria bassiana*, *Metarrhizium anisopliae* and *Verticillium chlamydosporium*, can also serve as biocontrol agents (9), suppressing harmful pathogens and pests and reducing the need for synthetic agrochemicals. By incorporating these microbial inoculants, farmers can decrease their reliance on synthetic fertilizers and pesticides, fostering a more sustainable and environmentally friendly agricultural system (10).

Endophytes are present in nearly all plant species, making their existence a common and natural phenomenon in the plant kingdom (11). Residing within plant tissues, these microbes are less exposed to the competitive environment of the rhizosphere, where numerous organisms vie for resources (12). This reduced competition from other rhizospheric microbes enables endophytes to thrive and benefit the plant more effectively (13), providing a sustainable and eco-friendly approach to enhancing crop productivity.

Several examples highlight the tangible benefits of microbial endophytes. In Brazil, soybean crops have shown significant improvement when co-inoculated with *Bradyrhizobium* and other microbial strains, particularly enhancing nodulation and performance under drought conditions (14). Similarly, in Pakistan, sweet potato yields have increased by 1-2% with microbial inoculants used to combat disease-causing agents (15). In Africa, the productivity of lettuce has benefited from the co-inoculation of the diazotrophic bacterium *Azotobacter chroococcum* and the arbuscular mycorrhizal fungus *Glomus fasciculatum*, which boost phytochemical constituents such as total phenolics, anthocyanins and carotenoids, thereby enhancing the crop's nutraceutical value (16). By promoting nutrient accessibility and the decomposition of organic matter, endophytes stimulate natural soil microbiota, improving soil microbial health when used as biofertilizers (17).

Endophytes

The study of endophytes and their relationships with crops has a long history. A wide range of bacterial and fungal endophytes has been identified through the analysis of plant samples (18). These endophytes encompass a diverse group of microorganisms, including bacteria and fungi, that reside within plant tissues without causing any apparent harm. This unique association enables endophytes to coexist with their host plants, often benefiting both parties (19). Perotti made the first documented observation of non pathogenic organisms in root tissues (20). These endophytes are believed to originate from the external environment, entering the plant through various pathways such as stomata, lateral root emergence, germinating radicles, wounds and lenticels (21).

The focus on non-pathogenic microbes within plants, rather than pathogenic ones, was pioneered by Bary (22), who identified microbial cells within plant tissues. His work ultimately led to the initial definition of endophytes as “any organism that grows within plant tissues”. This definition has since evolved, Petrini (23) later offering a more widely accepted description: “any organism that at some part of its life cycle colonizes the internal plant tissues without causing any harm to the host plant.” This redefinition emphasized the mutualistic nature of many endophytic relationships, setting them apart from pathogenic microbes. Over recent years, the discovery of endophytes in different plant species has accelerated, with numerous studies dedicated to uncovering these associations (24).

Most scientists categorize plant-associated microbes as epiphytes (organisms that live on or near plant tissues) or endophytes (organisms that inhabit plant tissues) (25). Expanding our understanding of endophytes, their roles and their significance can lead to the discovery of novel bioactive compounds with applications in medicine, agriculture and environmental management (26).

Endophytes have been isolated from various plants and can form complex interactions with their hosts. Some endophytes maintain a mutualistic relationship with their host plants, providing benefits such as improved nutrient uptake (Fig. 1) and increased resistance to pathogens and environmental stress. Others may exhibit antagonistic properties. For example, soybean performance is enhanced when co-inoculated with endophytic *Bradyrhizobium*, improving nodulation under drought conditions (27). Likewise, mycorrhizal fungi form beneficial associations with many plants, enhancing nutrient uptake and stress resilience. Conversely, certain endophytes, like *Penicillium* species in bananas, display antagonistic properties by reducing nematode populations, thereby protecting the plant (28).

These examples illustrate how endophytes promote plant growth or protect against pathogens, which is critical in sustainable agriculture.

The diverse interactions between endophytes and their hosts represent a fascinating area of research. Scientists are investigating the mechanisms by which endophytes establish and maintain relationships with plants and the specific benefits they offer. Understanding these interactions holds significant potential for agriculture, as leveraging the beneficial properties of endophytes can enhance crop health and productivity.

In a study by Fisher et al. (29), endophytic bacterial and fungal colonies were isolated from a maize field in Devon. Researchers found that most bacterial colonies occupied the lower portions of the maize plant, closer to the soil. In contrast, most fungal colonies were located in the stem's core and epidermis rather than the leaves, displaying tissue specificity. They also observed an inverse relationship, where tissues with fewer fungal colonies had higher bacterial counts and vice versa.

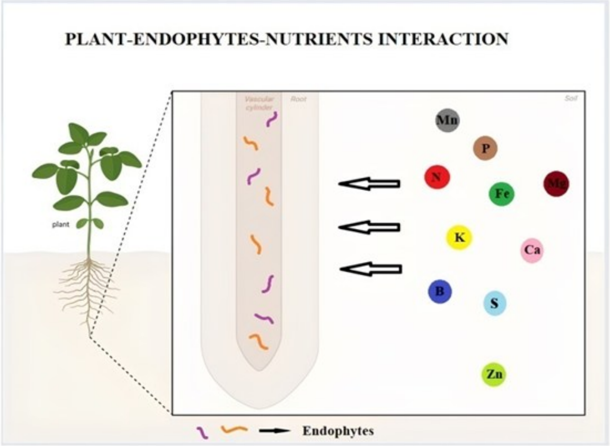


Fig. 1: Plant - Endophytes- Nutrients interactions in soil

Rhizobial endophytes

Rhizobial endophytes predominantly inhabit the nodules of legume crops and are well-known for their role in nitrogen (N) fixation. *Rhizobium* has attracted considerable attention from researchers due to its unique ability to form a beneficial symbiotic relationship with legume plants. Through the formation of root nodules, *Rhizobium* converts atmospheric N into a form that plants can utilize, thereby improving productivity in nitrogen-deficient soils (30). This process not only provides essential N to the plants but also offers rhizobia a suitable habitat within the root or stem nodules (31).

Rhizobial endophytic bacteria primarily belong to the class α-proteobacteria (32). This group includes diverse genera such as *Azorhizobium*, *Bradyrhizobium*, *Rhizobium* and *Mesorhizobium* all of which exhibit the capacity to form this symbiotic relationship (31). Other rhizobial bacteria within the Alphaproteobacterial group have been identified in genera such as *Ochrobactrum* (33), *Methylobacterium* (34), *Microvirga* (35), Phyllobacterium (36) and *Devosia* (37). Additionally, Beta-*Rhizobium* species within the Betaproteobacterial group, including *Cupriavidus* and *Burkholderia,* have been recognized over the past decade (38).

Scientists have identified two niches for rhizobial endophytes: soil, where they function as heterotroph and legume nodules, where they act assymbiont (39). Initially, endophytic rhizobia were believed to survive saprophytically in soils lacking legumes. However, later studies revaled that the life cycle of rhizobial endophytes can also include colonizing non-legume crops (40). In a notable study, Lupwayi and Clayton (40) investigated rhizobial endophytes in the roots of barley, wheat and canola, examining their effects on field pea-based crop rotations. They discovered that these microbes can improve the nutrition of non-legume crops.

Recent research has demonstrated that *Rhizobium* can establish endophytic relationships with certain cereal crops, including wheat, maize and rice (41). This endophytic colonization can positively impact plant growth and increase grain yield at harvest. Interestingly, these benefits seem to occur independently of the root nodulation and biological nitrogen fixation (BNF) traditionally associated with *Rhizobium*. Instead, *Rhizobium* appears to enhance plant growth through additional mechanisms. These include synthesizing growth-promoting compounds like indole acetic acid (IAA) and gibberellins (GA3) and producing enzymes such as phytase and protease, which facilitate nutrient acquisition. Furthermore, *Rhizobium* enhances nutrient uptake efficiency by solubilizing phosphorus (P) and producing siderophores that chelate iron (Fe), making it more available to plants. Studies have shown that inoculating crops like common beans with *Rhizobium* significantly boosts nutrient content and yields, underscoring the bacteria's multifaceted role in promoting plant growth (42). This discovery has sparked considerable interest within the agricultural community, opening new avenues for reducing dependence on chemical fertilizers and advancing sustainable farming practices. By leveraging *Rhizobium* as an endophyte, there is potential to enhance crop productivity while reducing environmental impacts (43).

Non-rhizobial endophytes

Microbes residing inside root nodules, other than *Rhizobium* species, are known as Non-Rhizobial Endophytes (NREs) (44). Endophytes that do not exhibit nodulation are classified as NREs (45). Initially, it was believed that rhizobial endophytes were solely responsible for nodule formation and development. However, recent studies have shown that in addition to rhizobial endophytes, some microbes residing within plants-specifically non-rhizobial endophytes-also contribute to nodule development. These microbes are known as nodule-associated bacteria (45). While legume crop nodules were traditionally thought to harbor rhizospheric microbial communities, recent research has revealed that other microbes, particularly NREs, are also present.

Non-rhizobial endophytes commonly belong to the α-, β- and δ-Proteobacteria groups (32). Numerous studies have found that *Bacillus* is the most dominant genus of non-rhizobial bacteria, followed by *Pseudomonas* (45). Additional research has identified various genera of NREs, including *Bacillus*, *Pantoea*, *Pseudomonas*, *Stenotrophomonas*, *Micromonospora*, *Paenibacillus*, *Mycobacterium*, *Serratia*, *Arthrobacter*, *Klebsiella*, *Bosea*, *Enterobacter*, *Acinetobacter*, *Agrobacterium* and *Phyllobacterium* (46-52).

The antifungal activity of both non-rhizobial endophytes and rhizobial colonies was studied by (53). Non-rhizobial endophytes enter plants through infection threads formed by rhizobial endophytes and subsequently colonize the nodules (54). While NREs cannot form nodules independently, they induce nodule formation and development in legumes when inoculated with specific rhizobial bacteria (55). NREs are considered active colonizers and when inoculated with rhizobial endophytes, promote plant growth, root exudation patterns and soil nutrient status. Additionally, they can modulate the rhizospheric microbiota in lentils (56).

Nutrient sequestration by endophytes

One of the most challenging processes for terrestrial plants is converting insoluble nutrients into soluble, bioavailable forms, a task facilitated by mobile microbes. These microbes are capable of transforming or solubilizing various unavailable nutrients, making them accessible to plants (57, 58).

Inoculating plants with endophytic bacteria or fungi can improve nutrient uptake, such as N and P, through increased root surface area and enhanced root symbiosis with soil microbes. This symbiotic relationship enables plants to access and absorb essential nutrients more efficiently, ultimately promoting growth and overall health(59).

The ‘rhizophagy cycle’ is a process in which microbes acquire nutrients from the soil and transfer them to plants. During this cycle, microbes alternate between an intracellular endophytic phase within the roots and a free-living soil phase. In the free-living phase, microbes collect nutrients from the soil and transfer them to the plants, while in the endophytic phase, they inhabit the plant tissues (58).

Research over the past two decades has demonstrated the solubility and availability of nutrients such as N, P, K and Fe (58, 60). Saddique, Ali (60) suggested that while significant research has focused on endophyte-mediated nutrient acquisition from root or seed endophytes, studies on the role of foliar endophytes-mediated nutrient acquisition from root or seed endophytes, studies on the role of foliar endophytes in nutrient acquisition are relatively limited. In a study on *Theobroma cacao*, foliar endophytes like *Colletotrichum tropicale* significantly enhanced N uptake and total plant biomass, especially when co-inoculated with the pathogen *Phytophthora palmivora* (61). Similarly, research on Northern oat grass revealed that foliar endophytes influenced plant responses, such as enhanced plant biomass from N fertilization and increased plant leaf area index from P fertilization, highlighting their critical role in nutrient acquisition and overall plant performance (62). Further research in this area could provide valuable insights into the potential benefits of foliar endophytes in enhancing nutrient uptake in plants.

Endophytic bacteria can improve plant growth by fixing atmospheric N into a form that plants can readily absorb, thus increasing N availability in the soil. This enhanced N availability helps plants thrive and develop more robust root systems, improving overall growth. In addition to N fixation, NRE bacteria can produce siderophores, molecules that facilitate the uptake of essential nutrients, particularly Fe. By enhancing Fe uptake, these bacteria support plant growth and development (45).

Mycorrhizal endophytes benefit host plants by improving the acquisition of soil nutrients such as P, potassium (K) and other inorganic elements. Other endophytes living in the roots and other plant parts are nitrogen-fixing entities, which help plants like sugarcane in Brazil to be cultivated for many more years without the need for additional nitrogenous fertilizers (63).

Mechanisms involved in nutrients acquisition

Fungal endophytic genera such as *Balansiopsis*, *Balansia*, *Echinodothis* and *Atkinsonella* can enhance the uptake of both macro and micronutrients from soil and organic matter. By forming symbiotic relationships with plants, these fungi help increase the availability of essential nutrients such as P, N, K, magnesium (Mg), Zn, Fe and copper (Cu) to their plant hosts. This mutualistic interaction benefits both the fungi and the plants by promoting nutrient uptake and improving overall plant health (64).

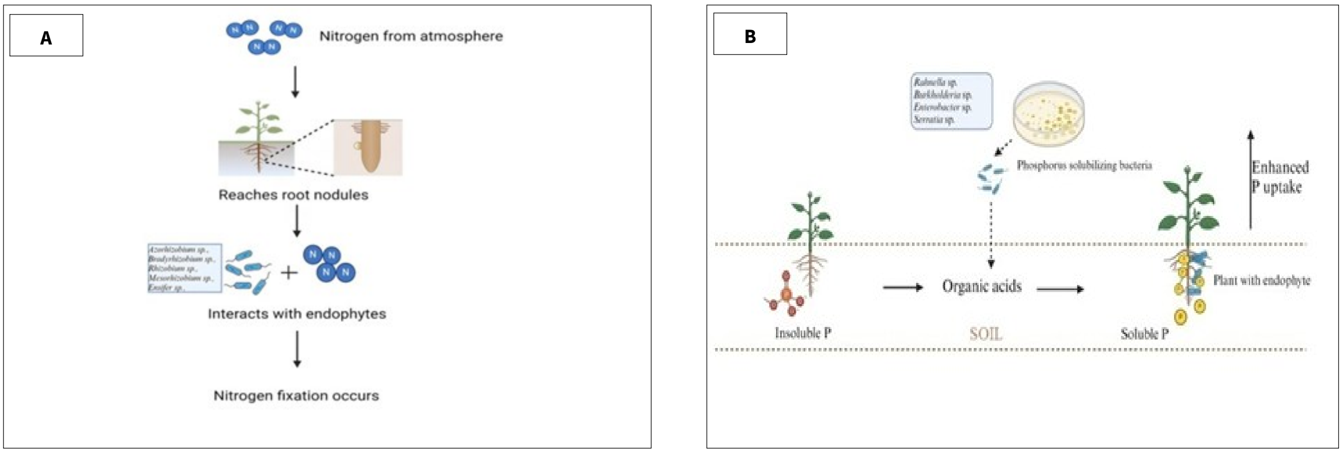
Bacteria in the endophyte category, including *Bacillus*, *Pseudomonas*, *Micrococcus* and *Methylobacterium*, can promote nutrient acquisition and plant growth through mechanisms such as N fixation, P , K solubilization and siderophore production (Fe chelation) (65).

The rhizophagy cycle is one of the common mechanisms by which soil microbes solubilize or acquire nutrients and transfer them back to the plant’s root intracellular periplasmic spaces. In this process, plants extract nutrients from microbes in the periplasmic space by producing reactive oxygen species (ROS), primarily NADPH superoxides. These ROS break down microbial cell walls, triggering the release of nutrients into the plants, enabling them to acquire more nutrients from the soil. Additionally, these ROS signal defense responses while protecting plant cells from damage. As microbes lose nutrients, they exit the root cell and typically return to the rhizosphere, where they may re-enter the cycle. This phase underscores a unique plant-microbe interaction for nutrient acquisition (57).

Various mechanisms are involved in the transformation of nutrients from the soil to plants by endophytic microbes (Fig. 2). These include N transformation through N fixation, conversion of insoluble P into soluble P via P solubilization, transformation of fixed K into soluble K via K solubilization and the conversion of unavailable micronutrients into available forms through siderophore production. Additionally, the rhizophagy cycle plays a significant role in nutrient transformation, as outlined by White, Kingsley (57).

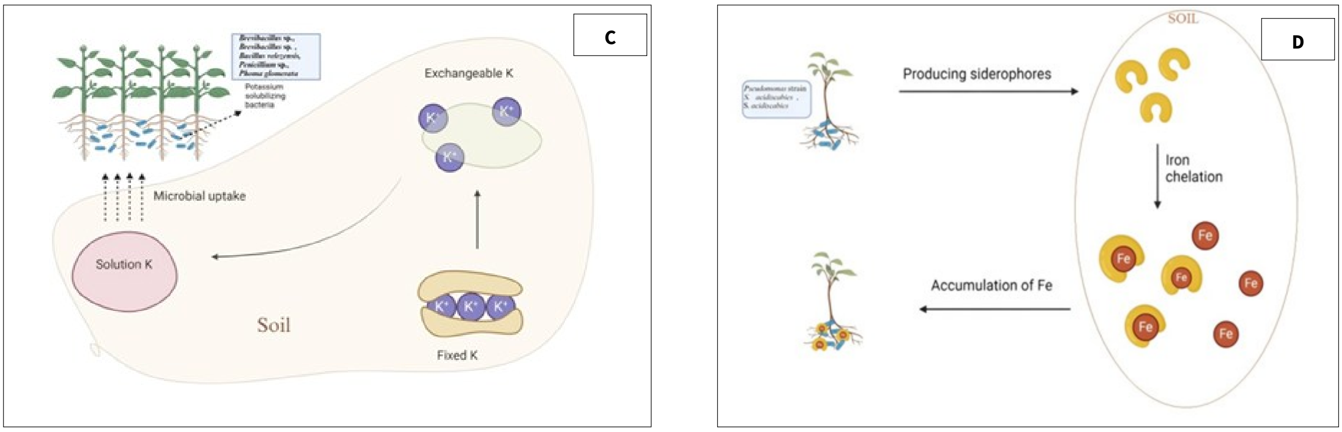
Primary nutrients

Nitrogen is a vital element for plant growth and development, playing critical roles in various essential functions such as protein synthesis, nucleic acid formation, chlorophyll production, enzyme activity, metabolic pathways, cellular structure formation and secondary metabolite production (66). Nitrogen gas makes up about 78% of the Earth's atmosphere, but most plants cannot directly utilize atmospheric N. The conversion of atmospheric N into ammonia (NH_3) or other nitrogenous compounds that plants can absorb is known as N fixation. This process is critical for making N available in a form that plants can assimilate. N fixation occurs through two main methods: physiological



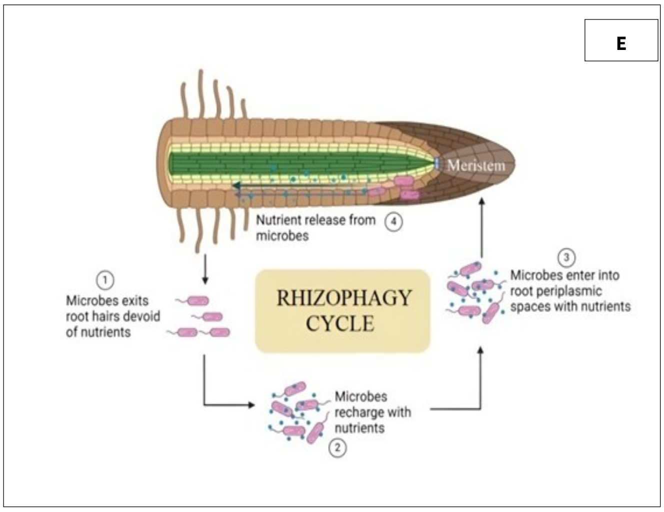
NITROGEN FIXATION MECHANISM

PHOSPHORUS SOLUBILIZATION MECHANISM



POTASSIUM SOLUBILIZATION MECHANISM

SIDEROPHORE PRODUCTION MECHANISM



RHIZOPHAGY CYCLE MECHANISM

Fig. 2. Mechanisms involved in the transformation of nutrients from soil to plants by endophytes

fixation, which accounts for about 10% of natural N fixation, and biological fixation by microbes, which contributes around 90% (67).

Peoples and Craswell (68) reported the expected amount of N fixation by rhizobial endophytes in crops such as groundnut, soybean, pigeonpea, cowpea, green gram and black gram (Fig. 3). According to their findings, the yield of rice, maize, wheat and sorghum increased by 11 to 353% due to the symbiotic relationship between endophytic Rhizobium and cereal crops. Additionally, N fixation is carried out by various endophytes in specific crops (Table 1).

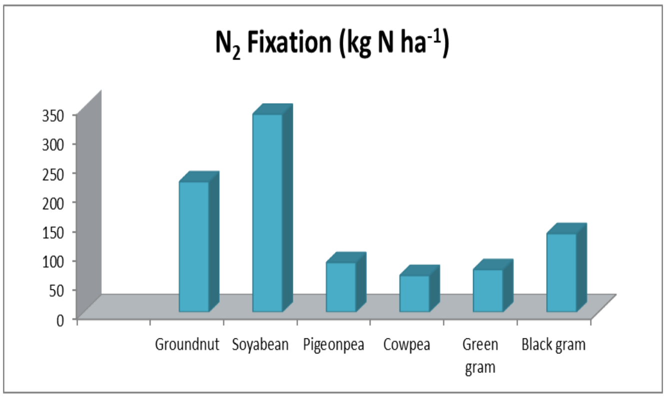


Fig. 3. Quantum of nitrogen fixation by endophytes in various crops

Table 1. Nitrogen fixation by various endophytes in specific crops

Crop	Endophytes	Beneficial Effects	Reference
Rice	*Burkholderia vietnamiensis* AR 1122, *Azospirillum amazonense* AR3122	10 to 29% increased grain yield	(92)
Rice	*Klebsiella pneumoniae* KW7-S06, KW7-S22,KW7-S27, KW7-S33; *Bacillus aryabhattai* HSS05; *Paenibacillus kribbensis* HS-R01, HS-R14;*Bacillus subtilis* CB-R05; *Bacillus megaterium* KW7-R08;*Microbacterium trichotecenolyticum* SW521-L21, SW521-L37; *Microbacterium binotii* CB-S18;	Increased plant growth, plant height, and dry weight. Antagonistic effects against fungal pathogens.	(93)
Rice	*Sphingomonas* spp., *Klebsiella* spp., *Burkholderia* spp., *Novosphingobium* spp.	Increased nitrogenase activity ranged from 86.39 to 888.37 nmol ethylene h^{-1} g^{-1} (dry weight)	(94)

Phosphorus is an essential nutrient for crops, playing a vital role in various physiological processes such as nucleic acid synthesis, energy transfer and root and flower development. However, its availability to plants is limited due to its tendency to form insoluble compounds in the soil. In the soil, P typically exists as phosphate ions (PO_4^{3-}), which often bind to minerals or organic matter, making it less accessible to plants. This insolubility is particularly pronounced in alkaline and acidic soils, where the availability of phosphate ions to plants is further reduced. The solubilization of inorganic phosphate by certain plant-associated microorganisms, such as fungi (*Penicillium* sp. and *Aspergillus* sp. in *Taxus wallichiana* (69)) and bacteria (*Aneurinibacillus* sp. and *Lysinibacillus* sp. in banana (70)), is crucial for enhancing P availability to plants (71). Various endophytes that carry out P solubilization in different crops is illustrated in Table 2.

Baghel et al. (72) evaluated the efficacy of bacterial endophytes, isolated from maize roots, in promoting plant development and facilitating nutrient uptake. They found that 10 of 24 isolates could solubilize P from tricalcium phosphate. They also discovered that the isolate FDN2-1, phylogenetically related to *Burkholderia* sp, was able to solubilize various sources of phosphate, as shown in Fig. 4.

Potassium is an essential nutrient for plant growth, critical in various physiological and biochemical processes. While the total amount of K in the soil may be substantial, only a small fraction is readily available to plants in a form they can absorb. This is where K-solubilizing endophytic bacteria come into play (73). In maize, *Bacillus* sp., *Pseudomonas* sp., and *Burkholderia* sp. have been identified as potent K-solubilizing endophytes (74). Similarly, in Moso bamboo, *Enterobacter* spp., *Alcaligenes* spp., and *Bacillus* spp. have demonstrated potential for K solubilization (75).

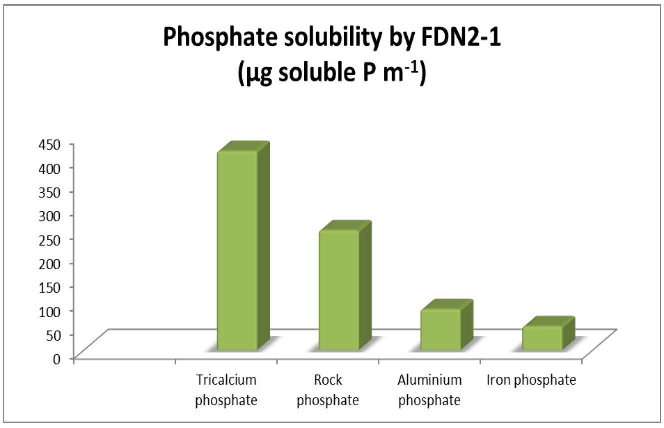


Fig. 4. Phosphate solubility by endophytic isolate FDN2-1 in maize crop

Potassium-solubilizing bacteria are endophytic microorganisms capable of solubilizing less available forms of K in the soil. These bacteria convert insoluble K compounds into soluble forms that plants can easily absorb and utilize for growth and development. This process entails the secretion of organic acids or other compounds by bacteria, facilitating the decomposition of K-containing complex minerals into a form accessible to plant roots . In agricultural practice, using K-solubilizing bacteria is a strategy to enhance K availability to plants. By incorporating these bacteria into biological fertilizers or using them as soil inoculants, farmers can improve soil fertility, leading to better nutrient uptake by plants (76). Different endophytes are involved in K solubilization in specific crops, as shown in Table 3.

Secondary nutrients

Nutrient availability plays a crucial role in determining crop yield and quality. While the fertilization of secondary nutrients can have limitations, soil microbes provide a sustainable and environmentally friendly solution to enhance plant secondary

Table 2. Phosphorus solubilization by various endophytes in specific crops

Crop	Endophytes	Beneficial Effects	Reference
Maize	*Burkholderia* FDN2-1	Increased indole acetic acid in the range of 17.47 to18.75µg/ml and available P in the range of 26.05 to 39.15 kg/ha	(72)
Soyabean, Maize, Peanut	*Enterobacter* sp. J49 or *Serratia* sp. S119	Significant increase in P in the tissues. Significant increase in growth.	(95)
Chickpea	*Mesorhizobium ciceri*, *Mesorhizobium mediterraneum*	Increased nodulating capacity. Increased P solubilization.	(96)
Poplar	*Rahnella* sp. *Burkholderia* sp.	Increased P solubilization to the extent of 1810 µg/kg. Increased wet root volume and root surface area	(71)
Pseudowintera colorata (horopito)	*Streptomyces* sp. UKCW/B *Streptomyces* sp. mhcr0816, *Nocardia* sp., *Streptomyces* sp. GMKU 3100	Mean shoot height of seedlings was (1.65×) longer. Higher shoot dry weight (1.6×) and number of internodes (1.67×).	(97)

Table 3. Potassium solubilization by various endophytes in specific crops

Crop	Endophytes	Beneficial effects	References
Rice	*Enterobacter cloaceae E, cloaceae* strain SBP-8	Increased potassium solubilization with 17.9 mm potassium solubility index	(76)
Soyabean	*Brevibacillus* sp. SAF9, *Brevibacillus* sp. SAF11, *Bacillus velezensis* SAC36	Increased Ca, Mg, P, K content High organic carbon and base saturation content	(98)
Cucumber	*Penicillium* sp. LWL3, *Phoma glomerata* LWL2	Increased plant biomass Higher assimilation of K, Ca and Mg	(99)

nutrient acquisition. These beneficial microbes can improve the efficiency of secondary nutrient uptake, helping to meet the nutritional needs of plants without the harmful effects associated with conventional fertilizers. Utilizing soil bacteria can enhance plant growth in a more sustainable way while reducing environmental harm (77).

Soil microbes, such as mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPRs) like *Bacillus* spp., *Pseudomonas* spp., and *Burkholderia* spp., as well as N-fixing bacteria like *Rhizobium*, are effective in enhancing secondary nutrient uptake. These microbes improve nutrient availability and efficiency by forming symbiotic relationships with plant roots, solubilizing nutrients and enhancing soil health. This offers a sustainable alternative to conventional fertilizers, promoting healthier plant growth without causing environmental harm (78). Secondary nutrients, such as calcium (Ca), Mg and sulfur (S), are sequestered by various endophytes in specific crops, as shown in Table 4.

Micronutrients

Nutrients may be sequestered in the rhizospheric soil due to the efficient activity of endophytic microbes. In addition to major nutrients, these microbes can also sequester certain micronutrients [including Fe, manganese (Mn), boron (B) and Zn] in the rhizospheric region using siderophores, which are biogenic ligands with a high affinity for metallic compounds (79).

While bacteria can serve as beneficial carriers of micronutrients for plant growth, it is important to note that the process of rhizophagy, in which plants extract nutrients from bacteria, is not solely oxidative. Rhizophagy involves a complex interaction between plants and bacteria, in which nutrients are released through various mechanisms, such as the oxidation of microbes, direct consumption of nutrients, and electrolyte leakage from bacteria. This symbiotic relationship plays a crucial role in nutrient cycling and plant health(57).

Various micronutrients have been acquired by different endophytes in specific plant species, as discussed by numerous researchers, and are listed in Table 5.

Complementary effects

In addition to nutrient acquisition and sequestration by endophytic microbes in plants, these microbes contribute to complementary effects such as biocontrol activity, phytohormone production and secondary metabolite production. These effects indirectly promote plant growth and enhance nutrient acquisition (65).

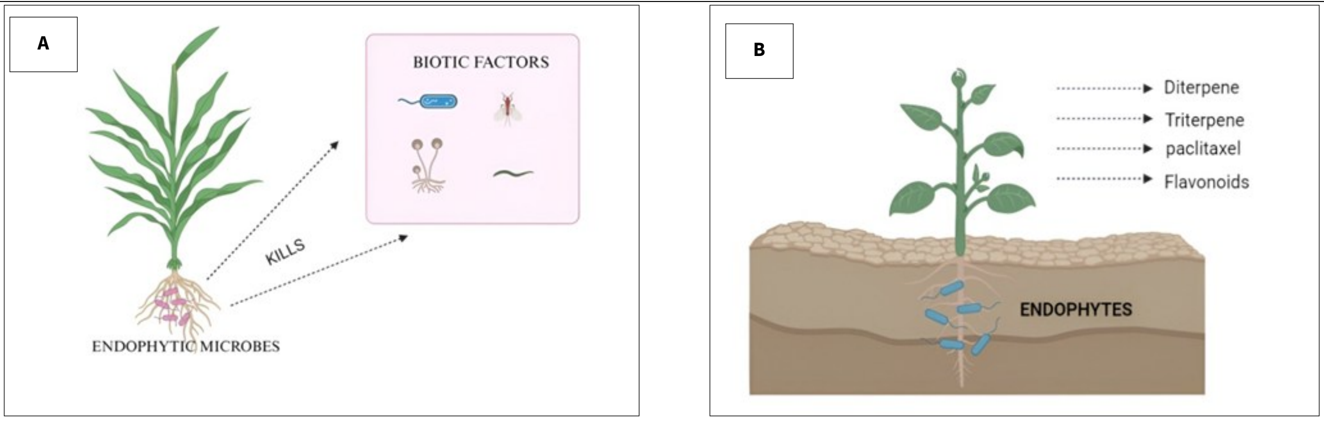
Pictorial representations of these complementary effects, including biocontrol activity, secondary metabolite production, and phytohormone production, are illustrated in Fig. 5a, 5b and 5c, respectively.

Table 4. Secondary nutrients acquisition by various endophytes in specific crops

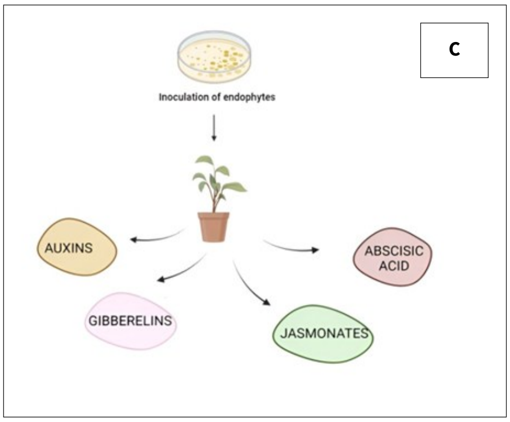
Crop	Nutrient	Endophytes	Beneficial effects	Reference
Soyabean	Mg	*Codinaeopsis* sp. 328EF, *E. keratinophyylum* SC4, *Bacillus cereus* SC5, *Pseudomonas sheari* SC15, *Paenibacillus alvei* PA12	Increased biomass accumulation, dry matter and nutrient content in plants	(100)
Soyabean	Ca and Mg	*Brevibacillus* sp. SAF9, *Brevibacillus* sp. SAF11, *Bacillus velezensis* SAC36	Increased Ca, Mg, P, K content; high organic carbon and base saturation content	(98)
Groundnut	Sulfur	*Thiobacillus thiooxidans* NCIM2426, coinoculated with *Rhizobium* sp. TNAU 14	Increased nodule number, nodule dry weight and plant biomass 136.9 plant^{-1}, 740.0 mg plant^{-1} and 15.0 g plant^{-1} respectively; enhanced pod yield by 18% and increased soil available S from 7.4 to 8.43 kg ha^{-1}.	(101)
Groundnut	Ca	*Funneliformis mosseae* (Arbuscular mycorrhiza)	Increased root and shoot biomass content ; increase in Ca content in Ca deficient condition	(102)
A. thaliana	Mg	*Piriformospora indica*	Increase in the total intracellular Mg content by two folds by the endophyte	(103)

Table 5. Micronutrients acquisition by various endophytes in specific crops

Crop	Nutrient	Endophytes	Beneficial Effects	Reference
Barley, *Arabidopsis thaliana*	Zn, Mn, Cu, B	*Piriformospora indica*	Improves crop productivity and enhanced crop tolerance against biotic and abiotic stresses	(104)
Soyabean	Cu	*B. cereus* SC5, *P. sheari* SC15 *P. alvei* PA12, *B. thuringiensis* SC10	Increased biomass accumulation, dry matter and nutrient contents in plants	(100)
Soyabean	Zn	*B. cereus* SC5, *P. sheari* SC15	Increased plant dry matter production and biomass content	(100)
Soyabean	B	*Paenibacillus alvei* PA12, *Codinaeopsis* sp. 328EF, *Hymenaea insecticol* 33EF	Increased micronutrient contents along with growth promoting attributes	(100)
Green gram	Fe	*Pseudomonas* strain GRP3	Reduction in chlorotic symptoms and increased chlorophyll content	(105)
Moss, ferns, angiosperms, gymnosperms	Zn, Mn, Cu, B	*Glomus* sp.	Increased in crop productivity and Zn, Cu, B, Mn uptake in the plants	(106)



BIOCONTROL ACTIVITY **SECONDARY METABOLITES PRODUCTION**



PHYTOHORMONE PRODUCTION

Fig. 5: Complementary effects of endophytic microbes in plants

Biocontrol activity

Endophytes are essential in protecting host plants throughout their life cycle, functioning effectively as biocontrol agents that defend against pathogens and other harmful organisms. This protection is achieved through mechanisms such as antibiosis, parasitism and competition (80). For example, endophytes can produce antimicrobial compounds that inhibit pathogen growth through antibiosis. Specifically, *Bacillus* spp. can suppress the fungal pathogen *Fusarium* spp., while *Pseudomonas* spp. are effective against *Rhizoctonia* spp., which causes root rot in various crops. Additionally, *Burkholderia* spp. help control *Phytophthora* spp., responsible for blights and rots (81).

Endophytes also engage in parasitism by directly attacking and feeding on pathogens, which limits the spread and growth of these harmful organisms within the plant. Competition mechanisms are another line of defense, where endophytes compete with pathogens for essential resources such as nutrients and space. This competitive exclusion creates an unfavorable environment for pathogens, further protecting the host plant. Collectively, these biocontrol mechanisms help suppress the population of harmful organisms, reduce disease incidence and promote the overall health and growth of the plant (82).

Excessive use of agrochemicals has led to the emergence of resistant phytopathogens, posing environmental and economic risks. The rise of resistant fungal pathogens is particularly concerning, as it undermines the effectiveness of conventional fungicides. Endophytes offer a promising, sustainable alternative for managing plant diseases and reducing reliance on chemical agents (80).

Moreover, endophytes can produce bioactive secondary metabolites with pharmacological properties, enhancing their biocontrol potential (80). This approach presents a viable alternative to chemical fungicides and has potential applications in commercial agriculture (83).

In recent decades, various studies have documented the biocontrol activities of endophytic microbes across multiple crops, as detailed in Table 6.

Production of secondary metabolites

Endophytes, including fungi and bacteria, have been identified as promising sources of high-value plant secondary metabolites (84). These metabolites, such as peptides, are produced by endophytes as part of their symbiotic relationships with host plants (85). However, industrial exploitation of endophytic microbes for metabolite production remains in its infancy, facing challenges like genomic instability and the need for advanced characterization methods (86).

Despite these challenges, the potential of endophytes as "tiny workrooms" for crop secondary metabolite production is compelling and warrants further research. The term "tiny workrooms" refers to endophytes' capability to synthesize secondary metabolites within plant tissues without harming the host. These endophytes produce bioactive compounds like alkaloids, phenolic acids, quinones, steroids, saponins, tannins and terpenoids, which possess antimicrobial, anti-insect and anticancer properties. By acting as miniature biochemical factories, endophytes enhance plant resilience against pathogens and environmental stress through these valuable secondary metabolites (87). Endophytic microorganisms that contribute to secondary metabolite production are regarded as essential agents for enhancing host plant survival and defensive mechanisms. Two theories have been suggested to elucidate how endophytes enhance host plant defenses via chemical mechanisms (88).

The "mosaic theory," proposed by Carroll (89), suggests that endophytes generate a heterogeneous chemical profile within genetically uniform plant organs, making these organs less attractive to herbivores and more resistant to pathogens. For example, endophytes in grasses like *Lolium perenne* (perennial ryegrass) produce loline alkaloids, diversifying the chemical environment among plant tissues. This chemical variability deters herbivores and reduces pathogen susceptibility, enhancing the plant's overall fitness and survival.

In contrast Arnold, Mejía (90) proposes that endophytes act as "acquired immune systems" in host plants. According to this theory, endophytes help the host develop an immune response against potential pathogens. They may produce secondary metabolites that directly inhibit pathogens or trigger plant defense pathways, effectively boosting the plant's immune system. Both theories underscore the essential role of endophytic fungi in supporting host plant chemical defenses. Endophytes enhance plant life by producing secondary metabolites, resulting in a diverse chemical profile or acting as acquired immune systems. Various endophytes are responsible for secondary metabolite production in specific crops (Table 7).

Phytohormone production

Endophytes produce phytohormones such as auxins, gibberellins (GAs), and cytokinins. While the significance of phytohormone production by endophytes, particularly gibberellins, is still not well understood, these molecules serve as necessary chemical signals and messengers that promote plant growth under various environmental conditions (91). A higher number of endophytes are responsible for producing phytohormones in specific crops (Table 8).

Table 6. Biocontrol activities by various endophytes in specific crops

Crop	Endophytes	Pest/Pathogen	References
Soyabean	*Verticillium lecanii*	*Heterodera glycines*	(107)
Chinese cabbage	*Pseudomonas* sp., *Rhizobia* sp., *Bacillus* sp.	*Pectobacterium carotovorum* sub sp. *carotovorum* (Pcc)	(108)
Tomato	*Pseudomonas* sp., *Rhizobia* sp., *Bacillus* sp.	*Alternaria solani*	(109)
Oil palm	*Pseudomonas* sp., *Rhizobia* sp., *Bacillus* sp.	*Ganoderma boninense*	(110)
Banana	*Fusarium oxysporum*	*Radopholus similis*	(111) (112)

Table 7: Secondary metabolites production by various endophytes in specific crop

S.No.	Crop	Endophytes	Beneficial Effects	Reference
1.	Celery cabbage	*Fusarium* E5	Increased production of triterpene and diterpene	(113)
2.	Japanese yew	*Fusarium* sp.	Increased production of paclitaxel	(114)

Table 8: Phytohormone production by various endophytes in specific crop

Crop	Endophytes	Beneficial Effects	Reference
Rice	*Penicillium citrinum* IR-3-3	Showed maximum plant growth and increased production of physiologically active gibberellins	(115)
Rice	*Cladosporium sp.* MH-6	Increased shoot length (12.9 cm) and enhanced physiologically active GAs	(116)
Rice	*Phoma glomerata* LWL2, *Penicillium* sp. LWL3	Increased production of GA and IAA	(99)
Cucumber	*Paecilomyces formosus* strain LHL10	Enhanced shoot length, reduced the effects of salinity by the accumulation of proline and antioxidants	(117)
Soybean, bean and maize	*Purpureocillium lavendulum*, *Purpureocillium lilacinum*, *Metarhizium marquandii*	Increased availability of P and N to the plants and increased production of IAA	(118)

Conclusion

In conclusion, the application of microbial endophytes in agriculture has emerged as an effective technique to augment nutrient availability, increase crop productivity and enhance environmental sustainability. This review has highlighted the complex interactions between rhizobial and non-rhizobial endophytes and their host plants, emphasizing the wide range of benefits these microorganisms offer. Through mechanisms such as biological N fixation, P and K solubilization and micronutrient mobilization, endophytes significantly improve soil nutrient status and promote plant growth.

Although challenges remain in translating laboratory findings into consistent field outcomes, the potential of microbial endophytes to reduce dependence on synthetic fertilizers, minimize environmental impact and improve crop yields is clear. of integrating endophytes into agricultural systems marks a significant step toward more sustainable and productive agroecosystems, providing a promising solution to meet the growing demands for global food security and environmental conservation.

Future perspectives

Future research on rhizobial and non-rhizobial endophytes in nutrient acquisition and crop enhancement should focus on comprehensively examining the endophytic microbes associated with a wide range of food and commercially important crops. This will help expand our understanding of crop-specific plant-microbe interactions. Such knowledge will facilitate the development of customized microbial or biofertilizer formulations tailored to specific crops, potentially maximizing nutrient acquisition efficiency and improving crop yields. Creating these crop-specific biofertilizers offers a significant opportunity to optimize agricultural practices across various cultivation systems.

Moreover, undertaking detailed microflora mapping of endophytes in different crops will provide valuable insights into the unique microbial communities associated with each plant species. This mapping could uncover novel beneficial microorganisms and clarify the synergistic relationships within the plant microbiome. By integrating these research directions, future studies can unlock the full potential of rhizobial and non-rhizobial endophytes in enhancing nutrient acquisition and fostering complementary effects in crops.

Additionally, further research is needed to fully understand the mechanisms underlying the interactions between these endophytes and plants in different soil types.

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References

1. Roberts DP, Mattoo AK. Sustainable agriculture-Enhancing environmental benefits, food nutritional quality and building crop resilience to abiotic and biotic stresses. Agriculture. 2018;8 (1):8. https://doi.org/10.3390/agriculture8010008
2. Doni F, Mispan MS, Suhaimi NSM, Ishak N, Uphoff N. Roles of microbes in supporting sustainable rice production using the system of rice intensification. Appl Microbiol. Biotechnol. 2019;103:5131-42. https://doi.org/10.1007/s00253-019-09879-9
3. Godfray HC, Beddington JR, Crute IR, Haddad L, et al. Food security: the challenge of feeding 9 billion people. Science. 2010;327(5967):812-8.
4. Hannah L, Steele M, Fung E, Imbach P, Flint L, Flint A. Climate change influences on pollinator, forest and farm interactions across a climate gradient. Clim Change. 2017;141:63-75. https://doi.org/10.1007/s10584-016-1868-x
5. Duan Y, Xu M, Gao S, Liu H, Huang S, Wang B. Long-term incorporation of manure with chemical fertilizers reduced total nitrogen loss in rain-fed cropping systems. Sci Rep. 2016;6 (1):33611. https://doi.org/10.1038/srep33611
6. Busby PE, Soman C, Wagner MR, Friesen ML, Kremer J, Bennett A, et al. Research priorities for harnessing plant microbiomes in sustainable agriculture. PLoS Biol. 2017;15(3):e2001793. https://doi.org/10.1371/journal.pbio.2001793
7. Granada CE, Passaglia LM, De Souza EM, Sperotto RA. Is phosphate solubilization the forgotten child of plant growth-

promoting rhizobacteria? Front Microbiol. 2018;9:2054. https://doi.org/10.3389/fmicb.2018.02054

8. Gull A, Lone AA, Wani NUI. Abiotic and Biotic Stress in Plants. In: Bosco de Oliveira A (ed). Abiotic and Biotic Stress in Plants. IntechOpen. 2019;7:1-8. https://doi.org/10.5772/intechopen.85832
9. Singh HB, Management of plant pathogens with microorganisms. Proc Indian Natl Sci Acad; 2014;80(2); 443-454. https://doi.org/10.16943/ptinsa/2014/v80i2/55120
10. Jambon I, Thijs S, Weyens N, Vangronsveld J. Harnessing plant-bacteria-fungi interactions to improve plant growth and degradation of organic pollutants. J Plant Interact. 2018;13 (1):119-30. https://doi.org/10.1080/17429145.2018.1441450
11. Zabalgogeazcoa I. Fungal endophytes and their interaction with plant pathogens: a review. Span J Agric Res. 2008;6:138-46. https://doi.org/10.5424/sjar/200806S1-382
12. Kumar A, Maurya VK, Susmita C, Chuarasiya U, et al. Chapter 15 - Environmental factors and plant-microbes (endophytes) interaction: an overview and future outlook. In: Solanki MK, Yadav MK, Singh BP, Gupta VK (eds). Microbial Endophytes and Plant Growth: Academic Press; 2023;245-57. https://doi.org/10.1016/B978-0-323-90620-3.00009-X
13. Cocking EC. Endophytic colonization of plant roots by nitrogen-fixing bacteria. Plant Soil 2003;252(1):169-75. https://doi.org/10.1023/A:1024106605806
14. Li J, Wang J, Liu H, Macdonald CA, Singh BK. Application of microbial inoculants significantly enhances crop productivity: a meta-analysis of studies from 2010 to 2020. J Sustain Agric Environ . 2022;1(3):216-25. https://doi.org/10.1002/sae2.12028
15. Aguk JA. Evaluate the effect of arbuscular mycorrhizal fungi and Rhizobacteria inoculation on performance of potato (*Solanum tuberosum*). University of Nairobi; 2013.
16. Alori ET, Babalola OO. Microbial inoculants for improving crop quality and human health in Africa. Front Microbiol.. 2018;9:2213. https://doi.org/10.3389/fmicb.2018.02213
17. Fasusi OA, Cruz C, Babalola OO. Agricultural sustainability: microbial biofertilizers in rhizosphere management. Agriculture. 2021;11(2):163.https://doi.org/10.3390/agriculture11020163
18. Owen NL, Hundley N. Endophytes-the chemical synthesizers inside plants. Sci Prog. 2004;87(2):79-99. https://doi.org/10.3184/003685004783238553
19. Pimentel MR, Molina G, Dionísio AP, Maróstica Junior MR, Pastore GM. The use of endophytes to obtain bioactive compounds and their application in biotransformation process. Biotechnol Res Int. 2011(1):576286.
20. Perotti R. On the limits of biological enquiry in soil science. Proceedings of International Society of Soil Science. 1926;2:146-61.
21. Gaiero JR, McCall CA, Thompson KA, Day NJ, Best AS, Dunfield KE. Inside the root microbiome: bacterial root endophytes and plant growth promotion. Am J Bot. 2013;100(9):1738-50. https://doi.org/10.3732/ajb.1200572
22. de Bary A. Morphologie und Physiologie der Pilze, Flechten und Myxomyceten. In: Handbuch der physiologischen Botanik, 2. Bd, 1. Abt. Leipzig, W. Engelmann. 1866;342. https://doi.org/10.5962/bhl.title.120970
23. Petrini O. Fungal Endophytes of Tree Leaves. In: Andrews JH, Hirano SS .(eds). Microbial Ecology of Leaves. Brock/Springer Series in Contemporary Bioscience. Springer, New York, NY. 1991;179-97. https://doi.org/10.1007/978-1-4612-3168-4_9
24. Mitter B, Petric A, Shin MW, Chain PS, et al. Comparative genome analysis of Burkholderia phytofirmans PsJN reveals a wide spectrum of endophytic lifestyles based on interaction strategies with host plants. Front Plant Sci. 2013;4:120. https://doi.org/10.3389/fpls.2013.00120
25. Turner TR, James EK, Poole PS. The plant microbiome. Genome Biol. 2013;14(6):209. https://doi.org/10.1186/gb-2013-14-6-209
26. Nair DN, Padmavathy S. Impact of endophytic microorganisms on plants, environment and humans. Sci World J. 2014;2014 (1):250693. https://doi.org/10.1155/2014/250693
27. Zeffa DM, Fantin LH, Koltun A, de Oliveira AL, Nunes MP, Canteri MG, et al. Effects of plant growth-promoting rhizobacteria on co-inoculation with Bradyrhizobium in soybean crop: a meta-analysis of studies from 1987 to 2018. PeerJ. 2020;8:e7905. https://doi.org/10.7717/peerj.7905
28. Su L, Shen Z, Ruan Y, Tao C, Chao Y, Li R, et al. Isolation of antagonistic endophytes from banana roots against *Meloidogyne javanica* and their effects on soil nematode community. Front Microbiol. 2017;8:2070. https://doi.org/10.3389/fmicb.2017.02070
29. Fisher PJ, Petrini O, Sutton BC. A comparative study of fungal endophytes in leaves, xylem and bark of *Eucalyptus* in Australia and England. Sydowia. 1993;45(2):338-45.
30. Long SR. Genes and signals in the Rhizobium-legume symbiosis1. Plant Physiol. 2001;125(1):69-72. https://doi.org/10.1104/pp.125.1.69
31. Sawada H, Kuykendall LD, Young JM. Changing concepts in the systematics of bacterial nitrogen-fixing legume symbionts. J Gen Appl Microbiol . 2003;49(3):155-79. https://doi.org/10.2323/jgam.49.155
32. Dhole A, Shelat H. Non-rhizobial endophytes in root nodules. MOJ Biol Med. 2018;3(1):1-2. https://doi.org/10.15406/mojbm.2018.03.00064
33. Trujillo ME, Willems A, Abril A, Planchuelo A-Ma, Rivas R, Ludena D, et al. Nodulation of *Lupinus albus* by strains of *Ochrobactrum lupini* sp. nov. Appl Environ Microbiol 2005;71(3):1318-27. https://doi.org/10.1128/AEM.71.3.1318-1327.2005
34. Sy A, Giraud E, Jourand P, Garcia N, Willems A, De Lajudie P, et al. Methylotrophic Methylobacterium bacteria nodulate and fix nitrogen in symbiosis with legumes. J Bacteriol. 2001;183(1):214-20. https://doi.org/10.1128/JB.183.1.214-220.2001
35. Ardley JK, Parker MA, De Meyer SE, Trengove RD, et al. *Microvirga lupini* sp. nov., *Microvirga lotononidis* sp. nov. and *Microvirga zambiensis* sp. nov. are alphaproteobacterial root-nodule bacteria that specifically nodulate and fix nitrogen with geographically and taxonomically separate legume hosts. Int J Syst Evol Microbiol. 2012;62(11):2579-88. https://doi.org/10.1099/ijs.0.035097-0
36. Zakhia F, Jeder H, Willems A, Gillis M, Dreyfus B, De Lajudie P. Diverse bacteria associated with root nodules of spontaneous legumes in Tunisia and first report for nifH-like gene within the genera Microbacterium and Starkeya. Microb Ecol. 2006;51:375-93. https://doi.org/10.1007/s00248-006-9025-0
37. Rivas R, Willems A, Subba-Rao NS, Mateos PF, et al. Description of *Devosia neptuniae* sp. nov. that nodulates and fixes nitrogen in symbiosis with *Neptunia natans*, an aquatic legume from India. Syst Appl Microbiol. 2003;26(1):47-53. https://doi.org/10.1078/072320203322337308
38. Chen W-M, Laevens S, Lee T-M, Coenye T, De Vos P, Mergeay M, et al. *Ralstonia taiwanensis* sp. nov., isolated from root nodules of *Mimosa* species and sputum of a cystic fibrosis patient. Int J Syst Evol Microbiol. 2001;51(5):1729-35. https://doi.org/10.1099/00207713-51-5-1729
39. Yanni YG, Rizk RY, Abd El-Fattah FK, Squartini A, Corich V, et al. The beneficial plant growth-promoting association of *Rhizobium leguminosarum* bv. *trifolii* with rice roots. Funct Plant Biol. 2001;28(9):845-70. https://doi.org/10.1071/PP01069
40. Lupwayi NZ, Clayton GW, Hanson KG, Rice WA, Biederbeck VO. Endophytic rhizobia in barley, wheat and canola roots. Can J

Plant Sci. 2004;84(1):37-45. https://doi.org/10.4141/P03-087

41. Potshangbam M, Devi SI, Sahoo D, Strobel GA. Functional characterization of endophytic fungal community associated with *Oryza sativa* L. and *Zea mays* L. Front Microbiol. 2017;8:325. https://doi.org/10.3389/fmicb.2017.00325
42. Fahde S, Boughribil S, Sijilmassi B, Amri A. Rhizobia: a promising source of plant growth-promoting molecules and their non-legume interactions: examining applications and mechanisms. Agriculture. 2023;13(7):1279. https://doi.org/10.3390/agriculture13071279
43. Biswas JC, Ladha JK, Dazzo FB, Yanni YG, Rolfe BG. Rhizobial inoculation influences seedling vigor and yield of rice. Agron J . 2000;92(5):880-86. https://doi.org/10.2134/agronj2000.925880x
44. Hardoim PR, van Overbeek LS, van Elsas JD. Properties of bacterial endophytes and their proposed role in plant growth. Trends Microbiol. 2008;16(10):463-71. https://doi.org/10.1016/j.tim.2008.07.008
45. De Meyer SE, De Beuf K, Vekeman B, Willems A. A large diversity of non-rhizobial endophytes found in legume root nodules in Flanders (Belgium). Soil Biol Biochem. 2015;83:1-11. https://doi.org/10.1016/j.soilbio.2015.01.002
46. Vandamme P, Goris J, Chen W-M, de Vos P, Willems A. *Burkholderia tuberum* sp. nov. and *Burkholderia phymatum* sp. nov., nodulate the roots of tropical legumes. Syst Appl Microbiol. 2002;25(4):507-12. https://doi.org/10.1078/07232020260517634
47. Srt R, Thangappan S, Uthandi S. Non-rhizobial nodule associated bacteria (NAB) from blackgram (*Vigna mungo* L.) and their possible role in plant growth promotion. Madras Agric J. 2019;451-459. https://doi.org/10.29321/MAJ.2019.000291
48. Valverde A, Velázquez E, Gutiérrez C, Cervantes E, Ventosa A, Igual J-M. *Herbaspirillum lusitanum* sp. nov., a novel nitrogen-fixing bacterium associated with root nodules of *Phaseolus vulgaris*. Int J Syst Evol Microbiol. 2003;53(6):1979-83. https://doi.org/10.1099/ijs.0.02677-0
49. Xu L, Zhang Y, Wang L, Chen W, Wei G. Diversity of endophytic bacteria associated with nodules of two indigenous legumes at different altitudes of the Qilian Mountains in China. Syst Appl Microbiol. 2014;37(6):457-65. https://doi.org/10.1016/j.syapm.2014.05.009
50. Dhole A, Shelat H, Vyas R, Jhala Y, Bhange M. Endophytic occupation of legume root nodules by nifH-positive non-rhizobial bacteria and their efficacy in the groundnut (*Arachis hypogaea*). Ann Microbiol. 2016;66:1397-407. https://doi.org/10.1007/s13213-016-1227-1
51. Velázquez E, Martínez-Hidalgo P, Carro L, Alonso P, et al. Nodular endophytes: an untapped diversity. Beneficial Plant–Microbial Interactions: Ecology and Applications. 2013 :215-35.
52. Zaheer A, Mirza BS, Mclean JE, Yasmin S, Shah TM, Malik KA, et al. Association of plant growth-promoting *Serratia* spp. with the root nodules of chickpea. Res Microbiol. 2016;167(6):510-20. https://doi.org/10.1016/j.resmic.2016.04.001
53. Dhole A, Shelat H. Non-rhizobial endophytes associated with nodules of *Vigna radiata* L. and their combined activity with *Rhizobium* sp. Curr Microbiol. 2022;79(4):103. https://doi.org/10.1007/s00284-022-02792-x
54. Pandya M, Rajput M, Rajkumar S. Exploring plant growth promoting potential of non rhizobial root nodules endophytes of *Vigna radiata*. Microbiology. 2015;84:80-89. https://doi.org/10.1134/S0026261715010105
55. Mushtaq S, Shafiq M, Tariq MR, Sami A, Nawaz-ul-Rehman MS, Bhatti MHT, et al. Interaction between bacterial endophytes and host plants. Front Plant Sci. 2023;13. https://doi.org/10.3389/fpls.2022.1092105
56. Debnath S, Chakraborty S, Langthasa M, Choure K, Agnihotri V, Srivastava A, et al. Non-rhizobial nodule endophytes improve nodulation, change root exudation pattern and promote the growth of lentil, for prospective application in fallow soil. Front Plant Sci. 2023;14. https://doi.org/10.3389/fpls.2023.1152875
57. White JF, Kingsley KL, Verma SK, Kowalski KP. Rhizophagy cycle: An oxidative process in plants for nutrient extraction from symbiotic microbes. Microorganisms. 2018;6(3):95. https://doi.org/10.3390/microorganisms6030095
58. Verma SK, Sahu PK, Kumar K, Pal G, Gond SK, Kharwar RN, et al. Endophyte roles in nutrient acquisition, root system architecture development and oxidative stress tolerance. J Appl Microbiol. 2021;131(5):2161-77. https://doi.org/10.1111/jam.15111
59. Carvalho TLG, Balsemão-Pires E, Saraiva RM, Ferreira PCG, Hemerly AS. Nitrogen signalling in plant interactions with associative and endophytic diazotrophic bacteria. J Exp Bot. 2014;65(19):5631-42. https://doi.org/10.1093/jxb/eru319
60. Saddique MAB, Ali Z, Khan AS, Rana IA, Shamsi IH. Inoculation with the endophyte Piriformospora indica significantly affects mechanisms involved in osmotic stress in rice. Rice. 2018;11(1):34. https://doi.org/10.1186/s12284-018-0226-1
61. Christian N, Herre EA, Clay K. Foliar endophytic fungi alter patterns of nitrogen uptake and distribution in *Theobroma cacao*. New Phytol. 2019;222(3):1573-83. https://doi.org/10.1111/nph.15693
62. Buckley H, Young CA, Charlton ND, Hendricks WQ, Haley B, Nagabhyru P, et al. Leaf endophytes mediate fertilizer effects on plant yield and traits in northern oat grass (*Trisetum spicatum*). Plant Soil. 2019;434:425-40. https://doi.org/10.1007/s11104-018-3848-6
63. Boddey RM, Urquiaga S, Alves BJR, Reis V. Endophytic nitrogen fixation in sugarcane: present knowledge and future applications. Plant Soil. 2003;252(1):139-49. https://doi.org/10.1023/A:1024152126541
64. Rana KL, Kour D, Kaur T, Devi R, Yadav AN, Yadav N, et al. Endophytic microbes: biodiversity, plant growth-promoting mechanisms and potential applications for agricultural sustainability. Antonie van Leeuwenhoek. 2020;113:1075-107. https://doi.org/10.1007/s10482-020-01429-y
65. Gopalakrishnan S, Sathya A, Vijayabharathi R, Varshney RK, et al. Plant growth promoting rhizobia: challenges and opportunities. 3 Biotech. 2015;5(4):355-77. https://doi.org/10.1007/s13205-014-0241-x
66. do Vale Barreto Figueiredo M, do Espírito Santo Mergulhão AC, Sobral JK, de Andrade Lira Junior M, de Araújo ASF. Biological nitrogen fixation: importance, associated diversity and estimates. In: Arora NK (ed). Plant Microbe Symbiosis: Fundamentals and Advances: Springer, New Delhi. 2013;267-89. https://doi.org/10.1007/978-81-322-1287-4_10
67. Kaur T, Devi R, Kumar S, Sheikh I, Kour D, Yadav AN. Microbial consortium with nitrogen fixing and mineral solubilizing attributes for growth of barley (*Hordeum vulgare* L.). Heliyon. 2022;8(4):e09326. https://doi.org/10.1016/j.heliyon.2022.e09326
68. Peoples MB, Craswell ET. Biological nitrogen fixation: Investments, expectations and actual contributions to agriculture. Plant Soil. 1992;141(1):13-39. https://doi.org/10.1007/BF00011308
69. Adhikari P, Pandey A. Phosphate solubilization potential of endophytic fungi isolated from *Taxus wallichiana* Zucc. roots. Rhizosphere. 2019;9:2-9. https://doi.org/10.1016/j.rhisph.2018.11.002
70. Matos AD, Gomes IC, Nietsche S, Xavier AA, Gomes WS, et al. Phosphate solubilization by endophytic bacteria isolated from banana trees. An Acad Bras Ciênc. 2017;89(04):2945-54. https://doi.org/10.1590/0001-3765201720160111
71. Varga T, Hixson KK, Ahkami AH, Sher AW, Barnes ME, Chu RK, et

al. Endophyte-promoted phosphorus solubilization in Populus. Front Plant Sci. 2020;11:567918. https://doi.org/10.3389/fpls.2020.567918

72. Baghel V, Thakur JK, Yadav SS, Manna MC, Mandal A, Shirale AO, et al. Phosphorus and potassium solubilization from rock minerals by endophytic *Burkholderia* sp. strain FDN2-1 in soil and shift in diversity of bacterial endophytes of corn root tissue with crop growth stage. Geomicrobiol J. 2020;37:550-63. https://doi.org/10.1080/01490451.2020.1734691

73. Don NT, Diep CN. Isolation, characterization and identification of phosphate-and potassium solubilizing bacteria from weathered materials of granite rock mountain, That Son, An Giang province, Vietnam. Am J Life Sci. 2014;2(5):282-91. https://doi.org/10.11648/j.ajls.20140205.16

74. Azizah H, Rahajeng SM, Jatmiko YD. Isolation and screening of phosphate and potassium solubilizing endophytic bacteria in Maize (*Zea mays* L.). J Exp Life Sci. 2020;10(3):165-70. https://doi.org/10.21776/ub.jels.2020.010.03.04

75. Yuan Z-S, Liu F, Zhang G-F. Characteristics and biodiversity of endophytic phosphorus-and potassium-solubilizing bacteria in Moso Bamboo (*Phyllostachys edulis*). Acta Biol Hung . 2015;66:449-59. https://doi.org/10.1556/018.66.2015.4.9

76. Warzatullisna W, Fitri L, Ismail YS. Potential of endophytic bacteria from rice root as potassium solvent. Biodiversitas. 2019;20(5):1303-308. https://doi.org/10.13057/biodiv/d200520

77. Singh RK, Singh P, Sharma A, Guo D-J, Upadhyay SK, Song Q-Q, et al. Unraveling nitrogen fixing potential of endophytic diazotrophs of different *Saccharum* species for sustainable sugarcane growth. Int J Mol Sci. 2022;23(11):6242. https://doi.org/10.3390/ijms23116242

78. Vincze É-B, Becze A, Laslo É, Mara G. Beneficial soil microbiomes and their potential role in plant growth and soil fertility. Agriculture. 2024;14(1):152. https://doi.org/10.3390/agriculture14010152

79. Johnstone TC, Nolan EM. Beyond iron: non-classical biological functions of bacterial siderophores. Dalton Trans. 2015;44(14):6320-39. https://doi.org/10.1039/C4DT03559C

80. Segaran G, Sathiavelu M. Fungal endophytes: A potent biocontrol agent and a bioactive metabolites reservoir. Biocatal Agric Biotechnol. 2019;21:101284. https://doi.org/10.1016/j.bcab.2019.101284

81. Pavithra G, Bindal S, Rana M, Srivastava S. Role of endophytic microbes against plant pathogens: a review. Asian J Plant Sci. 2020;19(1):54-62. https://doi.org/10.3923/ajps.2020.54.62

82. Anjum MZ, Ghazanfar MU, Hussain I. Bio-efficacy of *Trichoderma* isolates and *Bacillus subtilis* against root rot of muskmelon *Cucumis melo* L. caused by *Phytophthora drechsleri* under controlled and field conditions. Pak J Bot. 2019;51(5):1877-82. https://doi.org/10.30848/PJB2019-5(13)

83. De Silva NI, Brooks S, Lumyong S, Hyde KD. Use of endophytes as biocontrol agents. Fungal Biol Rev. 2019;33(2):133-48. https://doi.org/10.1016/j.fbr.2018.10.001

84. Venugopalan A, Srivastava S. Endophytes as *in vitro* production platforms of high value plant secondary metabolites. Biotechnol Adv. 2015;33(6):873-87. https://doi.org/10.1016/j.biotechadv.2015.07.004

85. Abdalla MA, Matasyoh JC. Endophytes as producers of peptides: an overview about the recently discovered peptides from endophytic microbes. Nat prod bioprospect. 2014;4:257-70. https://doi.org/10.1007/s13659-014-0038-y

86. Mishra S, Sahu PK, Agarwal V, Singh N. Exploiting endophytic microbes as micro-factories for plant secondary metabolite production. Appl Microbiol Biotechnol. 2021;105(18):6579-96. https://doi.org/10.1007/s00253-021-11527-0

87. Gouda S, Das G, Sen SK, Shin H-S, Patra JK. Endophytes: a treasure house of bioactive compounds of medicinal importance. Front Microbiol. 2016;7. https://doi.org/10.3389/fmicb.2016.01538

88. Kusari P, Kusari S, Spiteller M, Kayser O. Endophytic fungi harbored in *Cannabis sativa* L.: diversity and potential as biocontrol agents against host plant-specific phytopathogens. Fungal Divers. 2013;60(1):137-51. https://doi.org/10.1007/s13225-012-0216-3

89. Carroll GC. Beyond pest deterrence-alternative strategies and hidden costs of endophytic mutualisms in vascular plants. In: Andrews JH, Hirano SS. (eds) Microbial Ecology of Leaves. Brock/Springer Series in Contemporary Bioscience. Springer, New York, NY 1991; 358-75. https://doi.org/10.1007/978-1-4612-3168-4_18

90. Arnold AE, Mejía LC, Kyllo D, Rojas EI, Maynard Z, et al. Fungal endophytes limit pathogen damage in a tropical tree. Proc Natl Acad Sci. 2003;100(26):15649-54. https://doi.org/10.1073/pnas.2533483100

91. Khan AR, Ullah I, Waqas M, Shahzad R, Hong S-J, Park G-S, et al. Plant growth-promoting potential of endophytic fungi isolated from *Solanum nigrum* leaves. World J Microbiol Biotechnol . 2015;31(9):1461-66. https://doi.org/10.1007/s11274-015-1888-0

92. Araújo AEDS, Baldani VLD, Galisa PDS, Pereira JA, Baldani JI. Response of traditional upland rice varieties to inoculation with selected diazotrophic bacteria isolated from rice cropped at the Northeast region of Brazil. Appl Soil Ecol. 2013;64:49-55. https://doi.org/10.1016/j.apsoil.2012.10.004

93. Ji SH, Gururani MA, Chun S-C. Isolation and characterization of plant growth promoting endophytic diazotrophic bacteria from Korean rice cultivars. Microbiol Res. 2014;169(1):83-98. https://doi.org/10.1016/j.micres.2013.06.003

94. Rangjaroen C, Rerkasem B, Teaumroong N, Noisangiam R, Lumyong S. Promoting plant growth in a commercial rice cultivar by endophytic diazotrophic bacteria isolated from rice landraces. Ann Microbiol. 2015;65(1):253-66. https://doi.org/10.1007/s13213-014-0857-4

95. Lucero CT, Lorda GS, Anzuay MS, Ludueña LM, Taurian T. Peanut endophytic phosphate solubilizing bacteria increase growth and P content of soybean and maize plants. Curr Microbiol. 2021;78:1961-72. https://doi.org/10.1007/s00284-021-02469-x

96. Rivas R, Peix A, Mateos P, Trujillo M, et al. Biodiversity of populations of phosphate solubilizing rhizobia that nodulates chickpea in different Spanish soils. In: Velázquez E, Rodríguez-Barrueco C. (eds). First International Meeting on Microbial Phosphate Solubilization. Developments in Plant and Soil Sciences 2007;102:23-33. https://doi.org/10.1007/978-1-4020-5765-6_3

97. Purushotham N, Jones E, Monk J, Ridgway H. Community structure of endophytic actinobacteria in a New Zealand native medicinal plant *Pseudowintera colorata* (Horopito) and their influence on plant growth. Microb Ecol. 2018;76(3):729-40. https://doi.org/10.1007/s00248-018-1153-9

98. Fiuza DAF, Vitorino LC, Souchie EL, Neto MR, Bessa LA, Silva CFd, Trombela NT. Effect of rhizobacteria inoculation via soil and seeds on *Glycine max* L. plants grown on soils with different cropping history. Microorganisms. 2022;10(4):691. https://doi.org/10.3390/microorganisms10040691

99. Waqas M, Khan AL, Kamran M, Hamayun M, Kang S-M, et al. Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. Molecules. 2012;17(9):10754-73. https://doi.org/10.3390/molecules170910754

100. Reis MNO, Vitorino LC, Lourenço LL, Bessa LA. Microbial inoculation improves growth, nutritional and physiological aspects of *Glycine max* (L.) Merr. Microorganisms. 2022;10(7):1386. https://doi.org/10.3390/microorganisms10071386

101. Anandham R, Sridar R, Nalayini P, Poonguzhali S, Madhaiyan M, sa T. Potential for plant growth promotion in groundnut (*Arachis hypogaea* L.) cv. ALR-2 by co-inoculation of sulfur-oxidizing bacteria and *Rhizobium*. Microbiol Res. 2007;162(2):139-53. https://doi.org/10.1016/j.micres.2006.02.005
102. Cui L, Guo F, Zhang J, Yang S, Meng J, Geng Y, Li X, Wan S. Synergy of arbuscular mycorrhizal symbiosis and exogenous Ca^{2+} benefits peanut (*Arachis hypogaea* L.) growth through the shared hormone and flavonoid pathway. Sci Rep 2019;9(1):16281. https://doi.org/10.1038/s41598-019-52630-7
103. Prasad D, Verma N, Bakshi M, Narayan OP, Singh AK, Dua M, Johro AK. Functional characterization of a magnesium transporter of root endophytic fungus *Piriformospora indica*. Front Microbiol. 2019;9:3231. https://doi.org/10.3389/fmicb.2018.03231
104. Sharma N, Varma A. Role of endophytic fungus *Piriformospora indica* in nutrient acquisition and plant health. In: Shrivastava N, Mahajan S, Varma A. (eds). Symbiotic Soil Microorganisms: Biology and Applications. Soil Biology. Cham: Springer International Publishing. 2021:161-69. https://doi.org/10.1007/978-3-030-51916-2_10
105. Sharma A, Johri BN, Sharma AK, Glick BR. Plant growth-promoting bacterium *Pseudomonas* sp. strain GRP3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilzeck). Soil Biol Biochem. 2003;35(7):887-94. https://doi.org/10.1016/S0038-0717(03)00119-6
106. Vishwakarma K, Kumar N, Shandilya C, Varma A. Unravelling the role of endophytes in micronutrient uptake and enhanced crop productivity. In: Shrivastava N, Mahajan S, Varma A. (eds). Symbiotic Soil Microorganisms: Biology and Applications. Soil Biology. Cham: Springer International Publishing; 2021;63-85. https://doi.org/10.1007/978-3-030-51916-2_4
107. Agrios GN. Plant pathology. Elsevier. 2005.
108. Cui W, He P, Munir S, He P, et al. Biocontrol of soft rot of Chinese cabbage using an endophytic bacterial strain. Front Microbiol. 2019;10:1471. https://doi.org/10.3389/fmicb.2019.01471
109. Arab YA, Abd-El-Rahman TG, Eisa N-jMM. Introducing an endophyte for controlling tomato early blight disease. J Plant Prot Pathol. 2009;34(6):6835-42. https://doi.org/10.21608/jppp.2009.208768
110. Sapak Z, Meon S, Ahmad ZAM. Effect of endophytic bacteria on growth and suppression of *Ganoderma* infection in oil palm. Int J Agri Biol. 2008;10: 127-132.
111. Niere BI, Speijer PR, Sikora RA,. A novel approach to the biological control of banana nematodes. In: Deutscher Tropentag 1999 in Berlin Session. Sustainable Technology Development in Crop Production, 1999
112. Pocasangre L, Sikora RA, Vilich V, Schuster RP. Survey of banana endophytic fungi from Central America and screening for biological control of *Radopholus similis*. Acta Hortic. 2000;531:283-90. https://doi.org/10.17660/ActaHortic.2000.531.47
113. Fadiji AE, Babalola OO. Elucidating mechanisms of endophytes used in plant protection and other bioactivities with multifunctional prospects. Front Bioeng Biotechnol. 2020;8:467. https://doi.org/10.3389/fbioe.2020.00467
114. Li Y-C, Tao W-Y. Effects of paclitaxel-producing fungal endophytes on growth and paclitaxel formation of *Taxus cuspidata* cells. Plant Growth Regul. 2009;58:97-105. https://doi.org/10.1007/s10725-008-9355-7
115. Khan SA, Hamayun M, Yoon H, Kim H-Y, Suh S-J, Hwang S-K, et al. Plant growth promotion and *Penicillium citrinum*. BMC Microbiol. 2008;8:231. https://doi.org/10.1186/1471-2180-8-231
116. Hamayun M, Khan SA, Khan AL, Rehman G, Kim Y-H, Iqbal I, et al. Gibberellin production and plant growth promotion from pure cultures of *Cladosporium* sp. MH-6 isolated from cucumber (*Cucumis sativus* L.). Mycologia. 2010;102(5):989-95. https://doi.org/10.3852/09-261
117. Khan AL, Hamayun M, Kang S-M, Kim Y-H, Jung H-Y, Lee J-H, et al. Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10. BMC Microbio. 2012;12:3. https://doi.org/10.1186/1471-2180-12-3
118. Baron NC, de Souza Pollo A, Rigobelo EC. *Purpureocillium lilacinum* and *Metarhizium marquandii* as plant growth-promoting fungi. PeerJ. 2020;8:e9005. https://doi.org/10.7717/peerj.9005