Review Paper:

Bioprospecting of endophytic diazotrophic microbes in sustainable agriculture: Review and prospects

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Abstract
Endophytic diazotrophic bacteria play an important role in developing sustainable modern agriculture. Endophytic bacteria can increase plant growth and yield by exhibiting antibiosis against phytopathogens. Biological mechanisms of atmospheric nitrogen fixation, phosphate solubilization, production of phytohormones and inhibition of plant pathogens and pests promote plant growth avoiding the need for chemical fertilizers and control agents. This review evaluates the groups of different endophytic bacteria, their prospects and challenges for sustainable agriculture.

Several new bacterial strains were protected as bioinoculants or biopesticides. Formulations containing endophytic bacteria mainly were intended for seed coating or spraying and acted directly in the control of pests and diseases, as well as in increasing resistance to environmental stress. In many cases, they performed well in promoting the growth of plants by producing hormones that regulate or increase nutrient uptake. Bioprospecting in the case of this review is a systematic overview of the rational approach in harnessing beneficial plant-associated microbes to ensure food security in the future.

Keywords: Diazotrophs, Endophytes, Growth promotion, Biocontrol, Biofertilizer.

Introduction

The need for the food is increasing as the population rises rapidly each day. The land for farming is not growing with the people and is becoming a limited source with the increasing population and industrialization. Hence, more efficient use of the existing agricultural land should be needed to produce more food from limited sources to fulfil the growing demand by using suitable agricultural practices. Due to the negative impacts of excessive chemical fertilizer and other agrochemicals, it is not an eco-friendly method to achieve a higher yield. Using fertilizers appropriately also affects soil health. Rhizosphere auto-toxicity occurs with the use of pesticides and continuous monoculture cropping. Aquatic ecosystems are also affected due to the mixing of water from agriculturally and chemically treated fields and different water sources.

Therefore, experts concentrate on various opportunities to attain ideal agricultural land usage. Among various alternatives, PGPR attracts more researchers as an environment-friendly way to boost crop production and an efficient option for agrochemicals[57,66]. Microorganisms in the rhizosphere benefit plant growth by positively affecting the host's survival. Plants' growth positively affects the host's survival with the help of plant growth-promoting (PGP) substances. They aid plants in their resistance to abiotic and biotic environmental stress. The beneficial bacteria present on the root or within the rhizosphere are called plant growth-promoting rhizobacteria (PGPR).

The rhizosphere contains these beneficial microbes plenteously, but they are not fully utilized as bio-inoculants to enhance crop yield under environmental pressure. The rhizosphere is home to a treasure trove of different groups of beneficial microbes that work alongside the plant roots through direct or indirect processes. The rhizosphere soil microorganisms are linked to plant development[26,27,57]. To stimulate microbial growth and production, plant roots deliver various organic nutrients viz. sugars and amino acids[66]. The root exudates have the most significant carbon source which is helpful in the bacteria culture. So, the rhizosphere contains many microbial communities that are related to plants. This microbial community is called the rhizo-microbiome. Microorganisms have been reported to enhance the growth of their host plant within the rhizome microbiome, directly or indirectly[11,51,57]. The mutual reciprocation of plant roots and microbes supports the plant's development.

The microorganisms living within the plants or inside the host microenvironment are called endophytes[73,74]. Endophytic bacteria are found everywhere and have high biodiversity. They have many potential characteristics, some of which still need to be studied in detail[26,27]. Endophytes uniquely adopt the particular chemical environment of the host plant[26,27]. As they reside inside the host plant, they have higher nutrient supplements than rhizosphere and phyllosphere bacteria[56,73]. Plant intercellular spaces are rich in nutrients like carbohydrates, amino acids, phosphorous, potassium, chlorine, sulfur, calcium and organic acids.

Hence it is a good site for endophyte multiplication[73,74]. Endophytes enter the plant, remain alive and continue their development by producing different bioactive compounds and hydrolytic enzymes. Their life-sustaining actions aid in the development and growth of plants. Endophytes help the host plant by producing plant-growth regulators, providing immunity to diseases and aiding in phytoremediation[26,27].

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Endophytes can promote plant growth implicitly or explicitly. They can enhance plant development explicitly by producing phytohormones like abscisic acid, cytokinin and indole acetic acid (IAA), nitrogen fixation, phosphate solubilization and forming symbiotic associations. They indirectly help plants to resist biotic stresses by producing antibiotics, HCN, siderophore, cell wall deteriorating enzymes, lipopeptides, unstable compounds and abiotic stresses by immunizing against temperature, salts, pesticides, droughts and metal stresses[21]. They indirectly promote growth by reducing episodes of plant disease. The effects of "endophytes" on the plant are direct and intense as they closely interact with the plants compared to rhizosphere and "phyllosphere" bacteria[73].

Rhizosphere and plant endophytes

The rhizosphere is the region around the plant root system where the root microbiome affects the features of the soil. The rhizosphere is an active region regulated by complex exchanges between plants and microorganisms. The rhizosphere is the storehouse of diverse microorganisms known as rhizobacteria. The rhizospheric microbes found around the plant root surfaces are called rhizobacteria[49]. Most of the endophytic bacteria are found in the roots. Plant roots release many substances such as sugars and amino acids as root exudates. They function as a chemoattractant, helping several microbial communities by stimulating the growth and production of microbes near plant roots. The composition and pattern of root exudates affect microbial growth, activity and population numbers. Changes in soil physical and chemical properties caused by several chemical compounds in the root exudates regulate soil microbial communities.

Plant endophytes are the microbes present inside the plant or host microenvironment. Endophytes enter plant tissues through root hair cells and injury[66]. Under the root hair region and with sufficient injury, they can puncture the epidermis of the lateral root[66]. They enter the plant tissues, transfer to the plant's intercellular spaces and colonize aerial parts of roots by occupying the localized point of entry (Fig. 1)[66,71]. They produce bioactive compounds and hydrolytic enzymes to survive inside the host plant's microenvironment[26,27]. The root exudates are the sources of carbon and nitrogen for the rhizomicrobiome and plants absorb organic molecules derived by microbes for their development[56-58]. They were rooting patterns and the supply of accessible supplements to plants was affected by microbial interactions in the rhizosphere[47]. This symbiotic relationship helps both the plant and endophytes in their development.

Endophytes and their beneficial attributes: Rhizospheric bacteria that occupy the spaces over the roots and boost plant growth are called growth-promoting rhizobacteria (PGPR). They can survive outside and enter the host plant through root hair cells or injury. The PGPR that colonizes and grows at the surface of the host plant's roots, is called extracellular PGPR; the PGPR that grows inside the host plant is called an endophyte. The genera of *Acinetobacter, Micrococcus, Arthrobacter, Azotobacter, Bacillus, Bradyrhizobium, Chromobacterium, Burkholderia, Caulobacter, Enterobacter, Azospirillum, Erwinia, Flavobacterium, Frankia, Klebsiella, Pseudomonas, Rhizobium* and *Serratia* contain more PGPR than others[37,66].

In recent times, many studies have been conducted regarding the functions of endophytes in and around the rhizosphere and the interactions between plants and the endophytes. Researchers today are more attracted to it and give much more attention to developing sustainable agricultural practices due to its positive effects on plant development. Farming frameworks can be improved by using PGPRs, emerging as sustainable agriculture devices[66].

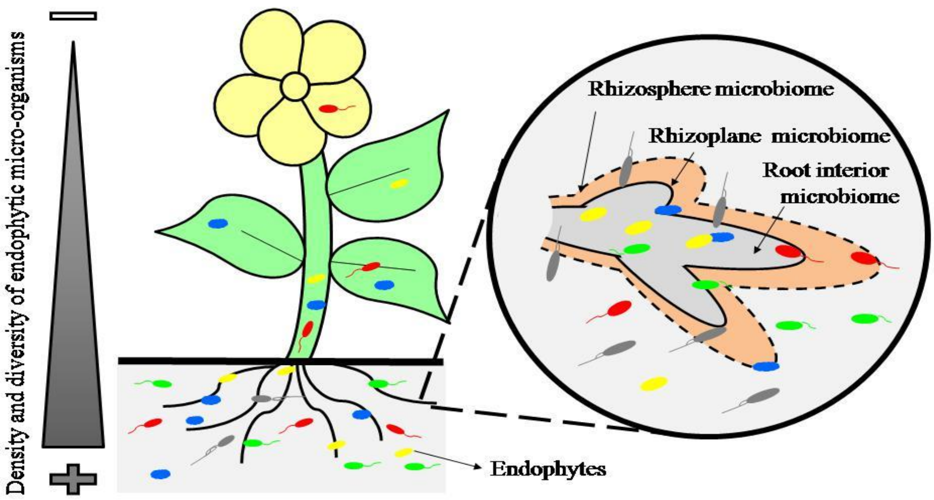

Fig. 1: Occurrence of endophytic microorganisms in the aerial parts and roots of plants originating in the rhizosphere, the rhizoplane and the internal root tissue.
Source: Santos et al[54]

Table 1
Different microbial endophytes and their interactions with host plants for growth-promoting attributes

S.N.	Crop plants used as host	Different endophytes	Growth-promoting attributes of plants
1.	*Lilium lancifolium*	*Paenibacilluspolymyxa* SK1	1-Aminocycloprapane-1-carboxylic acid (ACC), deaminase, indole-3-acetic acid (IAA), siderophores, nitrogen fixation, phosphate solubilization, showed antifungal activities against plant pathogens[36]
2.	Lupine root	*Paenibacillus glycanilyticus* LJ121 and *Pseudomonas brenneri* LJ215	Increase shoot Dry weight, number of nodules per plant, photosynthetic assimilation rate and chlorophyll a and b content and shoot nitrogen and phosphorus content[18]
3.	*Echinacea purpurea*	*Arthrobacter sp.* EpS/L16	IAA production, increase in the number of leaves[44]
4.	Tea (*Camellia sinensis* L.)	*Lysinibacillus sp.* S24 *Brevibacterium sp.* S91	Highest phosphate solubilization, IAA and ammonia production
5.	Maize root	*Enterobacter cloacae* R7	IAA (35.4 mg mL_1), ACC deaminase (+), siderophore (+) and phosphate solubilization (+), alleviating heavy metal stress[1]
6.	Maize root	*Bacillus cereus* N5	IAA (47.3 mg mL_1), ACC deaminase (+), siderophore (+) and phosphate solubilization (+), tolerance of this plant to environmental stresses[1]
7.	Lettuce roots	*Streptomyces exfoliatus* FT05W	solubilize phosphates and synthesize IAA, active against other soil-borne fungal pathogens[12]
8.	Soybean	*Stenotrophomonas rhizophila* ep-17	Beneficial association with *Bradyrhizobium* in the rhizosphere and promote plant growth, nutrient uptake and grown soybean under salt stress condition[16]
9.	Wheat	*Bacillus subtilis* SU47 and *Arthrobacter sp.* SU18	*Bacillus subtilis* SU47 and Arthrobacter sp. SU18[65]
10.	Sugar beat	*Bacillus pumilus* 2-1, *Chryseobacterium indologene* 2-2, and *Acinetobacter johnsonii* 3-1	Increased photosynthetic capacity, increased concentration of carbohydrates[62]
11.	Potato, tomato, Onion, maize, barley	*Burkholderia phytofirmans* strain PsJN	ACC deaminase activity, IAA synthesis[68]
12.	Arabidopsis thaliana	*Pseudomonas syringae*	IAA and abscisic acid biosynthesis[14]
13.	Sugarcane	*Gluconacetobacter Diazotrophicus*	Nitrogen fixation[10]
14.	Rice roots	*Rhizobium leguminosarum*bv. Trifolii	Biological nitrogen fixation[72]

PGPR improves plant growth and development by synthesizing specific compounds necessary for growth, amplifying the absorption of particular additives from the soil, protecting the plant from phytopathogens and decreasing the activity of infectious microbes[7]. The PGPR influences plant development explicitly by producing plant growth-regulating hormones, phosphate solubilization, synthesis of 1-aminocyclopropane-1-carboxylatedeaminase (ACC), nitrogen fixation and implicitly inducing systemic resistance (ISR), while producing antimicrobial metabolites, antibiotics, or siderophores to hinder pathogenic microorganisms[26,27,66].

Some scientific reports disclosed that growth enhancement in crops like peas, rice, wheat, maize, etc., had been done using PGPR[45]. Table 1 represents some endophytes' synopsized notes and their helpful interactions with the host plants.

Mechanism of plant endophytes' interaction for growth promotion: Similar mechanisms are used to promote plant growth by rhizospheric bacteria and endophytes. However, the main difference is that endophytic bacteria are present inside the plant microenvironment and do not face uncontrolled changes in soil conditions. However, the rhizospheric bacteria must adapt to outer changes to survive. Endophytes enhance plant growth through direct or indirect mechanisms.

Direct Mechanism

Nitrogen fixation: Nitrogen-containing chemical fertilizers are used extensively to overcome nitrogen deficiency inside the soil and achieve high yields. Nitrogen-fixing bacteria transform nitrogen into ammonia, which is suitable for plants[2,56-58]. Nitrogen-fixing bacteria can fix environmental nitrogen through a symbiotic relationship with specific plants such as legumes. PGPR produces ammonia and indirectly helps in plant growth. Some ammonia-producing PGPRs are *Bacillus*, *Pseudomonas* and *Serratia*[2,55]. Endophytes in the root nodules of plants promote plant growth. The nitrogen-fixing endophytes Ensifer, Shinella and *Rhizobium tropici* were isolated from root nodules of Vicia[40]. A special symbiotic relationship has been noted in the Rhizobiaceae family of nitrogen-fixing endophytes[67]. Vascular rhizobial endophytes can symbiotically fix nitrogen by diazotrophs in the xylem of the host plant because the xylem is the site for metabolite exchange which is necessary for nitrogen fixation.

For example, *Azorhizobium caulinodans* ORS571 has been reported to secrete cellulases and pectinases to colonize the xylem elements in Sesbaniaro strata to form nodules[10]. *Glucono acetobacter diazotrophicus* (*Acetobacter diazotrophicus*) can help fix nitrogen in sugarcane[42]. Endophytic diazotrophs *Azoarcus* can boost non-legume yields, such as cash crops and nitrogen fixation in Kallar grass[24]. High levels of nitrogenase in the aerenchyma of rice roots expressed by *Azoarcus* spp. are abundant in rice roots[17].

Phosphate solubilization: After nitrogen, phosphorus is essential for plant growth inside the soil. Two soluble forms of phosphorus called monobasic phosphate ions (H_2PO_4) and dibasic phosphate ions (HPO_4) can be taken up by plants. Due to the insoluble forms of phosphorus inside the soil, the plants cannot access it and phosphorus deficiency occurs. Phosphate fertilizers are used on a large scale to supply phosphorus to plants in agriculture. Phosphate fertilizers when used regularly, can harm the soil and our environment because plants absorb the low amount of phosphate from the fertilizer and the soluble resin forms stay inside the soil[3].

Phosphate-solubilizing microbes can alter the insoluble phosphate into its soluble forms and make them available for plants (Fig. 2). *Azotobacter, Burkholderia, Rhizobium, Serratia, Streptomyces, Bacillus, Pseudomonas, Enterobacter, Bradyrhizobium, Cladosporium* etc. are reported as improved phosphate-solubilizing PGPR[8,55].

Phosphate-solubilizing endophytes can enhance the plant's phosphorus supply. Because of the chelation of metal cations embedded with them by low molecular weight acids released by endophytes, phosphorus becomes easily accessible to plants[33]. Some phosphate solubilizing endophytes are *Achromobacter xiloxidans* and *Bacillus pumilus* in sunflower[19] and endophytes isolated from soybean[34].

IAA Production: IAA helps in cell-division, lengthening cells and tissue distinction in plants. Multiple strains of plant growth-promoting bacteria are reported to produce IAA[63]. Several IAA-producing endophytes are *Bacillus aryabhattai, Klebsiella pneumoniae, B. subtilis, Microbacterium trichotecenolyticum and Paenibacillus kribbensis*[29].

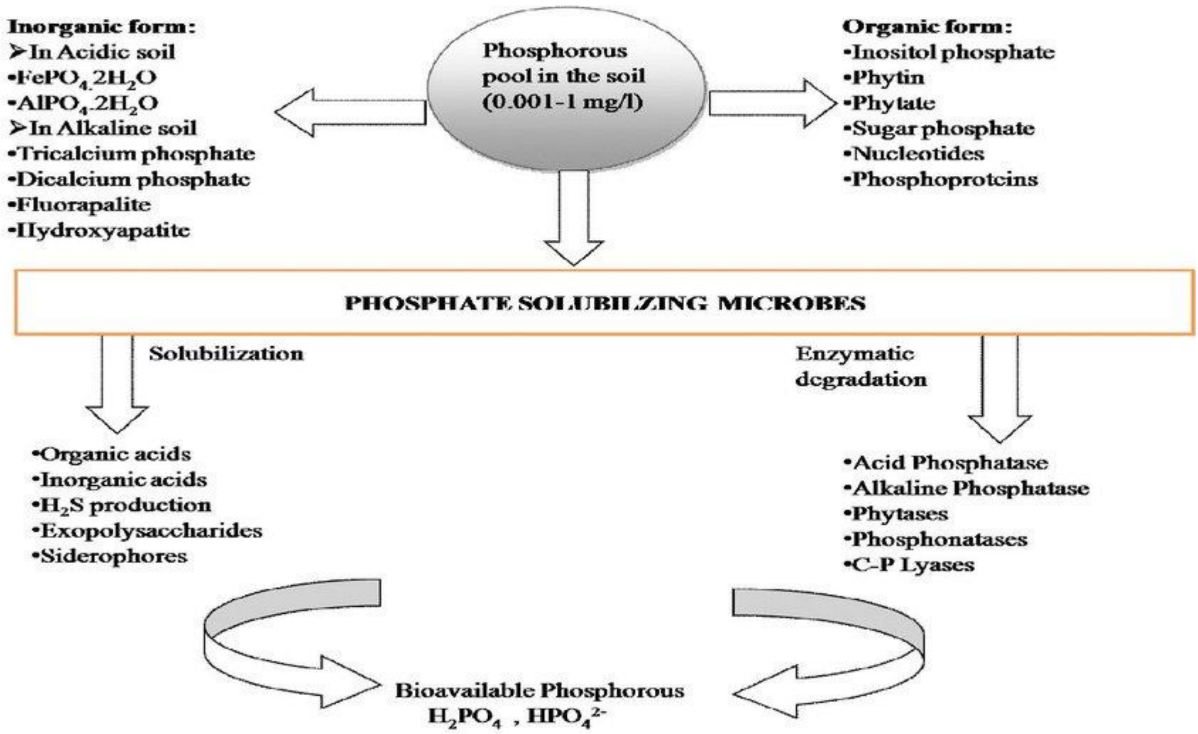

Fig. 2: Mechanism of phosphate solubilization by microorganisms
Source: Kaur and Kaur[31]

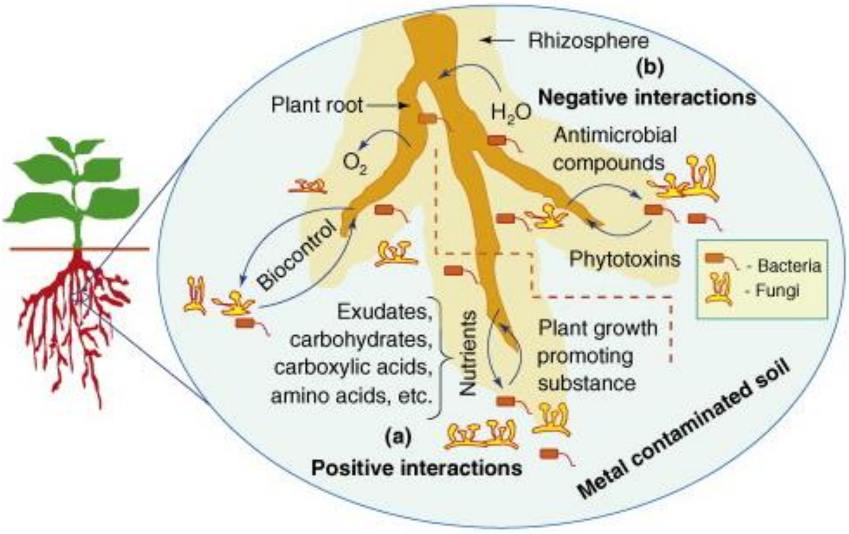

Fig. 3: Potential of siderophore-producing bacteria for improving heavy metal phytoextraction
Source: Rajkumar et al[53]

The natural root exudate tryptophan is used as a precursor in many IAA-producing pathways of endophytes like the indole-3-acetamide (IAM) pathway, the tryptamine (TAM) pathway, the indole-3-pyruvate (IPyA)pathway and the tryptophan sidechain oxidase (TSO) pathway[63]. IAA production has multiple roles in plant development.

ACC deaminase activity: Under adverse conditions, the level of the plant phytohormone ethylene rises and negatively regulates plant growth, promoting fruit ageing and ripening by limiting root growth and auxin transport. Ethylene protects plants from biotic stresses[25].

Under stress conditions, the activity of the primary precursor of ethylene synthesis, 1-aminocyclopropane-1-carboxylate (ACC), increases and a high amount of ethylene production occurs, which leads to the negative growth of the plant[52]. ACC is degraded by various microbes resulting in the elongation of the roots[22,23] and again the plant grows.

Droughts, pathogenic attacks, metal radiation, salt, heat stress etc. are some biotic and abiotic stresses that can be decreased by ACC deaminase[43]. Hence it is called a stress-release enzyme. Plants can grow in stressed conditions due to the ACC deaminase-producing endophytes such as *Enterobacter*, *Klebsiella* and *Pseudomonas*[26,27]. Also, the capability of endophytes to reduce ACC by using them as nitrogen sources can prevent ethylene-mediated plant growth inhibition.

Indirect Mechanism

Production of siderophore: Iron is a micronutrient necessary for plant growth. Fe^{3+}, the natural form of iron, is insoluble in plants. In stressed conditions, plants face iron deficiency. To overcome this deficiency, PGPR produces a siderophore that chelates ferric ions (Fe^{3+}) and helps the plants increase their Fe supply[3,70]. In the rhizosphere, microbes produce siderophores during the metal-stressed condition. Bacterial siderophores help alleviate plant stresses because besides iron, they can form stable complexes with heavy metals, increasing the concentration of soluble metals in the soil (Fig. 3)[53]. Endophytes can survive inside plants with low levels of free iron. This viability made endophytes nickel-resistant (Ni). Some nickel-resistant endophytes are *Sphimgomonas spp.* and *Methylobacterium mesophilic*[37].

HCN production: HCN production is a biocontrol process due to its harmful effects against plant parasites[35]. HCN-producing rhizospheric microbes are essential in protecting the plant from several diseases. In avocados and black grapes, endophytic *Bacillus* produces HCN. *Pseudomonas putida* produces HCN with antibacterial activity against *Escherichia coli* and *Klebsiella pneumoniae* and antifungal activity against *Pythium ultimum*[48]. Endophytic bacteria such as *Pseudomonas* and *Serratia* isolated from various plants also improve seed germination, seedling length and plant growth in oilseed rape and tomato. Also, seeds treated with endophytes can reduce disease caused by vascular wilt pathogens such as *Verticillium dahlia* and *Fusarium oxysporum f. sp. lycopersici (Sacc.).* Plants can resist soil-borne pathogens cultured in their vascular tissues, thanks to induced resistance produced by endophytes[50].

Cell wall - degrading enzymes: Endophytes produce hydrolytic enzymes to degrade cellular components such as chitin, hemicellulose, cellulose, proteins and DNA[46] which are important for colonizing the plant roots[55,64]. While colonizing, the endophytes dissolve plant cell walls by producing enzymes.

Plant pathogens such as fungi and oomycetes can be suppressed directly by disintegrating their cell walls with hydrolytic enzymes[28]. The ability of endophytic enzymes to degrade the glycosidic bonds of the fungal cell wall component chitin makes it a biocontrol agent[6].

Chitinase, protease, glucanase and cellulase are important among various hydrolytic enzymes due to their ability to dissolve the cell wall of fungi[59]. Some examples of endophytic bacteria that can be used as biocontrol agents are *Enterobacter, Pseudomonas, Burkholderia, Bacillus and Azospirillium*[41,55].

Endophytes as biocontrol against phytopathogens: Plant diseases caused a 10–16% reduction in global food production. Microbes like nematodes, bacteria, fungi, protozoa and viruses are the causative agents of diseases in plants. Fungal pathogens primarily affect plants by infecting the majority of plant parts including roots, stems, leaves, flowers and fruits. Endophytes can be used to reduce these plant diseases due to their positive effects on plant growth. Endophytic bacteria live inside the plant tissues with phytopathogens in the same microenvironment and act against bacterial pathogens as biocontrol agents. Plant-beneficial endophytic bacteria can inhibit fungal, viral and bacterial pathogens and protect the plant from diseases (Fig. 4).

Fruitful effects from endophytic bacteria are analogous to those of rhizospheric bacteria; however, endophytic bacteria are more fitting as biocontrol agents due to their ability to transmit to the next generation. Fungal endophytes also present inside the host plant can act as biocontrol agents. Fungal endophytes benefit the plant by promoting growth, improving resistance to multiple stressors and protecting it from diseases and insects.

Recently, many researchers have studied the effects of endophytes as a biocontrol agent for pathogens and insects[20] and reported their successful applications to plant protection. A few documented bacterial and fungal endophytes as biocontrol agents are listed in tables 2 and 3. The results uphold the hypothesis that endophytic bacteria act as biocontrol agents in plants, but the complex mechanism, the biocontrol activity and the inter-species signaling pathways of endophytic bacteria engaged in biocontrol activities have yet to be explained. Therefore, more studies are needed for the hands-on use of endophytes as biocontrol agents.

Conclusion

Endophytes have attracted many researchers due to their ability to enhance plant growth through active or passive mechanisms. For a sustainable future, these are preferable alternatives to chemicals. In the coming future, tackling the environmental degradation caused by agrochemicals will be our utmost responsibility and endophytes can play a pivotal role in agriculture. However, there are notable gaps in our understanding of endophytes such as turning rhizospheric microbes into endophytes, the plant adapting the endophytes and integrating and using them to fight pathogens. To fill such gaps, the need of the hour is to establish an understanding of the interactions of endophytes, plants, the environment and phytopathogens. Although *in vitro* experiments are conducted on time and under standardized conditions, field experiments under a variety of environmental conditions are also required to develop a proper method of using endophytes for crop improvement in agriculture.

Table 2
Different potential endophytic bacteria used as biocontrol agents for different phytopathogens

S. N.	Host plants	Endophytic bacteria	Target pathogens
1	*Panax ginseng*	*P. polymyxa GS01*	*Rhizoctoniasolani*
2	*Panax ginseng*	*Bacillus sp. GS07*	*R. solani*
3	*Panax ginseng*	*Pseudomonas poae JA01*	*R. solani*
4	*Panax notoginseng*	*B. amyloliquefaciens sub sp. plantarum*	*Fusarium oxysporum, Ralstonia sp., Meloidogyne hapla*
5	*Panax notoginseng*	*B. methylotrophicus*	*F. oxysporum, Ralstonia sp., M. hapla*
6	*Triticum aestivum*	*B. subtilis*	*Gaeumannomycesgraminisvar. tritici*
7	*Platycodon grandiflorum*	*B. licheniformis*	*Phytophthora capsici, F. oxysporum, R. solani, Pythium ultimum*
8	*Platycodon grandiflorum, Codonopsislanceolata*	*B. pumilus*	*P. capsici, F. oxysporum, R. solani, P. ultimum*
9	*Manihot esculenta*	*Paenibacillus sp.*	*R. solani*
10	*Piper nigrum L*	*P. aeruginosa*	*P. capsici*
11	*Piper nigrum L*	*P. putida*	*P. capsici*
12	*Piper nigrum L*	*B. megaterium*	*P. capsici*
13	*thaliana*	*thuringiensis KB1*	*F. oxysporum, P. syringaepv. Tomato DC3000*
14	*thaliana*	*Rhodococcus sp. KB6*	*Ceratocystis fimbriata, P. syringaepv. tomato DC3000*
15	*Capsicum annuum*	P. polymyxa AC-1	*P. capsici, C. fimbriata, P. syringaepv. tomato DC3000*

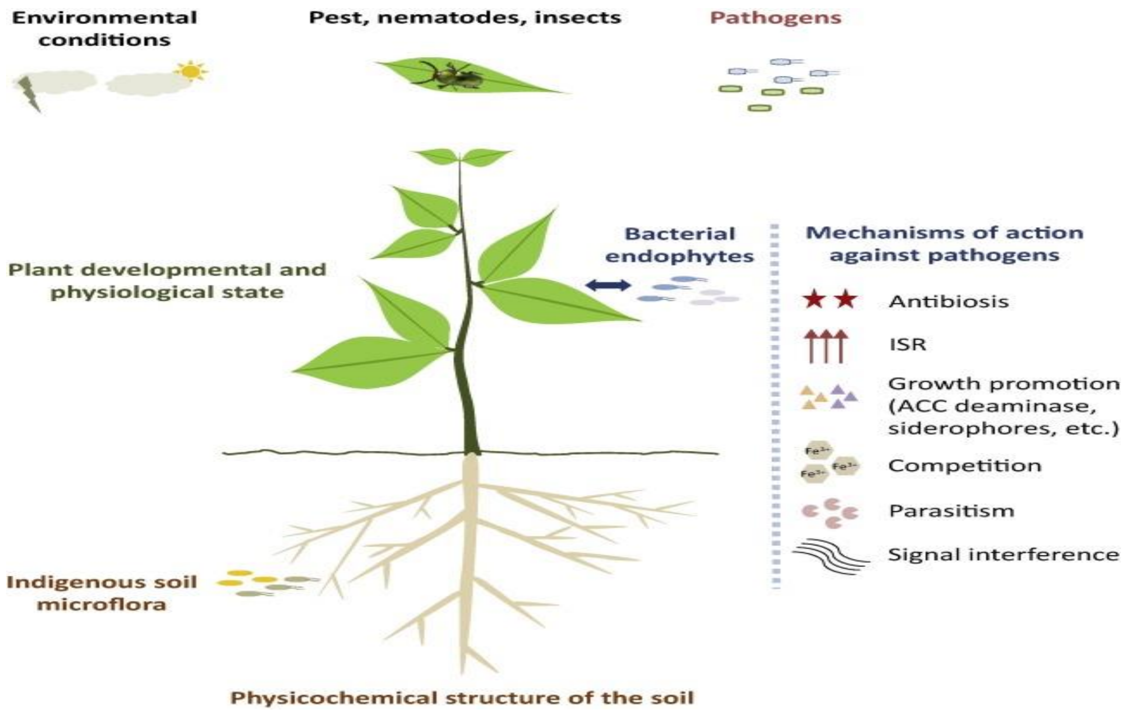

Fig. 4: Bacterial endophytes as potential biocontrol agents
Source: Kaouthar et al[30]

Table 3
List of different plant endophytic fungi used as biocontrol agents against phytopathogens (Gao et al[20])

S. N.	Host plant	Fungal endophyte	Target pathogens
1	Maize	*Acremonium zeae*	*Aspergillus flavus, Fusarium verticillioides*[69]
2.	Rice	*Trichoderma* sp.	*Sclerotium rofsii, Sclerotium oryzae, Rhizoctonia solani* [59]
2	Rehmanniagultinosa	*Vertidillium*sp.	*Pyriculariaoryzae*P-2b
3	*Cassia spectabilis*	*Phomopiscassiae*	*Cladosporium sphaerospermum, Cladosporium cladosporioides*[61]
4	*Tropical tree*	*Muscodoralbus*	*Stachybotryschartarum*[5]
5	*Taxus cuspidata*	*Periconia sp.*	*Bacillus subtilis, Staphylococcus aureus, Klebsiella pneumoniae, Salmonella typhimurium*[32]
6	*Urospermumpicroides*	*Ampelomyces sp.*	*Staphylococcus aureus, S. epidermidis, Enterococcus faecalis*[40]

Also, to minimize the economic and environmental costs, the commercialization of endophytes and endophytic products is needed. Despite these gaps, endophytes are sustainable agriculture's most significant substitute for harmful and toxic chemical fertilizers.

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