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A study on the potential of endophytic bacteria to promote plant growth: Uses in agriculture and future directions

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Abstract

The increasing demand for chemical-free fertilizers in agriculture arises from the adverse effects of chemical fertilizers on both human and animal health as well as environmental pollution. To address these issues, plant-based microorganisms offers a promising solution for developing environmentally sustainable biofertilizers. Among these microorganisms, endophytic bacteria, living within plant tissues without harming the host plant, shows exceptional qualities that promote plant growth. Notably, these bacteria produce phytohormones, ammonia and are capable of minerals solubilization and nitrogen fixation. Additionally, endophytic bacteria synthesize hydrolytic enzymes, produce siderophores and exhibit antimicrobial activity against pathogens. These characteristics significantly enhance the growth and development of host plants and improve their tolerance to environmental stresses. This manuscript aims to provide a comprehensive review of the plant growth-promoting activities of endophytic bacteria, detailing their diversity and isolation from various plants. It also explores potential future directions in this emerging field of research, envisioning the development of endophytic bacterial strains that could replace traditional chemical fertilizers. Future research endeavours hold the promise of discovering novel and effective endophytic bacterial strains, potentially leading to a sustainable shift in agricultural fertilization practices.

Keywords

Endophytic bacteria; plant growth promotion activity; abiotic stress tolerance; disease management; diversity; phosphate-solubilization

Introduction

Ensuring food safety for the growing global population is a critical priority and strengthening agriculture is essential to achieving this goal (1). To address the global challenges, chemical fertilizers are often used to enhance productivity, improve crop quality and extend crop shelf life. However, these practices come with significant drawbacks, including ecosystem degradation, climate change, soil erosion and reduced biodiversity (2). Environmental friendly biofertilizers offers a sustainable alternative to chemical fertilizers. A biofertilizers is a material containing living microorganisms that, when applied to soil, plant surfaces or seeds, colonises the rhizosphere or the interior of the plant. This colonization promotes growth by increasing the availability of primary nutrients to the host plant (3). Innovative approaches utilizing microbes are increasingly recognized as effective means to mitigate the negative impacts of traditional agricultural practices (4). Plant-associated microbes represent a vast and underutilized resource of unique phytochemical compounds, biofertilizers and growth promoters that offer sustainable and natural alternatives to agrochemicals (2). Plant growth-promoting rhizobacteria (PGPR), found in the rhizosphere, plays a crucial role in plant growth and development. Their functions include phosphate solubilization, nitrogen fixation and symbiosis. PGPR also enhance plant defence by developing systemic resistance against various disease and pests (5). Another important group of microorganisms, known as endophytes, reside within plant tissues and contribute significantly to plant growth and development. The term "endophyte", first introduced by De Barry in 1866, refers to any organism—bacteria, fungi, or their combinations—that multiplies intracellularly or intercellularly within host plants at least once during its lifecycle without causing visible symptoms of disease (6). Endophytic bacteria, which are harmless microorganisms residing within plant hosts are well-known for their role in supporting plant growth and development. These bacterial endophytes colonize the interior plant tissues without causing significant morphological changes or disease symptoms (7). Some endophytic bacteria are attracted to plants by root exudates, while others are seed-borne. Effective colonization by endophytes requires compatible plant-microbe interactions (8). Endophytic bacteria promote plant growth directly by fixing atmospheric nitrogen, absorbing phosphorus, potassium and zinc, producing molecules that chelate iron and secreting various phytohormones such as auxins, ethylene, gibberellins and cytokinins (Fig. 1) (9). Indirectly, they contribute to plant resistance or tolerance against biotic and abiotic stresses through the production of siderophores, the release of antimicrobial compounds, competition for resources and space and the modulation of the plant's resistance (Fig. 1) (10). Endophytic bacteria can be isolated from surface-sterilized plant tissues, including roots, stems, leaves and occasionally from flowers, fruits and seeds. They are present in almost all plants (11). Roots serve as the primary habitat and entry point for bacterial endophytes, with root hairs, root fractures or wounds caused by nematode or microbial activity providing main routes for bacterial colonization (1). The interaction between the host plant and endophytic bacteria can be both mutualistic and antagonistic. The presence of endophytic bacteria is influenced by temporal and environmental factors, as endophytic populations vary between different plants and species, with certain plant species harbouring unique populations of endophytes in diverse environments (12). Endophytic bacteria can be isolated using various selective media and techniques, and their plant growth-promoting activities can be analyzed through analytical and molecular technologies (13).

The relationship between endophytic bacteria and host plants remain a largely unexplored field of research.

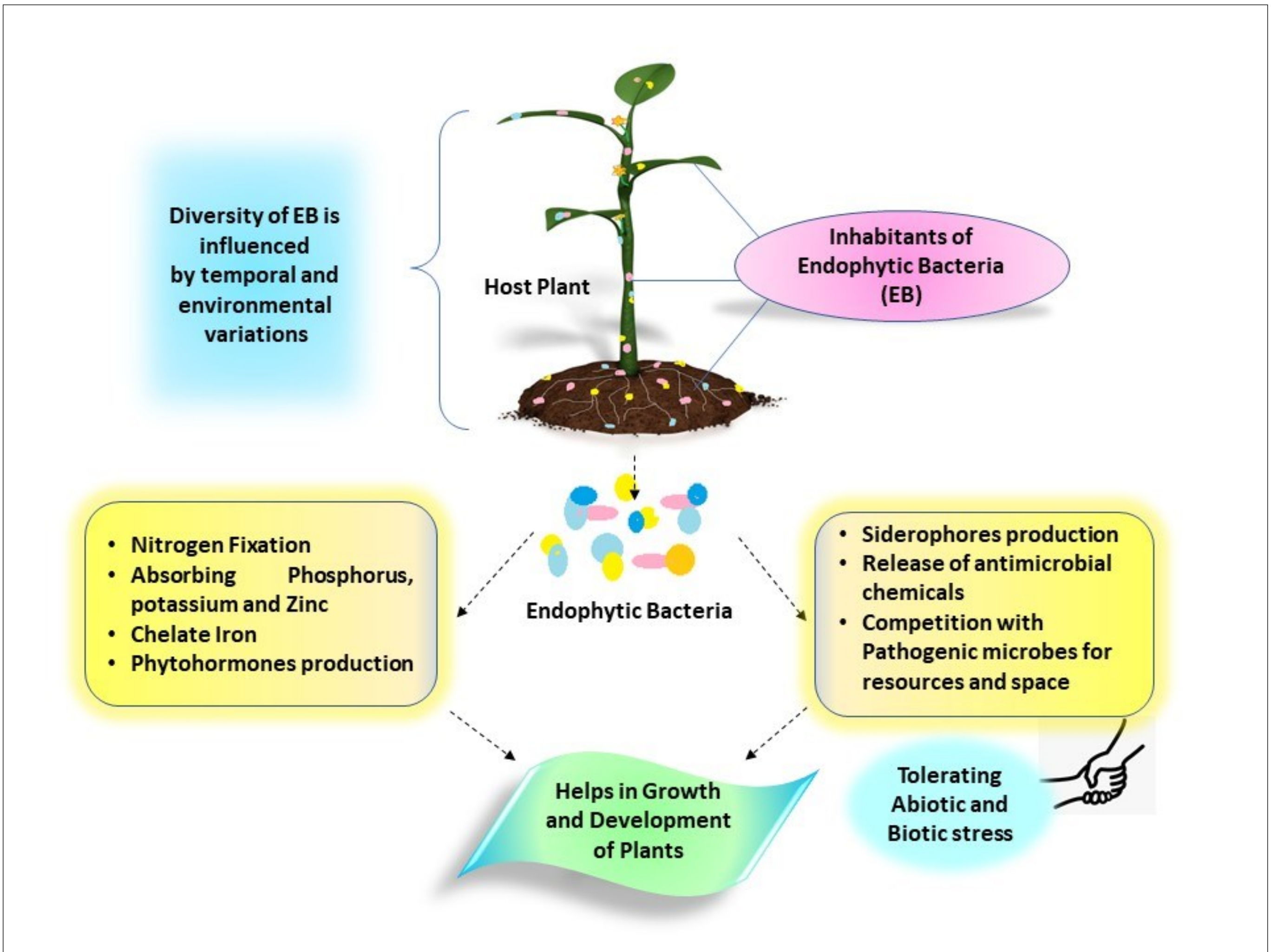

Fig. 1. The role of endophytic bacteria in plant growth and development.

The specific bacterial genes responsible for colonizing the host plant's genome are still unknown (14). However, some genes in bacterial endophytes have been identified as playing a role in promoting plant growth. For example; nifH gene was found in *P. cichorii* and other plant growth-promoting genes like ipdC, asb and AcPho were detected in different endophytic bacteria isolated from the host plant *Passiflora incarnata* (15). Endophytic bacteria support the growth and development of host plant under both normal and stressed conditions. Several bacterial genera, including *Pseudomonas*, *Enterobacter*, *Bacillus*, *Klebsiella* and *Burkholderia,* have been shown to aid in plant growth and development in these conditions (16). These microbes produce a variety of bioactive substances that can benefit the host plant by significantly influencing its interactions with the environment, enhancing defense and adaptability. The defense mechanisms of endophytic bacteria support the host plants growth and development by protecting against pathogens, insects, nematodes, etc (17).

The primary aim of this review is to describe the various plant growth- promoting activities of endophytic bacteria isolated from different plants, including minerals solubilisation, phytohormones production and nitrogen fixation. This review also provides insights into how these microbes supports the host plant by activating defense mechanisms and enhancing tolerance to various environmental stresses through the production of bioactive compounds.

Isolation of endophytic bacteria

The most critical step in isolating endophytic bacteria is the surface sterilization of plant tissues to eliminate epiphytes. To achieve thorough surface sterilization while minimizing harm to the diversity of endophytes, it is crucial to use the appropriate sterilant solution, concentration and exposure time. Commonly used surface sterilants include formaldehyde (40 %), ethanol (70 %-90 %), sodium hypochlorite (2 %–10 %) and mercuric chloride (0.1 %) (18). Plant tissues showing visible surface damage are excluded from the isolation process of endophytic bacteria.

For example, endophytic bacteria were isolated from the leaves of common bean using 70 % alcohol for 1 min, 2.5 % sodium hypochlorite (Cl^-) for 4 min and ethanol for 30 sec, followed by 3 rinses in sterile distilled water (19). Different plants and plant parts require different sterilization treatments (Table 1). Endophytic bacteria were extracted from the roots of the medicinal plant *Alkanna tinctorial* using 70 % ethanol for 5 min, 1.4 % NaOCl for 20 min and 2 % $Na_2S_2O_3$ for 10 min (20). In contrast, 70 % ethanol and 0.5 % NaOCl were used to isolate endophytic bacteria from the roots of *Momordica charantia* L. Endophytic bacteria were isolated from crushed root, transverse section of the roots and root fragments (21).

Endophytic bacteria can also be isolated from a plant's apoplastic fluid. For instance, *Alcaligenes* sp. MZ895490 and *Bacillus amyloliquefaciens* MZ895491 were isolated from the apoplastic fluid of maize root and leaves. To isolate endophytic bacteria from apoplastic fluid, the plant tissue is surface sterilised and apoplastic fluid is extracted by immersing small plant fragments in KCl and applying pressure until the tissue darkens. The extraction is then completed by centrifugation (22).

Endophytic bacteria were extracted from various plant species' leaves, stems, roots, flowers and seeds (23). The plant tissue pieces were placed on media plates and aliquots of the sterile distilled water used in the final rinse were also plated on the same medium to ensure the effectiveness of the sterilization process. After being incubated at 28 °C for 3 days, the plates were checked for growth (24).

Diversity of endophytic bacteria

Endophytic microbes resides within the internal tissues of plants without causing harm to their host. They play vital roles in the growth, development and defense processes of plants (25). Endophytic bacteria are highly diverse, with each species exhibiting specific adaptations to its host plant (26). Due to the highly selective conditions of the rhizosphere, it has been found that plant variety significantly influences the diversity, composition, network and function of microbial community (27).

Endophytic bacteria typically enter plants through the root zone and their ability to colonize the host endophytically is controlled by various bacterial characteristics. The complex process of colonization usually begins at the roots, where endophytic bacteria must recognize specific chemicals in the exudates from the roots. These exudates are produced by plants to interact with beneficial microbes for their ecological advantage (25).

The colonization process involves several stages: the bacteria first identify root exudates and move toward the plant, then attach to the root surface. This is followed by the formation of biofilms that invade the root surface, leading to the colonization of the plant's internal tissues. The biomolecules involved in these stages can influence

Table 1. Surface sterilization of different plant parts for isolation of endophytic bacteria.

Plant/Plant organs	Sterilant	Concentration	Exposure	References
Leaves of common bean	Alcohol	70 %	1 min	(19)
	Sodium hypochlorite	2.5 % Cl^-	4 min	
	Ethanol		30 sec	
Roots of medicinal plant, *Alkanna tinctoria*	Ethanol	70 %	5 min	(20)
	NaOCl	1.4 %	20 min	
	$Na_2S_2O_3$	2 %	10 min	
Roots of *Momordica charantia*	Ethanol	70 %	-	(21)
	NaOCl	0.5 %	-	

gene expression in both the host plant and the endophytic bacteria (28). Plants detect bacteria using pattern-recognition receptors (PRRs) that recognize microbial- or pathogen-associated molecular patterns (MAMPs/PAMPs). The plant's innate immunity is triggered by early signaling, which begins with PRRs, a class of cell surface recognition proteins. The 2 most well-characterized MAMPs/PAMPs are elongation factor Tu (EF-Tu) and the flagellin protein (flg22). Most of the pathways targeted by miRNAs for plant defence systems are blocked during the development of symbiosis, which would have otherwise prevented endophyte proliferation (29).

Endophytic bacteria belong to various taxonomic groups, including the Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes (30). This taxonomic diversity is linked to the wide range of ecological niches provided by different host plant species. Studies have shown that the host cultivar and season are the most significant factors influencing mulberry endophytic bacterial populations. In particular, spring samples exhibited more bacterial operational taxonomic units (OTUs), higher α-diversity and greater bacterial community complexity compared to autumn samples. An analysis of the taxonomic composition of endophytes revealed that Proteobacteria (at the genus level: *Pantoea* and *Pseudomonas*) were predominant in autumn, whereas Proteobacteria (at the genus level: *Methylobaterium*) and Actinobacteria were more abundant in spring (31).

The diversity of flora and microbial ecosystems is greater due to climatic variations. The geographical diversity of host plants is closely linked to their physiological diversity. The presence of endophytic actinobacteria in plants from various climates, including saline habitats, aquatic ecosystems and other ecological niches, highlights the ubiquity of these organisms (32). It was previously observed that *Populus trichocarpa* plants exhibited difference in diversity when grown in native, nutrient-limited habitats, which ranged from hot-dry riparian zones to riparian zones with mid-hot-dry and moist climates. Alpha-diversity measurements indicates that plants in hot, dry areas had lower levels of diversity compared to those in mid-hot-dry and moist climates. Beta-diversity measurements revealed substantial differences in bacterial composition among the sampling sites (33). A study on the diversity of endophytic bacteria linked to the leaves of *Cinnamomum camphora* (L.) Presl., across three seasons—spring (April), summer (July) and early winter (October)—found that the most diverse endophyte samples were collected in October (34). Additionally, even within the same grapevine cultivars, variations in the endophytic bacterial microbiota were observed in the shoot xylems, depending on the cultivar, the grapevine-growing location and the stage of shoot growth (35).

Some bacterial strains are more commonly associated with particular plant species than others. This is because plants can release large amounts of photosynthates or other compounds from their roots, which can influence rhizosphere microbial communities. Proteins, amino acids and organic acids found in root exudates may have a role in attracting bacterial endophytes from the rhizosphere (10). Different types and functions of endophytic bacteria were observed in various tissues of the same plant. For instance, in the rice plant, it was reported that root tissues contained 4 types of isolates with a population density of $1.526x10^5$ CFU/g, while the leaf tissue had 2 types of isolates with a population density of $0.0395x10^5$ CFU/g. This indicates that the diversity and population density of endophytic phosphate-solubilizing bacteria were higher in the root tissue compared to the leaf tissue. Conversely, while the leaf tissue had a lower population density of $5.976x10^5$ CFU/g compared to 11.55x105 CFU/g in the root tissue, the diversity of endophytic nitrogen-fixing bacteria was higher in the leaf tissue, consisting of 5 types compared to 3 types in the root tissue (36).

Research has shown that the diversity and richness of the endophytic bacterial community in *Dendrobium* stems are influenced by stem length. Specifically, Group J having 10-15 cm of stems exhibited the highest endophytic bacterial diversity and richness, indicating a significant difference from other stem length groups (37). Similarly, *in-vitro* wheat cultures subjected to drought stress exhibited alterations in endophytic bacterial diversity. The study revealed that these variations in bacterial endophytes were more closely associated with the drought -resistant characteristics of the wheat variety being studied than with the stress conditions themselves (38). Exploring the diversity of endophytic bacteria could contribute to the development of sustainable farming practices that may reduce or replace the need for pesticides and chemical fertilizers.

Plant growth promotion mechanisms

Endophytic bacteria employ various strategies to promote plant growth, such as:

Nitrogen fixation

Nitrogen is the most critical nutrient limiting plant growth. Since plants cannot directly utilize atmospheric N_2, they rely on externally fixed nitrogen for their growth and development. For plants to use atmospheric N_2, it must first be converted into ammonia (39). Nitrogen-fixing microbes absorb nitrogen from the atmosphere when there is a lack of excess mineral nitrogen compounds in the environment (40). Endophytic bacteria, which are widely distributed and adaptable, play a crucial role in nitrogen fixation within plants. To assess the impact on enzymatic activity and biomass associated with nitrogen and carbon metabolism, sugarcane cultivars were inoculated with the endophytic nitrogen-fixing bacteria *Klebsiella variicola* DX120E. It enhanced the enzymatic activity linked to gluconeogenesis and nitrogen metabolism. The inoculation also enhanced the plant's height, cane juice Brix, biomass, chlorophyll content and soluble sugar levels (41). The amount of nitrogen fixed by these bacteria has been measured using various direct and indirect methods, such as the robust and precise 15N isotopic dilution test and the rapid but indirect acetylene reduction assay (42). Nitrogen-fixing endophytic bacteria, including species like *Burkholderia*, *Rhizobium*, *Pseudomonas*, *Bradyrhizobium*, *Bacillus*, *Frankia*, *Enterobacter* and *Azospirillum*, have been reported in several host plants (43).

Minerals solubilization and availability

Phosphorus is a key element necessary for plant growth, but the bioavailability of this vital macronutrient in soil is often reduced due to its tendency to form complexes with calcium, iron and aluminum. To enhance crop productivity, phosphate fertilizers are frequently used in agriculture. However, excessive use of these fertilizers had led to environmental problems, such as contamination of surface and ground waters, eutrophication of water bodies and the occurrence of algae blooms in lakes and oceans (44). Endophytic bacteria can increase the solubility and bioavailability of essential nutrients like phosphorus, potassium and zinc in the rhizosphere, thereby facilitating their uptake by plants (45). For plants to absorb phosphorus, it must be in the form of orthophosphate anions (46). Endophytic bacteria achieve this by secreting organic acids into the soil, which dissolve phosphate complexes and convert them into ortho-phosphate, making them available for plant absorption (Fig. 2). For examples, endophytic bacteria like *Pseudomonas fluorescens* and *Pseudomonas* sp. are known to produce gluconic acid, which aids in phosphate solubilization (Table 2) (47). One of the primary mechanisms through which endophytic bacteria solubilize insoluble phosphate is by lowering the pH of the soil through the production of organic acid (44). Additionally, *Aneurinibacillus* sp. and *Lysinibacillus* sp., isolated from banana roots, have demonstrated significant phosphate solubilization ability (Table 2) (48). Pikovaskaya's medium is used to determine the phosphate solubilization abilities. Pikovskaya's agar medium is a selective medium for isolating phosphate-soluble microorganisms. The isolates are inoculated on PVK medium and incubated at 28 °C for approximately 5 to 7 days. The presence of a clearing zone around the colony indicates the ability to solubilize phospahte (49). Further assessment of phosphate solubilization is conducted using National Botanical Research Institute Phosphate (NBRIP) media, supplemented with various phosphorus sources like $Ca_3(PO4)_2$ and Fe_3PO_4 (48). It has been observed that underground plant tissues contained a higher concentration of phosphate-solubilizing endophytic bacteria compared to above-ground tissues (36). Phosphate solubilizing microorganisms (PSM) not only increase the availability of soluble phosphate but also enhance biological nitrogen fixation, thereby promoting plant growth. Studies have reported increased production of rice, maize and other cereals when inoculated with phosphate-solubilizing bacteria (50).

Zinc is an essential micronutrient required for optimal plant growth. Zinc-solubilizing bacteria can serve as an alternative to zinc supplements by converting applied inorganic zinc into soluble forms (8). To evaluate the zinc-solubilizing capacity of bacterial isolates *in vitro*, they were inoculated on Tris-minimal agar medium supplemented with 0.1 % zinc in the form of carbonate, phos-

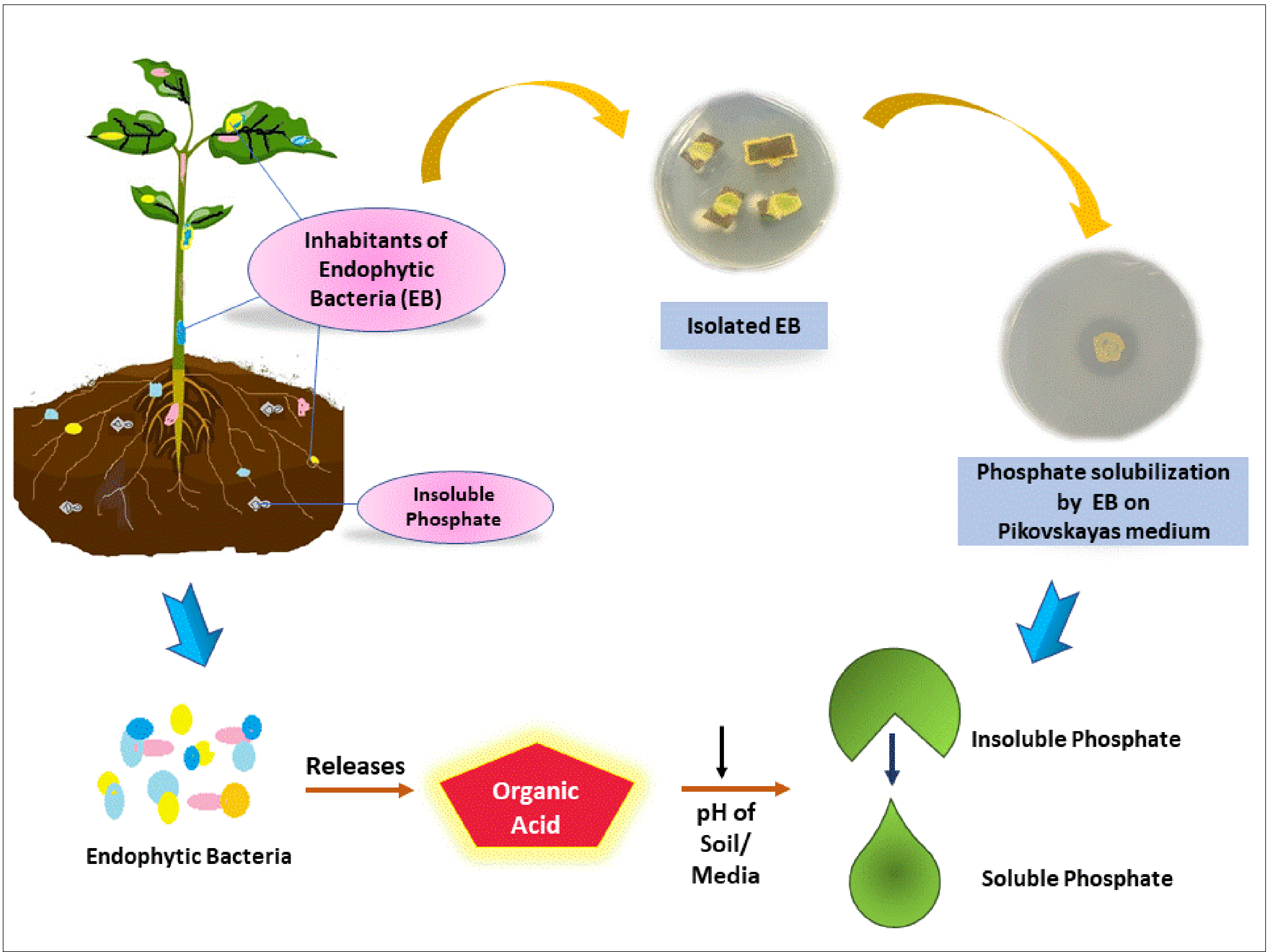

Fig. 2. Phosphate solubilization activity of endophytic bacteria.

Table 2. List of some endophytic bacteria having different plant growth promotion activity.

Sl. No.	Host plant	Endophytic bacteria	Functions	References
1	*Miscanthus giganteus*	*Pseudomonas fluorescens* and *Pseudomonas* sp.	Phosphate solubilization	(47)
2	Banana root	*Aneurinibacillus* sp. and *Lysinibacillus* sp.	Phosphate solubilization	(48)
3	*Alkanna tinctoria*	*Chitinophaga* sp., *Allorhizobium* sp., *Duganella* sp., and *Micromonospora* sp.	Antimicrobial	(20)
4	*Momordica charantia* L.	*Bacillus licheniformis*, *Bacillus* sp., *Bacillus subtilis*, *Lysinibacillus fusiformis*	IAA production, siderophore production and phosphate solubilization	(21)
5	*Momordica charantia* L.	*Bacillus licheniformis* and *Bacillus subtilis*	Tolerate up to 10 % of NaCl	(21)
6	*Anredera cordifolia*	*Pseudomonas aeruginosa*	Anti-bacterial activity	(64)
7	Poaceae family plants	*Bacillus toyonensis*, *Bacillus halotolerans*, and *Bacillus subtilis* subsp. *inaquosorum*	Cellulase enzyme activity	(68)
8	*Oryza sativa*	*Achromobacter xylosoxidans*, *Bacillus aryabhattai*, *Stenotrophomonas pavanii* and *Enterobacter cloacae*	Tolerate different salt concentrations 1.37 mol/L, 2.57 mol/L, 2.05 mol/L, 2.05 mol/L respectively.	(84)
9	Wheat	*Burkholderia gladioli*, and *Bacillus aryabhattai*	Salt toterance	(9)
10	*Lilium davidii* var. *unicolor*	*Bacillus halotolerans*	Tolerate 10 % NaCl and 20 % polyethylene glycol (PEG) Antagonistic activities against plant pathogens including *Botrytis cinerea*, *Botryosphaeria dothidea*, and *Fusarium oxysporum*. ACC deaminase activity	(67)
11	*Swertia chirata*	*Staphylococcus* sp.	Anti-microbial activity against *Xanthomonas oryzae* and *Fusarium oxysporum*	(71)
		Bacillus sp.	Anti-bacterial activity against *Ralstonia solanacearum*	
12	*Datura stramonium*	*Rhodococcus jialingiae*	Anti-bacterial activity against *Ralstonia solanacearum*	
13	Wheat	*Bacillus subtilis* and *Arthrobacter* sp.	Help in zinc accumulation in grains	(53)
14	*Achillea fragrantissima*	*Brevibacillus* sp.	Ammonia production, IAA production	(60)
15	*Fagonia mollis*	*Bacillus* sp.	IAA production	
16	*Alkanna tinctoria*	*Stenotrophomonas* sp.	Siderophore production	(20)
		Brevibacillus sp.	Cellulase and pectinase activities	
17	*Pistacia atlantica* L.	*Serratia plymuthica*	IAA and siderophore production, Nitrogen fixation	(61)
18	*Curcuma longa* L.	*Acinetobacter* sp., *Pseudomonas aeruginosa* BacDOB- E15, *Pseudomonas aeruginosa* BacDOB- E19, *Enterobacter* sp.	IAA production	(91)
		Pseudomonas aeruginosa BacDOB- E19	Antagonistic activity against *Pythium aphanidermatum*, *Rhizoctonia solani*	

phate or oxide. A positive result for Zn solubilization is indicated by the formation of a clearing zone after incubation (51). From 17 rhizosphere soils of soybeans grown in the Nimar region of central India, 115 bacterial isolates were identified. Among these, 20 isolates demonstrated significant potential for solubilizing inorganic zinc compounds in both plate and broth experiments. These promising isolates were identified as strains of *Bacillus cereus* and closely related strains, including *B. thuringiensis*, *B. anthracis* and *B. tequilensis* (52). In addition, several endophytic bacteria isolated from a group of 13 wheat genotypes were found to be effective zinc solubilizers. Among various zinc salts, the highest number of isolates could solubilize zinc oxide at concentrations of 5 and 15 mM. However, only 30 % of the isolates were able to solubilize zinc phosphate (53).

Phytohormones production

Phytohormones, also known as plant growth regulators are chemical compounds that, in small amounts, influence plant growth and development by altering, suppressing or stimulating various process. Indole-3-acetic acid (IAA) primarily promote cell elongation and differentiation in plants. The main phytohormones produced by endophytic bacteria include auxins, cytokinins, abscisic acid, ethylene, brassinosteroids, gibberellins, strigolactones and jasmonates (54). Phytohormones are among the most important growth regulators, known for their profound effects on plant metabolism and their ability to activate plant defense mechanisms under stress conditions (55). Endophytic bacteria such as *Paecilomyces formosus* LHL10 and *Sphingomonas* sp. LK11 have been observed to produce gibberellins (GAs) and indole-3-acetic acid (IAA).

These bacteria were found to enhance plant growth and reduce metal toxicity in soybean tissues by blocking the uptake and translocation of metals, increasing the absorption of essential nutrients and altering extracellular enzymatic activities in the soil (56). Phytohormones help plants respond to various environmental challenges by activating or deactivating the expression of specific plant genes (57). To assess the IAA production capability of bacterial isolates, Tryptone Soy Broth (TSB) medium supplemented with L-tryptophan (5 mM) was used as the inoculation medium. The isolates were then cultured at room temperature in a shaker at 100 rpm (58). IAA can be produced *in vitro*, either with or without tryptophan. For instance, isolates from Redgram and Blackgram produced the highest amount of IAA, 6.46 μg/mL, in the presence of tryptophan, while isolates from blackgram produced 0.12 μg/mL in the absence of tryptophan (59). When tryptophan was added at concentrations of 1 to 5 mg/mL, the amount of IAA produced by the bacteria increased from 10 to 60 μg/mL (60).

Previous studies have shown that numerous endophytic bacteria, such as *Pseudomonas*, *Serratia* and *Bacillus* are capable of synthesizing IAA. Among the examined strains, *Serratia plymuthica* isolated from *Pistacia atlantica* L., produced the highest amount of IAA, with a concentration of 57.6 μg/mL (61).

Disease Suppression

In addition to reducing damage caused by phytopathogens, endophytes exhibit antagonistic activity against disease-causing pathogens (1). They contribute to pathogen defense by directly synthesizing and releasing secondary metabolites or antimicrobial substances, such as hydrolytic enzymes, antibiotics, and siderophores. These compounds help inhibit or reduce pathogen invasion. Endophytes can also indirectly defend against pathogens by competing for nutrients and space (8). Most endophytic microorganisms produce various antibiotics, including novel ones like ecomycin, pseudomycin, and kacadumycin (62). Endophytic bacteria such as *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas* and *Streptomyces* are used as microbial formulations to combat various phytopathogens. Endophytes produce a range of metabolites, including alkaloids, polypeptides, polyketides, terpenoids and others, which play a crucial role in protecting plant health. These bioactive metabolites help host plants survive biotic and abiotic stressors, either directly or indirectly (63). For example, *Pseudomonas aeruginosa* isolated from the medicinal plant *Anredera cordifolia* CIX1 demonstrated antimicrobial activity against *Escherichia coli* (ATCC 25922), *Bacillus cereus* (ATCC 10102) and *Staphylococcus aureus* (ATCC 25925). This bacterium was found to produce an antimicrobial compound called diisooctyl phthalate (64). Additionally, the endophytic bacteria *Stenotrophomonas maltophilia* and *Alcaligenes faecalis*, isolated from the leaves of *Moringa oleifera*, were found to produce several phytochemicals such as phenolics, tannins, flavonoids, alkaloids and other bioactive compounds like octadecanoic acid, hexadecanoic acid, linoleic acid ethyl ester, octadecenoic acid methyl ester, methyl stearate, nonacosane, indolizine, palmitoleic acid, heptacosane, cis-2-phenyl-1,3-dioxolane-4-methyl and ergotamine. These compounds exhibit antimicrobial, anticancer and antioxidant activities (65).

Furthermore, *Stenotrophomonas maltophilia* isolated from *Fagonia indica* was found to produce antimicrobial compounds such as N-(5-benzyl-10b-hydroxy-2-methyl-3,6-dioxooctahydro-8H-oxazolo[3,2-α]pyrrolo[2,1c] pyrazin-2-yl)-7-methyl2,3,3a,3a^1,6,6a,7,8,9,10,10a,10b-dodecahydro-1H-4λ^2-indolo[4,3-*fg*]quinoline-9-carboxamide (66).

Bacillus halotolerans, isolated from the roots of *Lilium davidii* var. unicolor, has demonstrated antagonistic activity against plant pathogens such as *Botrytis cinerea*, *Botryosphaeria dothidea* and *Fusarium oxysporum* (67). Additionally, high levels of cellulase activity were demonstrated by *Bacillus toyonensis*, *Bacillus halotolerans* and *Bacillus subtilis* subsp. *inaquosorum*, which were isolated from plants of the Poaceae family (68). Cellulase is one of the lytic enzymes that play a crucial role in preventing pathogen invasion in plants (69). Rhizoctonia root-rot disease causes significant financial losses in tomato cultivation. To combat this disease and introduce defense mechanisms as well as growth-promoting strategies in tomato plants, *Bacillus velezensis*, *Bacillus megaterium* and *Herbaspirillum huttiense* were effective (70).

Endophytic bacteria were isolated from 2 widely used medicinal herbs in India's northeastern states, *Swertia chirata* (Chirata) and *Datura stramonium* (Datura). The isolates were studied for their antibacterial and antifungal activities. *Staphylococcus* sp., isolated from the root of Chirata, exhibited antibacterial activity against *Xanthomonas oryzae* and antifungal activity against *Fusarium oxysporum*. Additionally, *Bacillus* sp. also isolated from Chirata, demonstrated antibacterial activity against *Ralstonia solanacearum*. An endophytic bacterial isolate, *Rhodococcus jialingiae*, from the Datura plant, showed antibacterial activity against *Ralstonia solanacearum* (Table 2) (71). Metabolites produced by endophytic bacteria often resemble those of their host plants. For instance, *Rhizophora mucronata* Lam. is reported to contain secondary metabolites such as alkaloids, tannins, saponins, phenolics, flavonoids, terpenoids, steroids and glycosides in extracts from its leaves, stems, roots, fruits and flowers. Endophytic bacteria found in this plant have shown strong inhibitory activity against pathogenic microbes, including *Bacillus cereus* and *Pseudomonas aeruginosa*. These findings suggest that endophytic bacteria isolated from *R. mucronata* Lam. mangroves hold great potential as a novel source of antibacterials, particularly against the pathogenic bacteria *B. cereus* and *P. aeruginosa* (72).

Endophytic bacteria have the potential to serve as effective biocontrol agents in agricultural settings. Extracts from most endophytic bacteria isolated from the needle, stem and root tissues of *Pinus densiflora*, *Pinus rigida*, *Pinus thunbergii* and *Pinus koraiensis* were shown to inhibit the pine wood nematode (*Bursaphelenchus xylophilus*), which causes pine wilt disease. Among these, *Stenotrophomonas* and *Bacillus* sp. demonstrated significant inhibitory efficacy against the nematode during its embryonic phases (73). Additionally, *Enterobacter* endophytic strains isolated from *Mimosa pudica* nodules exhibited nematicidal activity against *Panagrellus redivivus* and *Nacobbus aberrans* (74). The endophytic bacterium *Klebsiella quasivaricola* was effective in suppressing egg hatching and juvenile mortality of the guava root knot nematode (*Meloidogyne enterolobii*) (75). In the control of lepidopteran insect pests, *Bacillus thuringiensis* (Bt) is the most effective microbial insecticides globally. Recent research suggests that Bt can be established as an endophytic bacterium for insect pest management (76). The insecticidal bacterium *Brevibacillus laterosporus* has been shown to be toxic to a variety of invertebrates when ingested. Initially, *B. laterosporus* isolates were obtained from seeds of surface-sterilized cabbage (77). Plant endophytic bacteria are also a valuable source of natural pesticides. *Serratia marcescens* isolated from sugarcane exhibits moderate insecticidal activity, significantly affecting the growth, development and reproduction of the armyworm *Mythimna separata*. The death rates from injectable and oral infections were 91 % and 47.06 % respectively (78). In chilli cultivation, where *Bemisia tabaci* is a significant pest and vector for the yellow curl virus, the endophytic bacterium *Bacillus pseudomycoides* strain SLBE1.1SN was found to be the most effective formula for suppressing whiteflies after 6 weeks of storage when rice straw was used as the carrier material. This formulation of preserved endophytic bacteria inhibited the growth of nymphs and adults as well as reduced egg deposition (79). The pest *Spodoptera frugiperda* affects cereal crops, diminishing yields. Co-inoculation of maize with 2 endophytes, *Glomus intraradices* and *Bacillus amyloliquefaciens*, has been shown to influence antioxidant levels and defense enzyme activities in the grain, altering *S. frugiperda's* feeding behavior. After 96 h of feeding, maize treated with *B. amyloliquefaciens* and *G. intraradices* displayed increased activity of antioxidants (catalases: 106.26 %, peroxidases: 62.71 %, superoxide dismutase: -17.39 %, ascorbate oxidase: 160.00 %) and defensive enzymes (polyphenol oxidases: 205.86 %, phenylalanine ammonia lyases: 126.00 %, lipoxygenases: 33.33 %) in its leaves (80). Overall, bacterial endophytes hold promise as plant protection agents in future agricultural practices.

Abiotic stress tolerance

Endophytic bacteria enhance the natural resistance of their host plants to stressors such as drought, salinity and heavy metals, helping them survive in challenging conditions. These bacteria can improve the solubility of metals and minerals in the soil by releasing metal-specific ligands, such as siderophores and low-molecular-weight organic acids. These compounds alter the pH of the soil and enhance metal binding activity (81). Researchers have realized that a detailed analysis of the interactions between endophytes and their host plants may be crucial for developing multi-factor control strategies to address common stressors affecting plants, especially under adverse conditions (82). Recent studies have highlighted the potential biotechnological applications of microbes isolated from harsh environments in industry, agriculture and medicine (83).

The ability of endophytic bacteria to tolerate high salt concentrations and heavy metals was observed in the isolates recovered from stress-tolerant parts of various plant species, including *Hemerocallis fulva*, *Lantana camara*, *Phoenix dactylifera*, *Salvia rosmarinus*, *Commiphora wightii* and *Abutilon indicum*. Isolates R1L2 and A2L2L2 demonstrated maximum salt tolerance with restricted growth at up to 16 % NaCl concentration. Isolates DL2R2, R1L2 and A1S1S showed the highest tolerance against 6 % w/v lead concentration, while strains R1L2, DL3R2 and DP1L1L1 exhibited the highest resistance to cadmium at 6 % w/v concentration (81). In the southern coastal region of Bangladesh, 75 endophytic bacteria were isolated from the roots of healthy *Oryza sativa* plants grown in saline environment. Most of these isolates demonstrated traits that promote plant growth, such as indole acetic acid synthesis, phosphate solubilization and nitrogen fixation. Among them, 4 endophytic bacteria exhibited high salt tolerance (84). Salt tolerance was also demonstrated by *Burkholderia gladioli* and *Bacillus aryabhattai*, which were isolated from wheat plant seeds (Table 2) (8). *Bacillus aryabhattai*, isolated from both the roots of *Oryza sativa* and wheat seeds, showed significant salt tolerance (Table 2) (9, 84). Endophytes derived from halophyte plants may help mitigate salinity stress in crops. Halotolerant strains of *Bacillus*, *Oceanobacillus*, *Brachybacterium*, *Micrococcus* and *Salinicoccus* have been reported to withstand up to 3 M NaCl (85).

Global crop growth and productivity are severely impacted by drought. Water scarcity in the early stages of crop development leads to low energy availability, poor water uptake and impaired enzyme activity, which inhibits crop growth and productivity (6). Three drought-tolerant endophytic actinobacteria, *Streptomyces coelicolor*, *S. olivaceus* and *Streptomyces geysiriensis*, were identified from cultivated plants in dry and drought-affected districts of Rajasthan, India. Experiments with these isolates showed that the maximum yield of wheat under water stress conditions was achieved with the inoculation of *S. olivaceus* culture, recording 492.77 kg/ha. Co-inoculation of *S. olivaceus* and *S. geysiriensis* resulted in the highest yield of 550.09 kg/ha (86). *Bacillus amyloliquefaciens*, isolated from *Panicum sumatrense* L., produced a variety of drought-tolerant metabolites, including organic acids, fatty acids, amino acids and their derivatives, organoheterocyclic compounds and benzenoids (87). Co-inoculation of *Endostemon obtusifolius* with endophytes under water stress led to enhanced growth and stress tolerance. This improvement was associated with increased production of osmolytes (soluble sugars, proline), up-regulation of the enzymatic antioxidant system (superoxide dismutase) and higher content of antioxidant metabolites (total phenolics, flavonoids) (88).

Applying the right endophytic bacteria can strengthen detoxification processes and prevent heavy metal hyperaccumulation. Two glutathione-producing bacterial strains, *Enterobacter ludwigii* SAK5 and *Exiguobacterium indicum* SA22, were tested for their tolerance to cadmium (Cd) and nickel (Ni), showing resistance up to 1.0 mM (89). These bacteria have adapted to environments with heavy metal pollution by bioaccumulating heavy metals and enzymatically reduce or oxidise them into non-toxic forms. Additionally, manipulating ethylene levels in plants by altering 1-aminocyclopropane-1-carboxylate (ACC) levels with different bacteria can directly impact heavy metal tolerance (90). *Bacillus halotolerans*, isolated from the root of the lily plant, exhibited ACC deaminase activity and was able to cleave 58.41 ± 2.62 n mol α-ketobutyrate (mg protein)$^{-1}$ min^{-1} (67).

Conclusions and Future Directions

The isolation, characterization and identification of endophytic bacterial populations from various plant tissues present a formidable challenge. This difficulty is mainly due to the fact that some endophytic bacteria are difficult to cultivate under laboratory conditions. Additionally, the surface sterilization methods used vary not only across different plant species but also among different tissues of the same plant. This variability poses a risk of impeding the isolation of certain endophytic bacteria, highlighting the need for standardized methodologies and conditions in future research. Previous studies indicate that endophytic bacteria may reside in plant tissues for specific durations or throughout the plant's lifespan. Exploring endophytic bacterial diversity is intricate and time-consuming, influenced by factors such as the age of plant tissues, seasonal variations and differences among diverse plant species and tissues. A comprehensive investigation is indispensable to draw definitive conclusions regarding the endophytic bacterial diversity. Many endophytic bacteria exhibit various activities related to plant health, and deciphering the genetic factors underlying these activities remains a significant challenge for researchers. Moreover, translating laboratory findings into practical field applications adds another layer of complexity, underscoring the multifaceted nature of advancing our understanding of the roles of endophytic bacteria in agriculture.

In this comprehensive review, we have explored various endophytic bacteria derived from a range of plant species, including *Curcuma longa* L., *Pistacia atlantica* L., *Alkanna tinctoria*, *Fagonia mollis*, *Achillea fragrantissima*, *Datura stramonium*, *Swertia chirata*, *Lilium davidii* var. unicolor, *Oryza sativa*, Poaceae, *Anredera cordifolia*, *Momordica charantia* L., *Miscanthus giganteus* and banana, among others. Our analysis encompasses a thorough exploration of their potential plant growth promotion activities, such as phosphate solubilization, nitrogen fixation, indole-3-acetic acid (IAA) production, abiotic stress tolerance and disease management mechanisms. Notably, *Bacillus aryabhattai*, isolated from both the roots of *Oryza sativa* and the seeds of wheat plants, demonstrated remarkable salt tolerance in the respective studies. These findings suggest that this particular isolate holds promising potential for agricultural applications, particularly in mitigating salinity stress.

The use of endophytes and their metabolites for plant disease management is a crucial and fascinating area of research. It holds the potential to provide ground-breaking insights for developing antibiotics, insecticides and fungicides that are not only more effective but also environmentally friendly. This field promises to advance modern agricultural practices by offering innovative solutions to the challenges of disease control. Investigating endophytes and their derivatives as a means to enhance the efficacy of agricultural agents is poised to make significant contributions to sustainable and eco-friendly crop protection strategies.

Research into producing endophytic bacterial-based biofertilizers offers a promising and environmentally sustainable approach to agriculture. Investigating the genes responsible for key functions, such as phytohormone production, phosphate solubilization, nitrogen fixation, enzyme production and stress tolerance, provides valuable insights into the beneficial interactions between these microorganisms and plants. Studying bioactive compound-producing endophytic bacteria opens the potential for their large-scale production and application. Furthermore, examining the impact of different bacterial generations on bioactive compound production enhances our understanding of their long-term effects. Future research on engineered endophytic bacteria could lead to the development of strains with significant agricultural and pharmacological importance. Overall, advancements in this field contribute to the well-being of humans, plants and soil, making it a critical area of study with far-reaching implications.

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Authors' contributions

DD developed the structure and prepared the manuscript; SD made critical revisions and approved the final version. All authors reviewed and approved the final manuscript.

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