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Endophytes and their significance in plant health and agricultural sustainability

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ABSTRACT

Endophyte refers to the endosymbiotic microorganisms that reside asymptomatically in plant tissues. They aid in plant growth promotion and disease resistance. Most plant species have endophytic associations and their functions are now well documented. These microorganisms help plants take up nutrients, stimulate the production of phytohormones, and fix atmospheric nitrogen. This makes plants more tolerant against biotic and abiotic stress. They are natural rivals of plant pathogens since they produce anti-microbial metabolites, compete for nutrients and space, and induce systemic resistance in their host plants. The use of endophytes in agriculture can be an environment friendly alternative to chemical fertilizers and pesticides for the long-term protection of crops. By investigating the diversity and functional traits of beneficial microorganisms, novel bio-stimulants, bio-inoculants, and biocontrol agents can be developed. Despite the advantages, endophytes have certain limitations, such as host specificity, environmental variability, and inconsistent colonization, often failing to perform reliably under field conditions. Competition with native microbiota, safety concerns, and commercialization challenges further restrict their widespread application. The review highlights the natural diversity, antagonistic mechanism toward pathogens, and potential agricultural applications of endophytes, which has immense potential toward agro-ecosystem sustainability and resilience.

1. INTRODUCTION

Endophyte microbes include a diverse group of organisms, inhabiting the internal tissues of the plant in a non-pathogenic, symptomless fashion [1]. These endophytes, after establishing a close association with their host, support plant growth and augment tolerance to various biotic as well as abiotic stresses [2-4]. They activate systemic resistance in the host, contributing to reduced dependency on synthetic agrochemicals [5]. These beneficial microbes improve plant resilience, through stabilization of membrane integrity, regulation of water balance, and induction of stress-related proteins [6]. A certain group of endophytes alters root architecture for better water absorption and produces osmo-protectants to retain water and confer drought tolerance to host plants. Extensive colonization of the plant tissue by endophytes creates a "barrier effect", where the local endophytes outcompete and prevent pathogenic organisms from taking hold.

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Endophytes are ubiquitous and have been found in all species of plants studied to date; however, most of the endophyte/plant relationships are not well understood. Studying endophytic microbes provides new avenues for developing innovative technologies, such as biofertilizers and biopesticides, which are potent enough for improving crop productivity [7,8]. Being eco-friendly, they promote sustainable agriculture by reducing the use of synthetic inputs [9,10]. Exploring the dynamic relationship between host and endophytes has paved ways to sustain food production amid emerging global environmental concerns [11]. This review talks about the beneficial endophytes, their diversity, mode of action against phytopathogens, and their role in abiotic stress management. Special emphasis is placed on their substantial role in promoting sustainability as an alternative to conventional agrochemicals.

2. DIVERSITY OF ENDOPHYTES

Plants are colonized by a wide range of microorganisms, collectively referred to as the plant microbiomes. The composition of the microbial community varies significantly across different plant parts [12]. The communities of microbes living in the rhizosphere, endosphere, and phyllosphere, are essential for promoting plant health and defending against pathogens [13]. Mutual regulation between plants and microbes fosters a harmonious micro-ecological environment [14]. Plants supply carbohydrates, essential for endophyte growth, while endophytes provide metabolites that help plants tolerate stresses, such as drought and salinity [15].

Plant endophytes bridge below and above-ground microbiomes, with specific microbes recruited from the rhizosphere and phyllosphere into plant tissues [16]. These endophytic microbes employ different strategies to penetrate [Figure 1] and colonize plant tissues [17]. The series of events involved in successful colonization are attachment, entry, motility, transmission, and multiplication within the host plant [18].

Remarkable morphological variability has been observed in endophytes isolated from different hosts [20]. Endophytes engage with plants in a number of ways that extend from symbiotic to opportunistically pathogenic [21].

2.1. Fungal Endophytes

Endophytic fungi constitute an integral component of the plant microbiome [Table 1]. They colonize a wide range of plant parts, including roots, stems, leaves, petioles, buds, fruits, and even seeds [22]. Numerous endophytic fungi associated with monocots, such as ryegrass, rice, barley, and corn, synthesize alkaloids [23], which display broad-spectrum bioactivity, particularly targeting pathogens and nematodes [24]. Endophytic fungi play a pivotal role in enhancing growth and fortifying resistance to environmental stresses in dicotyledonous plants [25,26].

Investigations of endophytes in roughly 300,000 plant species indicate that virtually all plants harbor at least one form of endophytic microorganisms [27]. Several studies [28-30] have reported a wide diversity of endophytic fungi, encompassing genera, such as *Fusarium, Trichoderma, Penicillium, Alternaria, Paecilomyces, Glomus, Colletotrichum, Rhizopus, Aspergillus, Curvularia, Serendipita, Microdochium, Claviceps, Leptospora, Phaemoniella, Epichloe*, and *Gyomyces* [31]. Plant-associated endophytic fungi are predominantly distributed across three major phyla – Ascomycota, Basidiomycota, and Mucoromycota [32,33].

Fungal endophytes are transmitted through horizontal and vertical transmission. Vertical transmission through seeds, while horizontal transmission from soil or the environment [51]. Endophytic fungi

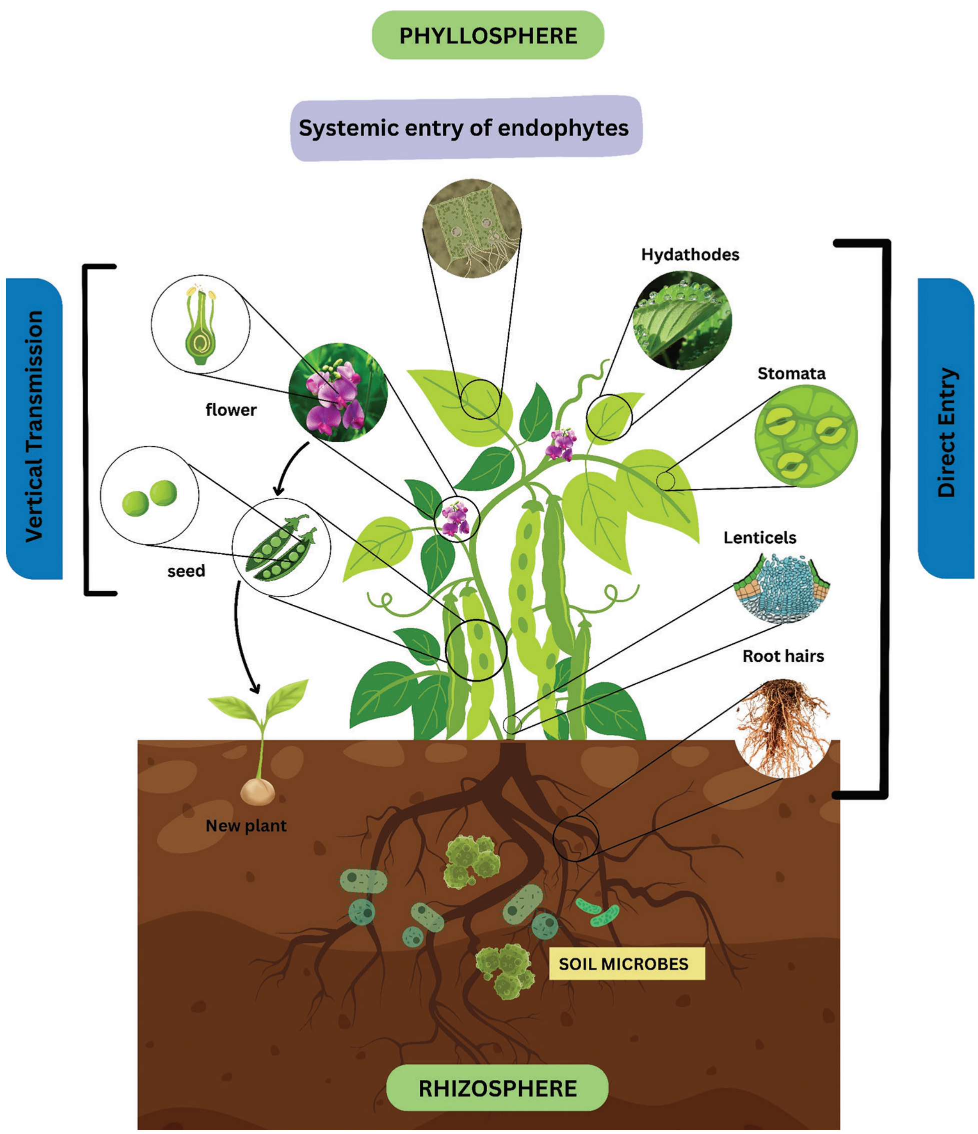

Figure 1: Entry and establishment of endophytes within the plant [19].

Table 1: Key fungal endophytes with their functional role and applications.

Category	Endophytic fungal genera	Key metabolites	Functional role in agriculture	References
Antagonistic Endophytes	*Trichoderma, Cladosporium, Chaetomium, Talaromyces, Epicoccum, Pestalotiopsis*	Enzymes, siderophores, antifungal compounds, VOCs	Induce resistance and suppress the pathogen, leading to broad-spectrum disease control in major crops	[34-39]
Plant growth promoters/ Biofertilizers	*Serendipita, Mortierella, Colletotrichum, Fusarium, Penicillium*	Auxins, phosphatases, lipids	Root enhancement and improved nutrient uptake contributing to higher crop yields	[40-44]
Stress-tolerance enhancers	*Alternaria, Epichloe, Nigrospora, Aspergillus*	Hormones, antioxidants, P- solubilizers	Enhancement of stress tolerance and nutrient mobilization, improving crop resilience and soil health	[45-48]
Pest-deterrent/ suppression endophytes	*Phyllosticta, Beauveria*	Alkaloids, Beauvericin, bassianolide	Herbivore/pest suppression, resulting in improved protection of grasses, fruits, and legumes, is useful in IPM	[49,50]

VOCs: Volatile organic compounds.

belonging to the phylum Ascomycota are recognized for synthesizing a wide range of bioactive compounds that enhance plant growth [52] and strengthen tolerance to environmental stresses [Figure 2]. The fungal genera *Fusarium* and *Trichoderma* synthesize secondary metabolites that help plants develop resistance to pathogenic infections [53,54]. These fungi expand their hyphal networks into the soil, enhancing the plant's absorption of key nutrients, such as phosphorus and nitrogen [55].

2.2. Bacterial Endophytes

Most dominant endophytic bacteria belong to the Proteobacteria, Firmicutes, and Actinobacteria phyla [Table 2], and dominant genera include *Bacillus*, *Pseudomonas*, and *Burkholderia* [56]. Endophytic bacteria are proved to improve plant growth, suppress the growth of pathogens, and enhance stress tolerance [57]. Endophytic bacteria enhance plant growth by improving nutrient uptake (K, N_2, P, and Fe) and by regulating growth hormones, such as cytokinin, auxin, and ethylene (ET) [58]. These further assist plants in coping with harsh environmental conditions, notably drought, salinity, and temperature extremes [27]. Two endophytic isolates, that is, *Staphylococcus warneri* and *Bacillus velezensis* from *Gnetum gnemon,* successfully controlled the bacterial wilt disease [59]. The growth of *Phytophthora parasitica* was inhibited by over 80% due to volatiles produced by *Pseudomonas taiwanensis* [60].

Both rhizobial and non-rhizobial endophytes, including *Klebsiella, Burkholderia, Azoarcus, Achromobacter*, *Serratia, Gluconoacetobacter,* and *Herbaspirillum,* serve as effective biofertilizers, among which *Azoarcus* is widely recognized for its strong nitrogen-fixation activity [76]. To function as biofertilizers, endophytic bacteria are isolated, cultured, and processed into stable formulations for field use.

2.3. Endophytic Actinomycetes

Actinobacteria, which are characterized by high G+C DNA content and filamentous growth, constitute one of the largest bacterial phyla [Table 3] and are ubiquitously found in aquatic and terrestrial habitats [77]. They are widely distributed in natural ecosystem habitats, such as soil, rhizosphere soil, ectomycorrhizal plants, hypersaline soil, limestone, freshwater, marine, sponges, volcanic cave-hot spot, desert, air, insect gut, earthworm castings, and goat feces [78]. These microorganisms produce a range of plant growth-promoting substances, including phytohormones, such as indole-3-acetic acid (IAA), gibberellins (GA), and cytokinins (CK), which are essential for plant growth and development [79]. They help in the solubilization of phosphate [80] and serve as biological fertilizers [81] and can control phyto-pathogens [82]. Moreover, they also aid in bioremediation [14].

3. ENDOPHYTE-MEDIATED PLANT PROTECTION MECHANISMS

Endophytes possess a number of strategies that they employ to suppress a broad variety of phytopathogens. They are increasingly recognized as natural allies of plants because of their capacity to exhibit multiple antagonistic strategies against harmful microbes. These strategies induce chemical, enzymatic, spatial, and nutritional defenses, which form a shield for safeguarding plants. These endophytes confer protection against pathogens through both direct and indirect strategies. Direct suppression occurs through antibiosis, competition, siderophore and phytohormone production, whereas indirect suppression is achieved by induction of plant resistance [Figure 2], secretion of secondary metabolites, and hyperparasitism [102].

Endophytes produce bacteriocins, antibiotics, bio-surfactants, lipopolysaccharides, cell wall-degrading enzymes, and volatile compounds, which obstruct the metabolism of the pathogen [103]. Moreover, the competition for space and nutrition between pathogens and endophytes plays an important role in lessening the plant's invasion by pathogens. Chitinases and pectinases enzymes interfere with the disease-causing ability of the pathogen. *Trichoderma* spp. and *Aspergillus* spp. produce enzymes, such as chitinases, β-1,3-glucanases, cellulases, and proteases that degrade fungal cell walls, leading to rupturing of hyphae and eventually the pathogen dies [104,105]. Banana wilt-affected plantations exhibit increased activity of enzymes, transcripts of chitinase and β-1,3-glucanases have been reported from pathogen-induced cultures [106].

Endophytes are also capable of producing metabolites having antifungal and antibacterial properties [107-109]. They are known to produce bioactive compounds, such as terpenoids, alkaloids, polypeptides, and phenolic compounds [110-112]. Fungal endophytes belonging to the genera *Trichoderma, Muscodor*, *Fusarium,* and *Xylaria* are capable of producing volatile compounds that are helpful post-harvest crop protection [113]. Clavicipitaceous endophytes produce ergot alkaloids, which possess antimicrobial properties against post-harvest

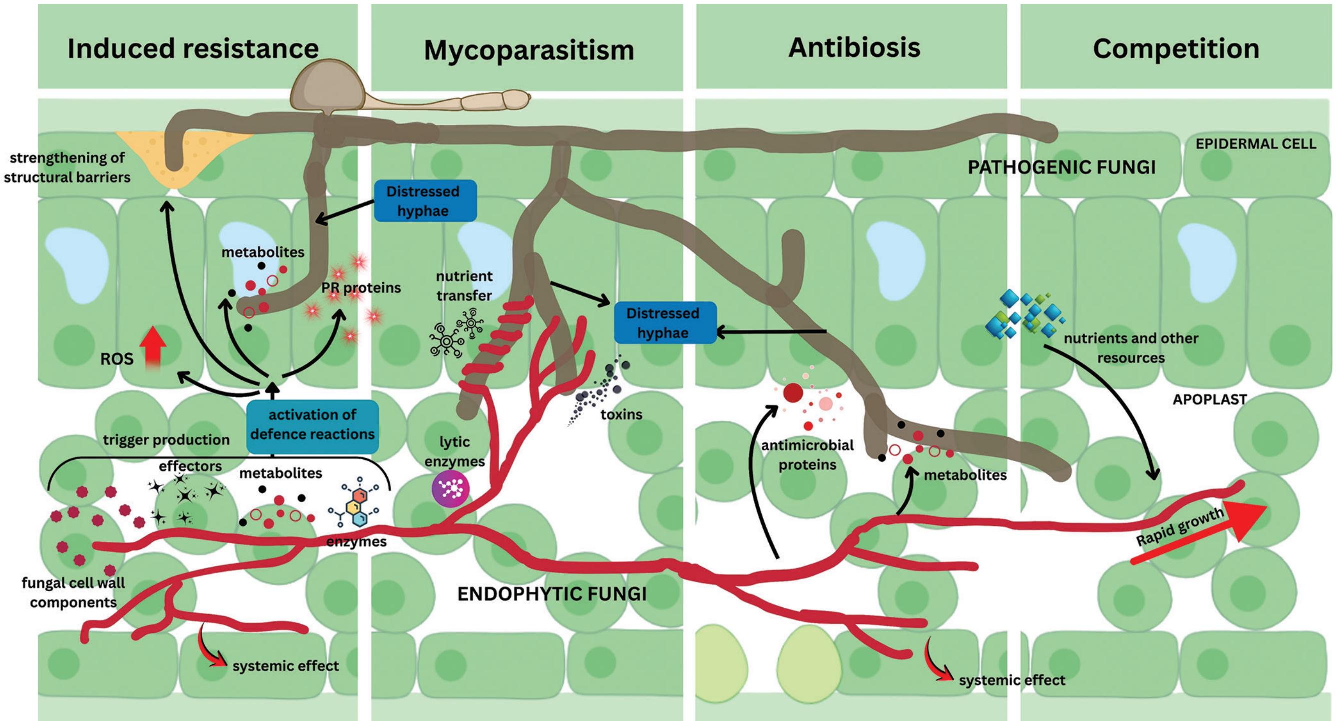

Figure 2: Biocontrol mechanism of fungal endophytes against phytopathogens [19].

pathogens [114]. Endophytes attack pathogen invading the host, and cause twisting, perforation, and coiling of fungal hyphae and release enzymes that degrades pathogen's cell wall, leading to inhibition and lysis of the pathogen [115].

The phytohormones, such as salicylic acid (SA), ET, and jasmonic acid (JA) act as signaling molecules [28,116] to curb the pathogen invasion [117]. These signals alert the plant regarding being attacked and activate defense pathways. These pathways upregulate defense-related genes, including those coding for pathogenesis-related (PR) proteins and oxidative enzymes, which strengthen the plant's ability to resist future pathogen attack [111,118,119]. This primes the immune system of the plant by inducing induced systemic resistance (ISR), resulting in durable defense responses, in case of pathogen attack in the future [120,121]. Such priming reduces the incidence of disease while conserving metabolic resources, and it has been shown to decrease dependence on chemical fungicides in cropping systems [49,105]. ET and jasmonic acid are effective against necrotrophic infections and are helpful in host-pathogen interactions [122].

Endophyte-mediated resistance is a specialized form of defense mechanism shown by the endophytes. This operates through a localized and pathway- independent mechanism that strengthens the roots of the host-plant as they are the most common entry sites for pathogens [123]. For instance, endophytic strains of *Fusarium oxysporum* Fo47 are known to activate resistance responses in roots. Endophytes, such as *Pseudomonas* and *Bacillus*, induce a defense system that functions independently of the JA and SA pathways yet results in robust protection against root-invading pathogens [124].

4. ENDOPHYTE- MEDIATED ABIOTIC STRESS MANAGEMENT

One of the significant abiotic stresses, responsible for global drought conditions is water scarcity, which further leads to reduced agricultural production. Plant growth-promoting bacteria, are gaining recognition because of their ability to enhance plants' tolerance to drought conditions by regulating physiological and molecular mechanisms [125-127]. *Serendipita indica*, the fungal endophyte present in Chinese cabbage, is capable of showing enhanced antioxidant activity leading to improved drought tolerance [128]. *Bacillus* spp. helps in maintaining cellular osmotic balance by encouraging the production of osmolytes and stimulating root elongation [129]. The bacterial endophyte *Bacillus pumilus,* accelerates osmoprotectant accumulation and increasing nitrogen metabolism to improve the drought tolerance in *Glycyrrhiza uralensis* [130].

Soil salinity has an adverse impact on agriculture, as it hampers overall agricultural output through inhibiting germination of seed, uptake of nutrients, activity of beneficial microbes, caused by ionic stress and osmotic instability [131]. Endophytes are potent enough to suppress these adverse effects through improved physiological and biological mechanisms [132,133]. The bacterial endophyte *Pseudomonas geniculata* reduces stress caused by high salinity through the production of siderophores, mobilization of nutrients, and production of phytohormones [134]. Enhanced wheat growth has been reported under a saline environment, in the presence of salt tolerant strain *Priestia aryabhattai* [135]. Moreover, reduced ionic stress is observed in the presence of endophytes, which synthesize exopolysaccharides in the rhizosphere [136].

The physiology of the plant is highly disrupted by the temperature extremes, as it interferes with the structure of the proteins and also alters the enzymatic functions [137]. Heat induced stress, hampers seed germination, reduces photosynthetic efficiency, and increases membrane permeability, which ultimately leads to reduced crop production [138]. The endophytes colonizing heat-tolerant plant species, *Cupressus dupreziana, Triticum aestivum,* and *Sporobolus indicus,* help them survive under temperature extremes [139] by fixing nitrogen, solubilizing nutrients, synthesizing phytohormones, hydrogen cyanide, and siderophores [140]. Heat-tolerant endophytic

Table 2: Key bacterial endophytes with their functional role and applications.

S. No.	Bacterial endophytes	Functions	Agricultural importance	References
1.	*Pseudomonas fluorescens*	Produces siderophores, IAA, antibiotics; activates ISR; suppresses soil-borne pathogens	Widely used as a bioinoculant for cereals, vegetables	[61]
2.	*Bacillus subtilis*	Produces lipopeptides (iturin, surfactin), hydrolytic enzymes, IAA; biocontrol agent	Commercial biofertilizers; foliar sprays and seed coatings	[62]
3.	*Burkholderia* spp.	Nitrogen fixation, phosphate solubilization, and production of antifungal compounds	Enhances the growth of rice, maize, and legumes	[63]
4.	*Rhizobium* spp.	Symbiotic nitrogen fixation in legumes; phytohormone production	Used in legume inoculants for sustainable N supply	[64]
5.	*Enterobacter* spp.	Produces IAA, siderophores, ACC deaminase; enhances abiotic stress tolerance	Promotes growth under salinity and drought stress	[65]
6.	*Azospirillum* spp.	Nitrogen fixation; production of auxins and gibberellins	Biofertilizers for cereals, such as wheat and maize	[66]
7.	*Serratia marcescens*	Produces antibiotics, proteases, and chitinases; inhibits fungal pathogens	Used in biocontrol formulations for vegetables & pulses	[65]
8.	*Microbacterium testaceum*	Produces IAA, siderophores, and promotes nutrient uptake	Enhances plant vigor and stress tolerance in rice	[67]
9,	*Paenibacillus polymyxa*	Produces antibiotics, exopolysaccharides, and phytohormones	Biocontrol and biofertilizer; used in cereals	[66]
10.	*Arthrobacter* spp.	Degrades xenobiotics; produces stress tolerance enzymes	Used for phytoremediation and stress management	[68]
11.	*Klebsiella pneumonia* (QS24-6)	Nitrogen fixation, ACC deaminase activity	Improves growth in rice and maize	[69]
12.	*Pantoea agglomerans*	Produces antibiotics, siderophores, and auxins	Biocontrol and plant growth promotion in vegetables	[70]
13.	*Bacillus velezensis*	Produces lipopeptides, surfactin, antimicrobial metabolites, and plant hormone modulation	Seed coating and soil inoculant for vegetables and cereals to suppress pathogens	[71]
14.	*Pseudomonas putida*	Siderophore production, phosphate solubilization, and IAA production	Biofertilizer for growth enhancement in vegetables under nutrient-deficient conditions	[72]
15.	*Microbacterium oxydans*	IAA production, stress tolerance enzymes, nutrient mobilization	Root/seed endophyte for cereals under water-stress environments	[73]
16.	*Enterobacter cloacae*	IAA, siderophore, nitrogen fixation potential	Growth promoter in vegetable crops under low-fertility soils	[65]
17.	*Methylobacterium populi*	Cytokinin production, methanol utilization, and plant growth promotion	Enhances photosynthesis and growth in field crops	[74]
18.	*Stenotrophomonas rhizophila*	ACC deaminase, siderophores, and hydrolytic enzymes	Abiotic stress management (salinity, drought) in horticultural crops	[75]

IAA: Indole-3-acetic acid, ISR: Induced systemic resistance.

fungal genera *Aspergillus, Scytalidium, Myceliophthora,* and *Talaromyces* release growth-enhancing hormones and improve uptake of nutrients, contributing to the overall growth of the plant [141]. Endophytes are capable of producing antifreeze proteins and protective metabolites to maintain the integrity of the cells under the cold induced stress [142,143].

The accumulation of toxic heavy metals in the agricultural soils is a growing concern, as it impacts the physiology and productivity of the plant [144]. Rice crop contaminated with lead (Pb) and Cadmium (Cd) has a detrimental impact on human health and global food sustainability [145]; the endophyte *Deinococcus radiodurans*, increases rice crop tolerance to these heavy metals by scavenging reactive oxygen species and enhancing the activity of antioxidants [146]. The probability of exposure among humans is elevated once these toxic metals enter the food chain [147]. Bacterial endophytes, such as *Enterobacter* spp., *Pseudoalteromonas* spp., and *Salmonella* spp. produce IAA to reduce metal toxicity [148-151].

5. OMICS APPROACHES TO UNRAVEL ENDOPHYTE ROLE IN AGRICULTURE

Genomics provides insights at the molecular level and has substantially increased our understanding of plant-microbiome associations [152,153]. These insights help us formulate biotechnological methodologies to encourage better crop performance [154]. The genes essential for survival of the endophytes within the plant, production of bioactive compounds, and secretion of beneficial metabolites that support plant growth can be identified using these approaches [155-157]. Next-generation sequencing is one such approach that has unraveled the genes essential for various metabolic processes and colonization of the endophytes [158,159]. The molecular level studies enabled us to differentiate beneficial microbes from the harmful ones through evolutionary adaptations and regulatory pathways [160]. Novel strains are discovered through 16 S rRNA of endophytes [161].

Table 3: Key actinomycete endophytes with their functional role and applications.

Category	Endophytic actinomycete genera	Key metabolites	Agricultural importance	References
Biocontrol agents	*Streptomyces*	Antibiotics, IAA	Broad-spectrum pathogen control	[83]
	Micromonospora	Antimicrobials	Pathogen suppression	[84]
	Actinoplanes	Antifungal metabolites	Root disease control	[85]
	Saccharopolyspora	Antibiotics	Biocontrol in multiple crops	[86]
	Actinokineospora	Lytic enzymes	Defense activation	[87]
	Kribbella spp.	Polyketides, alkaloids	Biocontrol + growth	[88]
	Dactylosporangium	Peptides, alkaloids	Crop protection	[89]
	Spirillospora	Antifungal proteins	Cereal disease control	[90]
	Actinomadura	Antibiotics	Solanaceous crop protection	[91]
	Streptosporangium	Polyketides	Soil health improvement	[92]
	Amycolatopsis.	Antibiotics compounds	Soil-borne pathogens control	[93]
	Kibdelosporangium	Macrolides	Potent biocontrol	[94]
Biofertilizers and Nutrient Enhancement	*Frankia*	Nitrogen-fixing	Fertility in actinorhizal crops	[95]
	Kitasatospora	Polyketides, siderophores	Root protection & nutrient uptake	[96]
	Planomonospora spp.	Siderophores	Root promotion	[97]
Stress Tolerance and Plant Growth Promotion	*Nocardiopsis*	Antioxidants	Abiotic stress tolerance	[86]
	Rhodococcus	Auxins, degradation	Stress tolerance, bioremediation	[91,98]
	Salinispora	Polyketides,	Salt-tolerant crop protection	[86]
	Actinophytocola	Siderophores, enzymes	Drought tolerance	[99]
	Thermomonospora spp.	Enzymes	Immunity enhancement	[100]
	Crossiella	Enzymes	Support legumes	[101]

IAA: Indole-3-acetic acid.

Metabolomic profiling of endophytes, revealed bioactive compounds essential for enhancing the vitality of the plants [162-164]. It helps in decoding biochemical networks that govern plant response under abiotic stresses[165] by the quantification of metabolites involved in stress adaptation [166]. In addition, integration of metabolomic, proteomic, and genomic analyses offer a comprehensive view of mechanisms involved in stress tolerance, facilitating targeted strategies to strengthen the performance of the crops under global challenges [167].

6. CHALLENGES AND FUTURE DIRECTIONS

The potential of endophytes to inhabit different sites within the plant has paved the way for their use in multiple biological applications. However, there are an immense number of endophytes that are still unidentified and uncultured because of insufficient knowledge about their cultivation requirements [168]. One of the major limitations of endophytes is host-specificity, and the effectiveness of endophytes often depends on the crop genotype and environmental conditions [169]. Another issue related to endophytic probiotics is their commercialization, as they encounter regulatory and production barriers. In addition, field consistency is one of the limitations; strains that perform well under laboratory trials sometimes fail to reproduce the same results under open-field conditions, which makes the farmers doubtful about the field performance of endophytes [49]. Lack of standardized inoculation methods complicates their integration into large-scale farming systems [112].

Future strategies required to overcome the challenges include:

- Integration of multi-omics techniques for better understanding of the plant-endophytic interactions
- Development of cultivars, highly compatible with beneficial endophytes for better performance across environments
- Conduction of large-scale field trials to enhance reliability, stability, and commercialization of the endophytic products
- Collaboration among policymakers, researchers, and industry stakeholders to accelerate endophyte-based innovations.

7. CONCLUSION

Presently, agriculture is facing numerous challenges, including climate change, biotic and abiotic stresses, soil degradation and pollution, all of which significantly affect crop yield and threaten food security. Therefore, it is essential to develop strategies that can enhance disease resistance and boost crop productivity over the long run. Thus, exploiting the beneficial plant microbiomes and their products is essential for developing effective strategies. By understanding the complexities of plant microbiome interactions and harnessing their benefits, researchers can develop innovative strategies for disease management. Plants have the ability to modulate their beneficial microbiomes under various stress conditions to enhance their own protection. Their benefits extend even after harvest, where they delay spoilage and extend shelf life through antifungal activity, offering a natural solution to food loss. However, translating laboratory discoveries into consistent field applications remains challenging due to host specificity, environmental variability, and lack of standardized protocols. Interdisciplinary research and collaborations are essential to fully harness its potential for promoting sustainable agricultural practices. Future studies should investigate how the plant immune system interacts with different beneficial microbiomes and how these interactions shape the specific microbiota that enhance crop health and productivity.

8. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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10. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

11. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

12. DATA AVAILABILITY

Data is available with the authors and shall be provided upon request.

13. PUBLISHER'S NOTE

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The authors declare that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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