

Original Research Article

Endophytic Microbial Inoculation Modulates Plant Defense Responses and Growth Performance

Sindhuja Suram¹ , Poly Saha² , Abhijit Debnath^{3*} , A. K. Mohanty⁴ , Chakpram Birendrajit⁵ ,
Athokpam Haribhushan⁶ , Lahar Jyoti Bordoloi⁷ , Moaakum Pongen⁸ 

¹PGIHS, SKLTGHU, Siddipet, Telangana – 502279, India.

²College of Agriculture, Burdwan, BCKV, WB – 713101, India.

³Krishi Vigyan Kendra Dhalai – 799278, Tripura, India.

⁴ICAR–Agricultural Technology Application Research Institute (ATARI), Zone VII, Umiam, Meghalaya, India.

⁵Training and Monitoring Cell, Directorate of Extension Education, CAU, Imphal – 795004, Manipur, India.

⁶Krishi Vigyan Kendra, Central Agricultural University, Imphal, South Garo Hills – 794005, India.

⁷KVK Kiphire, ICAR Research Complex for NEH Region, Nagaland Centre, Nagaland – 798611, India.

⁸ICAR KVK Wokha – 797111, Nagaland, India.

Corresponding Author: Abhijit Debnath

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Abstract

Endophytic microorganisms inhabit internal plant tissues without causing visible disease and can substantially modify plant growth, immunity, nutrient acquisition and tolerance to environmental stress. Their effects arise from coordinated interactions among microbial colonization traits, plant immune surveillance, phytohormonal signalling, redox regulation, nutrient exchange and resident microbial communities. Endophytes are not immunologically invisible; rather, successful strains regulate the amplitude, duration and spatial distribution of pattern-triggered immunity. Controlled immune accommodation permits internal colonization, whereas reactive oxygen species, mitogen-activated protein kinase cascades and specialized metabolites constrain excessive microbial proliferation. Many endophytes simultaneously prime systemic tissues through jasmonic acid, ethylene, salicylic acid and N-hydroxyphenylpyruvic acid-associated pathways, enabling faster defence activation after pathogen challenge without the metabolic cost of constitutive resistance. Growth promotion results from microbial auxin production, 1-aminocyclopropane-1-carboxylate deaminase activity, biological nitrogen fixation, phosphorus transfer, siderophore production, improved root architecture and maintenance of photosynthesis under stress. Representative systems include *Bacillus velezensis* FZB42, *Enterobacter* sp. SA187, *Paraburkholderia phytofirmans* PsJN, *Colletotrichum tofieldiae*, *Serendipita indica* and endophytic *Beauveria*, *Metarhizium* and *Epichloë* species. Synthetic communities and bacterial–fungal combinations can broaden disease suppression and environmental stability, although strain identity and functional compatibility are often more important than taxonomic richness. Multi-omics, spatial imaging, stable-isotope tracing and synthetic biology are improving mechanistic resolution, while encapsulation and hydrogel technologies are enhancing inoculant delivery. However, field performance remains constrained by host genotype, resident microbiota, formulation, environmental variability and biosafety concerns. This review integrates current understanding of endophyte diversity, colonization, immune modulation, growth promotion, stress adaptation and field translation, emphasizing the need for mechanism-guided, ecology-aware and genomically validated inoculant development.

Keywords: endophytes; plant immunity; defence priming; induced systemic resistance; phytohormonal crosstalk; plant growth promotion; synthetic microbial communities; multi-omics; microbial inoculants

1. Introduction

Global crop productivity is increasingly constrained by climate variability, soil degradation, nutrient-use inefficiency, emerging pathogens and declining agrochemical effectiveness. Drought, salinity, heat, flooding, nutrient deficiency and pathogen infection frequently occur together, disrupting photosynthesis, hormonal regulation, redox balance, nutrient acquisition and reproductive development. These challenges have increased interest in microbiome-assisted crop management, particularly the use of endophytic microorganisms capable of colonizing internal tissues and directly regulating plant metabolism, immunity and stress adaptation.

Plants are increasingly regarded as holobionts whose performance reflects interactions among the host genome, associated microbiota and environment. The endosphere is a selectively assembled habitat influenced by host genotype, organ identity, developmental stage, immune status, nutrition and microbial competition. Arabidopsis studies demonstrated progressive microbial filtering from bulk soil to the rhizosphere and endosphere [1–3], with comparable patterns reported in rice, maize, wheat and barley [4–7]. Comparative genomic studies have identified microbial genes associated with motility, nutrient acquisition, stress tolerance, immune interaction and plant adaptation [8–11].

Endophytism is a context-dependent ecological state rather than a fixed taxonomic property. Microorganisms may shift between mutualism, commensalism and pathogenicity depending on strain identity, host genotype, microbial abundance, tissue localization, nutritional status and environmental conditions. *Colletotrichum tofieldiae* promotes Arabidopsis growth by transferring phosphorus under phosphate deficiency [12], whereas fungal endophytic competence is linked to specific genomic and transcriptional features [13]. Regulatory changes in fungal secondary metabolism can also shift the association towards pathogenicity, illustrating the molecular plasticity of endophytic lifestyles [14].

Endophytic colonization involves chemotaxis, attachment, biofilm formation, tissue penetration, apoplastic adaptation and competition with resident microorganisms. Motility, adhesins, exopolysaccharides, siderophores, cell-wall-modifying enzymes and oxidative-stress tolerance contribute to establishment [15–19]. Metatranscriptomic analysis of a 106-member bacterial–fungal community identified more than 3,000 microbial genes associated with root-interface adaptation, energy metabolism and colonization [20].

Plant immunity is a major determinant of colonization. Pattern-recognition receptors perceive flagellin, elongation factor Tu, peptidoglycan, lipopolysaccharides and fungal chitin, activating calcium influx, reactive oxygen species, mitogen-activated protein kinase cascades, callose deposition and antimicrobial metabolism [21–23]. Beneficial microorganisms are therefore not immunologically invisible; they modulate the intensity, duration and spatial distribution of defence.

Root commensals suppress selected immune pathways and microbial-pattern-induced growth inhibition [9,24–25]. Spatial restriction of immune perception prevents root-meristem damage and permits colonization without severe growth penalties [26]. Controlled immune activation may also support mutualism. Plant-derived reactive oxygen species stimulated auxin production by *Bacillus velezensis* FZB42, increasing lateral-root development, bacterial survival and fungal protection [19]. RBOHD-dependent reactive oxygen species also suppressed the secretion system of a potentially harmful *Xanthomonas* commensal while preserving its protective function [27].

Endophytes induce systemic resistance and defence priming. Root colonization by *Pseudomonas fluorescens* WCS417 enhanced distal resistance through jasmonic acid- and ethylene-associated signalling without constitutive salicylic acid accumulation [28–30]. Colonized plants maintained limited basal defence but responded more rapidly after pathogen challenge [31]. More recently, fungal colonization was shown to regulate FMO1- and UGT76B1-dependent N-hydroxyphenylpyruvic acid homeostasis, providing a molecular mechanism for dose-dependent regulation of shoot growth and immunity [32].

Endophytes also regulate auxin, cytokinins, gibberellins, ethylene, salicylic acid, jasmonates, abscisic acid and brassinosteroids. Microbial auxin promotes root branching, whereas ACC deaminase reduces stress-induced ethylene accumulation [33–35]. *Enterobacter* sp. SA187 improved salinity tolerance through ethylene-pathway reprogramming and coordinated sulfur metabolism [36–37]. Endophytes also improve nitrogen, phosphorus, iron, zinc and potassium acquisition and regulate specialized metabolites involved in microbial recruitment and immunity [38–42].

The resulting phenotype reflects interactions among the microbial strain, host genotype, resident microbiome and environment. This review synthesizes the diversity, ecological origin, colonization, immune regulation, growth promotion, stress protection, multi-

omics analysis and agricultural translation of bacterial and fungal endophytes [43].

2. Diversity, Ecological Origin and Functional Classification

Endophytic communities include bacteria, actinobacteria, filamentous fungi and yeasts. Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes commonly dominate bacterial communities, whereas Ascomycota and Basidiomycota dominate fungal communities [1,5,7]. Host genotype and tissue type strongly influence endophytic community composition. Proteobacteria were reported as the dominant bacterial group in the roots and shoots of *Pelargonium graveolens* [44]. Both shared and genotype-specific endophytic microorganisms have been identified in different rice genotypes [45]. Substantial functional variation has also been observed among fungal endophytes isolated from hairy vetch [46].

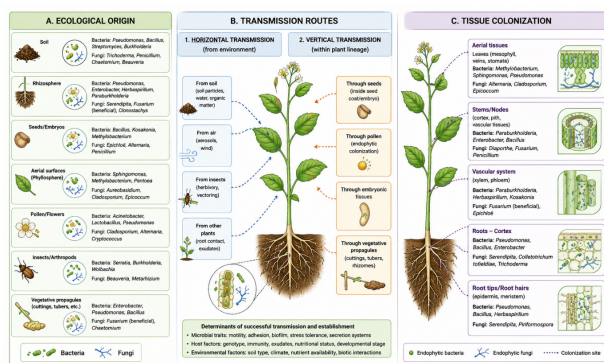


Figure 1. Ecological origin, transmission routes and tissue colonization of bacterial and fungal endophytes.

Important bacterial genera include *Pseudomonas*, *Paraburkholderia*, *Enterobacter*, *Kosakonia*, *Herbaspirillum*, *Azoarcus*, *Gluconacetobacter*, *Bacillus*, *Paenibacillus*, *Streptomyces*, *Sphingomonas* and *Methylobacterium* [8,10,17,47]. Proteobacterial endophytes are common in roots because of their motility and metabolic versatility, whereas *Sphingomonas* and *Methylobacterium* frequently occupy aerial tissues. *Paraburkholderia phytofirmans* PsJN can colonize roots, cortex, xylem, stems, leaves and reproductive structures and has been associated with improved growth, chilling tolerance, salinity tolerance and pathogen resistance [16,48–51]. *Bacillus* species are valuable because of durable endospores and production of lipopeptides, siderophores and hydrolytic enzymes. Diazotrophic *Herbaspirillum*, *Azoarcus*, *Gluconacetobacter* and *Kosakonia* can colonize cortical and vascular tissues and improve nitrogen acquisition [15,17].

Fungal endophytes include *Serendipita*, *Colletotrichum*,

Trichoderma, *Fusarium*, *Clonostachys*, *Epichloë*, *Beauveria*, *Metarhizium*, *Alternaria*, *Penicillium*, *Chaetomium* and *Diaporthe*. *Serendipita indica* and *S. vermifera* colonize root epidermal and cortical tissues and influence calcium signalling, auxin homeostasis, nutrient transport and systemic defence [52–54]. Entomopathogenic *Beauveria* and *Metarhizium* species may establish endophytically after seed, root, soil or foliar application and improve resistance to insects and pathogens [55–58]. Vertically transmitted *Epichloë* species colonize cool-season grasses and produce alkaloids that reduce herbivory, although some metabolites may cause livestock toxicity [59–61]. Endophytes originate from soil, rhizosphere, seeds, aerial surfaces, pollen, insects and vegetative propagules. Horizontal transmission occurs from soil, air or water, whereas vertical transmission occurs through seeds, embryos, pollen or vegetative tissues [62–64]. Persistent bacterial and fungal taxa can be transmitted across successive rice generations [64]. Seed-associated bacteria also contribute to the assembly of spermosphere and rhizosphere microbial communities in wheat [65]. Functionally, endophytes can be classified as nutrient-acquisition facilitators, phytohormone regulators, defence-priming microorganisms, biocontrol agents, abiotic-stress modulators, phytoremediation partners and producers of bioactive metabolites [66]. These categories overlap because effective strains commonly combine several functions.

3. Establishment and Colonization

Successful inoculation requires attraction to host-derived metabolites, attachment, competition with resident microbiota, tissue entry and maintenance of a compatible internal population. Root exudates containing sugars, amino acids, organic acids and phenolics act as nutrients and signalling molecules. Chemotaxis, motility, pili, adhesins, exopolysaccharides, biofilm formation and oxidative-stress tolerance are major colonization determinants [10,16–17,19].

Entry occurs through lateral-root emergence zones, root hairs, wounds, stomata and hydathodes. Bacteria may occupy intercellular spaces, cortical tissues and xylem, whereas fungal hyphae commonly occupy epidermal and cortical tissues. PsJN spreads from grapevine roots to aerial organs through vascular tissues [16,48], while *C. tofieldiae* and *S. indica* remain primarily associated with roots [12,52].

Host nutrition regulates colonization outcomes. Under phosphate deficiency, *Arabidopsis* permits *C. tofieldiae* colonization and receives phosphorus, whereas phosphate sufficiency strengthens fungal restriction [12,67]. Priority effects are also important. Early seed

Table 1. Representative bacterial and fungal endophytes and their principal functions

Endophyte	Host or origin	Colonized tissue or application	Major mechanism	Reported response	Key references
<i>Paraburkholderia phytofirmans</i> PsJN	Onion-derived; grapevine, rice and quinoa	Root or soil application; roots, xylem and shoots	Systemic defence, ion and redox regulation	Growth, chilling and salinity tolerance	[16,48–51]
<i>Bacillus velezensis</i> FZB42	<i>Arabidopsis</i> root association	Root inoculation	ROS-induced bacterial auxin production	Root branching and fungal protection	[19]
<i>Enterobacter</i> sp. SA187	<i>Indigofera argentea</i>	Root inoculation	Ethylene signalling, KMBA and sulfur metabolism	Salinity and heat tolerance	[36,37]
<i>Herbaspirillum seropedicae</i>	Rice, maize and grasses	Seed or root application; cortical and vascular tissues	Nitrogen fixation and nutrient regulation	Improved nitrogen acquisition and biomass	[15,17]
<i>Pseudomonas</i> spp.	Diverse crops	Seed, root or soil application	JA–ET-dependent resistance, siderophores and antibiotics	Root growth and disease suppression	[28–31]
<i>Colletotrichum tofieldiae</i>	<i>Arabidopsis</i>	Root cortex	Phosphorus transfer and immune accommodation	Growth under phosphate deficiency	[12,67]
<i>Serendipita indica</i>	Broad host range	Root epidermis and cortex	Calcium, auxin and nutrient signalling	Root growth and stress tolerance	[52,54]
<i>Beauveria bassiana</i>	Tomato, maize, wheat and legumes	Seed, root, soil or foliar application	JA, SA, antioxidants and insect pathogenicity	Growth and pest resistance	[56–58]
<i>Epichloë</i> spp.	Cool-season grasses	Vertical seed transmission	Alkaloid-mediated herbivore defence	Persistence and insect resistance	[59–61]

endophytes may occupy niches before soil microorganisms, whereas established resident communities may exclude introduced strains [11,68].

Colonization should therefore be verified through validated surface sterilization, strain-specific quantitative PCR, fluorescence imaging, confocal microscopy and temporal abundance measurements. Recovery from surface-sterilized tissues alone is insufficient evidence of stable internal colonization.

4. Modulation of Plant Defence

4.1 Immune Perception and Accommodation

Pattern-recognition receptors activate calcium signalling, reactive oxygen species, MAP kinase cascades, callose deposition and defence metabolism following microbial recognition [21–23]. Beneficial endophytes can selectively attenuate or spatially restrict these responses, while root commensals may suppress pattern-induced root growth inhibition and defence-related transcription [9,24,25].

Immune-suppressive bacteria can facilitate colonization by non-suppressive members of the microbial community, indicating that immune accommodation may function at the community level [24]. However, complete immune suppression could permit excessive microbial proliferation, so successful endophytic colonization requires balanced immune regulation. Inap-

propriate immune activation in root meristems may cause growth arrest, whereas restriction of immune responses to differentiated tissues permits microbial accommodation [26]. Regenerative agricultural practices may enhance soil microbial diversity and nutrient cycling, while conventional farming systems may increase the abundance of pathogens and antimicrobial-resistance genes [69].

4.2 Reactive Oxygen Species and Redox Control

Reactive oxygen species restrict microorganisms at high concentrations but act as signalling molecules when maintained at controlled levels. Host-derived reactive oxygen species can stimulate bacterial auxin synthesis in *Bacillus velezensis* FZB42, promoting lateral-root formation and plant protection [19]. RBOHD-derived reactive oxygen species can also suppress virulence-associated secretion in commensal *Xanthomonas*, thereby maintaining a protective rather than damaging interaction [27].

Endophytes also modify superoxide dismutase, catalase, peroxidase, ascorbate peroxidase and glutathione reductase. These changes can reduce lipid peroxidation, electrolyte leakage and photosynthetic damage under biotic or abiotic stress [70].

4.3 Induced Systemic Resistance and Priming

Root-associated *P. fluorescens* WCS417 induces systemic resistance through jasmonic acid- and ethylene-associated pathways [28–30]. Colonized plants may maintain only limited basal defence but respond more rapidly and strongly after pathogen challenge [31]. This primed state enhances calcium influx, oxidative bursts, MAP kinase activation, callose deposition and antimicrobial metabolism without requiring continuous expenditure of metabolic resources [71,72]. An N-hydroxyphenylpyruvic acid-dependent root-to-shoot signalling system regulates the balance between plant growth and immunity [32]. Fungal colonization alters FMO1- and UGT76B1-dependent NHP homeostasis. Moderate NHP levels support plant growth with limited immune activation, whereas higher NHP concentrations enhance defence responses but restrict growth [32].

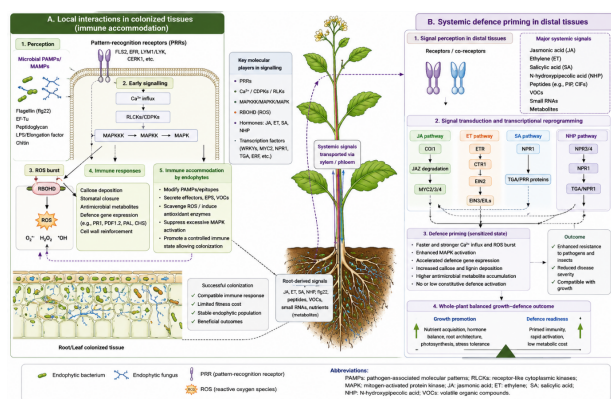


Figure 2. Endophyte-mediated local immune accommodation and systemic defence priming.

4.4 Direct Antagonism and Community Protection

Endophytes directly suppress pathogens through nutrient competition, siderophore-mediated iron sequestration, antibiotics, lipopeptides, volatile compounds, chitinases, glucanases, quorum quenching and mycoparasitism. *Bacillus*, *Pseudomonas*, *Streptomyces*, *Trichoderma*, *Clonostachys* and non-pathogenic *Fusarium* commonly combine these activities.

A consortium of *Bacillus velezensis*, *B. megaterium* and *Herbaspirillum huttiense* reduced *Rhizoctonia solani* root rot in tomato and increased phenolic content and antioxidant activity [73]. Disease suppression may also result from microbiome restructuring through the recruitment or activation of protective microbial communities [74–76]. Interactions between bacterial and fungal community members can also be essential for plant survival under fungal pathogen pressure [77].

5. Plant Growth and Physiological Performance

Endophytes regulate plant development through auxins, cytokinins, gibberellins, ethylene, abscisic acid, salicylic acid, jasmonates and brassinosteroids. Microbial indole-3-acetic acid promotes lateral roots and root hairs, increasing water and nutrient absorption. ACC deaminase lowers the ethylene precursor ACC and helps maintain root elongation under drought, salinity, flooding and pathogen pressure [33–35]. ACC deaminase is required for growth promotion by the foliar symbiont *Paraburkholderia dioscraeae*, although this enzyme is not essential for microbial colonization of the host plant [78].

Endophytes enhance nutrient acquisition through nitrogen fixation, phosphorus and potassium solubilization, siderophore production and regulation of root transporters. Diazotrophic *Herbaspirillum*, *Azoarcus*, *Gluconacetobacter* and *Kosakonia* improve nitrogen availability [15,17]. *C. tofieldiae* transfers phosphorus under deficient conditions [12], while root microbial communities integrate phosphate-starvation signalling with immunity [38].

Endophytic inoculation may improve chlorophyll content, photosystem stability, stomatal conductance, carbon assimilation and water-use efficiency. Pteridic acids H and F produced by *Streptomyces iranensis* HM35 act as potent growth-regulatory metabolites and can alleviate drought and salinity stress even at nanomolar concentrations [79].

Under salinity, endophytes may maintain favourable potassium-to-sodium ratios, increase osmolytes and protect photosynthetic systems. Under drought, increased root depth, branching, antioxidant activity and water-use efficiency improve plant hydration. Under heat, endophytes regulate membrane stability, heat-shock responses and cellular redox balance.

Growth promotion and defence nevertheless compete for carbon, energy and nutrients. Endophytes reduce this trade-off by maintaining defence in a primed state, improving resource acquisition and spatially separating local accommodation from systemic resistance. A microbiota–root–shoot signalling circuit coordinates plant growth and defence under low-light conditions through MYC2-mediated regulation [80]. The NHP signalling system further demonstrates that plant growth and immunity are quantitatively coordinated rather than functioning as strictly opposing processes [32].

Table 2. Principal defence mechanisms regulated by endophytes

Mechanism	Representative endophytes	Major components	Consequence	References
Local immune accommodation	Root <i>Pseudomonas</i> , <i>Xanthomonas</i> and synthetic communities	PRRs, MAPKs and tissue-specific immunity	Colonization with reduced growth penalty	[24–26]
ROS-mediated regulation	<i>Bacillus velezensis</i> FZB42 and <i>Xanthomonas commensals</i>	RBOHD and microbial auxin or secretion systems	Restricted virulence and stable mutualism	[19,27]
Systemic resistance	<i>Pseudomonas fluorescens</i> WCS417, <i>Bacillus</i> and <i>Trichoderma</i>	JA, ET, MYC2 and defence priming	Faster response to subsequent attack	[28,29,31]
NHP-mediated signalling	Root-associated fungi	FMO1, UGT76B1 and NHP	Dose-dependent regulation of growth and immunity	[32]
Direct antagonism	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Streptomyces</i> and <i>Trichoderma</i>	Siderophores, antibiotics and hydrolytic enzymes	Inhibition of pathogen growth	[73,74]
Microbiome restructuring	Bacterial–fungal consortia	Exudates, metabolites and microbial competition	Assembly of disease-suppressive microbial communities	[75–77]

6. Multi-Omics, Formulation and Field Translocation

Whole-genome sequencing identifies genes involved in motility, adhesion, secretion, nutrient acquisition, secondary metabolism and biosafety. Comparative genomics can distinguish beneficial strains from related pathogens. Beneficial and pathogenic *Colletotrichum* species may possess similar genomic repertoires but differ in effector expression and the host responses they induce [67].

Host transcriptomics reveals changes in immune receptors, transcription factors, phytohormonal pathways, nutrient transporters, antioxidant systems and photosynthetic processes. Dual RNA sequencing simultaneously examines transcriptional responses in both the plant host and the associated microorganism, whereas metatranscriptomics evaluates the active functions of entire microbial communities. Members of synthetic microbial communities can activate strain-specific colonization programmes while sharing broader functions related to energy metabolism and environmental adaptation [20]. Effective formulations must maintain microbial viability, physiological activity and genetic stability during storage and application. Common carrier materials include peat, talc, lignite, biochar, alginate, starch, chitosan and polymeric hydrogels. A carboxymethyl-chitosan–alginate hydrogel containing *Ensifer* C5 protected the bacterial inoculant, improved root colonization and increased the field yield of *Brassica napus* [81].

Single-strain inoculants are comparatively easier to characterize, formulate and regulate, but they may provide a limited range of functions. Microbial con-

sortia can combine nutrient acquisition, hormonal regulation, pathogen suppression and stress protection. However, antagonistic interactions, unequal growth rates and poor compatibility among component strains may reduce community stability. Strain identity and specific microbial interactions may therefore be more important than total species richness in determining pathogen protection [82].

Field performance remains less predictable than greenhouse performance because of indigenous microbial competition, environmental variability and differences among host genotypes. Multi-location and multi-season trials should quantify colonization persistence, yield, nutrient-use efficiency, disease severity, product quality and non-target microbiome effects [83].

7. Constraints, Biosafety and Future Directions

A major limitation is inconsistent verification of endophytic colonization. Recovery after surface sterilization does not prove stable internal residence if sterilization is incomplete. Colonization should be confirmed through surface-sterility controls, molecular quantification, microscopy and temporal persistence.

Microbial performance is context dependent. Nutritional conditions, host genotype and environmental stress may shift an association from beneficial to neutral or detrimental. *C. tofieldiae* benefits *Arabidopsis* under phosphate deficiency but is more strongly restricted under phosphate sufficiency [12,67]. Changes in microbial secondary metabolism may also alter the mutualist–pathogen balance [14].

Candidate strains related to opportunistic human, ani-

Table 3. Tools and translational requirements for endophyte development

Component	Information or advantage	Principal limitation
Whole-genome sequencing	Colonization, metabolism and biosafety genes	Gene presence does not demonstrate in planta expression
Dual transcriptomics	Simultaneous host and microbial responses	Requires sufficient microbial RNA
Metabolomics and proteomics	Active metabolites, enzymes and effectors	Molecular origin may be difficult to assign
Stable-isotope tracing	Quantitative nutrient transfer	Requires specialized facilities
Spatial imaging	Tissue- and cell-specific colonization	High cost and complex preparation
Seed coating	Economical and early root exposure	Compatibility with pesticides and seed storage
Root dipping or soil drenching	Direct exposure of root entry sites	High inoculum demand and soil competition
Encapsulation and hydrogels	Improved viability and controlled release	Additional formulation cost
Synthetic communities	Functional complementarity	Interaction instability and regulatory complexity
Multi-location field trials	Agronomic validation	High environmental and genotype variability

mal or plant pathogens require genomic safety assessment. Whole-genome screening should identify virulence genes, toxins, transferable antibiotic-resistance determinants and mobile genetic elements. Effects on indigenous microbiota, horizontal gene transfer and persistence beyond the crop cycle must also be evaluated.

Future inoculant development should integrate host genotype, microbial ecology and defined mechanisms. Microbiome-assisted breeding may identify plant alleles that favour beneficial colonization without increasing pathogen susceptibility. Root-exudate chemistry, immune-receptor diversity and nutrient-transporter activity are promising breeding targets.

Synthetic communities should be assembled using functional complementarity, niche compatibility and stable interaction networks rather than richness alone. Machine learning and metabolic modelling may assist community design, although experimental validation remains essential. Defined microbial metabolites, including pteridic acids, may offer standardized alternatives to living inoculants [79].

Responsive delivery systems, biodegradable coatings and hydrogels can improve survival and tissue targeting. Engineered endophytes could eventually sense drought, nutrient deficiency or pathogen signals and conditionally produce protective compounds. Such systems will require genetic safeguards, ecological containment and transparent risk assessment.

Future research must also examine combined stresses, multiple host genotypes and long-term field effects. Standardized reporting of inoculum concentration, formulation, colonization abundance, soil characteristics and environmental conditions would improve reproducibility and meta-analysis.

8. Conclusion

Endophytic microorganisms regulate plant defence and growth through interconnected effects on colonization, immunity, phytohormones, nutrient acquisition, redox homeostasis and microbiome structure.

Successful strains establish controlled immune accommodation in colonized tissues while priming systemic tissues for faster responses to subsequent attack.

Growth promotion results from microbial auxin and ACC deaminase activity, biological nitrogen fixation, phosphorus transfer, siderophore production, sulfur metabolism and specialized metabolites. These functions can improve drought, salinity, heat and disease tolerance, but their expression depends strongly on microbial strain, host genotype, resident microbiota and environment.

The major challenge is converting promising laboratory responses into reproducible field performance. Reliable inoculants require verified internal colonization, genomic safety, host compatibility, formulation stability and multi-environment validation. Multi-omics, spatial biology, synthetic communities and advanced delivery systems provide promising routes for overcoming current limitations.

Endophytic inoculation should therefore be viewed as ecological and molecular engineering of the plant holobiont rather than simple application of a growth-promoting microorganism. Integration of microbial genetics, plant immunity, community ecology, formulation science and field agronomy will be essential for developing dependable endophyte-based technologies that enhance crop productivity while reducing reliance on chemical inputs.

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