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Endophytes Unveiled: Microbial Allies in Plant Growth and Stress Management

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Abstract

Endophytes are microscopic creatures that live in plants' inner tissues and don't seem to inflict any harm there. In particular, they improve nutrient uptake, produce growth-regulating hormones, and make plants more resistant to drought, salt, and severe temperatures, all of which contribute to plant development. Moreover, these microbes help defend plants against pathogens and herbivores by generating antimicrobial substances and activating plant defense mechanisms. Their functions in nitrogen fixation, phosphate mobilization, and siderophore secretion also contribute significantly to plant growth and yield. With the advent of molecular and genomic tools, the intricate relationships between endophytes and their host plants are being increasingly understood, highlighting their potential in eco-friendly agriculture. Utilizing endophytes as natural inoculants or biological control agents offers a promising alternative to synthetic agrochemicals, paving the way for sustainable and resilient farming systems. This review highlights the pivotal role of endophytes in enhancing plant performance and supports their broader application in contemporary crop management.

Keywords: Endophytes, crop management, Stress Management, eco-friendly agriculture, agrochemicals

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Introduction

There is a critical need to find ecologically appropriate substitutes for chemical inputs in agriculture due to the growing number of global concerns like climate change, decreasing soil fertility, and the rising demand for sustainable farming practices. Endophytes, which are harmless microbes that live in plant tissues, are one potential option. Once considered passive inhabitants, endophytes are now recognized as active partners that significantly influence plant physiology, development, and resilience. Endophytes contribute to plant growth promotion through mechanisms such as nutrient acquisition, phytohormone production, and nitrogen fixation. Equally important is their role in stress management, where they help plants withstand adverse conditions including drought, salinity, and temperature extremes by modulating stress-responsive pathways. In addition, many endophytes exhibit biocontrol potential, producing antimicrobial compounds and inducing systemic resistance to pathogens and pests.

Nature harbours an immense and largely untapped reservoir of chemical diversity, much of which remains to be fully understood. Among the most explored sources of this natural wealth are plants and microorganisms, which serve as rich repositories of bioactive compounds. In recent years, the quest for beneficial microbes and their metabolites has gained significant momentum, largely driven by increasing societal demand to reduce dependence on synthetic fertilizers and chemical pesticides. This shift reflects a broader commitment to adopting environmentally sustainable and ecologically sound agricultural practices (Morelli *et al*., 2020).Using endophytic microorganisms as biofertilizers may be an effective way to enhance soil microbial status since it encourages the natural soil microflora, which in turn affects nutrient accessibility and organic matter breakdown. Living inside the host plant, endophytes are microorganisms that may colonize plant roots without endangering the plants (Chaudhary *et al*., 2022). One of the most important ways endophytic microbes contribute to plant health is via improving nutrient uptake. These microorganisms help plants get the nitrogen and phosphate they need by transforming these nutrients into forms plants can use. Higher agricultural output and enhanced plant development are outcomes of this enhanced nutrient uptake. Furthermore, certain endophytes produce hormones that enhance plant growth and development, such as auxins, gibberellins, and cytokinins. The role that endophytes play in plant defence mechanisms is an important advantage of these organisms. As an added layer of defence, several of these bacteria secrete antibiotic chemicals that stop dangerous pathogens from multiplying. Chemical pesticides are often associated with health and environmental hazards; this biocontrol capability helps lessen reliance on them. According to Gakuubi *et al*. (2021), endophytes have the ability to activate systemic resistance in plants, which means they can prime their immune systems to respond better when future pathogens attack.

Sustainable agriculture's guiding principles—which include the utilisation of endophytic microbes—highlight the significance of socially responsible, commercially successful, and ecologically sound approaches. Soil erosion, water contamination, and the lack of biodiversity are some of the negative environmental implications of conventional farming. Endophytes help to mitigate these impacts by minimising the need for synthetic fertilisers and pesticides. More robust and fruitful agroecosystems are supported by these bacteria because they improve soil quality by increasing microbial diversity and promoting biological activity (Wilson *et al*., 2023). Additionally, endophytes play a crucial role in plant health by protecting plants from harmful organisms, improving nutrient absorption, and producing important phytohormones. They accomplish this in a number of ways, one of which is by activating plant defence hormones and another is by producing antibacterial chemicals, lytic enzymes, and secondary metabolites. Plants having these traits are better able to endure biotic stress, which in turn boosts soil fertility and agricultural yields. Therefore, endophytes provide a sustainable and environmentally acceptable alternative to toxic agrochemicals when used as biofertilizers and biocontrol agents in contemporary farming systems.

Plant-microbe interactions have garnered significant attention in recent years due to their expanding roles in agriculture, ecology, and pharmacology. Among these interactions, mycorrhizal fungi and endophytes associated with plants are particularly important, as they enhance nutrient uptake and help plants adapt to environmental challenges (Chitnis *et al*., 2020; Tedersoo *et al*., 2020; Tiwari *et al*., 2020c, 2021a). Both microbial and plant partners are known to produce a diverse array of metabolites and proteins that serve multiple purposes, particularly in mediating biological functions and environmental responses. These biochemical compounds not only contribute to plant survival and adaptation but also hold promising potential in the field of drug discovery, given their pharmacological properties and natural origin (Tiwari *et al*., 2021b, 2021c, 2021d, 2022b, 2022c).

What are Endophytes?

German scientist Heinrich Anton De Barry (1866) was the first person to coin the word "endophyte" to describe fungi and bacteria that invade plant tissues without endangering their host (Akram *et al*., 2023).

Although many researchers have different definitions of endophytes, White and Bacon (2000) proposed a clear-cut as well as recognized definition as: "microbes that colonize living, internal tissues of plants without causing any immediate, overt negative effect."

Endophytes are microbes that perpetuates inside plants and usually do not interfere with their development. Endophytes, in contrast to harmful microbes, are known to improve the fitness of their plant hosts. Although endophytes are believed to be a subpopulation of the rhizosphere microbiome, they differ from rhizospheric bacteria in certain ways, indicating that not all of the latter can enter plants and/or that alter their metabolism and adapt to their internal environment once they are inside their hosts.

Mangroves are an abundant source of endophytic fungi. Mangrove plants have a diverse fungal population due to their unique host-endophyte association. Plants rely on their unique genetic information to protect themselves against predators.

Even while endophytic microbes still have a lot of potential in the agricultural sector, there are several obstacles to their widespread usage that arise from their field use. There are numerous elements that need to be considered for their broad use from lab to field when injected into a crop plant. Initially, a lot of fungal endophytes create harmful secondary metabolites, like mycotoxins, which infect their host plants after colonizing them and spread to fruits and seeds. Research on their colonization and the viability of the intended inoculants is still necessary (Chitnis et.al, 2020).

Nitrogen fixation, phosphate solubilisation, siderophore production, phytohormone synthesis, and enhanced stress resistance are just a few of the many processes that endophytic bacteria and fungi help crop plants with, helping them thrive in a wide range of environments. Some nitrogen-fixing endophytes have genes that allow them to fix nitrogen biologically. This helps plants grow and acquire nutrients. Examples of such endophytes include Bradyrhizobium, Kosakonia, and Paraburkholderia, which were found in rice, Novosphingobium sediminicola, and Ochrobactrum intermedium, which were found in sugarcane (Okamoto *et al*., 2021).

The development of multiple-factor control techniques for the most prevalent stress drivers impacting plants, particularly in unfavourable conditions, may be facilitated by a careful analysis of the interaction between endophytes and their host plants, according to researchers. This innovative method also offers a more favourable viewpoint for researching the possibilities of biological processes connected to endophytes, including metabolite production, biocontrol, and bioremediation (Pirttilä et. al., 2021).

In recent times, endophytic microorganisms have gained significant interest for their role in plant disease management. These microbes, which include both fungi and bacteria, establish symbiotic associations with plants, frequently enhancing growth, boosting resistance to environmental stress, and offering protection against various plant pathogens (Anjum *et al*., 2019). Their application in sustainable agriculture presents an environmentally friendly alternative to chemical pesticides, supporting effective and green disease control strategies.

Types of Endophytes

Unlike pathogenic organisms, endophytes (often fungi or bacteria) may live in plants and safely inhabit their roots, stems, leaves, and seeds. On the contrary, they improve the plant's health and, in many cases, make it more resistant to biotic and abiotic challenges (Dubey *et al*., 2020).

Associating with grasses and a number of other plant species, fungal endophytes have shown that they can shield their hosts from predators, diseases, and even drought. According to Grabka *et al*. (2023), these microbes have the ability to create bioactive substances that can strengthen the immune response of plants or inhibit the spread of harmful diseases.

In addition to colonising the same plant sections as beneficial bacteria, bacterial endophytes are essential for plant growth, nutrition absorption, and defence against pathogenic germs. In order to prevent plant diseases, several of these bacteria produce antibiotics and other antimicrobials (Xia *et al*., 2022).

Bacterial Endophytes

Common genera of bacterial endophytes known for enhancing plant growth include Pseudomonas, Bacillus, Burkholderia, Stenotrophomonas, Pantoea, and Microbacterium. These microbes maintain a stable symbiotic association with their host plants while producing a range of metabolites that influence the plant’s physiological and biochemical processes. They contribute to plant development through both direct and indirect pathways. Directly, they assist in synthesizing essential biomolecules like phytohormones and improving nutrient availability. Indirectly, they offer protection to plants by acting as biocontrol agents, employing strategies such as producing hydrolytic enzymes, toxins, and antifungal compounds, competing for nutrients, engaging in mycoparasitism, and triggering the plant’s own defense mechanisms.

Several bacterial genera—such as Bacillus, Paenibacillus, Pseudomonas, Burkholderia, Enterobacter, Klebsiella, and Arthrobacter—have been studied for their roles in promoting plant growth and acting as biocontrol agents, with their endophytic behaviour well documented (M.A. Khan *et al*., 2020; C.A. Christakis *et al*., 2021; A.M. Mowafy *et al*., 2021; P.M. Mutungi *et al*., 2021; T. Ahmad *et al*., 2022).

Bacillus species can endure adverse environmental conditions by forming resilient endospores, enabling them to survive stress. These bacteria are also known for enhancing plant growth, activating plant defense responses, and exhibiting a wide spectrum of biocontrol capabilities (S. Compant *et al*., 2005; Vega *et al*., 2018). Similarly, Paenibacillus species are equipped to withstand extreme environments, form endospores, and combat plant diseases either through antibiotic production or by triggering systemic resistance in the host plant (E.N. Grady *et al*., 2016).

Due to their diverse metabolic capabilities, Pseudomonas species are adaptable to various environmental settings. They also play a significant role in suppressing plant pathogens and stimulating plant development (M.A. Khan *et al*., 2020; K. Craig *et al*., 2021).

Fungal Endophytes

fungus that live inside plants, known as endophytic fungus, are a common biological control agent for plant diseases. There are a lot of these fungi that help keep plant diseases at bay. Once fungal endophytes have colonised plant tissues, they compete with other microorganisms for nutrients and space while producing a wide range of antifungal secondary metabolites, including antibiotics, lipopeptides, and enzymes. In addition to suppressing phytopathogens, these effects promote growth and enhance systemic resistance, which improve plant health. According to Saikkonen *et al*. (2006), fungal endophytes create asymptomatic partnerships with plants and colonise many parts of them, including roots, stems, leaves, flowers, fruits, and branches. They are well-known for the ecological advantages they bring to their hosts and constitute a significant portion of the fungal biodiversity. Keeping pests at bay is an important part of what they do. Plants that host these endophytes have a natural defence against pests, according to studies. This is probably because these endophytes produce bioactive chemicals that disrupt the life cycle of pests. For example, in maize and several other crops—including banana, tomato, cotton, coffee, faba bean, and common bean—endophytic fungi have demonstrated their potential to reduce pest-related damage. This protective effect is largely attributed to the synthesis of mycotoxigenic secondary metabolites within the host plant, which act as natural pest deterrents (Cherry *et al*., 2004; Gurulingappa *et al*., 2010; Qayyum *et al*., 2015; Resquín-Romero *et al*., 2016; Klieber *et al*., 2016; Sánchez-Rodríguez *et al*., 2018; Vega *et al*., 2018; Jaber *et al*., 2018; Rondot *et al*., 2018). By residing in the internal, healthy tissues of plants for a portion or the all of their life cycle, endophytic fungi—particularly those belonging to the phylum Ascomycota—have a substantial impact on plant ecology, adaptation, and evolution. In a typical case, these fungi have a symbiotic relationship with the host plant, helping the host plant develop faster and more resilient to stress without really harming the host plant. "Plant" means the entire organism, but "host" describes the plant in its role as an endophyte's living environment. Roots, stems, and leaves are just a few of the plant tissues that these symbionts can colonise, beginning a mutually beneficial relationship.

Biocontrol Potential of Endophytes

A number of characteristics, such as marketability, storage, application, stability, and survival, have been deemed important in the investigation of endophytes as biological control agents. Only a few numbers of microbiological strains—whether they be bacteria, fungus, or yeast—have been commercialised despite extensive research into using them as BCAs in vitro or in vivo. This could be due to the stability or survivability of BCAs. In comparison to other microbial strains, Bacillus subtilis's endospore formation or Trichoderma's chlamydospore structure makes them the most ideal due to their stability or survivability under adverse conditions, which satisfies the criteria of commercial exploitation. In contrast to other microorganisms, which have a complicated colonisation process, the endophytic microbiome is easily delivered, entering and colonising the host tissue. However, a number of variables, including as the plant's growth or physiological status, genotype, colonisation pattern, population dynamics, and environmental conditions, may also affect how effective BCAs are against the pathogen (Card *et al*., 2016)

Recent studies have highlighted the presence of diverse endophytic communities on the surface of fruits that exhibit antagonistic activity. These microbial inhabitants—comprising bacteria, actinomycetes, and fungi—can significantly influence the development of postharvest diseases. Common bacterial genera such as Pseudomonas, Citrobacter, Paenibacillus, Burkholderia, and Bacillus are frequently found on fruit surfaces and show similar biocontrol potential to those observed under field conditions. For example, the growth of Alternaria alternata on table grapes was successfully suppressed by using a combination of chitosan and the endophytic yeast Metschnikowia pulcherrima.

Recent Discoveries in Endophytes

Reduced fertilizer Application Using Endophytic Bacterial species

Research has shown that certain bacterial strains capable of nitrogen fixation, phosphorus and potassium solubilization, and indole-3-acetic acid (IAA) production can significantly enhance the availability of key nutrients in the soil. For instance, Klebsiella pneumoniae has been identified as a high IAA producer, while species like Azotobacter chroococcum and Klebsiella variicola contribute to improving nitrogen, phosphorus, and potassium levels, thereby promoting soil fertility and plant growth. Wheat plant growth and N/P/K absorption were significantly enhanced by a mix of growth-promoting bacteria with various roles. Compared to conventional fertilization techniques, these bacterial isolates offer a higher potential for field application and enable the use of lower chemical fertilizer dosages. To confirm the validity of the current study, additional research is required to examine different circumstances, regions, and crops (Wang *et al*., 2020)

Bacterial Microbiota – A Valuable Resource in Xylem of Maize

It has been observed that maize specifically recruits a stable core microbiota within its xylem sap, which remains consistent across different genotypes and environmental conditions. This microbial community contributes to plant nitrogen nutrition by facilitating biological nitrogen fixation and plays a role in enhancing root development. However, the precise mechanisms and functions governing the interaction between the xylem sap microbiota and the host plant remain to be fully explored. In sustainable agriculture, this core microbiota may be a valuable resource for creating alternative microbial biotechnologies that improve crop performance (Zhang *et al*., 2022)

Endophytes as Biological Control Agents

Species of the genus Trichoderma are widely recognized as effective endophytic fungi used to control crop diseases. According to Silva *et al*., two different isolates—T. asperelloides and T. lentiforme—demonstrated strong biocontrol activity against the cotton pathogen Sclerotinia sclerotiorum. These isolates not only parasitized the sclerotia produced by the pathogen but also inhibited the growth of its mycelium through the emission of volatile compounds (Silva *et al*., 2022).

Role of Endophytes in Plant Growth and Productivity

Endophytes help plants grow in part by increasing the accessibility of nutrients. Soil fertility can be enhanced naturally, without the use of synthetic fertilisers, by specific bacterial endophytes that fix atmospheric nitrogen and transform it into plant-accessible forms. Some break down soil insoluble substances, allowing important macronutrients like phosphorus and potassium to be soluble. Strong plant development and increased harvest yields are both aided by this process of nutrient mobilisation.

Also, endophytes affect root architecture and promote cell division and elongation through the production of plant growth regulators like cytokinins, gibberellins, and indole-3-acetic acid (IAA). These microorganisms aid plants in nutrient absorption optimisation and stress adaptation by regulating hormonal balance. When it comes to the early phases of growth, this hormone support is crucial for making sure seedlings establish themselves vigorously.

Plant genotype and environmental variables impact the specificity of the symbiotic connection between endophytes and plants. Modern molecular biology has uncovered intricate signalling networks that regulate endophyte colonisation and function. To maximise the benefits of endophytes for agriculture, it is necessary to understand these interactions so that bioinoculants can be developed that are specific to crops and growing conditions.

Role of Endophytes in Plant Stress Management

Drought, salt, high temperatures, heavy metal toxicity, and disease infections are just a few of the challenges that plants face throughout their life cycle. Reduced growth and production are common results of these stress factors, which create major problems for farmers around the world. A new ally in the fight against these pressures has arisen: endophytes, which are microscopic organisms like bacteria and fungus that live harmlessly inside plant tissues. Endophytes accomplish a lot to help plants thrive in harsh environments by boosting their resistance and general health through a variety of processes.

Improved plant tolerance to abiotic stimuli, such as drought and salinity, is a critical mechanism via which endophytes contribute to stress management. Metabolites produced by some endophytic bacteria and fungi regulate osmolyte levels and the activity of antioxidant enzymes, helping plants to keep their internal water balance. In response to salt stress or dehydration, biological components and enzymes are shielded by osmoprotectants such proline and glycine betaine, which are frequently triggered by endophyte activity. Endophytes enhance the plant's internal defence system and reduce oxidative damage, allowing plants to thrive in challenging environments.

When it comes to temperature fluctuations, endophytes are just as helpful as those that help plants deal with drought and salt. Endophytes from certain fungi have the ability to alter gene expression in ways that are associated with cold tolerance and heat shock proteins. Because of these molecular changes, plants can tolerate temperature changes that would normally damage their cells.

One of the most important factors limiting agricultural yields is heavy metal pollution of the soil. By creating chelating agents and enzymes that convert hazardous metals into less dangerous forms, endophytes can immobilise or detoxify heavy metals. Endophytes are a valuable asset in the management of polluted settings due to their ability to shield plants from metal-induced damage and aid in soil restoration.

When it comes to protecting plants from biotic challenges including fungal, bacterial, viral, and insect diseases, endophytes are just as vital as they are when it comes to abiotic stresses. In order to directly hinder the growth of pathogens or impede the development of pests, numerous endophytes create volatile chemical compounds, lytic enzymes, and antibiotics. In addition, endophytes have the ability to make the host plant develop a resistance to future pathogens by priming its immune system. Sustainable agricultural methods are bolstered by its biocontrol function, which lessens the need for chemical pesticides.

Endophytes have both direct and indirect effects on plant stress management, with the former involving nutrient acquisition and the latter encompassing hormone modulation and enhanced root architecture. For example, in stressful environments, certain endophytic bacteria produce auxins and other phytohormones that encourage root growth and improve nutrient and water intake. The plant's vitality and resilience in the face of stress are enhanced by these all-encompassing advantages.

The possibility for generating crop-and environment-specific bioinoculants is being highlighted by ongoing research into the intricate relationships between plants and their endophytic partners. To make crops more resistant to the effects of climate change and other environmental stresses, microbial formulations like this may play a significant role in agricultural practices of the future.

IAA Improved Drought Resistance in V. radiata Plants

Colonized seedlings with IAA-producing fungal endophytes showed improved salinity tolerance, increased fresh weight, and induced early shoot development. The study found that the fungal endophyte producing IAA improved drought resistance in V. radiata plants by increasing photosynthetic processes, allowing them to overcome stress.

Auxin Interaction with Brassinosteroids and Abscisic Acid regulates Biotrophic Transition in Endophytic Bipolaris spp.

Auxin is the class of signalling molecules that are essential to the interaction between microbes and plants. Through the yucasin pathway, maize seedlings primarily produce IAA.

Yousaf *et al*. showed that the hormones present affect the behaviour of an endophyte linked to the host plant. Bipolaris species were used in the study, and the effects of auxin overload caused them to change from endophytic to biotrophic pathogens. An endophyte called Bipolaris spp. promoted plant growth by raising the plant's IAA levels, which in turn disrupted the plants' phytoalexins and brassinosteroids. Plant growth was consequently suppressed. The conducted in-silico analysis further confirmed that brassinosteroid (BR) signalling was downregulated as a result of elevated IAA levels (Yousaf MJ *et al*., 2021).

Discussion and Conclusion

The interaction between plants and endophytes holds great promise for agriculture and environmental sustainability due to their wide-ranging beneficial effects. Endophytes are increasingly recognized as sustainable and eco-friendly tools to address various challenges, particularly in areas like bioremediation, discovery of high-value bioactive compounds for therapeutic applications, and enhancing agricultural productivity through their role as natural bio-stimulants. With the advancement of functional genomics and high-throughput screening techniques, our understanding of how endophytes contribute to the production of valuable secondary metabolites has expanded significantly.

The potential of endophytes to yield novel bioactive compounds offers a valuable strategy in combating drug-resistant plant and human pathogens. Screening endophytic microorganisms for antimicrobial production can lead to the identification of compounds with pharmaceutical relevance, making them promising candidates in the search for new antibiotics. This bioprospecting approach can accelerate the development of clinically effective antimicrobials.

Nevertheless, several challenges hinder the full exploitation of endophytes in drug development. These include the typically low concentrations of desired compounds produced in laboratory cultures, the broad toxicity spectrum of certain antimicrobials, and insufficient knowledge about the biosynthetic routes and intermediary processes involved. Despite these hurdles, the continued exploration of natural products derived from endophytes remains a valuable direction in drug discovery. The goal is to enhance the potency and specificity of antimicrobial metabolites, minimize side effects, and better understand the genetic and biochemical regulation of their biosynthesis. As sources of novel biochemical compounds, endophytes have the potential to serve as innovative platforms for developing next-generation therapeutic agents (Tiwari *et al*., 2023).

To ensure food security and maintain a healthy ecosystem for future generations, it has become essential to enhance agricultural productivity without degrading soil health. However, frequent outbreaks of pests and plant diseases contribute to reduced crop yields and lead to considerable annual agricultural losses. To address this issue, effective and sustainable disease and pest management strategies must be implemented. Endophytes have emerged as a promising solution in eco-friendly farming practices, often serving as alternatives to chemical fertilizers. They are valued for being non-toxic, environmentally sustainable, easy to use, and cost-effective. Despite their growing use, more research is needed to fully understand the biochemical, molecular, and genetic pathways through which endophytes help crops withstand various forms of stress.

Bacterial and fungal endophytes serve as powerful tools in managing plant diseases through various mechanisms, such as parasitism, induced systemic resistance (ISR), competition for nutrients and space, and the production of antimicrobial compounds. These beneficial microbes help reduce dependence on chemical pesticides and contribute to environmentally friendly farming practices. Beyond agriculture, endophytes also hold potential in the discovery of novel bioactive compounds, highlighting their relevance in addressing global challenges like sustainable development and food availability.

Given their increasing importance in promoting agricultural resilience and food security, integrating endophytes into farming practices is a vital step toward achieving long-term sustainability. While considerable progress has been made in understanding how endophytes enhance plant growth and defense, significant gaps remain. In particular, limited research has explored the molecular basis of endophyte-plant interactions in diverse Indian agroclimatic zones. Although some studies have examined the genetic and biochemical pathways involved, comprehensive insights will require the application of advanced omics technologies, including genomics, transcriptomics, and metabolomics. Moreover, much of the current knowledge is limited to specific host species, underscoring the need to assess the broader effectiveness of endophytes across various crops and ecological conditions. The lack of extensive field testing to validate the lab-based results also impedes the creation of biofertilizers and biocontrol agents that are commercially feasible. Through the combination of laboratory research and practical agricultural applications, this review suggests a more integrated approach to endophyte research.

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