Fungal Biology

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Endophytic Fungi

The Hidden Sustainable Jewels for the Pharmaceutical and Agricultural Industries

Springer

Fungal Biology

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Fungal biology has an integral role to play in the development of the biotechnology and biomedical sectors. It has become a subject of increasing importance as new fungi and their associated biomolecules are identified. The interaction between fungi and their environment is central to many natural processes that occur in the biosphere. The hosts and habitats of these eukaryotic microorganisms are very diverse; fungi are present in every ecosystem on Earth. The fungal kingdom is equally diverse, consisting of seven different known phyla. Yet detailed knowledge is limited to relatively few species. The relationship between fungi and humans has been characterized by the juxtaposed viewpoints of fungi as infectious agents of much dread and their exploitation as highly versatile systems for a range of economically important biotechnological applications. Understanding the biology of different fungi in diverse ecosystems as well as their interactions with living and non-living is essential to underpin effective and innovative technological developments. This series will provide a detailed compendium of methods and information used to investigate different aspects of mycology, including fungal biology and biochemistry, genetics, phylogenetics, genomics, proteomics, molecular enzymology, and biotechnological applications in a manner that reflects the many recent developments of relevance to researchers and scientists investigating the Kingdom Fungi. Rapid screening techniques based on screening specific regions in the DNA of fungi have been used in species comparison and identification, and are now being extended across fungal phyla. The majorities of fungi are multicellular eukaryotic systems and therefore may be excellent model systems by which to answer fundamental biological questions. A greater understanding of the cell biology of these versatile eukaryotes will underpin efforts to engineer certain fungal species to provide novel cell factories for production of proteins for pharmaceutical applications. Renewed interest in all aspects of the biology and biotechnology of fungi may also enable the development of "one pot" microbial cell factories to meet consumer energy needs in the 21st century. To realize this potential and to truly understand the diversity and biology of these eukaryotes, continued development of scientific tools and techniques is essential. As a professional reference, this series will be very helpful to all people who work with fungi and should be useful both to academic institutions and research teams, as well as to teachers, and graduate and postgraduate students with its information on the continuous developments in fungal biology with the publication of each volume.

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Foreword

With immense joy and anticipation, I am delighted to present this extraordinary addition to Springer Nature's esteemed collection of works. This book opens the door to a realm of knowledge and exploration in the field of endophytic fungal research, inviting readers to comprehend the crucial role and significance of these fungi across various industries.

Encompassing contributions from distinguished scholars, this volume delves into a myriad of topics, ranging from the symbiotic relationships of endophytes with their hosts to their potential applications in agriculture and pharmaceuticals. The chapters are meticulously arranged to facilitate a comprehensive understanding of the roles and importance of endophytic fungi.

This book serves as an all-in-one solution for researchers and students engaged in the study of endophytic fungi, while also providing valuable reference material for professionals in the agriculture and pharmaceutical sectors. I extend my heartfelt appreciation to the editors and contributors who have poured their passion and expertise into laying the foundation for this remarkable volume. Their collective contributions enrich the academic discourse that shapes our world.

Lastly, I hope this book will inspire and empower readers to reach new heights of expertise in endophytic fungal research. May it ignite a spark of curiosity that leads to remarkable advancements in this field.

Panjab Singh

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Preface

Every book has a beginning, and this one is no exception. As we read the compiled chapters on various aspects of endophytic fungi, we are filled with their importance in the agriculture, health, and pharmaceutical industries. This preface captures the intentions and motivations driving us to bring book volume on *Endophytic Fungi: The Hidden Sustainable Jewels for the Pharmaceutical and Agricultural Industries*.

The genesis of this book lies in a confluence of experiences and questions. It is born out of countless conversations, moments of introspection, and a deep-seated desire to share insights that have shaped our understanding of the role of endophytic fungi in our life. In this book volume, you will find contributions from academicians working in the area and understanding the potential of endophytic fungi for sustainable development.

In this book, you will encounter chapters on broad aspects of endophytic fungi that may challenge, resonate, or inspire you and will generate your interest in this group of microorganisms. Others might encourage you to pause, reflect, and weave your interpretations into the narrative.

Ultimately, this book is a gesture of sharing – an offering of thoughts, perspectives, and facts on the latest developments on the role of endophytic fungi in agriculture and pharmaceutical industries. We hope readers will find the content appropriate for teaching and research.

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Acknowledgments

The completion of this book volume marks a significant milestone, and it is with great humility and gratitude that we acknowledge the individuals whose contributions have made this achievement possible.

First and foremost, we extend our heartfelt appreciation to all the contributors who contributed to this book volume in the form of a book review. Your knowledge and invaluable insights have been instrumental in shaping the direction and depth of this book. We also thank the Springer Nature team for their continuous support and cooperation in bringing the volume in final shape.

Finally, we extend our gratitude to the readers who will embark on this journey. We hope the contents covered in this volume will match the reader's expectations.

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Chapter 1
Endophytic Fungi: Symbiotic Bioresource for Production of Plant Secondary Metabolites

Lovelesh Singh Saini, Swati Patel, Arti Gaur, Priti Warghane, Rashmi Saini, and Ashish Warghane

Abstract Endophytes are a diverse group of microbes that asymptomatically colonize the interior organs of higher plants. Fungi and bacteria are also considered endophytes, although the former is more common, adaptable, and pervasive microorganisms that colonize plants growing in practically all geoclimatic situations. Endophytic fungi are a kind of symbiotic fungus that lives inside the tissues of a plant. These fungi have a symbiotic relationship with the plant, providing nutrients and protection while receiving shelter and food from its host. Endophytic fungi can play a significant role in the sustainability of a plant species. Different strains of endophytic fungus are being researched, and the accompanying restrictions are being addressed for maximum use/multidimensional applications as beneficial metabolites with multifaceted environmental effects are progressively being discovered. The current chapter reveals that endophytic fungi are a chemical reservoir of novel compounds and elicit plant secondary metabolites with numerous applications in the pharmaceutical and agrochemical industries. Various bioactive metabolites produced by endophytic fungi have shown socioeconomic value and found uses in agriculture and the environment, as well as biofuels and biocatalysts.

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1 Introduction

Higher plants provide complex, multilayered, diversified environments in spatial and temporal habitats that are home to assemblages of microorganisms of various species. Plants inside and outside their tissues contain many microorganisms, including bacteria, fungi, archaea, algae, and protists. Complex interactions between these species have progressively developed over a long-term, resulting in their symbiosis as a group rather than leaving them as separate species (Hassani et al. 2018). The interactions between these microbes and plants positively impact plant sustainability, biodiversity, and ecological stability (Rosier et al. 2016; Bai et al. 2017; Sasse et al. 2017).

Microorganisms, known as endophytes, inhabit plants for at least a portion of their life cycle without producing disease symptoms (Bacon and White 2000). Thus, “endophytism” is a special plant-microbe relationship defined by “location” (not “function”) that is momentarily symptomless, inconspicuous, and established within the living host plant tissues (Kusari and Spiteller 2012). Plants that possess poisonous alkaloids and interact with endophytes show high resistance to biotic and abiotic stresses (Carroll 1988; Chagas et al. 2018). Later on, a large body of evidence suggested that endophytic associations were crucial for the development of the plant immune system (Soliman et al. 2015), the control of disease (Terhonen et al. 2016), the uptake of nutrients (Hiruma et al. 2016), and to enhance the ability to withstand abiotic pressures (Khan et al. 2013).

In the accumulations of plants and microbes, microfungi predominate, colonizing the surfaces of leaves and twigs (epiphytes), the tissues inside leaves (foliar endophytes), the young and old bark (bark endophytes), and the wood (xylem endophytes and wood decomposers) (Stone et al. 2004). Endophytic fungus is highly varied and polyphyletic; it includes organisms that can live asymptomatically in the above- and belowground tissues of plants and play a wide range of ecological tasks (Saikkonen et al. 1998). Numerous endophytes can produce a range of bioactive compounds that may be employed directly or indirectly as therapeutic agents against a variety of ailments (Strobel et al. 2004; Staniek et al. 2008; Aly et al. 2010; Kharwar et al. 2011; Kusari and Spiteller 2012; Passari et al. 2015, 2016). Additionally, a large number of endophytic fungi are sources of cytotoxic compounds and secondary metabolites that are biologically active, like paclitaxel, podophyllotoxin, deoxypodophyllotoxin, camptothecin, hypericin, emodin, and azadirachtin (Stierle et al. 1993; Eyberger et al. 2006; Puri et al. 2005, 2006; Kusari et al. 2008, 2009, 2012; Shweta et al. 2010). Various coniferous and deciduous tree hosts for endophytic *Pezicula* species strains produce bioactive secondary metabolites in culture (Noble et al. 1991; Schulz et al. 1995). Cytochalasins and indole diterpenes with significant biological activity are commonly produced by endophytic species of the *Xylariaceae* (Brunner and Petrini 1992).

Endophyte synthesis of bioactive substances, mainly those unique to their host plants, is significant from a biochemical, pharmacological, and ecological standpoint. Exciting opportunities exist to use endophytic fungus to produce a wide range of recognized and undiscovered physiologically active secondary metabolites.

2 Evolution of Endophytic Fungi in Plants

Endophytic fungi, which dwell inside plant tissues permanently or for a specific time during their life cycles, colonize plants, especially perennials (Stone et al. 2004; Demain 2014), causing no apparent harm or morphological alterations. These microorganisms typically coexist alongside diseases and comprise fungi and bacteria (Zhang et al. 2006; Gouda et al. 2016). In plant tissues, fungal endophytes exist internally, intercellularly or intracellularly, and asymptomatically. Endophytes are distinguishable from mycorrhizae by missing external hyphae or mantels, and they often reside in aboveground plant tissues but can also occasionally be found in roots. Over the past 10 years, the definition of "endophyte" has undergone several changes (Sinclair and Cerkauskas 1996; Bills 1996; Saikkonen et al. 1998).

Parasitic or pathogenic fungi are believed to have originated endophytes on both grasses and woody plants (Carroll 1986, 1991, 1992). Woody plant endophytes are closely related to pathogenic fungi and are thought to have descended from them by lengthening their latency periods and decreasing their pathogenicity (Petrini et al. 1992). It is also believed that the fungal grass diseases of the genus *Epichloe* are the ancestors of the *Neotyphodium* grass endophytes. But there doesn't seem to be a clear coevolutionary route between the host plant and the endophyte. Plants have faced a variety of abiotic and biotic stressors throughout evolution. Since they cannot move, plants have relied on vegetative growth, sophisticated physiology, and seed dissemination to avoid or lessen stress's effects. All plants are known to sense signals, transfer them, and react to stresses, including disease, salt, heat, and drought (Bohnert et al. 1995; Bartels and Sunkar 2005).

Surprisingly complex microscopic specimens have been found in the Canadian Arctic. The earliest documented appearance of fungus may have occurred around 1 billion years ago, more than 500 million years earlier than previously thought, according to tiny fossils discovered in remote Arctic Canada. Endophytes have developed unique biotransformation skills due to the long-term coevolution of fungal endophytes and host plants, which can significantly affect the metabolism and makeup of plants.

Geographical considerations, interactions with other species in the community, phylogenetic and life history restrictions, and abiotic factors all affect the continuum of antagonistic-mutualistic interactions between any two interacting species (Thompson and Pellmyr 1992; Thompson 1994). Similar to this, even during the life span of the microbe and host plant, complex microbial mutualisms with host plants fluctuate along a continuum from pathogenic to mutualistic (Sinclair and Cerkauskas 1996). Although endophytic fungal-host plant interactions are complex and variable, evolutionary traits like mode of transmission and infection patterns as well as ecological factors like host condition, competition with other microorganisms, population structure, and prevailing abiotic factors allow predictions of where endophyte-plant associations are likely to fall along the continuum.

The byproducts of main metabolic pathways are termed primary metabolites, encompassing lipids, proteins, carbohydrates, and amino acids. They are crucial to the metabolism of building blocks and an organism's growth. Without them, the organism's growth and development are very likely to have flaws. The fact that the by-products of several crucial stages serve as precursors for producing secondary metabolites is an essential function of basic metabolism. These precursors are used by both endophytes and their host plants in their separate secondary metabolites (SMs) biosynthesis processes. According to Kirby and Keasling (2009) and Deepika et al. (2016), SMs in EFs may imitate the host pathways and use those pathways as their biosynthetic route. Using blocking mutant and radiolabeling approaches, researchers have explored the synthesis of certain phytochemicals, including ergot alkaloids, aflatoxin, and lovastatin (Keller et al. 2005; Rekadwad et al. 2022). Although varied, a few shared biosynthetic pathways synthesize SMs, and endophytic fungal communities and their host plants' metabolomic pathways are comparable. It is unclear whether these low-molecular-weight phytochemicals are produced by plants directly or through symbiosis with microbes inside them.

3 Biodiversity of Endophytic Fungi

Nearly every plant on the earth has endophytes, which are the most distinctive microbes. It has mainly been extracted from the soil of large and small trees, coastal grasses, and lichens. Many different microbes, such as bacteria, actinobacteria, fungi, and algae, are found inside the plant tissue (Saini et al. 2015; Zhang et al. 2018; Passari et al. 2020; Sriravali et al. 2022). They all establish symbiotic or asymbiotic biological relationships with the host-plant body. Prokaryotic cells connected with plants through vertical or horizontal transmission through stomata and colonizing the internal plant tissue make up the wide endophytic variety in our ecosystem. Endophytic microorganisms target various parts of the host-plant body, so they can enter and establish a habitat.

Fungal endophytes are a common type of endophyte. Endophytic fungi can sustainably increase crop output and growth by enduring severe biotic and abiotic stress conditions, including drought, high temperatures, and salinity (Rodriguez et al. 2009). Due to their extensive adaption, the fungal endophytes colonize the plant tissue's intra- and intercellular regions, forming a symbiotic or mutualistic relationship with the host (Aly et al. 2011). The host plant provides the fungal strain with food and protection, and the fungal endophyte confers resistance to pathogens and numerous abiotic stresses. The transfer of a fungal cell to a damaged wound region through surface contact or channels is called external fungal endophytes. Endogenous fungal endophytes, however, travel through inner organelles like mitochondria and chloroplasts (Yadav 2020). There are two ways that fungal endophytes can spread: vertically or systemically from the host plant body to the offspring or seeds of the host plant or horizontally or nonsystematic through sexual reproduction or infection (Malik et al. 2023).

Endophytic fungi belong to diverse phyla, including Ascomycota, Basidiomycota, and Mucoromycota. The majority of endophytic fungi belong to Ascomycota (89%), followed by Basidiomycota (9%), and the remaining to Mucoromycota (2%) (Rana et al. 2019). The diversity of fungal endophyte species in these phyla is summarized in Table 1.1.

The variety of all fungal endophytes can be divided into two major groups. These include *Clavicipitaceae* (CE), which are widely dispersed and occur in asymptomatic tissues of nonvascular plants, conifers, ferns, and angiosperms, which infect specific grasses restricted to chilly climates and nonclavicipitaceous endophytes (NCE). NCE, however, is reportedly only found in the Ascomycota and Basidiomycota groups (Maldonado-González et al. 2015). On every continent, fungi have been found to colonize terrestrial plants. They have been isolated from ferns, gymnosperms, angiosperms, arctic habitats, tropical climes, various xeric environments, and boreal woods (Suryanarayanan et al. 2000; Mohali et al. 2005; Šraj-Kržič et al. 2006; Selim et al. 2017).

Different fungal species with a variety of chemical productions are found in the various fungal areas of plants. A study of the microbial diversity in *Paris polyphylla* var. *yunnanensis* plants (Liu et al. 2017) found that *Trichoderma viride* and *Leptodontidium* sp. coexisted with the dominating species *Fusarium oxysporum* in the rhizospheric endophytes. Along with these three predominant fungi, the presence of *Alternaria* sp., *Pyrenochaeta* sp., *Truncatella* sp., *T. viride*, *Chaetomium* sp., *Penicillium swiecickii*, and *Cylindrocarpon* sp. was also noted.

4 Interaction of Endophytic Fungi with Host Plant

Filamentous fungus and vesicular–arbuscular mycorrhiza (VAM) are the most paramount groups included and investigated as endophytes. Certain fungi that belong to the genus *Trichoderma*, *Colletotrichum*, *Penicillium*, *Aspergillus*, *Purpureocillium*, *Fusarium*, *Claviceps*, *Metarhizium*, *Xylaria*, *Curvularia*, *Cladosporium*, *Dreschlera*, *Alternaria*, etc. colonizes either roots, shoots, or leaves (Uzma et al. 2018; Attia et al. 2020; Baron and Rigobelo 2021). They are populating in the endosphere of plants and are transmitted horizontally or vertically. Endophytes can uphold in

Table 1.1 Biodiversity of different groups of endophytic fungi associated with different hosts

Phyla	Species	References
Ascomycota	*Curvularia* sp., *Setosphaeria* sp., *Guehomyces* sp., *Annulohypoxylon* sp., *Trichoderma* sp., *Xylaria* sp., *Septoria* sp., *Trichosporon* sp., *Filobasidium* sp., *Mucor* sp., *Neurospora* sp., *Ampelomyces* sp., *Microdochium* sp., *Helminthosporium* sp., *Tilletiopsis* sp., *Anthostomella* sp., *Ophiocordyceps* sp., *Plectosphaerella* sp., *Emericella* sp., *Talaromyces* sp., *Glomus* sp., *Stagonospora* sp., *Gibberella* sp., *Alternaria* sp., *Cryptococcus* sp., *Nectria* sp., *Sordariomycetes* sp., *Ilyonectria* sp., *Davidella* sp., *Chaetomium* sp., *Rhodosporidium* sp., *Eurotium* sp., *Stemphylium* sp., *Didymella* sp., *Rigidoporus* sp., *Bipolaris* sp., *Coniothyrium* sp., *Ulocladium* sp., *Cercospora* sp., *Engyodontium* sp., *Porostereum* sp., *Paraconiothyrium* sp., *Phaeosphaeria* sp., *Boeremia* sp., *Cochliobolus* sp., *Exserohilum* sp., *Calonectria* sp., *Paraphoma* sp., *Diaporthe* sp., *Eutypella* sp., *Cladophialophora* sp., *Macrophomina* sp., *Rhizopus* sp., *Phaeosphaeriopsis* sp., *Corynespora* sp., *Nigrospora* sp., *Lasiodiplodia* sp., *Wallemia* sp., *Paecilomyces* sp., *Puccinia* sp., *Williopsis* sp., *Lecanicillium* sp., *Leptospira* sp., *Fusarium* sp., *Nemania* sp., *Neofusicoccum* sp., *Dichotomopilus* sp., *Cylindrocarpon* sp., *Leptosphaeria* sp., *Aspergillus* sp., *Pleosporales* sp., *Peyronellaea* sp., *Marasmius* sp., *Crinipellis* sp., *Mortierella* sp., *Eupenicillium* sp., *Bipolaris* sp., *Clonostachys* sp., *Phomopsis* sp.	Sieber et al. (1988), Fisher and Petrini (1992), Larran et al. (2001), Wakelin et al. (2004), Tian et al. (2004), Nassar et al. (2005), Pan et al. (2008), Saunders and Kohn (2008), Naik et al. (2009), Yuan et al. (2010), Khan et al. (2011, 2012), Gao et al. (2011, 2012), de Souza Leite et al. (2013), Tenguria and Firodiya (2013), Impullitti and Malvick (2013), Amin (2013), Zhao et al. (2012, 2013, 2014), Tian et al. (2014), Fernandes et al. (2015), Colla et al. (2015), Gonzaga et al. (2015), Köhl et al. (2015), Chadha et al. (2015), Pierre et al. (2016), Marcenaro and Valkonen (2016), dos Santos et al. (2016), Parsa et al. (2016), Keyser et al. (2016), Ofek-Lalzar et al. (2016), Wang et al. (2016), Renuka and Ramanujam (2016), Bogner et al. (2016), Rothen et al. (2017), Potshangbam et al. (2017), Hamayun et al. (2017), Singh and Gaur (2017), Spagnoletti et al. (2017), Narayan et al. (2017), Comby et al. (2017), Larran et al. (2002, 2007, 2018), Yang et al. (2014a, 2018), Zhao et al. (2018), Xing et al. (2018), and Rana et al. (2019)
Basidiomycota	*Cryptococcus* sp., *Trichosporon* sp., *Puccinia* sp., *Porostereum* sp., *Rigidoporus* sp., *Filobasidium* sp., *Rhodotorula* sp., *Guehomyces* sp., *Tilletiopsis* sp., *Crinipellis* sp., *Marasmius* sp., *Wallemia* sp., *Rhodosporidium* sp., *Sporobolomyces* sp., *Cryptococcus* sp., *Cystobasidium* sp., *Sporobolomyces* sp., *Rhizoctonia* sp.	
Mucoromycota	*Glomus* sp., *Mucor* sp., *Mortierella* sp.	

environments like high temperatures, temperate forests, mangrove forests, and tropical forests (Arnold 2008), insinuating they can survive under diverse climatic conditions. Endophytic fungi are distinct in their colonization due to the expression of genes required for the molecules necessitated for their colonization. However, there are the least details available for the accountable genes (Behie and Bidochka 2014). It can enter the plant system via wounding of plant tissues that further secrete nutrient metabolites and chemoattractants of endophytes. There is the germination of fungal mycelia in roots and its extensive penetration into the root cortex. Thereby, it commences its colonization. It spreads through the cell wall to the adjacent cells of plants and moves further in the plant system (Yan et al. 2019). Endophytes are observed in almost all plant parts, such as root, shoot, stem, leaves, and reproductive tissues. The existence of endophytes is validated via surface sterilization of plant tissue followed by its growth on a specific media or with metagenome analysis. The internal parts of the plant are the protective, secure zones for the endophytic fungus to get the required nourishment and ameliorate competition. In turn, the fungi also favor plants through direct and indirect courses. They benefit plants directly with nutrient acquisition, secreting molecules that facilitate plant growth. Indirectly with the production of important secondary metabolites and other compounds, endophytic fungus protects plants from biotic and abiotic stress (Fig. 1.1).

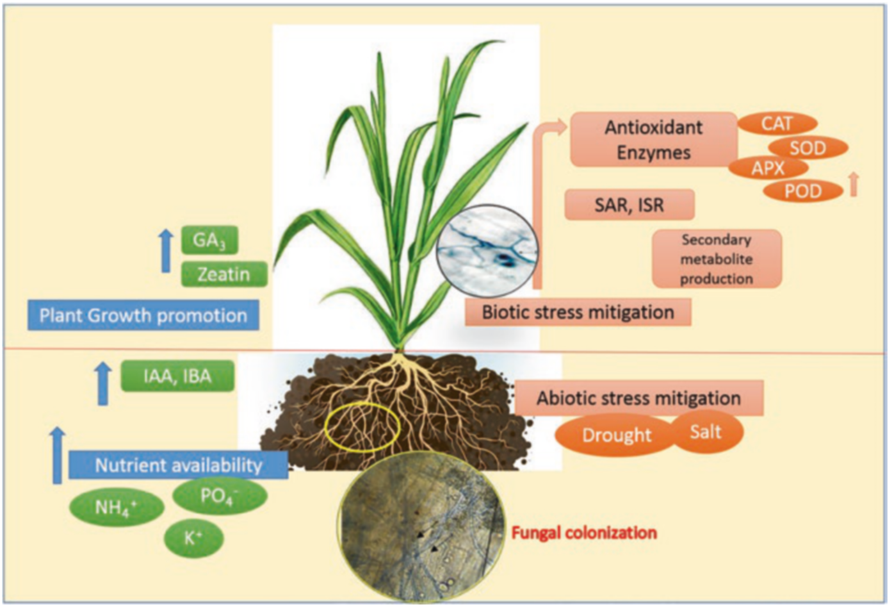

Fig. 1.1 Direct and indirect benefits offered by endophytic fungal colonization. Parameters in blue and green boxes show the direct effects of plant growth promotion. Pink and orange boxes indicate the indirect use of biotic and biotic stress tolerance to the colonized plant

4.1 For Sustainable Agriculture

A global climate change concern is due to deforestation, domestication, urbanization, soil salinization, and soil pollution through the extensive use of chemical fertilizers and pesticides. Plants are also losing important valuable microorganisms due to the abovementioned situations. Therefore, they are not acquiring the direct and indirect advantages imparted by them, which makes them more resistant to stress.

Nutrient Availability

Endophytes do have a role in facilitating macroelements (nitrogen, potassium, phosphorous, calcium, magnesium, sulfur) and microelements (zinc, iron, copper, etc.) for the plants, which make efficient use of fertilizers applied. They can also play a role as biofertilizers. The first report of colonization by the endophytic fungus *Piriformospora indica* revealed that external hyphae of the fungus possess phosphate transporter (*PiPT*) expression that helps to absorb phosphate and make it available to maize plants. Mycorrhizal fungi *Metarhizium* and *Beauveria* have been reported to augment the availability of nitrogen and phosphorous in their symbiosis (Behie and Bidochka 2014). Under conditions of low nitrogen, the genes associated with nitrogen uptake and metabolism, including *OSAMT1;1*, *OSAMT2;2*, OSNR1, and OSGS1, are upregulated in rice due to endophytic colonization by Phomopsis liquidambari. This upregulation is accompanied by elevated levels of total nitrogen, amino acids, proteins, and free $NH4^{+}$ (Yang et al. 2014b).

Plant Growth Promotion

Phytohormone production is also characteristic of many endophytic fungi. They can produce auxin, cytokinin, and gibberellic acid, mainly with siderophore (Mishra et al. 2016; Tochhawng et al. 2019; Abdalla et al. 2020). The endophytic fungi *Aspergillus fumigatus TS1* and *Fusarium proliferatum* symbionts of *Oxalis corniculata* roots have been screened to have indole acetic acid production and siderophore production with an eclectic derivative of gibberellic acid, such as GA_1, GA_3, and GA_7 (Bilal et al. 2018). Endophytic fungus belongs to the genus *Fusarium*, *Alternaria*, *Xylogone*, and *Didymella* isolated from a medicinally important plant *Sophora flavescens* found to produce a significant concentration of IAA (indole acetic acid), and it has been proven with application and observation of primary root length in *Arabidopsis* plant (Turbat et al. 2020). Endophytic colonization in root cortical cells with *Chaetomium globosum* strain ND35 fostered the growth of cucumber plants with the production of hormones zeatin, gibberellic acid, indole-3 acetic acid (IAA), and indole butyric acid (IBA) (Tian et al. 2022).