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

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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).

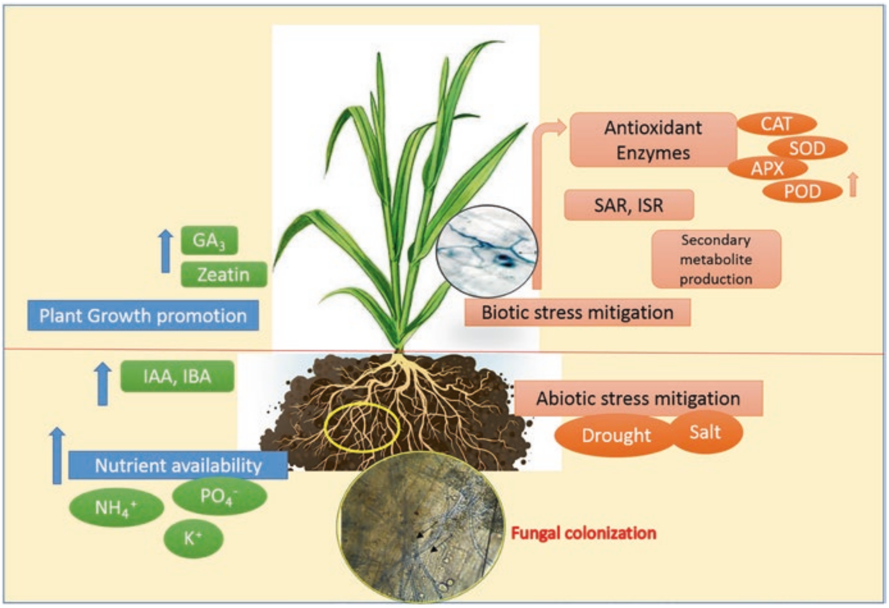

Fig. 1.1 Direct and indirect benefits offered by endophytic fungal colonization. Parameters in blue and green boxes show the direct effects of plant growth promotion. Pink and orange boxes indicate the indirect use of biotic and biotic stress tolerance to the colonized plant

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).

4.2 For Stress Management

A mutualistic relationship of plants with endophytic fungus has been observed to produce considerable bioactive compounds and metabolites that impart stress tolerance to the plant. Under abiotic stress conditions like drought and salt stress, these endophytes encountered to regulate the levels of antioxidant enzymes catalase (CAT), peroxidase (POD), ascorbic peroxidase (APX), glutathione (GSH), and superoxide dismutase (SOD) to mitigate stress-induced injury for the cell. The global loss due to plant disease is expected to be 16% (Fontana et al. 2021), and endophytic fungi have been documented to activate induced systemic resistance (ISR) or systemic acquired resistance (SAR) to fight against biotic stress. The banana (*Musa* spp.) crop faces a significant loss due to a fungal pathogen. Endophytic root colonization with *Serendipita indica* increases SOD, POD, CAT, and APX activities, thereby obtaining resistance to *Fusarium oxysporum* f. sp. *cubense* (*Foc*) (Cheng et al. 2020). Under extreme agroecosystems of salt and drought conditions, endophytic colonization with fungi belonging to genus *Periconia macrospinosa*, *Neocamarosporium chichastianum*, and *N. goegapense* obtained from Salt Lake plants alleviates the adverse effect of stress in *Hordeum vulgare* L. that reminisces with the improvement of biomass, shoot length, proline content, and antioxidant enzyme activity (Moghaddam et al. 2022). Endophytic fungi bares the prospect as a biocontrol agent through the secretion of several enzymes (cellulase, amylase, protease, and xylanase), hydrogen cyanide, and certain secondary metabolites; this will reduce the use of synthetic insecticides or pesticides (Yadav et al. 2010). *Penicillium* sp. NAUSF2 can solubilize hard phosphate sources in saline conditions and makes phosphate available to plants with endophytic colonization. It also reduces the disease severity index for bacterial leaf spots caused by *Xanthomonas axonopodis* pv. *V. radiate* in *Vigna radiata* with a significant increase in jasmonic acid and antioxidant enzyme concentration (Patel et al. 2021).

5 Production of Secondary Metabolites by Endophytic Fungi

Plant secondary metabolites are a class of substances that are not essential for basic bodily processes but are crucial for plants to adapt to their environment (Bourgaud et al. 2001). Plants generate low-molecular-weight antimicrobial molecules known as phytoalexins, which comprise a variety of chemicals such as flavonoids, terpenoids, etc. Several studies spotlight the production of phytoalexins by pathogens under numerous nonbiological stress stimuli, such as UV radiation, heavy metal ions, or salt stress (Abraham et al. 1999). Co-culturing with an endophytic elicitor is an additional strategy for enhancing plant secondary metabolites and boosting plant resistance (Li and Tao 2009).

Endophytic fungi are categorized by biological processes that affect plant systems and the proliferation of endophytic fungi. Group I endophytic fungi move a genetic element into plant systems by vertical gene transfer, whereas group II endophytes generally help to combat external stresses. Group III endophytic fungi acquire genes from other fungal species via horizontal gene transfer that produces bioactive chemicals. Depending on the plant's state and age, endophytes present in plant systems create secondary metabolites. Endophytic fungi generate a variety of metabolites from different structural classes, such as terpenoids, steroids, aliphatic chemicals, flavonoids, alkaloids, quinines, phenols, coumarins, peptides, etc. (Calhoun et al. 1992). These metabolites are produced in different pathways like shikimate pathway (alkaloids, flavonoids) (Tohge et al. 2013; Peek and Christendat 2015) and TCA cycle (isoprenoids, polyketide, terpenoids) (Meena et al. 2019). Tejesvi et al. (2007) found that endophytic fungi of medicinal plants create secondary metabolites that can be researched for treating various ailments. All of these studies show that endophytic fungi are a chemical reservoir of novel compounds that have numerous applications in the pharmaceutical and agrochemical industries, including those for antimicrobial, antiviral, antifungal, anticancer, antiparasitic, antitubercular, antioxidant, immunomodulatory, and insecticidal properties (Fig. 1.2) (Calhoun et al. 1992).

In addition to providing novel sources for cytotoxic chemicals, including anticancer and antibacterial compounds (Uzma et al. 2018; Radic and Strukelj 2012), endophytic fungi (EFs) also operate as biostimulants for the production of essential oils (Enshasy et al. 2019). This has led to a great deal of attention in the field. They might function as biological control agents (Poveda and Baptista 2021), encourage plant growth (Mehta et al. 2019), increase nutrient solubilization in the rhizosphere

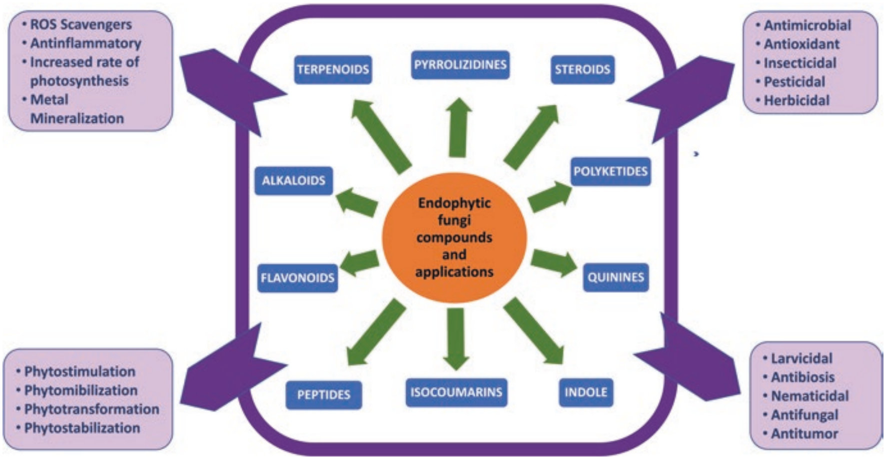

Fig. 1.2 Applications of different bioactive secondary metabolites compounds produced by endophytic fungi

of the plant (Poveda et al. 2021), or activate systemic plant defenses against biotic (Poveda et al. 2020) or abiotic (Cui et al. 2021) stresses.

5.1 *Symbiotic Interaction*

Endophytes create various connections with their host plants throughout their growth inside the living tissues of the plant, including symbiotic, mutualistic, or parasitic ones. The host plant's cells or intercellular space are home to fungal endophytes, which appear to inflict no harm (Saikkonen et al. 1998). In mutualistic symbiosis, EF partners and host plants benefit from this advantageous symbiotic continuum and eventually succeed in evolution and the environment (Fig. 1.3) (Jia et al. 2016). The host plants' metabolic processes are changed by EFs, which also increase drought and metal tolerance, growth, and nutrient uptake (Poveda et al. 2021; Cui et al. 2021).

However, EFs can also sporulate quickly and interact with host plants in a latent pathogenic or commensalism relationship, with or without appreciable positive impacts on plant physiology (Fig. 1.3) (Hiruma et al. 2016). They can also colonize and flourish asymptomatically inside healthy plant tissues (Saikkonen et al. 1998; Kogel et al. 2006). These endophytes can trigger host plant disease symptoms under stress (Schulz and Boyle 2005), such as those caused by *Cordana*, *Deightoniella*, *Verticillium*, *Curvularia*, *Nigrospora*, *Periconiella*, *Colletotrichum*, *Guignardia*, *Phoma*, *Cladosporium*, and *Fusarium* (Photita et al. 2004; Cui et al. 2021). Equilibrium between these organisms has been achieved during the long-term coevolution of endophytes and plants. Thus, the real endophyte will exist once a balance is reached between fungal activity and the plant response and is sustained throughout time (Gimenez et al. 2007).

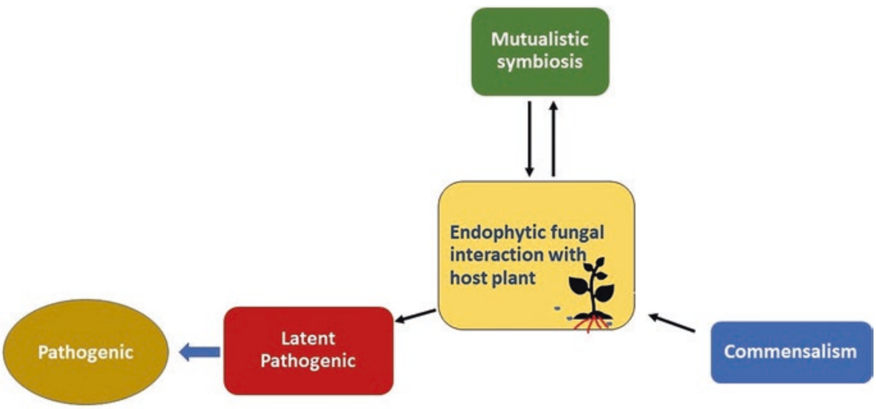

Fig. 1.3 Interaction of endophytic fungi with host plant

5.2 In Stress Conditions

Plants create many different pathways, such as jasmonic acid, abscisic acid, and salicylic acid, due to abiotic stress stimuli and function as defense signaling chemicals. As fungal endophytes may develop from plant pathogenic fungi, they may act as pathogens and cause plants to defend themselves. To promote plant development under stressful conditions, fungal endophytes produce siderophores, antibiotics, and phytohormones; mineralize nutrients; and perform other tasks (Yung et al. 2021). Siderophores increase iron intake and phosphate solubilization and plant uptake of these nutrients, promoting plant development and executing defense against many pathogens (Chowdappa et al. 2020). Endophytes also accelerate biomass formation and nitrogen intake while biodegrading the trash (Idbella et al. 2019). Over 500 siderophores from different fungi have been identified (Chowdappa et al. 2020). *Aspergillus fumigatus*, *Aspergillus niger*, *Curvularia*, *Trichoderma*, and other fungal endophytes have all been recently discovered to solubilize and mobilize phosphorus, potassium, and zinc salts, which in turn promote plant growth and high crop production (Mehta et al. 2019; Haro and Benito 2019).

Phytohormone gibberellins are secreted by *Penicillium* sp., which inhabits *Suaeda japonica*, as an example of the reduced amount of plant growth-promoting compounds the fungal endophytes release during stress. The fungi *Penicillium* sp., *Ascomycete* sp., *Aspergillus* sp., *Verticillium* sp., *Cladosporium* sp., and *Fusarium* sp., which live on *Panax ginseng*, also release triterpenoid, ginsenosides, and saponins, which improve stress resistance and root development (Sahoo et al. 2017). To increase the phytoimmobilization and availability of zinc, nitrogen, and phosphorus for the host, siderophores can biodegrade biomass and recycle it in the environment (Yung et al. 2021). They can also lower levels of the hormone ethylene by inhibiting 1-aminocyclopropane-1-carboxylate deaminase (ACC) in plants. Hence by immobilizing osmolytes and regulating membrane ion conductivity during stress, phytoimmobilization by endophytes eventually aids in withstanding abiotic stressors by plants.

Endophytic fungi are also accountable for protecting crops from biotic stress in the wake of the chain of events (Singh et al. 2021a). The three main ways fungi defend themselves from phytopathogens are competition within the biological niche, antibiotics production, and mycoparasitism, which strengthens plant defenses and raises tolerance to virulence factors generated by pathogenic bacteria. The primary endophytes that begin to tolerate biotic stress while simultaneously enhancing the host plant's development and yield components are *Trichoderma* species, *Epicoccum* species, *Aspergillus* species, *Colletotrichum* species, *Gliocladium* species, *Fusarium* species, *Petriella* species, *Piriformospora* species, *Epichloe* species, etc.; mildews, rots, nematodes, blights, and leaf mosaics are just a few of the diseases that *P. indica* can successfully treat (Ali et al. 2019). They ought to be considered as potential biocontrol agents as a result. According to Laihonen et al. (2022), *Epichloe* sp. controls herbivorous insects and offers its host plant biotic resilience. Host plants' roots, twigs, and stems are colonized by the filamentous anamorphic saprophytic fungus known as *Trichoderma* sp. due to its antibacterial, antifungal, and cytotoxic qualities; it can be utilized as a biocontrol agent.

6 Biotic Potential of Secondary Metabolites Produced by Entophytic Fungi

Many secondary metabolites are produced by endophytic fungi, such as phenols, alkaloids, polyketides, quinones, steroids, enzymes, and peptides, which have a higher therapeutic value than primary metabolites (Xu et al. 2021). They can protect the plants from disease-causing invaders. This protection is made possible by producing secondary metabolites, which act as a defense against the invasion of pathogens (Kaur et al. 2022). These secondary metabolites, such as bioactive compounds, are the primary source of the beneficial characteristics of endophytic fungi. Endophytes can stop the development of resistance mechanisms in plants, which can lead to disease. The production of these bioactive compounds also allows for the release of enzymes, antioxidants, and other beneficial compounds that help protect the plant from external threats (Wen et al. 2022). Additionally, these secondary metabolites can be used for plant growth and development as well as for the improvement of crop yields. Endophytic fungi are crucial for protecting plants from disease and promoting growth, and their ability to produce secondary metabolites is key to their beneficial qualities (Manganyi and Ateba 2020).

Endophytic fungi are an essential source of secondary metabolites, including terpenoids, polyketides, shikimic acid derivatives, and terpenes. They are found in many plants and play an important role in the pharmaceutical and drug industries through the production of alcohol, antibiotics, enzymes, and other medicinal ingredients (Singh et al. 2021b). These secondary metabolites can create new drugs and treatments and provide a valuable treasure for medical research. Endophytic fungi benefit both the environment and humans, since they are natural sources of these compounds, which can decrease the need for chemical synthesis. Additionally, they offer substitutes for chemical-based drugs, which can have a number of health hazards. Endophytic fungi are also valuable in developing treatments for diseases such as cancer and Alzheimer's, since they can produce compounds that can be used to fight these diseases. These compounds have potential applications in drug discovery and can be used to treat various disease conditions. Endophyte-derived natural products can also be used as pesticides, insecticides, and herbicides to control agricultural pests (Zheng et al. 2021; Wen et al. 2022)

Endophytic fungi potentially produce novel bioactive compounds. Suitable media, growth parameters, and nutrient limitations should be explored to gain insight into fungal metabolism and discover novel pharmaceutical products; such compounds can be used to treat many diseases. Furthermore, endophytic fungi provide a sustainable source of novel bioactive compounds which is environmentally friendly (Adeleke and Babalola 2021).

7 Application of Secondary Metabolites Produced from Symbiotic Fungi

Endophytic fungi have recently gained tremendous attention due to their ability to produce novel bioactive compounds with a wide range of biological properties. These compounds have been used in a variety of applications, especially in the fields of medicine, pharmaceuticals, and agriculture. In addition to their bioactive compounds, endophytic fungi have also been found to possess many other beneficial attributes, including the ability to increase a plant's resistance to pathogens, reduce the amount of fertilizer needed, and promote crop yield (Manganyi and Ateba 2020). Moreover, endophytic fungi can act as a natural source of antibiotics, providing potential alternatives to traditional antibiotics. Endophytic fungi can also be used for bioremediation and to clean up contaminated soil and water. Overall, endophytic fungi have a wide range of potential applications, and their ability to produce novel bioactive compounds is an invaluable asset to many industries (Stępniewska and Kuźniar 2013).

The antimicrobial and antifungal properties of endophytic fungi metabolites have been especially noted, as these compounds have the potential to provide novel solutions to existing and emerging drug-resistant microbial and fungal infections (Deshmukh et al. 2022). For instance, endophytic fungi metabolites have been proven to effectively inhibit the growth of several drug-resistant bacterial and fungal pathogens, such as methicillin-resistant *Staphylococcus aureus* (MRSA), vancomycin-resistant *Enterococci* (VRE), and *Candida albicans*. In addition, the antifungal activities of endophytic fungi metabolites have been demonstrated against several fungal species, such as *Aspergillus flavus*, *Fusarium solani*, and *Rhizoctonia solani*. Additionally, the antiprotozoal activity of endophytic fungi metabolites has been shown against several protozoan species, such as *Trypanosoma cruzi*, *Toxoplasma gondii*, and *Leishmania*. Moreover, the antiparasitic activity of endophytic fungi metabolites has been demonstrated against several parasitic species, such as *Plasmodium falciparum*, *Schistosoma mansoni*, and *Fasciola hepatica* (Liu et al. 2019; Deshmukh et al. 2022).

Several studies have also reported the antioxidant, immunosuppressant, and anticancer activities of endophytic fungi metabolites. Endophytic fungi metabolites have been demonstrated to possess antioxidant activities, which are beneficial in reducing oxidative stress and protecting against numerous diseases (Almustafa and Yehia 2023). In addition, the immunosuppressant activities of these metabolites have been demonstrated in several studies, as these compounds have been found to reduce inflammation and suppress the immune system. Finally, the anticancer activities of endophytic fungi metabolites have been demonstrated in several studies, as these compounds have been found to inhibit the growth of cancer cells (Table 1.2) (Sharma et al. 2020).

Table 1.2 Examples of biotechnologically relevant fungal secondary metabolites

S. no.	Secondary metabolite	Producing fungus	Application
1	Cephalosporin C	*Acremonium chrysogenum*	Resource for the production of Cephalosporins
2	*B*-carotene	*Blakeslea trispora*	Pigment
3	Astaxanthin	*Phaffia rhodozyma*	Pigment
4	Griseofulvin	*Penicillium griseofulvum*	Antifungal agent
5	Cyclosporine A	*Tolypocladium inflatum*	Immunosuppressant
6	Gibberellic acid	*Gibberella fujikuroi*	Plant growth regulator
7	Penicillin G	*Penicillium rubens*	Antibiotic
8	Taxol	*Taxomyces andreanae*	Anticancer drug
9	Lovastatin	*Aspergillus terreus*	Cholesterol-lowering drug

8 Challenges and Future Perspectives of Endophytic Fungi

To regulate and manipulate the biosynthesis process for increased production, we must elucidate the entire biosynthesis pathway, including all of the enzymes and associated genes. To solve the issues of poor yield and attenuation, the two main obstacles to commercial success, we need to learn more about the functions of host plant-endophyte interactions. For the successful industrial-scale synthesis of pharmaceutically valuable compounds or leads, scientists working in this area and the pharmacological business must collaborate. The pharmaceutical sector must prioritize the endophyte-dependent production of natural plant chemicals. For the pharmaceutical and healthcare sectors, as well as for a "green drug revolution," the concept of endophyte-dependent improved in vivo and in vitro production of plant-derived useful metabolites is crucial.

9 Conclusion

In conclusion, endophytic fungi represent a fascinating group of microorganisms that reside within the tissues of plants without causing any apparent harm. These fungi have coevolved with their host plants, establishing mutualistic relationships that can profoundly affect the fungi and the plants. Over the years, extensive research has revealed various applications for endophytic fungi in various fields. Moreover, endophytic fungi have demonstrated remarkable potential as a source of bioactive compounds with pharmaceutical and industrial importance. Many endophytic fungi produce secondary metabolites with antimicrobial, antiviral, anticancer, and antioxidant properties. These bioactive compounds promise to develop new drugs, nutraceuticals, and natural products for various applications, including medicine, cosmetics, and agriculture.

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