



## Investigating the effectiveness of endophytic fungi under biotic and abiotic agricultural stress conditions

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### Abstract

Endophytic fungi play crucial roles in promoting plant growth and enhancing stress tolerance, making them valuable allies in agriculture. This reviewer explores the advantageous roles and implications of endophytic fungi in plant stress tolerance, focusing on hormonal regulation, nutrient uptake, and their management of various abiotic and biotic stresses. Endophytic fungi influence the production of plant hormones such as auxins, cytokinins, and gibberellins; thus, contributing to enhanced growth and stress resilience. They also assist in nutrient uptake, solubilizing minerals, and fixing atmospheric nitrogen; thereby improving overall plant nutrition. This reviewer discusses the mechanism of endophytic fungi's effectiveness in managing biotic and abiotic stresses, including; high CO<sub>2</sub> levels, waterlogging/drought, salinity, high temperatures, salinity, heavy metal stress as well as plant pathogens and parasitic attacks. Furthermore, the bio-control capabilities of endophytic fungi against biotic stresses are highlighted, showcasing mechanisms such as induced resistance, mycoparasitism, antibiosis, and competition. The biological activities of recently isolated compounds and associated endophytic fungi are also discussed. Thus, as research in this field progresses, harnessing the full potential of endophytic fungi holds promise for promoting resilient and sustainable agriculture in the face of changing environmental conditions.

### 1. INTRODUCTION

Fungi that form a mutually advantageous symbiotic connection with their host plant and reside in plant tissues for the entirety or a portion of their life cycle are referred to as endophytic fungi since they do not cause disease or other negative effects (Hyde, 2019; Patchett and Newman, 2021). They are naturally occurring elements of the plant micro-ecosystem that have a positive impact on the host plant's physiological activities in several ways, such as generating hormones like indoleacetic acid, biosynthesizing and obtaining nutrients for plant growth and development, secreting metabolites that act as stress-adaptors to shield the host plant from pathogens and herbivores, and enhancing the host's resistance to abiotic stressors. In exchange, endophytic fungi receive nutrients and habitats from plants (Odelade and

Babalola, 2019; Igiehon et al., 2021). According to Jin et al. (2018), endophytic fungi can create a wide range of bioactive chemicals, including molecules that bear resemblance or identity to pharmacological activity found in plants. They generate a variety of metabolites belonging to many chemical classes, including phenolic chemicals, alkaloids, flavonoids, steroids, and terpenoids. Some substances have intriguing and pleiotropic pharmacological effects, such as antioxidant, anticancer, antibacterial, and anti-diabetic qualities (Wen et al., 2022).

Endophytic bacteria and fungi are associated with almost all vascular plant species (Arnold et al., 2000; Khan et al., 2018). Furthermore, it has previously been established that endophytes colonize mosses, ferns, and marine algae (Raviraja et al., 1996; Stanley, 1996). Endophytic fungi have recently attracted a lot of attention

for their ability to shield plants from pathogens, insect pests, and even domestic herbivores (Malinowski and Belesky, 2006; Shiomi et al., 2006). This is even though numerous studies have demonstrated the mutualistic interactions between plants and their associated endophytes and their distribution in plant communities worldwide, through increasing host fitness and assisting in adaptation to environmental and biological stresses (Naseem et al., 2018).

## 2. ORIGIN OF ENDOPHYTIC FUNGI

Following the successful use of the antibiotic Penicillin, which was developed from *Penicillium notatum* in 1928, and anticancer medication Taxol, which was derived from *Taxomyces andreanae* in the 1990s, the origin of endophytic fungi has been expanded (Strobel et al., 1993). These medications and antibiotics stimulated new ideas for the production of a wide range of biologically derived medications. Scientists have recently been investigating endophytic fungi for their natural compounds, such as Micafungin, an antifungal drug derived from *Coleophoma empetri* (Frattarelli et al., 2004). Because of coevolutionary processes, the endophyte-plant relationship may have originated with the genesis of higher plants, which may be traced back millions of years (Pamphile and Azevedo, 2002). Furthermore, fungi are far older and may have formed more than a billion years ago, according to findings based on molecular data and fossil records (Parfrey et al., 2011). These endophytic microbes may coevolve with higher plants because of their genetic affinities with fossilized conifer tissues (Jasinski and Payette, 2007).

## 3. ENDOPHYTIC FUNGAL DIVERSITY

The endophytic communities are closely linked to their host plants during their whole life cycle, or they spend a portion of it inside the tissues of the host without posing a threat to the host or causing illness (Hardoim et al., 2015; Puri et al., 2016). The endophytic community that is bearing the host plant may reside in facultative associations or as competent, obligate, or passenger types of microbial population (passenger endophytes are those that enter living tissues without any kind of selection pressure and remain there) (Hardoim et al., 2008). Fungal endophytes, such as *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycota: Hypocreales), can sometimes protect plants from disease-causing pathogenic fungi and nematodes as well as pests (arthropods) and

promote plant growth (Akello and Sikora, 2012; Biswas et al., 2013).

Some fungal endophytes, such as the insect pathogen *Clonostachys rosea*, *B. bassiana*, *Isaria farinosa*, and *Acremonium* sp. (now known as *Neotyphodium*), have been isolated from asymptomatic plant tissues. Following artificial inoculation, some endophytic entomopathogenic fungi, such as *Metarhizium anisopliae* (Akello and Sikora, 2012; Greenfield et al., 2016), *B. bassiana* (Parsa et al., 2013; Russo et al., 2015), *Hypocrea lixii*, *Gibberella moniliformis*, and *Trichoderma asperellum* (Akello and Sikora, 2012; Akutse et al., 2013), have been recovered from colonized host plants. Artificial inoculation techniques have been used to access endophytic fungal diversity in several economically significant crops, such as tomato (*Lycopersicon esculentum*) (Qayyum et al., 2015), soybeans (*Glycine max*) (Russo et al., 2015), cassava (*Manihot esculenta*) (Greenfield et al., 2016), cotton (*Gossypium hirsutum*) (Lopez et al., 2014; Lopez and Sword, 2015), tomato (*Phaseolus vulgaris*) (Akutse et al., 2013; Parsa et al., 2013; Parsa et al., 2016), soybeans (*Glycine max*) (Russo et al., 2015), and other crops of economic importance. According to Nair and Padmavathy (2014), endophytes and their hosts have intimate relationships that lead to complex interactions without causing losses or disease to plants. These interactions are primarily classed as mutualism, occasionally as antagonism, and very infrequently as parasitism (Nair and Padmavathy, 2014).

## 4. ENDOPHYTE DISTRIBUTION AND CLASSIFICATION

Endophyte density is typically higher in roots and subsurface areas than in aboveground areas (Miliute et al., 2015). This number could, however, differ because endophytes have been shown to migrate from rice roots to leaves (Chi et al., 2005), indicating that endophytes reach the host plant through the roots (Miliute et al., 2015). Even though bacterial endophytes are internal to plants, their population density and distribution are affected by biotic and abiotic factors that plants encounter, such as interactions between plants and microbes as well as environmental stresses (Ryan et al., 2008; Kamran et al., 2022).

According to more than a century of research, the majority of plants in natural environments work in symbiotic relationships with mycorrhizal fungi or fungal endophytes (Petrini,

1991). Plant evolution may be significantly impacted by this fungal companion. This fungus can define plant communities (Clay and Holah, 1999) and have a significant impact on plant evolution, fitness, and dispersion (Brundrett, 2006). According to fossil records, plant and fungal mycorrhizal and endophytic associations date back more than 400 million years (Redecker et al., 2000; Krings et al., 2007). These associations were probably formed at the time when plants first left their mark on land, and they therefore played a significant role in the evolution of life on land (Rodriguez et al., 2009). Fungal endophytes, like their bacterial counterparts, are contained within the plant host, where they can grow in both aboveground and underground sections and sporulate when the host tissue or plant ages (Mueller et al., 2004). Based on their host range and manner of transmission, fungi endophytes are divided into four classes (Rodriguez et al., 2009; Kamran et al., 2022).

## 5. ADVANTAGEOUS ROLES AND IMPLICATION OF ENDOPHYTIC FUNGAL IN PLANT STRESS TOLERANCE

### 5.1. Promotion of growth in host plants

#### 5.1.1. Hormonal regulation

Endophytic fungi can produce or influence the production of plant hormones, such as auxins, cytokinins, and gibberellins, which play essential roles in plant growth and stress responses. This hormonal regulation can contribute to enhanced plant resilience under stressful conditions (Khan et al., 2011).

Important physiological and ecological roles are played by endophytic fungi in the lives of their hosts. According to recent studies, endophytic fungi are important for industry and agriculture, can produce bioactive metabolites (Alloush, 2004; Tintjer and Rudgers, 2006), and have special structures and bioactivities against a variety of diseases. Gibberellins (GAs), auxin (IAA), and abscisic acid are only a few of the plant hormones that endophytic fungi produce in response to their connection with plants, which controls plant growth (Khan et al., 2008).

Auxins are imperative plant hormones, and among these hormones, indole-3-acetic acid has been shown to stimulate various growth and developmental actions, like cell division, cell elongation, and differentiation of a cell (Asgher et al., 2015). Gibberellin is a vital plant growth regulator, which has an important role in seed

germination growth of floral organs, and lateral shoot formation (Olszewski et al., 2012). The obtainable literature exposes the ameliorative influence of gibberellic acid against salt stress. Gibberellic acid was observed to encourage plant growth and improvement under numerous abiotic stress situations (Tuna et al., 2008; Ahmad, 2010).

#### 5.1.2. Nutrient uptake and enhanced nutrition

Endophytic fungi can assist in nutrient uptake and absorption by the host plant. They can enhance the availability of essential nutrients, such as phosphorus and nitrogen, by solubilizing minerals or fixing atmospheric nitrogen. This contributes to improved plant nutrition and overall stress tolerance (Rodriguez et al., 2009).

Endophytic fungi can affect plant uptake and production of nitrogen and are crucial to the health of agroecosystems (Behie and Bidochka, 2014). It has been shown in numerous studies that fungal endophytes increase the growth of host plants by improving the uptake of nutrients from the soil by the plants (Yang et al., 2014a; Yang et al., 2014b). In a symbiotic relationship, *P. liquidambari* helps rice absorb and accumulate nitrogen, which greatly increases rice output and growth (Yang et al., 2014b). Yang et al. (2014a) revealed that the fungal endophyte *P. liquidambari* stimulated the expression of many genes related to N-uptake and rice seedling metabolism. *P. liquidambari* raised the levels of organic acids, total free amino acids, and soluble saccharides in the rice root exudates thus, promoting the growth of the plant (Yang et al., 2015).

Several endophytic fungi have demonstrated the role of inorganic phosphate solubilization as one of the main processes promoting plant growth. The phosphate solubilization capacity of endophytic fungi isolated from *Taxus wallichiana* Zucc. roots was reported by Adhikari and Pandey (2019). *P. indica* can grow saprotrophically on poorly soluble inorganic Phosphorus forms like  $\text{Ca}_3(\text{PO}_4)_2$  or rock phosphate, according to research by Ngwene et al. (2016) on the physiological and molecular changes related to phosphorus dynamics in *P. indica* supplied with different forms of organic and inorganic phosphorus. The functional mechanism of endophytic fungus promoting plant growth was assessed in a study using 26 fungi from the genera *Alternaria*, *Aspergillus*, *Fusarium*, *Paecilomyces*, *Penicillium* sp., and a

few sterile mycelia. Absorption of mineral nutrients, enhanced water uptake, and build-up of osmolytes under stress circumstances are some of the mechanisms that promote plant growth. These mechanisms collectively improve the metabolic processes of the host plants, resulting in growth and stress resistance (Yang et al., 2014b; Yang et al., 2015).

## 5.2. Abiotic stress management

Plant growth is significantly impacted by abiotic stresses, and to survive, plants require a robust system. Endophytes, which live in the stem, petiole, and leaves of plants, play a crucial role in providing nutrients, acclimatizing to the environment, and promoting biotic and abiotic stress tolerance. These endophytes can persist throughout a plant's life cycle, enabling it to overcome environmental constraints. They are essential for resilience and sustainability in agriculture, as they collaborate with host plants and mobilize insoluble phosphate, providing nitrogen, and promoting plant growth (Redman et al., 2021; Yung et al., 2021; Grabka et al., 2022).

During stress, they secrete metabolites that promote plant growth, such as phytohormones and triterpenoid saponins. They also perform phosphate solubilization, siderophores production, antibiotic production, phytohormone production, and nutrient mineralization (Sahoo et al., 2017). The fungal endophytes secrete an alleviated amount of plant growth-promoting metabolites; for example, *Penicillium* sp. inhabiting *Suaeda japonica* secretes phytohormone Gibberellins. Likewise, *Aspergillus* sp., *Cladosporium* sp., *Fusarium* sp., *Penicillium* sp., *Verticillium* sp., and *Ascomycete* sp. inhabiting *Panax ginseng* secretes triterpenoid saponins and ginsenosides (enhances root growth and biotic and abiotic stress tolerance) (Sahoo et al., 2017). During abiotic stress, they produce defense-signaling substances like abscisic acid, jasmonic acid, and salicylic acid. In acidic soil, phosphorus is insufficient, leading to the fixation of aluminum and iron hydroxides (Johnson, 2008). These endophytes increase iron uptake and solubilization of phosphates, promoting growth. They also biodegrade litter, enhancing biomass production and nutrient uptake (Idbella et al., 2019).

### 5.2.1. High carbon di-oxide

Endophytic fungi increase internal hyphal growth and colonization, carbon sequestration,

biomass, and yield via increased photosynthesis and induced compositional changes in elevated CO<sub>2</sub> (Galani et al., 2022). In this context, various researchers found symbiotic relationship beneficial as it escalates plant growth in crops viz. tomato, rice, beans, cereals, potato, etc., secreting ascorbate and glutathione reducing Reactive Oxygen Species (ROS), following antioxidants and allelochemicals production (Yadav and Yadav, 2017). This renders efficient nutrient uptake, photosynthetic rate, water use efficiency (Elhindi et al., 2016), elevating phytohormone production, amplifying gene expression, supplementing protein function, metabolite synthesis, signaling molecules secretion, and triggering stress-responsive pathways, for better survival without hampering the yield (Ma et al., 2019).

However, some contrast results revealing decreased root and shoot growth exaggerated that endophytes vary in their effects on the same host plants subjected to the specific niche, preferentially under a particular growth condition (Gavito et al., 2000). Furthermore, colonization is also affected by the type of plants; for example, C3 plants consume additional carbon for biomass production and thus are less likely to benefit from colonization, whilst C4 plants allocate more carbohydrates resulting in a profit from endophytic fungi association (Tang et al., 2009). Therefore, according to the present studies, the role of microbiota in biological and ecological processes remains a challenge, especially for possible application in agriculture as endophytes adopt a molecular mechanism to induce stress-responsive genes, anti-stress metabolites, and Reactive Oxygen Species (ROS) scavenger molecules synthesis (Rehman et al., 2016).

### 5.2.2. Water stress management

Water stress can be divided into excess water stress (i.e., waterlogging or flooding) and water shortage stress (i.e., drought) (Wang and Komatsu, 2018). Excess water stress caused by soil waterlogging and/or submergence leads to oxygen deficiency in plants and severely suppresses their growth (Takahashi et al., 2018). Drought stress affects plant growth by a marked reduction in water uptake. It lowers water potential, leads to osmotic stress (Santander et al., 2017), causes stomatal closure, damages chloroplast structure, and decreases photosynthesis-related enzyme activity (He et al., 2016). It also destroys fungi and makes pathogen infiltration easier (Lee et al., 2014)

Drought is one of the significant stresses diminishing agricultural productivity and directly challenging food security attainment goals in developing countries (Santander et al., 2017). Fungal endophyte *Piriformospora indica* colonizes many plant roots, and its hyphae are present in the outer layer of the host's roots aiding in plant growth, higher chlorophyll content, and elevated yield under drought stress conditions (Bogati and Walczak, 2022, Joly et al., 2023). The fungal genus studied for plant growth parameters and stress tolerance were *Fusarium* sp., *Trichoderma* sp., *Penicillium* sp., *Aspergillus* sp., *Alternaria* sp., etc. Most of them were found to confer drought resistance to wheat. Endophytic fungus-associated plants (rice, tomato, and dune grass) have used significantly less water and increased biomass than non-symbiotic plants (Bogati and Walczak, 2022; Mukhtar et al., 2023).

The drought tolerance phenomenon may be explained by an enhanced accumulation of solutes in tissues of endophyte-infected plants compared to non-infected plants, by reduced leaf conductance and a slowdown of the transpiration stream, or due to thicker cuticle formation (Ripa et al., 2019). Characterization of *Trichoderma* sp. inhabiting *Theobroma cacao* revealed changes in gene expression patterns, implying that *Trichoderma* sp. could induce tolerance to abiotic stresses, possibly including drought (Bailey et al., 2006). Drought, heat, and salt stress affect the plant-water relationship, triggering complex plant responses, including increased osmolytes production. According to Marquez et al. (2007), the osmotic potential is determined primarily by solute potential and matrix potential; symbiotic fungi are likely to contribute to the matrix potential, which is particularly important in helping plants retain water and enhancing plant drought tolerance. Accordingly, the symbiotic fungi-associated plants consume significantly less water than non-symbiotic plants (Marquez et al., 2007).

### 5.2.3. Salinity

Salinity is another significant abiotic stress limiting the growth and productivity of plants worldwide. Tolerance of plants to salt stress is associated with the alleviation of antioxidant enzymes, i.e., ROS scavengers including glutathione, ascorbate, and tocopherol, and the enzymes superoxide dismutases (SOD), catalases (CAT), ascorbate- or thiol-dependent peroxidases (APX), glutathione reductases (GR), dehydroascorbate reductases (DHAR) and

mono-dehydroascorbate reductases (MDHAR) (Rouhier et al., 2008). They are involved in removing ROS directly (SOD, CAT, and APX) or indirectly via regenerating ascorbate and glutathione in the cell. For instance, *Piriformospora indica*, a root fungal endophyte, upraised biomass production in salt stress conditions by intensifying antioxidative capacity, fatty acid composition, lipid peroxidase, dehydroascorbate reductase, catalase, and glutathione reductase enzymes accumulation in barley (Baltruschat et al., 2008).

In another instance, the endophytic fungus *Exopiala* sp. LHL08 isolated from cucumber root appeared to confer tolerance against salinity and drought stress in rice (Murphy et al., 2018). Similarly, *P. indica* and *S. vermifera* showed salinity tolerance with increased growth and yield, and strong effects were observed by combining biological agents (Franken, 2012). Endophytic fungi *Fusarium culmorum* (FcRed1) was found to have a symbiotic relationship with rice seedlings under salinity and drought, resulting in increased plant height, root length, biomass, and higher osmolyte accumulation than the non-symbiotic rice seedlings. Nonetheless, there is a great need to unveil how fungal endophytes stimulate plant defense response against abiotic stress (Egamberdieva et al., 2017; Ma et al., 2019).

### 5.2.4. High temperature

Endophytic fungi may mediate the effect of high temperature by adjusting, regulating, or modifying plant physiological, biochemical, and metabolic activity depending on their biology, developmental stage, and cultivar of the host plant. Environmental conditions that affect the endophytic community may also escalate the number and variety of endophytic populations influencing metabolite production. Many researchers have assayed several isolated fungal endophytes, their multifarious interactions beneficial for the host against high-temperature stress environments, and their precise roles in environment acclimatization and conferring tolerance. For instance, a study found that *Curvularia protuberata*, a fungal endophyte, confers thermo-tolerance to tomato and panic grass (Lata et al., 2018).

*Paraphaeosphaeri aquadrioseptata* produces a heat shock protein 90 (HSP90) inhibitor conferring heat tolerance to *Arabidopsis* sp. When infected by a virus, as exemplified in a study of the potential of *Stenotrophomonas*

*maltophilia* SBP-9 to promote the growth of wheat under salt stress plant, the plant may confer heat tolerance (Marquez et al., 2007; Yadav and Yadav, 2017). Thus, a critical evaluation of a more intriguing and inexplicable issue with many fungal endophytes to produce host metabolites needed to be harnessed for potential use in a diverse environment (Khare et al., 2018; Galani et al., 2022).

### 5.2.5. Heavy metal stress

Heavy metal pollution is of great concern in developing countries where industrial wastes and pollutants are directly dumped into rivers or left open on soil surfaces. Cultivable areas may be affected by the application of excessive agrochemicals and polluted water as the direct passage from waterways. Accumulation of such heavy metals in the plants through the soil and irrigated water, hampering their growth and giving direct entry into the food chain, may pose health hazards to humans and animals; hence, bioremediation is crucial. In this context, plant endophyte symbiotic interactions enhance antioxidant enzyme activity via the uptake of heavy metal (cadmium) from soil followed by detoxification and transport led by three genes, namely ZYP, PCS, and MTP. Various fungal endophytes (*Penicillium sp.*, *Mucor sp.*, *Alternaria sp.*, *Microsphaeropsis sp.*, etc.) have ameliorated the adverse effects of heavy metal stress in plants (Ma et al., 2016; Wang et al., 2016).

Fungal endophytes are found to be involved in the bio-absorption of cadmium (Xiao et al., 2010), copper (Li et al., 2012), and sodium chloride (Khan et al., 2013) by stabilizing the negative effect of heavy metal toxicity (Khan et al., 2013). Zahoor et al. (2017) isolated and screened some innate endophytes and cultured them on heavy metal (chromium, cobalt, copper, manganese, and zinc) contaminated soils and found *Mucor sp.* (strain MHR-7) to confer a multiple heavy metal toxicity tolerance. Recently, the endophyte-mediated biosensor concept has also received much attention, promising a better bioremediation-controlled process (Khanam et al., 2020). Some endophytes induce phytohormone production, especially gibberellins, which contribute to fungus in eradicating heavy metal toxicity, thus serving an eco-friendly approach to bioremediation benefiting a healthy diet environment (Khan et al., 2013; Zahoor et al., 2017; Khanam et al., 2020).

### 5.3. Biotic stress management

Pesticides and agrochemicals resistance is a growing concern, and sustainable solutions are needed to address this issue (Baron and Rigobelo, 2021). Management of biotic stresses and disease-causing pathogens using biological resources is a welcomed approach as they reduce the release of harmful chemicals into the environment and favor ecological sustainability. Endophytic fungi protect plants from pathogenic microbes via several mechanisms such as competition, antibiosis, mycoparasitism, induced resistance, etc., and also serve as a biocontrol agent (Latz et al., 2018).

Induced resistance stands out as a crucial mechanism provided by endophytes for disease management. Numerous studies have highlighted the potential of the root endophyte *Serendipita indica* in promoting plant growth and enhancing resistance to diseases (Harrach et al., 2013; Varma et al., 2013; Nassimi and Taheri, 2017). The basidiomycetous fungi *P. indica* has demonstrated a broad spectrum of symbiosis with plants. In symbiotic plants, the defense response involves the systemic induction of resistance. Additionally, the altered state of "defense readiness" is characterized by the activation of the glutathione-ascorbate cycle, leading to increased antioxidative enzymatic activities and ultimately higher crop yields (Nassimi and Taheri, 2017).

Since the beneficial fungus can thrive independently of its host, it suggests the potential for leveraging these fungi in sustainable agricultural practices. Competitive exclusion emerges as a regulatory factor influencing the composition of the plant microbiome, offering a likely mechanism through which inhabiting endophytes can prevent the colonization of hosts by pathogens (Martinuz et al., 2012). Arnold et al. (2003) observed that the foliar application of a mixture of commonly isolated endophytes from cacao tree leaves to endophyte-free seedlings localized the reduction of disease symptoms caused by *Phytophthora* spp. on foliage, indicating competition as a viable mechanism (Arnold et al., 2003).

Non-pathogenic fungal endophytes, such as *Aspergillus sp.*, *Colletotrichum sp.*, *Gliocladium sp.*, *Fusarium sp.*, *Petriella sp.*, *Piriformospora sp.*, *Trichoderma sp.*, *Epicoccum sp.*, and *Epichloe sp.*, have shown the ability to help plants withstand pathogen attacks and protect crops from biotic stress (Mane et al., 2018; Grabka et al., 2022). These endophytes regulate bioactive molecules,

antioxidants, phytoalexins, phytohormone production, and ecological occupancy, making them potential biocontrol agents (Singh et al., 2021).

*Epichloe* sp. offers biotic resistance to its host plant and controls herbivorous insects (Laihonen et al., 2022). *Piriformospora indica*, a root colonizing filamentous fungus, counter-attacks pests/pathogens by accelerating the production of phytoalexins, anti-microbial compounds, and antioxidant defense enzymes (Arora et al., 2022). *Trichoderma* sp., an anamorphic filamentous saprophytic fungus, colonizes roots, twigs, and stems of host plants, producing anti-fungal, anti-bacterial, and cytotoxic effects. They can also produce phytohormones, siderophores, and other plant growth-promoting substances, enriching soil microflora and aiding soil fertility (Srivastava et al., 2012; Srivastava et al., 2014).

*Myrothecium verrucaria*, a soil-borne ascomycete fungal endophyte with antagonist properties, is considered a natural mycoherbicide due to its high phytotoxin and lytic enzyme production (Clarke et al., 2007). *Aureobasidium pullulans* and *Candida orthopsilosis* can fight against *Alternaria* sp. in citrus. These fungal endophytes are safe, eco-friendly, and effective bio-control agents for various crop species (Sukmawati et al., 2021). Table 1 shows the activities of some endophytic fungi of plant sources/inoculated with the fungus.

### 5.3.1. Induced resistance

The activation of the host's resistance system, particularly through barriers like physical and chemical defenses against diseases caused by biotic or abiotic agents, has been emphasized (Kloepper et al., 1992). The stimulating agent triggers the synthesis of signaling molecules in the host, resulting in the development of a more pathogen-resistant plant through distinct expression of genes and protein functions. This leads to alterations in the plant's metabolic processes, making the host more relevant and reducing the severity of the disease. Both biotic and abiotic agents can induce resistance in host plants, either localized or throughout the entire plant body (Martinez-Medina et al., 2016).

The induction of host resistance to disease is mediated by stimulating infection-induced defense responses (Conrath et al., 2002). The enhanced capacity of the host to resist diseases is not temporary or moderately triggered but is a response to specific defense stimuli (Martinez-

Medina et al., 2016). The fungal endophyte *S. indica*, isolated from roots, has been shown to promote increased growth and resistance in various plants (Table 1) (Varma et al., 2013; Nassimi and Taheri, 2017).

### 5.3.2. Mycoparasitism

Mycoparasitism refers to the condition in which a fungus acts as a parasite on another fungus (Jeffries, 1995). Biotrophic fungi acquire their nutrients from living host cells, utilizing haustoria to kill plant cells in the process (Kim and Vujanovic, 2016). In the context of endophyte and pathogen interactions, specific metabolites are produced, as seen in the example of *Stachybotris elegans* parasitizing *Thanatephorus cucumeris* (Chamoun et al., 2015). This parasitic fungus employs various mechanisms such as direct attachment, hyphal puncture, and aggregate formation around the hyphae, ultimately leading to the formation of abnormal hyphae. *Geotrichum* sp. (isolate EF-ds104-16), as studied by Donayre and Dalisay (2016), is a fungus that obtains nutrients and parasitizes *T. cucumeris*. Endophytes isolated from *Phragmites australis* exhibit antagonistic behavior against eight pathogens, involving coiling around hyphae and the breakdown of fungal cell walls through the action of chitinases and  $\beta$ -1,3-glucanases (Cao et al., 2009).

### 5.3.3. Antibiosis

Antibiosis refers to the prevention of pathogens through the action of chemical compounds produced by endophytic fungi, which are utilized as biocontrol agents (Dipietro, 1995). Endophytes isolated from plants have the potential to produce various antimicrobial compounds, including flavonoids, alkaloids, peptides, phenols, steroids, terpenoids, polyketides, and volatile organic compounds (VOCs). These specific metabolites play a role in suppressing the growth of aggressive pathogens (Thines et al., 2004; Yu et al., 2010; Mousa and Raizada, 2013; Lugtenberg et al., 2016). It is crucial to study potential endophytic fungi to identify and understand the specific chemical compounds produced by biocontrol agents used in antimicrobial activities (Suryanarayanan, 2013; Daguerre et al., 2017).

According to Kusari et al. (2012), endophytic fungi grown on distinct media produce various metabolites. These endophytic fungi synthesize metabolites and VOCs, which can be transferred and spread to the entry point of pathogens (Lugtenberg et al., 2016; Gabriel et al., 2018).

While it has been reported that endophytes produce metabolites capable of inhibiting the growth of pathogens in vitro, there is currently no evidence confirming that the prevention of pathogens occurs inside the host (Kohl et al., 2011; Deketelaere et al., 2017; Laur et al., 2018).

### 5.3.4. Competition

Competition is a key aspect of the endophyte's role as it resides within the plant, impeding the growth of pathogens by competing with them for space and nutrient utilization (Martinuz et al., 2012). Endophytes demonstrate rapid growth

**Table 1.** Activities of some endophytic fungus of plants sources/inoculated with the fungus.

| Plant Source/Host               | Endophytic fungus                                | Activity/Mechanism of action                             | Reference                                |
|---------------------------------|--------------------------------------------------|----------------------------------------------------------|------------------------------------------|
| <i>Cucumis sativus</i>          | <i>Paecilomyces formosus</i>                     | Production of indole-acetic-acid (IAA)                   | Waqas et al. (2014)                      |
| <i>Glycine max</i> (L.) Merr.   | <i>Chrysosporium Pseudomerdarium</i>             | Production of indole-acetic-acid (IAA)                   | Waqas et al. (2014)                      |
| <i>Atractylodes lancea</i>      | <i>Gilmaniella</i> sp.                           | Defense response induced by production of jasmonic acid  | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Cirsium arvense</i>          | <i>Chaetomium cochliodes</i>                     | Pathogen toxic activities                                | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Glycyrrhiza uralensis</i>    | <i>Penicillium griseofulvum</i>                  | Protective enzymes production under stress               | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Chrysanthemum morifolium</i> | <i>Chaetomium globosum</i>                       | POD activities                                           | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Oryza sativa</i>             | <i>Absidia</i>                                   | Promotion of plant growth                                | Atugala and Deshappriya (2015)           |
| <i>Glycine max</i>              | <i>Phoma glomerata</i>                           | Production of gibberellin                                | Waqas et al. (2014)                      |
| <i>Oryza sativa</i>             | <i>Cylindrocladium</i>                           | Promotion of plant growth                                | Atugala and Deshappriya (2015)           |
| <i>Glycine max</i>              | <i>Paecilomyces formosus</i>                     | Production of gibberellin                                | Waqas et al. (2014)                      |
| <i>Hordeum vulgare</i>          | <i>Serendipita indica</i>                        | Mitigation of some biotic stress                         | Nizam et al. (2019)                      |
| <i>Chenopodium quinoa</i>       | <i>Penicillium minioluteum</i>                   | Mitigation of some biotic stress                         | Gonza'lez-Teuber et al. (2018)           |
| <i>Hordeum vulgare</i>          | <i>Aspergillus fumigatus</i>                     | Prevents pathogen colonization                           | Maciá-Vicente et al. (2009)              |
| <i>Telfairia</i> (inoculated)   | <i>occidentalis</i> <i>Glomus geosporum</i>      | Promotion of plant growth under salt stress              | Okon et al. (2022)                       |
| <i>Cucurbita</i> (inoculated)   | <i>maxima</i> <i>Rhizophagus irregularis</i>     | Promotion of plant growth under salt stress              | Okon et al. (2022)                       |
| <i>Angelica sinensis</i>        | <i>Fusarium oxysporum</i>                        | Production of toxins antagonistic to pathogens           | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Maytenus hookeri</i>         | <i>Trichothecium roseum</i>                      | Production of toxins antagonistic to pathogens           | Zhang et al. (2010)                      |
| <i>Cucumis sativus</i>          | <i>Chaetomium</i> Ch1001                         | Absciscic acid production                                | Aamir et al. (2020); Ikram et al. (2019) |
| <i>Withania somnifera</i>       | <i>Penicillium oxalicum</i> strain 5aWF          | Increased production of anolides in the leaves and roots | Kushwaha et al. (2019)                   |
| <i>Withania somnifera</i>       | <i>Sarocladium kiliense</i> strain 10aWF (10aWF) | Increased production of anolides in the leaves and roots | Kushwaha et al. (2019)                   |

and efficient nutrient exploitation compared to pathogens harbored within plant tissues (Rodriguez et al., 2009). Mohandoss and Suryanarayanan (2009) found that fungicide treatment on mango leaves led to the exclusion of beneficial endophytes, creating space for the invasion of harmful microorganisms. An endophyte, *Heteroconium chaetospora*, isolated from oilseed rape roots, was observed to inhibit the pathogen responsible for clubroot disease (Lahlali et al., 2014). However, the effectiveness of the competition mechanism diminishes under elevated disease intensity, as the density of pathogens on the host surface increases, leading to reduced control efficiency (Martinuz et al., 2012). Endophytes isolated from cacao plant leaves, spreading onto endophyte-free seedlings, have been shown to reduce foliar diseases caused by *Phytophthora* sp. through competitive means (Arnold et al., 2003). Card et al. (2016) proposed that for endophytes used as biocontrol agents, aggregation at access points is crucial for effectively removing pathogens.

5.3.5. Bio-control agents

The utilization of endophytic fungi as bio-control agents is a common approach in fungal bio-control strategies, primarily targeting pathogens associated with plant diseases. Endophytic antagonistic fungi employ various mechanisms to suppress pathogens, including mycoparasitism, antibiotic (toxin) production, competition for space and nutrients, production of enzymes, and induction of the plant defense system (Benhamou et al., 2000; Walters et al., 2005; El-Hasan et al., 2009; Ting et al., 2010). Endophytic fungi reside internally in plant bodies without causing obvious injury, providing tolerance to both biotic and abiotic stresses (Walters et al., 2005). Diverse groups of systematically and biologically heterogeneous

endophytic fungi have been identified in various plants, including medicinal, crop, woody, and others (Wilson, 1995).

Numerous endophytic fungi have been evaluated for their biocontrol potential against a variety of pests and pathogens responsible for numerous plant diseases (Holmes et al., 2004; Ting et al., 2010). The global market for potential inoculants of endophytic fungi applied as biocontrol agents has experienced approximately a 10% annual growth rate (Lahlali and Hijri, 2010). There is a need to explore novel endophytic fungi with biocontrol capabilities that induce plant defense systems, thereby protecting crops against various plant diseases. Lahlali and Hijri (2010) demonstrated that *Trichoderma atroviridae*, an endophyte, exhibited in vitro inhibitory effects on *Rhizoctonia solani* AG3, the causal agent of black scurf on potatoes. Additionally, various endophytes, including *Fusarium chlamydosporum*, *Fusarium oxysporum*, and *Fusarium redolens*, were identified from *Monarda citriodora* Cerv. These endophytes displayed a broad spectrum of antagonistic activity against *Sclerotinia* sp., *Colletotrichum capsici*, *Aspergillus flavus*, *Aspergillus fumigatus*, and *Fusarium solani* (Katoch and Pull, 2017). Furthermore, a novel endophyte named *Muscodor yucatanensis* KJ572191, isolated from *M. citriodora* Cerv., was found to completely inhibit the growth of *Sclerotinia* sp., *C. capsici*, *A. flavus*, and *A. fumigatus* in dual culture assays (Katoch and Pull, 2017).

5.4. Current discovery of metabolites isolated from endophytic fungi

Recent studies have reported that about 220 new chemical compounds with relevant biological applications/activities. Table 2 shows

Table 2. Biological activities of recently isolated compounds and associated endophytic fungi

| S/N | Chemical Compound                     | Biological effect                            | Endophytic fungi                  | Plant Source                    |
|-----|---------------------------------------|----------------------------------------------|-----------------------------------|---------------------------------|
| 1   | Huperzine A                           | Effective in the treatment of Alzheimers'    | <i>Fusarium verticillioides</i>   | <i>Huperzia serrata</i>         |
| 2   | Corynesidone D                        | Anticancer/anti-inflammatory                 | <i>Corynespora cassiicola</i>     | <i>Gongronema latifolium</i>    |
| 3   | punctaporonin H                       | antibacterial                                | <i>Pestalotiopsis theae</i>       | <i>Camellia sinensis</i>        |
| 4   | Podophyllotoxin                       | Antiviral                                    | <i>Phialocephala fortinii</i>     | <i>Podophyllum peltatum</i>     |
| 5   | Napthaquinones<br>Azaanthraquinones   | Antimicrobial                                | <i>Fusarium solani</i>            | <i>Cassia alata</i>             |
| 6   | Scorpinone                            | Antibacterial                                | <i>Lophiostoma</i> sp.            | <i>Eucalyptus exserta</i>       |
| 7   | Terezine E                            | Antifungal                                   | <i>Mucor</i> sp.                  | <i>Centaurea stoebe</i>         |
| 8   | Myriocin                              | Antifungal                                   | <i>Mycosphaerella</i> sp.         | <i>Myrciaria floribunda</i>     |
| 9   | 4b-hydroxy-1213-epoxytrichothec-9-ene | Antimicrobial and antiproliferative activity | <i>Trichoderma brevicompactum</i> | <i>Vinca herbacea</i>           |
| 10  | Sterigmatocystin                      | Antiproliferative                            | <i>Aspergillus nidulans</i>       | <i>Nyctanthes arbor-tristis</i> |

some of these compounds and associated endophytic fungi (Wen et al., 2022).

## 6. CONCLUSION

In conclusion, endophytic fungi emerge as versatile contributors to plant health and productivity by influencing various physiological and biochemical processes. Their ability to modulate hormonal levels, enhance nutrient uptake, and manage both abiotic and biotic stresses underscores their potential as sustainable agricultural tools. Understanding the intricate interactions between endophytic fungi and their host plants opens avenues for developing eco-friendly strategies to address challenges such as drought, salinity, and pest resistance. The diverse mechanisms employed by endophytic fungi, including mycoparasitism and antibiosis, make them promising biocontrol agents against pathogenic threats. As research in this field progresses, harnessing the full potential of endophytic fungi holds promise for promoting resilient and sustainable agriculture in the face of changing environmental conditions.

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