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Unraveling endophytic fungal communities: Diversity, global biogeography, and biological activities

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ABSTRACT

Endophytes are microorganisms, including bacteria, fungi, and actinomycetes, which colonize the internal tissues of plants for at least part of their life cycle without causing apparent disease symptoms or adverse effects to the host. Endophytic fungi, also regarded as plant-associated fungi, include a diverse collection of microorganisms normally found in plant tissues or intercellular gaps and are rich in biodiversity. There are five major phyla of endophytic fungal communities, namely, Ascomycota, Basidiomycota, Mucoromycota, Glomeromycota, and Chytridiomycota. Fungal endophytes contribute to plant growth and sustainable productivity by improving host tolerance to diverse biotic and abiotic stresses. Endophytic fungi perform remarkable functions in the environment, including stress tolerance (abiotic and biotic), eco-adaptation, boosting plant growth and development, and maintaining their host's health. Endophytes have the ability to modify phytochemical profiles, mediate the expression of plant functional traits, and reduce a plant's susceptibility to disease. The beneficial activities of endophytes are mediated by the synthesis of secondary metabolites and enzymes, regulation of host physiological functions, and their ability to act as biological control agents against pests and plant pathogens. The lack of understanding surrounding endophyte biogeography has hindered both scientific and applied research concerning endophytes. Since they are relatively undiscovered, endophytic fungi may be sources of novel products that can be utilized in industry, agriculture, and medicine. So, this review mainly focuses on the diversity and biogeography of endophytic fungal communities and their potential contribution in promoting agro-environmental sustainability.

1. INTRODUCTION

The concept of endophytes was introduced by De Bary [1] and refers to microorganisms that colonize the internal tissues of living plants without causing visible disease symptoms. Since the term "symbiosis" was introduced, numerous forms of symbiotic interactions have been identified among living organisms. The term is described as "the mutual living of dissimilar organisms" [2]. These definitions have been established based on fitness benefits or impacts on both microscopic symbionts and macroscopic hosts [3]. The mutualistic relationship fungi possess with plant species has grown to be one of the major concerns in biology. Fungal species classified as endophytic reside in plant tissues throughout their life cycle or a specific portion of it without producing visible signs of disease. These fungi mostly inhabit the inter or intracellular spaces of the host plants in many organs, including the leaf, root, stem, fruit, flower, and seed. Most investigated plant species, harbor endophytes, yet only a small fraction of the endophytic fungi associated with the world's plant diversity has been characterized, suggesting that plants represent an immense and largely untapped reservoir of microbial diversity and biotechnological potential. Endophytic fungi have gained increasing attention since they have huge potential to produce a wide variety of metabolites that are significant for medicine [4].

Only a small number of these phytobiome-associated fungal endophytes have been investigated, suggesting that there is a good chance of discovering fascinating endophytes among a wide variety of plants in various niches and habitats. In addition, research on plant endophytes is required to furnish basic data for evaluating fungal diversity and distribution worldwide and for the identification of new species. Endophytic fungi inhabit plant tissues and establish symbiotic associations with their hosts, contributing to plant growth

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and development, enhancing tolerance to biotic and abiotic stresses, and stimulating the production of secondary metabolites [5,6]. Host plants along with their microbiota are referred to as holobionts. Certain endophytes may have developed as holobionts alongside their host and may have important implications for agriculture, medicine, or the environment [7,8]. Numerous studies have demonstrated that nearly all plants are colonized by endophytic fungi. Fungal diversity in plants has been influenced by a variety of parameters, such as host plant species, organs, geographic location, seasonal environment, and more [9].

Ascomycota, Basidiomycota, Mucoromycota, Glomeromycota, and Chytridiomycota are the current fungal taxa that have been documented to be endophytes of various plant species [10]. Numerous endophytic fungal species and a wide variety of metabolites with various purposes have been found in recent investigations [11–13]. They may also function as biocontrol agents [14], promote plant growth and generate enzymes [15]. Due to their relative underuse, endophytic fungi may provide a wide range of novel products that could be used in industry, the agricultural sector, as well as in medicines [16]. Abiotic and biotic stresses such as drought, heavy metals, salt, and other environmental pollutants such as floods, extremely high or low temperatures, predators, and infections can be mitigated by these endophytes. In addition to offering stimulants for plant growth and development, they confer advantageous biological characteristics on their hosts, including the ability to ward off harmful bacteria, insects, and other herbivores [17].

Endophytes have gained much attention as they produce valuable compounds. In order to find natural molecules that can be used as agrochemicals, researchers have been investigating secondary metabolites produced from these endophytes. Various chemicals have been extracted and isolated using top–down techniques from certain taxonomic orders of fungi [18]. A study reported that remarkable diversity of bioactive compounds, including glucosides, cytochalasans, azaphilones, terpenoids, nonribosomal peptides, macrolide polyketides, benzenoids, and lactones from *Xylariales* [18]. Endophytic fungi are relatively unknown sources of innovative natural compounds with uses in industry and agriculture. In fact, a variety of chemicals produced by endophytes have therapeutic utility [19]. The present review gives readers an overview of endophytic fungi, discovers the remarkable diversity of endophytic fungi, their distribution, function, and immense biological potential. Thus, the variety and biogeography of endophytic fungal communities, as well as their potential to support the sustainability of the agro-environment, are the primary subjects of this chapter. It also suggests potential paths to close the knowledge gaps and encourages more investigations.

2. DIVERSITY, TAXONOMY, AND BIOGEOGRAPHY OF ENDOPHYTIC FUNGAL COMMUNITIES

The variety of fungal endophytes within the tissues of plants can differ even among species, depending on the physiological conditions of each individual plant [20]. As a result, the variety of plant-associated fungal endophytes varies considerably [9]. Furthermore, the population profile of these fungi might be influenced by the age of the plant. Certain fungal endophytes can colonize a wide variety of plant species, while others are highly specialized and can only be found inside a small number of plants. This specialization may also exist with respect to the area of the plant that has been colonized [21]. In contrast to horizontally transmitted fungi, which are more probably to be antagonists, vertically transmitted fungi appear to exhibit plant interactions with a more mutualistic profile [9]. To maintain ecosystem functioning and variety across a wide range of plant species, it is imperative to do research on the endophytic fungal community in an evolutionary framework [22].

Research on the distribution and variety of endophytic fungi has been conducted throughout a broad range of geographical areas, including freshwater, marine, terrestrial, and semi-aquatic settings. Likewise, a wide range of phototrophs, including forest trees, mangroves, ferns, medicinal plants, seaweeds, vegetables, seagrass, and orchids, have been checked for endophytic fungi. The variety of these endophytes also varies substantially based on the location and is influenced by a variety of factors, including the growth season, anthropogenic effects, host plant physiology and genotype, and the environment. It varies greatly in abundance and variety among host plants, even within the same geographic region, and even inside the same host plant [23,24]. It was observed that, in comparison to other places, the fungal diversity is significantly higher in tropical and subtropical areas [25,26]. Seasonal fluctuations have also been identified as a significant factor influencing the variety and spread of these endophytes. The focus of endophytic fungal research has primarily shifted from taxonomic novelty to applications. It has been noted that numerous fungal endophytes are unknown to science [27]. Even though fungal endophytes are abundant and diverse throughout a wide range of biomes, research on their uses and functions is still in its early stages.

2.1. Taxonomic Basis of Endophytic Fungi

Fungal endophytes are commonly classified according to their phylogeny, host range, tissue colonization pattern, and mode of transmission [12,28]. Based on phylogenetic relationships, they are broadly categorized into clavicipitaceous (Class 1) and non-clavicipitaceous (Classes 2–4) endophytes. Clavicipitaceous endophytes are predominantly associated with cool-season grasses and exhibit a relatively narrow host range, whereas non-clavicipitaceous endophytes colonize a broad spectrum of vascular plants and inhabit various internal tissues, including leaves, stems, roots, and seeds [28]. Endophytic fungi may also be classified according to the plant organ they colonize, such as foliar, root, stem, or seed endophytes, and by their mode of transmission as vertically transmitted (seed-borne) or horizontally transmitted (environmentally acquired) [12,27]. By definition, endophytic fungi inhabit living plant tissues without causing visible disease symptoms for at least a part of their life cycle, although certain species may transition to latent pathogenic, saprotrophic, or mutualistic lifestyles in response to host developmental stage or environmental conditions [28,29]. Unlike saprotrophs, which derive nutrients from dead organic matter, necrotrophic fungi are pathogens that actively kill host cells and subsequently utilize the dead tissues as a nutrient source; therefore, necrotrophy should not be considered a nutritional strategy of endophytic fungi [5,30].

2.2. Distribution of Fungal Endophytes in the Terrestrial Habitat

Being a varied and diverse guild in ecology, an endophytic fungus possesses a huge range of functional features related to host phytogeography, adaptation, and defense. Fungal endophytes have been distributed in the terrestrial habitat and share niches with trees, orchids, shrubs, medicinal plants, ferns, etc. (Fig. 1). Arnold and Lutzoni [31] recognized tropical trees and their leaves as unique hotspots with a wide diversity of endophytes based on the amount of mutualistic fungal colonization. The endophytic fungal diversity in the dry tropics was not particularly great, regardless of the type of habitat or tree species; nonetheless, there is a tendency toward the dominance of a small number of core group fungi, such as *Colletotrichum*, *Pestalotiopsis*, *Phomopsis*, and *Xylaria* [32]. In two dry tropical forests in southern India, 24 tree hosts from 17 families revealed 81 endophytes in 3,600 segments [33]. In northern China, 2,065 endophytes isolated from 4,320 tissue sections of *Pinus tabulaeformis*

[34]. Twenty-six fungal endophytes were reported from *Juniperus procera* in Saudi Arabia [35].

There are numerous cases where the fungi live in association with plants of medicinal importance and create some of the value-added compounds [36,37]. Based on morphological and genetic approaches, 46 endophytic fungi were found in the foliar section of six medicinal herbs from central India, whereas 34 fungal species were found in three medicinal shrubs [38]. Eleven species of aquatic hyphomycetes as endophytes have been identified by Sati and Belwal [39] in the roots of numerous riparian pteridophytes at two places in Kumaun, Himalaya. There is little information available about endophytic fungi, despite the fact that orchids must be in close proximity to fungi in order to meet their nutritional and seed germination needs [40,41]. To learn more about orchids' relationship with mycorrhizal fungi, evaluations of up to 200 genera of orchids have been conducted [42]. Thirty-three samples of roots and tubers from five different species of Mediterranean orchids were examined, and *Fusarium*, *Papulaspora*, and *Rhizoctonia* were identified [43]. The orchid *Odontoglossum* sp. was shown to harbor endophytic *Phomopsis* sp. in Northern Ecuador [44]. *Anoectochilus setaceus*, a type of orchid found in Sri Lanka, included the endophytic *Xylaria* sp. [45]. Endophytic fungi were evaluated in 90 segments of two major orchid species from the Western Ghats of India, *Bulbophyllum neilgherrense* and *Vanda testacea* [46]. Further, considerable numbers of fungi were recorded in the leaf segments of both orchids rather than in the bulb, stem, or roots.

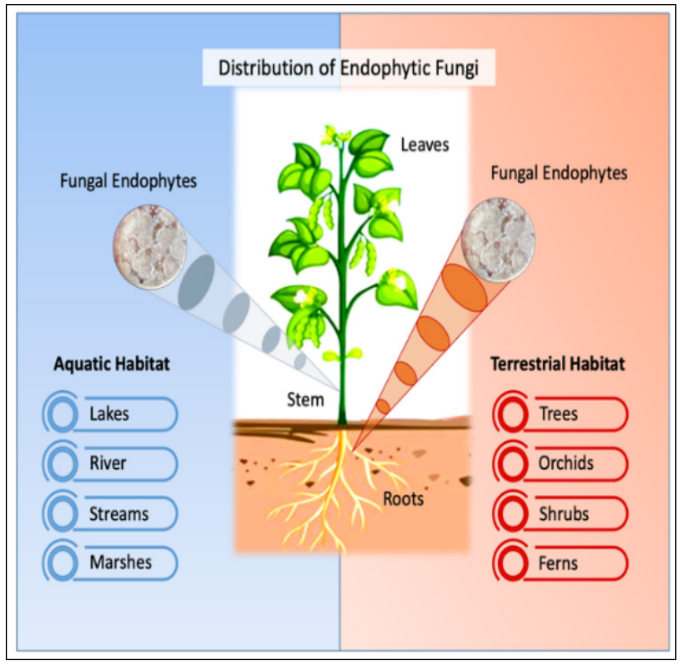

Figure 1. Distribution of endophytic fungi.

2.3. Distribution of Fungal Endophytes in the Aquatic Habitat

Research on the distribution and diversity of endophytic fungi in aquatic habitats is rather rare [47]. Compared to terrestrial and marine areas, less research has been done on endophytic fungi in freshwater environments. A variety of plant species are influenced by freshwater environments, including lakes, rivers, streams, and marshes (Fig. 1). Numerous species of riparian trees extend their roots into flowing waters that could be possible sites for fungal colonization. This hinders the complete elimination of fungi from higher portions of streams and rivers. The endophytic stage of two common aquatic *hyphomycetes* (*Campylospora parvula and Tricladium splendens*) was initially shown by Fisher and Petrini in 1989. The occurrence of *Filosporella fistucella, Fontanospora fusiramosa, Filosporella versimorpha* and *Tetracladium nainitalense* as endophytes of riparian plants has subsequently been documented by Sati and Belwal [39]. New aquatic hyphomycetes (*Filosporella fistucella*, *Fontanospora fusiramosa*, *Filosporella versimorpha,* and *Tetracladium nainitalense*) were discovered in numerous riparian tree roots during the research of endophytic fungi. In tropical and subtropical climates, plant varieties found in river mouths (estuaries and mangroves) offer possible sites for endophytic fungi colonization. In mangrove plant species found along India's east coast, common foliar endophytes are *Acremonium, Phomopsis, Phyllosticta*, and *Sporormiella minima*. There are 619 endophytic fungi on Thai mangrove trees, with *Bruguiera cylindrica* having the highest colonization [48]. Twenty-five endophytic fungi were isolated from the mangrove shrub and fern, which include *Acanthus ilicifolius* and *Acrostichum aureum,* respectively [49].

Sesbania bispinosa, a mangrove legume native to southwest India, contained 25 endophytic fungi, the majority of which were found in the root segments [50]. A study reported that fungal species of the wild legume *S. bispinosa*, which is acclimated to mangroves and coastal sand dunes [51]. Worldwide, seaweeds are home to about 100 known endophytic fungi, of which up to 75% have been documented from the North Sea, the Baltic Sea, Canada, the United Kingdom, India, and China [52]. The diversity of fungal endophytes associated with red, brown, and green seaweeds from the coastal areas of India has been comprehensively compiled and discussed [53]. The east coast of India *Halophila ovalis* revealed a low colonization density of 14 endophytic fungi in its petiole, rhizome, and leaf blade [54]. The endophytic fungi inhabiting the leaf tissues and rhizomes of ten seagrass species collected from the east coast of India were examined by Venkatachalam et al. [55]. Three seagrass species, *Zostera japonica, Zostera marina*, and *Thalassia testudinum* gathered from Hong Kong (China), and the Philippines, are reported to have approximately 26 endophytic fungi [56].

3. SPECIFIC BIOACTIVE METABOLITES PRODUCED BY ENDOPHYTIC FUNGI

The ability of endophytic fungi to produce secondary metabolites that are precious for the manufacturing of novel drugs makes them of biotechnological interest [57]. It is thought that these fungi are a good source of novel bioactive substances [58]. They have been found to produce bioactive compounds, including resveratrol, taxol, podophyllotoxin, huperzine, and vinca alkaloids [59,60]. These compounds have the potential to be used as therapeutic agents for the treatment of a variety of illnesses, either directly or indirectly [61]. Steroids, alkaloids, phenols, isocoumarins, xanthones, quinones, and terpenoids are some secondary metabolites produced by endophytic fungi [62,63] (Table 1). Novel, advantageous bioactive compounds with biological properties [64] such as antituberculosis [65], anti-inflammatory [66], antiprotozoal [67], insecticidal [68], antiviral, anticancer activities [69], immunomodulatory [70], and anthelmintic activity [62] have been reported in a number of studies. Abundant pharmacologically significant compounds, including the antimicrobial metabolite 5α,8α-epidioxyergosta-6,22-dien-3β-ol [71], the anticancer cajanol [72], the podophyllotoxin and kaempferol [73], the anti-inflammatory ergoflavin [74], the antioxidant lectin [75], the insecticidal heptelidic acid [76], the immunosuppressive sydoxanthone A, B [77], and the cytotoxic radicicol [78] were produced by fungal endophytes. Various enzymes with important clinical and industrial applications, including lipases, amylases, catalases, laccases, and proteases, have also been reported from endophytic fungi.

4. ROLE OF FUNGAL ENDOPHYTES IN BIOLOGICAL ACTIVITIES

It has been discovered that endophytic fungi are a novel source of bioactive secondary metabolites with a wide range of biological activities, including biocontrol activities, antibiotic production, immunosuppressive, antimycotic, and anticancerous activities. They play an important role as plant growth promoters (PGP) [79] and help in nutrient recycling bioremediation and biotransformation (Fig. 2).

4.1. Biological Control Agents

Biological control is the process of reducing the detrimental effects of plant pathogens and encouraging beneficial responses by the plant by utilizing beneficial organisms, their genes, and/or products, such as metabolites. Various crop plant varieties that were derived from wild types are used in current agricultural techniques. Since these crop plants cannot acquire resistance against the new pathogens, new pathogens may arise and occasionally trigger disease epidemics [80]. Excessive pesticide use lowers agricultural sustainability and has negative consequences for human health and ecological function. Agrochemicals deplete soil fertility, disrupt natural equilibrium, and pollute the environment and food chains [81].

Fungal entomopathogens are thought to be a diverse group of organisms on this planet, Earth, and are natural enemies of arthropods. They are the subject of extensive global research and have great potential as biocontrol agents. Adoption and application of these fungal entomopathogens in biocontrol is an alternative to chemical pesticides that harm the ecosystem [82]. The use of fungal biopesticides provides an environmentally friendly and highly efficient substitute. Endophytes have the capacity to modify their interactions with pathogens and pests and may even serve as potential biocontrol agents. Endophytic fungi can shield their host plant against insect infection by producing peramine, which prevents insects, nematodes, and other phytoparasites from eating the plant [83]. Important biocontrol agents include *Aspergillus* spp., *Gliocladium* spp., nonpathogenic *Fusarium* spp., *Trichoderma* spp. etc. *Acremonium alternatum*, an endophyte, protects Chinese cabbage from *Plasmodiophora brassicae* [84].

A fungal endophyte called *Phomopsis* sp. was identified from cotton plants, and it helped the plants resist caterpillar herbivory [85]. Occasionally, a certain endophytic species shows promise as a biocontrol agent. Considering the added benefits; the same endophyte species may promote the growth of the host plant, fitness, and stress tolerance, and protect the host plant from pests and diseases. Endophytic fungi such as *Aspergillus*, *Cladosporium*, *Paecilomyces*, and *Diaporthe* were also found to be promising biocontrol agents against *Duponchelia fovealis* [86]. Endophytic fungal isolates obtained from *T. wilfordii* exhibited larvicidal activity against mosquito larvae. [87]. *Cladosporium uredinicola* has been reported to manage the population of *Spodoptera litura*. *Sarocladium strictum* also exhibits insecticidal properties against *Spodoptera littoralis* [88]. *Acremonium vitellinum* serves as a potential biocontrol agent against *Helicoverpa armigera* [89].

Species of *Trichoderma* can colonize a variety of crops, including cotton, soybeans, wheat, and corn. Although it demonstrates an impressive capacity to parasitize a wide range of plant infections, this fungus is most recognized for its ability to develop resistance in plants [90]. Furthermore, a number of strains have been documented to parasitize eggs and juveniles (second stage) of *Meloidogyne javanica* and the incredibly tough cysts of *Heterodera avenae* [91]. As a result, a variety of hosts are present for *Trichoderma* species, including plants and other plant pathogens that are parasitic or symbiotic, respectively. *Purpureocillium lilacinum* is a well-known biocontrol agent for insects and nematodes that parasitize plants. It has been reported as a promising nematicide to manage plant pathogenic nematodes [92]. It has also been found to manage the *Blatta orientalis* and *Shelfordella* populations under laboratory condition [93].

4.2. Antimicrobial Actions

Endophytic fungi have been discovered as a potent source of naturally occurring biomolecules that possess antimicrobial activities such as antioxidant, antibiotic, cytotoxic, antimalarial, antitumor, enzyme-inhibition, and anti-filarial activities [63]. These biomolecules are actually the secondary metabolites produced by endophytic fungi (Table 1). A number of metabolites isolated from fungal endophytes have shown antimicrobial properties. The leaf tissues of the medicinal plant *Callistemon subulatus* were used to isolate *Aspergillus* sp. ASCLA, which produces isoshamixanthone, and it showed antibacterial properties against pathogenic microorganisms [94]. Three novel α-pyrone derivatives were discovered from *Penicillium ochrochloronthe*, and these compounds have antibacterial action against some strains of pathogenic bacteria and fungi [95]. Ramos *et al.* [96] reported two endophytic fungi, namely *Papulaspora immersa* and *Apiospora montagnei,* from *Smallanthus sonchifolius* in Brazil; these endophytes showed antibacterial efficacy against a variety of test species in different extract forms. *Aspergillus fumigatus* was isolated from the leaves of *Albizia lucidior* [97] and *Ocimum basilicum* [98], and it may have antibacterial and antifungal properties against the majority of common resistant microorganisms. *Colletotrichum gloeosporioides* was also reported to have antibacterial activities against *Bacillus subtilis*, *Staphylococcus aureus*, *Pseudomonas aeruginosa,* and *Escherichia coli* and antimycotic activities against *Candida albicans* [99].

Alternaria alternata extract was obtained from *Picrorhiza kurroa*, possesses antioxidant and antibacterial action against *S. aureus* and *B. subtilis* [100]. Antibacterial and antifungal properties against *B. subtilis, Bacillus cereus, C. albicans, S. aureus, S. typhimurium, E. coli, P. aeruginosa,* and *K. pneumoniae,* were discovered in *Aspergillus flavus* [98]. *Aspergillus nidulans,* discovered in *O. basilicum,* also showed antimicrobial activities against several microorganisms [98]. *Aspergillus welwitschiae,* isolated from *Aloe ferox,* has potential antibacterial activity against disease-causing microorganisms [101]. Similarly, *Penicillium citrinum* isolated from *Azadirachta indica* also exhibits antimicrobial potential against human disease-causing bacteria and fungi [102]. The endophytic *Aspergillus tubingensis* has demonstrated potential antibacterial efficacy against gram-positive, gram-negative, and unicellular fungi. It may also prevent the production of biofilms [103]. Promising antimicrobial activities were observed from the endophytic *Aspergillus niger* against *S. aureus*, *E. coli*, *P. aeruginosa*, *Micrococcus luteus*, and *C. albicans* [104].

Stephania dielsiana exhibits the fungal endophyte *Penicillium* sp. that showed significant antimicrobial properties toward pathogenic bacteria [105]. The antimicrobial potential was also reported in the extracts of *Penicillium funiculosum* and *Penicillium pinophilum* [106,107]. Pathogenic microorganisms are susceptible to the antibacterial activity of *Nigrospora* spp. [108]. *Emericella nidulans*, which possesses potent antifungal activity against *A. niger*, *Microsporum audouinii,* and *Penicillium* sp. [109]. Antibacterial activities against *B. cereus* and *Staphylococcus epidermidis* were reported from *Diaporthe* sp. [110]. It was recently reported that nigranoic acid was extracted from an endophytic *Trichoderma sp*. and exhibited potent antiviral activity [111]. Pulchranin, an anticancer drug, was produced by the *Aspergillus*

Table 1. Secondary metabolites produced by endophytic fungi and their activities.

Fungal species	Host plant	Compounds produced	Activities	Target	References
Alternaria alternata AE1	*Azadirachta indica*	Phenanthrene, 7-isopropyl-1-methyl (Retene), Dichloronitromethane	Antibacterial	*Bacillus subtilis, Staphylococcus aureus, Escherichia coli, Listeria monocytogenes, Salmonella typhimurium*	[138]
Alternaria alternata	*Phyllanthus reticulatus*	Phenanthrene, 7-isopropyl-1-methyl (Retene), Dichloronitromethane	Antimicrobial	*E.coli, Staphylococcus aureus, Pseudomonas aeruginosa , Candida albicans*	[139]
Alternaria sp.	*Calophyllum inophyllum*	Coumarin	Antiviral	HIV	[140]
Aplosporella javeedii	*Orychophragmus violaceus*	Aplojaveediins A–F	Antimicrobial	*Candida albicans* ATCC 24433	[141]
Aspergillus sp.	*Bauhinia guianensis*	Alkaloids Fumigaclavine C and Pseurotin C	Antibacterial	*B. subtilis, E. coli, S. aureus, P. aeruginosa*	[142]
Aspergillus fumigatus	*Ceriops decandra*	Azaspirofuran B, Fumigaclavine C, Fraxetin	Antibacterial	*E. coli, S. aureus, P. aeruginosa, Micrococcus luteus*	[143]
Aspergillus flavus	*Lannea coromandelica*	Kojic acid, Octadecanoic acid, Diethyl phthalate 3-Phenyl propionic acid	Antimicrobial	*C. albicans, Malassezia pachydermatis*	[144]
Aspergillus clavatonanicus MJ31	*Mirabilis jalapa*	6-PP (6 Pentyl-2H Pyrone-2-one), 1, 2 butadiene, m-camphorene, 3-Thietanol, Thiopivalic acid, Phthalic acid Heneicosane, Pyrazole, and benzene derivatives	Antimicrobial	*E. coli, S. aureus, M. luteus, B. subtilis*	[145]
Aspergillus niger	*Opuntia ficus-indica*	Cristatumin B, Dihydroauroglaucin	Antibacterial	*S. aureus, Klebsiella pneumoniae E. faecalis, P. aeruginosa*	[146]
Aspergillus cejpii	*Nelumbo nucifera*	5-(1H-Indol-3-yl)-4,5-dihydro-[1,2,4] triazin-3-ylamine	Antibacterial	Methicillin-resistant *S. aureus*	[147]
Arthrinium sp. MFLUCC16-1053	*Zingiber cassumunar*	3-p-menthone, Bornyl acetate, γ-curcumene, Bicyclogermacrene, and β-isocomene	Antibacterial	*E. coli, S. aureus*	[148]
Botryosphaeria dothidea X-4	*Camptotheca acuminata*	9-methoxycamptothecin	Antibacterial	*B. subtilis, E. coli*	[149]
Curvularia papendorfii	*Vernonia amygdalina*	Polyhydroxy acid, Kheiric acid	Antibacterial	Methicillin resistant *S. aureus*	[147]
Curvularia lunata	*Paepalanthus chiquitensis*	Curvulinic acid	Antibacterial	*E. coli*	[150]
Curvularia protuberata	*Paspalidium flavidum*	Diphenyl sulfone, 7-Hydroxycoumarin Griseofulvin, β-Asarone	Antifungal	*A. alternata, F. oxysporum*	[151]
Curvularia sp. T12	*Rauwolfia macrophylla*	2′-deoxyribolactone, Hexylitaconic acid, Ergosterol	Antibacterial	*Pseudomonas agarici, E. coli, Staphylococcus warneri, M. luteus*	[152]
Cladosporium delicatulum	*Terminalia pallida, Rhynchosia beddomei, Pterocarpus santalinus*	Plumbagin (5-hydroxyl- 2-methylnaphthalene-1,4-dione)	Antimicrobial	*C. albicans, C. tropicalis, F. moniliforme*	[153]
Cladosporium cladosporioides	*Zygophyllum mandavillei*	3-phenylpropionic acid	Antifungal	*A. flavus, F. solani*	[154]
Colletotrichum sp.	*Artemisia annua*	Steroids	Antifungal	*Phytophthora capsici, Rhizoctonia cerealis, Gaeumannomyces graminis, Helminthosporium sativum*	[155]
Colletotrichum sp. BS4	*Buxus sinica*	Colletotrichone A, B, C and Chermesinone B	Antibacterial	*S. aureus, E. coli, B. subtilis, P. aeruginosa*	[156]
Colletotrichum sp.	*Umbelliferae*	Colletonoic acid	Antibacterial	*Bacillus megaterium*	[157]
Chaetomium globosum TW1-1	*Armadillidium vulgare*	Armochaetoglobins K–R	Antiviral	HIV	[158]
Diaporthe phaseolorum	*Laguncularia racemosa*	3-hydroxypropionic acid	Antibacterial	*S. aureus, S. typhi*	[159]

(*Continued*)

Fungal species	Host plant	Compounds produced	Activities	Target	References
Diaporthe sp.	*Pteroceltis tatarinowii*	Diaporone A	Antibacterial	*B. subtilis*	[160]
Emericella sp. (HK-ZJ)	*Aegiceras corniculatum*	Emerimidine A–B and Emeriphenolicins A–D	Antiviral	H1N1	[161]
Eupenicillium sp. LG41	*Xanthium sibiricum*	Eupenicinicols A and B, (2S)-butylitaconic acid, (2S)-hexylitaconic acid	Antibacterial	*Acinetobacter* sp., *B. subtilis*, *E. coli, S. aureus*	[162]
Emericella quadrilineata (RS-5)	Pteris pellucida	Benzyl benzoate, Benzaldehyde dimethyl acetal, and Benzoic acid	Antibacterial	*S. aureus, Aeromonas hydrophila*	[163]
Emericella sp.	*Panax notoginseng*	Quiannulatic acid	Antibacterial	Multidrug-resistant *Enterococcus faecium*	[164]
Epicoccum nigrum	*Entada abyssinica*	Quinizarin, indole-3-carboxylic acid, and Parahydroxybenzaldehyde	Antibacterial	*B. cereus, S. typhimurium*	[165]
Fusarium sp.	*Crescentia cujete*	-	Antibacterial	All human pathogenic bacteria except *S. aureus, S. typhi, Shigella* sp.	[166]
F. oxysporum KU527806	Dendrobium lindleyi	gibepyrone A, Pyrrolo[1,2-a] pyrazine-1, 4-dione, hexahydro-3-(2-methylpropyl), and indoleacetic acid	Antimicrobial	*C. albicans, C. tropicalis, Curvularia* sp.	[167]
Fusarium sambucinum TE-6L	*Nicotiana tabacum*	Amoenamide C, Sclerotiamide B	Antibacterial	*E. coli, M. luteus, P. aeruginosa*	[68]
Geotrichum candidum	*Phyllanthus reticulatus*	-	Antibacterial and antifungal	*E. coli, P. aeruginosa, S. aureus, Candida albicans*	[139]
Gliomastix murorum Ppf8	*Paris polyphylla*	Ergosta-5,7,22-trien-3-ol, 2,3-dihydro-5-hydroxy-α,α-dimethyl-2-benzofuranmethanol	Antibacterial	*E. coli, Pseudomonas lachrymans, Staphylococcus haemolyticus, B. subtilis*	[168]
Hypoxylon sp. 6269	*Artemisia annua*	Integracide E and Isointegracide E	Antiviral	HIV	[169]
Hyalodendriella sp. Ponipodef12	*Populus deltoides*	Palmariol B, 4-hydroxymellein, Alternariol 9-methyl ether	Antibacterial	*B. subtilis, P. lachrymans*	[170]
Lophodermium sp.	*Pinus strobus*	Methyl (2Z,4E)-6(acetyloxy)-5-formyl-7-oxoocta-2,4-dienoate, 5-(hydroxymethyl)-2-(20, 60, 60-trimethyltetrahydro-2H-pyran-2-yl)phenol, pyrenophorol	Antimicrobial	*Saccharomyces cerevisiae*	[171]
Lophodermium nitens DAOM 250027	*Pinus strobus*	(7R)-(-)-methoxysydonol and its derivatives, (7R,7′R)-(-)-pyrenophorin	Antimicrobial	*S. cerevisiae*	[172]
Microsphaeropsis sp.	*Salsola oppositifolia*	Microsphaerol, Seimatorone		*E. coli, Bacillus megaterium*	[173]
Muscodor albus	*Tropical tree* and *rainforest*	Peptide	Antimycotic	*Candida albicans*	[174,175]
MR1B and MRB.2	*Catharanthus roseus* and *Euphorbia hirta*	Citreoisocoumarin, paxilline, nigricinol, fatty acid, sceptrin, cladosporin	Antibacterial and antifungal	*C. albicans, E. coli, B. subtilis, S. typhi, A. fumigatus* and *S. aureus*	[176]
Nigrospora sp. YE3033	*Aconitum carmichaeli*	6-O-demethyl-4-dehydroxyaltersolanol A, 4-dehydroxyaltersolanol A, Altersolanol B, Cermesinone B	Antiviral	H1N1	[177]
Nigrospora sp.	*Crescentia cujete*	Griseofulvin, pyrone and spirobenzofuran	Antibacterial	All human pathogenic bacteria except *S. aureus, S. typhi, Shigella* sp.	[166]
Nigrospora sphaerica	*Indigofera suffruticosa*	Alkaloids	Antibacterial	*S. aureus*	[178]
Phomopsis cassiae	*Cassia spectabilis*	Terpenoids	Antimycotic	*Cladosporium sphaerospermum, Cladosporium cladosporioides*	[179]
Phoma species	*Saurauia scaberrinae*	Phomodione	Antibacterial	*S. aureus*	[180]
Pestalotiopsis maculans	*Indigofera suffruticosa*	Alkaloids	Antibacterial	*S. aureus*	[178]
Pestalotiopsis neglecta	*Cupressus torulosa*		antibacterial	*Escherichia coli, Salmonella typhimurium, Bacillus subtilis and Staphylococcus aureus*	[181]

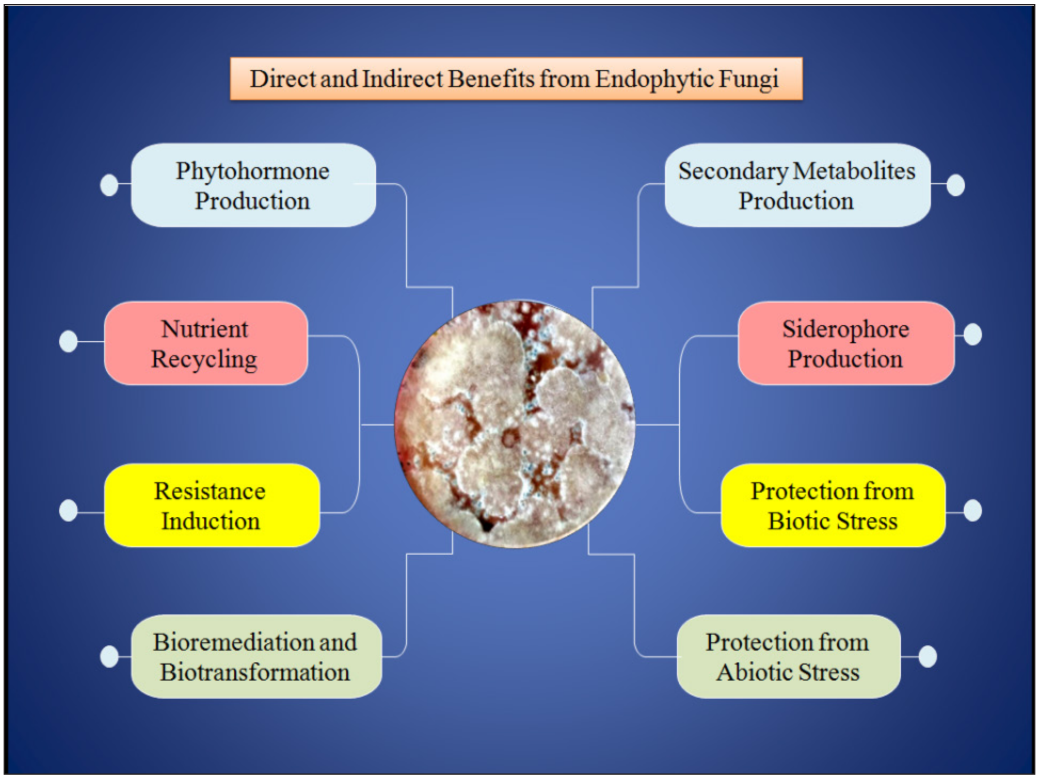

Figure 2. Benefits provided by endophytic fungi.

TRL1, was isolated from *Tabebuia rosea*. It was reported that this molecule effectively suppresses human tumor cells, including liver (Hep-G2) cell lines and breast (MCF-7) cell lines [112].

4.3. Production of Phytohormone and PGP

The interactions between the fungal endophytes and the host plants showed a neutral antagonism because the identification of the plant as a host necessitates the enactment of virulence factors for fungal colonization and the induction of host defenses by these processes [113]. This connection maintains equilibrium between fungi and host, since the fungus benefits the host plant by surviving on its resources and by providing resistance to both biotic and abiotic stresses [21]. The plant provides endophytes with a protected habitat, limited competition with other microbes, and the nutrients needed for fungal survival and growth [114]. Thus, through a variety of processes, fungi enhance plant fitness in return for this secure environment.

Recently, the use of endophytic fungi to stimulate plant growth has garnered attention due to the significant role these fungi play in increasing plant tolerance to both biotic and abiotic stressors and raising yield [115]. Through two primary pathways, that is, direct and indirect, these endophytes have considerable potential to cause PGP. Direct mechanisms include the synthesis of phytohormones and the uptake of nutrients. The production of antibiotics, siderophores, secondary metabolites, induced resistance, and defense against ecological stressors are included in the indirect mechanism [116]. Fungal endophytes can produce cytokinins, auxins, and gibberellins. Even though gibberellins are equally crucial to plant growth in many environmental situations as chemical signaling and messengers, the ability of endophytic fungi to produce phytohormones is understudied [117]. The primary auxin that fungi make is called indole-3-acetic acid (IAA). It is the primary controller of plant growth and is responsible for the growth of shoots and roots, including the commencement of the root formation process, vascular tissue differentiation, and tropism responses [118]. Gibberellins are necessary for a number of plant responses, including fruit production, senescence, flowering, stem elongation, sexual expression, and seed germination [119].

Purpureocillium lavendulum, *P. lilacinum*, and *Metarhizium marquandii* have been shown to produce IAA and solubilize phosphorus (P) from fluorapatite. After testing on plants of maize, beans, and soybeans, the colonization of these fungal endophytes was found to improve and enhance growth factors such as shoots and roots and nutrient availability such as sulfur (S) and nitrogen (N) [120]. In addition to increasing nitrogen fixation and phosphate solubilization, promoting the synthesis of siderophores, inhibiting ethylene production through the action of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and influencing enzyme synthesis, fungal endophytes can also have an impact on plant development by producing phytohormones [121–124].

Fungal endophytes such as those reported from *Teucrium polium* showed unpredictable ability for phosphate solubilization, which acts as a promising PGP [125]. Three fungal endophytes from *Oryza coarctata,* namely *Talaromyces adpressus*, *Talaromyces argentinensis,* and *A. welwitschiae,* have been reported in Bangladesh that exhibit PGP capability. IAA, ACC deaminase, and siderophore production were recorded from *T. adpressus* and *T. argentinensis*, along with phosphate, and zinc solubilization as well as N fixation under *in vitro* conditions having high salinity. Furthermore, *A. welwitschiae* showed improved metabolite and chlorophyll content [126]. *Trichoderma longibrachiatum* T6 has been documented to boost the plants' tolerance to NaCl stress and encourage the growth of *Triticum aestivum* [124].

Macrophomina phaseolina isolate MP-1, *Macrophomina phaseolina* isolate MP-3, *Diaporthe phaseolorum, Daldinia eschscholtzii,* *Trichoderma koningii,* and *Trichoderma erinaceum* exhibited high phosphate-solubilizing ability and extracellular enzyme production under greenhouse conditions [127]. A study recorded that the biomass yield, nutritional value, and mineral status of *Trifolium subterraneum* feed were impacted by fungal endophytes; however, the impacts differed depending on the type of fungus. In the field, *Chaetosphaeronema* sp. boosted fodder productivity by about 80%. In the greenhouse experiment, *Fusarium lateritium* and *Pleosporales* decreased the concentration of aluminum, while *Epicoccum nigrum* decreased the lead content of the feed. *Stemphylium globuliferum* was the primary source of a rise in vital nutrients, such as zinc [128]. The application of *Xylariaceae* sp., *Fusarium avenaceum*, and *Sarocladium terricola* has been reported to enhance the germination of *Lolium multiflorum* seeds by over 70%. The use of fungus filtrates had a favorable effect on shoot and root length, plant dry weight, and root count [129].

Trichoderma species, *Aspergillus flavus*, *Penicillium digitatum*, *Podospora bulbillosa*, *Actinomucor elegans*, *Gliocladium virens*, Arbuscular mycorrhizal fungi, etc. have demonstrated their environmentally friendly ability to enhance crop production by promoting the growth of crop plants' shoots and roots, seed germination, chlorophyll production for photosynthesis, and an abundance of crop yields [130]. Numerous studies have documented the benefits of fungal endophytes such as *Gliocladium*, *Penicillium*, *Phoma*, *Phytophthora*, *Rhizoctonia*, *Talaromyces*, *Trichoderma* in plant growth promotion. These genera have been shown to enhance the growth of orange, tomato, apple, pear, cucumber, carrot, and other plants, as well as to further support the innate immunity and the production of various necessary secondary metabolites by the plants [131–136]. Plant growth-promoting fungi (PGPF) enhance plant growth through phytohormone production, nutrient acquisition, induced systemic resistance, and suppression of phytopathogens [137].

5. FUTURE PROSPECT AND CHALLENGES

Endophyte-plant interactions can be used as an effective and reasonable integrated disease management technique and can be essential in promoting low-cost sustainable agriculture applications due to their substantial significance as a possible biocontrol agent. More knowledge of the metabolite structures created by endophytic fungi and plant support protection mechanisms may help with integrated management strategies. However, because of regulatory requirements, challenges with mass production, inoculant efficacy, and farmer and consumer resistance, their agricultural application is still restricted. The use of fungal endophytes can be employed by small marginal farmers, but it cannot be utilized for large-scale production. Particularly, in extreme habitats, the conflict between inoculated fungal endophytes and native microbiomes could result in adverse effects or lower efficacy. Several endophytes have been reported to enhance plant growth and productivity, but they also affect invertebrates and vertebrate species.

Researchers might be able to investigate and make extensive use of endophyte resources in the future. One option is to look for unique endophytes in plants that thrive under harsh conditions. Another is to look for appropriate and productive ways to extract more potent bioactive substances from a variety of endophytes. Ultimately, it will be promising for large-scale manufacturing to increase the yield and content of active compounds in recognized strains based on metabolic regulation and genetic engineering. Endophytes have only recently been investigated, despite the fact that fungi have been shown to be economically significant suppliers of enzymes for restoration of the environment and other applications. Endophytes are therefore a fascinating niche that is just waiting to be exploited.

6. CONCLUSION

Climate change, population expansion, and other stressors are posing growing concerns about global food security, highlighting the urgent need to increase agricultural yields in vulnerable areas. The study of fungal endophytes provides insight on the diversity, biogeography, and various biological activities of fungal endophytes. Endophytic fungi perform remarkable functions in the ecosystem, including abiotic and biotic stress tolerance, eco-adaptation, boosting growth and development, and maintaining the health of their host. It is an affordable and environmentally responsible alternative to increase food production and advance sustainable agricultural methods. Because they produce biologically active chemicals against both biotic and abiotic stresses by activating useful products for agricultural output under rapid climate change scenarios, fungal endophytes can be regarded as a crucial tool in regulating both types of stresses. Endophytic fungi are a valuable tool for research and businesses, as evidenced by their usage as an alternative with significant potential in the sectors of biocontrol, bioremediation, biotransformation, and biofertilization.

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This study does not involve experiments on animals or human subjects.

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13. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declare that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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