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Review article

A review on fungal endophytes of the family Fabaceae, their metabolic diversity and biological applications

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ABSTRACT

Fabaceae is considered the third largest family of the plant kingdom, comprising of a large number of plants, belonging to 650 genera and 20,000 species of plants. Out of the various plant species that are reported in the family Fabaceae, many of the species have been reported to exhibit diverse pharmacological activities and are of economic importance to agriculturists and scientists across the globe. Studies over the last few decades have unraveled a lot of concrete information about different plants, ranging from the mutualistic interdependence of plants and microbes for their survival to the innumerable benefits of plants in the sectors of agriculture, food industry, medicine, and healthcare. The survival and effective maintenance of plant homeostasis is largely regulated by the diverse microbial population that co-exists in symbiotic relationships with plants. This endophytic microbial population can be either categorized as endophytic bacteria or endophytic fungi. The studies over the past decades have highlighted the crucial role of both endophytic bacteria and fungi in the growth and development of plants. This review explores the ameliorative roles of endophytic fungi in alleviating biotic and abiotic stresses in plants. Additionally, it highlights the vast diversity of secondary metabolites produced by these fungi and their potential applications. Secondary metabolites exhibit a wide range of biologically significant activities, including anticancer, antimicrobial, antimalarial, and nematicidal properties, which hold substantial importance in therapeutic and agricultural applications. Furthermore, the role of various endophytic fungi of the Fabaceae family has been shown in phytoremediation.

1. Introduction

Endophytic fungi represent a class of highly diverse fungi belonging to ascomycetous fungi that are characterized by their ability to reside inside the plant tissues without causing any noticeable effect on the plants. Fungal endophytes usually transcend into an inactive quiescent state once they make their entry into the host plant. Dormant latent fungal endophytes remain inactive until favorable environmental conditions arise or the host plants reach a specific stage in their development. At that point, these endophytes activate, initiate their metabolic processes, and fully engage in their role within the host [1]. The earth, home to nearly 300,000 species of higher plants, operates within intricate symbiotic networks where microbial endophytes play a critical role in plant survival and ecosystem functionality. Endophytes, including bacteria, fungi, and protists, colonize plant tissues without causing disease and contribute significantly to plant growth, stress tolerance, and adaptation. Studies show that endophytes can enhance plant growth by

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15–30 % under nutrient-poor conditions through improved nutrient uptake and modulation of hormone pathways, including auxin and cytokinin production [2]. Endophytes also produce secondary metabolites like flavonoids, alkaloids, and terpenoids, which serve as plant defense compounds and have medicinal importance [3]. For instance, 60 % of secondary metabolites in plants such as *Artemisia annua* are influenced by endophytic interactions, underscoring their role in phytochemical diversity [4]. Mycorrhizal and fungal endophytes are pivotal in facilitating phosphorus acquisition, increasing uptake efficiency by up to 80 % in some grassland species, thereby reducing dependency on chemical fertilizers [2].

Different plant species have been found to host a large number of fungal endophytes in various parts including their stem, petioles, leaves (foliar), fruits, buds, and sometimes even in their inflorescences [5]. Fungal endophytes exhibit maximum density in the foliar leaves of plants due to the leaves' high photosynthetic efficiency, which provides an abundant source of nutrition through photosynthates. Studies have shown that mature leaves harbor a greater colonization frequency of endophytes, with significant diversity observed in species such as *Aspergillus* and *Cladosporium*, which produce various extracellular enzymes beneficial for both the fungi and the host plant [6,7]. Fungal endophytes play a crucial role in the plant life cycle owing to their various functions (Fig. 1) which include:

(A) Growth and development of plants

Fungal endophytes significantly enhance plant growth and resilience through multiple mechanisms, including nutrient uptake optimization, stress mitigation, and phytohormone production. These fungi solubilize insoluble phosphates, improving phosphate availability and enhancing nitrogen fixation, which collectively increases crop yields by up to 30 % under nutrient-limited conditions [8]. Additionally, endophytes secrete phytohormones like auxins, gibberellins, and cytokinins, which promote root elongation, seedling growth, and overall biomass development. For instance, auxin production by fungal endophytes increases root surface area by approximately 25 %, enhancing nutrient interception and uptake efficiency [9]. Fungal endophytes also improve plant health through secondary metabolite production. They produce siderophores that chelate iron (Fe^{3+}) from the rhizosphere, facilitating iron uptake in plants while simultaneously reducing its availability to phytopathogens, thus enhancing disease resistance [10]. Furthermore, their role extends to mitigating abiotic stresses, such as drought and salinity, by enhancing water use efficiency and modulating osmolyte production. Recent research highlights the ecological and environmental benefits of leveraging fungal endophytes in sustainable agriculture. By integrating these microbes, reliance on chemical fertilizers can be reduced by up to 40 %, offering an eco-friendly approach to boosting agricultural productivity. Synthetic biology approaches are beginning to harness these endophytes to engineer plants with enhanced nutrient uptake and stress resilience, offering promising solutions for global food security in the face of climate change [11].

(B) Providing resistance to plants against abiotic stress

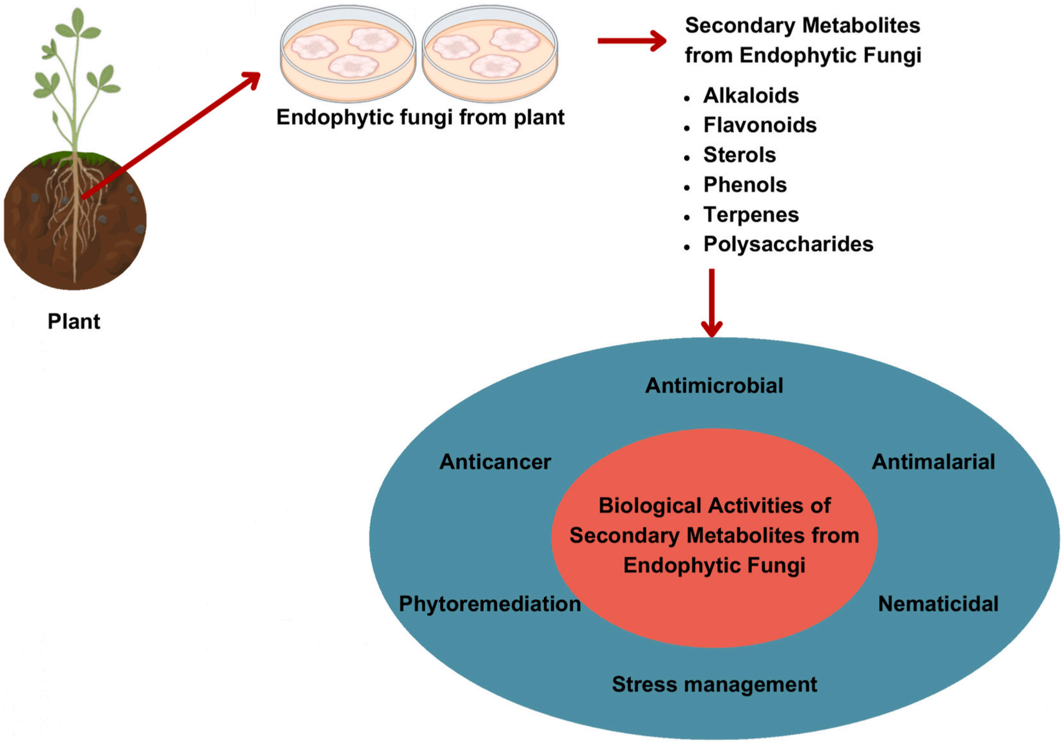

Fig. 1. Schematic representation of endophytic fungi isolation, their secondary metabolites and biological activities.

Fungal endophytes provide robust support for plants under abiotic stress by leveraging various biochemical and molecular mechanisms. They maintain ionic balance and optimize sodium ion/potassium ion (Na^+/K^+) ratios by upregulating key ion transporters, ensuring osmotic stability during saline conditions. For instance, *Acremonium alternatum* inoculation in *Brassica napus* enhanced ion sequestration via V-ATPase activity, reducing chloride content and mitigating salinity-induced damage [12]. Endophytes also bolster oxidative equilibrium by enhancing the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase, and peroxidases. Inoculation with *Aspergillus terreus* increased SOD activity by up to 50 %, reducing malondialdehyde (MDA) levels and electrolyte leakage in plants exposed to 150 mM NaCl stress [13]. Additionally, they promote osmolyte accumulation, including proline and glycine betaine, which stabilize proteins and membranes under drought and salinity stress. At the molecular level, endophytes trigger the expression of stress-related genes and transcription factors such as DREB, WRKY, and NAC, which modulate adaptive pathways to abiotic stresses like drought and heat. Furthermore, they produce phytohormones such as abscisic acid (ABA), enhancing drought resilience, and secrete organic acids that improve heavy metal chelation and reduce toxicity in contaminated soils [14]. Management of abiotic stress via endophytes presents a sustainable approach to alleviating the effects of climate change. Stress-adapted endophytes, particularly drought-tolerant species such as *Aspergillus fumigatus*, *A. terreus*, and *Talaromyces variabilis*, improve tomato resilience during drought conditions. They improve key physiological traits, including pollen viability, trichome and stomatal density, and overall yield in stressed and non-stressed environments. These fungi enhance fruit quality by elevating total soluble solids and titratable acidity, simultaneously decreasing pH levels. *A. fumigatus* significantly promoted growth, while *T. variabilis* enhanced fruit characteristics. Increased levels of GA_3 were associated with benefits such as enhanced chlorophyll and carotenoid content, improved chlorophyll fluorescence, and the development of trichomes [15]. A unique metallophilic strain of *Aspergillus*, closely related to *Aspergillus luchuensis*, demonstrated exceptional tolerance to increased doses of Cu, Zn and Pb. This strain, named *A. luchuensis* C7, was further examined for its dual role in heavy metal cleanup and plant growth promotion under greenhouse conditions. Inoculation with strain *A. luchuensis* C7 considerably improved the development of *Prosopis laevigata* compared to other treatments, indicating its potential as a growth-promoting agent. Additionally, *A. luchuensis* C7 promoted the translocation of metals, particularly enhancing copper transport from roots to leaves. Demonstrating endophytic behavior, high metal tolerance and plant growth-promoting activity, *A. luchuensis* C7 proposes a potential, sustainable bioremediation technique for copper-contaminated soils [16].

(C) Providing resistance to plants against biotic stress

Fungal endophytes significantly enhance biotic stress tolerance in plants by employing a suite of biochemical and molecular mechanisms. These microorganisms promote the production of plant antimicrobial compounds and secondary metabolites, many of which exhibit broad-spectrum activity against pathogens. For instance, endophyte-derived bioactive compounds have demonstrated antimicrobial efficacy against fungal and bacterial phytopathogens, with some metabolites showing over 80 % pathogen inhibition [17]. Furthermore, they stimulate the expression of defense-related genes such as WRKY and MYB families, which regulate systemic acquired resistance and plant immune responses [18]. Fungal endophytes also induce systemic tolerance by triggering pathways like induced systemic resistance (ISR), enhancing the plant's ability to withstand pathogen attacks. For example, colonization by *Trichoderma atroviride* increased plant biomass and reduced pathogen impact by activating ISR pathways, as shown in controlled trials with cucurbits and tomatoes [13]. Additionally, endophytes facilitate the synthesis of volatile organic compounds (VOCs) such as terpenes and benzenoids, which act as signaling molecules to deter herbivores and attract beneficial organisms. Enhanced activity of antioxidant enzymes like superoxide dismutase (SOD) and catalase further mitigates reactive oxygen species (ROS), bolstering plant resilience during biotic stress events. Biological control is influenced by various factors, including host specificity, soil structure, the type of inoculum used, and environmental conditions. Biological control agents that can effectively colonize plant tissues tend to be more compatible and efficient when applied to plants, making them superior in terms of biological control [19]. The endophytic fungi *Aspergillus oryzae* and *Aspergillus tubingensis*, isolated from the seeds of *Vigna unguiculata*, play a protective role in tomato plants against *Fusarium* wilt disease by enhancing immune responses. The primary strategy for mitigating this biotic stress involves improving the levels of photosynthetic pigments, sugars, proteins, and phenols, as well as enhancing the activity of antioxidant enzymes [20]. In another study, it was observed that the activity of photosystem II increased in endophyte-inoculated host plants compared to non-inoculated host plants under stress conditions. Additionally, leaf nitrogen and carbohydrate content also increased. The potent endophyte identified was *Penicillium* sp., found in *Prosopis chilensis*, a vulnerable and threatened arid-adapted tree [21]. Endophytic entomopathogenic fungi (EEPF) have the potential to serve as effective tools for biological control. They enhance plant growth, nutrition, and morpho-physiology, as well as improve tolerance to factors like salt and iron. EEPF influences insect behavior and performance through mechanisms such as antixenosis, antibiosis, and increased plant tolerance [22]. By colonizing plants, EEPF slows down herbivore development, reduce food consumption, and decreases oviposition and larval survival. Additionally, EEPF alters the plant's physio-chemical properties, including volatile emission profiles and the production of secondary metabolites, to regulate defenses against insect pests [23]. Possible mechanisms behind tolerance to biotic stress include hyphal coiling, induction of resistance, and production of lytic enzymes, which help protect older plants from root rot. Biocontrol through endophytes can occur either by directly inhibiting pathogens or indirectly by enhancing the plant's systemic resistance [24]. Other contributing mechanisms involve competition for ecological niches and resources, the production of enzymes that degrade cell walls, the activation of induced systemic resistance (ISR), and the suppression of pathogen quorum sensing [25]. In addition, a variety of antibiotic compounds and lytic enzymes produced by endophytes help mitigate disease severity in numerous plants. For example, fungal genera like *Fusarium*, *Trichoderma*, and *Botryosphaeria* secrete enzymes such as cellulose, 1,3-glucanases, amylase, and glutaminase, which contribute to controlling phytopathogens by disrupting their cell walls [26].

2. Diversity of endophytic fungi in family Fabaceae

The Fabaceae family, often referred to as the bean, legume, or pea family, has evolved over time in a mutualistic relationship with several endophytic fungi. These fungi have become closely associated with various members of the Fabaceae family, forming unique partnerships that are passed down through vertical transmission from one generation to the next [27]. A large number of endophytic fungi have been found to be closely linked to plants within this family. For example, *Albizia* species have been found to harbour 20 genera of endophytic fungi, while species of *Bauhinia*, *Senna*, *Astragalus*, and *Glycyrrhiza* host 16, 14, 12, and 9 genera of fungi, respectively [28]. In comparison, plants belonging to *Cercis*, *Oxytropis*, or *Medicago* contain 6 genera of endophytic fungi, while *Styphnolobium*, *Trifolium*, and *Leucaena leucocephala* are home to 4, 2, and 1 genera of fungi, respectively [29]. A study by DeMers & May [30] suggests that many endophyte taxa have the capacity to disperse over large distances and across heterogeneous biotic and abiotic environments. The interplay of biotic and abiotic factors helps maintain the high diversity of endophyte communities. A study by Herrera et al. [31] demonstrated that *Ulex europaeus* L. (Fabaceae) plantlets host four fungal endophytes belonging to Sordariomycetes and twelve bacterial endophytes belonging to Proteobacteria and Actinobacteria in their roots. Some of these, such as *Fusarium acuminatum*, exhibited biocontrol capabilities and plant growth-promoting traits, which could contribute to the rapid growth rates of the shrub during its juvenile stages. Endophytic fungi present in the leaves of *Copaifera oblongifolia* affect seed germination and seedling development in the host plant. The species *Neofusicoccum parvum*, *Curvularia intermedia*, *Phomopsis* sp. and *Pseudofusicoccum stromaticum* negatively impacted seed germination, with *N. parvum* showing the most pronounced negative effects. *Cochliobolus intermedius* adversely affected seedling development. Therefore, the combined use of *C. intermedius* and *N. parvum* or products derived from the metabolism of these microorganisms, for controlling invasive plants warrants further investigation in future studies [32]. In a study involving 11 endophytic fungi isolated from four species of Fabaceae family (*Arachis hypogaea* L., *Cajanus cajan* L., *Vigna unguiculate* L., and *Vigna radiatus* L.), endophyte identified as *Trichoderma hamatum* demonstrated significant antibacterial activity against test pathogen *Agrobacterium tumefaciens* [33]. An endophytic fungus, *Beauveria bassiana*, was isolated from the plant *Phaseolus vulgaris* L., and it was observed that its colonization provides protection to the host from the pest *Tetranychus urticae*. Colonization of this endophytic fungus adversely affected mite growth, adult lifespan, fecundity, reproductive rate, and the intrinsic rate of increase [34]. Two plants from the Fabaceae family, *Copaifera langsdorffii* and *Copaifera pubiflora*, are well known for their ethnomedicinal properties. These plants are colonized by 64 taxa and 22 genera of endophytic fungi. Among them, fungal extracts of *Diaporthe* and *Alternaria* displayed antibacterial activities against *Candida albicans* ATCC 60193, *Candida krusei* ATCC 6258, *Cladosporium sphaerospermum* CCT 1740, *Escherichia coli* ATCC 11775, *Pseudomonas aeruginosa* ATCC 10145, and *Staphylococcus aureus* ATCC 12600 [35]. A total of 27 different taxa of endophytic fungi were isolated from *Phaseolus vulgaris* using tissue fragmentation. These fungi were identified through morphological analysis and sequencing of the internal transcribed spacer (ITS) regions and the large subunit (LSU) of rDNA. The genus *Colletotrichum* was the most prevalent. To quickly differentiate *Colletotrichum lindemuthianum* from other *Colletotrichum* species, the IRAP (inter-retrotransposon amplified polymorphism) and REMAP (retrotransposon-microsatellite amplified polymorphism) markers were employed [36]. These studies provide baseline data on the fungal associations with host plants and their positive impacts on these plants. In the future, managing different endophytes could benefit agricultural systems and animal husbandry.

3. Secondary metabolites of endophytic fungi isolated from the Fabaceae family

Endophytes are a powerful source of bioactive compounds that resemble plant-derived metabolites. The interaction between the host plant and endophyte plays a crucial role in influencing fungal colonization and the extraction of bioactive compounds produced by the endophyte [37]. Endophytic fungi obtained from different plants of the family Fabaceae are a rich source of the diverse array of secondary metabolites, which found usage in a number of commercial as well as healthcare applications ranging from their role as antitumorigenic agents to the antibacterial, antimalarial, and nematocidal activity [38]. These secondary metabolites also play a pivotal role in both biotic as well as abiotic stress tolerance in plants, overcoming plant infections by instigating plant defense systems and serving as biocontrol agents, thus contributing a crucial part in phytoremediation [39].

Different classes of secondary metabolites present in endophytic fungi obtained from different beans can be classified into various categories including terpenoids (sesquiterpenes, diterpenoids, and triterpenoid), alkaloids, phenolic compounds, flavonoids, aliphatic compounds, polyketides and peptides [40,41]. The UHPLC-QTOF fingerprinting of the ethyl acetate extract of the endophytic fungus *Aspergillus fumigatus* isolated from *Albizia lucidior* leaves identified forty-two metabolites, among which three major metabolites-ergosterol, helvolic acid, and monomethyl sulochrin-4-sulfate were found to exhibit antibacterial activity against *Staphylococcus aureus* [42]. A total of eighteen fungal endophytes were isolated from the leaves of eight ethnomedicinal plants of Nigeria. The fungal extracts from these endophytes demonstrated free radical scavenging activity, which was attributed to the presence of various bioactive compounds. These compounds include pyrogallol, phenol (2,6-dimethoxy-), phytol, dl-alpha-tocopherol, alpha-tocospiro, oleamide, methyl stearate, oleic acid, palmitic acid, campesterol, stigmasterol, β-sitosterol, urs-12-en-24-oic acid (3-oxo-, methyl ester), lup-20(29)-en-3-one and lupeol. These bioactive compounds contribute to the observed antioxidant potential [28]. The extract of *Curvularia* sp., an endophyte isolated from the leaves of the medicinal plant *Piliostigma thonningii*, was found to contain alkaloids, flavonoids, phenolics, tannins, and saponins. Due to the presence of these bioactive compounds, the fungal extract exhibited antibacterial activity against *Escherichia coli* and *Pseudomonas aeruginosa*, as well as antioxidant activity [43,44]. A study by Kononenko & Burkin [45] discussed the formation of metabolic equilibrium in plants with the involvement of microscopic fungi, using five species of the genus *Trifolium* selected from different stages of vegetation. Alternariol, cyclopiazonic acid, and emodin were consistently present in the aerial parts of the plants. The levels of contamination varied significantly, particularly in *Trifolium pratense*

L. and *Trifolium repens* L. A total of 82 endophytic fungi were isolated from the stems and barks of *Caesalpinia echinata* Lam. (Fabaceae). The organic extracts of these endophytes exhibited antibacterial and antitumor activities. Among them, fungal extracts of *Fusarium* sp. demonstrated trypanocidal effects against *Trypanosoma cruzi*, attributed to the presence of the bioactive compound beauvericin, a depsipeptide [46]. Three endophytic fungi isolated from *Medicago sativa* were molecularly identified as belonging to the same species, *Aspergillus terreus*. LC-MS-based metabolomic analysis of the fungal extracts revealed the presence of phenolics, coumarins, and polyketides, which exhibited antioxidant properties and inhibitory activity against the prooxidant enzyme xanthine oxidase [47]. *Sophora alopecuroides* L. is a well-known medicinal plant recognized for its antitumor properties. Endophytic fungi inhabiting the plant predominantly include genera such as *Alternaria*, *Cladosporium*, *Filobasidium*, and various members of Ascomycota. These endophytes produce a range of bioactive metabolites, with quinolizidine alkaloids, oxymatrine, and oxysophocarpine being the major components [48]. *Cochliobolus* sp., an endophytic fungus isolated from the plant *Piptadenia adiantoides* J.F. Macbr., produces cochlioquinone A and isocochlioquinone A as its major metabolites. Both compounds have been identified as having potent leishmanicidal activity [49]. Three endophytic fungi (*Fusarium avenaceum*, *Sarocladium terricola*, and *Xylariaceae* sp.) were isolated from the leaves of *Biserrula pelecinus* and *Ornithopus compressus*. These fungi produce phytohormone-like substances, such as gibberellin A2 and zeatin, as well as the antioxidant acetyl eugenol, which demonstrate plant-growth-promoting activity in *Lolium multiflorum* [8]. Endophytic fungi isolated from *Bauhinia guianensis* produce several bioactive metabolites, including ergosterol, ergosterol peroxide, mevalonolactone, cytochalasin B, and cytochalasin H. Among these metabolites, cytochalasin B and its diacetate derivative were found to be more lethal to *Artemia salina* [50]. Some compounds of biological importance produced by endophytic fungi associated with plants of the Fabaceae family exhibit diverse and significant biological functions, some are shown in Fig. 2. The secondary metabolites present in endophytic fungi inhabiting host plants from the family Fabaceae have been summarized in Table 1.

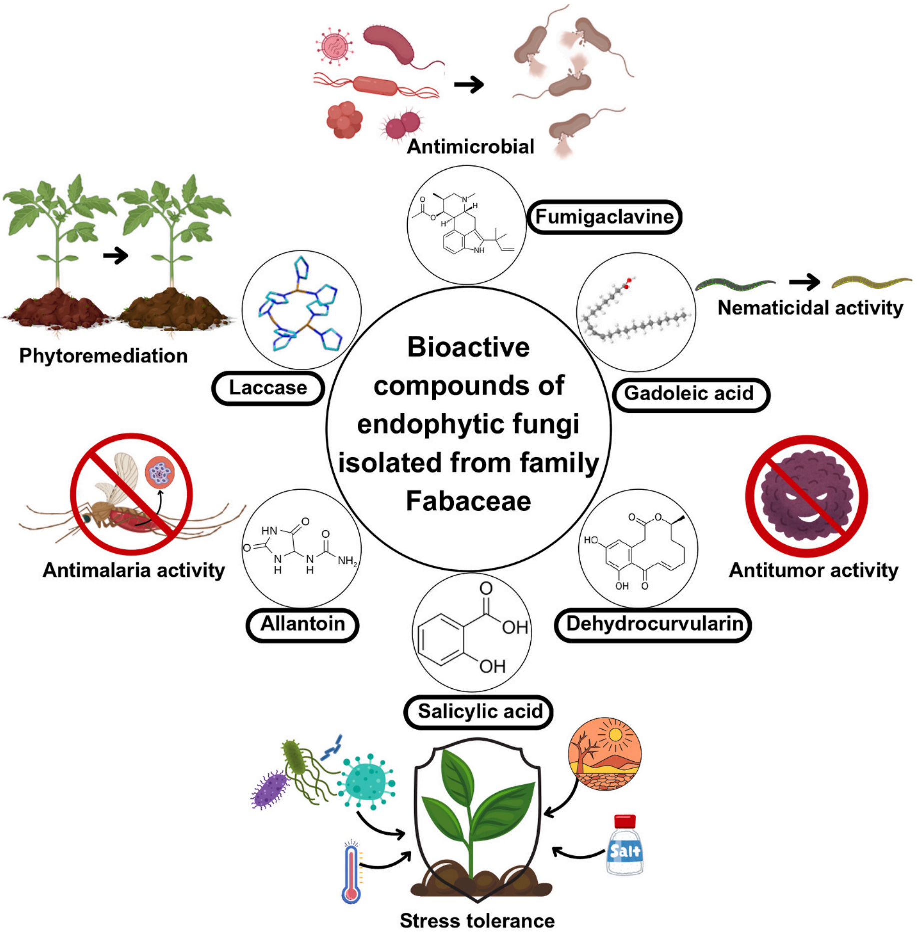

Fig. 2. Bioactive compounds produced by endophytic fungi isolated from Fabaceae family plants and their associated biological activities. Laccase aids in phytoremediation, while fumigaclavine exhibits antimicrobial activity. Gadoleic acid demonstrates nematicidal activity, and dehydrocurvularin shows antitumor potential. Allantoin contributes to antimalarial activity, whereas salicylic acid enhances plant stress tolerance against pathogens, extreme temperatures, and salt stress. These compounds highlight the multifaceted applications of fungal metabolites in medicine, agriculture, and environmental remediation.

4. Biological activity of endophytic fungi

4.1. Anticancer activity of endophytic fungi

The anticancer activity of secondary metabolites extracted from endophytic fungi colonizing leguminous plants has been elucidated in a number of studies. For instance, *Fusarium* species secretes three different bioactive compounds, out of which the first compound has antitumor activity against MOLT-4, A549, HL -60, and BEL-7402 cells. The second compound acts as a potent anticancer drug in combination with doxorubicin and the third one is capable of inhibiting actin polymerization [58]. In another study, it has been reported that *Alternaria* sp. residing in the host plant *A. membranaceus*, is capable of synthesizing five different compounds, all of which possess potent antitumor activity against NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231; all of which are human cancer cell lines [51]. Liu et al. [54] reported different bioactive compounds from *Aspergillus* sp. of *A. membranaceus*, which showed potent antitumor activity against prostate cancer, liver cancer, cervical cancer, breast cancer, and colon cancer. In another study, Kuriakose et al. [57], showed anticancer activity of bioactive compounds from *Penicillium sclerotiorum* inhabiting *Cassia tora*, against A549, A431, U251, and HeLa by activation of the mitochondrial apoptotic pathway. Other studies showing the anticancer activity of secondary metabolites from different endophytic fungi inhabiting the Fabaceae family have been summarized in Table 2.

4.2. Antimicrobial activity of endophytic fungi

A number of studies have shown the potent antimicrobial activity of bioactive compounds obtained from endophytic fungi inhabiting plants of the Fabaceae family. The endophytic fungi have been found to display potent antibacterial activity against various bacterial strains such as *Staphylococcus aureus*, methicillin-resistant *S. aureus*, *Listeria monocytogenes*, *Salmonella enterica* and *Escherichia coli* and other pathogenic bacteria. Studies showing the antimicrobial activity of secondary metabolites from different endophytic fungi inhabiting the Fabaceae family have been summarized in Table 2.

4.3. Antimalarial activity of endophytic fungi

Malaria is one of the major infectious diseases concerning the healthcare workers and scientific community throughout the country owing to the severe morbidity and mortality in subtropical and tropical regions. The situation has really intensified in the past few years because of increased resistance of the malarial parasite to the prevalent antimalarial drugs in the market [73]. This scenario is further complicated by the growing insecticide resistance of mosquito vectors to currently available insecticides. Considering the currently prevalent anarchical scenario, the hunt is on for new antimalarial drugs with improved efficacy and minimum toxicity. In this context, research over the past few years has shown the immense potential of secondary metabolites from endophytic fungi to serve as potent antimalarial drugs. In a recent review by Ibrahim et al. [74], the reviewers have elaborately discussed about the huge potential of endophytic fungi to act as antiplasmodial agents. However, till date, only one study has shown the antimalarial efficacy of secondary metabolites from *Fusarium* sp. inhabiting the *A. membranaceus* plant belonging to the Fabaceae family [58].

Table 1
Various secondary metabolites present in endophytic fungi inhabiting host plants from the family Fabaceae.

S. No.	Endophytic fungi	Plant host	Group of metabolites	Reference
1.	*Alternaria* sp.	*Astragalus lentiginosus*	Quinones and alkaloids	[51]
2.	*Aspergillus* sp.	*A. lentiginosus*	Peptides; Sesquiterpenes (Diterpenes)	[52–54]
3.	*Fusarium* sp.	*Cercis alata*	Terpenoids (diterpenes); VOCS	[55]
4.	*Fusarium solani*	*Cassia tora*	Terpenoids (diterpenes); VOCS	[55,56]
5.	*Penicillium sclerotiorum*	*C. alata*	VOCs and steroids	[57]
6.	*Fusarium* sp.	*Astragalus membranaceus*	Terpenoids (diterpenes); VOCS	[58]
7.	*Aspergillus* sp.	*A. membranaceus*	Peptides; Sesquiterpenes (Diterpenes)	[54]
8.	*Alternaria alternata*	*Cercis chinensis*	Quinones and alkaloids	[59]
9.	*Aspergillus* sp.	*Medicago sativa* L.	Peptides; Sesquiterpenes (Diterpenes)	[60]
10.	*Aspergillus ochraceus* MSEF6	*M. sativa* L.	Phenolics, quinones, benzofurans, and isochromanones	[61]
11.	*Aspergillus terreus*	*Sophora flavescens*	Peptides; Sesquiterpenes (Diterpenes)	[62]
12.	*Penicillium vulpinum*	*S. flavescent*	VOCs; Steroids	[63,64]
13.	*Xylaria* sp.	*S. flavescens* and *Sophora tonkinensis*	Pheromones; Sesquiterpenes (Diterpenes)	[63,64]
14.	*Penicillium* sp.	*S. flavescens*	VOCs; Steroids	[65–67]
15.	*Aspergillus* sp.	*Trifolium repens* and *Bauhinia guianensis*	Peptides; Sesquiterpenes (Diterpenes)	[58,68]
16.	*A. alternata*	*C. chinensis*	Peptides; Sesquiterpenes (Diterpenes)	[59]
17.	*Epicoccum nigrum*	*Entada abyssinica* Steud. ex A.Rich.	Depsipeptide, indole carboxylic acids, anthraquinone	[69]
18.	*Phomopsis* sp.	*Senna spectabilis*	3,4-Fused isocoumarins	[70]
19.	*Aspergillus niger* and *Fusarium oxysporum*	*Crotalaria pallida*	Tannin, flavonoids, terpenoids, phenol and saponins	[71]
20.	*Aspergillus eucalypticola* SBU-11AE	*Glycyrrhiza glabra* L.	Isoflavone	[72]

Table 2
Biological activities of secondary metabolites present in endophytic fungi inhabiting various host plants belonging to the family Fabaceae.

S. No.	Plant host	Endophytic fungi	Compound(s) name	Activity	Result	Reference
1.	*Astragalus membranaceus*	*Alternaria* sp.	(−)-(10E,15S)-4,6-Dichloro-10(11)-dehydrocurvularin	Anticancer	NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231	[51]
2.	*A. membranaceus*	*Alternaria* sp.	(−)-(10E,15S)-6-Chloro-10(11)-dehydrocurvularin	Anticancer	NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231	[51]
3.	*A. membranaceus*	*Alternaria* sp.	(−)-(10E,15S)-10(11)-Dehydrocurvularin	Anticancer	NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231	[51]
4.	*A. membranaceus*	*Alternaria* sp.	Alterperylenepoxide A	Anticancer	NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231	[51]
5.	*A. membranaceus*	*Alternaria* sp.	Thioperylenol	Anticancer	NCI-H460, SF-268, MCF-7, PC-3M, and MDAMB-231	[51]
6.	*A. membranaceus*	*Aspergillus* sp.	(−)-6-Methoxymellein	Anticancer	Effective against breast cancer cell lines	[52–54].
7.	*Cercis alata*	*Fusarium* sp.	Ergosterol	Anticancer	Effective against vero tumor cells	[55]
8.	*C. alata*	*Fusarium* sp.	4-Hydroxybenzaldehyde	Anticancer	Effective against vero tumor cells	[55]
9.	*C. alata*	*Fusarium* sp.	Bostrycoidin	Anticancer	Effective against vero tumor cells	[55]
10.	*C. alata*	*Fusarium* sp.	Fusarubin	Anticancer	Effective against haematological tumor cells	[55]
11.	*C. alata*	*F. solani*	3-Deoxyfusarubin	Anticancer	Effective against haematological tumor cells	[55]
12.	*C. alata*	*F. solani*	3,5,9-Trihydroxyergosta-7,22-diene-6-one	Anticancer	Effective against haematological tumor cells	[55]
13.	*C. tora*	*F.solani*	Anhydrofusarubin	Anticancer	Effective against haematological tumor cells	[55,56]
14.	*C. alata*	*Penicillium sclerotiorum*	Hexadecanoic acid	Anticancer	Effective against cervical cancer cells	[57]
15.	*C. alata*	*P. sclerotiorum*	Oleic acid	Anticancer	Effective against cervical cancer cells	[57]
16.	*C. alata*	*P. sclerotiorum*	Benzoic acid	Anticancer	Effective against cervical cancer cells	[57]
17.	*A. membranaceus*	*Fusarium* sp.	Fumitremorgin B	Anticancer	MOLT-4, A549, HL-60, and BEL-7402	[58]
18.	*A. membranaceus*	*Fusarium* sp.	Fumitremorgin C	Anticancer	Overcome drug resistance with doxorubicin	[58,75]
19.	*A. membranaceus*	*Fusarium* sp.	Cyclotryprostatin B	Anticancer	Prevents actin polymerization	[58,76]
20.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Pro-Gly)	Anticancer	Effective against breast cancer cell lines	[54]
21.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Pro-Leu)	Anticancer	Effective against breast cancer cell lines	[54]
22.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Pro-Ile)	Anticancer	Effective against breast cancer cell lines	[54]
23.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Phe-Gly)	Anticancer	Effective against breast cancer cell lines	[54]
24.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Phe-Ala)	Anticancer	Effective against breast cancer cell lines	[54]
25.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Pro-Tyr)	Anticancer	Effective against breast cancer cell lines	[54]
26.	*A. membranaceus*	*Aspergillus* sp.	Cyclo-(Pro-Phe)	Anticancer	Effective against breast cancer cell lines	[54]
27.	*Cercis chinensis*	*A. alternata*	(+)-5′-Dehydroxytalaroflavone	Anticancer	Inhibits communication between cancer cells	[59]
28.	*C. chinensis*	*A. alternata*	Altertoxin I	Anticancer	Inhibits communication between cancer cells	[59,77]
29.	*A. membranaceus*	*Fusarium* sp.	Ergosterol	Antifungal	Fungus-target of action of azoles and ketones	[58, 78–80]
30.	*A. membranaceus*	*Fusarium* sp.	Cerevisterol	Antibacterial	Antibacterial activity	[58,81]
31.	*A. membranaceus*	*Fusarium* sp.	Ergosterol peroxide	Antifungal	Fungal pathogens	[58,78,79, 82]
32.	*A. membranaceus*	*Fusarium* sp.	Allantoin	Antimycobacterial and antimalarial	*Mycobacterium tuberculosis* and *Plasmodium falciparum*	[58,82]
33.	*A. membranaceus*	*Fusarium* sp.	Verruculogen	Antifungal	*F. solani*, *F. moniliforme*, *F. equiseti*, *R. solan*, and *C. astragalis*	[58]
34.	*A. membranaceus*	*Fusarium* sp.	Fumitremorgin C	Antibacterial	Antibacterial activity	[58]
35.	*A. membranaceus*	*Aspergillus* sp.	(−)-6,7-Dihydroxymellein	Antibacterial, cytotoxic, phytotoxic and nematicidal activities	Antibacterial, cytotoxic, phytotoxic, and nematicidal activities	[51,52]

(continued on next page)

Table 2 (*continued*)

S. No.	Plant host	Endophytic fungi	Compound(s) name	Activity	Result	Reference
36.	*A. membranaceus*	*Aspergillus* sp.	(+)-Terrein	Natural antibacterial and antiproliferative activity	Natural antibacterial and antiproliferative activity	[51,52]
37.	*A. membranaceus*	*Penicillium* sp.	Cyclotryprostatin B	Antifungal	*F. solani*, *F. moniliforme*, *F. equiseti*, and *R. solani*	[83]
38.	*A. membranaceus*	*Penicillium* sp.	Tryprostatin B	Antifungal	*F. moniliforme*	[83]
39.	*A. membranaceus*	*Penicillium* sp.	Tryprostatin A	Antifungal	*R. Solani* and *C. astragalis*	[83]
40.	*A. membranaceus*	*Penicillium* sp.	Cyclotryprostatin A	Antifungal	*F. moniliforme* and *F. equiseti*	[83]
41.	*A. membranaceus*	*Penicillium* sp.	Cyclotryprostatin C	Antifungal	*R. Solani* and *C. astragalis*	[83]
42.	*A. membranaceus*	*Penicillium* sp.	Cyclotryprostatin D	Antifungal	*R. Solani* and *C. astragalis*	[83]
43.	*B. guianensis*	*Aspergillus* sp.	Monocerin	Antibacterial	*E. coli*, *P. aeruginosa*, *B. subtilis*, *S. aureus*, and *S. typhimurium*	[50]
44.	*C. chinensis*	*A. alternata*	3-*O*-Methylfusarubin	Antibacterial	Antibacterial activity	[84]
45.	*C. chinensis*	*A. alternata*	Javanicin	Antibacterial	*E. coli*, *Klebsiella pneumonia*, *S. aureus*, and *M. tuberculosis*	[84]
46.	*C. spectabilis*	*Phomopis cassiae*	3,12-Dihydroxycadalene	Antifungal	*C. sphaerospermum* and *C. cladosporioides*	[85]
47.	*C. spectabilis*	*P. cassia*	3,11,12-Trihydroxycadalene	Antifungal	*C. sphaerospermum* and *C. cladosporioides*	[85]
48.	*L. leucocephala*	*D. apiculatum*	γ-Terpinene	Antibacterial	Antibacterial activity	[86]
49.	*L. leucocephala*	*D. apiculatum*	(−)-4-Terpineol	Antibacterial	Antibacterial activity	[86,87]
50.	*L. leucocephala*	*D. apiculatum*	α-Terpinene	Antibacterial	Antibacterial activity	[86,88]
51.	*M. sativa*	*Aspergillus* sp.	3-Hydroxytoluquinone	Antibacterial	Antibacterial activity	[60]
52.	*M. sativa*	*Aspergillus* sp.	Phenoxyacetic acid	Antibacterial	Antibacterial activity	[60,89,90]
53.	*M. sativa*	*Aspergillus* sp.	Terreic acid	Antibacterial	*Nterobacter cloacae* and *Escherichia coli*	[60,89,90]
54.	*M. sativa*	*Aspergillus* sp.	Terredionol	Antibacterial	Antibacterial activity potential	[60]
55.	*M. sativa*	*Aspergillus* sp.	Isoaspinonene	Antibacterial	Antibacterial activity	[60]
56.	*M. sativa*	*Aspergillus* sp.	4-Hydroxymellein	Antibacterial	Antibiotic activity with structure of iso-chromone	[60]
57.	*M. sativa*	*Aspergillus* sp.	Nidulol	Antibacterial	Antibacterial activity	[60]
58.	*M. sativa*	*Aspergillus* sp.	Terreinol	Antibacterial	Antibacterial activity	[60]
59.	*M. sativa*	*Aspergillus* sp.	Versicolin	Antibacterial	*A. versicolor-pathogens* of *B. variabilis*	[60]
60.	*S. flavescen*	*Penicillium vulpinum*	(−)-3-Carboxypropyl-7-hydroxyphthalide methyl ester	Antibacterial	*E. areogenes*	[63,64]
61.	*S. flavescens*	*P. vulpinum*	(−)-3-Carboxypropyl-7-hydroxyphthalide	Antibacterial	*B. subtilis*, *Shigella dysenteriae*, and *Enterobacter areogenes*	[63]
62.	*S. flavescens*	*Xylaria* sp.	6-Heptanoyl-4-methoxy-2*H*-pyran-2-one	Antibacterial	*B. Subtilis*, *Escherichia coli*, *B. Megaterium*, *S. aureus*, *Shigella dysenteriae*, and *S. paratyphi*	[63]
63.	*S. flavescens*	*Xylaria* sp.	Xylarphthalide A	Antibacterial	*B. subtilis* and *B. cereus*	[63]
64.	*S. flavescens*	*Xylaria* sp.	(−)-5-Carboxylmellein	Antibacterial	*B. subtilis*, *B. anthracis*, *B. megaterium*, *S. aureus*, and *E. coli*	[63]
65.	*S. flavescens*	*Xylaria* sp.	(−)-5-Methylmellein	Antibacterial	*B. Subtilis*, *S. Aureus*, *B. megaterium*, *E. coli*, and *S. dysenteriae*	[63]
66.	*S. flavescens*	*Penicillium* sp.	1,2-Benzenedicarboxylic acid butyl cyclohexyl ester	Antibacterial	Anti-corrosion bactericidal effect-industrial production	[65,91,92]
67.	*S. tonkinensis*	*Xylaria* sp.	Xylapeptides B	Antibacterial	*B. subtilis*, *B. cereus*, *B. megaterium*, *Micrococcus luteus*, *S. aureus*, *Shigella castellani*, and *Canidia albicans*	[63,64]
68.	*S. flavescens*	*Aspergillus terreus*	Anshanmycin	Antifungal	Fungi, bacteria, actinomycetes, and other pathogens in varying degrees, especially on fungi	[62]
69.	*T. repens* and *B. guianensis*	*Aspergillus* sp.	Monomethylsulochrin	Antibacterial	*E. coli*, *P. aeruginosa*, *S. aureus*, *B. subtilis*, and *Helicobacter pylori*	[93,94]
70.	*T. repens* and *B. guianensis*	*Aspergillus* sp.	Fumigaclavine C	Antibacterial	*E. coli*, *Pseudomonas aeruginosa*, *S. aureus*, and *B. subtilis*	[29,58,68,95]

4.4. *Nematicidal activity of endophytic fungi*

Plant-parasitic nematodes including root-knot nematodes (*Meloidogyne* spp.), cyst nematodes (*Heterodera* spp., *Globodera* spp.), and root lesion nematodes (*Pratylenchus* spp.) are significant agricultural pests that inflict considerable yield losses on numerous crops globally. They predominantly assault the root system by establishing feeding sites, including solitary giant cells, syncytia, nonhypertrophied nurse cells, and coenocytes, which create a safeguarded feeding environment [96]. Nematodes have been a menace for agriculturists and food scientists all over the world owing to their deteriorative role in crop losses due to their extensive host variety, short generation period and high reproduction potential, which makes their management a humongous task to accomplish. These nematodes are mainly microscopic soil-borne pathogens that can feed on various plant parts (including roots, stems, leaves, flowers, and seeds), however, most species feed on roots. They require a protruding style to feed and penetrate plant cells. The stylet is affixed to three to five pharyngeal glands that produce effector chemicals, which are typically secreted, facilitating penetration, internal migration, and parasitism [97,98]. Based on their feeding habitats, plant-parasitic nematodes can be roughly categorized as either ectoparasitic or endoparasitic. The most important nematodes in terms of agricultural losses are sedentary endoparasites, the root-knot (*Meloidogyne* spp.), and cyst nematodes (*Heterodera* spp. and *Globodera* spp.) [99]. Estimates indicate that plant parasitic nematodes inflict significantly greater annual harm than insect pests. The loss of crop productivity attributable to these microscopic pests in numerous nations is substantial. They resulted in an anticipated yield loss of 12.3 % ($157 billion) globally. From this, $40.3 million is reported from India [100]. Therefore, a number of strategies have been used to control the infection of nematodes in agricultural as well as medicinal plants. One of the most crucial of these strategies is the application of chemical nematicides [101].

The soybean cyst nematode (*Heterodera glycines*) is an important plant pest causing significant crop losses globally. This study assessed the efficiency of *Piriformospora indica*, a plant-growth-promoting endophytic fungus, in mitigating damage to soybean (*Glycine max*) seedlings induced by this nematode. The soil was treated with 2.5 % and 5 % *P. indica* (w/w) and inoculated with second-stage juvenile nematodes (J2). After 60 days, *P. indica* dramatically reduced nematode egg densities by 29.7 % and 36.7 %, respectively, compared to controls. Despite reduced root biomass (27.9 % and 33.5 %), shoot biomass grew by 30.8 % and 8.2 % in 2.5 % and 5 % treatments, respectively. Accelerated plant development was seen, with flowering increasing by 75 % in the 2.5 % treatment group. These data imply that *P. indica* successfully lowers nematode populations and enhances soybean development, presenting a feasible technique to balance production losses caused by plant-parasitic nematodes. However, there are several concerns over the usage of

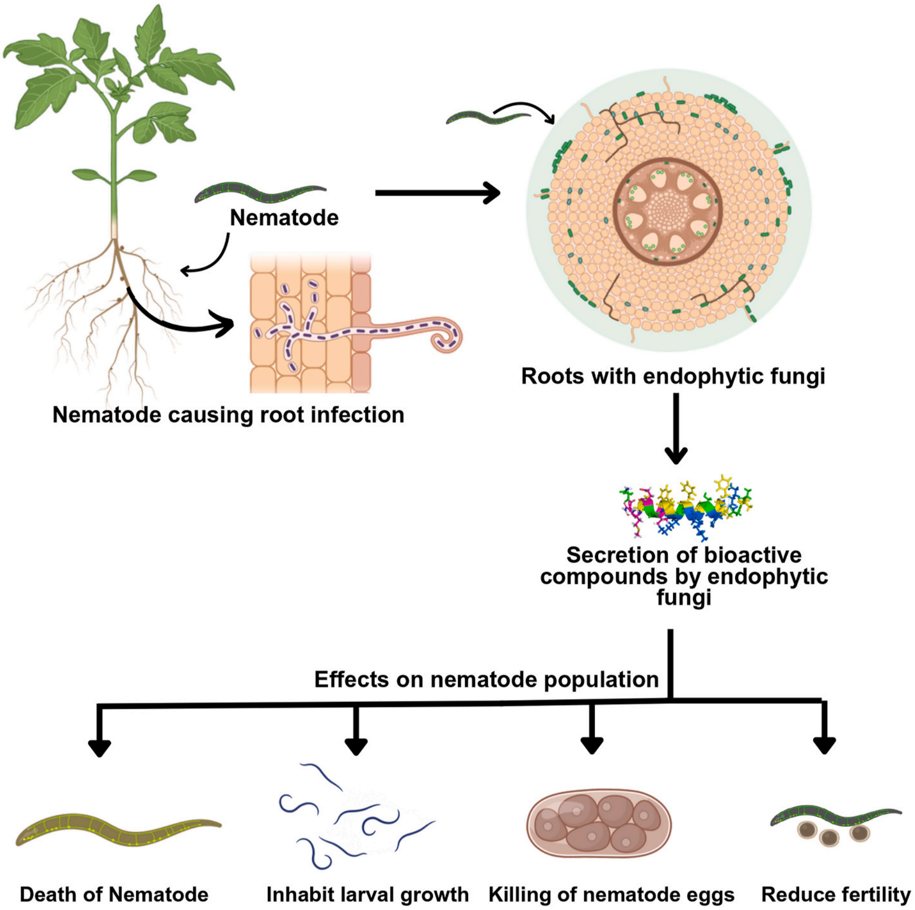

Fig. 3. Schematic representation of the biocontrol mechanism of endophytic fungi against root-infecting nematode. The figure depicts the process by which nematodes infect plant roots, leading to root damage. Endophytic fungi colonize the plant roots, secreting bioactive compounds that target nematode populations. These compounds exhibit nematicidal effects, including the death of nematodes, inhibition of larval growth, killing of nematode eggs, and reduced fertility of nematodes. This demonstrates the role of endophytic fungi in providing bioprotection against nematode infections through bioactive metabolite production.

chemical nematicides for controlling the nematode population because of the degradation of environmental quality by these agents [102]. Considering this, there is an urgent need to look for other alternative strategies to control nematode infections. This is where endophytic fungi come into the picture. Several studies have shown the ameliorative role of endophytic fungi as biocontrol agents for controlling nematode infections [103]. Endophytic fungi mainly adopt two main strategies for their biocontrol action: the first one being competing for space and nutrition with the nematode followed by activation of the plant immune system; while the second one is antagonism of the nematode via antibiosis. Studies by Bashyal et al. [51], Khan et al. [104], Rajendran et al. [105], Strom et al. [106] Messa et al. [107] and Yadav & Meena [154] have demonstrated nematicidal activities of endophytic fungi such as *Aspergillus* sp., *Trichoderma virens*, *Purpureocillium lilacinum*, *Fusarium* sp. and *Claroideoglomus etunicatum* against several nematicidal infections in *Cicer arietinum* and *Glycine max*.

The study by Ghareeb et al. [108] analyzes the nematicidal effects of *Aspergillus flavus*, an endophytic fungus from *Trigonella foenum-graecum*, on root-knot nematodes (*Meloidogyne incognita*) in potatoes. The fungus generates bioactive metabolites such as gadoleic and oleic acids, which impede nematode development, diminish egg hatching, and augment plant defense enzymes, resulting in up to 97 % juvenile mortality. This environmentally sustainable method mitigates nematode damage and promotes sustainable potato cultivation. An investigation by Zhou et al. [109] reported the antagonistic capability of 55 fungal strains, originally isolated as foliar endophytes from *Gossypium hirsutum* (upland cotton) and one commercial *Beauveria bassiana* strain against root-knot nematodes (*Meloidogyne incognita*). Using a seed treatment approach, root gall counts on treated cotton seedlings were measured three weeks post-inoculation. Most fungal strains significantly lowered gall levels, and 22 of the most efficient strains were retested for repeatability, with 95 % confirming their efficacy. Fungal strains from *Alternaria*, *Chaetomium*, *Cladosporium*, *Diaporthe*, *Epicoccum*, *Gibellulopsis*, and *Purpureocillium* genera revealed substantial antagonistic effects, whereas some *Alternaria* and *Curvularia* strains unexpectedly promoted galling. These results show that cotton-associated endophytic fungi constitute a good reservoir of opportunities for developing biocontrol drugs against root-knot nematodes.

The study by Anbalagan et al. [110] evaluated the biocontrol efficacy of four *Trichoderma* spp. against the wilt-nematode complex in tomato, caused by *Fusarium oxysporum* f.sp. *lycopersici* and *Meloidogyne incognita*. Molecular identification confirmed the fungi as *Trichoderma asperellum* (Tv1), *T. asperelloides* (Tasd1), *T. harzianum* (Th1), and *T. koningiopsis* (Tk1). *T. asperellum* (Tv1) demonstrated the highest effectiveness, inhibiting pathogen mycelial growth and achieving up to 100 % juvenile mortality and 90.20 % egg hatching inhibition of *M. incognita*. *Trichoderma asperellum* (Tv1) treatment also enhanced tomato plant growth parameters and reduced disease incidence by 64.57 %, comparable to carbendazim (82.32 %). Pot trials showed that Tv1 significantly reduced root galling and nematode reproduction (RF = 0.53). The findings confirm Tv1's potential as a biocontrol agent for managing nematode and wilt disease in tomato crops. An endophytic fungus *Acremonium implicatum*, isolated from tomato root galls infected with *Meloidogyne incognita*, exhibits remarkable biocontrol potential [111]. It was identified through morphological and ITS sequence analysis. *A. implicatum* destroyed 96 % of second-stage nematode juveniles and reduced egg hatching to 36.3 % in vitro. Pot studies revealed it greatly lowered root gall counts (40.6 galls per treated plant vs. 121.6 in controls) and nematode population in soil (151.1 vs. 375.1 per 100 g soil). Field trials also indicated a considerable drop in the root gall index (25 in treated plants vs. 96 in controls), showing *A. implicatum* as an effective biocontrol agent against root-knot nematodes in tomatoes. Fig. 3 depicts a schematic representation of the biocontrol mechanism of endophytic fungi against root-infecting nematodes.

5. Role of endophytic fungi in phytoremediation

Phytoremediation is a novel technology that is non-intrusive, economical, and aesthetically pleasing [112]. There are several approaches that are employed for the phytoremediation of xenobiotics including xenobiotic uptake, translocation, extraction, bioaccumulation, and detoxification process**.** The main drawback associated with the bioremediation of soil using hyperaccumulator plants is that their growth rate is slow, which largely limits their remediation efficiency [113]. On top of that, the complex interactions between plant root exudates and different soil components impede the bioavailability of chelating metal ions. This drawback is overcome by endophytic fungi, which offer enhanced ligand exchange, increased secretion of metabolite-rich exudates, production of siderophores, pH-regulated mobilization, and immobilization of chemicals thus ensuring the provision of tolerance to plants under stressful unfavorable conditions. The bioaccumulation of heavy metals leading to toxicity in biological systems of humans, animals, microbes, and plants constitutes a significant concern for environmental health and safety [114].

A number of endophytic fungi associated with Fabaceae have been found to play a crucial role in phytoremediation. For instance, in a study by Garg et al. [115], the researchers pointed out the toxic effects of heavy metal accumulation in plants in the form of stunted growth, imbalance in mineral nutrition, and compromised membrane structure and permeability. The ameliorative effect of fungus in heavy metal detoxification was evident from the significant enhancement of plant dry mass, nitrogen metabolism, and amount of GSH and phytochelatins in the plant tissue. The ameliorative role of endophytic fungi, namely, *Phoma* sp., *Alternaria* sp., and *Peyronellaea* sp. associated with *Acacia decurrens* Willd have been reported in a study by Li et al. [116]. In this study, the researchers reported alleviation of Pb- and Zn-induced heavy metal toxicity in *Acacia decurrens* Willd in the presence of endophytic fungi.

Another recent study by Pietro-Souza et al. [117] analyzed the bioremediation role of different endophytic fungi belonging to *Aspergillus* sp., *Curvularia geniculata*, Lindgomycetaceae and *Westerdykella* in Hg bioremediation in *Aeschynomene fluminensi* plants belonging to Fabaceae family. The results indicated the ameliorative role of *Aspergillus* sp. A31, *Curvularia geniculata* P1, Lindgomycetaceae P87, and *Westerdykella* sp. in Hg bioremediation as evident from the fact that Lindgomycetaceae P87 promoted plant growth in *A. fluminensis* and removed nearly 100 % of the mercury from the culture medium. Elimination of mercury from the soil may be attributed to mercury compartmentalization inside the host tissues or mercury volatilization. A unique strain of *Aspergillus* (strain *A. luchuensis* C7), closely related to *A. luchuensis*, was isolated from the metal hyperaccumulator plant *Prosopis laevigata* [118]. This strain was identified as a metallophile and exhibited significant tolerance to elevated concentrations of Cu, Zn, and Pb. The fungus also induced higher size features in *P. laevigata* individuals, indicating that the *A. luchuensis* C7 strain serves as a growth-promoting agent for *P. laevigata*. Furthermore, the fungus facilitated the translocation of metals from the roots to the leaves in *P. laevigata*, enhancing copper translocation. The study proved that novel *A. luchuensis* strain exhibits endophytic characteristics, promotes plant development, demonstrates significant metal tolerance, and enhances copper translocation. Therefore, study advocate itself as an innovative, efficient, and sustainable bioremediation approach for copper-contaminated soils.

Mercury-resistant endophytic fungi demonstrate significant promise for phytoremediation by enhancing plant health and mitigating metal toxicity in polluted environments [119]. The study examined the functional features of fungal strains isolated from the Fabaceae plant *Aeschynomene fluminensis* Vell. specifically, *Westerdykella aquatica* P71 and *Pseudomonodictys pantanalensis* A73, which exhibit remarkable capacities. These fungi produced indole-3-acetic acid, excreted siderophores, and solubilized phosphate, enhancing maize (*Zea mays*) growth by as much as 76.25 %. The fungi facilitated mercury absorption in plants, predominantly concentrating it in the roots, therefore mitigating phytotoxic effects. Genomic investigation of *P. pantanalensis* and *W. aquatica* identified essential genes for mercury resistance (merA and merR1), oxidative stress regulation (PRX1 and TRX1), and growth enhancement (trpS and iscU). Moreover, their genomes encoded secondary metabolites including dimethylcoprogen and melanin, which function as metal chelators with antioxidant characteristics. The findings identify *P. pantanalensis* and *W. aquatica* as effective agents for remediating mercury-contaminated soils, successfully integrating diminished phytotoxicity with improved plant growth and environmental restoration.

6. Role of endophytic fungi in stress management

The productivity of plants is greatly limited by both abiotic and biotic stresses. In this context, endophytic fungi play a significant role in the alleviation of both abiotic and biotic stresses in plant systems. Plants may face abiotic stress in the form of increased carbon dioxide concentration, high temperature, salinity stress, drought stress, and heavy metal stress. Under such stressful conditions, endophytic fungi trigger plant defense systems in a number of ways: by inducing ROS scavengers, phosphorus mobilization, stress hormone production, production of secondary metabolites, production of antioxidant molecules, ion balance, protein synthesis, and production of allelochemicals. All these defense mechanisms may induce a cascade of fight and flight response in plants, characterized by induction of an array of ameliorative events such as increased nutrient uptake, increased carbon sequestration, increased photosynthetic efficiency in plants, enhanced phosphorus solubilization, increased nutrient efficiency, increased uptake of nitrogen and phosphorus, high water use efficiency and improved membrane integrity. All these events further lead to enhanced crop production due to the development of abiotic stress tolerance in plants. The ameliorative role of endophytic fungi in overcoming abiotic stress in leguminous plants has been shown in many studies. For instance, Khan et al. [120] showed the ameliorative role of endophytic fungus GMC-2A in overcoming salinity stress in soybean plants as evident from soybean growth attributes such as shoot length, shoot fresh/dry biomass, chlorophyll content, photosynthesis rate, and leaf area. In addition to these, soybean plants exposed to salinity stress in the presence of GMC-2A were found to possess a lower level of abscisic acid and a higher level of jasmonic acid as well as isoflavones.

Hedysarum scoparium recognized for its quick growth and great drought resistance, is extensively employed in dry region restoration in Northwest China. Addressing the potential of dark septate endophytes (DSEs) isolated from non-host desert plants, this study assessed their symbiotic advantages for *H. scoparium* under varied soil moisture levels [121]. Four DSE strains (*Phialophora* sp., *Knufia* sp., *Leptosphaeria* sp., and *Embellisia chlamydospora*) successfully colonized *H. scoparium* roots, with considerable growth and physiological improvements under water stress. In water-limited settings, *Phialophora* sp. and *Leptosphaeria* sp. improved root biomass, total biomass, and nutrient absorption, while enhancing antioxidant enzyme activity in the host. These findings emphasize the ecological importance of DSE fungi in arid environments, stressing their potential in enhancing drought resistance and assisting desert revegetation initiatives. Similarly, another study by Kumari et al. [122] showed the ameliorative role of endophytic fungi in drought stress tolerance in chickpea as evident from decreased ROS concentration and augmented oxidative stress tolerance evident from decreased activity of antioxidant genes, proline, and antioxidant enzymes. Abiotic stress tolerance in leguminous plants due to the beneficial role of endophytic fungi has also been demonstrated in a number of other studies [123,124].

Global warming presents a significant threat to crops such as soybean and sunflower, demanding the development of innovative methods to mitigate heat stress. Fungal endophytes, known for synthesizing growth-enhancing secondary metabolites, present a viable option. The work comprised the isolation of *Aspergillus flavus* from *Euphorbia indica*, a plant that grows in the desert, and the examination of its ability to enhance plant development under stress conditions. The fungal culture yielded higher levels of advantageous chemicals, such as indole acetic acid (IAA), salicylic acid (SA), flavonoids, and phenolics. Seedlings of soybean and sunflower inoculated with *A. flavus* were evaluated against uninoculated controls under normal (25 °C) and heat-stressed (40 °C) conditions in a growth chamber. Under heat stress, control plants displayed higher levels of stress indicators such as abscisic acid (ABA) and proline, while exhibiting a decrease of defensive compounds like phenols, flavonoids, catalase, and ascorbic acid oxidase. They had more significant declines in chlorophyll content, root and shoot development, and dry biomass. On the other hand, plants inoculated with *A. flavus* demonstrated enhanced growth and stress resilience, underscoring the potential of fungal endophytes in improving crop performance against elevated temperatures [125].

Heat stress can adversely harm crops, but endophytic fungi provide a viable answer. Ismail et al. [126] isolated *Aspergillus niger* (SonchL-7) from *Sonchus asper* and evaluated its effects on sunflower and soybean under high temperatures (40 °C). Plants inoculated with *A. niger* demonstrated enhanced height, biomass, and chlorophyll content, along with reduced lipid peroxidation and reactive oxygen species (ROS). The fungus strengthened ROS-scavenging enzymes like catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD), while promoting proline and phenolics levels. It also decreased abscisic acid (ABA), a stress-related hormone. These findings show that *A. niger* could be a beneficial tool for protecting crops from heat stress in the future.

Desert plants rely on endophytic fungi to stay survive in harsh situations like drought and heat. Researchers obtained *Thermomyces lanuginosus*, a thermophilic fungal endophyte from a desert plant *Cullen plicata* Delile. Plants incubated with the fungus (E+) were compared to uninoculated controls (E−). The results showed that *T. lanuginosus* not only boosted the host plant's growth but also improved its resistance to heat stress. This shows the potential of thermophilic endophytes to strengthen desert plants against extreme environmental challenges while supporting their growth [127].

Another study suggests dark septate endophytes (DSEs) have a crucial role in increasing drought resistance in *Ormosia hosiei* [128]. Inoculation with *Acrocalymma vagum* stimulated growth by increasing leaf size, palisade tissue thickness, and vascular bundle area. Photosynthetic efficiency, pigment content, and transpiration rates were similarly improved in infected seedlings compared to controls. Notably, inoculation protected chloroplast ultrastructure and membrane integrity under drought stress, whereas non-inoculated seedlings revealed substantial cellular damage. These results show the potential of DSE inoculation as a biological technique to promote drought resilience and survival in trees.

Salinity stress is a major environmental problem that severely impacts plant growth. The investigation assessed the ability of *Bipolaris* sp. CSL-1, a plant growth-promoting fungus, to strengthen soybean tolerance to salinity stress [129]. CSL-1 displayed various growth-promoting properties, including the generation of indole-3-acetic acid (IAA), gibberellins (GAs), and organic acids, coupled with resistance to high sodium chloride (NaCl) levels. Inoculation with CSL-1 significantly increased soybean shoot and root length, biomass, and chlorophyll content under 200 mM NaCl stress. It lowered endogenous abscisic acid (ABA) levels while increasing salicylic acid (SA) levels, contributing to better stress management. Additionally, CSL-1 reduced oxidative stress markers like peroxidase, polyphenol oxidase (PPO), malondialdehyde (MDA), and superoxide anion (SOA) in treated plants. Molecular investigation indicated lower expression of stress-associated genes (GmFDL19, GmNARK and GmSIN1), confirming CSL-1's role in moderating stress responses. This endophytic fungus offers a promising eco-friendly alternative for enhancing agricultural output in salt-affected soils.

In another study, four endophytic fungi (GM-1, GM-2, GM-3, and GM-4) tested for their capacity to promote soybean growth under salinity stress. Soybean seedlings sprayed with fungal cultures indicated improved germination and growth compared to untreated controls. Gibberellin (GA) profiling of fungal culture filtrates (CFs) revealed a diverse array of GAs, including GA4, GA7, GA8, GA9, GA12, and GA20, suggesting the fungi's potential to synthesize bioactive growth regulators. Among those studied isolates, GM-1 demonstrated the most pronounced impact on plant growth, considerably raising plant length and fresh weight under salinity stress. GM-1 reduced salinity-induced damage by decreasing lipid peroxidation, enhancing protein synthesis, and promoting the activities of antioxidant enzymes such as catalase, superoxide dismutase, and peroxidase. In addition, GM-1 treatment led to lower abscisic acid levels and elevated salicylic acid levels, further adding to stress tolerance. Other isolates (GM-2, GM-3, and GM-4) similarly decreased oxidative stress by decreasing lipid peroxidation and maintained plant growth metrics, however, their positive aspects were less obvious compared to GM-1. Molecular analysis of GM-1 confirmed it as *Fusarium verticillioides* (teleomorph: *Gibberella moniliformis*), isolate RK01. The findings reveal the potential of *F. verticillioides* as a bioinoculant for enhancing soybean growth and stress tolerance under salt conditions, presenting a promising strategy for sustainable agriculture in saline environments [130].

The study analyzes how dark septate endophytic fungus (DSE), specifically Sordariomycetes sp1-B′2 and *Melanconiella elegans*-21W2, influence cowpea plants under salt stress [131]. The fungus was initially isolated from the roots of *Vochysia divergens* and identified using ITS region sequencing. These fungi are noted for generating typical black septate structures in roots. Cowpea plants either inoculated or not with the fungi, were cultivated under greenhouse conditions using irrigation water with varied salt levels (1.2, 2.2, 3.6, and 5.0 dS m^{-1}). Salt stress often lowers potassium (K) levels in the leaves while increasing calcium, sodium, and chlorine. However, the fungi did not modify these leaf mineral reactions. The genuine benefits of fungal colonization were found in plant roots. Inoculated plants showed improved nitrogen (N) and phosphorus (P) uptake, leading to greater growth and enhanced photosynthesis under moderate salinity. These findings emphasize the potential of DSE fungus to improve plant health in tough conditions, although their favorable impacts may could diminish under severe salinity. Another investigation highlights the impact of dark septate endophytes (DSE) (*Acrocalymma vagum*, *Paraboeremia putaminum*, and *Fusarium acuminatum*) on the growth, physiological performance, and rhizosphere microbial profile of licorice (*Glycyrrhiza uralensis*) subjected to drought stress [132]. All three DSE species effectively colonized licorice roots and created species-dependent harmonious relationships. Notably, inoculation with *A. vagum* and *P. putaminum* considerably increased plant biomass and glycyrrhizin content, while *A. vagum* and *F. acuminatum* increased glycyrrhizic acid synthesis. However, *F. acuminatum* significantly influenced overall plant biomass. DSE application increased root development, photosynthesis, antioxidant activity, and nutrient uptake while modifying rhizosphere microbial diversity, including a substantial increase in arbuscular mycorrhizal fungi under drought-prone circumstances. Soil organic matter, phosphate availability, and plant metabolic activity were enhanced by DSE, with *A. vagum* being identified as the most advantageous strain due to its advantageous impacts on plant growth and active component production. These findings underline the ecological and agronomic potential of DSE for drought resistance in dryland farming systems.

Biotic stress, caused by microbes that are pathogenic, hampers plant growth and exerts negative consequences globally [9]. Fungal endophytes offer an alternative for addressing the challenges associated with traditional farming by invading plant tissues without harming them. Fungal endophytes participate in enhancing the fitness of hosts in response to biotic stress by facilitating nutrient uptake, synthesizing phytohormones, and mitigating injury caused by pathogens through various mechanisms such as antibiosis, lytic enzyme production, secondary metabolites biosynthesis, mycoparasitism, and the activation of induced systemic resistance [10]. Microbes, pests, and nematodes are major biotic stressors and generally produce reactive oxygen species (ROS) which interfere with plant molecular and physiological processes, ultimately lowering the productivity of crops and even killing plants [133]. Agriculture is significantly affected by fungal pathogens because they produce plant diseases that reduce crop yields and quality [134,135]. Phytopathogenic fungi generally produce toxins that play a pivotal role in development of plant diseases and consequently harm host plants [136].

The majority of phytopathogenic toxins are low molecular weight secondary metabolites that can cause certain disease symptoms such as wilting, necrotic spots, stunted growth, chlorosis, and plant death. These toxins can impair normal physiological functioning, even at very low levels [17]. Chemical fungicides are frequently being employed for the management of phytopathogenic fungus, and having detrimental effects on the environment. Fungal endophytes can greatly regulate the impact of fungal infections, minimizing the negative environmental impacts of chemical fungicides [137–139]. Fungal endophytes deploy many strategies to overcome fungal infections and the development of plant resistance, including stimulating defense-related gene expression and producing bioactive compounds and hormonal signaling molecules [140]. The generation of antimicrobial secondary metabolites by fungal endophytes can effectively suppress the growth and multiplication of pathogenic microbes. These chemicals diminish the prevalence and virulence of pathogens within the host plant by either directly targeting viability or inhibiting their infective mechanisms. This interaction adds to the host plant's improved resistance to fungal infections and plays a critical role in preserving plant health under biotic stress [141].

Endophytic fungi trigger biotic stress tolerance in plants in three different ways: antibiosis or production of antibiotics, competition for nutrients, and mycoparasitism [142]. For instance, a recent study by Sallam et al. [143] showed protective action of *Trichoderma longibrachiatum*, *T. asperellum*, and *T. atroviride* associated with soybean in the protection of host plants from root rot caused by *Rhizoctonia solani.* The protective effects of the endophytic fungi in safeguarding the host plant soybean were attributed to the presence of several bioactive compounds such as pectinase, chitinase, and siderophore production by the fungus. White mold of common bean caused by *Sclerotinia sclerotiorum* is a serious disease in temperate and subtropical climates [144]. The investigation demonstrated that *Purpureocillium lilacinum* culture filtrates (75 % concentrated) successfully suppressed mycelial growth (100 %), sclerotia formation (100 %), myceliogenic (93.5 %), and carpogenic germination (90 %). The filtrates promoted lipid peroxidation and cell membrane permeability while lowering oxalic acid in *S. sclerotiorum*. In greenhouse studies, disease severity fell by 83.3 %, and plant defense enzymes (PAL, PPO, and POD) were considerably activated. NMR data indicated leucinostatins H and K as the primary bioactive peptides, underlining their involvement in antifungal action and disease control. This shows *P. lilacinum*'s potential as a biocontrol agent against *S. sclerotiorum.*

The fungal endophyte *Simplicillium lanosoniveum* demonstrates a mycoparasitic mode of antagonistic activity towards *Phakopsora pachyrhizi*, the pathogen responsible for rust in soybean [145]. *P. pachyrhizi* Sydow poses a significant threat to soybean crop production on a global scale. The infection significantly impacts grain weight and quality [146]. Yield losses can be as high as 80 % when environmental conditions support fungal growth, and even a minimal disease incidence of 0.05 % can impact crop yield [147,148]. Both in vitro and in vivo tests were performed to assess the antagonistic capability of the endophytic insect-pathogenic fungus *Metarhizium robertsii* against the root rot pathogen *Fusarium solani* f. sp. *Phaseoli* in *Phaseolus vulgaris* [149]. *M. robertsii* suppressed *F. solani* growth by around 60 %, according to dual-culture experiments. Additionally, *M. robertsii* cell-free culture filtrates inhibited *F. solani* conidial germination by 83 %; this was ascribed to a heat-stable metabolite. In vivo tests exhibited that in comparison to non-colonized plants, bean plants colonized by *M. robertsii* showed enhanced growth and decreased disease severity when later challenged with *F. solani*. These results indicate that *M. robertsii* can serve as a dual-purpose biocontrol agent, offering defense against soilborne plant diseases and insect pests. This demonstrates how useful it could be in integrated approaches to managing diseases and pests. Another investigation demonstrates the protective role of endophytic fungus in modifying plant defense mechanisms against aphids. Endophyte seed treatments in *Vicia faba* considerably reduced populations of *Acyrthosiphon pisum* and *Aphis fabae* compared to untreated controls [150]. The most effective isolates were *Trichoderma asperellum*, *Gibberella moniliformis* and *Beauveria bassiana*, which not only inhibited aphid population growth but also impacted offspring fitness, development, and fertility. Offspring birth rates were considerably reduced across two generations of aphids feeding on treated plants, resulting in 1.6–14.6 and 3.7–11.0 times fewer nymphs for *A. fabae* and *A. pisum* respectively, at final evaluation. Furthermore, endophyte-treated plants displayed enhanced seedling survivorship, with survival rates between 20 and 100 % compared to 0 % in untreated plants at 20 days post-infestation. These findings suggest that endophytic fungus can boost plant resilience to aphids and have the potential to be integrated into integrated pest management (IPM) systems as a sustainable biocontrol technique. The common bean (*Phaseolus vulgaris*), an essential food and cash crop in Africa, faces significant challenges from bean stem maggots (BSM, *Ophiomyia* spp.), which inflict damage on seedlings. This investigation evaluated 11 fungal isolates regarding their efficacy to colonize bean plants and inhibit various stages of the BSM lifecycle [151]. All isolates except *Metarhizium anisopliae* and *Beauveria bassiana* (ICIPE 273), effectively colonized the roots, stems and leaves of bean plants. The highest level of colonization was observed in the roots with significant variation noted among the different isolates. The application of fungal inoculation led to a notable decrease in BSM feeding, oviposition, pupation and adult emergence when compared to the control group. *M. anisopliae* ICIPE 20 demonstrated the highest efficacy in interrupting the lifecycle of BSM. While *M. anisopliae* ICIPE 78 exhibited comparable feeding punctures to the control, it significantly diminished pupae and adult emergence, indicating a potential inhibitory effect on BSM growth. The results emphasize the potential of fungal endophytes as effective biocontrol agents for addressing BSM in bean production systems across East Africa.

Field trials over two seasons in Sagana and Naromoru, Kenya, examined the efficacy of *Beauveria bassiana* (G1LU3) and *Hypocrea lixii* (F3ST1) as seed inoculants for reducing *Liriomyza* leafminers in *Phaseolus vulgaris* [152]. An autodissemination device (AD) with *Metarhizium anisopliae* (ICIPE 20) conidia was also tried. Both fungal isolates successfully colonized bean plants, with higher colonization rates for *H. lixii*. Leafminer infestations were reduced in endophyte-treated plants compared to controls during the second season. Pupae counts on treated plants varied from 110 to 252 compared to 331–523 in controls. Despite no significant variations in parasitoid emergence between treatments, endophyte sprays resulted in increased seed yields. The AD treatment demonstrated a modest impact on pest parameters but boosted yield. These findings highlight the potential of *B. bassiana* and *H. lixii* for *Liriomyza* management in beans, warranting further research for integrated pest management strategies. Russo et al. [153] evaluated endophytic *Beauveria bassiana* potential to colonize soybeans and its influence on various biological and reproductive parameters and the food preference of *Helicoverpa gelotopoeon*, a polyphagous pest of several agronomic crops. A suspension of 1×10^8 conidia ml^{-1} of *B. bassiana* (LPSC 1098), was inoculated in soybean plants using the leaf spraying method. *H. gelotopoeon* survival, development, fecundity, and fertility were registered to investigate fungal influence. Also, meal preference was determined via the free-choice method. *B. bassiana* as an endophyte adversely influenced the duration of the larval stages (L1, L2, L3, L4) and the adult stages, as well as the total duration of the life cycle. Furthermore, the oviposition duration, fecundity, and fertility of *H. gelotopoeon* were reduced. This is the first report of decreased eating of soybean leaves by *H. gelotopoeon* due to endophytic *B. bassiana*. The study reveals that endophytic fungi could be considered as valuable microorganisms for integrated pest management.

7. Conclusion

The overuse of chemical pesticides and fertilizers for boosting the agricultural production and minimizing the productivity losses due to biotic and abiotic stress may somehow have solved the problem of food scarcity but led to a considerable deterioration of the environmental quality. This is evident from the deteriorating condition of the environment as well as degradation of different ecosystems with every passing day. However, use of endophytic fungi has been a great initiative to boost plant productivity and pave way for safer and sustainable forms of agriculture without harming the environmental resources. Endophytic fungi play a crucial role in augmenting plant growth and productivity and helping plants cope with different biotic as well as abiotic stresses. Furthermore, the inuumerable plethora of bioactive secondary metabolites harvested from different forms of endophytic fungi have been reported to play pivotal role as anticancer, antimicrobial, nematocidal and antimalarial agents. Endophytic fungi have also been reported to play a crucial role in phytoremediation and stress management of plants against both biotic and abiotic stresses. A plenty of strategies have been explored to reduce the infection of nematodes in agricultural as well as medicinal crops. One of the most crucial of these approaches may be the deployment of fungal endophytes as bionematicides. In future, fungal endophytes may be employed to assist crops cope with both biotic as well as abiotic stress, encouraging agriculture to continue even in the face of harsh environmental circumstances. Chemical fungicides are frequently being employed for management of pathogenic fungus, having detrimental effect on the environment. Fungal endophytes can greatly regulate the impact of fungal infections, also utilized for minimizing the negative environmental impacts of chemical fungicides Endophytic fungus could be considered as valuable microorganisms for the integrated pest management. Bioinformatics tools in addition to the latest techniques such as metabolomics, next generation sequence typing can potentially address the gaps in fungal endophytes studies. However, there are many challenges that need to be addressed before the translational use of endophytic fungi of plants for human welfare such as the survival and cultivation of endophytic fungi outside the plant host is a challenging task and unwinding the complex intricacies of different metabolic pathways that regulate interactions between plants and endophytic fungi.

CRediT authorship contribution statement

Hanuman Prasad Saini: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Mukesh Meena:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Abhishek Sahoo:** Writing – review & editing, Visualization, Validation, Investigation. **Tushar Mehta:** Writing – review & editing, Visualization, Validation, Investigation.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethical approval and consent to participate

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Declaration of competing interest

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