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Biocontrol mechanisms of endophytic fungi

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Abstract

Background: Scientific approaches into modern agricultural systems, as opposed to the use of synthetic pesticides in food production, became important by exploring endophytic fungi capable of protecting plants against pathogens for maximum crop productivity.

Main body: Diverse endophytic microbes colonizing the internal tissue of plants exhibit beneficial and pathological effects on plants. The beneficial endophytic fungi assisted plants in the control of pathogenic endophytic fungi in plants due to their ability to directly or indirectly promote plant health. Inefficient agricultural practices and environmental factors contribute to the disease emergence in plants. Endophytic fungi employed diverse mechanisms in phytopathogen control by activating and inducing plant resistance through gene expression, synthesis of fungi-derived metabolite compounds, and hormonal signaling molecules. The mutual coexistence between endophytic fungi and host plants remains an important mechanism in disease suppression. An in-depth understanding and selection of beneficial endophytic fungi and interaction between pathogens and host plants are important in managing challenges associated with the endophyte biocontrol mechanisms.

Conclusion: Research findings on the use of endophytic fungi as bioinoculants are advancing, and understanding endophytic fungi antibiosis action through the synthesis of biocontrol agents (BCAs) can, however, be explored in integrated plant disease management. Therefore, in this review, the biocontrol mechanism of endophytic fungi against plant pathogens was highlighted.

Keywords: Biocontrol mechanism, Endophytic microbiome, Fungal diversity, Plant-soil interface, Sustainable agriculture

Background

The scientific approaches to the study of plant-fungal interactions are becoming interesting in modern agriculture with prospects to ensure food security and zero malnutrition among the world populace (Sharma et al. 2021). In recent times, a higher world population index by 2050 has been envisaged with emphasis and recommendations on the use of biological approaches in tackling food demand pressure, food insecurity, and future food scarcity (Sahu and Mishra 2021). From antiquity, farmers employed diverse approaches to enhance food

production using agrochemicals, which are not sustainable due to negative threats to the ecosystem (Glick et al. 2001). To this premise, checkmating these threats to the ecosystem and exploring potential endophytic microbes will help achieve a stable ecosystem and grow pathogen-free plants for higher crop productivity (Akanmu et al. 2021).

Researches focusing on endophytic microbes and exploration as bioinoculants have created many opportunities as a substitute for synthetic pesticides usage in modern agricultural systems (Orozco-Mosqueda et al. 2021). Nevertheless, information on the endophytic fungi antibiosis action through the synthesis of biocontrol agents (BCAs) can, however, be explored in integrated plant disease management, which is the focus of this review paper.

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Literarily, the discreet regions in the internal tissue of plants are referred to as the endosphere and the microorganisms found in these regions are called endophytic microbes (Dubey et al. 2020). Of most interesting, microbial endophytes establish mutualism or antagonism association with the host plants, depending on their similar or dissimilar genetic make-up. The beneficial types that do not express any pathological effects with unique plant growth-promoting (PGP) attributes, such as phytohormone synthesis, nutrient acquisition, secretion of BCAs, and stress induction mechanism, are referred to as plant growth-promoting endophytes (Adeleke et al. 2021).

The endosymbiotic relationship of endophytic fungi with the host plants aimed to contribute to plant growth and pathogen control depending on their colonization and secretion of biocontrol agents (Reshma et al. 2019). Most endophytic microbiomes in the plant endosphere have been reported to influence plant phenotypic functions against environmental stresses and control plant pathogens (Yu et al. 2019). Recent findings have pointed out the need to elucidate how endophytic microbes can be engineered in agricultural biotechnology for plant health sustainability and integration in crop breeding (Zhang et al. 2020). Depending on the plant organ location, some endophytic fungi inhabiting below ground level easily change form to become endophytes due to proximity to the root endosphere. Interestingly, evidence has shown the dynamic nature, colonization, and infiltration of endophytic fungi from the external root environment (rhizosphere) into the internal tissue of plants (endosphere) to establish endophytic microbial communities (Yan et al. 2019).

Endophytic microbes directly or indirectly stimulate plant growth and sustain plant health based on their genes involved in metabolic pathways (Baghel et al. 2020). The biocontrol potential of endophytic microbes can be attributed to their ability to colonize plant tissues, produce hydrogen cyanide, and exopolysaccharide, and stimulate novel genes involved in secretion systems and secondary metabolite secretions (Singh et al. 2021). Due to the under-exploration of endophytic fungi in plant disease control; research efforts toward harnessing their bioactive secondary metabolites as biopesticides and incorporation into plant disease control remain fundamental and will help mitigate the effect of synthetic pesticides application on plant growth for improved crop production. Therefore, this review provided an update of the unique features of endophytic fungi, and the mechanisms necessitating their roles in plant protection against phytopathogens.

Main body

Endophytic fungi classification and characteristics in the endosphere

Screening of endophytic fungi against some plant pathogens has been recently intensified by Abaya et al. (2021), due to their effectiveness as a source biocontrol agent. Endophytic microbes enhance plant growth, diseases tolerance and control, and carbon sequestration (Wang et al. 2022). Endophytic fungi inhabiting various plant compartments broadly promote plant growth through different mechanisms classified as direct and indirect mechanisms (Adeleke and Babalola 2022). In the direct mechanism, the endophytes regulate various plant hormones, such as cytokinin, ethylene, and auxins, enhance soil nutrient availability, which includes phosphorus and iron solubilization, siderophore production, and nitrogen fixation; whereas in the indirect mechanism, the endophytes prevent damage to the plants by releasing enzymes, antibiotics, hydrogen cyanide, and volatile compounds which inhibit the activities of pathogens, and induce systemic resistance (Segaran and Sathiavelu 2019).

Suebrasri et al. (2020) reported the production of plant growth-promoting metabolites, such as the enzymes (protease, xylanase, amylase, and cellulase), and indole-3-acetic acid by endophytic fungi, namely; *Daldinia eschscholtzii*, *Diaporthe phaseolorum*, *Macrophomina phaseolina*, *Trichoderma koningii*, and *T. erinaceum* from *Sunchocke* and medicinal plants. It is interesting to note that *M. phaseolina*, a notorious plant pathogen, can be beneficial to plants as reported by Suebrasri et al. (2020); hence, it could be explored for more plant beneficial activities. Also, the strain of *T. koningii* (ST-KKU1) discovered by Suebrasri et al. (2020) is also different from the strain *T. koningii* SMF2, which has previously been reported by Xiao-Yan et al. (2006) to be active against phytopathogens. Sravani et al. (2020) also reported the ability of endophytic fungi from the *Hypocreales* family to prevent their host plant from insect infection by releasing peramine, which prevented nematodes, insects, and other parasites from feeding on them. Also, authors reported secretion of indole-like compounds, such as; diacetamide and sesquiterpene from endophytic fungi, which exerted lethal effects on the other microbes, which could be pathogenic to their host plant. Furthermore, endophytic fungi contributed to the enhancement of root development patterns in their host plants to increase access to water and other nutrients.

Fungal endophytes are classified according to different criteria. For instance; (i) based on ecology, they are classified into clavicipitaceous and non-clavicipitaceous endophytes, (ii) based on the mode of reproduction, they are classified as sexual and asexual endophytes, (iii)

according to transmission, they are classified as vertically and horizontally transmitted endophytes, (iv) according to the source of nutrition, they are classified as biotrophic or necrotrophic endophytes, (v) according to the expression of infection, they are classified as symptomatic and asymptomatic endophytes and (vi) based on the body part they attack, they are classified as foliar and root endophytes (Bamisile et al. 2018). The summary of endophytic fungi classification was presented in Table 1.

Systemic frontline networking of endophytic fungi for plant protection

In recent times, research into the plant-microbial interactions in the below-and-above plant levels has been conceptualized on the endosphere inhabitants. The microbial networking in the root endosphere regions can be influenced by diverse biotic and abiotic factors (Adeleke and Babalola 2021a). The microbial domain tends to show high biomass below ground level compared to the phyllosphere depending on the prevailing environmental factors (Ananda and Sridhar 2002). Urbina et al. (2018) reported a higher microbial population in the below plant parts compared to the stem due to the high rhizodeposition of organic molecules, which mediated microbial activities below ground.

From the literature, studies on fungal isolation from the plant environments capable of sustaining plant growth and health were known with less exploration in phytopathogen control (Bilal et al. 2018). The aforementioned might be due to a lack of information on their transitional networking in the plant-root interface and the type of metabolite produced. Plant roots inhabiting fungi have been classified as natural micro-flora in the endo-rhizosphere, whereas those causing diseases in plants were classified to be found dominant in the soil-root environment (Sylvia and Chellemi 2001). Research into the understanding of association that exists among endophyte colonizing plant roots have enabled scientists to deduce their functional traits by *in vitro* assay (Vélez et al. 2017). The rhizosphere is regarded as a subset of root endophytes because they can easily infiltrate from the external soil environment into the plant roots and colonize the region (Ghaffari et al. 2019). The potential of endophytic fungi to induce plant resistance to environmental stress adaptors and phytopathogens has necessitated more research in their exploration in plant disease management. Additionally, the beneficial plant-microbe cooperation for increased biomass yield can be linked to the diverse functions of these microbes in the environment.

Insights into the community structure and lifestyle of the endophytic fungi in some plants by combining diverse approaches have been reported to determine

their functional profiling (Manzotti et al. 2020). The frontline networking of diverse fungal communities in the plant-root interface can be influenced by environmental factors; biotic, such as pathogens, abiotic, salinity, drought, and high temperature. (Nadeem et al. 2014). Root exudate secretion and substrate metabolism; however, serve as key frontline components and driving factors mediating biodiversity and metabolism of fungal communities' belowground level (Woźniak et al. 2019). Based on the nutrient pool in the soil-root interface, this region has been recognized as a 'hotspot', which facilitates the establishment of microbial communities and colonization of root-associated endophytic microbes (Liu et al. 2019).

Critical evaluation of metabolite secretion, which facilitates plant-microbe communication, is important to reveal the complex dynamics and type of interactions that exist between endophytic microbes and the host plants (Adeleke and Babalola 2021b). An approach by reductionists stated an impressive production of root exudates from plants (Qu et al. 2020). The advancement in endosphere biology through the combined strategies in understanding plant-fungal interactions can help develop a stable approach to fungal biodiversity in plants.

Several beneficial endophytes with bioprospecting in agriculture have been identified in diverse plant species under different climatic and geographical locations (Jia et al. 2016). They can be isolated and identified either by using direct observation or culture-dependent techniques. The direct observation enabled direct visualization of fungal in plant tissues with the aid of a light and electron microscope, which reflect endophytic fungal species and those that cannot be cultured on normal growth media (Nazir and Rahman 2018). However, this method can only be used to detect the presence of endophytic fungi by revealing the hyphal structure without the taxonomic grouping, which suggested the need for the cultivation-dependent method. In the culture-dependent technique, endophytic fungi can be isolated from plant tissues and subjected to conventional or molecular evaluation. The conventional method involves the morphological characterization, whereas molecularly, ribosomal DNA Internal Transcribed Spacer (ITS) sequence analysis was employed (Nazir and Rahman 2018).

Endophytes peculiar to different plants protect them from phytopathogens and promote their growth through different mechanisms. This protection was conferred on the plants to enhance crop productivity and consequently food security. The majority of plant endophytic fungi are active against plant insects; hence, the production of plant insecticides for commercial purposes from these endophytes and their metabolites will go a long way in improving food security.

Table 1 Classification of fungal endophytes

Mode of classification (MOC)	Type-based on MOC	Characteristics	Plant host	Specific endophytic fungi	References
Ecology	Clavicipitaceous	They are associated with sedges and grasses; they phylogenetically belong to the hypocreales family. They help to protect the host plants against insects who feed on them	Hypocreales family (Grasses and sedges)	<i>Balansia</i> spp., <i>Acremonium coenophialum</i> , <i>Epichloe</i> spp., <i>Neotyphodium coenophialum</i> , and <i>Epichloe festucae</i>	Rodriguez et al. (2009), Khiralla et al. (2016), Sravani et al. (2020)
Mode of reproduction	Non- Clavicipitaceous	They are majority associated with conifers, ferns, and non-vascular plants	Non-vascular plants, ferns, and conifers	<i>Fusarium culmorum</i> , <i>T. diticcoides</i> , <i>Curvularia protuberata</i> , <i>Colletotrichum</i> spp. and <i>A. sharonensis</i> ,	Llorens et al. (2019)
	Sexual	These fungi reproduce sexually; their stomata which are produced during sexual reproduction, reduce seed and flower production, a condition referred to as "choke" in grasses	Angiosperm trees, such as <i>Picea abies</i>	<i>Ph. nodosa</i> , <i>Acer saccharum</i> , <i>Epichloe</i> spp., <i>Ph. Piceae</i> and <i>Ph. Scopiformis</i> ,	Schardl and Craven (2003), Schardl et al. (2004), Tannev et al. (2016), Li et al. (2017), Bamisile et al. (2018), Hume et al. (2020)
Mode of transmission	Asexual	This group of endophytes shows no symptoms in plants: however, they colonize plant embryos and thus could be transmitted through the plant seeds	Ericaceous plants (such as <i>Empetrum nigrum</i> , <i>Calluna vulgaris</i> , <i>Vaccinium myrtilloides</i>) and coniferous trees (such as <i>Picea</i> spp., <i>Pinus</i> spp., and <i>Abies</i> spp.)	<i>Phialocephala dimorphospora</i> , <i>Ph. scopiformis</i> , <i>Neotyphodium</i> spp., <i>Ph. Fortinii</i> , and <i>Ph. sphaeroides</i>	Schardl and Craven (2003), Schardl et al. (2004), Tannev et al. (2016), Li et al. (2017), Bamisile et al. (2018), Hume et al. (2020)
	Vertically transmitted	It involves the transmission of fungi through the seeds of plants. There are often differences in the proportion of the offspring of plants that carry the seeds; also, there could be variation in the concentration of the mycelia and secondary compounds present in the seeds	Grasses, e.g., switch grass, <i>Rumex acetosa</i> , <i>Senecio vulgaris</i> , <i>C. nigra</i> , <i>Plantago lanceolata</i> , <i>Papaver rhoeas</i> , and <i>Centaurea cyanus</i>	<i>Epichloe</i> spp., <i>A. alternata</i> and <i>C. spheerosperum</i>	Hodgson et al. (2014), Gundel et al. (2017)
	Horizontally transmitted	The majority of the fungi in this group are natural inhabitants of the soil from which they get into the plants. However, they could be transmitted through the air or air-borne spores	<i>Panicum rigidulum</i> <i>Lolium perenne</i>	<i>Balansia henningsiana</i> <i>Neotyphodium lolii</i>	Ren and Clay (2009), Wiewióra et al. (2015)
Sources of nutrition	Biotrophs	They derive their nutrients from the tissue of living matters	<i>Oryza sativa</i>	<i>Aspergillus</i> spp., <i>Magnaporthe oryzae</i> , <i>Penicillium Chrysogenum</i> , and <i>Hymenochaete</i> sp.	Su et al. (2013)
	Necrotrophs	They kill the host cells and live in them	<i>Syngonium podophyllum</i>	<i>Bjerkandera fumosa</i> , <i>Phanerochaete</i> spp., <i>Phlebiopsis flavidoliba</i> and <i>Hymenochaete ustulata</i>	García-Guzmán et al. (2017)

Table 1 (continued)

Mode of classification (MOC)	Type-based on MOC	Characteristics	Plant host	Specific endophytic fungi	References
Expression of infection	Symptomatic	They cause diseases in plants and show symptoms	<i>Vitis vinifera</i>	<i>Acremonium</i> spp., <i>Cadophora</i> spp., <i>Coniothyrium</i> spp., <i>Fomitiporia</i> spp., <i>Hypoxylon</i> spp., <i>Paecilomyces</i> spp., and <i>Paraphoma</i> spp.	Nerva et al. (2019)
	Asymptomatic	They cause diseases in plants and show no symptoms	<i>Vitis vinifera</i>	<i>Leptosphaeriulina</i> spp., <i>Microdiplozia</i> spp., <i>Scopulariopsis</i> spp., <i>Fusarium</i> spp., and <i>Myrothecium</i> spp.	Nerva et al. (2019)
Body part attacked	Foliar	They exist on the leaves and stems of plants	<i>Theobroma cacao</i>	<i>Colletotrichum tropicale</i>	Christian et al. (2017), Christian et al. (2019)
	Root	They are generally found in the root of plants	<i>Phoenix dactylifera</i>	<i>Aspergillus tubingensis</i> , <i>Corynespora cassicola</i> , <i>Clonostachys rosea</i> , <i>Penicillium commune</i> , <i>Beauveria bassiana</i> , <i>Fusarium solani</i> , <i>Campanella olivaceonigra</i> , <i>Phomopsis lagerstroemiae</i> , <i>Ilyonectria radiciicola</i> , <i>Aspergillus sclerotiorum</i> , <i>Phomopsis lagerstroemiae</i> , and <i>Fusarium equiseti</i>	Mahmoud et al. (2017)

Mechanisms employed by endophytic fungi in phytopathogen control

Fungal induced resistance in plant

Endophytic fungi colonize the internal part of both monocotyledonous and dicotyledonous plants, help to induce resistance, and promote plant growth in a diverse number of systems (Waqas et al. 2012). Though, most endophytes solely colonize the root, inducing a system that protects other parts of the plant (Adeleke et al. 2021). Induced resistance to plant pathogen is a preventive mechanism that is actively favored by the host plant's chemical and physical barriers and induced by both abiotic and biotic factors (Wani et al. 2016). These agents (especially fungi) induce exchangeable signals in the host plant, so that they activate an acquired response to subsequent threats from the pathogen(s). An induced response is usually triggered by some agents that impel distinctive expression of genes, metabolic changes, and protein synthesis. The plant's metabolic swift and change in the eligibility of the plant as a host has led to the reduction in disease level (Latz et al. 2018). As mentioned above, both biotic and abiotic factors can induce host response locally or systemically. The activation of defense mechanisms produced by plants for protection against pathogens is usually referred to as priming (Martinez-Medina et al. 2016). Plant-induced resistance is most often linked to the mobilization potential for cellular defense responses against nonself.

Molitor et al. (2011) reported the mechanisms of *S. indica* in inducing plants' resistance to barley powdery mildew. Authors inferred that the induced resistance to powdery mildew by *S. indica* can be a result of physiological responses by reducing pathogen penetration via an increase in local cell death and papillae formation of barley with an up-regulation of *HvPRI7b* (a *PR* gene) in foliage. Other changes in the expression of *PR* gene in the plant root were also noticed. Likewise, genes denoting *Hsp70*, *PR1*, *PR2*, and *BCI-7* (barley chemically induced 7) are a set of genes instigating protein synthesis, which activate defense reactions as a result of inoculating barley with *Blumeria graminis* f. sp. *hordei* (Molitor et al. 2011). These *PR*-complex are exclusively involved in both direct and indirect plant growth promotion and antifungal activities.

An investigation conducted on rice roots showed that *Harpophora oryzae* suppressed the effect of *Pyricularia oryzae* in rice (Su et al. 2013). Also, Polonio et al. (2015) showed the effect of endophyte—*Diaporthe citri* on Guaco (*Mikania glomerata* Spreng.) associated pathogens, such as *Fusarium solani* and *Didymella bryoniae*. Endophytic fungi induced antimicrobial activity against both pathogens and also increased the growth of the plant (Table 2). Furthermore, *OsWRKY4*—an

SA-dependent transcription gene known to induce resistance against rice blast was up-regulated in research by Shimono et al. (2007) using *Harpophora oryzae*—an endophytic fungus, to prevent root-necrotization by *Pyricularia oryzae* infection in rice. Efforts to unravel fungal metabolites associated with plant resistance for commercial purposes in striving against phytopathogens have been documented (Peng et al. 2021). Many natural bioproducts, such as terpenoids, polyketides, steroids, quinones, flavonoids, alkaloids, and peptides, have been extracted from endophytes, with most reported to have antimicrobial activities against plant pathogens (Latz et al. 2018).

The combined effect of diverse microorganisms in the root endosphere can trigger synergistic effects and the production of BCAs used to control the growth of phytopathogens (Rojas et al. 2020). Often based on specificity, endophyte-induced metabolites can share similar pathways to induce metabolism. A familiar instance is the recent finding that most endophytic fungi produce anticancer substances in *Taxus brevifolia* (El-Bialy and El-Bastawisy 2020). But, many of these endophytes were discovered working simultaneously with other organisms as producers (Heinig et al. 2013).

To confirm the potency of an antimicrobial substance produced by an endophyte against pathogens, most importantly, close contact with the pathogen should be confirmed. Although, it is quite difficult to confirm this finding since endophytic fungi are embedded in the plant endosphere and the rate of metabolite synthesis may be hard to quantify. Nonetheless, metabolites induced by plant endophyte could be translocated through the microorganism to the base of these pathogens within the plant; whereas, organic compounds secreted can easily spread to the site of infection (Mejía et al. 2008). Meanwhile, it is yet to be confirmed whether the number of compounds secreted at the site of infection could be enough to control the invasion of phytopathogens, or may be other mechanisms are involved in the plant pathogen management.

Endophytic fungi-derived compounds activating plant defenses

Just like human responses, nonself/microbial components are easily recognized by the plant as specific foreign substances. Host plants can easily be prepared for potentially harmful microorganisms by inducing defense responses. Although both endophytes and pathogens are recognized by the host plant, in the same manner, the response to both foreign bodies is quite different (Wani et al. 2016). Invariably, the favorable coexistence between endophyte and host plant revealed that fungal-induced resistance remains an important mechanism

Table 2 Endophytic fungi and mechanisms of phytopathogen management and disease suppression

Endophyte(s)	Host plant	Pathogen	Mode of action (Biocontrol process)	Inference	Reference
Endophytic fungi belonging to genera, viz., <i>Aspergillus</i> , <i>Botrytis</i> , <i>Colletotrichum</i> , <i>Penicillium</i> , etc	<i>Panax notoginseng</i>	<i>Mycocentrospora acerina</i> <i>Fusarium oxysporum</i> , <i>F. solani</i> , <i>Alternaria panax</i> , <i>Phoma herbarum</i> ,	Bioactive compounds production	Endophytes isolated from <i>P. notoginseng</i> protected plants against root disease-causing organisms	Zheng et al. (2017)
<i>Cladosporium cladosporioides</i>	<i>Zygophyllum mandavillei</i>	<i>Pseudomonas syringae</i> , <i>Xanthomonas oryzae</i> , <i>Aspergillus flavus</i> , <i>Fusarium solani</i>	Antimicrobial metabolites, viz., 3-phenylpropionic acid, 1-acetyl-17-methoxy aspidospermidin-20-ol, Isocladosporin, Cladosporin, etc	3-phenylpropionic acid was the most active compound against potential fungal and bacterial phytopathogens	Yehia et al. (2020)
<i>Cryptosporiopsis</i> sp., <i>Phialocephala sphaeroideis</i>	<i>Picea abies</i>	<i>Botrytis cinerea</i> , <i>Phytophthora pini</i> , <i>Heterobasidium panivporum</i>	New antimicrobial metabolites were secreted by both endophytes	<i>P. sphaeroideis</i> inhibited all pathogens with improved growth of the plant, while <i>Cryptosporiopsis</i> sp. gave a stronger inhibitory effect but retarded the root growth of Norway spruce	Terhonen et al. (2016)
<i>Trichoderma asperellum</i>	<i>Lactuca sativa</i> L	<i>Curvularia aeria</i> , <i>Corynespora cassicola</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Baiyee et al. (2019)
<i>Trichoderma viride</i>	<i>Spilanthes pariculata</i>	<i>Alternaria solani</i> , <i>Fusarium solani</i> , <i>Colletotrichum acutatum</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Talapatra et al. (2017)
<i>Penicillium simplicissimum</i> , <i>Leptosphaeria</i> sp.	<i>Gossypium arboretum</i> L	<i>Verticillium dahlia</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Yuan et al. (2017)
<i>Diaporthe</i> sp., <i>Leptosphaeria</i> spp., <i>Nigrospora oryzae</i>	<i>Olea europaea</i> L	<i>Colletotrichum acutatum</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Landum et al. (2016)
<i>Fomitopsis</i> sp., <i>Fusarium solani</i> , <i>Nigrospora sphaerica</i> , <i>Purpureocillium lilacinum</i>	<i>Sophora tonkinensis</i> Gapnep	<i>Colletotrichum gloeosporioides</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Yao et al. (2017)
<i>Trichoderma citrinoviridae</i>	<i>Cornus florida</i>	<i>Macrophomina phaseolina</i> , <i>F. solani</i> , <i>F. oxysporum</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Mmbaga et al. (2018)
<i>Paenibacillus polymyxa</i>	<i>Morinda citrifolia</i> L	<i>Botrytis cinerea</i> , <i>Alternaria panax</i> , <i>Rhizoctonia solani</i> , <i>Pythium</i> spp.	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Park et al. (2019)
		<i>Aspergillus aculeatus</i>	Antagonistic activity with mycoparasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Liu et al. (2018)

Table 2 (continued)

Endophyte(s)	Host plant	Pathogen	Mode of action (Biocontrol process)	Inference	Reference
<i>Rhizopycnis vagnum</i>	<i>Zingiber officinale</i> Rosc	<i>Fusarium oxysporum</i> , <i>Sclerotium rolfsii</i> , <i>Rhizoctonia solani</i>	Antagonistic activity with myco-parasitism	Endophytes inhibited the growth of highlighted pathogen(s)	Anisha et al. (2018)
<i>Paraconiothyrium variabile</i>	<i>Cephalotaxus harringtonia</i>	<i>Fusarium oxysporum</i>	The Biocontrol process include the production of metabolites, viz., 13-oxo-9,11-octadecadienoic acid, beauvericin	Metabolites produced from endophyte showed inhibitory effect against <i>F. oxysporum</i>	Combès et al. (2012)
<i>Induratia coffeana</i> , <i>I. yucatanensis</i>	<i>Phaseolus vulgaris</i> L	<i>Pseudocercospora griseola</i> , <i>Sclerotinia sclerotiorum</i> , <i>Colletotrichum lindermuthianum</i>	Antagonistic activity with myco-parasitism	Both species of <i>Induratia</i> control diseases caused by the three pathogens on common beans	Mota et al. (2021)
<i>Hypoxyton anthochroam</i> , <i>Nodulisporium</i> spp.	<i>Solanum lycopersicum</i> var. <i>cerasiforme</i>	<i>Fusarium oxysporum</i>	Volatile organic compounds synthesized include; Phenylethyl alcohol, 2-methyl-1-butanol, ocimene, terpinolene, etc	VOC showed antifungal activity both <i>in planta</i> and <i>in vitro</i> assessment	Medina-Romero et al. (2017)
Fungal genus from <i>Aspergillus</i> , <i>Chaetomium</i> , <i>Paecilomyces</i> , <i>Penicillium</i>	<i>Cannabis sativa</i> L	<i>Botrytis cinerea</i> , <i>Trichothecium roseum</i>	Antagonistic activity with myco-parasitism	Endophytes inhibited the growth of phytopathogens	Kusari et al. (2013)
<i>Diaporthe citri</i>	<i>Mikania glomerata</i> Spreng	<i>Fusarium solani</i> , <i>Didymella bryoniae</i>	Antagonistic activity with myco-parasitism	Endophytes induced antimicrobial activity against both pathogens	Polonio et al. (2015)
<i>Bipolaris</i> sp., <i>Fusarium</i> sp., <i>Phoma</i> sp., etc	<i>Vitis labrusca</i> L	<i>Alternaria</i> spp., <i>Glomerella</i> spp., <i>Sphaeloma</i> spp.	Antibiosis, parasitism, and production of lytic enzymes	Biological control agents help in the control of phytopathogens	Felber et al. (2016)
<i>Muscodora yucatanensis</i> , <i>Penicillium commune</i> , <i>A. oryzae</i>	<i>Monarda citriodora</i>	<i>Sclerotinia</i> spp., <i>Colletotrichum capsica</i> , <i>A. flavus</i> , <i>A. fumigatus</i>	Antagonistic activity by direct contact suspected to have bioactive compounds	Endophytes showed biocontrol activity against highlighted pathogens	Katoch and Pull (2017)
<i>Lasioidiplodia theobromae</i> , <i>Phoma herbarum</i> , <i>Schizophyllum commune</i>	<i>Piper hispidum</i> Sw	<i>Alternaria alternata</i> ,			
<i>Colletotrichum</i> spp., <i>Phyllosticta citricarpa</i> , <i>Monilophthora perniciosa</i>	<i>P. herbarum</i> and <i>S. commune</i> produce proteolytic enzymes	Both endophytes had a high enzymatic halo and were able to protect the plant against pathogens	Orlandelli et al. (2015)		
<i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pichia</i> spp., <i>Postaltopsis</i> sp., <i>Xylaria</i> sp.	<i>Camellia oleifera</i>	Anthracnose phytopathogenic fungus	Mycoparasitism	Endophytes inhibited the growth of pathogens (especially <i>Oidium</i> sp.)	Yu et al. (2018)
<i>Apoaspora terricola</i> , <i>Aureobasidium pullulans</i> , <i>Bjerkandera adusta</i> , <i>Colletotrichum boninense</i> , <i>C. gloeosporioides</i> , <i>Flavodon flavus</i> ,	<i>Vitis labrusca</i> L	<i>Fusarium oxysporum</i> f. spp. <i>herbomantis</i>	Antibiosis against plant pathogens	Both <i>F. flavus</i> and <i>C. gloeosporioides</i> showed antagonistic activity against <i>F. oxysporum</i>	Brum et al. (2012)

Table 2 (continued)

Endophyte(s)	Host plant	Pathogen	Mode of action (Biocontrol process)	Inference	Reference
<i>Cladosporium</i> sp., <i>Ophiognomonia</i> sp., <i>Trichoderma</i> sp., etc	<i>Coffea arabica</i> L. cultivar IAPAR-59	<i>Glomerella</i> spp. (CNPUV 378), <i>Colletotrichum</i> spp., <i>Sclerotinia sclerotiorum</i>	Antagonistic effect against phytopathogens	Endophytes inhibit the growth of pathogens	Bongiorno et al. (2016)
<i>Muscador coffeanum</i> , <i>M. vitigenus</i> , <i>M. yucatanensis</i> , <i>Simplicilium</i> sp.	<i>Coffea arabica</i>	<i>Rhizoctonia solani</i> (LAPS 369), <i>Fusarium oxysporum</i> (LAPS 152), <i>Phoma</i> spp. (DFP 01), <i>F. solani</i> (LAPS 298), <i>F. verticillioides</i> (CML 1896), <i>Cercospora coffeicola</i> (CML 2984), <i>Pestalotia longisetula</i> (DFP 02), <i>A. ochraceus</i> (SCM 1.15)	Volatile organic compounds produced	VOC produced by endophytes, which helps to inhibit the growth of pathogens	Monteiro et al. (2017)
<i>Diaporthe citri</i> , <i>Phomopsis</i> spp.	<i>Sapindus Saponaria</i> L	<i>Fusarium solani</i> , <i>Glomerella</i> spp., <i>Monilophthora perniciosa</i>	Amylase, pectinase, and cellulase produced	Phyto-protective properties of these compounds were observed against pathogens	Santos et al. (2019)

used by endophytic microorganisms in disease suppression (Fig. 1). Normally, specific endophytic fungal components, viz., cell wall, lipids, protein substances, volatile compounds, BCA, and some molecules with hormonal responses, are usually recognized by the host plant. These compounds/components are selective endophyte-derived compounds that induce plant defense mechanisms (Latz et al. 2018).

Components of microbial origin are oftentimes referred to as MAMPS—microbe-associated molecular patterns or PAMPS pathogen-associated molecular patterns, which induce MAMP/PAMP-triggered immunological response (Nürnberg and Kemmerling 2009). Components of the fungal cell wall, such as β -glucans and chitin, are referred to as MAMPs, they are usually recognized by the receptors of plants to trigger immune responses. Endophytic secretions, such as peptides and proteins, have been described by most researchers as agents that trigger host plant responses (Rojas et al. 2020). Other secreted enzymes, viz., cellulase, xylanases, and chitinases, were produced as a result of infection also induce plant defense and are easily identified by hosts via their decomposed products (Druzhinina et al. 2011).

Proteins rich in cysteine and fungal effectors are secreted as a result of endophytic and pathogenic inhabitation processes to increase host plant compatibility, by inducing physiological and defense responses (Ku et al. 2020). Nonetheless, different studies have shown that compounds produced to inhibit the growth of competing microorganisms can also instigate resistance (Akinola and Babalola 2021). The above-mentioned products obtained from endophytic fungi have the complexity and potential to induce plant defense responses necessary to reduce the menace posed by plant pathogens and other soil-related anomalies.

Hormonal signaling and its ability to induce resistance

Plant hormones are crucial in the transmission of structural and comprehensively inherent resistance. The systemically induced plant resistance can be classified into two; namely; ISR-induced systemic resistance and SAR—systemically acquired resistance. Ethylene and hormonal jasmonic acid (JA) are the most important secretion produced in ISR, whereas SA—salicylic acid plays a pivotal role in systemically acquired resistance (Latz et al. 2018). The coherent relationship among hormonal responses is induced by the coexistence of ethylene, JA, and SA maintains defensive responses in the plant (Latz et al. 2018). For instance, the defensive response induced by the biological agents, viz., *Serendipita indica*, *Penicillium* sp., and *Trichoderma asperellum*, has induced the production of ethylene and JA-dependent systemic resistance that plays important role in preventing the inhabitation

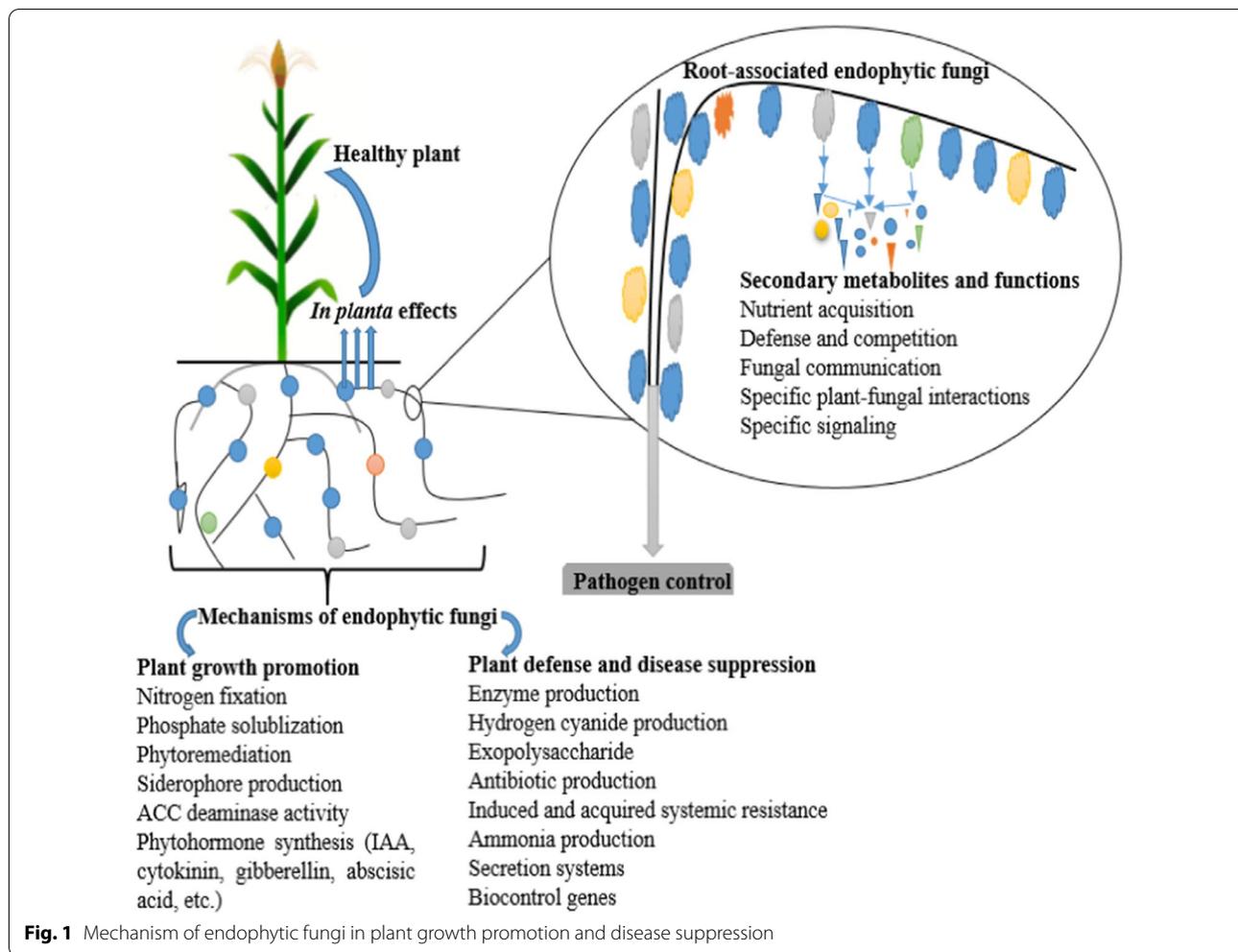
of host pathogens (Hossain et al. 2008). Meanwhile, *S. indica* instigated other resistance pathways different from ethylene/JA in other pathophysiological responses. In another scenario, SA-dependent pathway is induced in a *T. asperellum* inhabited plant (Yoshioka et al. 2012). This showed that hormonal responses and interaction with the host plant were very complex, withal, numerous events; and cross-communication is normally involved in plant-induced responses. Microbial inhabitation changes a plant's normal reflexes and profile, at times, rather than affecting only a single hormonal response, it brings together a couple of them. Nevertheless, the coexistence between microbial strain and the host of the inducing agent also determines variations in hormonal responses. Despite the tremendous progress in the studies on signal transfer in induced resistance, there is still a lacuna in attributing functions to each hormone in signal transduction, especially in complex systems. Therefore, there is a need to intensify the defense mechanisms in a plant and adopt it as a biomarker to detect an induced resistance.

Use of plant defense mechanisms to detect induced resistance

An induced resistance occurs as a result of activated plant-defense mechanisms to make the plant less susceptible to a variety of pathogens. Most of these mechanisms are activated simultaneously to help strengthen plant physical barriers, and secretion of pathogen-repellants in the form of proteins and enzymes with antimicrobial properties to prevent phytopathogens (Farhangi-Abri and Ghassemi-Golezani 2019).

To study if an endophytic fungus induces a resistance mechanism against a specific pathogen, two (2) criteria are used to test and classify plant responses. Firstly, the induced responses should control the targeted plant pathogen(s). There should be proven that fungal-induced response could effectively eradicate the pathogens, and expressions observed therewith should be related to hindering pathogen infection. Secondly, the elimination process of phytopathogen should be correlated with Koch's postulate. This can be verified by noticing the defense response expression after introducing the pathogen to the plant. In essence, adopting the principle of exclusion is an acceptable condition to evaluate the effectiveness of induced resistance in plant protection. With that said, excluding a direct in vitro assessment of an induced resistance assumes the effect of the induced response to the pathogen is unacceptable.

Another conserved process is the ability to strengthen a plant's structural barriers to resist the easy invasion of pathogens and reinforcement of cell wall appositions, which might have been involved (Waller et al. 2005). According to different studies, this effect occurred as a



result of inducing agents. For instance, a study on *Trichoderma harzianum* (T-22) showed the expression of an enzyme (phenylalanine ammonia-lyase—PAL) involved in lignin formation was well enhanced in maize (Shoresh et al. 2010), whereas in the case of another strain *T. harzianum* (T-203), the cortical and epidermal cell walls of cucumber fruit were strengthened and the process was confirmed to have been induced by intercellular inhabitation of endophytic fungi (Yedidia et al. 1999). Systemic introduction of inducing agents has been very useful in the promotion/activation of important proteins and metabolites in plants, with antimicrobial properties that are very effective against plant pathogens. Another example of a useful metabolite was phytoalexin-type compounds reported by Oliveira et al. (2016). The pathogen-related (PR) proteins produced as a result of the colonization of endophytic fungus also perform other roles, such as stress response and antimicrobial properties. These metabolites include peptides and enzymes, viz., thaumatin-like proteins, lipid transfer proteins, and

thionins (Sels et al. 2008). In research by Lahlali et al. (2014), a plant-related protein (PR2) — β -1, 3-glucanase was enhanced in oilseed rape plants infected by *Plasmodiophora brassicae* when an endophytic fungus—*Heteroconium chaetospira* colonized the plant. Also, Combès et al. (2012) detected a systemic resistance induced by an endophytic fungus—*Paraconiothyrium variable* on *Cephalotaxus harringtonia* infected by *Fusarium oxysporum*, which led to the production of important metabolites such as 13-oxo-9,11-octadecadienoic acid and beauvericin that are capably inhibiting the growth and pathogenic effect of *F. oxysporum* as shown in Table 2.

An induced resistance activated by *F. solani* (strain Fs-K)—infested tomato enhanced the expression of thaumatin-like (PR5) and endo-proteinase (PR7) enzymes in the plant (Kavrulakis et al. 2007). More so, Waller et al. (2008) also hypothesized the up-regulation of protein *HvPR17b* was suspected to have antifungal activity in a barley-infested with endophytic—*Serendipita indica* against *Blumeria graminis* f. sp. *hordei*. The synergistic

effect of *Fusarium graminearum* and *S. indica* on barley was also reported by Deshmukh and Kogel (2007) with the reduced expression of pathogen-related genes (*PR1b* and *PR5*), which means *PR* genes are not always involved/pronounced in all systems.

Antibiosis activities of endophytic fungi against plant pathogens

Antibiosis—an antagonistic relationship involving endophytic fungal control of potential plant pathogens using metabolic substances was produced by endophytes. A purified form of *Efe-AfpA* mined from an apoplastic fluid of endophyte-inoculated red fescue showed anti-parasitic activity against *Sclerotinia homoeocarpa* (Ambrose and Belanger 2012). The same result was also observed in the recombinant product of *Efe-AfpA* expressed gene found in *Pichia pastoris*. In a transcriptome study to detect the percentage protein (*Efe-AfpA*) produced from the endophytic relationship between *Epichloë festucae* and *Festuca rubra* sp., a 6%—*Efe-AfpA* was produced from the fungal transcriptome. The product mined from the study was observed to have the same property as the product secreted in a relationship between *Aspergillus* spp. and *Penicillium* sp. as reported by Tian et al. (2017).

The synergy between endophytic funguses—*Paraconiothyrium* strain SSM001 and a yew tree producing Taxol against wood-decaying fungus was investigated by Rafiqi et al. (2013). Although, the yew tree usually forms bark cracks that allow easy penetration of pathogen. Meanwhile, the endophytic fungus was observed growing toward these cracks in a way to prevent Taxol accumulation and also down-regulated the transcription of *Taxus* genes, viz., DXP reductoisomerase and taxadiene synthase, that is very crucial for Taxol secretion. An *in vitro* assessment of strain SSM001 endophytic fungus and Taxol treatment prevented the growth of important wood-decaying fungal species, such as: *Perenniporia subacida*, *Phaeolus schweinitzii*, and *Heterobasidion annosum*, meanwhile, the growth of the endophyte strain SSM001 was not hindered by Taxol (Soliman et al. 2015).

Competition

Microbial competition remains an important factor determining plant tissue inhabitation and a probable way endophytes inhibit pathogens from colonization (Martinuz et al. 2012). The endophytic fungus colonizes plant tissues systemically and locally, within or outside the tissues. Through this method, rapid inhabitation and feeding on available nutrients are easily explored, and also occupy the space that could have been filled by potential pathogens. A study by Mohandoss and Suryanarayanan (2009) on mango leaves showed that the fumigation of

the tree eliminated specific endophytes, creating space for pathogens to grow.

Phyto-pathological control mechanisms involving competitive exclusion incorporate the co-occurrence of other mechanisms and also require endophytic colonization of intracellular plant parts where the pathogen might have attacked. For instance, the treatment of a sterile seed with endophytic fungus isolated from a cacao tree reduced the effect of *Phytophthora* spp. on the plant leaves (Arnold et al. 2003). The colonization of the oilseed roots by an endophytic fungus—*Heteroconium chaetospira*, negatively correlated with the symptoms of clubroot disease (Lahlali et al. 2014). Withal, an increase in the inoculum size of the pathogen reduced the control effect, showing the restraints of competition. Competitive exclusion could be well studied using *in planta* microscopic assessment and quantification of endophyte biomass related to phytopathogen management. To evaluate endophyte—pathogen *in planta* interaction, visualization using microscopy is advisable, when investigating pathogen strains and fungal BCA (Latz et al. 2018). *In situ* detection of metabolite distribution, microorganism involved and genomic evaluation of the role of mined metabolites could be determined using molecular 3D cartography-mass spectrometry as described by Floros et al. (2017).

Mycoparasitism

Fungal parasitism involves the direct reliance of a fungus on another fungus for nutrients. The process of mycoparasitism occurs either through necrotrophic or biotrophic relationships. In necro-trophism, parasites live on the dead cells of the host, while bio-trophism is a situation, whereby the parasite takes nutrients from a living host (Kim and Vujanovic 2016).

Normally, *in planta* verification of mycoparasitism is very hard, since the transfer of nutrients among microorganisms is very tedious to detect. In essence, most studies claiming mycoparasitism only based their verifications on circumstantial shreds of evidence. The close relationship between two fungi is not enough to claim a mycoparasitism, rather they are referred to as a fungicolous relationship. Mycoparasitism may occur directly or indirectly. In indirect fungal-parasitism, a metabolite produced by the parasite releases nutrients from the host at a distance, while direct contact with the prey is referred to as direct mycoparasitism (Latz et al. 2018). In either case, the parasite secretes some metabolites to release host nutrients such as toxins, antibiotics, and cell wall degrading enzymes (Kim and Vujanovic 2016). For instance, a study by Chamoun et al. (2015) showed the production of specialized compounds in a relationship between *Manatephorus cucumeris* and *Stachybotris elegans*, where *S. elegans* was preying on *T. cucumeris*.

A lot of researchers misplace mycoparasitism and antibiosis with potential intermingling relatedness making it very hard to differentiate interactions, but this has shown that parasitic relationships among microorganisms could employ several mechanisms to prey on each other.

Since microbial interactions are easily studied using conventional methods, the inhibitory relationship among microorganisms becomes very easy to study using traditional methods, such as microscopy techniques and culturing in Petri dishes than *in planta* screening. Using simple microscopic methods, mycoparasite is observed having direct contact with the host either by coiling around the hyphae of the prey for easy acquisition of nutrients. This relationship was demonstrated in a study by Donayre and Dalisay (2016). An endophytic fungus, *Geotrichum* sp. isolated from *Echinochloa glabrescens* was observed having a direct mycoparasitic relationship with a soil-borne pathogen, *Thanatephorus cucumeris*. Likewise, three (3) endophytic fungi isolated from *Phragmites australis* were observed penetrating and coiling around the hyphae of soil-borne pathogens to degrade their cytoplasm, meanwhile, other degrading enzymes, viz., β -1, 3-glucanase, and extracellular cell wall degrading enzymes, were involved in the process (Cao et al. 2009).

Challenges associated with endophyte biocontrol mechanisms

For an in-depth understanding, utilization, and selection of endophytic fungi, an assessment of the biology behind the interaction between pathogen, host plant, and endophytic fungus is required in addition to the physiological activities involved in the tie-in. Some important principles are generally acceptable for the study of endophytic fungus and biological control agents (BCAs). These include; (i) activation of plant defense mechanism induced by endophyte, (ii) inhibition via mycoparasitism, (iii) inhibition through antibiosis, and (iv) competition for nutrient and space (Latz et al. 2018). Also, the most times and several mechanisms may be activated at the same time. Nutrient acquisition for plant growth promotion or modification of the level of plant growth hormone can generally improve plant health and disease suppression (Berthelot et al. 2016). Studying the complex interaction between pathogen, host plant, BCAs and the process of pathogen inhibition are complicated to study. To better explore the relationship between highlighted factors, several questions are raised and these include; (i) are the mechanisms involved in BCAs really assessable within the tissue of plant (*in planta*)? Because most mechanisms associated with endophytic metabolite production in plants are usually performed under *in vitro* conditions. Putting out one of the factors from the tripartite

interaction put a lacuna on the importance of endophytes on disease suppression in the plant. Therefore, evaluating endophyte-pathogen interaction using *in vitro* assessment will only result in false conclusions. For instance, an *in vitro* experiment on *Pseudozyma flocculosa*- an endophytic yeast suggested to inhibit the growth of *Blumeria graminis* in barley via antibiosis, but after adopting cellular microscopy and transcriptomics to study the control mechanism, it was concluded that the parasitic relationship was mycoparasitism not antibiosis (Laur et al. 2018). (ii) what are the pattern and colonization methods of a biological control agent? Understanding the mechanism involved in BCA infiltration and pattern will help link intra-and-intercellular endophytic structure to a disease suppression mechanism (Compant et al. 2005), (iii) what is the pathosystem involved in the BCA mechanism of action? Understanding the mechanisms of biological control agents in phytopathogen management is also very important. Conclusively, if a BCA was isolated from an external surface and identified to be of endophytic origin when applied *in planta*, does the BCA grow intracellularly? It is necessary to confirm the function of the biological control agent within the plant tissue, to confirm its potency in phytopathogen control (Busby et al. 2016).

Conclusions

Endophytic microbes employ direct and indirect mechanism options in plant growth promotion and protection against pathogens. Exploring endophytic microbes as bioinoculants, upon inoculation can cause changes in the plant's physiological and phenotypic modifications, thus boosting plant tolerance to biotic and abiotic stressors. The biotechnological importance of valuable metabolites produced by endophytic fungi, which stimulate antibiosis against phytopathogens for plant protection is less to be fully explored in plant disease management.

The combined application of culture-dependent and culture-independent techniques helps in the predictive functional analysis of notable genes involved in phytohormone synthesis, secretion systems, biocontrol, and synthesis of cellular components, metabolic pathway, and secondary metabolites (SM) from endophytic microbes. The presence of biocontrol genes in some endophytic fungi was suggested their ability to control plant diseases. Studies have successfully shown the biocontrol activity of endophytic fungi, which promise to be used in the synthesis of certain novel BCA to confront the challenges associated with phytopathogens control in plants. Nevertheless, how endophyte infiltrates plant endosphere is still a question that demands clarification by researchers.

The SM biosynthesis potential of endophytic fungi is characterized by complex biocontrol activity, which can be explored as valuable bioproducts. Hence, providing

updated information on the plant growth-promoting endophytic fungal species or yet-to-be culture endophytic fungi will help discover their potential in producing desirable metabolite compounds, which can be harnessed as a biocontrol agent in the control of plant diseases. For endophytic fungi to be successfully used in sustaining plant health, it is necessary to understand factors mediating endophyte bioactivity on disease suppression, source and type of BCAs, how they are produced, and the amount required to cause pathogen inhibition. This review further recommended future studies on how a specific amount of BCAs from endophytic fungi can be obtained to confront challenges associated with the use of endophyte fungi in plant disease suppression.

Abbreviations

BCA: Biological control agent; MAMPS: Microbe-associated molecular patterns; PAMP: Pathogen-associated molecular patterns; ISR: Induced systemic resistance; SAR: Systemically acquired resistance; JA: Jasmonic acid; SA: Salicylic acid; PAL: Phenylalanine ammonia-lyase.

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Author contributions

BSA and OOB had the idea for the review article and suggested the review topic. BSA, MSA, and SAA performed the literature search and wrote the first draft. BSA revised and formatted the manuscript. OOB made substantial and technical contributions to the structure of the various manuscript drafts. All authors read and approved the final revised manuscript.

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