

Fungal Endophytes and Agricultural Plant Protection

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Virtually all examined plant species harbour fungal endophytes which asymptotically infect or colonize living plant tissues, including leaves, branches, stems and roots. Endophyte-host interactions are complex and span the mutualist–pathogen continuum. Notably, mutualist endophytes can confer increased fitness to their host plants compared with uncolonized plants, which has attracted interest in their potential application in integrated plant health management strategies.

endophytic fungus

plant protection

biocontrol

antagonism

defence activation

1. Introduction

Endophytes are microorganisms that live inside the plant for all or part of their life cycle while not causing damage or disease symptoms in their host most of the time ^{[1][2]}. Almost all vascular plants examined to date harbor endophytes that are believed to originate in the rhizosphere and phyllosphere and enter the host plant through natural openings or wounds.

Endophytic microorganisms promote plant growth and provide protection against pests and pathogens through different mechanisms ^{[3][4][5]}. Endophytes produce and secrete secondary metabolites/biochemicals that suppress/reduce the negative effects from plant pathogens, including volatile compounds that are able to suppress pathogen growth ^[6]. Other endophytes protect their host plant by inducing plant defence mechanisms ^[7], which can be achieved by systemic acquired resistance (SAR) or induced systemic resistance (ISR) ^{[4][8]}. An example of a host-induced defence mechanism is *Piriformospora indica*, inducing a jasmonic acid-dependent defence response in *Arabidopsis thaliana* by co-inoculation with a pathogen ^[9]. Some endophytes may demonstrate their biocontrol potential by secreting antifungal and antibacterial compounds, thereby inhibiting the competition of pathogens, or they may exhibit mycoparasitic activity (i.e., parasitism of one fungus by another) ^[10]. Recently, it has been shown that an *Enterobacter* sp. strain isolated from finger millet (*Eleusine coracana*) is able to suppress the grass pathogen *Fusarium graminearum* in the root system of its host plants and simultaneously produces several antifungal compounds that kills the fungus ^[11]. Endophytes also directly compete with the host pathogens for space and nutrients ^{[12][13]}. Foliar application of endophyte-free leaves of *Theobroma cacao* with a mixture of endophytes protected against leaf necrosis and leaf mortality in leaves challenged with a *Phytophthora* sp. ^[14]. This protection was localized in inoculated leaves and could not be readily correlated with in vitro endophyte interactions, suggesting that complex interspecific interactions (such as competition and mutual antagonism) may play an important role in mediating host defence outcomes.

In addition to protecting their host plants against pathogens directly, several endophytes have plant growth promoting (PGP) properties that result in a stronger plant. These PGP endophytes not only provide nutrients such as nitrogen, phosphate and/or iron, but can facilitate plant growth and development by growth stimulation [15]. Associated with roots, PGP microbes can produce several chemical compounds that influence plant growth and development. These include the plant hormones indole-3-acetic acid (IAA), gibberellins, and cytokinins, and/or 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity [16][17]. The latter was shown to promote plant mycorrhization [18]. Endophytes can also modulate plant hormones such as auxin, cytokinin, ethylene and gibberellin, and produce other bioactive compounds [19][20]. These PGP microbes can play an indirect role in plant protection against pathogens and pests by improving growth and overall health of their hosts compared to non-colonized counterparts.

Fungal endophytes are asymptomatic inhabitants of plant tissue and are reported from all parts of plants [21][22][23]. A plant may harbour numerous endophytic species, which may remain localized and lead to tissue-specific protection from disease [23][24] or can spread systemically in herbaceous plants [25][26]. These symbiotic, and potentially mutualistic, interactions between plants and endophytes are diverse and span both wild and cultivated plant species [27]. In almost every instance, examining host plants reveals the presence of endophytes [28]. The ubiquitous nature of endophytes is increasingly a focus in plant-fungal studies, which have traditionally focused on phytopathogenic or mycorrhizal fungi [27]. More than 1 million endophytic species are estimated to exist in 300,000 different plant species, but only a small fraction have been isolated and investigated for their roles within the plants they inhabit [29].

Some endophytes can offer a range of benefits to their plant hosts, offering an increase in plant fitness over uninhabited counterparts [30][31]. Endophytes can alleviate abiotic and biotic stressors such as drought, salinity, heavy metals and other toxic compounds introduced by the environment, flood, extreme temperatures, predators and pathogens [31][32]. Endophytes provide beneficial biological properties to the hosts, such as deterring pathogenic microbes, insects and other herbivores, while also providing stimulants for plant growth and development [33]. As plant pathogens and pests are well known for reducing global crop yield by an estimated 30 to 50% annually [28], endophytes, whose beneficial properties can improve plant fitness and crop yield while still maintaining quality and safety, represent a notable avenue in combatting plant loss.

2. Fungal Endophytes and Their Effects on Fungal Pathogens

Fungal pathogens cause some of the most devastating damage to crops by killing plants, reducing yield and quality, and causing postharvest losses [28]. Some fungal pathogens also produce mycotoxins that are detrimental to the health of humans and livestock [28]. Biocontrol endophytes, such as *Ampelomyces*, one of the first biocontrol fungi used against pathogenic fungi, are environmentally friendly alternatives to chemical fungicides, decreasing pathogen prevalence while maintaining mutualistic fungi. As biocontrol endophytes are capable of reducing adverse environmental effects of chemical fungicides [34], the inclusion of such biocontrol agents in integrated pest management approaches can improve sustainability in the agricultural sector and maintain or even enhance soil

health. In addition, applying diverse pest management strategies may also reduce the occurrence of, or manage for, chemical pesticide resistance.

The antifungal activities of compounds produced by some endophytes have been studied for their mode of effectiveness against several different pathogenic fungi and their ability to increase host plant fitness [25]. In many cases, however, the mechanism of how these endophytes provide such benefits to their host remains elusive or understudied [25].

Endophytes can also enhance host plant resistance to fungal pathogens by inducing a systemic response after endophytic colonization [35][36]. The plant initiates a defensive strategy using cell wall deposits to strengthen cell walls and defend them from penetration [35]. Endophytes possess mechanisms such as exoenzymes to allow them access to these strengthened cells, but the deposits may prevent pathogens from doing the same [35]. Endophytes can also act as priming stimuli that induce plant defence responses through transcriptional reprogramming. Colonization by endophytes (and pathogens) and subsequent metabolite secretion have also been associated with increasing the rate of photosynthesis (*Sclerotinia sclerotiorum*), chlorophyll content of plant cells, density of trichomes and stomata on plant tissues (*Beauveria bassiana*), antioxidant enzyme activity, callose deposition, cell lignification and phytoalexin accumulation (*Diaporthe liquidambaris*) [37][38][39]. Along with these modes of protection, competitive exclusion between endophytes and pathogenic fungi may occur [13][36]. Competitive exclusion describes the general suppression of pathogen establishment by endophytes colonizing and occupying the same potential niche. This method of protection can occur in the absence of the aforementioned mechanisms.

Fungal endophytes from the genus *Daldinia* inhibit the growth of the plant pathogens *Colletotrichum acutatum* and *Sclerotium rolfsii* [40][41]. *Daldinia eschscholtzii* isolated from ginger, *Zingiber officinale*, and *Stemona* root, *Stemona tuberosa*, was found to produce 60 identifiable compounds, the major ones being elemicin (24%), benzaldehyde dimethyl acetal (8%), ethyl sorbate (7%), methyl geranate (6%), trans-sabinene hydrate (5%) and 3,5-dimethyl-4-heptanone (5%) [41].

The genus *Fusarium* contains many species known as both plant pathogens and endophytes capable of inhibiting other fungal pathogens [42]. Many studies have investigated *Fusarium* metabolites for their application as pharmaceutical antimicrobial agents, but less focus has been placed on the antifungal properties of these compounds and their application in agricultural systems [42]. A crude extract of *F. proliferatum*, isolated from the medicinal plant *Cissus quadrangularis*, inhibited the growth of *Rhizoctonia solani* and *F. oxysporum* at concentrations of 0.2–2.5 mg/mL [43].

3. Fungal Endophytes and Their Activities against Bacterial Pathogens

In addition to antifungal compounds, endophytes also produce antibacterial compounds that may protect the host plant against bacterial pathogens. These antibacterial compounds vary, with some being broad spectrum but others providing protection against a narrower target group [25]. One such compound, javanicin, showed activity

against many microbes, but is most effective against *Bacillus* spp. and *Escherichia coli* [25]. Other broadly antimicrobial secondary metabolites that endophytes produce include terpenoids, alkaloids, phenylpropanoids, aliphatic compounds, polyketides, acetol, hexanoic acid, acetic acid and peptides [28][44]. Phomadecalin E and 8 α -acetoxyphomadecalin C are two examples of terpenoids produced by some endophytes of the genus *Microdiplodia* that show effective antibacterial properties against antagonistic strains of *Pseudomonas aeruginosa* [28]. Some strains of *Pseudomonas aeruginosa* can cause soft root rot in plants such as *Panax ginseng*, *Arabidopsis* and *Ocimum basilicum* and can also be opportunistic human pathogens [45][46].

Another fungal endophyte that produces broad-spectrum antimicrobial compounds is *Chaetomium globosum*, which exhibits activity against several pathogenic microorganisms and also has anti-biofilm activities [47]. Similarly, *Penicillium* sp. isolated from the medicinal plant *Stephania dielsiana* shows remarkable broad-spectrum antimicrobial activity.

4. Fungal Endophytes and Their Effects against Plant-Parasitic Nematodes

Nematodes form feeding sites on plant roots and stems, from which nutrients are extracted, which creates wounds through which secondary opportunistic fungal, bacterial or viral pathogens can enter the plant [48]. They also serve as vectors for viruses that may infect crop plants and cause disease or death in host plants [28]. Several fungal endophytes have been reported that either produce nematocidal compounds, parasitize nematode eggs and larvae or utilize hyphal loops and other means to trap nematodes and their eggs [49]. Some fungal species appear to produce bioactive compounds that directly or indirectly impact nematode colonization of the plant and/or surrounding soil, but the exact chemical compounds responsible for these effects are still being elucidated [49].

Root-knot nematodes, represented by *Meloidogyne* species, are globally ubiquitous and impact over 2000 plant species including economically important crops such as tomato, cotton, cucumber, melon, soybean and rice [48][49][50][51][52][53][54][55]. Many fungal genera have been reported as having inhibitory effects on *Meloidogyne* species, including: *Acremonium*, *Alternaria*, *Arthrobotrys*, *Chaetomium*, *Cladosporium*, *Clonostachys*, *Diaporthe*, *Drechslerella*, *Epichloë*, *Epiccocum*, *Fusarium*, *Gibellulopsis*, *Melanconium*, *Metacordyceps*, *Monacrosporium*, *Neotyphodium*, *Paecilomyces*, *Phialemonium*, *Phyllosticta*, *Piriformospora*, *Purpureocillium*, *Talaromyces* and *Trichoderma* [49][53][54][55][56][57][58][59][60][61][62][63][64][65][66][67][68][69]. Species from one or more of these genera have also been reported as having similar antagonistic effects towards other species of nematodes [49]. The presence of one or more species has been reported as significantly decreasing the occurrence of root knots and the nematodes that cause them.

Compounds produced by *Alternaria*, *Chaetomium*, *Cladosporium*, *Clonostachys*, *Fusarium*, *Phyllosticta*, *Piriformospora* and *Trichoderma* strains have been shown to alter the chemical composition of existing metabolites, or increase their production, within the host plant resulting in plant growth promotion or induced resistance to invading nematodes [55][56][63][67][70][71]. Alternatively, *Acremonium*, *Diaporthe*, *Epichloë*, *Melanconium*, *Phialemonium* and *Purpureocillium* species can produce bioactive compounds that directly inhibit nematode eggs,

juveniles, and females [51][58][64][67][71][72]. Strains of *Chaetomium*, *Clonostachys*, *Phyllosticta* and *Trichoderma* have also been reported as hyper colonizers that can outcompete plant pathogens, including nematodes, for space and nutrients within the plant host [53][55][56][66][67].

Endophytic fungi have been used as a seed treatment of agricultural plants for the control of nematodes, with other practices involving root inoculation [55][62]. The full capacity of fungal endophytes as nematode control agents remains understudied but shows potential for the development of effective biocontrol methods. The elucidation of the bioactive compounds produced by the endophytes, or whose production is induced within the host plant to combat nematodes will aid in understanding the mode of action for these compounds and how they directly or indirectly inhibit nematode development. Fungal species known to parasitize nematodes need to be further investigated for their abilities against different genera of nematodes for their use as biocontrol agents.

5. The Effect of Fungal Endophytes against Plant Viral Diseases

Fungal endophytes reduce viral diseases either by increasing plant defences or by reducing the spread of viruses by having entomopathogenic activities against vectors that spread the viruses. Inoculation of *Lolium pratense* (meadow ryegrass) with *Neotyphodium uncinatum* reduced viral infection of *Barley yellow dwarf virus* in inoculated plants, likely due to the production of alkaloids that deterred viruliferous aphid vectors and indirectly reduced the spread of virus infection [73]. In another study, inoculation of squash plants with different strains of *Beauveria bassiana* provided protection against *Zucchini yellow mosaic virus* compared to the non-inoculated control plants [74]. The antiviral defence of fungal endophytes may be specific against different viruses infecting the same plant species. Maize plants inoculated with *Trichoderma harzianum* and *Metarhizium anisopliae* were more resistant to *Sugarcane mosaic virus* compared to the control plants, while the same inoculated plants were not significantly resistant to *Maize chlorotic mottle virus* [75]. Environmental conditions also play a role in endophyte-induced plant resistance against plant viruses. Inoculation of tomato plants with *Piriformospora indica* repressed the amount of *Pepino mosaic virus* in shoots under higher light intensities, while significantly increasing fruit biomass [76]. In general, the most prevalent way to protect against viral infection of plants is by attempting to limit the potential viral vectors prior to infection [77]. Typically, this process involves the use of insecticides or other potentially harmful compounds for control [77]. Endophytic priming of plants represents a potential treatment option that could reduce the application of insecticides and may also provide persistent protection if insecticidal treatments fail [77].

6. The Role of Fungal Endophytes against Mites

Phytophagous mites are globally important pests of agricultural crops and ornamental plants, causing damage through feeding and by transmitting viruses and subsequently reducing photosynthetic capacity, overall health, yield, and market value.

A control tool involves the application of mycoacaricides, which include well-known entomopathogenic hypocrealean fungi such as *Akanthomyces muscarius*, *Beauveria bassiana*, *Cordyceps fumosorosea*, *Hirsutella thompsonii*, *Metarhizium anisopliae* and *Purpureocillium lilacinum* [78][79][80][81]. These generalist entomopathogens typically infect insects via conidia, which land on the insect cuticle, germinate, and form an appressorium that penetrates the cuticle through a combination of mechanical pressure and cuticle-degrading enzymes [82]. The fungus then proliferates throughout the insect hemolymph via yeast-like hyphal bodies or blastospores, colonizes internal tissues and may produce toxic secondary metabolites. Dead insects appear mummified and are the source for new infective propagules.

Hypocrealean entomopathogens/acaripathogens are well-studied and have been extensively reviewed, primarily as biocontrol agents of insects but also of mites [83][81][84][85][86][87][88][89][90][91]. *Beauveria* and *Metarhizium* are by far the most studied mycoacaricides and mycoinsecticides and can endophytically colonize a broad range of host plants naturally and when applied by methods such as seed soaking and coating, root dip, foliar spray, wound inoculation and soil treatment [89]. Interestingly, entomopathogenic endophytes can be recovered from both root and foliar tissues following seed inoculation, suggesting systemic acropetal growth, which offers a convenient and effective method of application [92][93]. For example, foliar endophyte colonization was confirmed in cotton seeds (*Gossypium hirsutum*) that were soaked in conidia suspensions of either *Beauveria bassiana* or *Purpureocillium lilacinum*, both of which subsequently reduced cotton aphid (*Aphis gossypii*) reproduction in field trials [94]. Composted cabbage waste (*Brassica oleracea* var. *capitata*) inoculated with *Clonostachys rosea* and used as a medium to cultivate tomatoes resulted in a 100% endophyte colonization rate; however, the endophyte colonization did not significantly decrease populations of TSSM [95].

Hypocrealean entomopathogens/acaripathogens are the most promising insect and mite biocontrol fungi. Species with endophytic life histories may be particularly useful as they can be conveniently applied (e.g., via seed soaking or coating), persist and spread within the host crop plant, prime host defence pathways and offer protection against a broad range of pests (not limited to mites) and may be less susceptible to factors limiting efficacy in the field (low moisture and UV light) [89][96][97][98]. Furthermore, evidence suggests that some acaripathogens may be compatible with predatory mites and, in some cases, can have a synergistic effect [99][100][101][102][103][104][105][106][107] although negative interactions are reported [108][109][110][111]. Endophytic mycoacaricides may therefore play an increasingly important role in future integrated pest management systems to control phytophagous mites and reduce acaricide resistance [112].

7. Environmental Factors Affecting Endophytic Fungi and Plants

The symbiosis between endophyte and plant can be affected by various environmental factors [113]. Weather is among the top factors and can influence the frequency of endophyte occurrence [113]. For example, wind is a primary spore dispersal mechanism for endophytes and, therefore, dispersal would be increased in areas of higher winds [114]. Similarly, increased precipitation is also linked to enhanced prevalence of endophytes, specifically those that are transmitted horizontally due, in part, to spore dispersal [113][114]. Along with dispersal, these

endophytes rely on moisture to germinate and colonize the host plant. Factors such as temperature and solar radiation can make environments either welcoming or inhospitable to endophytes, which generally only survive in specific temperature ranges [115].

Data suggest that the diversity and colonization rate of endophytes is not static [116]. Seasonal changes, specifically in the spring, have shown higher colonization rates and diversity than in the fall [116]. These data are complicated by the previously discussed environmental factors associated with season, but season can be used to generalize those environmental factors [115]. The location and age of plants can have an effect on the endophyte density as well, with older leaves having stronger resistance to colonization than younger leaves [117][118]. Surprisingly, both leaf chemistry and toughness have not been shown to significantly change colonization [118].

Data exists on the ability of endophytes to enhance their host plant ability to tolerate stressors such as salinity, drought, and other extreme weather events [31]. Stress tolerance may be increased due to antioxidant compounds such as phenolic acids, isobenzofuranones, isobenzofurans, mannitol and other carbohydrates [35]. Endophytes may produce antioxidants, and they have also been shown to release reactive oxygen species to stimulate the host plant to produce such antioxidants [35].

8. Host Plant Feedback on Endophytes

Generally mutualistic, the symbioses between endophytes and plants provide the endophyte with protection from abiotic and biotic stress and enhanced competitive abilities, while the plant receives protection and in some cases nutrients [31][119]. This mutual feedback is often essential for the survival of both partners [35]. However, endophytes may turn pathogenic due to nutrient shortages or prolonged severe weather [119]. A fungal species may be endophytic in one host species and pathogenic to another, so endophytic status cannot be assumed [35]. These co-evolved interactions are plastic and can be expected to destabilize under severe climate change scenarios [120][121].

Secondary metabolites can be made by either the endophyte or plant [122]. They give plants control in the relationship, allowing them to limit endophytic growth within their tissues by using lignin and other cell wall deposits to restrict or allow further colonization [35][122]. This process is also crucial for initiating the relationship and allowing colonization. Endophytes must bypass plant defence mechanisms to initially colonize the plant [21]. When plants sense an invader, they have numerous defences to try to thwart the attempt. These defence signaling cascades are initiated from recognition of fungal invasion and damage to plant tissue and may include cell wall thickening and production of secondary metabolites [123]. Host plants may also manipulate the secondary metabolites produced by endophytes to give them increased benefits for certain stressors, allowing the plant to adjust what is needed and when [122]. They may also modify the metabolites if they are too toxic and are causing harm to the plant [122].

9. Endophyte Transmission

The transmission of endophytes can occur vertically, with the parent plant passing on endophytes to their offspring through seeds. In this manner, the endophyte is present for the entire plant life cycle [124]. Vertical transmission is most common among grass species, which may only have one endophyte species and have only a single genotype for that endophyte [113]. Endophytes are also transmitted horizontally, often by spores present in the surrounding environment [124][125]. Seedlings may begin their lives free of endophytic colonization and gradually become colonized, with an accumulation at the end of the growing season, by spores from rain, air or passing organisms such as insects or mammals [114]. This mode of transmission provides a heterogeneous endophytic community that is different from that of the parent plant and may lead to more resilient populations [113]. Modulating crop plant microbiomes can incorporate both vertical and horizontal transmission [126][127]. Studying the transmission and life histories of endophytes will therefore provide practical knowledge that can be applied to developing more effective inoculants and application techniques.

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