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Review

Fungal Endophytes: An Alternative Biocontrol Agent against Phytopathogenic Fungi

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Abstract: There has been renewed interest in the application of endophytic fungi to control phytopathogenic fungi, which cause significant damage to crop health, ultimately leading to losses in agricultural productivity. Endophytic fungi inhibit pathogens via different modes of action—mycoparasitism, competition (for nutrients and ecological niches), antibiosis, and induction of plant defense—thus demonstrating the ability to control a wide range of phytopathogenic fungi in different growth phases and habitats. However, many studies have been conducted under laboratory conditions, and there is a huge lack of studies in which real field testing was performed. *Aspergillus*, *Clonostachys*, *Coniothyrium*, *Trichoderma*, and *Verticillium* have been proven to be the most effective fungal biocontrol agents. *Trichoderma* is regarded as the most promising group in commercial formulations. In this study, we attempted to emphasize the significance of fungal endophytes in controlling phytopathogenic fungi, while reporting recent advances in endophytic biology and application.

Keywords: biocontrol agents; dual culture method; mycoparasitism; plant disease; *Trichoderma*

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1. Introduction

1.1. Phytopathogenic Fungi and Their Significance

The exponential growth of the human population is one of the major problems facing today's world. More than 7.884 billion people are alive today [1], and it is predicted that the population will reach 9.2 billion by 2050 [2]. Feeding this growing population is becoming a huge problem, putting enormous pressure on various agricultural production systems. Land expansions for agriculture may not be always possible, although increasing the production per hectare and reducing harvest losses due to various biotic and abiotic factors would be ideal [3]. In this regard, the key roles of pests are significant, since according to the Food and Agriculture Organization of the United Nations (FAO) [4], plant diseases are responsible for about USD 220 billion in annual losses to the world economy. Plant diseases result in the loss of 10–42% of the world's major crops [5]. Of these diseases, 70–80% are caused by pathogenic fungi [6]. Several fungal epidemics have been reported throughout the history of agriculture. The coffee rust epidemic in the 1870s due to *Hemileia vastatrix* caused a huge drop in the harvest in eastern Africa and Ceylon (now Sri Lanka). At the time, Ceylon was the leading coffee exporting country in the world; however, coffee production fell from 45 million kg in 1870 to 2.5 million in 1889. This island nation could not recover its production, and tea plantations replaced the majority of the coffee producing land. This scenario brings changes in the beverage habits of British people, from coffee to tea [7]. In 1943, the Great Bengal Famine, particularly due to the brown spot disease in rice caused by the *Cochliobolus miyabeanus* (formerly known as *Helminthosporium*

oryzae, current name *Bipolaris oryzae*), led to the death of nearly three million people, who suffered from severe hunger owing to the yield reductions of their staple food, rice, by up to 92% [8]. While the southern corn leaf blight epidemic in 1970 caused by *Cochliobolus heterostrophus* (also known as *Bipolaris maydis*, previously *Helminthosporium maydis*) caused corn losses of up to 50% in the USA [9]. At present, *Blumeria graminis*, *Botrytis cinerea*, *Colletotrichum* spp., *Fusarium graminearum*, *F. oxysporum*, *Magnaporthe oryzae*, *Melampsora lini*, *Mycosphaerella graminicola*, *Puccinia* spp., and *Ustilago maydis* are the top ten fungi groups based on the scientific/economic importance and possess great potential to emerge as devastating disease-causing agents [10]. Most fungal plant pathogens belong to the phyla Ascomycota and Basidiomycota. Fungal plant pathogens can be classified into several classes among Ascomycota, such as the Dothideomycetes (e.g., *Cladosporium* spp.), Sordariomycetes (e.g., *Magnaporthe* spp.), and the Leotiomycetes (e.g., *Botrytis* spp.). Rusts (Pucciniomycetes) and smuts (spread among the subphylum of Ustilaginomycotina), the two major plant pathogen groups, belong to the Basidiomycota [11]. These fungi can cause damage to plants as well. Upon infection, phytopathogenic fungi interfere with plant metabolism and affect their normal/regular functions (and hence diseases) by producing enzymes, toxins, and other metabolic inhibitors such as hormones or absorbing nutrients from the host plants by growing internally or externally to the plant host [6,12]. Plants switch to active defense mechanisms to counteract the virulence factors of the fungi, while fungi may not resist or die; in contrast, if plants succumb to the virulence of the fungi, plants get sick, and the fungi become phytopathogenic [13,14].

1.2. Endophytic Fungi and Their Benefits

The term endophyte was first coined by De Bary in 1866. He referred to any organism that grows within plant tissues as an endophyte. Endophytes are generally not considered pathogens, and they often form a symbiotic relationship with plant hosts without causing any immediate adverse effects or disease symptoms [15–17]. Those endophytes that do not cause diseases in plants are called true endophytes, while others cause diseases in plants at some stage of their lifecycle due to various reasons, such as the weakening of the plant, environmental changes, and the type of host. For example, *Fusarium* species are found as harmless (latent) endophytes in carrots, though they cause head blight disease in cereals. Similarly, *Ramularia collo-cygni*, which causes necrotic disease in barley, can be found as a harmless endophyte in many other cereals [18].

Based on their phylogeny and life cycle characteristics, endophytic fungi have been divided into two major groups: clavicipitaceous (infecting some grasses limited to cool regions) and non-clavicipitaceous endophytes (from asymptomatic tissues of non-vascular plants, ferns and allies, conifers and angiosperms, also restricted to the Ascomycota or Basidiomycota) [19]. They have coexisted with plants for over 400 million years [20]. Today, over 300,000 plant species have been identified, and it is believed that each of them harbors at least one endophyte [21]. They propagate horizontally or vertically, thus increasing their survivability [22,23]. They have also been extensively examined in a range of geographic and climatic regions that are home to many ecological habitats from xeric to arctic, temperate to tropical forests, grasslands to croplands, and savannahs [24].

The benefits of endophytes to their host plants are significant; in their review, Baron and Rigobelo [25] described the advantageous role of endophytic fungi in depth. Endophytic fungi give direct benefits to their plant host (through mutualistic symbiosis interactions) by enhancing nutrient acquisition (e.g., N, P, K, Mg, and other macro and micronutrients), siderophore production, phytohormone productions for plant growth and development (e.g., auxins, cytokinins, gibberellin), and increasing the photosynthetic activity of the plant. They also offer many indirect effects such as an increase in secondary metabolites (e.g., alkaloids, steroids, terpenoids), improve protection against abiotic stresses (e.g., drought, heavy metal, salinity, temperature), biotic stresses (e.g., microbial pathogens, herbivores animals, and other insect pests), and trigger plant active defense mechanisms. The collective effect of a few or more of them thereby supports improvements in the fitness

of the plant and also promotes plant growth and physiology, making the host plant robust, and leading to the inhibition of phytopathogens [26].

Today, the potential to use endophytes as a valuable source of novel products for utilization in agriculture, medicine, and other industries has been well identified [27]. The pharmacological properties of major bioactive compounds synthesized by endophytic fungi have been recognized; for example, Stierle and co-workers [28] identified that *Taxomyces andreanae* (associated with *Taxus brevifolia*) has the ability to synthesize taxol, which has an antitumor effect against breast and ovarian cancers. Many other anti-cancer drugs have been isolated, such as Asperfumoid (from *Aspergilus fumigatus*), Aspernigerin (from *Aspergillus niger*), and Camptothecin (from *Fusarium solani*, *Entrophospora infrequens*, *Neurospora* sp., *Nodulisiporium* sp.) [29]. Antidiabetic, antifungal, antimalaria/antiparasite, antimicrobial, antioxidants, antiviral and immunosuppressive properties of endophytic fungi have also been identified [30]. The utilization of endophytic fungi in agriculture as biofertilizers [31] and biocontrol of pests [32] has been well documented in recent years. Endophytic fungi are also recognized as a potential source of industrial enzyme producers, including in the food and biofuel industries [33].

In this review, we attempted to discuss the application of endophytic fungi to control phytopathogenic fungi. First, we discussed the current requirements of endophytes as biocontrol agents. Second, we stressed some basics of endophytic fungi in order to better understand their biocontrol ability, along with successful studies in this respect. Finally, the mode of action of endophytic fungi in controlling phytopathogenic fungi is described.

2. Urgent Need for Biocontrol Agents

The application of pesticides is the most common practice in agriculture, due to their improved productivity and reduced yield losses via efficient control of pathogens (including during disease outbreaks), ease of application/handling and minimal requirements in terms of labor cost, and so on. These advantages have not been acknowledged by many in the research community, however, due to their undeniable disadvantages, which include water, soil, and air pollution, impact on soil fertility and non-target organisms, and health risks to humans and their animals [34,35]. Because of these negative consequences, numerous chemicals have been banned worldwide. An example is methyl bromide (MeBr), a broad-spectrum soil fumigant. It was mainly applied to control soil-borne pathogens; however, due to its ozone-depleting nature, it was completely banned in 2005, with a few exceptions [36]. The development of efficient synthetic chemicals, while addressing the aforesaid negatives, remains a huge challenge for the pesticide industry, which has been struggling to improve its products and produce novel pesticides [37]. Public and governments of many countries are pushing for pesticide-free farming, aiming to find alternative approaches to control phytopathogens [38,39]. In this scenario, traditionally, many environmentally friendly approaches, including mixed cropping, crop rotation, resistant cultivars/selective breeding, application of biocontrol agents, flooding, solarization, steaming, pasteurization, hot water treatment, and bio-fumigation have been used to control the pathogens. The effectiveness of controlling pathogens is questionable, and they also have their own advantages and disadvantages. For example, today, the utilization of resistant cultivars has come to be of interest owing to the advancement of molecular techniques [40], although with the broad range of pathogens and the rise of virulent strains/populations of pathogens, it is difficult to improve the resistant cultivars and non-host-specific crops [41,42]. Nonetheless, among the aforementioned methods, the application of biocontrol agents has become one of the ongoing trends in the field, as it presents promising alternatives for the protection of plants [43]. For instance, due to the banning of MeBr, the only feasible method for eradicating the devastating *Fusarium* diseases in the field is to use resistant cultivars or rootstocks. Recent studies have shown the importance of the application of endophytic fungi in the biocontrol of *Fusarium* diseases [44,45].

Substantial technological, economic, and political discussion has been sparked by the idea of biocontrol with the goal of fostering sustainable agriculture at a lower environmen-

tal cost. Some countries have adopted protective strategies that can reduce pesticide usage by about 50% [46]. It is important to understand the meaning of the concept of biological control. Traditionally, biological control has been defined as using an organism (not human or plant) to control or decrease the population of a pathogen or disease [47]. In contrast, biological control is an attempt to translate a phenomenon that is common in nature to agricultural systems, taking advantage of natural and established relationships [48]. Biological control agents (most, but not all) have demonstrated the ability to interact with and/or colonize plants, and they are able to develop complex inter-kingdom communication in which signaling occurs through a biochemical language with plants [49,50]. To disrupt the life cycle of pathogens, biocontrol agents use different antagonistic mechanisms [51]; such effects lead to infection prevention and reduced colonization of host plant tissues, and reduced sporulation, ultimately affecting the pathogen's ability to survive [52,53]. Biocontrol agents enhance plant immunity by increasing the expression of defense-related genes and systemic resistance [48]. Fungi and bacteria are considered the most prominent agents for controlling plant pathogens. One of the most exciting groups that can be used in biological control is endophytic fungi [42]. It is also worth mentioning that endophytic fungi, once associated with plants, provide protection to the host plant throughout their entire life cycle. Endophytic fungi may endure various adverse conditions while continuing to benefit the plant [54]. The other important thing to consider is that endophytic fungi do not develop pathogen-resistant strains like synthetic fungicides do [52]. These characteristics have led researchers to use them as biocontrol agents for directing sustainable agriculture practices.

3. Endophytic Fungi as Successful Biocontrol Agents

3.1. Emergence of Endophytic Fungi as Biocontrol Agents

In 1914, Carl Freiherr von Tubeuf introduced the biological control of fungi plant diseases for the first time [55]. Despite their advantage in terms of environmentally friendly utilization, many other characteristics make them competitive for usage with other disease control strategies. The ability to colonize plant tissues makes them better biological control agents for surviving dangerous UV rays, temperature fluctuations, and continued availability against pathogens [56]. Along with the previously mentioned merited features, the biological control ability of phytopathogen began to emerge in the 1930s. Weindling [57] proved that *Trichoderma lignorum* protected citrus seedlings against the *Rhizoctonia solani*. Sutton et al. [58] acknowledged the use of *Gliocladium roseum*, as it consistently ranked high among other organisms with exceptional effectiveness against *Botrytis cinerea* in a variety of greenhouse-grown flowers and vegetables, including begonia (*Begonia* sp.), cucumber (*Cucumis sativus*), cyclamen (*Cyclamen* sp.), *Exacum affine*, geranium (*Geranium* sp.), pepper (*Piper nigrum*), poinsettia (*Euphorbia* sp.), and tomato (*Solanum lycopersicum*). Here, it was found that *G. roseum* was as effective as or more effective than fungicide treatments on leaves, bracts, stems, flowers, and fruits in nearly all cases.

The way in which biotrophic and necrotrophic fungi are influenced is of interest. Biotrophic pathogens, such as those that cause rust and mildew disease, often have a brief epiphytic phase, and require little to no exogenous nutrients to penetrate. Mycoparasitism (rather than competitors) could be the most useful strategy for the biocontrol of the targeted fungi at this stage of the cycle. However, the collective effects of other modes of actions of endophytes (which are described later in this review) add much effectiveness to their abilities to control phytopathogens. Meanwhile, unspecialized necrotrophs, such as *Alternaria* sp., *Botrytis* sp., *Cochliobolus* sp., *Phoma* sp., and *Septoria* sp., typically grow saprophytically on the phylloplane and absorb external nutrients before they penetrate. In such a situation, antagonists behaving as nutrient competitors might be useful. In addition, there is a general consensus that biocontrol agents that act as nutrient competitors (and not through antibiosis) can only be used in a prophylactic manner [59]. Rajani et al. [60] found the ability of the same genera of endophytic fungi to control several species of pathogens. In this context, they found that three *Trichoderma* species, namely *T. harzianum*, *T. longibrachiatum* and *T. pleuroti*, were capable of completely inhibiting the mycelial growth

of *Sclerotinia sclerotiorum*, *Sclerotium rolfsii*, and *Fusarium oxysporum*. Several endophytes from different genera can also be utilized to kill a single targeted fungal pathogen. For instance, the fungi *Acremonium alternatum*, *Acrodontium crateriforme*, and *Gliocladium virens* are able to parasitize the powdery mildew pathogen in Erysiphaceae [61].

3.2. In Vitro Assay for Recognition of the Antagonistic Ability of Endophytic Fungi

First, endophytic fungi should be isolated from the healthy plant part/s. Then, to remove the surface soil and appendages, repeated washing under tap water needs to be carried out. Selected plant materials should be further cut into appropriately sized pieces (e.g., length, 1–2 cm for leaves; 5–7 cm for roots) and subjected to proper surface sterilization to remove epiphytic microbes from the plant tissues while keeping only the true endophytes [62]. Earlier in the 1990s, Schulz et al. [63] recommended several methods of surface sterilization, of these, ethanol, formaldehyde, and diluted sodium hypochlorite-based methods are still common practices in laboratories. Pilot studies can be used to determine the required sterilant solution, concentration, and exposure time [64]. Sterilants ought to be powerful enough to sterilize the plants' surface without causing any damage to their tissues. The age, sensitivity, and tissue thickness of the selected plant parts should therefore be taken into account [65].

To investigate potential biocontrol agents, it is essential to obtain pure endophytic fungal cultures. After surface sterilization, the plant materials should undergo further serial washings to remove the excess sterilants, trimmed/sliced (e.g., 0.5 cm × 0.5 cm), and transferred to the culture medium [66]. Endophytic fungi can be recovered using a variety of culture media protocols, although potato dextrose agar (PDA) is one of the most popular. Other commonly used media include Agar containing Murashige and Skoog (MS) vitamins and sucrose, Czapek medium, Hagem minimal medium, Luria–Bertani medium, malt extract agar, tryptone bovine extract Aagar, and tryptone soybean agar. A common characteristic among these media is a slightly acidic pH range of 5.8–6.0, which enhances fungal growth [67]. Cultures should also contain antibiotics (e.g., penicillin, streptomycin) to inhibit bacterial growth. In general, the cultures are kept inside the incubator, maintaining a temperature regime between 23 and 29 °C for 3–14 days, according to requirements [66,68,69]. At this point, the initial identification of endophytics can be carried out using microscopic examination; however, genomic analysis is the most ideal and necessary for precise identification and confirmation [70,71].

The antagonistic activity against phytopathogenic fungi can be tested using dual culture methods [72–74]. A small portion of mycelia (e.g., 6 mm plugs) picked from the isolated cultures needs to be kept in a separate PDA along with the isolated phytopathogenic fungi mycelia, a few centimeters apart from one another. Then, the cultures should be incubated, and after 8–10 days, radial growth needs to be recorded by measuring the mean colony diameter [75]. Figure 1 shows dual culture assays for several endophytic fungi isolated from the coffee hosts (*Coffea arabica*) with fungal pathogens.

In addition to the dual culture method, the co-culture of more than two species is also popular among researchers. In this procedure, the endophyte is placed in the center of the culture media (PDA) and is surrounded by different phytopathogen plugs that are kept a few centimeters away [62,76]. As of today, many endophyte fungi have had their biocontrol ability identified through in vitro assays. Table 1 summarizes some of the recent findings related to endophyte fungi with their targeted pathogen for control.

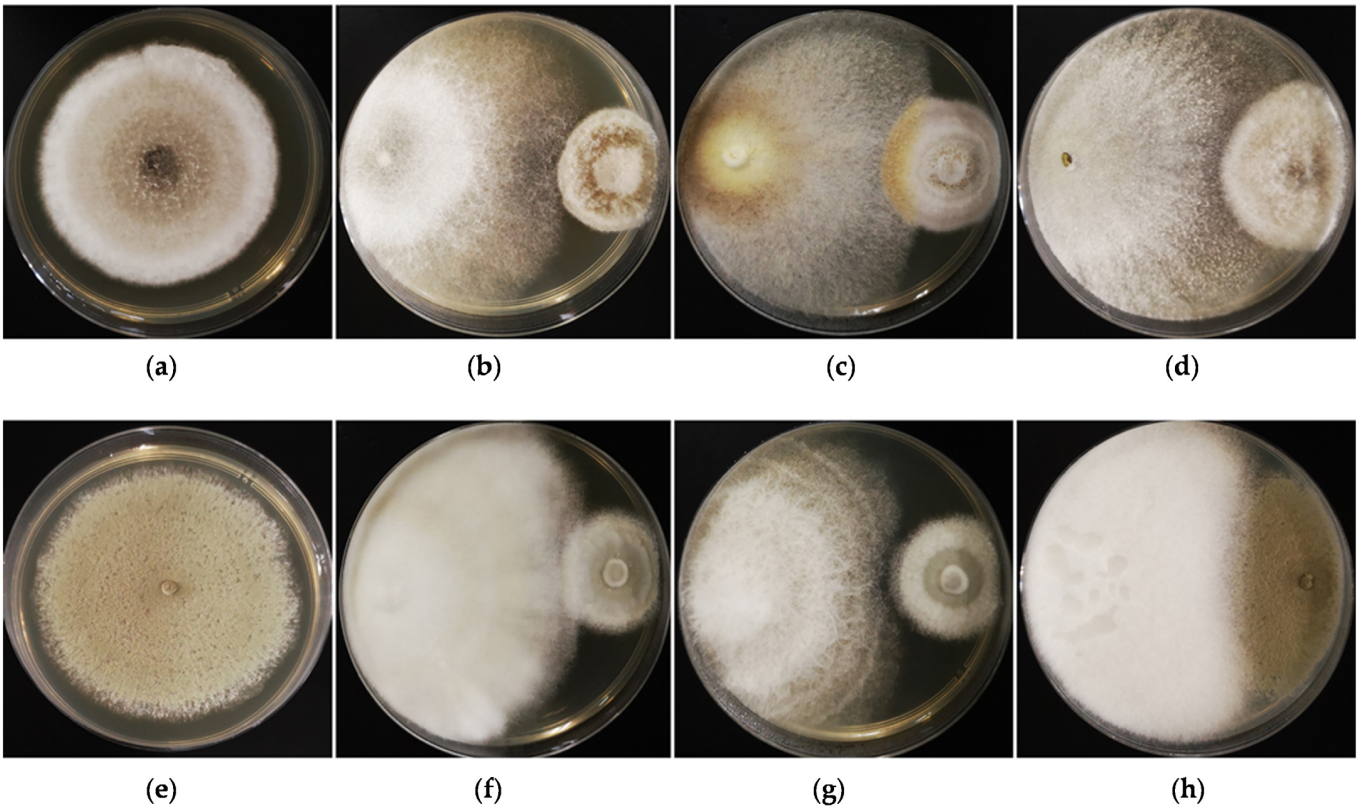

Figure 1. Screening of endophytic fungi for antagonistic activity against phytopathogenic fungi. (**a**) Pathogen *Alternaria alternata* (CGMCC 3.15535); (**b**) endophytic fungus *Arthrinium* sp. (left, KUMCC 21-0407) and *Alternaria alternata* (right); (**c**) endophytic fungus *Hypoxylon* sp. (left, KUMCC 21-0356) and *Alternaria alternata* (right); (**d**) endophytic fungus *Daldinia* sp. (left, KUMCC 21-0398) and *Alternaria alternata* (right); (**e**) pathogen *Penicillium digitatum* (CGMCC 3.15410); (**f**) endophytic fungus *Nodulisporium* sp. (left, KUMCC 21-0375) and *Penicillium digitatum* (right); (**g**) endophytic fungus *Colletotrichum* sp. (left, KUMCC 21-0351) and *Penicillium digitatum* (right); (**h**) endophytic fungus *Colletotrichum* sp. (left, KUMCC 21-0401) and *Penicillium digitatum* (right). The fungal cultures were grown on PDA at 28 °C. The photographs show the cultures on the 10th day. It shows that endophytes restrict the growth of pathogens by occupying space and minimizing their spread over time.

Table 1. Some endophytic fungi with biocontrol potential against phytopathogenic fungi.

Endophytic Fungus	Host Plant	Part of the Plant Utilized to Isolate the Endophytes	Target Fungal Pathogen	Highest Growth Inhibition%	References
Acrophialophora jodhpurensis	Tomato (*Lycopersicon esculentum*)	Roots	*Rhizoctonia solani*	52.5	[77]
Alternaria alternata	Japanese cornel dogwood (*Cornus officinalis*)	Biennial twigs	*Alternaria arborescens*	57.1	[78]
Alternaria destruens	Wheat (*Triticum aestivum*)	Stems or heads	*Fusarium graminearum*	-	[79]
Alternaria tenuissima	Japanese cornel dogwood (*Cornus officinalis*)	Biennial twigs	*Alternaria alternata*	53.5	[78]
			Alternaria arborescens	38.4	

Table 1. *Cont.*

Endophytic Fungus	Host Plant	Part of the Plant Utilized to Isolate the Endophytes	Target Fungal Pathogen	Highest Growth Inhibition%	References
Annulohypoxylon sp.	Agarwood (*Aquilaria sinensis*)	Bark from branches and twigs	*Alternaria alternate*	70.61 ± 0.03	[80]
			Penicillium digitatum	72.96 ± 0.58	
Aspergillus flavus	*Dysoxylum gotadhora*	Leaves, seeds, and stems	*Verticillium dahliae*	59.980 ± 0.889	[71]
			Fusarium oxysporum	52.678 ± 1.351	
Aspergillus fumigatus			*Verticillium dahliae*	48.550 ± 1.255	
			Fusarium oxysporum	40.184 ± 0.615	
Aspergillus niger			*Verticillium dahliae*	52.964 ± 1.369	
			Fusarium oxysporum	42.863 ± 0.657	
Botryosphaeria berengeriana	Japanese cornel dogwood (*Cornus officinalis*)	Triennial twigs	*Alternaria alternate*	29.3	[78]
			Botryosphaeria dothidea	59.6	
			Colletotrichum gloeosporioides	37.6	
Botryosphaeria dothidea			*Alternaria alternate*	72.4	
			Alternaria arborescens	75.3	
			Botryosphaeria dothidea	69.6	
			Colletotrichum gloeosporioides	71.2	
		-	*Rhizoctonia cerealis*	84.6	[73]
			Fusarium pseudograminearum	80.3	[81]
Cladosporium sp.	Tomato *(Lycopersicon esculentum)*	Stems	*Fusarium oxysporum*	38.2 ± 7.4	[82]
Cladosporium cladosporioides	*Zygophyllum mandavillei*	Leaves	*Aspergillus flavus Fusarium solani*	-	[83]
Colletotrichum gloeosporioides	Japanese cornel dogwood (*Cornus officinalis*)	Triennial twigs	*Alternaria alternata*	52.8	[78]
			Botryosphaeria dothidea	30.3	
Curvularia chiangmaiensis	Rice plants (*Oryza sativa*)	-	*Pyricularia oryzae*	-	[84]
Diaporthe spp.	*Avicennia nitida*	Branches	*Colletotrichum* sp.	33	[85]
			Fusarium oxysporum	50	
			Rhizopus microspores	62	
Epicoccum nigrum	Common ginger (*Zingiber officinale*) and *Salix* sp.	Leaves	*Ustilago maydis*	-	[86]

Table 1. *Cont.*

Endophytic Fungus	Host Plant	Part of the Plant Utilized to Isolate the Endophytes	Target Fungal Pathogen	Highest Growth Inhibition%	References
Eupenicillium javanicum	Agarwood (*Aquilaria sinensis*)	Leaves	*Fusarium oxysporum*	43.3 ± 0.7	[82]
Fusarium commune	Wheat (*Triticum aestivum*)	Stems or heads	*Fusarium graminearum*	-	[79]
Fusarium oxysporum	Wheat (*Triticum aestivum*)	Stems or heads	*Fusarium graminearum*	-	[79]
Fusarium solani	Rice plants (*Oryza sativa*)	-	*Pyricularia oryzae*	-	[84]
Fusarium subglutinans	*Thymus* spp.	-	*Botrytis cinerea*	61.33	[87]
Guignardia mangiferae	Mangrove (*Rhizophora stylosa*)	Stems	*Fusarium oxysporum*	47.3 ± 3.1	[82]
Hypocrea sp.	Agarwood (*Aquilaria sinensis*)	Leaves	*Fusarium oxysporum*	44.4 ± 0.4	[82]
Induratia coffeana	Common bean (*Phaseolus vulgaris*)	Seedlings	*Colletotrichum lindemuthianum*	99.64 ± 0.57	[88]
			Sclerotinia sclerotiorum	70.83 ± 2.60	
Induratia yucatanensis			*Colletotrichum lindemuthianum*	77.22 ± 4.19	
			Sclerotinia sclerotiorum	40.42 ± 4.39	
Lasiodiplodia theobromae	Agarwood (*Aquilaria sinensis*)	Leaves	*Fusarium oxysporum*	40.2 ± 0.3	[82]
Microdochium bolleyi	Wheat (*Triticum aestivum*)	Roots	*Fusarium culmorum*	-	[89]
Neurospora sp.	Agarwood (*Aquilaria sinensis*)	Leaves	*Fusarium oxysporum*	43.1 ± 1.0	[82]
Penicillium sp.	Tomato (*Lycopersicon esculentum*)	Stems	*Fusarium oxysporum*	66.4 ± 4.6	[82]
Penicillium thomii	*Dysoxylum gotadhora*	Leaves, seeds and stems	*Verticillium dahliae*	44.137 ± 1.141	[71]
			Fusarium oxysporum	58.914 ± 1.943	
Phyllosticta fallopiae	Japanese cornel dogwood (*Cornus officinalis*)	Leaves	*Alternaria alternate*	52.2	[78]
			Alternaria arborescens	54.1	
			Botryosphaeria dothidea	56.9	
			Colletotrichum gloeosporioides	53.2	
Porostereum sp.	*Dysoxylum gotadhora*	Leaves, seeds and stems	*Verticillium dahliae*	66.205 ± 1.711	[71]
			Fusarium oxysporum	66.974 ± 1.026	

Table 1. *Cont.*

Endophytic Fungus	Host Plant	Part of the Plant Utilized to Isolate the Endophytes	Target Fungal Pathogen	Highest Growth Inhibition%	References
Talaromyces pinophilus	Onion (*Allium cepa*)	Seeds	*Botrytis cinerea*	-	[90]
Trichoderma sp.	Star anise (*Illicium verum*)	Leaves	*Fusarium oxysporum*	39.3 ± 0.4	[82]
	Forest tree species	Leaves	*Colletotrichum truncatum*	50–70	[74]
			Lasiodiplodia theobromae	30–78	
			Macrophomina phaseolina	49–78	
			Sclerotium delphinii	6–62	
Trichoderma asperellum	Lettuce (*Lactuca sativa*)	Leaves	*Corynespora cassiicola*	83.79	[91]
			Curvularia aeria	85.71	
	Rice plants (*Oryza sativa*)	-	*Pyricularia oryzae*	-	[84]
	Soybean (*Glycine max*)	Roots	*Rhizoctonia solani*	42	[92]
Trichoderma atroviride	Soybean (*Glycine max*)	Roots	*Rhizoctonia solani*	55	[92]
Trichoderma harzianum	Common ginger (*Zingiber officinale*) and *Salix* sp.	Leaves	*Ustilago maydis*	-	[86]
	Rattan (*Calamus castaneus*)		*Colletotrichum scovellei*	85.80 ± 5.47	[72]
			Colletotrichum truncatum	89.33 ± 2.99	
			Diaporthe pascoei	66.96 ± 1.56	
			Fusarium fujikuroi	71.25 ± 1.50	
			Fusarium oxysporum	76.74 ± 4.45	
			Fusarium proliferatum	57.38 ± 17.22	
			Fusarium solani	62.28 ± 2.15	
			Lasiodiplodia pseudotheobromae	73.78 ± 1.09	
			Lasiodiplodia theobromae	82.86 ± 1.28	
			Pestalotiopsis mangiferae	88.89 ± 1.41	

Table 1. *Cont.*

Endophytic Fungus	Host Plant	Part of the Plant Utilized to Isolate the Endophytes	Target Fungal Pathogen	Highest Growth Inhibition%	References
Trichoderma koningiospsis		Spines	*Colletotrichum scovellei*	89.45 ± 2.55	[72]
			Colletotrichum truncatum	80.05 ± 5.75	
			Diaporthe pascoei	66.67 ± 9.30	
			Fusarium fujikuroi	59.94 ± 11.16	
			Fusarium oxysporum	76.04 ± 1.74	
			Fusarium proliferatum	51.63 ± 13.52	
			Fusarium solani	74.56 ± 2.72	
			Lasiodiplodia pseudotheobromae	93.56 ± 1.00	
			Lasiodiplodia theobromae	77.62 ± 6.30	
			Pestalotiopsis mangiferae	60.00 ± 1.99	
Trichoderma longibrachiatum	Soybean (*Glycine max*)	Roots	*Rhizoctonia solani*	87	[92]
Xylaria feejeensis	Mangrove trees (*Ceriops decandra*, *Rhizophora apiculate*, *R. mucronata*, and *Xylocarpus granatum*)	Leaves, petioles, and roots	*Alternaria solani*	60–75	[93]
			Fusarium oxysporum	87	

3.3. Application of Endophytic Fungi in Real Fields

Aspergillus, *Clonostachys*, *Coniothyrium*, *Trichoderma*, and *Verticillium* are recognized as being among the most successful fungal biocontrol agents [94–96]. A great deal of research has been performed, particularly on *Trichoderma*, owing to its diversity, abundant and frequent presence in many local environments, and ability to colonize all parts of the plants and substantially modulate plant responses to biotic and abiotic stresses [97–99]. Nowadays, many companies are developing *Trichoderma*-based commercial biocontrol products around the world, for example, *T. harzianum* strain T-22 (Bioworks, Geneva, Switzerland, New York, NY, USA and TGT Inc., New York, NY, USA), *T. virens* (Grace-Sierra Co., Baltimore, MD, USA), *T. viride* (Ecosense Laboratories, Mumbai, India), and *T. parceramosum* (BioSpark Corporation, Laguna, Philippines) [100].

It is also worth noting that the effectiveness of biological control is influenced by a variety of factors, and as such, success in this area is challenging. Most of the time, environmental conditions—temperature and relative humidity—have been showcased. However, solid edaphic factors, age and plant specificity, and the type and density of the inoculum also affect endophytic colonization [32,56]. For instance, in one study, Trutmann and Keane [101] found that the spore germination and infection (with *Sclerotinia sclerotiorum*) process of *Trichoderma koningii* was highly dependent on the pH and the temperature. They noticed that endophytic fungi germination and infection declined after pH 6 and at temperatures between 7 and 35 °C. Furthermore, the optimum temperature for germination was proven to be between 15 and 30 °C, and for infection of sclerotia, between 20 and 35 °C. In another study, Sutton et al. [58] indicated that the biocontrol activity of *Gliocladium roseum* against *Botrytis cinerea* was mainly dependent on the temperature conditions,

where the activity was highest at 20 and 25 °C, but progressively decreased at 15 and 10 °C. Conventionally, before releasing biocontrol agents for commercial usage, further assessments are needed to identify the growth medium (e.g., the composition also, pH, and sterility), effective formulation (e.g., powder, liquid, or granule), and the method of application, e.g., soil, seed, and vegetative part inoculation (foliar spraying and transplant dip), as these are the other key factors for the survivability of the endophyte in the field as well as for their sufficient colonization [102,103]. Formulations based on carriers frequently have a short shelf life, are of poor quality, and may have a greatly diminished antagonistic effect on endophytic fungi. Different substrates are now utilized as carriers to enhance quality, extend shelf life, and boost the activity of potent microbes [104]. Looking at the development of formulations for *Trichoderma asperellum*, Kodithuwakku and Wijekoon [105] developed both liquid and solid media. Each liquid medium contained 1% sucrose solution, 1% peptone water, 1% tryptone broth, and 1% tryptone soy broth and sterilized distilled water. Meanwhile, the solid media contained sterilized talc powder. In both, spore suspension of the endophyte was employed. However, they obtained negative results for all the liquid formulations due to the heavy contamination after four weeks of storage, noticeably reducing the spore suspension. Interestingly, talc powder showed preservation of spores for three months in a talc-based formulation stored under 25–30 °C in polypropylene bags without adding preservatives. Moreover, Kodithuwakku and Wijekoon [105] revealed that talc with sterilized cattle manure had proved to be an effective multiplication substrate for *T. asperellum* for commercial production. In a study, Thangavelu et al. [106] recognized that soil application of *T. harzianum* in dried banana leaves (treated with jaggery solution) shows the stimulation of the endophyte growth over the talc-based formulation. Thangavelu and co-workers [106] observed that dried banana leaf formulations and talc-based formulations had a maximum of 10^{11} CFU/g and 10^{7} CFU/g *Trichoderma* sp. in soil, respectively, 60 days after treatment. This was above the minimum requirement of *Trichoderma* sp. (105 CFU/g) in the soil to achieve effective disease control.

3.4. Control Mechanism of Phytopathogenic Fungi by Endophytic Fungi

Endophytic fungi use different modes of action to control phytopathogenic fungi, including mycoparasitism, competition for nutrients and ecological niches, antibiosis, rhizosphere colonization, and induction of the plant defense system [107,108]. Generally, many endophytic fungi may utilize a combination of all the above methods, (e.g., *Fusarium oxysporum* strain Fo47), resulting in a greater level of antagonism [15].

3.4.1. Mycoparasitism

In mycoparasitism, the endophytic fungi safeguard the ecology of the host by directly attacking the phytopathogenic fungi. Generally, mycoparasitic interaction includes recognition of the host, development towards the host, attachment, coiling around the host, penetration, and acquisition of nutrients. Spores of endophytic fungi can come into contact with the host fungi, and trigger the germination, protrusion of the germ tube, and further development towards the host and physical pressure allow penetration to occur [101]. Once extensive mycelia are available, when the host-derived signal is received (e.g., short oligomers, characteristically chitin, and β-1,3-glucan), it is recognized first by mycoparasitic fungi via the receptors located on their cell surface. Then, the chemotropic growth of the endophytic fungal mycelium toward the prey fungi takes place by sensing lectins released by the phytopathogenic fungi [109]. Often, endophytic fungi grow alongside/parallel to the host hyphae and branch out extensively, forming hyphal tips that are hooked and attached, and coiling more loosely/compactly or massively around them [90,110,111]. Penetration even can be occurred immediately after the hyphal contact in the absence of coiling. Conventionally, coiling happens due to defense by the host against penetration [111–113]. Additionally, tight coiling leads to complete loss of the pathogen's turgidity, resulting in considerable cell collapse, and they start to shrink/wrinkle. However, such coiling will not

happen if the phytopathogenic fungi are damaged or dead. Once the initial contact occurs, the fungi host starts to deform, at which pint hyphae become slightly granular [101,110].

Contact between the mycohost/prey and its parasitic fungi is made possible by lectins and proteins harboring cellulose binding modules present in their hyphae, respectively. This interaction helps trigger a signaling cascade comprising G-proteins and Mitogen-activated protein kinases (MAPKs) that can modulate the activities of as-yet-unknown transcription factors (TFs). These factors contribute to the constitutive expression of genes that encode enzymes responsible for the biosynthesis of secondary metabolites and the lysis of cell walls [114,115]. G-protein signaling pathways elicit cellular responses like cell division, growth, and further pathogenic development [109].

After this initial interaction, the endophyte begins to penetrate through the fungal cell wall, using mechanical pressure driven by hyphae and aspersoria (or similar structures), reinforced by a wide array of cell wall lytic enzymes, including chitinases, glucanases, and proteinases [101,116]. Dugan et al. [117] observed profuse coils and appressoria of *Clonostachys rosea* during infection of *Alternaria infectoria*, *Alternaria tenuissima*, *Stemphylium* sp., and *Ulocladium consortiale*. Similarly, Abdel-Rahim and Abo-Elyousr [90] reported the presence of appressoria (also called pseudo-appressoria, as they are not individualized cells) at the penetration site of *Talaromyces pinophilus* on *Botrytis cinerea*. In contrast, Trutmann and Keane [101] failed to detect any appressoria-like structures supporting the penetration of *Trichoderma koningii* hyphae while they were parasitic in *Sclerotinia sclerotiorum*. Pisi et al. [110] found that *Trichoderma harzianum* produced pincer-shaped structures supporting penetration on *Fusarium graminearum*. Similarly, they observed these structures when interactions occurred between *Penicillium frequentans* and *Fusarium nivale*.

In order to degrade the fungal cell wall completely, the coordinative work of all aforementioned lytic enzymes may be needed [116]. Chet and Baker [118] presented the biological mechanism, and according to their findings, when the *Trichoderma hamatum* and *Rhizoctonia solani* were cultured together in a petri dish, *T. hamatum* attacked the mycelium of *R. solani* through the chitinases and β-(1-3) glucanase. Chitinases break down the glycosidic bonds in chitin, which is among the major components of the fungal cell wall. For example, in filamentous fungi *Aspergillus* spp., it accounts for up to 10–20% of the cell wall dry weight [119]. Seidl-Seiboth and co-authors [120] showed that chitinases of *Trichoderma* species can be divided into three main groups, A, B, and C. These can be divided into subgroups A2, A4, A5, B1, B2, B5, C1, and C2, where the A5, B1, and B2 subgroups contain biochemically characterized members with chitinase activities. This may imply that numerous chitinase isozymes work together to cause the cell wall degradation of phytopathogenic fungi. Advancement of the molecular techniques led to a novel insight into chitinases; initially, for example, it was believed that in group A, 42-kDa endochitinase (Ech42) played a major role in cell wall degradation [121]; however, today it is recognized that it is also expressed during carbon starvation [122] and autolysis [123]. It is clear that Ech42 is not a mycoparasitic-specific chitinase. In group C, some subgroups are involved in a killer-toxin-like mechanism for permeabilizing antagonist cell walls during interactions between fungi [120]. Glucanase is needed to degrade α and β-glucans polysaccharides present in the phytopathogenic fungi cell wall [124]. Nevertheless, β-glucan (majorly β-(1,3)-glucan) accounted for between 30% and 80% of the cell wall dry weight, depending on the fungal species [125]. Thus, as highlighted above, chitinases and β-(1-3) glucanase are the primary enzymes playing a major role in the lysis of phytopathogenic fungal cell walls, particularly during the antagonistic action of *Trichoderma* spp. [126]. While proteases cleave peptide bonds in proteinaceous substrates, 20–30% of the dry weight of the cell wall of the filamentous fungi is made up of the proteins; this even rises to 30–50% in some cases in yeast-like fungi [127]. A comprehensive systematic review by Bezerra et al. [128] reported many protease studies of endophytic fungi. Nonetheless, endophytic fungi need to protect themselves against the host's hydrolytic enzymes during mycoparasitism. For instance, in a recent study, Romero-Contreras et al. [129] found that Lysin motif (LysM) effectors were

involved in resistance against chitinase activity, protecting *Trichoderma atroviride* from the chitinases of its mycohosts.

3.4.2. Competition for Nutrition and Ecological Niches

It has long been recognized that niche complementarities could be important factors in the coexistence of species [130]. Competitive exclusion, which states that two species cannot coexist in the same ecological niche, applies to fungi in the genus *Trichoderma*, which has been found to have the niche most comparable to that of *Colletotrichum* spp., thus eliminating the latter phytopathogenic species [131]. In turn, *Trichoderma* spp. have been identified as extremely fast colonizers, and are thought of as fierce competitors, keeping out slower-growing pathogens. The further ability to acquire nutrition from various substrates adds value for them [132]. Oszust et al. [131], on the basis of an in vitro assay, found that *Trichoderma* spp. nutritionally outcompeted (e.g., adonitol, D-arabitol, i-erythritol, glycerol, D-mannitol, and D-sorbitol) *Botrytis* sp., *Verticillium* sp., and *Phytophthora* sp. In a separate study, Sutton and co-authors [58] reported that, rather than being mycoparasitic, *Gliocladium roseum* acts as a nutrient competitor in controlling *Botrytis cinerea*. Morandi et al. [133] found that the nonpathogenic endophyte *Clonostachys rosea* controlled *B. cinerea* by suppressing the development and sporulation potential. To achieve this, *C. rosea* competes for nutrients that are in the moisture films on wounded leaves. *Clonostachys rosea* shows greater aggressiveness than the pathogen, and *B. cinerea* is eliminated owing to nutrition deprivation. Moreover, according to Morandi and colleagues [133], *C. rosea* inhibited *B. cinerea* colonization by as much as 40–50%, or even more, and conidiophore production of the pathogen was inhibited by 99–100%.

3.4.3. Antibiosis

Endophytic fungi inhibit phytopathogens through antibiosis, producing various antimicrobial chemical compounds, particularly secondary metabolites such as alkaloids, flavonoids, isocoumarins, lignans, peptides, phenolics, phenylpropanoids, quinones, steroids, terpenoids, volatile compounds, and so on [134,135]. Du et al. [66] recognized that many of the endophytic fungi of Ascomycota and Basidiomycota have a relatively high level of non-volatile-compound alkaloids, thus showing higher antimicrobial effects. In a separate study, Wu et al. [136] showed the effect of terpenoids extracted from *Xylaria* sp. isolation: nine oxygenated guaiane-type sesquiterpenes and three isopimarane diterpenes. Those guaiane-type sesquiterpenes presented moderate antifungal effect against *Candida albicans* and *Hormodendrum compactum*; however, more considerable inhibitory activity was demonstrated against *C. albicans* and *Pyricularia oryzae* by the diterpenes. Daroodi et al. [77] found that endophytic fungi produced volatile and non-volatile compounds; hence, the antibiosis was greater. Notably, antibiosis not only destroys the fungi mycelium, it also inhibits the germination of resistant structures like sclerotia [101]. Shi et al. [137] demonstrated the role of peptaibols, a family of peptides from *Trichoderma pseudokoningii*, against several pathogenic fungi. They demonstrated that peptaibols induced extensive apoptotic programmed cell death in the selected model organism, *Fusarium oxysporum*, while displaying strong antifungal activity in other studied species, *Ascochyta citrullina* and *Botrytis cinerea*. In a recent study, Yang et al. [138] found evidence of the higher antifungal activity of three volatile compounds, namely, 2-methoxy-4-vinylphenol (methoxyphenols), 3,4-dimethoxystyrol, and (-)-trans-caryophyllene, generated by *Sarocladium brachiariae* against *Fusarium oxysporum*. In addition, 2-methoxy-4-vinylphenol showed the strongest inhibition capacity, while (-)-trans-caryophyllene showed the least.

Kelemu et al. [139] isolated *Acremonium implicatum* fungus from *Brachiaria* grasses, showing the inhibition activity of cultured *Drechslera* sp. In a similar study, Gama and co-workers [140] evaluated the antifungal effect of several endophytic fungi (e.g., *Paraconiothyrium* sp., *Sarocladium kiliense*, *Acremonium curvulum*, *Setophoma terrestris*, *Dissoconium* sp., and *Cladosporium flabelliforme*) isolated from the *Brachiaria* grasses against *Sclerotinia sclerotiorum*. Mejía et al. [141] experimented with the antibiosis of fungal endophyte isolates from Cacao trees (*Theobroma cacao*) against *Moniliophthora roreri*, and reported that 13% of the

tested morphospecies showed clear antibiosis. Additionally, extensive studies conducted by Bailey et al. [142], Harwoko et al. [86], Zhao et al. [81], and Zhao et al. [78] recognized the antibiosis effect of endophytic fungi against phytopathogens.

3.4.4. Induction of Plant Defense System

Plants attempt to avoid the damage caused by phytopathogens through plant defense mechanisms. Pre-existing defense structures (e.g., cuticles and wax layers on plant leaves/stems, epidermal cell walls, thick-walled tissues) and biochemical compounds (e.g., exudates) initially restrict pathogen invasion; however, pathogens can generally overcome these mechanisms. Thus, induced defense mechanisms respond to pathogens, upon infection, by forming cytoplasmic, cellular, and histological defense structures, deposition of callose, formation of abscission and cork layers, formation of tyloses, and deposition of gum. Meanwhile, induced biochemical defense mechanisms include the production of various proteins, phenolic compounds, and hypersensitive responses [143]. In order to induce the plant defense system, endophytic fungi need to enter the host plant. To achieve this, the endophytes must get beyond the initial line of resistance provided by the plant immune system. This first layer of the defense system involves plants recognizing conserved molecules that are shared by microorganisms, referred to as microbe- or pathogen-associated molecular patterns (PAMPs or MAMPs). These PAMPs are recognized on the surface of plant cells by pattern recognition receptors (PRRs). Chitin-specific receptors (PR-3) in plants recognize chitin oligomers formed on the cell wall of endophytic fungi, and trigger further defensive response [16,144]. Additionally, chitosan, a chemical derived from chitin, which is also present in the endophytic cell wall, has also been found to trigger plant defense responses [145,146]. Endophytic fungi continue to induce PRR signaling and lead to the accumulation of plant antimicrobial compounds, as well as enzymes that disrupt pathogen cell structures [91].

Following PRR activation by endophytic fungi, alteration in phytohormone biosynthesis occurs, and plant cell walls are reinforced by callose deposition [17]. Furthermore, among the phytohormones, salicylic acid (SA) and jasmonic acid (JA) are central defense signaling molecules that regulate the plant's defense responses to pathogens [147]. Both SA and JA have the ability to increase the activity of the enzymes in plants' phenylpropane pathway and promote the production of phenolic compounds (e.g., coumarins, flavonoids, lignin, tannins) when PRR recognize the pathogens, initiating PAMP-triggered immunity (PTI) in plants, a long-lasting defense response [147–150]. In addition to the two aforementioned hormones, ethylene (ET) and abscisic acid (ABA) have been found to be implicated in plant defense signaling pathways, also possibly involving auxin, gibberellic acid (GA), cytokinin (CK), brassinosteroids, and peptide hormones [151]. In a study, Agostini et al. [152] indicated the role played by *Trichoderma atroviride* in maize (*Zea mays*), inducing SA, JA, and ABA synthesis pathways against *Fusarium verticillioides*. In a similar study, Ren and Dai [153] recognized that in addition to inducing JA biosynthesis in *Atractylodes lancea* as a result of interaction with *Gilmaniella* sp., the plant also synthesized volatile antimicrobial oils containing atractylone, hinesol, β-eudesmol, and atractylodin.

Note that endophytic fungi increase the production of enzymes involved in defense-related and cell-wall degrading enzymes. Baiyee et al. [91] found that *Trichoderma asperellum* induced the production of defense-related enzymes (peroxidase, polyphenol oxidase) and cell-wall-degrading enzymes in lettuce (*Lactuca sativa*) against leaf spot fungi. It is well known that peroxidases contribute significantly to the formation of lignin and are in charge of destroying excess hydrogen peroxide produced in plant tissues as a result of pathogen attacks. Meanwhile, polyphenol oxidase aids in preventing major oxidative damage when a plant responds to disease by catalyzing the oxygen-dependent oxidation of phenols to quinones [91,154]. Endophytic fungi need to establish compatible interaction with the plant while eliciting PTI. Therefore, the fungi should be able to cope with or suppress PTI that works against them. Endophytes use proteins secreted by effectors to protect them from the host immune system [144].

Those endophytic effectors activate the next phase of the plant immunity system, called effector-triggered immunity (ETI). Once the fungi produce the effectors, they are recognized by plant-resistance (R) proteins determined by disease-resistance (*R*) genes. Those R proteins have two conserved features, nucleotide binding (NB) and leucine-rich repeat (LRR) domains, called *NLR*s [155]. In plants, *NLR*s genes account for over 80% of identified *R* genes. A range of intracellular multi-domain proteins that directly or indirectly identify pathogen-derived effectors is encoded by the *NLR*s genes. Identifying effectors by the NLRs receptors leads to ETI [156]. The defense reaction of ETI is similar to that of PTI; nevertheless, to activate the complete defense-resistant mechanism in plants, PTI itself may not be enough, and a cooperative function with ETI is needed [157]. Endophytic fungi have adapted balanced antagonism, which equalizes the plant defense and virulence of endophytic fungi. Secondary metabolites produced by endophytes allow them to neutralize unwelcome plant defense responses; therefore, no disease symptoms are expressed by the plant, confirming the survivability of the endophytic fungi, and favoring endosymbiosis [158,159]. In turn, phytopathogenic fungi are affected by the readily available defense reactions, thus controlling the early stage of the infection.

4. Conclusions and Prospects

In light of the study findings, it is crystal clear that a wide range of endophytic fungi can serve as alternative sources of biocontrol agents, presenting an option for controlling certain plant diseases in a variety of ways; at the same time, they can produce a range of bioactive compounds that are beneficial to plants. Characterizing the potential endophytic fungi through in vitro experiments is an essential initial step in developing biocontrol agents, and field experiments also need to be performed under different environmental conditions before they are released as commercial products. Most research to date has taken place in controlled environments, and it is not yet known how the endophyte–pathogen interaction will develop when environmental conditions change and when in competition with other organisms in the field. Among the identified potential biological control agents, species from the genus *Trichoderma* have been studied extensively, although many other equally effective organisms from other endophytic groups have not been adequately considered. There is also a huge lack of primary studies aimed at understanding novel endophytic fungi with bio-controlling activity, and continuous investigations are needed in this regard.

Control of those pathogens is being carried out using synthetic fungicides that cause negative impacts on ecosystems. According to the available studies, endophytic fungi better control many deleterious diseases caused by phytopathogens than synthetic fungicides; however, environmental dependency makes them more vulnerable. Consequently, in an open-field setting, we recommend applying endophytic fungi as biocontrol agents and other disease precaution measurements. Endophytic fungi were found to be a golden alternative source to the application of fungicides. Undeniably, the utilization of endophytic fungi could lead to more eco-friendly agro farming.

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