Fungal Endophytes and Their Benefits for Plants

Subjects: Microbiology

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Plant pathogens are responsible for causing economic and production losses in several crops worldwide, thus reducing the quality and quantity of agricultural supplies. To reduce the usage of chemically synthesized pesticides, strategies and approaches using endophytic microorganisms are being used in plant disease management. Although the term "endophyte" was originally introduced by de Bary in 1866, the most used definition of endophytes was proposed by Petrini in 1991. It refers to a group of organisms "inhabiting plant organs that at some time in their life can colonize internal plant tissues without causing apparent harm to the host". These endophytes are usually fungi or bacteria that are present in the phyllosphere, endosphere or rhizosphere. These microorganisms live in the tissues of plants without causing any symptoms of disease, leading to beneficial effects for the hosts.

Keywords: antibacterial ; antifungal ; biofertilizers ; endophytes ; mycoherbicides

1. Introduction

In 1807, Bénédict Prévost found that germination of spores from *Tilletia caries* was inhibited by metallic copper when placed in the soil, thus describing it as the first compound with fungicidal properties [1]. The first organic fungicide was synthesized in the early 20th century. After that, several fungicides such as 2-methoxyethyl silicate and 2-hydroxyphenyl mercury, effective against the fungal species *Fusarium* spp. and *Dreschlera* spp., started also to be commercialized [2]. Nevertheless, the excessive use of agrochemicals has contributed to the environmental pollution (e.g., long degradation period), undesirable effects on human health (e.g., carcinogenicity) and the development of pathogen resistance [3]. Therefore, alternative methods for the safe control of plant pathogens and weed managements such as the use of biocontrol microorganisms and the application of naturally sourced metabolites have received increasing attention in the past decade [4][5].

Microorganisms are known for their ability to synthesize secondary metabolites, which exhibit promising bioactivities for the development of agrochemicals. Many natural antifungal fungicides have been obtained from microbial resources [6]. For instance, kasugamycin isolated from *Streptomyces kasugaensis* is widely used to control leaf spot, fire blight, rice blast and bacterial diseases in several crops [7]. The polyoxins, produced by *Streptomyces cacaoi*, are effective for rice fungal diseases as well as for the gray mold disease of fruits (*Botrytis cinerea*) [8]. Moreover, the antifungal antibiotic validamycin produced by *Streptomyces hygroscopicus* var. *limoneus* is commonly used to control sheath blight of rice plants caused by *Rhizoctonia solani* [9]. It is also well-stablished that several fungal genera may confer herbicidal activities by producing competent phytotoxins, such as species of the genus *Colletotrichum* and *Xylaria* [10].

The application of endophytic fungi to promote a sustainable agriculture has also been of interest, due to their role as plant-growth promoters [11]. This role is based on recognized mechanisms, such as the increase in nutrient and water acquisition and the production of plant hormones, leading to an increase in resistance to biotic and abiotic stresses [12]. Recent research has also demonstrated that the use of bacteria and fungi as biological control agents is advantageous to control plant diseases, thus improving agricultural yields [13]. The application of fungal biological control agents has largely increased due to their high reproductive rate (sexually and asexually), and their being target specific [14].

The genus *Diaporthe* comprises plant pathogens and endophytes, and it is a source of secondary metabolites. These have been explored for their potential applications in health care (e.g., antioxidant and anti-inflammatory properties), pharmacology (e.g., clinical toxicology assessment) and biomedicine (e.g., development of drugs) [15][16]. However, there is still a lack of information on the phytotoxins produced by species of *Diaporthe*, which should be explored given their potential application in agriculture as promising candidates for the development of natural herbicides [15]. Moreover, endophytic *Diaporthe* species are also reported as producing antimicrobial compounds to control plant pathogens, and as promising agents in the development of biofertilizers to promote plant growth [17].

2. Fungal Endophytes and Their Benefits for Plants

Although the term "endophyte" was originally introduced by de Bary in 1866, the most used definition of endophytes was proposed by Petrini in 1991 [18]. It refers to a group of organisms "inhabiting plant organs that at some time in their life can colonize internal plant tissues without causing apparent harm to the host" [19]. These endophytes are usually fungi or bacteria that are present in the phyllosphere, endosphere or rhizosphere. These microorganisms live in the tissues of plants without causing any symptoms of disease, leading to beneficial effects for the hosts (**Figure 1**) by:

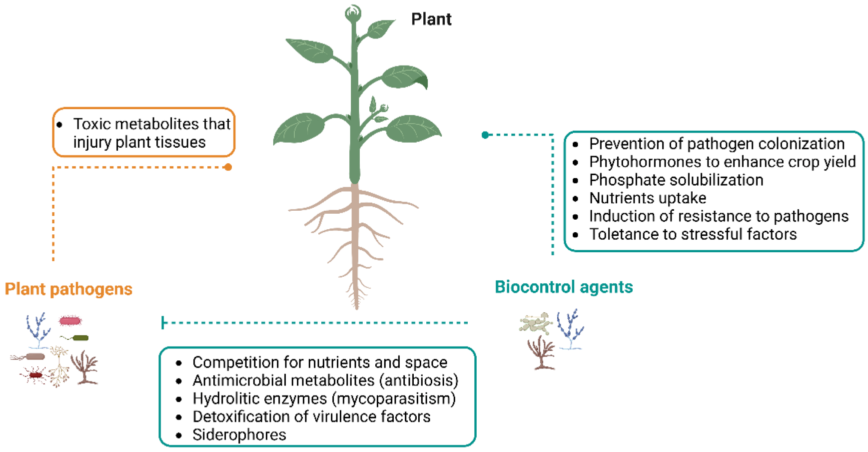

Figure 1. Overview of possible modes of action of endophytic fungi as biological control agents and plant-growth promoters. Beneficial microorganisms can exhibit direct antagonism against plant pathogens (inhibitor green line), as well as promote plant growth (dotted green line). Plant pathogens can also produce toxins to injure the plant (dot orange line). The figure was created with BioRender.com (accessed on 20 October 2022).

(1)Facilitating the acquisition of limited nutrients (e.g., nitrogen) [3];

(2)Producing phytohormones (e.g., gibberellins and indole acetic acid) that enhance crop yield and quality [20][21][22];

(3)Providing plant tolerance to environmental stresses factors (e.g., salinity, drought, heavy metal presence) [3][20];

(4)Improving resistance to pathogens [3].

In this regard, some fungal species have been studied due to their ability to promote plant growth. For instance, *Fusarium equiseti* increased the herbage yield of *Trifolium subterraneum* (subclover) by facilitating nitrogen uptake, while *Sporormiella intermedia* increased the mineral uptake of calcium, copper and zinc in subclover, thus enhancing the nutritional value of forage [23]. Similarly, Baron et al. [24] used *Aspergillus sydowii* to inoculate maize plants (*Zea mays*). The authors stated that those plants inoculated with the fungus accumulated significantly higher amounts of phosphorous in their tissues. The endophyte *Colletotrichum tropicale* can also enhance the nitrogen uptake and change its distribution in cacao plants [25]. *Trichoderma asperellum* was also reported to significantly increase seed vigor and the yield of *Sorghum bicolor* roots [26].

Moreover, Khan et al. [27] detected gibberellin production by *Penicillium citrinum*. These authors have thus demonstrated that the *P. citrinum* improved the length of seedlings in the sandy plant *Atriplex gmelinii*, thus promoting its growth. Baron et al. [28] also demonstrated that the fungal species *Purpureocillium lilacinum*, *P. lavendulum* and *Metarhizium marquandii* are able to produce indole acetic acid and to solubilize phosphorous. The authors showed that these strains were able to promote the availability of phosphorous and nitrogen in soybean, bean and maize plants. In another study, Ismail et al. 2020 [29] reported that soybean plants inoculated with the endophyte *Aspergillus niger* showed tolerance to high temperatures. The inoculation with this fungal endophyte promoted and increased plant height, biomass and chlorophyll content, as well as to reduced lipid peroxidation during heat stress [29].

The intensive use of chemical fungicides to suppress the growth of plant pathogens over a long period have led to pesticide-related pollution, resistant microbial strains, chemical consumption through bioaccumulation, biodiversity losses and the elimination of natural/beneficial microorganisms [30]. Considering that the most current strategies contained in the United Nations 2030 Agenda (17 Sustainable Development Goals) aim at achieving sustainable development, the biopesticides application creates an equilibrium between economic productivity and environmental protection that is crucial to sustainable agriculture [30][31]. In this regard, the growing search for new biopesticides to replace synthetic chemicals is supported by its low toxicity properties, eco-friendliness, specificity, biodegradability, low post-harvest contamination and compatibility in integrated pest management [32].

The drawbacks of biopesticides usage are defined as the high cost of commercial products, standard method of preparations and dose determination of active substances [32]. Nevertheless, the application of antagonistic endophytic fungi as biocontrol agents, has drawn special attention for being a sustainable option for the management of some plant diseases, thus resulting in minimal impact on the environment [4][17][33]. The main interaction between endophytic fungi and pathogens is the limitation of mycelium growth by contact, or through the formation of inhibition zones in dual culture [34]. Such facts indicate that the endophytes that act as biocontrol agents harbor multiple mechanisms to control the pathogens (**Figure 1**) by:

(1)Competing for nutrients and space [35][36];

(2)Antibiosis-production of inhibitory metabolites or antibiotics [33][35][37];

(3)Induction of plant defense response against plant pathogens [35][38];

(4)Secretion of extracellular hydrolytic enzymes [38];

(5)Detoxification of virulence factors [38].

Since early times, man has attempted to increase and improve crop production and to control plant diseases by using antagonistic microorganisms [39]. For instance, Roberts, in 1874 [40], introduced the term antagonism in microbiology after showing the antagonistic action between the fungus *Penicillium glaucum* and a bacterial strain. Later in 1921, Hartley inoculated forest nursery soils with antagonistic fungi to control damping-off caused by *Pythium debaryanum* [41]. In 1941, Weindling [42] noted that species of *Trichoderma* produced an antifungal compound, the gliotoxin, that was toxic to plant pathogens including *Rhizoctonia solani* and *Sclerotinia americana*. This study conducted by Weindling [42] was the first to record the use of gliotoxin in plant disease control [43]. Since the discovery of penicillin by Alexander Fleming in 1928 with pharmaceutical application, the studies on the discovery of biological control agents against plant pathogens have been increasing, attempting to unveil secondary metabolites with promising applications in agriculture [14][44].

It is noteworthy that endophytic fungi produce large numbers of metabolites with different chemical structures from, including alkaloids, terpenoids, benzopyranones or quinones [45]. These compounds are crucial for agricultural application once they exhibit promising bioactivities such as antifungal, antibacterial, herbicidal and other agricultural activities [3][16]. For instance, the fungal genus *Xylaria* associated with the *Azadirachta indica* plant produces antifungal compounds with activities against *Aspergillus niger* and *Fusarium avenaceum* [46][47]. Sangeetha et al. [48] demonstrated that species of *Trichoderma* may produce antifungal compounds due to their biocontrol potential against *Colletotrichum musae*, *Fusarium verticillioides* and *Lasiodiplodia theobromae* (causing postharvest crown rot of banana). Griseofulvin, a secondary metabolite initially isolated from the fungus *Penicillium griseofulvum*, has drawn special attention due to many reports of antifungal activities against plant pathogenic fungi such as *Cytospora* sp., *Cladosporium gloeosporioides*, *Botrytis cinerea*, *Alternaria solani* and *Fusarium solani* [49]. Therefore, endophytic fungi are promising leads for the discovery of novel secondary metabolites with potential for agricultural applications as biocontrol agents, biostimulants, biofertilizers and bioherbicides [3][4][13][50].

3. Conclusions

Regardless of the recognized benefits of endophytic fungi on plants and their potential in both biocontrol and biofertilization, they have been rarely studied regarding their application in agriculture. Nevertheless, due to the actual climate change scenarios (e.g., drought and high levels of soil salinity), it is crucial to understand the impacts of these environmental stresses on agriculture, as well as to unravel adaptation patterns of the endophytic community. Moreover, an effective utilization of endophytic fungi aids in promoting a sustainable agriculture for a safe environment and a positive impact on human health.

In recent years, accumulating evidence has provided important advances regarding biological control agents for the development of commercialized bacterial and fungal-based biopesticides to control plant diseases. However, the implementation of large-scale studies to expand the knowledge on the usage of biopesticides is still hampered by the high cost of commercial products, the standard methods of preparations, the dose determination of active substances and the susceptibility of biopesticides to environmental conditions. In this regard, and taking into consideration the possibility of using endophytic microorganisms as promising leads for the development of biopesticides and biofertilizers, some strategies should be adopted to improve the performance of these endophytic fungi. For instance, the development of specific delivery systems such as biopriming, encapsulation or foliar spraying should be favored to support the success of biocontrol and biofertilization programs. Moreover, the development of effective microbial consortium composed of endophytic fungi could also be a promising strategy, not only to ensure the microbial diversity in the soil, but also in the phylosphere; phylosphere colonization is of paramount importance to ensure crop development and plant health management, regulating plant physiology under climate change scenarios.

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