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Endophytic fungi in economically important plants: ecological aspects, diversity and potential biotechnological applications

Fungos endofíticos em plantas economicamente importantes: aspectos ecológicos, diversidade e potenciais aplicações biotecnológicas

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ABSTRACT

The aim of the present study was to perform a review of the literature to provide a brief overview of the ecological aspects, diversity and potential biotechnological applications of endophytic fungi associated with economically important plants, such as the common bean (*Phaseolus vulgaris*), cocoa (*Theobroma cacao*) and soybean (*Glycine max*). A high diversity of fungi has been reported on the leaves, stems and other organs of such plants. Studies on this subject are of considerable importance and directly contribute to the knowledge and conservation of fungal biodiversity, especially in Neotropical areas. Furthermore, such studies can open the door to a wide range of potential uses and/or modulations of fungal microbiota with the aim of enhancing the health and productivity of plants in agricultural practices, such as promoting plant growth or the biological control of diseases caused by phytopathogenic microorganisms. These endophytic fungi also represent a valuable source for prospecting secondary metabolites for biotechnological purposes.

Keywords: Biotechnology. Biological control. Symbiotic interactions. Secondary metabolites. Plant growth promotion

RESUMO

O presente estudo, que consiste em uma revisão de literatura, teve o objetivo de apresentar um breve panorama acerca de aspectos ecológicos, diversidade e potenciais aplicações biotecnológicas de fungos endofíticos associados a plantas economicamente importantes, tais como o cacau (*Theobroma cacao*), o feijão comum (*Phaseolus vulgaris*) e a soja (*Glycine max*). Uma alta diversidade de fungos tem sido revelada em associação com folhas, caules e outros órgãos dessas plantas. Estudos com essa temática são de grande importância, uma vez que eles contribuem diretamente para o conhecimento e conservação da biodiversidade fúngica, sobretudo em áreas neotropicais. Além disso, podem abrir portas para uma vasta gama de potenciais usos e/ou modulações da microbiota fúngica associada a fim de incrementar a sanidade e, consequentemente, a produtividade do hospedeiro em práticas agrícolas, tais como a promoção do crescimento vegetal ou o controle biológico de doenças causadas por micro-organismos fitopatogênicos. Fungos endofíticos de plantas economicamente importantes podem, ainda, representar uma valiosa fonte para prospecção de metabólitos secundários de interesse biotecnológico.

Palavras-chaves: Biotecnologia. Controle biológico. Interação simbiótica. Metabólitos secundários. Promoção de crescimento vegetal.

INTRODUCTION

Endophytic fungi are microorganisms that live in plant tissues for at least a part of their life cycle, apparently without causing any harm to the host (PETRINI, 1991; CABRAL et al., 1993). In recent years, considerable attention has been given to these fungi, with the conduction of a large number of studies involving a variety of approaches (AZEVEDO et al., 2000; HYDE; SOYTONG, 2008; KUMAR; KAUSHIK, 2012; NISA et al., 2015). The most commonly discussed issues regard the clarification of aspects related to the symbiosis between endophytic fungi and host plants (ARNOLD et al., 2001; FERREIRA et al., 2015), the composition of fungal communities associated with plant species in both temperate and tropical regions (GONZAGA et al., 2014; FERNANDES et al., 2015; SANTOS et al., 2016) and the functions of these microorganisms that favor the host, such as protection against pathogens (CLARKE et al., 2006; HANADA et al., 2008; GAO et al., 2010) and the promotion of plant growth (CLARKE et al., 2006; HANADA et al., 2008; Gao et al., 2010; OWNLEY et al., 2010). Focus has also been on the exploration of secondary metabolites of fungi to obtain new bioactive molecules with potential applications in the medical, pharmaceutical, industrial, agricultural and environmental fields (BUDHIRAJA et al., 2013; CAMPOS et al., 2015; CHEN et al., 2015; KUMAR et al., 2016).

Endophytic microorganisms are ubiquitous, having been encountered in many plant species growing under natural conditions (RODRIGUEZ et al., 2009; NISA et al., 2015). Endophytic fungi, in particular, have been investigated in a variety of plants ranging from grasses (MÜLLER; KRAUSS, 2005; REKHA; SHIVANA, 2014) to trees (Arnold et al., 2003; Campos et al., 2015). Studies have been conducted on medical plants (MUSSI-DIAS et al., 2012; FERREIRA et al., 2015), toxic plants (SOUZA et al., 2004; CAFÊU et al., 2005) and plants with recognized economic importance in Brazil and other countries, such as the common bean (GONZAGA et al., 2014; SANTOS et al., 2016), cocoa (MEJÍA et al., 2008; HANADA et al., 2010) and soybean (LEITE et al., 2013; Fernandes et al., 2015), which are responsible for the movement of large sums of money every year through local marketing and exportation. Moreover, many economically important plants are cultivated over large areas and are often affected by phytopathogenic fungi, pests and other organisms, which can result in decreased productivity. Thus, the study of endophytic fungi living in these plants can provide insights into the mediation of these and other common problems in agricultural production systems.

The aim of the present review was to provide a brief overview of the ecological aspects, diversity and potential biotechnological applications of endophytic fungi associated with economically important plants.

ENDOPHYTIC FUNGAL DIVERSITY IN ECONOMICALLY IMPORTANT PLANTS

Some factors exert a qualitative and quantitative influence on the biodiversity of the endophytic fungal community of a plant, such as the age of the plant, the tissue or organ studied and methods employed for the isolation of fungi (PEIXOTO NETO et al., 2002; HYDE; SOYTONG, 2008). The endophytic fungal community inhabits different plant structures, such as leaves, petioles, reproductive structures, twigs, bark and roots (RODRIGUEZ *et al*., 2009). A wealth of such fungi (most belonging to the phylum Ascomycota) has been detected (HYDE; SOYTONG, 2008). As summarized in Table 1, endophytic fungi have been investigated in different organs of a wide variety of plant species of economic interest, including food crops such as the common bean (*Phaseolus vulgaris* L.), cocoa (*Theobroma cacao* L.), soybean (*Glycine max* (L.) Merr.) and wheat (*Triticum aestivum* L.). A high diversity of fungi has been reported in association with the leaves, stems and other organs of such plants. Studies on this subject are of considerable importance and directly contribute to the knowledge and conservation of fungal biodiversity, especially in Neotropical areas.

Table 1. Host plants, isolation parts, and frequent taxonomic groups of endophytic fungi isolated from economically important plants.

Host plants		Isolation parts	Frequent taxonomic groups	References
Common names	Scientific names			
Banana	*Musa acuminata* Colla	leaves	*Xylaria* sp., *Colletotrichum musae* and *Cordana musae*	Pereira; Vieira; Azevedo, 1999
Cocoa	*Theobroma cacao* L.	branches	*Fusarium* spp.	Rubini et al., 2005
		stems and pods	*Coprinellus* sp.	Crozier et al., 2006
		leaves and fruits	(*1)	Mejía et al., 2008
		branches, twigs and stem bark	*Trichoderma* spp., *Pestalotiopsis* spp. and *Fusarium* spp.	Hanada et al., 2010
Coffee	*Coffea arabica* L.	leaves	*Colletotrichum*, *Xylaria* and *Guignardia*	Santamaría; Bayman, 2005
		leaves	(*1)	Fernandes et al., 2009
	C. arabica L. and other coffee species	leaves, roots, stems and berries	*Colletotrichum*, *Fusarium*, *Penicillium* and *Xylariaceae*	Vega et al.,2010
Common bean	*Phaseolus vulgaris* L.	leaves	*Colletotrichum, Hannaella, Cochliobolus* and *Phomopsis*.	Gonzaga et al., 2014
Cowpea	*Vigna unguiculata* (L.) Walp.	seeds	*Aspergillus* spp., *Penicillium* spp. and *Fusarium* spp.	Rodrigues; Menezes, 2002
Cupuassu	*Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum.	branches, twigs and stem bark	*Pestalotiopsis* spp.	Hanada et al., 2010
Grapevine	*Vitis vinifera* L.	stems	*Alternaria sp., Epicoccum nigrum* and *Aureobasidium pullulans*	Pancher et al., 2012
Maize	*Zea mays* L.	leaves and stems	*Alternaria alternata* and *Aureobasidium pullulans* var. *melanigerum*	Fisher et al, 1992
		grains and roots	(*1)	Orole; Adejumo, 2011

To be continued

Table 1. Continued

Host plants		Isolation parts	Frequent taxonomic groups	References
Common names	Scientific names			
Orange	*Citrus* spp.	leaves and seeds	*Colletotrichum gloeosporioides, Guignardia citricarpa* and *Cladosporium sp.*	Araújo et al., 2001
Pejibaye	*Bactris gasipaes* Kunth	shoot tips	*Fusarium* spp., *Neotyphodium* sp., *Epicoccum nigrum*; *Colletotrichum* sp. and *Alternaria gaisen*	Almeida; Yara; Almeida, 2005
Rice	*Oryza sativa* L.	leaves and roots	*Chaetomium globosum, Penicillium chrysogenum, Fusarium oxysporum* and *Cladosporium cladosporioides*	Naik; Shashikala; Krishnamurthy, 2009
Rubber trees	*Hevea brasiliensis* L.	leaves and stems	*Penicillium, Pestalotiopsis* and *Trichoderma*	Gazis; Chaverri, 2010
Soybean	*Glycine max* (L.) Merr.	leaves and stems	(*1)	Pimentel et al., 2006
		roots	(*1)	Hamayun et al., 2009a; 2009b
		leaves	*Colletotrichum, Cochliobolus, Fusarium* and *Xylaria*	Leite et al., 2013
		leaves and roots	*Ampelomyces* sp., *Cladosporium cladosporioides, Colletotrichum gloeosporioides, Diaporthe helianthi, Guignardia mangiferae, Phoma* sp., *Fusarium oxysporum, Fusarium solani* and *Fusarium* sp.	Fernandes et al., 2015
Sugarcane	*Saccharum* spp.	leaves	Ascomycota phylum	Stuart et al., 2010
		leaves	(*1)	Leme et al., 2013
Wheat	*Triticum aestivum* L.	leaves, stems, glumes and grains	*Alternaria alternata, Cladosporium herbarum, Epicoccum nigrum, Cryptococcus* sp., Rhodotorula rubra, *Penicillium* sp., and *Fusarium graminearum*	Larran et al, 2007

(*1): Unavailable or unclear information in reference.

Analyzing the data displayed in Table 1, spatial and seasonal fluctuations in endophytic fungi are evident. For example, an endophytic fungus may or may not occur in a given plant species, depending on the cultivation locality, environmental conditions and the growth stage of the plant. Moreover, same species of endophytes have been isolated from different host species (GAO et al., 2005; MUSSI-DIAS et al., 2012).

Endophytic fungi have been encountered in the leaves, fruit, branches and other parts of the cocoa plant (*T. cacao*) (RUBINI et al., 2005; MEJÍA et al., 2008; HANADA et al., 2010). The most frequent taxa are not the same for all plant organs.

However, there are taxa in common, the genus *Fusarium*, which Rubini et al. (2005) and Hanada et al. (2010) found to be dominant and Mejia et al. (2008) also detected as endophytic in the cocoa plant. Moreover, species of the genus *Fusarium* have been reported to be members of the endophytic fungal community of other crops, such as the cowpea (RODRIGUES; MENEZES, 2002), coffee (VEGA et al., 2010) and common bean (GONZAGA et al., 2014). Fungi from the genera *Colletotrichum*, *Epicoccum*, *Phomopsis* and *Xylaria* are also frequently reported endophytic taxa associated with economically important plants (ARAÚJO et al., 2001; SANTAMARÍA; BAYMAN, 2005; LEITE et al., 2013; TALONTSI et al., 2013; GONZAGA et al., 2014; SANTOS et al., 2016).

ENDOPHYTIC FUNGI PROVIDE BENEFITS TO THE HOST

Through interactions with the host plant, endophytic fungi play several beneficial roles that contribute to the health of the host and either directly or indirectly lead to an increase in plant productivity, such as protection against diseases caused by pathogenic microorganisms, protection against herbivory, the promotion of plant growth and the production of secondary metabolites.

A) Protection against diseases caused by pathogenic microorganisms

This aspect is a major benefit of endophytic fungi, which are capable of protecting the plant against pathogens through different strategies, such as competition with pathogens for colonization sites and nutrients, the production of antibiotics, the induction of resistance in the host plant and other mechanisms (AZEVEDO et al., 2000; STROBEL et al., 2001; ARNOLD et al., 2003; CLARKE et al., 2006; OWNLEY et al., 2010).

B) Protection against herbivory

Another activity that has been attributed to endophytic fungi is the protection of plants against attacks from herbivorous insects through the production of toxins (Raps and Vidal, 1998). Investigations have shown that endophytic fungi can influence the preference and performance of herbivorous insects, which minimizes the harm caused to the plant (RAPS; VIDAL, 1998; MEISTER et al., 2006; OKI et al., 2009; CRAWFORD et al., 2010; GANGE et al., 2012).

C) Plant growth promotion

Endophytic fungi can promote the growth of the host plant through the synthesis of phytohormones and/or by increasing plant tolerance to abiotic stress (PEIXOTO NETO et al., 2002; REDMAN et al., 2002; BAE et al., 2009; HAMAYUN et al., 2009b; KHAN et al., 2015). This ability to stimulate plant growth is extremely important and can be explored in agricultural practices. Indeed, the use of plant growth-promoting microorganisms is an option to help modern agriculture face the challenges of increasing crop production and ensuring sustainability (LUZ et al., 2006).

Studies involving the use of endophytic fungi for the promotion of plants of economic interest have achieved promising results. Examples include the work done with corn (*Zea mays* L.), tobacco (*Nicotiana tabacum* L.) (VARMA et al., 1999), yellow passion fruit (*Passiflora edulis* Sims. f. sp. *flavicarpa* Deg.) (LUZ et al., 2006), cocoa (*T. cacao* L.) (BAE et al., 2009) and soybean (*G. max* (L.) Merr.) (HAMAYUN et al., 2009a; 2009b; KHAN et al., 2011). *Piriformospora indica*, which is a basidiomycete that endophytically colonizes the roots of numerous plants, is among the species of endophytic fungi most commonly used in plant growth promotion (VARMA et al., 1999; PEIXOTO NETO et al., 2002; KUMAR et al., 2011).

D) Production of secondary metabolites

Endophytic fungi produce a wide variety of secondary metabolites, which, unlike primary metabolites, play an important role in the physiological processes of microorganisms (STROBEL; DAISY, 2003; SURYANARAYANAN et al., 2009; RÖNSBERG et al., 2013). These compounds are produced for specific reasons, such as social interactions or predation, and are therefore related to the ecology of the producing organisms (BRAGA et al., 1999; CONTI et al., 2012). Secondary metabolites produced by endophytic fungi are also a potential source of novel bioactive natural products that may have applications in different fields of study (STROBEL; DAISY, 2003; SURYANARAYANAN et al., 2009; KUMAR; KAUSHIK, 2012; RÖNSBERG et al., 2013).

BIOTECHNOLOGICAL APPLICATIONS OF ENDOPHYTIC FUNGI

The two main biotechnological applications of endophytic fungi are the production of secondary metabolites of economic interest and the biological control of pathogens, which are the focus of the discussion in this review.

A) Secondary metabolites of biotechnological interest

In the context of the prospecting of natural products, microorganisms are considered excellent producers of chemicals with desirable bioactive properties and substantial potential in the pharmaceutical industry (SURYANARAYANAN et al., 2009; CONTI et al., 2012; KUMAR; KAUSHIK, 2012). Indeed, fungi produce a quantity of chemicals currently used in medicine as antimicrobial agents and are producers of different substances of economic interest, such as enzymes, vitamins, amino acids and steroids (BRAGA et al., 1999; CAFÊU et al., 2005; MARINHO et al., 2009; SURYANARAYANAN et al., 2012; BARA et al., 2013).

Endophytic fungi stand out among the microorganisms that have been prospected in search of natural products with biotechnological applications. The secondary metabolites produced by these fungi have been the focus of several studies and represent a promising source for the bioprospecting of novel molecules with potential applications in both the pharmaceutical industry as well as agricultural activities in the form of crop protection (STROBEL; DAISY, 2003; AMARAL; RODRIGUES-FILHO, 2010; KUMAR; Kaushik, 2013; TALONTSI et al., 2013).

As endophytic fungi have ubiquitous distribution (RODRIGUEZ et al., 2009), there is an excellent chance of finding new species in plants that make up different ecosystems (STROBEL; DAISY, 2003). Thus, there is a range of metabolites to be explored from the biotechnological standpoint.

The most striking account of metabolite production by endophytic fungi with bioactive properties is the cancer medication taxol, which was originally produced from the yew tree (*Taxus brevifolia*). The production of this compound by an endophytic fungus was first demonstrated in studies by Stierle et al. (1993), in which the authors demonstrated that *Taxomyces andreanea* found in the yew tree was able to produce taxol *in vitro* (STIERLE et al., 1993). Subsequent studies have also shown that different species of endophytic fungi are also able to produce taxol, such as *Pestalotiopsis microspora* isolated from *Taxus wallachiana* (Strobel et al., 1996), *Pestalotiopsis terminaliae* isolated from *Terminalia arjuna* (GANGADEVI; MUTHUMARY, 2009), *Gliocladium* sp. isolated from *Taxus baccata* (SREEKANTH et al., 2009) and *Guignardia mangiferae* isolated from *Taxus media* (XIONG et al., 2013).

The discovery that numerous endophytic fungi can produce taxol led to the emergence of the possibility of using a novel, more efficient, less expensive process to produce this important drug (PEIXOTO NETO et al., 2002). The laboratory cultivation of fungi does not require the extraction of the compound from *Taxus brevifolia* or other producing plants (PEIXOTO NETO et al., 2002; SREEKANTH et al., 2009; XIONG et al., 2013). This is one of the advantages of the exploration of secondary metabolites of a fungal origin in relation to other sources, as microorganisms can be grown in large-scale fermenters, which eliminates the harm to the ecosystem that occurs with the removal of plants from natural areas and minimizes the danger of the local extinction of plant species that are collected for the extraction of medicinal products (PEIXOTO NETO et al., 2002; TAKAHASHI; LUCAS, 2008).

In addition to taxol, the scientific literature reports the discovery of secondary metabolites produced by endophytic fungi with activity of biotechnological interest, such as the inhibition of pathogenic organisms (MOMESSO et al., 2008; SILVA et al., 2010; BUDHIRAJA et al., 2013). The following are examples of such metabolites: phomopsichalasin produced by *Phomopsis* sp., which has antibacterial activity (HORN et al., 1995); cryptocandin produced by *Cryptosporiopsis* cf. *quercina*, which has antifungal activity (STROBEL et al., 1999); cercosporin produced by *Mycosphaerella* sp., which has antiparasitic action (MORENO et al., 2011); and cytochalasins produced by *Chaetomium globosum* and *Xylaria* sp., which have diverse biological activities, including cytotoxic action (MOMESSO et al., 2008; SILVA et al., 2010).

As with endophytes of medicinal plants, the biological activity of endophytic fungi of crops, such as coffee (*Coffea arabica* L.) (SETTE et al., 2006; FERNANDES et al., 2009), rice (*Oryza sativa* L.) (NAIK et al., 2009), sugarcane (*Saccharum officinarum* L.) (FÁVARO et al., 2012), cocoa (*T. cacao* L.) (TALONTSI et al., 2013) and wheat (*Triticum durum* Desf.) (SADRATI et al., 2013), has also been investigated.

B) Endophytic fungi as biological control agents of phytopathogens

The biological control of phytopathogens involves the use of microorganisms that reduce the activity or survival of disease-causing agents in plants (OWNLEY et al., 2010). The most commonly described biocontrol mechanisms are antibiosis, competition for space, iron and other nutrients, parasitism and the induction of resistance in the host (MARIANO et al., 2004; BAILEY et al., 2008; CAO et al., 2009; OWNLEY et al., 2010).

Endophytic fungi have been studied with regard to the ability to act as inhibitors of other microorganisms for application as biocontrol agents as an alternative to chemical control. These fungi can be used either directly, in which the organism is applied live and acts as an antagonist, or indirectly, through the use of metabolites (LAZZARETTI; BETTIOL, 1997; GRIGOLETTI JÚNIOR et al., 2000; MORANDI; BETTIOL, 2009).

Hanada et al. (2010) conducted field experiments to assess the biocontrol properties of endophytic fungi isolated from cocoa (*T. cacao* L.) and cupuassu (*T. grandiflorum* (Willd. ex Spreng.) K. Schum.) against *Phytophthora palmivora*, the causal agent of cocoa black-pod rot disease, which is one of the most important pathogens in cocoa-producing areas throughout the world. Fungal species of the genera *Pestalotiopsis*, *Curvularia*, *Tolypocladium* and *Fusarium* have demonstrated the greatest activity against this pathogen (HANADA et al., 2010). Rubini et al. (2005), Bailey et al. (2008) and Mejía et al. (2008) also evaluated the potential use of endophytic fungi isolated from cocoa (*T. cacao* L.) for the biological control of phytopathogens.

Rocha et al. (2011) analyzed the potential application of endophytic fungi from rubber trees (*Hevea brasiliensis* L.) for the biological control of the pathogen *Microcyclus ulei*, which causes damage to rubber tree crops. Garoé et al. (2012) assessed the potential use of endophytic fungi from grapevine (*Vitis vinifera* L.) for the biological control of *Botrytis cinerea*, which affects grape crops. Similar studies should be conducted to assist in the development of sustainable strategies for the control of diseases that affect crops and lead to huge financial losses.

CLOSING REMARKS

The findings of the present review of the literature underscore the importance of endophytic fungi to host plants and the need for further studies on the isolation and identification of these organisms as well as the prospecting of secondary metabolites of biotechnological interest.

AUTHORS CONTRIBUTION

The biologist Beatriz dos Santos Souza, from UFOPA, carried out the selection of bibliographic data and contributed to the preparation of the manuscript. The Professor MSc. Taides Tavares dos Santos, from UFT, planned and guided the study, as well as approved the final proof of the manuscript.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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