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REVIEW ARTICLE

Diversity, distribution and biotechnological potential of endophytic fungi

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Abstract Endophytic fungi, living in the inner tissues of living plants, have attracted increasing attention among ecologists, taxonomists, chemists and agronomists. They are ubiquitously associated with almost all plants studied to date. Numerous studies have indicated that these fungi have an impressive array of biotechnological potential, such as enzyme production, biocontrol agents, plant-growth promoting agents, bioremediation, biodegradation, biotransformation, biosynthesis and nutrient cycling. These fungi may represent an underexplored reservoir of novel biological resources for exploitation in the pharmaceutical, industry and agriculture. This review focuses on new findings in isolation methods, biodiversity, ecological distribution and biotechnological potential.

Keywords Endophytic fungi · Diversity · Distribution · Biotechnological application

Introduction

Fungi that reside in the tissues of living plants without causing visible damage are known as endophytic fungi (Wang and Dai 2011). These fungi live in different organs (root, stem, leaf, flower, fruit, and seed) of the host plants, mainly in inter- or intra-cellular spaces. It is noteworthy that, of the nearly 300,000 plant species on our planet, each individual plant is considered to host at least one type of endophyte (Strobel and Daisy 2003), creating an enormous biodiversity. However, only a few of these plant-associated endophytic fungi have been studied, indicating that the opportunity to find interesting endophytes among myriad plants in different niches and ecosystems is great. Furthermore, studies on the endophytic fungi of plants are necessary to provide fundamental information for the assessment of global fungal diversity and distribution, as well as for the discovery of new species. To date, fungal taxa that have been reported to be endophytic of different plant species include *Ascomycota*, *Basidiomycota*, and *Zygomycota* (Carvalho et al. 2012). Recent studies have revealed a large richness of endophytic fungal species and diverse metabolites with different functions (Zimmerman and Vitousek 2012; Xiao et al. 2014; Zhang et al. 2014a, b). In some cases, they can enhance plant growth (Waller et al. 2005), act as biological control agents (Zhang et al. 2014c), and produce enzymes (Bezerra et al. 2012). The endophytic fungi are relatively unexplored and could be potential sources of novel natural products for exploitation in medicine, agriculture, and industry (Strobel et al. 2004).

This review aims to provide an overview of endophytic fungi, and to summarize their isolation and cultivation methods, new findings in the recent study of the astounding endophytic fungi diversity, and their ecological distribution, role and enormous biotechnological potential.

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Isolation and cultivation methods for endophytic fungi

In the early 1898, endophytic fungi were first isolated from seeds of *Lolium temulentum*, indicating that fungi can closely be associated with plants. From 1890 to 1980, however, only a handful of endophytic fungi were recorded and described (Hyde and Soytong 2008). Since the 1980s, endophytic fungi have been isolated from almost all examined tracheophytes, ranging from herbaceous species to woody plants. It is evident that colonization of terrestrial plants by fungi is ubiquitous in nature. Thus, endophytic fungi are important components of microbial biodiversity because of the vast number of plant species. Theoretically, any plant could be selected for fungi isolation (Qin et al. 2011). Strobel and Daisy (2003) stressed that plant selection is tactical. Those plants with an unconventional setting and biology as well as with established ethnobotanic value would be preferred and promising sources of endophytic fungi producing novel bioactive products. It is important to establish a specific protocol for the isolation of endophytic fungi from a given plant material, as isolation represents the most crucial step to obtain pure cultures, and host species, sampling strategy, host-endophyte and inter-endophyte interactions, tissue type and age, geographic and habitat distribution, culture conditions, surface sterilants and selective media all influence the detection and enumeration of endophytic fungi (Zhang et al. 2006). Some detailed isolation methods and procedures, including plant sampling, surface sterilization and media used have been reviewed by Hallmann et al. (2006) and introduced by Strobel and Daisy (2003). Plant selection is important to isolate novel endophytic fungi as well as those making novel bioactive products, and selection strategies have also been outlined (Strobel and Daisy 2003).

Surface sterilization is the first critical step for ensuing isolation of endophytic fungi avoiding contamination by those on the plant surface. Sodium hypochlorite (2–10 %), ethanol (70–90 %), H_2O_2 (3 %) and $KMnO_4$ (2 %) are commonly used as surface disinfectants. Sterilization with ethanol followed by sodium hypochlorite is used widely (Rivera-Orduña et al. 2011; Li et al. 2012b; Xiong et al. 2013). Some surfactants, such as Tween 20, Tween 80 and Triton X-100, have been used as soaking agents to enhance the effectiveness of surface sterilization (Zhang et al. 2006; Qin et al. 2011). A common protocol involves a three-step procedure as described by Coombs and Franco (2003). A five-step procedure was introduced by Qin et al. (2009), adding sodium thiosulfate solution after treatment with sodium hypochlorite since thiosulfate decreases residual traces of NaClO, and promotes endophyte growth and isolation. In general, the surface sterilization procedure should be optimized for each plant tissue, especially sterilization time, since the sensitivity varies with plant species, organ and age (Qin et al. 2011). In addition to surface sterilization, vacuum and pressure bomb techniques have been employed for isolating endophytes (Hallmann et al. 1997).

Pretreatment of plant issues is an important step in the isolation of endophytic fungi. Usually, sterilized plant materials are sectioned aseptically into small fragments, measuring approximately 0.5×0.5 cm for leaves or 0.3–0.5 cm in length for stems and roots (Zhang et al. 2006; Kharwar et al. 2011b; Rivera-Orduña et al. 2011; Li et al. 2012b; Zheng et al. 2013), and then distributed on isolation media. We recommend that plant tissues be crumbled aseptically into smaller fragments using a commercial blender in order to enlarge the colonization area of tissues on the agar medium, thus aiding recovery of endophytes (Qin et al. 2009). Moreover, tender or soft tissues can be crushed and homogenized in a mortar using an appropriate extraction solution or buffer, and prepared for plating with proper dilution ($1\times10^{-3}-1\times10^{-5}$). In summary, an efficient release of endophytes from the inner parts of plant material is an obligatory step of pure culture isolation.

Growth of microbes in the laboratory depends on the composition of the medium and on culture conditions. For endophytic fungi, some classical media are available, such as potato dextrose agar (PDA) (Rivera-Orduña et al. 2011; Li et al. 2012b), corn meal malt agar (CMMA) (Kleczewski et al. 2012), malt extract agar (MEA) (Sun et al. 2011; Tejesvi et al. 2011), water agar (WA) (Tejesvi et al. 2011; Qi et al. 2012), Sabouraud maltose agar (SMA) (Qi et al. 2012), Sabouraud dextrose agar (SAB) (de Siqueira et al. 2011), Czapek agar (CZA) (Qi et al. 2012), corn meal agar+2 % dextrose (CMD) (Gazis and Chaverri 2010), Kenknight-Munaier′s medium (Qadri et al. 2014), nutrient broth (Pancher et al. 2012), and so on. Some low nutrient media, such as synthetic low nutrient agar (SNA) and carnation leaf agar (CLA) have proved effective for isolation of specific endophytic fungi (Arnold and Herre 2003). To improve the diversity of isolates, various culture media should be employed. In our investigations, adding a certain amount of plant extracts is effective when growing endophytic colonies. This may be due to the different physiological properties of some microorganisms in plant tissues and soils (Qin et al. 2011). Thus it is a good strategy for isolation of endophytes to design media according to the characteristics of the inner micro-environments of plants.

The obtained endophytic fungi must be identified correctly. A combination of morphological and molecular analysis methods are used widely in the taxonomy of microbiology. Macro- and micro-morphological cultural characteristics, and the characteristics of the reproductive structures and metabolite profiles are the main criteria. Gene-based sequence techniques, such as 18S rDNA, internal transcribed spacer (ITS), combined small and large ribosomal subunits, are also used to determine phylogenetic relationships (Zhang et al. 2006).

Biodiversity of endophytic fungi

Endophytic fungi have been isolated from a variety of healthy plant species ranging from crops (Fisher et al. 1992; Larran et al. 2002; Kim et al. 2007; Usuki and Narisawa 2007; Yuan et al. 2010; Yan et al. 2011), invasive plants (Mei et al. 2014), woody tree species - especially medicinal plants - (Cui et al.

2011; Rhoden et al. 2012; Wu et al. 2013a), mosses (U'Ren et al. 2010), ferns (Del Olmo-Ruiz and Arnold 2014), and also lichens (U'Ren et al. 2010). In general, *Alternaria*, *Colletotrichum*, *Fusarium*, *Gibberella*, *Glomerella*, *Guignardia*, *Leptosphaerulina*, *Nigrospora*, *Phoma*, *Phomopsis* and *Xylaria* are the genera most commonly isolated (Table 1). For example, 81 fungi were isolated from *Taxus x media*, belonging to eight different genera (*Alternaria*, *Colletotrichum*, *Gibberella*, *Glomerella*, *Guignardia*, *Nigrospora*, *Phomopsis* and *Phoma*) (Xiong et al. 2013). From three woody plants (*Betula platyphylla*, *Quercus liaotungensis*, *Ulmus macrocarpa*) of China, Sun et al. (2012) isolated 1955 strains belonged to 61 taxa (*Alternaria*, *Fusarium*, *Phoma*, *Xylaria*, etc.), which were identified on the basis of morphological characteristics and DNA sequence data. The dominant endophytic fungi were *Melanconis* spp. and *Disculina* spp. in *B. platyphylla*, *Fusicoccum* spp. in *Q. liaotungensis*, *Alternaria* spp. and *Fusarium* spp. in *U. macrocarpa*, respectively. Mei et al. (2014) isolated 463 endophytic fungi grouped in 112 operational taxonomic units (OTUs) including 38 genera from leaves of the invasive plant *Ageratina adenophora*. *Colletotrichum* spp. were the most common isolates, followed by *Nemania* spp., *Phomopsis* spp. and *Xylaria* spp.

Investigators believe that the widest biodiversity of endophytes occurs in tropical and temperate regions (Arnold et al. 2000; Zhang et al. 2006; Hyde and Soytong 2008; Zimmerman and Vitousek 2012). Arnold and Lutzoni (2007) compared endophytic fungal communities along a broad latitudinal gradient from the Canadian arctic to the lowland tropical forest of central Panama. Among 21 plant species in six localities, endophytic fungi decreased linearly from the tropics to northern boreal forest. Diversity of endophytic fungi ranged from Fisher's α=2.6 in southern boreal forest to 17.9 in tropical forest. As reviewed by Banerjee (2011), more than 80 genera of endophytic fungi were isolated from tropical and subtropical plants, which illustrates the tremendous endophytic biodiversity in these areas.

Compared to tropical trees, the diversity of endophytic fungi and their ecological roles in cold environment plants have been underexplored. Li et al. (2012b) isolated 604 endophytic fungi from five different plants collected from the Baima Snow Mountain (altitude 4000–4300 m), Southwest China. Morphological characteristics and internal transcribed spacer (ITS) sequence analysis revealed that 43 different taxa were obtained, in which *Cephalosporium*, *Sirococcus*, *Penicillium* and *Aspergillus* were the dominant genera distributed widely in all five plant species. Zhang et al. (2013) investigated the endophytic fungi diversity associated with bryophytes (*Barbilophozia hatcheri*, *Chorisodontium aciphyllum*, *Sanionia uncinata*) in the Fildes Region, King George Island, maritime Antarctica. A total 128 endophytic fungi were identified to 21 different taxa, with 15 *Ascomycota*, 5 *Basidiomycota*, and 1 unidentified fungus. The number of fungal taxa isolated from *B. hatcheri*, *C. aciphyllum* and *S. uncinata* were 9, 6, and 12, respectively. Even these limited results suggest that cold environment plants will be an interesting source of fungal endophytes, and the diversity is also abundant.

Mangrove is another hot research point for endophytic fungi. De Souza Sebastianes et al. (2013) isolated 343 endophytic fungi from three mangrove plants (*Avicennia schaueriana*, *Laguncularia racemosa*, *Rhizophora mangle*) belonging to at least 34 different genera, the most frequent of which were *Diaporthe* spp., *Colletotrichum* spp., *Fusarium* spp., *Trichoderma* spp. and *Xylaria* spp. This indicates that the mangrove fungal community possesses an impressive diversity and richness of endophytic fungi. More than 200 endophytic fungi, mainly genera of *Alternaria* spp., *Aspergillus* spp., *Cladosporium* spp., *Colletotrichum* spp., *Fusarium* spp., *Paecilomyces* spp., *Penicillium* spp., *Pestalotiopsis* spp., *Phoma* spp., *Phomopsis* spp., *Phyllosticta* spp. and *Trichodema* spp., were isolated and identified from mangroves (Cheng et al. 2009). Most endophytic fungi found in mangroves have a wide range of hosts, but a few have only a single host.

Mycologists believe that there are a lot of endophytic fungal species in plants growing in areas of heavy-metal pollution. For instance, 495 endophytic fungi belonging to 20 taxa were obtained from six dominant plant species in a Pb-Zn mine in China, and *Phoma* spp. were the most common isolates, followed by *Alternaria* spp. and *Peyronellaea* spp. (Li et al. 2012a). In our study (Zheng et al. 2013), 186 endophytic fungi were isolated from different plant species in a Pb-Zn mine in Southwest China. The endophytic fungi isolation rate ranged from 43 % to 85 %. These results suggest that fungal endophyte colonization in Pb-Zn polluted plants is moderately abundant. However, their ecological function in such extreme environments is still not clear, and needs further investigation.

Research on endophytic fungi has focused on terrestrial plants, while the ecologically and economically important plants present in aquatic ecosystems (except for rice) remain unexplored. Recently, Sandberg et al. (2014) investigated the diversity of fungal endophytes associated with aquatic macrophytes (*Elodea bifoliata*, *Myriophyllum sibiricum*, *Persicaria amphibia*, *Stuckenia pectinata*) in lentic waters in northern Arizona in the United States. A total of 226 isolates representing 60 putative species was recovered from 9600 plant tissue segments. Although isolation frequency was low, endophytes were phylogenetically diverse and rich at species level.

It has been estimated that less than 1 % of microorganism species are currently known, indicating that millions of microorganism species remain to be discovered (Davis et al. 2005). Gene-based culture-independent molecular approaches, such as PCR-based ITS gene clone libraries, 18S rDNA, and denaturing gradient gel electrophoresis (DGGE), are useful methods with which to reveal the complex fungal endophyte

Table 1 Biodiversity of endophytic fungi in some plants

Host plant	Family	Endophytic fungi (genera)	Reference
Colobanthus quitensis	*Caryophyllaceae*	*Aspergillus*, *Cadophora*, *Davidiella*, *Entrophospora*, *Fusarium*, *Geomyces*, *Gyoerffyella*, *Microdochium*, *Mycocentrospora*, *Phaeosphaeria*	Rosa et al. 2010
Dendrobium loddigesii	*Orchidaceae*	*Acremonium*, *Alternaria*, *Ampelomyces*, *Bionectria*, *Cercophora*, *Chaetomella*, *Cladosporium*, *Colletotrichum*, *Davidiella*, *Fusarium*, *Lasiodiplodia*, *Nigrospora*, *Paraconiothyrium*, *Pyrenochaeta*, *Sirodesmium*, *Verticillium*, *Xylaria*	Chen et al. 2010
Hevea brasiliensis	*Euphorbiaceae*	*Alternaria*, *Arthrinium*, *Cladosporium*, *Endomelanconiopsis*, *Entonaema*, *Fimetariella*, *Fusarium*, *Guignardia*, *Penicillium*, *Perisporiopsis*, *Pestalotiopsis*, *Nigrospora*, *Trichoderma*, *Umbelopsis*	Gazis and Chaverri 2010
Magnolia liliifera	*Magnoliaceae*	*Colletotrichum*, *Corynespora*, *Fusarium*, *Guignardia*, *Leptosphaeria*, *Phomopsis*	Promputtha et al. 2010
Theobroma cacao	*Malvaceae*	*Acremonium*, *Arthrinium*, *Aspergillus*, *Clonostachys*, *Colletotrichum*, *Coniothyrium*, *Curvularia*, *Cylindrocladium*, *Fusarium*, *Gliocladium*, *Lasiodiplodia*, *Myrothecium*, *Paecilomyces*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Septoria*, *Talaromyces*, *Tolypocladium*, *Trichoderma*, *Verticillium*	Hanada et al. 2010
Theobroma grandiflorum	*Malvaceae*	*Acremonium*, *Asteromella*, *Lasiodiplodia*, *Pestalotiopsis*, *Phoma*	Hanada et al. 2010
Acer truncatum	*Sapindaceae*	*Alternaria*, *Ascochytopsis*, *Bipolaris*, *Cladosporium*, *Clypeopycnis*, *Colletotrichum*, *Coniothyrium*, *Coprinellus*, *Cryptodiaporthe*, *Cyclothyrium*, *Diaporthe*, *Discula*, *Drechslera*, *Epicoccum*, *Fusarium*, *Geniculosporium*, *Gibberella*, *Glomerella*, *Guignardia*, *Helminthosporium*, *Leptosphaeria*, *Melanconis*, *Microdiplodia*, *Microsphaeropsis*, *Nigrospora*, *Paraconiothyrium*, *Phoma*, *Phomopsis*, *Podosordaria*, *Preussia*, *Pseudocercosporella*, *Sclerostagonospora*, *Septoria*, *Sirococcus*, *Xylaria*	Sun et al. 2011
Aquilaria sinensis	*Thymelaeaceae*	*Chaetomium*, *Cladosporium*, *Coniothyrium*, *Epicoccum*, *Fusarium*, *Hypocrea*, *Lasiodiplodia*, *Leptosphaerulina*, *Paraconiothyrium*, *Phaeoacremonium*, *Phoma*, *Pichia*, *Rhizomucor*, *Xylaria*	Cui et al. 2011
Dendrobium devonianum	*Orchidaceae*	*Acremonium*, *Arthrinium*, *Cladosporium*, *Fusarium*, *Glomerella*, *Leptosphaerulina*, *Phoma*, *Pestalotiopsis*, *Rhizopus*, *Trichoderma*, *Xylaria*,	Xing et al. 2011
Dendrobium thyrsiflorum	*Orchidaceae*	*Alternaria*, *Colletotrichum*, *Epicoccum*, *Fusarium*, *Glomerella*, *Leptosphaerulina*, *Pestalotiopsis*, *Phoma*, *Rhizopus*, *Xylaria*	Xing et al. 2011
Ledum palustre	*Ericaceae*	*Arthrinium*, *Fusarium*, *Lecythophora*, *Penicillium*, *Sordaria*, *Sphaeriothyrium*	Tejesvi et al. 2011
Lippia sidoides	*Verbenaceae*	*Alternaria*, *Colletotrichum*, *Corynespora*, *Curvularia*, *Drechslera*, *Fusarium*, *Guignardia*, *Microascus*, *Peacilomyces*, *Periconia*, *Phoma*, *Phomopsis*	de Siqueira et al. 2011
Mansoa alliacea	*Bignoniaceae*	*Alternaria*, *Aspergillus*, *Chaetomium*, *Curvularia*, *Fusarium*, *Penicillium*, *Phomopsis*, *Rhizoctonia*, *Stenella*, *Trichoderma*	Kharwar et al. 2011b
Pinus halepensis	*Pinaceae*	*Alternaria*, *Aureobasidium*, *Camarosporium*, *Chaetomium*, *Chalastospora*, *Davidiella*, *Diplodia*, *Epicoccum*, *Fusarium*, *Gremmeniella*, *Leptosphaeria*, *Lophodermium*, *Naemacyclus*, *Paraconiothyrium*, *Penicillium*, *Pestalotiopsis*, *Peziza*, *Phaeomoniella*, *Phaeosphaeria*, *Phoma*, *Phomopsis*, *Pleospora*, *Preussia*, *Pyronema*, *Sordaria*, *Trichoderma*, *Tryblidiopsis*, *Truncatella*, *Ulocladium*, *Xylaria*	Botella and Diez 2011
Solanum cernuum	*Solanaceae*	*Arthrobotrys*, *Bipolaris*, *Botryosphaeria*, *Candida*, *Cercospora*, *Colletotrichum*, *Coprinellus*, *Cryptococcus*, *Curvularia*, *Diatrypella*, *Edenia*, *Eutypella*, *Fusarium*, *Glomerella*, *Leptosphaeria*, *Mucor*, *Petriella*, *Phoma*, *Meyerozyma*, *Flavodon*, *Hapalopilus*, *Hohenbuehelia*, *Kwoniella*, *Oudemansiella*, *Phanerochaete*, *Phlebia*, *Phlebiopsis*, *Schizophyllum*	Vieira et al. 2011
Taxus globosa	*Taxaceae*	*Alternaria*, *Aspergillus*, *Annulohypoxylon*, *Cercophora*, *Cochliobolus*, *Colletotrichum*, *Conoplea*, *Coprinellus*, *Daldinia*, *Hypocrea*, *Hypoxylon*, *Lecythophora*, *Letendraea*, *Massarina*, *Nigrospora*, *Penicillium*, *Phialophorophoma*, *Phoma*, *Polyporus*, *Sporormia*, *Trametes*, *Trichophaea*, *Xylaria*, *Xylomelasma*	Rivera-Orduña et al. 2011
Tylophora indica	*Apocynaceae*	*Alternaria*, *Chaetomium*, *Colletotrichum*, *Nigrospora*, *Thielavia*	Kumar et al. 2011
Acer tataricum subsp. *ginnala*	*Sapindaceae*		Qi et al. 2012

Table 1 (continued)

Host plant	Family	Endophytic fungi (genera)	Reference
		Alternaria, *Cladosporium*, *Epicoccum*, *Fusarium*, *Neurospora*, *Penicillium*, *Phoma*, *Phomopsis*, *Trichoderma*	
Cinnamomum camphora	*Lauraceae*	*Alternaria*, *Arthrinium*, *Arthrobotrys*, *Aspergillus*, *Chaetomium*, *Chaetophoma*, *Cladosporium*, *Curvularia*, *Drechslera*, *Gliomastix*, *Humicola*, *Nigrospora*, *Penicillium*, *Periconia*, *Pestalotiopsis*, *Phacidium*, *Phomopsis*, *Phyllosticta*, *Stachybotrys*, *Trichoderma*	Kharwar et al. 2012
Echinacea purpurea	*Compositae*	*Ceratobasidium*, *Cladosporium*, *Colletotrichum*, *Fusarium*, *Glomerella*, *Mycoleptodiscus*	Rosa et al. 2012
Ginkgo biloba	*Ginkgoaceae*	*Alternaria*, *Cladosporium*, *Colletotrichum*, *Fusarium*, *Pestalotiopsis*, *Peyronellaea*, *Phoma*, *Phomopsis*, *Phyllosticta*	Thongsandee et al. 2012
Holcoglossum flavescens	*Orchidaceae*	*Alternaria*, *Cladosporium*, *Didymella*, *Epulorhiza*, *Fusarium*	Tan et al. 2012
Nyctanthes arbor-tristis	*Oleaceae*	*Acremonium*, *Alternaria*, *Aspergillus, Chaetomium*, *Cladosporium*, *Colletotrichum*, *Drechslera*, *Humicola*, *Fusarium*, *Nigrospora*, *Penicillium*, *Phomopsis*, *Rhizoctonia*	Gond et al. 2012
Opuntia ficus-indica	*Cactaceae*	*Acremonium*, *Aspergillus, Cladosporium*, *Fusarium*, *Monodictys*, *Nigrospora*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Tetraploa*, *Xylaria*	Bezerra et al. 2012
Panicum virgatum	*Poaceae*	*Alternaria*, *Ampelomyces*, *Aspergillus*, *Candida*, *Cladosporium*, *Colletotrichum*, *Epicoccum*, *Fusarium*, *Kretzschmaria*, *Monographella*, *Nemania*, *Nigrospora*, *Nodulisporium*, *Ophiosphaerella*, *Phaeosphaeria*, *Phoma*, *Phomopsis*, *Preussia*, *Schizosaccharomyces*, *Septoria*, *Stagonospora*, *Xylaria*	Kleczewski et al. 2012
Picea abies	*Pinaceae*	*Acephala*, *Chalara*, *Cistella*, *Cladosporium*, *Entomocorticium*, *Fomitopsis*, *Lophodermium*, *Mollisia*, *Mycena*, *Neonectria*, *Ophiostoma*, *Phacidiopycnis*, *Phacidium*, *Phialocephala*, *Rhizoscyphus*, *Rhizosphaera*, *Sarea*, *Scleroconidioma*, *Sirococcus*, *Valsa*, *Xylomelasma*, *Zalerion*	Koukol et al. 2012
Piper hispidum	*Piperaceae*	*Alternaria*, *Bipolaris*, *Colletotrichum*, *Glomerella*, *Guignardia*, *Lasiodiplodia*, *Marasmius*, *Phlebia*, *Phoma*, *Phomopsis*, *Schizophyllum*	Orlandelli et al. 2012
Reynoutria japonica	*Polygonaceae*	*Alternaria*, *Arthrinium*, *Bionectria*, *Colletotrichum*, *Didymella*, *Glomerella*, *Nigrospora*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Phyllosticta*, *Septoria*, *Xylaria*	Kurose et al. 2012
Sapindus saponaria	*Sapindaceae*	*Alternaria*, *Cochliobolus*, *Curvularia*, *Diaporthe*, *Phoma*, *Phomopsis*	García et al. 2012
Stryphnodendron adstringens	*Leguminosae*	*Alternaria*, *Arthrobotrys*, *Aspergillus*, *Botryosphaeria*, *Cladosporium*, *Colletotrichum*, *Coniochaeta*, *Cytospora*, *Diaporthe*, *Guignardia*, *Fimetariella*, *Massarina*, *Muscodor*, *Neofusicoccum*, *Nigrospora*, *Paraconiothyrium*, *Penicillium*, *Pestalotiopsis*, *Phomopsis*, *Preussia*, *Pseudofusicoccum*, *Sordaria*, *Sporormiella*, *Trichoderma*, *Xylaria*	Carvalho et al. 2012
Tinospora sinensis	*Menispermaceae*	*Acremonium*, *Alternaria*, *Aspergillus*, *Botryosphaeria*, *Botrytis*, *Cladosporium*, *Chaetomium*, *Colletotrichum*, *Curvularia*, *Drechslera*, *Emericella*, *Fusarium*, *Guignardia*, *Humicola*, *Monilia*, *Nigrospora*, *Penicillium*, *Pseudofusicoccum*, *Trichoderma*, *Veronaea*	Mishra et al. 2012
Trichilia elegans	*Meliaceae*	*Cordyceps*, *Diaporthe*, *Phomopsis*	Rhoden et al. 2012
Vitis vinifera	*Vitaceae*	*Absidia*, *Alternaria*, *Aspergillus*, *Aureobasidium*, *Botrytis, Cladosporium*, *Epicoccum*, *Fusarium*, *Mortierella*, *Mucor*, *Penicillium*, *Pithomyces*, *Rhizopus*, *Trichoderma*, *Umbelopsis*, *Zygorhynchus*	Pancher et al. 2012
Cannabis sativa	*Cannabaceae*	*Aspergillus*, *Chaetomium*, *Eupenicillium*, *Penicillium*	Kusari et al. 2013
Glycine max	*Leguminosae*	*Alternaria*, *Ampelomyces*, *Annulohypoxylon*, *Arthrinium*, *Cercospora*, *Chaetomium*, *Cladosporium*, *Cochliobolus*, *Colletotrichum*, *Curvularia*, *Davidiella*, *Diaporthe*, *Didymella*, *Epicoccum*, *Eutypella*, *Fusarium*, *Gibberella*, *Guignardia*, *Leptospora*, *Magnaporthe*, *Myrothecium*, *Nectria*, *Neofusicoccum*, *Nigrospora*, *Ophiognomonia*, *Paraconiothyrium*, *Phaeosphaeriopsis*, *Phoma*, *Phomopsis*, *Rhodotorula*, *Sporobolomyces*, *Stemphylium*, *Xylaria*	De Souza Leite et al. 2013
Jatropha curcas	*Euphorbiaceae*	*Alternaria*, *Chaetomium*, *Colletotrichum*, *Fusarium*, *Guignardia*, *Nigrospora*	Kumar and Kaushik 2013
Kigelia africana	*Bignoniaceae*	*Alternaria*, *Aspergillus*, *Botryodiplodia*, *Chaetomium*, *Colletotrichum*, *Curvularia*, *Drechslera*, *Fusarium*, *Mucor*, *Nigrospora*, *Nodulisporium*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Rhizopus*, *Trichoderma*	Maheswari and Rajagopal 2013

Table 1 (continued)

Host plant	Family	Endophytic fungi (genera)	Reference
Panax ginseng	*Araliaceae*	*Aspergillus*, *Cladosporium*, *Engyodontium*, *Fusarium*, *Penicillium*, *Plectosphaerella*, *Verticillium*	Wu et al. 2013a
Stellera chamaejasme	*Thymelaeaceae*	*Acremonium*, *Alternaria*, *Aporospora*, *Ascochyta*, *Aspergillus*, *Bionectria*, *Botryotinia*, *Cadophora*, *Colletotrichum*, *Dothiorella*, *Emericellopsis*, *Eucasphaeria*, *Eupenicillium*, *Fusarium*, *Geomyces*, *Ilyonectria*, *Leptosphaeria*, *Mucor*, *Nectria*, *Neonectria*, *Paecilomyces*, *Paraphoma*, *Penicillium*, *Schizophyllum*, *Scytalidium*, *Sordaria*, *Sporormiella*	Jin et al. 2013
Taxus x media	*Taxaceae*	*Alternaria*, *Colletotrichum*, *Gibberella*, *Glomerella*, *Guignardia*, *Nigrospora*, *Phoma*, *Phomopsis*	Xiong et al. 2013
Brassica napus	*Brassicaceae*	*Acremonium*, *Alternaria*, *Arthrinium*, *Aspergillus*, *Aureobasidium*, *Botrytis*, *Chaetomium*, *Clonostachys*, *Cryptococcus*, *Dioszegia*, *Dothidea*, *Dothiorella*, *Epicoccum*, *Fusarium*, *Guignardia*, *Hypoxylon*, *Leptosphaeria*, *Macrophomina*, *Nigrospora*, *Penicillium*, *Periconia*, *Phoma*, *Rhizoctonia*, *Rhizopus*, *Simplicillium*, *Sporidiobolus*, *Sporobolomyces*	Zhang et al. 2014c
Pinus wallichiana	*Pinaceae*	*Alternaria*, *Anthostomella*, *Aspergillus*, *Cadophora*, *Cladosporium*, *Cochliobolus*, *Coniochaeta*, *Coniothyrium*, *Epicoccum*, *Fimetariella*, *Fusarium*, *Geopyxis*, *Lecythophora*, *Leptosphaeria*, *Lophiostoma*, *Lophodermium*, *Microdiplodia*, *Neurospora*, *Nigrospora*, *Paraconiothyrium*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Preussia*, *Pseudoplectania*, *Rachicladosporium*, *Rosellinia*, *Sclerostagonospora*, *Sordaria*, *Sporormiella*, *Therrya*, *Tricharina*, *Trichoderma*, *Thielavia*, *Tritirachium*, *Truncatella*, *Xylaria*	Qadri et al. 2014

communities inhabiting various plants. To our knowledge, the culture-independent method relying on rRNA genes (rDNA) was used for the first time by Guo et al. (2001), and has proved a very valuable means of detecting and identifying endophytic fungi directly from plant tissues (Gao et al. 2005; Weiß et al. 2011; Bálint et al. 2013; Zhou et al. 2013). Sometimes, a combination of culturing methods and culture-independent analysis is needed for the study of endophytic communities (Götz et al. 2006). Zhou et al. (2013) compared endophytic fungi within foliar tissues of *Camellia oleifera* by the rDNA-ITS gene clone library method and the pure culture method, and found a richer endophytic fungal diversity using the former method. Seasons and organs also have an effect on the distribution and diversity of endophytes. Samples collected in spring harbored more abundant endophytic fungal communities than those collected in summer, implying a seasonal fluctuation for the endophytes in *Heterosmilax japonica* (Gao et al. 2005). However, culture-independent techniques still have their limits, and may prevent the identification of heterogeneous species. Recently, high-throughput sequencing technologies, including those commercialized by Applied Biosciences (SOLiD; http://www.appliedbiosystems.com), Dover Systems (Polonator; http://arep.med.harvard.edu/Polonator/soft.html), Illumina Incorporated (Solexa; http://www.illumina.com), 454 Life Science (Roche; http://www.454.com/) and Illumina HiSeq and MiSeq platforms (http://www.illumina.com) have been used to explore diverse microbial ecological communities (Mardis 2008; Quail et al. 2008; Zimmerman and Vitousek 2012; Kozich et al. 2013). In 2012, pyrosequencing was used for the first time to study fungal endophyte communities in the leaves of a single tree species (*Metrosideros polymorpha*), revealing very high levels of diversity of fungal foliar endophytes (Zimmerman and Vitousek 2012). This technique has also been used to examine the diversity of endophytic fungi inhabiting various plants in later research (Bálint et al. 2013; U'Ren et al. 2014). These discoveries greatly improved our understanding of the complexity and the ecological distribution of plant-associated fungi. However, the actual number and diversity of endophytic fungi are probably enormous and remain unknown.

Distribution of endophytic fungi

Endophytic fungal communities have different distributions in different tissues of a single tree species. Generally, the colonization rate of endophytic fungi is significantly higher in the stems than in the leaves. Fungal communities within leaf and root tissues are significantly different. Tao et al. (2008) investigated the endophytes within leaf and root tissues of *Bletilla ochracea* (Orchidaceae) using DGGE and random cloning analysis, and found that the diversity within leaves (H'= 2.354) was higher than that within roots (H'=1.560). This phenomenon was also confirmed by other researchers (Fisher et al. 1994; Sun et al. 2011; Li et al. 2012a; Zheng et al. 2013). One possible reason might be that the stems are persistent, whereas the leaves are deciduous (Li et al. 2012a). In contrast, Kharwar et al. (2011b) found that leaves harbored the maximum colonization of endophytic fungi (72.22 %), greater than stem (67.78 %), associated with the medicinal plant *Mansoa alliacea*.

Geographical different distribution also exists in the same kind of plants. Early in 1994, Fisher et al. (1994) detected that endophytic fungi communities in leaves of *Quercus ilex* from England, Majorca and Switzerland were significantly different. Vega et al. (2010) also detected that endophytic fungi diversity was significantly different in coffee plants from Colombia, Hawaii, Mexico and Puerto Rico. Investigation of endophytic fungi communities of *Taxus chinensis* var. *mairei*, distributed in Jiangxi, Zhejiang and Chongqing regions of China, gave similar results (Wu et al. 2013b). Endophytic fungi of the same plant species in the same area are basically similar, but for some fungi, the abundance and distribution differs with the age and the tissue of plants (Arnold and Herre 2003; Mei et al. 2014). Normally, the species and abundance of endophytic fungi increase as the host ages. There are two main reasons for this: on the one hand, fungi spread by air and rainfall affords older trees the opportunity for repeat infection; on the other hand, changes in plant physiological status and tree bark structure in aging trees create new access in the plant tissue, allowing fungal invasion (Fisher et al. 1994).

Distribution of endophytic fungal communities can also be affected by crown height and canopy cover (Arnold and Herre 2003). Commonly, the species diversity and abundance of endophytic fungi are higher in samples taken from densely wooded sites than in samples taken from more open sites (Petrini et al. 1982). Certainly, endophytic fungal communities are also affected by other environmental factors, such as ambient humidity (Lau et al. 2013), seasonal changes (Mishra et al. 2012), altitude (Davey et al. 2013), precipitation (Zimmerman and Vitousek 2012), temperature (Li et al. 2012b), other plant communities (Novas et al. 2007) and environmental pollution (Li et al. 2012a; Zheng et al. 2013).

Biogeography is the study of the distribution of biodiversity over space and time. It aims to reveal where organisms live, at what abundance, and why (Martiny et al. 2006). Since the eighteenth century, biologists have investigated the geographic distribution of plant and animal diversity. More recently, the geographic distribution of microorganisms has been examined. Ecologists describing microbial biogeography typically invoke Baas Becking's summary from a century ago: "Everything is everywhere, the environment selects" (the EisE hypothesis) (Baas Becking 1934; Green et al. 2008). The question now arises, does endophytic fungi biogeographical distribution and spatial variation reflect the proposition that "the environment selects"? Recently, Zimmerman and Vitousek (2012) surveyed endophytic fungi communities in leaves of a single tree species (*M. polymorpha*) across wide environmental gradients (500–5500 mm rain/year; 10–22 °C mean annual temperature) spanning short geographic distances on Hawaiian and the results seems to support the EisE hypothesis. But more research results are needed for this to be proved. Understanding biogeography is not simply of academic interest but also provides a fungal map for biodiscovery.

Role and biotechnological potential of endophytic fungi

Source of novel bioactive secondary metabolites

Endophytic fungi experience long-term relationships with their host plants and many endophytes produce bioactive compounds (Kumar and Kaushik 2013). Thus, it has been surmised that endophytic fungi and host plants have similar pathways for synthesizing secondary metabolites due to horizontal gene transfer (Wang and Dai 2011; Soliman et al. 2013), and that endophytic fungi could become an important source of novel bioactive secondary metabolites. Many bioactive substances are potentially useful to modern medicine, including cryptocin, gentiopicrin, spiroquinazoline alkaloids, taxol, vinblastine, vincristine, and so on (Stierle et al. 1993; Li et al. 2000; Barros and Rodrigues-Filho 2005; Yin et al. 2009; Kumar et al. 2013; Soliman et al. 2013). Several recently reported novel bioactive secondary metabolites produced by fungal endophytes (Asai et al. 2013; Xu et al. 2013; Akay et al. 2014; Xiao et al. 2014; Zhang et al. 2014a, b; Zhou et al. 2014a, b) are presented in Fig. 1.

Current interest in bioactive secondary metabolites from endophytes, especially endophytic fungi, is evident in several recent reviews focused on this field (Aly et al. 2010; Kharwar et al. 2011a; Kusari et al. 2012; Alvin et al. 2014). The reported compounds belong to diverse structural groups: alkaloids, benzofuran, cyclohexanone, dihydroisocoumarin, flavonoids, lipoids, organic acids, peptides, phenylpropanoids, pyridines, quinone, steroids, and terpenoids. Most novel substances showed antimicrobial, anti-insect, antioxidant, anticancer and antineoplastic activities, cytotoxicity, and other important biological functions (Kharwar et al. 2011a; Sun et al. 2011; Akay et al. 2014; Xiao et al. 2014; Zhou et al. 2014a, b). The screening of novel bioactive secondary metabolites from endophytic fungi has become a research hotspot for new drug discovery and development.

Enzyme production

As important biological catalysts, enzymes are employed widely in industrial and agricultural production (Suryanarayanan et al. 2012). Endophytic fungi are important producers of enzymes, and have high capability for production of extracellular enzymes

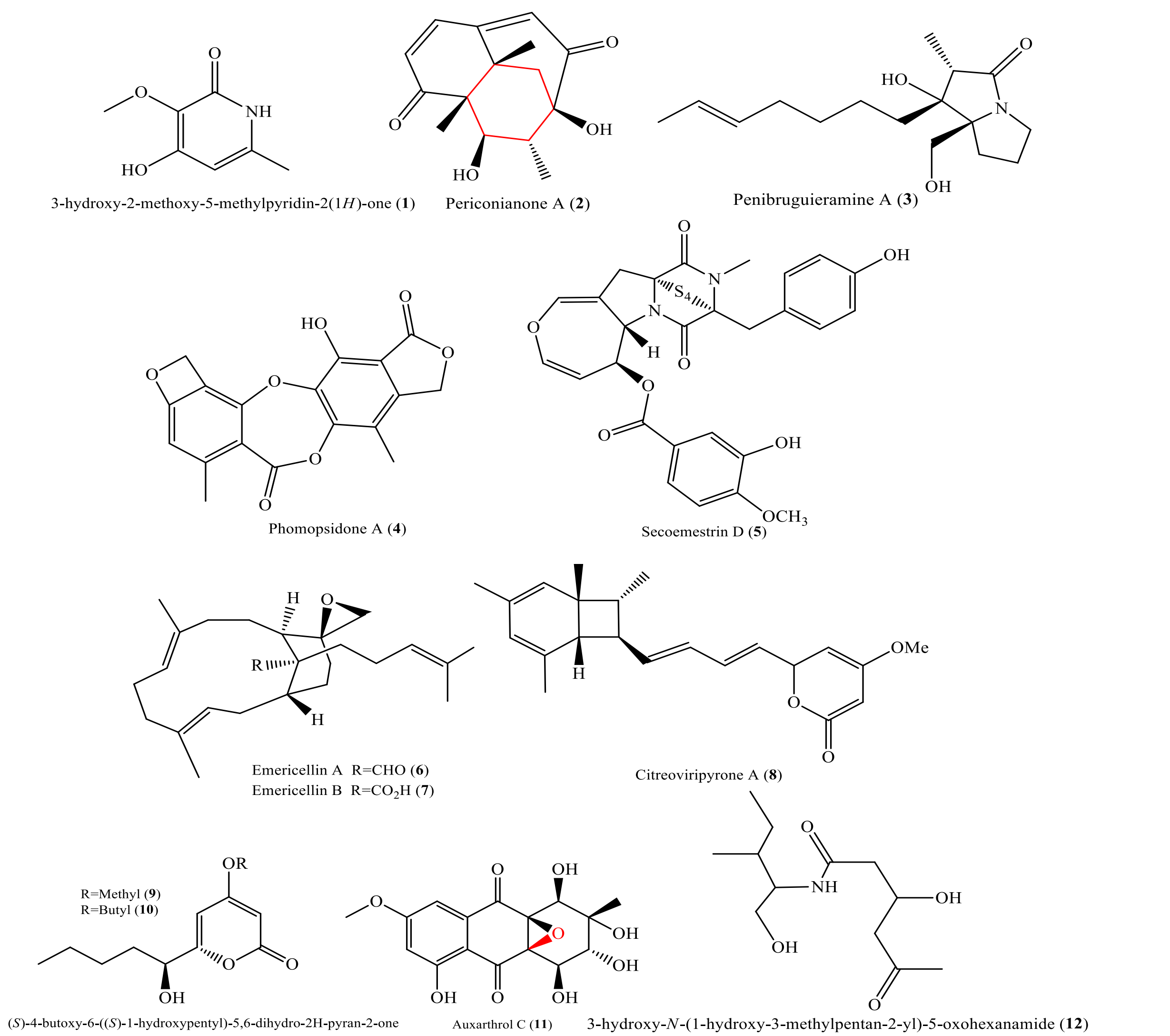

Fig. 1 Structures of compounds **1–12**, representing several novel bioactive secondary metabolites isolated from fungal endophytes (Asai et al. 2013; Xu et al. 2013; Akay et al. 2014; Xiao et al. 2014; Zhang et al. 2014a, b; Zhou et al. 2014a, b)

such as cellulases, chitinases, laccase, pectinases, xylanases, proteases, amylases, β-galactosidase and other catabolic enzymes (Jordaan et al. 2006; Bischoff et al. 2009; Borges et al. 2009; Rajulu et al. 2011; Bezerra et al. 2012). Chitinase is applied to the biological control of phytopathogens as it degrades the chitin of the pathogen cell wall. Phosphatases, especially acid phosphatases, have been used in enzyme-linked immunesorbent assay (ELISA) and western blotting tests. Both enzymes have also been found in the endophytic fungi *Neotyphodium* sp. and *Colletotrichum musae*, respectively. Endophytic species of the genera *Alternaria*, *Phoma* and *Phomopsis*, from the plant *Colophospermum mopane*, displayed lignocellulolytic activity that could accelerate significantly the dehiscence of pods and enable effective germination of seeds in arid environments under favorable conditions (Jordaan et al. 2006). *Sarocladium zeae*—a fungal endophyte isolated from maize—produces hemicellulase, which may be suitable for application in the bioconversion of lignocellulosic biomass into fermentable sugars (Bischoff et al. 2009). Therefore, research in this area might lead to the identification of enzymes with novel and improved biotechnological applications, and seems to be a promising research field.

Biological control agents

The exploitation of endophytic fungi as biological control agents (BCA) of phytopathogens has attracted many researchers, as this group of fungi shows plant colonizing ability and antimicrobial activities. They exhibit the abilities of protecting plants against various soil-borne pathogens, including *Aspergillus fumigatus*, *Botrytis cinerea*, *Blumeria graminis*, *Fusarium culmorum*, *F. oxysporum*, *Globisporangium ultimum*, *Monilinia laxa*, *Moniliophthora perniciosa*, *Penicillium expansum*, *Phytophthora* sp., *P. palmivora*, *Plasmopara viticola*, *Puccinia polygoni-amphibii*, *Sclerotinia sclerotiorum* and *Verticillium longisporum* (Arnold and Herre 2003; Waller et al. 2005; Kim et al. 2007; Chen et al. 2010; Hanada et al. 2010; Kurose et al. 2012; Zhang et al. 2014c). Endophytic fungi and their role as BCA have been partly discussed (Backman and Sikora 2008).

Reported biocontrol mechanisms include antibiosis, cell wall degrading enzyme, mycoparasitism, induction of defense response and competition for nutrients and space (Zhang et al. 2014c). *Piriformospora indica*—a plant-root-colonizing basidiomycete fungus—was capable of inducing resistance of barley to phytopathogen *F. culmorum* (Waller et al. 2005). Seven endophytic isolates from *Theobroma cacao* and *T. grandiflorum*, belonging to genera of *Curvularia*, *Fusarium*, *Pestalotiopsis* and *Tolypocladium*, showed a biocontrol effect on *P. palmivora*—the causal agent of the black-pod rot disease of cacao (Hanada et al. 2010). Fungal biological control is an exciting and rapidly developing research area with implications for plant productivity, health, food safety and the environment. Endophytic fungi should be a potential source for BCA development.

Plant growth promoting agents

Environmental problems caused by chemical pesticides and fertilizers, whether directly or indirectly, have prompted researchers to consider alternatives for facilitating plant growth in agriculture. Endophytic fungi are of special interest since they possess many properties that could benefit plant growth. The beneficial effects of plant growth promoting fungi (PGPF) on plant growth and development are well documented (Hamayun et al. 2010). The investigated plant growth promting mechanisms include producing biological control agents, phytohormones (indole acetic acid, gibberellins, cytokines, etc), siderophore to bind Fe^{3+} from the environment, enhancing host uptake of nutrient elements, and secreting substances to suppress ethylene production by 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (Arnold and Herre 2003; Hamayun et al. 2010; Khan et al. 2012a, b; Khan and Lee 2013). For example, the fungal endophyte *Phoma* sp. GAH7, isolated from cucumber roots, produced high amounts of GA_3, GA_4, GA_9 and GA_{19}, which was used as control for GA production (Hamayun et al. 2010). Endophytic *Paecilomyces variotii* LHL 10 from roots of cucumber plants could promote plant growth by producing high amounts of IAA and GAs (Khan et al. 2012a). The endophytic fungi plant growth promoting properties and the recent increase in our understanding of some of the mechanisms suggest that this promising source merits further investigation for potential application in agricultural production.

Antimicrobial/anticancer activity

Endophytic fungi from medicinal plants show broad-spectral antimicrobial and cytotoxic (antitumor) bioactivities. Endophtyes from *Dendrobium devonianum* and *D. thyrsiflorum* could produce inhibitory substances against pathogens such as *Aspergillus fumigatus*, *Bacillus subtilis*, *Candida albicans*, *Cryptococcus neoformans*, *Escherichia coli* and *Staphylococcus aureus* (Xing et al. 2011). Fungal endophytes from agarwood (*Aquilaria sinensis*) displayed antitumor activity against human cancer cell lines, HepG2, MCF7, SKVO3, HL-60 and 293-T (Cui et al. 2011). Carvalho et al. (2012) investigated the biodiversity and bioactivities of endophytic fungi harbored in the medicinal plant *Stryphnodendron adstringens*, and identified some isolates with antimicrobial activity against the pathogens *Candida albicans* and *Cladosporium sphaerospermum*, and growth inhibition on cancer cells MCF-7 and TK-10. As reviewed by Kharwar et al. (2011a) and Chandra (2012), endophytic fungi have become novel sources of anticancer molecules.

Bioremediation/biodegradation

Pollution caused by mines, pesticides, fertilizers, and other industrial waste become concentrated in the environment. We still lack effective approaches to deal with this problem. Biodegradation and/or bioremediation consists of removing pollutants and wastes from the environment by the use of biochemical processes in microorganisms. Endophytes have become a potential resource to help cope with these problems since they possess many systems that can break down complex compounds, degrade chemical pollutants, and effect biosorption of heavy metals (Xiao et al. 2010; Russell et al. 2011; Li et al. 2012c). A non pathogenic *F. oxysporum*, isolated from the Zn/ Cd co-hyperaccumulator *Sedum alfredii* grown in a Pb/ Zn mined area, was able to increase *S. alfredii* root systems and function, metal availability and accumulation, and plant biomass, and thus phytoextraction efficiency (Zhang et al. 2012). Similar results were obtained by Xiao et al. (2010), who demonstrated that the endophytic fungal strain *Microsphaeropsis* sp. LSE10 is helpful for cadmium (Cd) biosorption by *Solanum nigrum*. The endohytic fungus *Pestalotiopsis microspora* was uniquely able to grow on synthetic polymer polyester polyurethane as the sole carbon source under both aerobic and anaerobic conditions (Russell et al. 2011), suggesting its potential use for treatment of white plastic pollution.

Biotransformation/biosynthesis

Biotransformation can be defined as the use of biological systems to produce chemical changes in compounds that are not their natural substrates. Such alteration may inactivate the compound, or may result in the production of an active metabolite from an inactive parent compound (Wang and Dai 2011). Biotransformations have many advantages when compared to the corresponding chemical methods. Many research results show that endophytic fungi play an important role in biotransformation (Zikmundová et al. 2002; Wang and Dai 2011). For instance, Zikmundová et al. (2002) studied biotransformation of the phytoanticipins 2-benzoxazolinone (BOA) and 2-hydroxy-1,4-benzoxazin-3-one (HBOA) by four endophytic fungi isolated from *Aphelandra arborea*. *Gibberella pulicaris* detoxified BOA and HBOA to *N*-(2-hydroxyphenyl) malonamic acid. *Monographella cucumerina*, *Gliocladium cibotii* and *Chaetosphaeria* sp. transformed HBOA to 2-hydroxy-*N*-(2-hydroxyphenyl)acetamide (compound **1**), *N*-(2-hydroxyphenyl)acetamide (compound **2**), *N*-(2-hydroxy-5-nitrophenyl)acetamide (compound **3**), *N*-(2-hydroxy-3-nitrophenyl)acetamide (compound **4**), 2-amino-3*H*-phenoxazin-3-one (compound **7**), 2-acetylamino-3*H*-phenoxazin-3-one (compound **8**), and 2-(*N*-hydroxy) acetylamino-3*H*-phenoxazin-3-one (compound **9**) (Fig. 2). Verma et al. (2010) employed the endophytic fungus *Aspergillus clavatus*, isolated from *Azadirachta indica*, to biosynthesize silver nanoparticles (AgNPs) 10–25 nM in size.

Nutrient cycling

Nutrient cycling is a very important process that happens continuously to balance existing nutrients and to make them available to all components of the ecosystem. Endophytic fungi are thought to play an important role in nutrient recycling in natural ecosystems (Sun et al. 2011). Endophytic fungi were found by Müller et al. (2001) to be capable of decomposing Norway spruce (*Picea abies*) needles in vitro and in situ. Some endophytic species could decompose *Cinnamomum camphora* leaf litter in pure

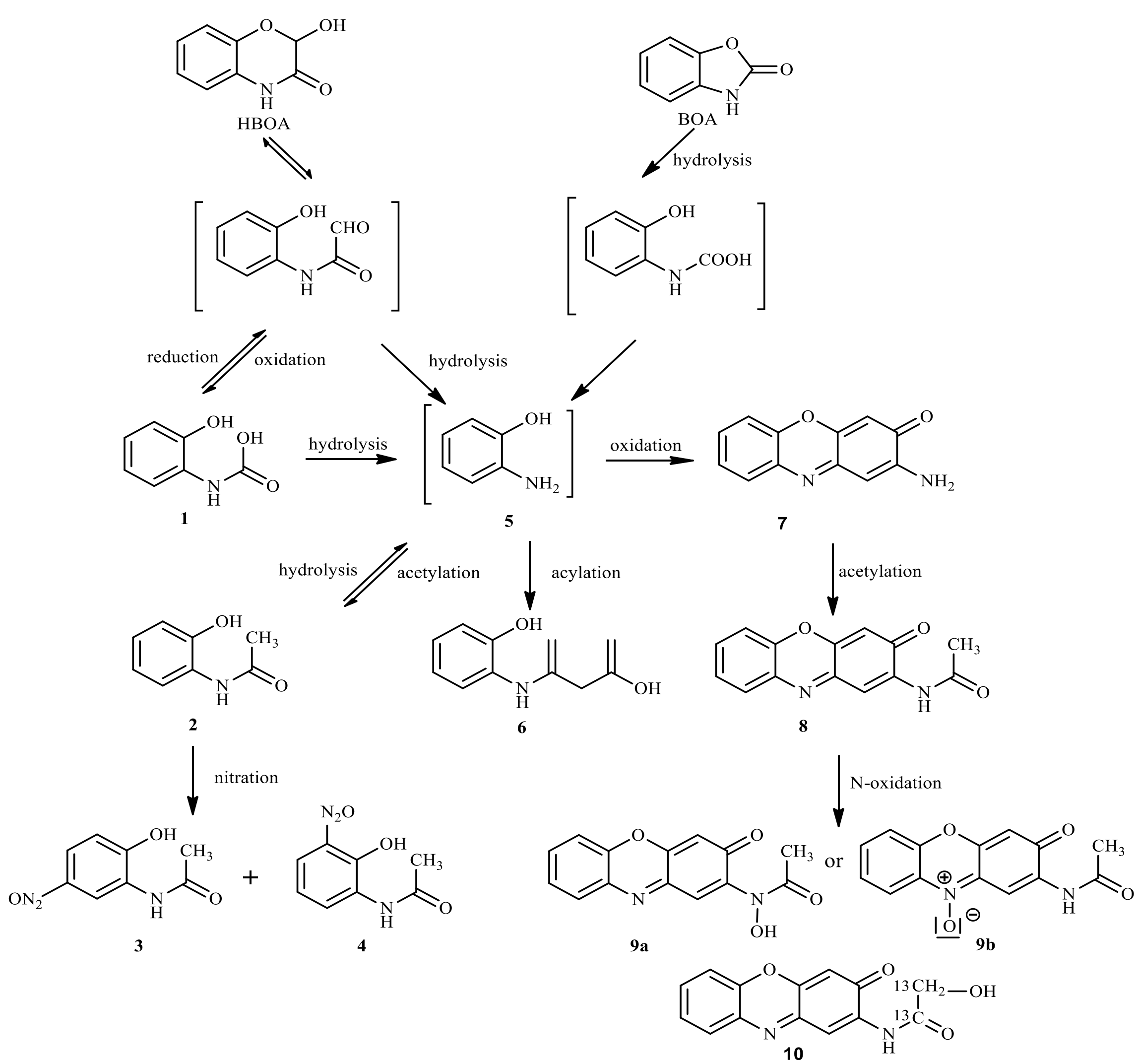

Fig. 2 Proposed schema of biotransformation of 2-hydroxy-1,4-benzoxazin-3-one (HBOA) and 2-benzoxazolinone (BOA) by *Chaetosphaeria* sp., *Gliocladium cibotii*, *Gibberella pulicaris*, and *Monographella cucumerina* (Zikmundová et al. 2002)

culture (He et al. 2012). During biodegradation of the litter, endophytic fungi colonize initially within the plants and facilitate the actio of the saprophytic fungi through antagonistic interaction, thus increasing litter decomposition (Nair and Padmavathy 2014). Another study demonstrated that the endophytic fungus *Phomopsis liquidambari* had the ability to stimulate organic mineralization and promote NH_4^+-N release in vitro. Such effects triggered a soil ammonia-oxidizing bacteria (AOB)-driven nitrification process (Chen et al. 2013).

Concluding remarks and future perspectives

Over the past decade, endophytes have emerged as a hot research topic. Rapidly increasing information on endophyte biodiversity, natural products, potential uses and biotechnological applications is found in a rich literature, and should be reviewed regularly for interested readers.

As reviewed here, the endophytic fungi have abundant biodiversity and are useful in pharmaceuticals, agriculture, and industry. Even so, the study of endophytic fungi is just at the beginning. In the future, it may be possible to explore and utilize fungal endophyte resources in many ways. Firstly, we can seek novel endophytic fungi from plants in extreme environments. Secondly, we should try to search for suitable and efficient methods to find more effective bioactive compounds from numerous endophytic fungi. Finally, increasing the yield and content of active substances in known strains by exploiting genetic engineering and metabolic regulation will be promising for large-scale production (Wang and Dai 2011). Further success in developing the molecular and proteomic technologies of key endophytes (fungi, bacteria and actinobacteria) will help us understand complicated plant–endophyte interactions and mechanisms. More focus should be put on biotechnological applications in biocontrol of plant diseases, bioremediation, production growth and areas such as environmental and food safety. Endophytes are a resource for all humankind, and require comprehensive cooperation among multi-disciplinary researchers.

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References

Akay Ş, Ekiz G, Kocabaş F, Hameş-Kocabaş EE, Korkmaz KS, Bedir E (2014) A new 5, 6-dihydro-2-pyrone derivative from *Phomopsis amygdali*, an endophytic fungus isolated from hazelnut (*Corylus avellana*). Phytochem Lett 7:93–96

Alvin A, Miller KI, Neilan BA (2014) Exploring the potential of endophytes from medicinal plants as sources of antimycobacterial compounds. Microbiol Res 169(7):483–495

Aly AH, Debbab A, Kjer J, Proksch P (2010) Fungal endophytes from higher plants: a prolific source of phytochemicals and other bioactive natural products. Fungal Divers 41:1–16

Arnold AE, Herre EA (2003) Canopy cover and leaf age affect colonization by tropical fungal endophytes: ecological pattern and process in *Theobroma cacao* (*Malvaceae*). Mycologia 95(3):388–398

Arnold AE, Lutzoni F (2007) Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88(3):541–549

Arnold AE, Maynard Z, Gilbert GS, Coley PD, Kursar TA (2000) Are tropical fungal endophytes hyperdiverse? Ecol Lett 3(4):267–274

Asai T, Luo D, Yamashita K, Oshima Y (2013) Structures and biomimetic synthesis of novel α-pyrone polyketides of an endophytic *Penicillium* sp. in *Catharanthus roseus*. Org Lett 15(5):1020–1023

Baas Becking LGM (1934) Geobiologie of inleiding tot de milieukunde. van Stockum, The Hague

Backman PA, Sikora RA (2008) Endophytes: an emerging tool for biological control. Biol Control 46(1):1–3

Bálint M, Tiffin P, Hallström B, O'Hara RB, Olson MS, Fankhauser JD, Piepenbring M, Schmitt I (2013) Host genotype shapes the foliar fungal microbiome of balsam poplar (*Populus balsamifera*). PLoS One 8(1), e53987

Banerjee D (2011) Endophytic fungal diversity in tropical and subtropical plants. Res J Microbiol 6(1):54–62

Barros FAP, Rodrigues-Filho E (2005) Four spiroquinazoline alkaloids from *Eupenicillium* sp. isolated as an endophytic fungus from leaves of *Murraya paniculata* (*Rutaceae*). Biochem Syst Ecol 33(3):257–268

Bezerra JDP, Santos MGS, Svedese VM, Lima DMM, Fernandes MJS, Paiva LM, Souza-Motta CM (2012) Richness of endophytic fungi isolated from *Opuntia ficus-indica* Mill. (*Cactaceae*) and preliminary screening for enzyme production. World J Microbiol Biotechnol 28(5):1989–1995

Bischoff KM, Wicklow DT, Jordan DB, de Rezende ST, Liu S, Hughes SR, Rich JO (2009) Extracellular hemicellulolytic enzymes from the maize endophyte *Acremonium zeae*. Curr Microbiol 58(5):499–503

Borges WS, Borges KB, Bonato PS, Said S, Pupo MT (2009) Endophytic fungi: natural products, enzymes and biotransformation reactions. Curr Org Chem 13(12):1137–1163

Botella L, Diez JJ (2011) Phylogenic diversity of fungal endophytes in Spanish stands of *Pinus halepensis*. Fungal Divers 47(1):9–18

Carvalho CR, Gonçalves VN, Pereira CB, Johann S, Galliza IV, Alves TMA, Rabello A, Sobral MEG, Zani CL, Rosa CA, Rosa LH (2012) The diversity, antimicrobial and anticancer activity of endophytic fungi associated with the medicinal plant *Stryphnodendron adstringens* (Mart.) Coville (*Fabaceae*) from the Brazilian savannah. Symbiosis 57(2):95–107

Chandra S (2012) Endophytic fungi: novel sources of anticancer lead molecules. Appl Microbiol Biotechnol 95(1):47–59

Chen XM, Dong HL, Hu KX, Sun ZR, Chen J, Guo SX (2010) Diversity and antimicrobial and plant-growth-promoting activities of endophytic fungi in *Dendrobium loddigesii* Rolfe. J Plant Growth Regul 29(3):328–337

Chen Y, Ren CG, Yang B, Peng Y, Dai CC (2013) Priming effects of the endophytic fungus *Phomopsis liquidambari* on soil mineral N transformations. Microb Ecol 65(1):161–170

Cheng ZS, Pan JH, Tang WC, Chen QJ, Lin YC (2009) Biodiversity and biotechnological potential of mangrove-associated fungi. J For Res 20(1):63–72

Coombs JT, Franco CMM (2003) Isolation and identification of actinobacteria from surface-sterilized wheat roots. Appl Environ Microbiol 69(9):5603–5608

Cui J, Guo S, Xiao P (2011) Antitumor and antimicrobial activities of endophytic fungi from medicinal parts of *Aquilaria sinensis*. J Zhejiang Univ Sci B 12(5):385–392

Davey ML, Heegaard E, Halvorsen R, Kauserud H, Ohlson M (2013) Amplicon-pyrosequencing-based detection of compositional shifts in bryophyte-associated fungal communities along an elevation gradient. Mol Ecol 22(2):368–383

Davis KER, Joseph SJ, Janssen PH (2005) Effects of growth medium, inoculum size, and incubation time on culturability and isolation of soil bacteria. Appl Environ Microbiol 71(2):826–834

De Siqueira VM, Conti R, de Araújo JM, Souza-Motta CM (2011) Endophytic fungi from the medicinal plant *Lippia sidoides* Cham. and their antimicrobial activity. Symbiosis 53(2):89–95

De Souza Sebastianes FL, Romao-Dumaresq AS, Lacava PT, Harakava R, Azevedo JL, de Melo IS, Pizzirani-Kleiner AA (2013) Species diversity of culturable endophytic fungi from Brazilian mangrove forests. Curr Genet 59(3):153–166

De Souza Leite T, Cnossen-Fassoni A, Pereira OL, Mizubuti ESG, de Araújo EF, de Queiroz MV (2013) Novel and highly diverse fungal endophytes in soybean revealed by the consortium of two different techniques. J Microbiol 51(1):56–69

Del Olmo-Ruiz M, Arnold AE (2014) Interannual variation and host affiliations of endophytic fungi associated with ferns at La Selva, Costa Rica. Mycologia 106(1):8–21

Fisher PJ, Petrini O, Scott HML (1992) The distribution of some fungal and bacterial endophytes in maize (*Zea mays* L.). New Phytol 122(2):299–305

Fisher PJ, Petrini O, Petrini LE, Sutton BC (1994) Fungal endophytes from the leaves and twigs of *Quercus ilex* L. from England, Majorca and Switzerland. New Phytol 127(1):133–137

Gao XX, Zhou H, Xu DY, Yu CH, Chen YQ, Qu LH (2005) High diversity of endophytic fungi from the pharmaceutical plant, *Heterosmilax japonica* Kunth revealed by cultivation-independent approach. FEMS Microbiol Lett 249(2):255–266

García A, Rhoden SA, Rubin Filho CJ, Nakamura CV, Pamphile JA (2012) Diversity of foliar endophytic fungi from the medicinal plant *Sapindus saponaria* L. and their localization by scanning electron microscopy. Biol Res 45(2):139–148

Gazis R, Chaverri P (2010) Diversity of fungal endophytes in leaves and stems of wild rubber trees (*Hevea brasiliensis*) in Peru. Fungal Ecol 3(3):240–254

Gond SK, Mishra A, Sharma VK, Verma SK, Kumar J, Klharwar RN, Kumar A (2012) Diversity and antimicrobial activity of endophytic fungi isolated from *Nyctanthes arbor-tristis*, a well-known medicinal plant of India. Mycoscience 53(2):113–121

Götz M, Nirenberg H, Krause S, Wolters H, Draeger S, Buchner A, Lottmann J, Berg G, Smalla K (2006) Fungal endophytes in potato roots studied by traditional isolation and cultivation-independent DNA-based methods. FEMS Microbiol Ecol 58(3):404–413

Green JL, Bohannan BJM, Whitaker RJ (2008) Microbial biogeography: from taxonomy to traits. Science 320(5879):1039–1043

Guo LD, Hyde KD, Liew ECY (2001) Detection and taxonomic placement of endophytic fungi within frond tissues of *Livistona chinensis* based on rDNA sequences. Mol Phylogenet Evol 20(1):1–13

Hallmann J, Kloepper JW, Rodríguez-Kábana R (1997) Application of the Scholander pressure bomb to studies on endophytic bacteria of plants. Can J Microbiol 43(5):411–416

Hallmann J, Berg G, Schulz B (2006) Isolation procedures for endophytic microorganisms. In: Schulz BJE, Boyle CJC, Sieber TN (eds) Microbial Root Endophytes. Springer, New York, pp 299–319

Hamayun M, Khan SA, Khan AL, Tang DS, Hussain J, Ahmad B, Anwar Y, Lee IJ (2010) Growth promotion of cucumber by pure cultures of gibberellin-producing *Phoma* sp. GAH7. World J Microbiol Biotechnol 26(5):889–894

Hanada RE, Pomella AWV, Costa HS, Bezerra JL, Loguercio LL, Pereira JO (2010) Endophytic fungal diversity in *Theobroma cacao* (cacao) and *T. grandiflorum* (cupuaçu) trees and their potential for growth promotion and biocontrol of black-pod disease. Fungal Biol 114(11):901–910

He X, Han G, Lin Y, Tian X, Xiang C, Tian Q, Wang F, He Z (2012) Diversity and decomposition potential of endophytes in leaves of a *Cinnamomum camphora* plantation in China. Ecol Res 27(2):273–284

Hyde KD, Soytong K (2008) The fungal endophyte dilemma. Fungal Divers 33:163–173

Jin H, Yan Z, Liu Q, Yang X, Chen J, Qin B (2013) Diversity and dynamics of fungal endophytes in leaves, stems and roots of *Stellera chamaejasme* L. in northwestern China. Antonie Van Leeuwenhoek 104:949–963

Jordaan A, Taylor JE, Rossenkhan R (2006) Occurrence and possible role of endophytic fungi associated with seed pods of *Colophospermum mopane* (*Fabaceae*) in Botswana. S Afr J Bot 72(2):245–255

Khan AL, Lee IJ (2013) Endophytic *Penicillium funiculosum* LHL06 secretes gibberellin that reprograms *Glycine max* L. growth during copper stress. BMC Plant Biol 13(1):86

Khan AL, Hamayun M, Kang SM, Kim YH, Jung HY, Lee JH, Lee IJ (2012a) Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10. BMC Microbiol 12(1):3

Khan AL, Hamayun M, Khan SA, Kang SM, Shinwari ZK, Kamran M, Rehman S, Kim JG, Lee IJ (2012b) Pure culture of *Metarhizium anisopliae* LHL07 reprograms soybean to higher growth and mitigates salt stress. World J Microbiol Biotechnol 28(4):1483–1494

Kharwar RN, Mishra A, Gond SK, Stierle A, Stierle D (2011a) Anticancer compounds derived from fungal endophytes: their importance and future challenges. Nat Prod Rep 28(7):1208–1228

Kharwar RN, Verma SK, Mishra A, Gond SK, Sharma VK, Afreen T, Kumar A (2011b) Assessment of diversity, distribution and antibacterial activity of endophytic fungi isolated from a medicinal plant *Adenocalymma alliaceum* Miers. Symbiosis 55(1):39–46

Kharwar RN, Maurya AL, Verma VC, Kumar A, Gond SK, Mishra A (2012) Diversity and antimicrobial activity of endophytic fungal community isolated from medicinal plant *Cinnamomum camphora*. Proc Natl Acad Sci India Sect B: Biol Sci 82(4):557–565

Kim HY, Choi GJ, Lee HB, Lee SW, Lim HK, Jang KS, Son SW, Lee SO, Cho KY, Sung ND, Kim JC (2007) Some fungal endophytes from vegetable crops and their anti-oomycete activities against tomato late blight. Lett Appl Microbiol 44(3):332–337

Kleczewski NM, Bauer JT, Bever JD, Clay K, Reynolds HL (2012) A survey of endophytic fungi of switchgrass (*Panicum virgatum*) in the Midwest, and their putative roles in plant growth. Fungal Ecol 5(5):521–529

Koukol O, Kolařík M, Kolářová Z, Baldrian P (2012) Diversity of foliar endophytes in wind-fallen *Picea abies* trees. Fungal Divers 54:69–77

Kozich JJ, Westcott SL, Baxter NT, Highlander SK, Schloss PD (2013) Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. Appl Environ Microbiol 79(17):5112–5120

Kumar S, Kaushik N (2013) Endophytic fungi isolated from oil-seed crop *Jatropha curcas* produces oil and exhibit antifungal activity. PLoS One 8(2):e56202

Kumar S, Kaushik N, Edrada-Ebel R, Ebel R, Proksch P (2011) Isolation, characterization, and bioactivity of endophytic fungi of *Tylophora indica*. World J Microbiol Biotechnol 27(3):571–577

Kumar A, Patil D, Rajamohanan PR, Ahmad A (2013) Isolation, purification and characterization of vinblastine and vincristine from endophytic fungus *Fusarium oxysporum* isolated from *Catharanthus roseus*. PLoS One 8(9):e71805

Kurose D, Furuya N, Tsuchiya K, Tsushima S, Evans HC (2012) Endophytic fungi associated with *Fallopia japonica* (*Polygonaceae*) in Japan and their interactions with *Puccinia polygoni-amphibii* var. *tovariae*, a candidate for classical biological control. Fungal Biol 116(7):785–791

Kusari S, Hertweck C, Spiteller M (2012) Chemical ecology of endophytic fungi: origins of secondary metabolites. Chem Biol 19(7): 792–798

Kusari P, Kusari S, Spiteller M, Kayser O (2013) Endophytic fungi harbored in *Cannabis sativa* L.: diversity and potential as biocontrol agents against host plant-specific phytopathogens. Fungal Divers 60:137–151

Larran S, Perelló A, Simón MR, Moreno V (2002) Isolation and analysis of endophytic microorganisms in wheat (*Triticum aestivum* L.) leaves. World J Microbiol Biotechnol 18(7):683–686

Lau MK, Arnold AE, Johnson NC (2013) Factors influencing communities of foliar fungal endophytes in riparian woody plants. Fungal Ecol 6(5):365–378

Li JY, Strobel G, Harper J, Lobkovsky E, Clardy J (2000) Cryptocin, a potent tetramic acid antimycotic from the endophytic fungus *Cryptosporiopsis cf. q uercina*. Org Lett 2(6):767–770

Li HY, Li DW, He CM, Zhou ZP, Mei T, Xu HM (2012a) Diversity and heavy metal tolerance of endophytic fungi from six dominant plant species in a Pb–Zn mine wasteland in China. Fungal Ecol 5(3):309–315

Li HY, Shen M, Zhou ZP, Li T, Wei YL, Lin LB (2012b) Diversity and cold adaptation of endophytic fungi from five dominant plant species collected from the Baima Snow Mountain, Southwest China. Fungal Divers 54:79–86

Li HY, Wei DQ, Shen M, Zhou ZP (2012c) Endophytes and their role in phytoremediation. Fungal Divers 54(1):11–18

Maheswari S, Rajagopal K (2013) Biodiversity of endophytic fungi in *Kigelia pinnata* during two different seasons. Curr Sci 104(4):515–518

Mardis ER (2008) Next-generation DNA sequencing methods. Annu Rev Genomics Hum Genet 9:387–402

Martiny JBH, Bohannan BJM, Brown JH, Colwell RK, Fuhrman JA, Green JL, Horner-Devine MC, Kane M, Krumins JA, Kuske CR, Morin P, Naeem S, Øvreås L, Reysenbach AL, Smith VH, Staley JT (2006) Microbial biogeography: putting microorganisms on the map. Nat Rev Microbiol 4(2):102–112

Mei L, Zhu M, Zhang DZ, Wang YZ, Guo J, Zhang HB (2014) Geographical and temporal changes of foliar fungal endophytes associated with the invasive plant *Ageratina adenophora*. Microb Ecol 67(2):402–409

Mishra A, Gond SK, Kumar A, Sharma VK, Verma SK, Kharwar RN, Sieber TN (2012) Season and tissue type affect fungal endophyte communities of the Indian medicinal plant *Tinospora cordifolia* more strongly than geographic location. Microb Ecol 64(2):388–398

Müller MM, Valjakka R, Suokko A, Hantula J (2001) Diversity of endophytic fungi of single Norway spruce needles and their role as pioneer decomposers. Mol Ecol 10(7):1801–1810

Nair DN, Padmavathy S (2014) Impact of endophytic microorganisms on plants, environment and humans. Sci World J 2014:250693. doi:10.1155/2014/250693

Novas VM, Collantes M, Cabral D (2007) Environmental effects on grass-endophyte associations in the harsh conditions of south Patagonia. FEMS Microbiol Ecol 61(1):164–173

Orlandelli RC, Alberto RN, Rubin Filho CJ, Pamphile JA (2012) Diversity of endophytic fungal community associated with *Piper hispidum* (*Piperaceae*) leaves. Genet Mol Res 11(2):1575–1585

Pancher M, Ceol M, Corneo PE, Longa CMO, Yousaf S, Pertot I, Campisano A (2012) Fungal endophytic communities in grapevines (*Vitis vinifera* L.) respond to crop management. Appl Environ Microbiol 78(12):4308–4317

Petrini O, Stone J, Carroll FE (1982) Endophytic fungi in evergreen shrubs in western Oregon: a preliminary study. Can J Bot 60(6): 789–796

Promputtha I, Hyde KD, McKenzie EHC, Peberdy JF, Lumyong S (2010) Can leaf degrading enzymes provide evidence that endophytic fungi becoming saprobes? Fungal Divers 41:89–99

Qadri M, Rajput R, Abdin MZ, Vishwakarma RA, Riyaz-Ul-Hassan S (2014) Diversity, molecular phylogeny, and bioactive potential of fungal endophytes associated with the Himalayan blue pine (*Pinus wallichiana*). Microb Ecol 67(4):877–887

Qi F, Jing T, Zhan Y (2012) Characterization of endophytic fungi from *Acer ginnala* Maxim. in an artificial plantation: media effect and tissue-dependent variation. PLoS One 7(10), e46785

Qin S, Li J, Chen HH, Zhao GZ, Zhu WY, Jiang CL, Xu LH, Li WJ (2009) Isolation, diversity, and antimicrobial activity of rare actinobacteria from medicinal plants of tropical rain forests in Xishuangbanna, China. Appl Environ Microbiol 75(19):6176–6186

Qin S, Xing K, Jiang JH, Xu LH, Li WJ (2011) Biodiversity, bioactive natural products and biotechnological potential of plant-associated endophytic actinobacteria. Appl Microbiol Biotechnol 89(3):457–473

Quail MA, Kozarewa I, Smith F, Scally A, Stephens PJ, Durbin R, Swerdlow H, Turner DJ (2008) A large genome center's improvements to the Illumina sequencing system. Nat Methods 5(12):1005–1010

Rajulu MBG, Thirunavukkarasu N, Suryanarayanan TS, Ravishankar JP, Gueddari NEE, Moerschbacher BM (2011) Chitinolytic enzymes from endophytic fungi. Fungal Divers 47:43–53

Rhoden SA, Garcia A, Rubin Filho CJ, Azevedo JL, Pamphile JA (2012) Phylogenetic diversity of endophytic leaf fungus isolates from the medicinal tree *Trichilia elegans* (*Meliaceae*). Genet Mol Res 11(3): 2513–2522

Rivera-Orduña FN, Suarez-Sanchez RA, Flores-Bustamante ZR, Gracida-Rodriguez JN, Flores-Cotera LB (2011) Diversity of endophytic fungi of *Taxus globosa* (Mexican yew). Fungal Divers 47:65–74

Rosa LH, Almeida Vieira ML, Santiago IF, Rosa CA (2010) Endophytic fungi community associated with the dicotyledonous plant *Colobanthus quitensis* (Kunth) Bartl. (*Caryophyllaceae*) in Antarctica. FEMS Microbiol Ecol 73(1):178–189

Rosa LH, Tabanca N, Techen N, Wedge DE, Pan Z, Bernier UR, Becnel JJ, Agramonte NM, Walker LA, Moraes RM (2012) Diversity and biological activities of endophytic fungi associated with micropropagated medicinal plant *Echinacea purpurea* (L.) Moench. Am J Plant Sci 3:1105–1114

Russell JR, Huang J, Anand P, Kucera K, Sandoval AG, Dantzler KW, Hickman D, Jee J, Kimovec FM, Koppstein D, Marks DH, Mittermiller PA, Núñez SJ, Santiago M, Townes MA, Vishnevetsky M, Williams NE, Vargas MPN, Boulanger L, Bascom-Slack C, Strobel SA (2011) Biodegradation of polyester polyurethane by endophytic fungi. Appl Environ Microbiol 77(17):6076–6084

Sandberg DC, Battista LJ, Arnold AE (2014) Fungal endophytes of aquatic macrophytes: diverse host-generalists characterized by tissue preferences and geographic structure. Microb Ecol 67(4):735–747

Soliman SSM, Trobacher CP, Tsao R, Greenwood JS, Raizada MN (2013) A fungal endophyte induces transcription of genes encoding a redundant fungicide pathway in its host plant. BMC Plant Biol 13(1):93

Stierle A, Strobel G, Stierle D (1993) Taxol and taxane production by *Taxomyces andreanae*, an endophytic fungus of Pacific yew. Science 260(5105):214–216

Strobel G, Daisy B (2003) Bioprospecting for microbial endophytes and their natural products. Microbiol Mol Biol Rev 67(4):491–502

Strobel G, Daisy B, Castillo U, Harper J (2004) Natural products from endophytic microorganisms. J Nat Prod 67(2):257–268

Sun X, Guo LD, Hyde KD (2011) Community composition of endophytic fungi in *Acer truncatum* and their role in decomposition. Fungal Divers 47:85–95

Sun X, Ding Q, Hyde KD, Guo LD (2012) Community structure and preference of endophytic fungi of three woody plants in a mixed forest. Fungal Ecol 5(5):624–632

Suryanarayanan TS, Thirunavukkarasu N, Govindarajulu MB, Gopalan V (2012) Fungal endophytes: an untapped source of biocatalysts. Fungal Divers 54(1):19–30

Tan XM, Chen XM, Wang CL, Jin XH, Cui JL, Chen J, Guo SX, Zhang LF (2012) Isolation and identification of endophytic fungi in roots of nine *Holcoglossum* plants (*Orchidaceae*) collected from Yunnan, Guangxi, and Hainan provinces of China. Curr Microbiol 64(2): 140–147

Tao G, Liu ZY, Hyde KD, Liu XZ, Yu ZN (2008) Whole rDNA analysis reveals novel and endophytic fungi in *Bletilla ochracea* (*Orchidaceae*). Fungal Divers 33:101–122

Tejesvi MV, Kajula M, Mattila S, Pirttilä (2011) Bioactivity and genetic diversity of endophytic fungi in *Rhododendron tomentosum* Harmaja. Fungal Divers 47:97–107

Thongsandee W, Matsuda Y, Ito S (2012) Temporal variations in endophytic fungal assemblages of *Ginkgo biloba* L. J For Res 17(2):213–218

U'Ren JM, Lutzoni F, Miadlikowska J, Arnold AE (2010) Community analysis reveals close affinities between endophytic and endolichenic fungi in mosses and lichens. Microb Ecol 60(2):340–353

U'Ren JM, Riddle JM, Monacell JT, Carbone I, Miadlikowska J, Arnold AE (2014) Tissue storage and primer selection influence pyrosequencing-based inferences of diversity and community composition of endolichenic and endophytic fungi. Mol Ecol Resour 14(5):1032–1048

Usuki F, Narisawa K (2007) A mutualistic symbiosis between a dark septate endophytic fungus, *Heteroconium chaetospira*, and a nonmycorrhizal plant, Chinese cabbage. Mycologia 99(2):175–184

Vega FE, Simpkins A, Aime MC, Posada F, Peterson SW, Rehner SA, Infante F, Castillo A, Arnold AE (2010) Fungal endophyte diversity in coffee plants from Colombia, Hawai'i, Mexico and Puerto Rico. Fungal Ecol 3(3):122–138

Verma VC, Kharwar RN, Gange AC (2010) Biosynthesis of antimicrobial silver nanoparticles by the endophytic fungus *Aspergillus clavatus*. Nanomedicine 5(1):33–40

Vieira MLA, Hughes AFS, Gil VB, Vaz ABM, Alves TMA, Zani CL, Rosa CA, Rosa LH (2011) Diversity and antimicrobial activities of the fungal endophyte community associated with the traditional Brazilian medicinal plant *Solanum cernuum* Vell. (*Solanaceae*). Can J Microbiol 58(1):54–66

Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Hückelhoven R, Neumann C, von Wettstein D, Franken P, Kogel KH (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. Proc Natl Acad Sci USA 102(38):13386–13391

Wang Y, Dai CC (2011) Endophytes: a potential resource for biosynthesis, biotransformation, and biodegradation. Ann Microbiol 61(2):207–215

Weiss M, Sýkorová Z, Garnica S, Riess K, Martos F, Krause C, Oberwinkler F, Bauer R, Redecker D (2011) Sebacinales everywhere: previously overlooked ubiquitous fungal endophytes. PLoS One 6(2), e16793

Wu H, Yang HY, You XL, Li YH (2013a) Diversity of endophytic fungi from roots of *Panax ginseng* and their saponin yield capacities. SpringerPlus 2:1–9

Wu L, Han T, Li W, Jia M, Xue L, Rahman K, Qin L (2013b) Geographic and tissue influences on endophytic fungal communities of *Taxus chinensis* var. *mairei* in China. Curr Microbiol 66(1):40–48

Xiao X, Luo S, Zeng G, Wei W, Wan Y, Chen L, Guo H, Cao Z, Yang L, Chen J, Xi Q (2010) Biosorption of cadmium by endophytic fungus (EF) *Microsphaeropsis* sp. LSE10 isolated from cadmium hyperaccumulator *Solanum nigrum* L. Bioresour Technol 101(6): 1668–1674

Xiao J, Zhang Q, Gao YQ, Tang JJ, Zhang AL, Gao JM (2014) Secondary metabolites from the endophytic *Botryosphaeria dothidea* of *Melia azedarach* and their antifungal, antibacterial, antioxidant, and cytotoxic activities. J Agric Food Chem 62:3584–3590

Xing YM, Chen J, Cui JL, Chen XM, Guo SX (2011) Antimicrobial activity and biodiversity of endophytic fungi in *Dendrobium devonianum* and *Dendrobium thyrsiflorum* from Vietman. Curr Microbiol 62(4):1218–1224

Xiong ZQ, Yang YY, Zhao N (2013) Diversity of endophytic fungi and screening of fungal paclitaxel producer from Anglojap yew, *Taxus x media*. BMC Microbiol 13(1):71

Xu Y, Espinosa-Artiles P, Liu MX, Arnold AE, Gunatilaka AAL (2013) Secoemestrin D, a cytotoxic epitetrathiodioxopiperizine, and emericellenes A-E, five sesterterpenoids from *Emericella* sp. AST0036, a fungal endophyte of *Astragalus lentiginosus*. J Nat Prod 76(12):2330–2336

Yan X, Sikora RA, Zheng J (2011) Potential use of cucumber (*Cucumis sativus* L.) endophytic fungi as seed treatment agents against root-knot nematode *Meloidogyne incognita*. J Zhejiang Univ Sci B 12(3): 219–225

Yin H, Zhao Q, Sun FM, An T (2009) Gentiopicrin-producing endophytic fungus isolated from *Gentiana macrophylla*. Phytomedicine 16(8):793–797

Yuan ZL, Zhang CL, Lin FC, Kubicek CP (2010) Identity, diversity, and molecular phylogeny of the endophytic mycobiota in the roots of rare wild rice (*Oryza granulate*) from a nature reserve in Yunnan, China. Appl Environ Microbiol 76(5):1642–1652

Zhang HW, Song YC, Tan RX (2006) Biology and chemistry of endophytes. Nat Prod Rep 23(5):753–771

Zhang X, Lin L, Chen M, Zhu Z, Yang W, Chen B, Yang X, An Q (2012) A nonpathogenic *Fusarium oxysporum* strain enhances phytoextraction of heavy metals by the hyperaccumulator *Sedum alfredii* Hance. J Hazard Mater 229:361–370

Zhang T, Zhang YQ, Liu HY, Wei YZ, Li HL, Su J, Zhao LX, Yu LY (2013) Diversity and cold adaptation of culturable endophytic fungi from bryophytes in the Fildes Region, King George Island, maritime Antarctica. FEMS Microbiol Lett 341(1):52–61

Zhang D, Ge H, Zou J, Tao X, Chen R, Dai J (2014a) Periconianone A, a new 6/6/6 carbocyclic sesquiterpenoid from endophytic fungus *Periconia* sp. with neural anti-inflammatory activity. Org Lett 16(5):1410–1413

Zhang QH, Zhang J, Yang L, Zhang L, Jiang DH, Chen WD, Li GQ (2014b) Diversity and biocontrol potential of endophytic fungi in *Brassica napus*. Biol Control 72:98–108

Zhang W, Xu L, Yang L, Huang Y, Li S, Shen Y (2014c) Phomopsidone A, a novel depsidone metabolite from the mangrove endophytic fungus *Phomopsis* sp. A123. Fitoterapia 96:146–151

Zheng YK, Chen C, Ren D, Gu YF (2013) Genetic diversity of the plant endophytic fungi in a Pb-Zn mine area in Hanyuan, Sichuan Province, China. J Sichuan Agric Univ 31(3):308–313

Zhou SL, Yan SZ, Wu ZY, Chen SL (2013) Detection of endophytic fungi within foliar tissues of *Camellia oleifera* based on rDNA ITS sequences. Mycosystema 32(5):819–830

Zhou XM, Zheng CJ, Chen GY, Song XP, Han CR, Li GN, Fu YH, Chen WH, Niu ZG (2014a) Bioactive anthraquinone derivatives from the mangrove-derived fungus *Stemphylium* sp. 33231. J Nat Prod 77(9): 2021–2028

Zhou ZF, Kurtán T, Yang XH, Mándi A, Geng MY, Ye BP, Taglialatela-Scafati O, Guo YW (2014b) Penibruguieramine A, a novel pyrrolizidine alkaloid from the endophytic fungus *Penicillium* sp. GD6 associated with Chinese mangrove *Bruguiera gymnorrhiza*. Org Lett 16(5):1390–1393

Zikmundová M, Drandarov K, Bigler L, Hesse M, Werner C (2002) Biotransformation of 2-benzoxazolinone and 2-hydroxy-1, 4-benzoxazin-3-one by endophytic fungi isolated from *Aphelandra tetragona*. Appl Environ Microbiol 68(10):4863–4870

Zimmerman NB, Vitousek PM (2012) Fungal endophyte communities reflect environmental structuring across a Hawaiian landscape. Proc Natl Acad Sci USA 109(32):13022–13027