

Review

Mechanisms of fungal endophytes in plant protection against pathogens

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Fungal endophytes are a group of microorganism associated with plant and have attracted a great interest to botanist, microbiologist and ecologist. Since they have the ability to benefit host plant growth and defense and can produce various potential commercially valued secondary metabolites, an increasing number of reports pay attention to endophytic screening, identification and production. However, little is known about the regulation of plant-fungal endophytes interaction and how fungal endophytes protect plant from pathogens. This review summarized current researches on fungal endophytes as biocontrol agent against plant pathogens and proposed that endophytes inhibit plant pathogen mainly by inducing phytoalexins production and ecological occupation.

Key words: Fungal endophyte, pathogens, plant protection.

INTRODUCTION

Endophytic microbes are an intriguing group of organism associated with various tissues and organs of terrestrial and some aquatic plants, whose infections are inconspicuous and the infected host tissue are at least transiently symptomless (Stone et al., 2000). Also, fungal endophytes live in intercellular space or inside cells of host plant causing no apparent damage (Saikkonen et al., 1998). However, endophytic fungi, which colonize and grow asymptotically within healthy plant tissues, may evolve from plant pathogenic fungi and become non-pathogenic (Carroll, 1988; Freeman and Rodriguez, 1993; Saikkonen et al., 1998; Kogel et al., 2006). Although, disease symptoms of host plant can be caused by endophytes under stress conditions (Clay and Schardl, 2002; Schulz and Boyle, 2005), during the long term co-evolution of endophyte and plant, equilibrium between these organisms have been established. Thus, the true endophyte will exist once equilibrium is achieved between fungal activity and the plant reaction and is maintained over time (Giménez et al., 2007). Fungal endophytes benefit plant by promoting plant growth

(Dai et al., 2008), improving resistance to multiple stress (Lewis, 2004; Malinowski et al., 2004), protection from diseases and insects (Wilkinson et al., 2000; Tanaka et al., 2005; Vega et al., 2008).

Recently, many scholars focus on the study of endophytes as biocontrol agent of pathogen and insects and successfully applied endophytes to plant protection. Based on recent reports, we proposed that the potential mechanisms of endophytes inhibition of plant pathogen are by several means, including direct effects, indirect effects and ecological effects. It can be indicated that the main reasons for fungal endophytes in plant protection against pathogens might be by phytoalexins production induced by fungal endophytes and endophytic ecological occupation.

DIRECT INHIBITION OF PLANT PATHOGENS

Many studies recently found that endophyte fungal have the ability to protect host from diseases and limit the damage caused by pathogen microorganism (Arnold et al., 2003; Ganley et al., 2008; Mejia et al., 2008). The common methods of these researches were *in vitro* co-culture with pathogens and endophytes, or comparison of the survival rate of plant inoculated with fungal

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endophytes with endophyte-free plant. Although, some re-researches propose some potential mechanisms of endo-phyte limiting the pathogen damage, our knowledge about precise regulation among endophyte, pathogen and plant still remain in the early age. Here we will discuss the mechanisms as direct effect (interaction between endophytes and pathogens), indirect effect (enhanced plant defense) and ecological effects (occupation of ecological niche). In the case of direct effect, endophytes directly suppress pathogens by producing antibiotic, secreting lytic enzymes. However, the direct interactions between fungal endophytes and pathogens are complex and sensitive to species-specific antagonism (Arnold et al., 2000).

Antibiotics produced by endophytes

Many fungal endophytes produce secondary metabolites and some of these compounds are antifungal and antibacterial which strongly inhibit the growth of other microorganisms including plant pathogens (Gunatilaka, 2006). A group of biocontrol strains can produce single or multiple kinds of antibiotics including terpenoids, alkaloids, aromatic compounds and polypeptides which have been proved that plant pathogens are sensitive to. Five cadinane sesquiterpenes derivatives were isolated from *Phomopsis cassiae*, which is an endophytic fungus isolated from *Cassia spectabilis* and 3,11,12-trihydroxy-cadalene as one of those five derivatives was revealed as the most antifungal active compound against *Cladosporium sphaerospermum* and *Cladosporium clado-sporioides* (Silva et al., 2006). Alkaloids also strongly suppress microbes. For example, altersetin, a new alkaloid isolated from endophytic *Alternaria* spp., showed antibacterial activity against several pathogenic gram-positive bacteria (Hellwig et al., 2003). Volatile oil is another compound with antibiosis. *Muscodor albus*, an endophytic fungus of tropical tree species, can produce many volatile organic compounds including tetrahydrofuran, 2-methyl furan, 2-butanone and aciphyllene which have antibiotic activities (Atmosukarto et al., 2005). *In vitro*, endophytic fungi isolated from *Artemisia annua* can produce substances that inhibit the growth of all or a few of the tested phytopathogens and the major antifungal compounds were EtOAc and n-butanol (Liu et al., 2001). A number of studies reported fungal endophytes produced antibiotics that inhibit pathogens *in vitro* (Table 1). However, as low concentration of these substances are excreted by endophytes in host plant, the effects of antibiotics to pathogens *in vivo* need to be assessed.

Lytic enzymes secreted from endophytes

Many microorganisms produce and release lytic enzymes that can hydrolyze a wide variety of polymeric

compounds, including chitin, proteins, cellulose, hemicellulose and DNA (Tripathi et al., 2008). When endophytes colonize on the plant surface, they produce enzymes to hydrolyze plant cell walls. As a result, these enzymes also have the function to suppress plant pathogen activities directly and have the capability of degrading the cell walls of fungi and oomycetes. There are many kinds of these enzymes which include β -1,3-glucanases, chitinases and cellulases. Mutagenesis of β -1,3-glucanase genes in *Lysobacter enzymogenes* strain C3 resulted in reduced biological control activity toward bipolaris leaf spot of tall fescue and pythium damping-off of sugar beet (Palumbo et al., 2005). *Streptomyces* which produce lytic enzymes *in vitro* have an additional role in the antagonism to cacao witches' broom (Macagnan et al., 2008). Although, the enzymes may not be of most importance in antagonism, they may contribute to antagonistic activity through a combination of mechanisms.

INDIRECT EFFECTS TO ENHANCE PLANT RESISTANCE

Plants emerge a series of mechanisms against unfavorable environment such as drought, cold, salt stress or pathogens. Morphological and biochemical changes including cellular necrosis, hypersensitive response and phytoalexin production respond to the various stresses rapidly. During the long term evolution, two types of innate resistance: non-specific (general) resistance and specific resistance are formed to resist pathogens infestation (Kira'ly et al., 2007). The former form is effective against several pathogenic species, while the latter can resist infection of one or a few pathogenic strains. Since fungal endophytes may evolve from plant pathogenic fungi, plant defense could be triggered by fungal endophytes like pathogens. Actually, the defense of plant associated with endophytes is increased through resistance enhancement and secondary metabolites production.

Induction of plant resistance

Over the past two decades, many researches have focused on plant resistance responses to pathogens and parasites of various scales. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistances in which scholars are interested. SAR, induced by pathogen infection, is mediated by salicylic acid and associated with the accumulation of pathogenesis-related (PR) proteins. ISR, induced by some nonpathogenic rhizobacteria, is mediated by jasmonic acid or ethylene and is not associated with the accumulation of PR proteins (Vallad and Goodman, 2004; Tripathi et al., 2008). These PR proteins comprise a variety of enzymes, some of which may act

Table 1. Antibiotic produced by fungal endophytes.

Fungal endophyte	Host	Antibiotic	Target pathogens	Reference
<i>Acremonium zeae</i>	Maize	Pyrocidines A, B	<i>Aspergillus flavus</i> , <i>Fusarium verticillioides</i>	Wicklow et al. (2005)
<i>Verticillium</i> sp.	<i>Rehmannia glutinosa</i>	Massariphenone, ergosterol peroxide	<i>Pyricularia oryzae</i> P-2b	You et al. (2009)
<i>Phomopsis cassiae</i>	<i>Cassia spectabilis</i> .	Cadinane sesquiterpenes	<i>Cladosporium sphaerospermum</i> , <i>Cladosporium cladosporioides</i>	Silva et al. (2006)
<i>Muscodor albus</i>	Tropical tree	Tetrohydrofuran, 2-methyl furan, 2-butanone, aciphyllene	<i>Stachybotrys chartarum</i>	Atmosukarto et al. (2005)
<i>Periconia</i> sp.	<i>Taxus cuspidata</i>	Fusicoccane diterpenes	<i>Bacillus subtilis</i> , <i>Staphylococcus aureus</i> , <i>Klebsiella pneumoniae</i> , <i>Salmonella typhimurium</i>	Kim et al. (2004)
<i>Ampelomyces</i> sp.	<i>Urospermum picroides</i>	3-O-Methylalaternin, altersolanol A	<i>Staphylococcus aureus</i> , <i>S. epidermidis</i> , <i>Enterococcus faecalis</i>	ly et al. (2008)

directly to lyse the invading cells, including chitinases and β -1, 3-glucanases (Fukuda and Shinshi, 1994), reinforce cell wall boundaries to resist infections, or induce localized cell death. Fungal endophytes induced ISR may also associate with expression of pathogenesis-related genes.

Fusarium solani isolated from root tissues of tomato elicited induced systemic resistance against the tomato foliar pathogen *Septoria lycopersici* and triggered PR genes, PR5 and PR7 expression in roots (Kavroulakis et al., 2007). Besides, endophytes colonized plants have the ability to mount a defense response more rapidly. *Citrullus lanatus* and *Cucumis sativus* exposed to a nonpathogenic mutant of *Colletotrichum magna* exhibited high levels of lignin deposition, peroxidase activity and phenylalanine ammonialyase activity and obtained the protection against disease caused by *Colletotrichum orbiculare* and *Fusarium oxysporum* (Redman et al., 1999).

Endophyte *Neotyphodium lolii* reduced lesions on detached leaves caused by four pathogens through enhancing superoxide dismutase (SOD) and peroxidases (POD) activities of host (Tian et al., 2008). It is plausible that antioxidative systems including SOD and POD would control reactive oxygen species (ROS) damage induced by pathogen infection.

Stimulation of plant secondary metabolites

Plant secondary metabolites are a group of compounds, which do not play important role in basic life functions, but play a major role in the adaptation of plants to their environment (Bourgoud et al., 2001). Among these compounds, plants produce low molecular weight antimicrobial molecules called phytoalexins (Smith, 1996), which contain multiple substances including flavonoid, terpenoid, etc. Although

phytoalexins could be formed by various non-biological stress factors such as UV light, heavy metal ions or salt stress, phytoalexins was first discovered in *Orchis morio* and *Loroglossum hircinum* as response to fungal attack by the French botanist Noel Bernard (Stoessl and Arditti, 1984). And recently, many researches have focused on the phytoalexins induced by pathogens (Lo et al., 1999; Abraham et al., 1999; McNally et al., 2003; Pedras et al., 2008).

However, studies refer to the plant secondary metabolism mediated by the fungal endophytes is still on the early stage. Our preview study showed that endophytic fungi *Fusarium* spp. E4 and E5 could promote the growth of *Euphorbia pekinensis*, and increased its terpenoids content (Yong et al., 2009). Further research indicated that *Fusarium* E5 elicitor could induce diterpene and triterpene production in *E. pekinensis* cell suspension cultures and activities of defense-related enzymes including PAL, POD, CAT (data

have not been published). A similar situation was observed in suspension cultures of *Taxus cuspidate*, to which the addition of fungal endophyte culture supernatants led to the yield of paclitaxel; was 1.8-fold of the yield from control (Li and Tao, 2009).

It seems that co-culturing with endophytic elicitor is an alternative way to enhance plant secondary metabolites and increase plant resistance. Mechanism of endophytic elicitor induced plant secondary metabolites production is similar to stimulation of plant resistance. Colonization of fungal endophytes results in the secretion of hydrolase of plant cell to limit the growth of fungi, thus, fragments of endophytes, acting as elicitor, are produced by hydrolization. The elicitors such as lipopolysaccharides, polysaccharides and glycoprotein will stimulate plant defense and plant secondary metabolites, which would suppress pathogens attack efficiently. However, determination of how endophytes can survive in high concentration of secondary metabolites in host plant is still unknown.

Promotion of plant growth and physiology

Endophytes may contribute to their host plant defenses against phytopathogenic organisms through plant physiology control (Giménez et al., 2007). An increase in plant growth will prevent a variety of abiotic and biotic stresses, reflecting plant vigor or persistence and considered as a potential protection to pathogen challenge (Kuldau and Bacon, 2008). Many studies demonstrate that plants infected with endophytes obtain growth promotion (Barka et al., 2002), resistance to drought stress (Swarthout et al., 2009) and tolerance to unsuitable soil conditions (Belesky and Fedders, 1995; Malinowski et al., 2004). The enhancement of plant growth may be influenced by compounds like phytohormones produced by fungal endophytes. *Colletotrichum* sp., an endophytic fungus in *A. annua* produces substances like indole acetic acid (IAA) to regulate plant processes (Lu et al., 2000).

Our previous research indicated that *Fusarium* sp. E5 extract functions as an auxin. The mechanism of fungal endophyte stimulating the host growth might be attributed to the phytohormone effect produced by endophytic fungi (Dai et al., 2008). As defense responses are associated with increased demands for energy, reducing equivalents and carbon skeletons are provided by primary metabolic pathways (Bolton, 2009). It is reasonable to believe that enhancement of plant growth induced by fungal endophytes will increase indirect protection to pathogens.

ECOLOGICAL EFFECTS

The plant-pathogen-endophyte interaction depends on endophytic niche. Competition of ecological niche and

nutrition, hyperparasites and predation are between diverse micro-organism that live in endophytic niche, especially between endophytes and pathogens. Endophytic recognition and colonization rapidly occupy ecological niche and leave no space for pathogens, which would be the common and main reason that fungal endophytes inhibit pathogen infection in plant.

Occupation of ecological niche

Fungal endophytes have the ability to colonize inter- or intracellular and often are localized in single cell. The colonization of plant tissues by endophytes involves several steps including host recognition, spore germination, penetration of the epidermis and tissue colonization (Petrini, 1991; 1996). After endophytes are successfully colonized in host tissue, the endophytic niche becomes established. In the endophytic niche, endophytes will obtain a reliable source of nutrition provided from plant fragment, exudates and leachates and protect host against other microorganisms. Fungal endophytes are generally thought to protect plant by rapid colonization and thereby exhausting the limited available substrates so that none would be available for pathogens to grow (Pal and Gardener, 2006). Furthermore, the plants produce lignin and other cell-wall deposits to limit the growth of endophytes and cause it to be a virulent (Harman et al., 2004). As a result, the cell wall becomes re-reinforced after endophytic colonization, thus it becomes difficult for pathogens to infest.

Hyperparasites and predation

Hyperparasites is another ecological strategy that endophytes provide to protect host plant. In hyper parasitism, the pathogen is directly attacked by a specific endophyte that kills it or its propagules (Tripathi et al., 2008). Fungal endophytes parasitize around hyphae of pathogens by various means as twisting, penetrating the hyphae of pathogens and secreting lyase to decompose cell wall of pathogens. For example, *Trichoderma* are able to parasitize hyphae of plant pathogen *Rhizoctonia solani* and many of these observations are linked with biocontrol (Grosch et al., 2006). In contrast to hyper parasitism, microbial predation is a more general way to suppress plant pathogens. Some endophytes show predatory behavior under nutrient-limited conditions. For example, *Trichoderma* produce a range of enzymes that are directly used against cell walls of fungi to utilize the fragment of pathogens (Benhamou and Chet, 1997).

PROSPECT FOR BIOLOGICAL CONTROL

Plant-microorganism symbiotic association based on

mutual exploitation has more opportunity to survive in environment. The most successful example of mutualism is rhizobia-*Legumes* symbiont. There are increasing numbers of studies focusing on fungal endophytes because they benefit plant growth and protection. As noted above, plant inoculated with fungal endophytes have displayed promotion in growth and resistance to diseases caused by pathogens (Arnold et al., 2003; Kavroulakis et al., 2007; Meji'a et al., 2008; Ganley et al., 2008; Mendoza and Sikora, 2009). Fungal endophyte-mediated plant resistances to pathogens have been well studied in agricultural crops, grass systems (Terry and Joyce, 2004) and forest trees (Ganley et al., 2008).

However, some potential ecological problems need to be assessed. First, it must be considered that when an endophyte is used to inoculate a species which is not its natural host plant, the pattern of produced metabolites may be different significantly (Giménez et al., 2007). Thus, the security of crops infested with endophytes must be evaluated. Second, we should consider whether trilateral interaction is going to affect the plant-micro-organism symbiont. Endophytic inoculation will change the growth, physiology and metabolism of other beneficial fungi and bacteria, which could break the balance between endophyte and host plant. Third, we must also assess whether it is worthy or useful to promote crop yield and disease protection. Not all the endophyte-plant associations make plant more resistant to diseases and grow better. In general, it seems that further studies would be carried on interaction, regulation of fungal endophytes and host plant.

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