Role of *Epichloë* Endophytes in Defense Responses of Cool-Season Grasses to Pathogens: A Review

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Symbioses of plants and animals with microorganisms have led to major transitions in the evolution of life (Margulis 1996). Many cool-season grasses are hosts of the fungal genus *Epichloë*, for which the asexual members had previously been classified as *Neotyphodium* spp. (Leuchtmann et al. 2014). These endophytes spend their life cycle living in the intercellular space of aerial tissues without causing obvious symptoms in or injury to the host (Christensen et al. 2008; Kuldau and Bacon 2008; Nan and Li 2004). Although the first association involving a member of this genus was found in 1898 (Sampson 1933), the stimulus that led to the current interest in *Epichloë* endophytes was the link established in 1977 between the presence of an endophyte in tall fescue (*Festuca arundinacea*) and a toxicosis problem in grazing cattle (Bacon et al. 1977). Following this, the symbiosis between Pooideae grasses and *Epichloë* endophytes has attracted great interest from researchers around the world (Leuchtmann et al. 2014; Saikkonen et al. 2006; Song et al. 2016; Tadych et al. 2014). Presently, 45 species of *Epichloë* endophytes have been reported in the world (Leuchtmann et al. 2014; Shymonovich et al. 2017; Song et al. 2016).

The associations between grasses and these endophytic fungi are generally considered to be mutualistic (Müller and Krauss 2005). Host plants provide photosynthate and shelter for these endophytes, and their presence can improve the ability of the host grass to persist when exposed to abiotic stresses, such as drought (Gundel et al. 2016; Hahn et al. 2008; Hesse et al. 2003; Kane 2011; Malinowski and Belesky 2000), salt (Dinnyen 2015; Sabzalán and Mirlohi 2010; Song et al. 2015a), heavy metals (Malinowski et al. 2004; Zhang et al. 2010a, b), cold (Chen et al. 2016; Zhou et al. 2015), and waterlogging (Song et al. 2015b), and to biotic stresses, such as livestock (Cheplick and Clay 1988; Filipov et al. 1998), birds (Pennell and

Rolston 2012), insects (Barker et al. 2015; Shiba et al. 2011; Yule et al. 2011; Zhang et al. 2012), nematodes (Eerens et al. 1998; Guo et al. 2016; Latch 1993), and pathogens (Ma et al. 2015; Sabzalán et al. 2012; Vignale et al. 2013; Xia et al. 2015, 2016). Therefore, mutualism plays important roles in influencing species coexistence and determining community composition (Umbanhowar and McCann 2005; Yao et al. 2015).

Disease resistance is the key factor in the quality of all agricultural crops, including forage grasses (Wiewióra et al. 2015). The incidence and severity of plant disease, especially foliar diseases, pose a serious threat not only to cereal production (Fisher et al. 2012) but also to forage production, which further influences livestock production. Fungicide application can be employed to remit damage from fungal disease, but it should be noted that this strategy has its limitations (Walter et al. 2005). It almost certainly would cause environmental problems and probably result in pathogens acquiring fungicide tolerance. Therefore, breeding resistant cultivars is regarded as the most economical and environmentally friendly strategy because of the reduction in chemical input into the environment (Huang and Roder 2004). One of the underexplored approaches to breed resistant cultivars is the use of symbiotic fungal endophytes. In 1983, in a pioneering study, Shimanuki and Sato (1983) first found that the presence of *Epichloë* endophytes suppressed fungal diseases in the host grasses. Following this finding, this area of research has attracted great interest around the world. Therefore, it is necessary to summarize advances in research regarding resistance to plant diseases caused by *Epichloë* spp. endophytic fungi and to try to reveal the disease resistance mechanisms. Here, we highlight the latest advances in our understanding of the interactions among host plants, endophytic fungi, and pathogenic fungi and of the potential mechanisms of inhibition of plant pathogenic fungi by endophytic fungi to obtain a broader understanding of fungal endophyte effects on hosts that could create new opportunities for managing or introducing fungal symbioses in both non-agronomic and agronomic ecosystems.

The Interaction Between Symbiosis and Pathogenic Fungi

The effect of endophytes on the growth of pathogenic fungi in vitro using a dual-culture test. The previous research regarding the antagonistic effect of endophytes on pathogens in a dual-culture test mainly focused on the *Epichloë coenophialum*, *E. uncinatum*, and *E. festucae* var. *lolii* endophytes. These endophytes colonize tall fescue, meadow fescue (*Lolium pratensis*), and perennial ryegrass

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(*L. perenne*), respectively. These three *Epichloë* endophytes caused variable inhibition of the growth of fungi, including *Alternaria alternata*, *Bipolaris sorokiniana*, *Drechslera* spp., *Fusarium* spp., and *Rhizoctonia* spp. The resistances of some other *Epichloë* endophytes to pathogenic fungi were also occasionally reported (Table 1). For example, *E. gansuensis* endophytes could inhibit the growth of *Curvularia* sp., *Phomopsis* sp., and *Fusarium acuminatum* (Li et al. 2007b). All dual-culture tests to date show that the inhibitory effects of *Epichloë* endophytes on pathogenic fungi are influenced by the species and genotype of the endophyte, the temperature of the growing environment, and the time of the dual-culture test.

The positive effect of *Epichloë* endophytes on plant defense has been traditionally attributed to alkaloids, and the role of alkaloids in protecting grasses associated with *Epichloë* endophytes has been extensively documented (Bastias et al. 2017). Different species of endophyte associate with different grasses that produce different kinds of alkaloids (Table 2) (Bush et al. 1997; Schardl and Phillips 1997). Thus, the inhibitory effects on the growth of pathogenic fungi are different. Beyond that, the inhibitory effect is also influenced by the genotype of the endophyte. The same species of endophytes isolated from different grasses show different resistance to various pathogens. Ten strains of the *E. festucae* var. *lolii* endophyte were isolated from 22 perennial ryegrass plants, and seven of them significantly inhibited the growth of *F. avenaceum* and *Rhizoctonia solani*, while the other three strains had no effect on either pathogen's growth (Paňka 2008). In addition, even if the endophytes are the same species or were isolated from the same host grass, their resistance to pathogens may be different. For instance, there were four *Epichloë* endophyte strains isolated from perennial ryegrass, but only one of them had the strongest inhibitory activity against *A. alternata*.

Recent research also suggested that one potential novel species of *Epichloë* endophyte (recorded as XH03) isolated from Chinese fescue (*Festuca sinensis*) remarkably inhibited the growth of *A. alternata*, *B. sorokiniana*, and *C. lunata* by at least 50%, but the inhibitory effect was not effective in the long term (Zhou et al. 2015). This phenomenon indicated that the inhibitory effect of endophytes on pathogen growth may be time-constrained. After all, external culture conditions *in vitro* are quite different from the native

Pathogen	Endophyte	Host	References
<i>Alternaria alternata</i>	<i>Epichloë coenophialum</i>	<i>Festuca arundinacea</i>	White and Cole 1985
<i>Cladosporium cladosporioides</i>			
<i>Nigrospora sphaerice</i>			
<i>Periconia macrospinoso</i>			
<i>Phoma sorghina</i>			
<i>Rhizoctonia cerealis</i>			
<i>Trichoderma harzianum</i>			
<i>Colletorichum graminicola</i>	<i>E. festucae</i> var. <i>lolii</i>	<i>Lolium perenne</i>	Christensen et al. 1991
<i>Drechslera erythrosipila</i>	<i>E. festucae</i> var. <i>lolii</i>	<i>L. perenne</i>	Christensen 1996; Christensen et al. 1991
<i>C. graminicola</i>	<i>E. coenophialum</i> or possibly <i>E. typhinum</i>	<i>F. arundinacea</i>	Christensen and Latch 1991
<i>D. erythrosipila</i>	<i>E. coenophialum</i> or possibly <i>E. typhinum</i>	<i>F. arundinacea</i>	Christensen and Latch 1991
<i>Puccinia coronata</i>	<i>E. coenophialum</i> or possibly <i>E. typhinum</i>	<i>F. arundinacea</i>	Christensen and Latch 1991
<i>Rhizoctonia zeae</i>	<i>E. lolii</i>	<i>Festuca</i> spp. or <i>L. perenne</i>	Christensen 1996
<i>Drechslera andersenii</i>	<i>E. lolii</i>	No	Holzmann-Wirth et al. 2000
<i>Drechslera siccans</i>			
<i>Drechslera teres</i>			
<i>Drechslera poae</i>			
<i>A. alternata</i>	<i>E. gansuensis</i>	<i>Achnatherum inebrians</i>	Li et al. 2007a
<i>Bipolaris sorokiniana</i>			
<i>Curvularia lunata</i>			
<i>Fusarium acuminatum</i>			
<i>R. cerealis</i>	<i>E. lolii</i>	<i>L. perenne</i>	Paňka 2008
<i>Cladosporium</i> sp.	<i>Epichloë</i> sp.	<i>A. sibiricum</i>	Xie et al. 2008
<i>Curvularia</i> sp.			
<i>Phomopsis</i> sp.			
<i>A. alternata</i>	<i>Epichloë</i> sp.	<i>L. perenne</i>	Ma and Nan 2011a
<i>B. sorokiniana</i>			
<i>C. lunata</i>			
<i>Drechslera</i> sp.			
<i>B. sorokiniana</i>	<i>E. uncinatum</i> and <i>E. lolii</i>	<i>L. perenne</i> and <i>F. pratensis</i>	Paňka 2011
<i>Microdochium nivale</i>			
<i>Fusarium equiseti</i>			
<i>Rhizoctonia solani</i>			
<i>A. alternata</i>	<i>Epichloë</i> sp.	<i>F. sinensis</i>	Zhou et al., 2015
<i>B. sorokiniana</i>			
<i>C. lunata</i>			

growth conditions of endophyte fungi, and their slow growth rate is one of their weaknesses, especially when they face competition from rapid-growth pathogenic fungi for a long period under dual-culture conditions. Further, for secondary metabolites, which are regarded as crucial substances for symbiosis protection, the concentration produced by the endophyte itself is far lower than the concentration of substances such as alkaloids produced by endophyte-grass symbiosis (Li 2005).

The antagonistic effect of endophytes on pathogenic fungi on detached leaves. Most of the studies indicated that *Epichloë* endophytes inhibit the growth of various pathogenic fungi (Table 3). Endophyte infection could inhibit pathogen invasion, lesion development, or both, manifested as a reduction in the number or size of disease lesions of endophyte-infected (E+) leaves (Li et al. 2007a; Nan and Li 2000; Sun 2015; Tian et al. 2008; Zhou et al. 2015). However, the results of previous research on the antagonistic effect of endophytes on pathogens on detached leaves are inconsistent. There are some exceptions indicating that the growth of some pathogenic fungi would not be affected by the endophyte status of leaves; for example, the *E. festucae* var. *lolii* endophyte has no effect on the growth of *Ascochyta leptospora* on detached perennial ryegrass leaves (Tian et al. 2008), the *Epichloë* sp. endophyte did not affect the growth of *F. equiseti* on detached *Elymus cylindricus* leaves (Nan and Li 2000), and the growth of *C. lunata* was not affected by endophyte status on detached drunken horse grass (*Achnatherum inebrians*)

leaves (Li et al. 2007a). In sum, in addition to endophyte status, disease resistance of detached grass leaves was influenced by multiple factors, including the species and genotype of pathogenic fungi, grass genotypes or varieties, and growth conditions (Bonos et al. 2005; Christensen 1996; Latch 1993; Popay and Bonos 2005; Wäli et al. 2006).

The effect of endophytes on the resistance to fungal disease in planta. There is a difference between obtaining fungal inhibition in vitro and obtaining resistance to a plant disease in an endophyte-infected plant. The changes in the host grass induced by the endophyte and environmental factors can influence many relationships that may take place during later stages, including those with pathogens (Pérez et al. 2017). For instance, an endophyte originating from three different cultivars of meadow ryegrass inhibited the growth of *Typhula ishikariensis* in vitro in a dual-culture test. However, compared with the endophyte-free (E-) grasses, the presence of endophytes in the host plant led to the plant becoming more susceptible to *T. ishikariensis* in planta (Wäli et al. 2006). As another example, nearly all *E. gansuensis* endophytes isolated from drunken horse grass could inhibit the growth and sporulation of *B. sorokiniana* in in vitro dual-culture tests, while the endophyte infection of drunken horse grass did not significantly enhance resistance to leaf blight disease, which is caused by the same pathogen under uncontrolled natural field conditions in planta (Li et al. 2007b). This difference may be induced by the difference in inhibitory substance

Table 2. Some main symbioses of grasses with *Epichloë* endophytes and their symbiosis-related alkaloids (Modified from Schardl and Phillips [1997])^a

Endophyte	Host	EA ^b	ID ^c	SAP ^d	PP ^e
<i>Epichloë coenophialum</i>	<i>Festuca arundinacea</i>	+/-	-	+	+
<i>E. festucae</i> var. <i>lolii</i>	<i>Lolium perenne</i>	+/-	+/-	-	+/-
<i>E. festucae</i>	<i>Festuca</i> spp.	+/-	+/-	+/-	+/-
<i>E. gansuensis</i> / <i>E. inebrians</i>	<i>Achnatherum inebrians</i>	+	+	-	-
<i>E. uncinatum</i>	<i>F. pratensis</i>	-	-	+	-
<i>E. typhina</i>	Various C3 grasses	-	-	-	+/-

^a +: found in all associations to date; +/-: found in some but not all associations; -: found in none of the associations to date.

^b Ergot alkaloids.

^c Indole-diterpenes (tremorgens, such as lolitrem B).

^d Saturated aminopyrrolizidines (lolines).

^e Pyrrolopyrazines (peramine).

Table 3. The antagonistic effect of endophyte on pathogenic fungi in detached leaves^a

Symbiosis/pathogens	<i>Lolium perenne</i> - <i>Epichloë festucae</i> var. <i>lolii</i>		<i>Elymus</i> <i>cylindricus</i> - <i>Epichloë</i> sp.		<i>Festuca</i> <i>sinensis</i> - <i>Epichloë</i> sp.		<i>Achnatherum</i> <i>inebrians</i> - <i>Epichloë</i> <i>gansuensis</i>		<i>Hordeum</i> <i>brevisubulatum</i> - <i>Epichloë</i> sp.	
	NL ^b	SL ^c	NL	SL	NL	SL	NL	SL	NL	SL
<i>Alternaria alternata</i>	+	+	+	+	+	+	+	+	+	+
<i>Ascochyta leptospora</i>	-	-					+	+		
<i>Bipolaris sorokiniana</i>	+	+			+	+			+	+
<i>Claviceps purpurea</i>									+	+
<i>Clonostachys rosea</i>							-	+		
<i>Curvularia lunata</i>	+	+			+	+	-	-	+	+
<i>Drechslera erythrosipila</i>									+	+
<i>Fusarium acuminatum</i>	+	+			+	+	-	+		
<i>Fusarium avenaceum</i>	+	+	+	+			-	+	+	+
<i>Fusarium chlamydosporum</i>	+	+					+	+		
<i>Fusarium culmorum</i>			+	+						
<i>Fusarium equiseti</i>			+	+						
<i>Fusarium oxysporum</i>	+	+	+	+			+	+		
<i>Fusarium semitectum</i>									+	+
<i>Fusarium solani</i>	+	+					+	+	+	+

^a +: the effect of endophyte on plant resistance to pathogens is positive; -: the effect of endophyte on plant resistance to pathogens is neutral; empty: no investigation. References: Li et al. 2007a; Nan and Li 2000; Sun 2015; Tian et al. 2008; Zhou et al. 2015.

^b Number of lesions.

^c Length of lesions.

production in vitro compared with that *in planta* (Christensen 1996). However, the disease resistance observed during the in vitro test does not completely disappear *in planta*. Most of the previous research on disease resistance of grass-endophytic fungi symbioses, which were carried out in field conditions or in a greenhouse, obtained similar results with in vitro assays (Table 4).

The effect of endophytes on the resistance to fungal disease under field conditions. In 1983, pioneering research carried out by Shimanuki and Sato found that the infection rate of the pathogenic fungus *Blastocladia pringsheimii* of timothy grass (*Phleum pratense*) could notably decrease when the host plant was infected by the *E. typhina* endophyte under field conditions (Shimanuki and Sato 1983). This is the first study to ever report such an association. Since then, researchers have carried out many related field experiments to shed new light on the relationship between pathogenic fungi and

endophytic fungi, and most of them have obtained similar results. Infection by the *E. coenophialum* endophyte decreased the spore numbers of *Alternaria* sp. on tall fescue (Chu-Chou et al. 1992) and enhanced resistance to brown leaf spot, damping off (Schmidt and Seehovic 1994), and crown rust diseases (Li et al. 2007b). Research on perennial ryegrass parallels the results in tall fescue; the presence of the *E. festucae* var. *lolii* endophyte could notably increase the resistance of a host grass to a leaf spot disease induced by *Pyrenophora semeniperda* (Wheatley et al. 2000). Compared with E- grasses, endophyte-infected perennial ryegrass had a stronger resistance to rust disease caused by *Puccinia* sp. (Ma and Nan 2011b). The *E. occultans* endophyte reduced the disease incidence and severity caused by *Claviceps purpurea* on Italian ryegrass (*Lolium multiflorum*) (Pérez et al. 2017). In addition, the *Epichloë* sp. endophyte could alleviate the negative effects of head

Table 4. The effects of endophytes on the resistance to the pathogenic fungal in planta

Pathogens	Hosts	Endophytes	Effects	References
<i>Alternaria alternata</i>	<i>Lolium perenne</i>	<i>Epichloë festucae</i> var. <i>lolii</i>	E+ grass had higher SOD and POD enzyme activity and developed small lesions than those from E-	Tian et al. 2008
	<i>Hordeum brevisubulatum</i>	<i>Epichloë</i> sp.	E+ grass had higher plant height, tiller number and biomass than E- grass	Sun 2015
	<i>Agropyron cristatum</i>	<i>Epichloë</i> sp.	The percentage of fungi isolated from the E+ grass was significantly lower than that from E- grass	Nan and Li 2000
	<i>Elymus cylindricus</i>	<i>Epichloë</i> sp.	The percentage of fungi isolated from the E+ grass was significantly lower than that from E- grass	Nan and Li 2000
<i>Aspergillus flavus</i>	<i>Puccinellia distans</i>	<i>E. typhina</i>	The percentage of fungi isolated from the E+ seeds was significantly lower than that from E- seeds	Górzyńska et al. 2017
<i>Bipolaris sorokiniana</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	E+ grass had higher POD enzyme activity and developed small lesions than those from E-	Tian et al. 2008
	<i>Festuca pratensis</i>	<i>E. uncinatum</i>	Endophyte significantly decreased the infection of pathogen, but the infection was also affected by weather conditions.	Pańka et al. 2011
	<i>Leymus chinensis</i>	<i>Epichloë</i> sp.	E+ grasses had smaller lesion area of the leaves than E- grasses	Wang et al. 2016
	<i>H. brevisubulatum</i>	<i>Epichloë</i> sp.	E+ grasses had higher plant height, tiller number and biomass than E- grass	Sun 2015
<i>Blumeria graminis</i>	<i>Achnatherum inebrians</i>	<i>E. gansuensis</i>	E+ grasses had lower disease incidence, higher SOD and POD enzyme activity, chlorophyll and proline content.	Liu et al. 2015
			E+ grasses had lower disease incidence, higher tiller numbers biomass and greater photosynthetic ability than E- grasses	Xia et al. 2015, 2016
<i>Cladosporium herbarum</i>	<i>Agropyron cristatum</i>	<i>Epichloë</i> sp.	The percentage of fungi isolated from the E+ grass was significantly lower than that from E- grass	Nan and Li 2000
	<i>E. cylindricus</i>	<i>Epichloë</i> sp.	The percentage of fungi isolated from the E+ grass was significantly lower than that from E- grass	Nan and Li 2000
<i>Claviceps purpurea</i>	<i>Lolium multiflorum</i>	<i>E. occultans</i>	Both pathogen incidence and severity were twofold lower in E+ plants than in E- ones	Pérez et al. 2017
<i>Chaetomium nigricolor</i>	<i>P. distans</i>	<i>E. typhina</i>	The percentage of fungi isolated from the E+ seeds was significantly lower than that from E- seeds	Górzyńska et al. 2017
<i>Curvularia lunata</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	E+ grass had higher SOD and POD enzyme activity and developed small lesions than those from E-	Tian et al. 2008
	<i>L. chinensis</i>	<i>Epichloë</i> sp.	E+ grasses had smaller lesion area of the leaves than E- grasses	Wang et al. 2016
	<i>H. brevisubulatum</i>	<i>Epichloë</i> sp.	E+ grass had higher plant height and biomass than E- grass	Sun 2015
	<i>Festuca arundinacea</i>	<i>E. coenophialum</i>	Endophyte infection reduced lesion number and spore concentration of the pathogen	Chen et al. 2017

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smut caused by *Ustilago bullata* on *Bromus auleticus* grass (Iannone et al. 2017). The pathogenic fungus isolation rate of endophyte-infected leaves of wheatgrass (*Agropyron cristatum*), *E. cylindricus* grass, and red fescue (*Festuca rubra*) collected from northwest China was significantly lower than that of the leaves without an endophyte (Nan and Li 2000). The diversity and incidence of pathogenic fungi in *Puccinellia distans* seeds were also reduced by the presence of endophytes (Górzyńska et al. 2017). These results also indicated that, from another perspective, endophytes had a certain inhibitory effect on pathogenic fungi in host plants.

The effect of endophytes on resistance to fungal disease under greenhouse conditions. The resistance of symbioses to diseases was inconsistent under greenhouse conditions. The presence of the

E. coenophialum endophyte enhanced the resistance of tall fescue to a sheath blight disease caused by *Rhizoctonia zeae* (Gwinn and Gavin 1992) and to a leaf spot disease caused by *A. alternata* (Pańka et al. 2013b), but it did not significantly affect resistance to the rust diseases caused by *Puccinia graminis* (Pańka et al. 2011) and *P. graminis* subsp. *graminicola* (Welty et al. 1991), the powdery mildew disease caused by *Blumeria* sp., or the root rot caused by *Cochliobolus sativa* (Trevathan 1996) and foot rot caused by *Fusarium oxysporum* and *F. equiseti* (Hume et al. 1997). These results indicate not only that the disease resistance of tall fescue is affected by endophyte status but also that CO₂ concentration may be responsible for pathogen development. The research of Chen et al. (2017) found that elevated CO₂ decreases the severity of the disease caused by *C. lunata* in E+

Table 4. (Continued from previous page)

Pathogens	Hosts	Endophytes	Effects	References
<i>Drechslera erythrospila</i>	<i>F. pratensis</i>	<i>E. uncinatum</i>	Presence of the endophyte inhibited hyphal growth of various pathogenic fungi on diseased grass leaves.	Christensen 1996
<i>Drechslera siccans</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	E+ grasses had lower disease infection than E–, but this benefit effect was affected by the grass genotypes	Wiewióra et al. 2015
<i>Fusarium avenaeum</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	E+ grass had higher SOD enzyme activity and developed small lesions than those from E–	Tian et al. 2008
	<i>H. brevisubulatum</i>	<i>Epichloë</i> sp.	E+ grass had higher tiller number and biomass than E– grass	Sun 2015
<i>Fusarium oxysporum</i>	<i>Festuca arizonica</i>	<i>Epichloë</i> sp.	E+ grasses appear to be more resistant to the pathogen than E–	Reddy and Faeth 2010
	<i>Agropyron cristatum</i>	<i>Epichloë</i> sp.	The percentage of fungi isolated from the E+ grass was significantly lower than that from E– grass	Nan and Li 2000
<i>Fusarium poae</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	The E+ plants had lower disease severity, but this benefit effect was affected by the grass genotypes.	Pańka et al. 2013a
<i>Fusarium semitectum</i>	<i>H. brevisubulatum</i>	<i>Epichloë</i> sp.	E+ grass had higher plant height, tiller number and biomass than E– grass	Sun 2015
<i>Puccinia</i> spp.	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	The height and biomass of E+ grasses were significantly higher, and the contents of leaf relative water content, soluble sugar, chlorophyll, proline, and photosynthetic capacity and the activity of SOD and POD were significantly greater than those of E–	Ma and Nan 2011b
	<i>F. pratensis</i>	<i>E. uncinatum</i>	Endophyte did not significantly affect the infection rate of the pathogen on grasses	Pańka et al. 2011
<i>Pyrenophora semeniperda</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	E– grasses were more susceptible to infection with the pathogen than E+ grasses	Wheatley et al. 2000
<i>Puccinia graminis</i> subsp. <i>graminicola</i>	<i>F. arundinacea</i>	<i>E. coenophialum</i>	Endophyte did not significantly affect the infection rate of the pathogen on grasses	Welty et al. 1991
<i>Rhizoctonia zeae</i>	<i>L. perenne</i>	<i>E. festucae</i> var. <i>lolii</i>	The presence of endophyte inhibited, at different degrees, the pathogenic fungi hyphal growth on diseased grass leaves.	Christensen 1996
	<i>F. arundinacea</i>	<i>E. coenophialum</i>	The presence of endophyte inhibited, at different degrees, the pathogenic fungi hyphal growth on diseased grass leaves.	Christensen 1996
			The E+ grasses had reduced pathogen infection, but this benefit effect was affected by the grass genotypes. Additionally, E+ grasses had a higher phenolic compounds content	Pańka et al. 2013b
	<i>F. pratensis</i>	<i>E. uncinatum</i>	The presence of endophyte inhibited, at different degrees, the pathogenic fungi hyphal growth on diseased grass leaves.	Christensen 1996
<i>Rhizopus nigricans</i>	<i>P. distans</i>	<i>E. typhina</i>	The percentage of fungi isolated from the E+ seeds was significantly lower than that from E– seeds	Górzyńska et al. 2017
<i>Sclerotinia homoeocarpa</i>	<i>Festuca rubra</i>	<i>E. festucae</i>	E+ grasses had greater plant density and support less foliar mycelium of pathogens than E– grasses	Clarke et al. 2006
<i>Typhula ishikariensis</i>	<i>F. pratensis</i>	<i>E. uncinatum</i>	E– grass had significantly less pathogen infections than E+	Wäli et al. 2006

and E- tall fescue, and the advantage of E+ over E- grass in pathogen resistance under ambient CO₂ disappeared with elevated CO₂. The researchers ascribed this change to the change in nutritive quality of grass leaves under various CO₂ concentrations. Other relevant studies on *Festuca* grasses showed that the presence of *Epichloë* endophytes increased the resistance of fine fescue (*Festuca stapfli*) to the red thread disease caused by *Laetisaria fuciformis* and *Limnomyces roseipellis* (Bonos et al. 2005). An *Epichloë* endophyte that infected red fescue had stronger resistance than endophyte-free grass to a leaf spot disease caused by *Sclerotinia sclerotiorum* (Clarke et al. 2006). However, the *E. uncinatum* endophyte makes meadow ryegrass more susceptible to *T. ishikariensis*, which is considered the pathogen of winter snow mold (Wäli et al. 2006). The studies on other genera of grasses found similar results to those for *Festuca*. The resistance of perennial ryegrass and wild barley (*Hordeum brevisubulatum*) to various pathogenic fungi were also enhanced when the plants were infected by endophytes, manifesting as more biomass and higher antioxidant substance content of endophyte-infected grasses under pathogen stress (Sun 2015; Tian et al. 2008). *E. gansuensis* endophytes could enhance the resistance of drunken horse grass to powdery mildew disease caused by *Blumeria graminis*, manifesting as greater accumulation of dry matter, improved photosynthesis (Xia et al. 2015, 2016), amelioration of the osmotic adjustment substance content, and increased antioxidant substance content (Li et al. 2007b; Liu et al. 2015). Additionally, a study on Chinese wild-rye (*Leymus chinensis*) indicated that endophytes could enhance the resistance to *B. sorokiniana* and *C. lunata* of host grasses by activating a rapid defense reaction in the plants, and this advantage of E+ over E- plants could be strengthened by predrought treatment (Wang et al. 2016).

The effect of endophytes on resistance to viral diseases. *Epichloë* is an endophyte that not only can inhibit the expansion of disease caused by fungal pathogens but also has a certain resistance to viral diseases. Previous studies showed that *Epichloë* endophytes could also enhance the resistance of host grasses to viral diseases via deterrence of aphids because some of the aphids are important vectors of viral diseases (Guy and Davis 2002; Mahmood et al. 1993). Studies carried out in America and Australia found that *E. coenophialum* could deter feeding by aphids (*Rhopalosiphum padi*), and this kind of aphid is regarded as one of the most important vectors of barley yellow dwarf virus (BYDV). Therefore, the presence of endophytes decreased the incidence of BYDV in their host grass (Guy and Davis 2002; Mahmood et al. 1993). However, there was no positive or negative correlation between BYDV incidence and the infection rate of the perennial ryegrass endophyte *E. festucae* var. *lolii* (Guy 1992). This may be explained by the finding of Latch et al. (1985) that *R. padi* showed no preference for *E. festucae* var. *lolii*-infected or uninfected ryegrass, but most of the *R. padi* attempted to move from *E. coenophialum*-infected to uninfected tall fescue grasses.

How Do *Epichloë* Endophytes Help Host Grasses Tolerate Plant Disease?

There is clear evidence that a diverse group of microbes is essential for promoting their host plant's adaptation to pathogenic fungi stress (Van Wees et al. 2008). Endophytes might be critical for host plants to address the three-way interaction among plant, pathogen, and endophyte. In this section, we aim to summarize current knowledge regarding the mechanisms of action of *Epichloë* endophytes accompanied by the physical, physiological, and molecular response of grass to pathogenic fungi stress. Based on previous studies, we propose that the *Epichloë* endophyte reduces the disease incidence rate of the host grass mainly through two different ways, one of which is preventing the occurrence of disease, and the other is inhibiting the development of disease. All in all, ecological occupation and antifungal substance production might be two of the major reasons that endophytes promote the resistance of hosts to pathogenic microorganisms. During recent years, it has been assumed that there is great potential for fungal endophytes as biological control agents based on production of antifungal chemicals, mycoparasitism, or physical occupation (Pal and Gardener 2006; Rivera-Varas et al. 2007).

Preventing the occurrence of disease. *Control of pathogen transmission.* Secondary metabolites are a class of chemical compounds of considerable biological and medical importance (Jarmusch et al. 2016) and play a key role in the adaptation of plants to various environments (Bourgaud et al. 2001). Most studies of secondary metabolites of the symbioses between grass and the *Epichloë* endophytes have considered alkaloids (Ludwig-Müller 2015; Young et al. 2015). Alkaloids have been regarded as some of the toxins that cause mammalian herbivore and insect poisoning (Philippe 2016; Schardl et al. 2004; Young et al. 2013); thus, an endophyte could provide a refuge for its host grass from grazing animals and insects in grassland ecosystems by deterring mammalian herbivores and insect vectors of pathogenic fungi from feeding on it (Yao et al. 2015). In this way, the possibility of pathogens infecting the grass by mechanical wounds caused by mammalian herbivore foraging would be greatly decreased (Daleo et al. 2009). In addition, excluding mammalian herbivores and insect vectors of pathogenic fungi contributed to a decrease in the concentration of pathogenic fungi around E+ grasses (Gao and Nan 2007; Latch 1993; Nan and Li 2004), consequently reducing the risk of host plants being infected by disease pathogens (Fig. 1A). The relevant research carried out by West et al. (1990) using tall fescue has confirmed this view.

In addition to alkaloids, volatile organic compounds (VOCs) are another kind of crucial secondary metabolite in grass-endophyte symbioses that act as a defense mechanism to regulate plant resistance (Bakkali et al. 2008). They are usually substances that are relatively low in molecular weight (less than 300 Da), have strong volatility, and have organic compounds with low polarity but very high vapor pressure (Vespermann et al. 2007). VOCs, derived from plant tissues, play a crucial role in plant-insect interaction systems (Yue et al. 2001), and their types and contents are different between E+ and E- grasses (Zhang et al. 2012, 2014, 2015), especially when the grasses are infected by pathogens (Pańka et al. 2013b). Similar to alkaloids, by repelling insects, the VOCs could cut off the transmission route of pathogen spores caused by the insects visiting the host and neighboring grasses (García Parisi et al. 2014). Thereby, VOCs also indirectly reduce the possibility of host plants being infected by disease pathogens (Fig. 1A).

Occupation of ecological niches. The first step in the colonization of plants by many pathogens is the penetration of the leaf surface to grow and develop inside plant tissues. The presence of endophytes may form a defensive barrier against initial colonization of the leaf surface. Moreover, the endophyte mycelium on the leaf (epiphyllous net) may occupy space and use available nutrients, although not every species of endophyte has an epiphyllous stage (Clarke et al. 2006). Thus, potential pathogens cannot obtain nutrients and are not able to continue successful growth (Moy et al. 2000). In other words, endophytes could enhance disease resistance through competition for nutrients with pathogens and spatial niche exclusion.

When pathogens break through the physical barriers of plants, the pattern recognition receptors of plants recognize the general features of the microbial pathogens, and inducible defenses can be activated (Jones and Dangl 2006; Pel and Pieterse 2013). In consideration of the fact that *Epichloë* endophytes may be derived from biotrophic pathogens (Wang et al. 2016), it is tempting to speculate that endophytes, although usually not causing any disease effects, induce a weak resistance response or cause the host's immune system to enter a latent activation state in infected plants (Malinowski and Belesky 2000). This makes the E+ plants much more sensitive than E- plants to biotrophic pathogen invasion, and symbiotic plants can activate a defense reaction more rapidly than nonsymbiotic plants when being attacked (Pańka et al. 2013a). In other words, endophytes could enhance disease resistance through an advanced activation of the host's immune system by occupying a temporal niche.

Promotion of host grass growth. In some cases, endophytes can accelerate seedling emergence and promote plant establishment under adverse conditions and enhance plant growth and development. Furthermore, they can improve the resistance of host plants to disease (Xia et al. 2016). However, the better growth and appearance of the grasses may sometimes in turn contribute indirectly to the development

of disease (Wiewióra et al. 2015). Overall protection mediated by an endophyte has been observed in several symbioses occurring during different stages of the plant life cycle (Pérez et al. 2013, 2016; Tian et al. 2008; Vignale et al. 2013; Wäli et al. 2006; Welty et al. 1991).

Inhibiting the development of disease. Molecules and proteins. A SOLiD-SAGE quantitative transcriptome comparison of E- and *E. festucae*-infected red fescue indicated that many of the abundantly expressed fungal genes were for a secreted antifungal protein, and these genes were similar to the antifungal activity genes found in *Penicillium* and *Aspergillus* spp. This evidence suggests that these abundantly expressed genes may be involved in the disease resistance conferred to the host by the *Epichloë* endophyte (Ambrose and Belanger 2012). The second most abundantly expressed gene, *Efe-afpA*, has been shown to encode an antifungal protein, *Efe-AfpA*. This protein is abundant in host plant apoplasts, which suggests it could come into contact with invading fungal pathogens and may be a factor in the disease resistance observed in E+ red fescue. This is because the purified *Efe-AfpA* protein has shown strong inhibition of the growth of the pathogen *Sclerotinia homoeocarpa* by damaging the fungi's plasma membrane in vitro (Tian et al. 2017). In addition to *E. festucae*, *E. inebrians* is another type of *Epichloë* endophyte of the 10 with whole genome sequences available that has related antifungal protein genes (Ambrose and Belanger 2012). However, there are some other studies indicating that the presence of an endophyte would down-regulate the pathogenesis-related (PR) genes in tall fescue (Johnson et al. 2003) and perennial ryegrass (Dupont et al. 2015). However, it is important to note that this effect was observed under a normal growth environment without any pathogenic stress, and there is still no definitive proof showing that the down-regulated PR genes are directly related to lower disease resistance.

Antioxidant substances. Plants produce and accumulate reactive oxygen species (ROS) during aerobic metabolism (Apel and Hirt 2004). Under normal situations, the antioxidant production of plants would be sufficient to meet the need to scavenge these ROS. The equilibrium between ROS production and antioxidant scavenging would be perturbed when responding to various stresses, consequently increasing the possibility of cell death (Foyer and Noctor 2011; Hamilton and Bauerle 2012), and ROS production may induce a switch in the *Epichloë* endophyte from being a mutualist to being a pathogen (Eaton et al. 2011). In addition to aerobic metabolism, plants also produce and accumulate ROS following recognition of various pathogens, which is regarded as one of the earliest cellular responses for successful pathogen recognition (Auh and Murphy 1995; Grant et al. 2000). It has been reported that the presence of endophytes increased the activity of antioxidants in host grasses, further increasing the ability of the host plant to scavenge ROS resulting from abiotic stress (Fig. 1B) (Hamilton et al. 2012). The process of endophyte resistance to plant disease also manifested as the same phenomena under pathogenic stress, with the activity of antioxidant substances such as superoxide dismutase (SOD) and peroxidases (POD) in E+ perennial ryegrass being stronger than that in E- grass (Ma et al. 2015; Tian et al. 2008). E+ drunken horse grass also had a stronger active SOD and POD under powdery mildew stress than E- grass. A trial assessing disease resistance of wild barley also obtained the same results, namely, that the presence of endophytes increased the SOD and catalase (CAT) activity of the host grass under five types of pathogenic stress (Sun 2015). Another scavenger substance of ROS, proline, which can be involved in cell wall reinforcement, also increased in E+ grass under pathogen stress (Ma et al. 2015). Malondialdehyde (MDA) is a key indicator for evaluating the status of plants' redox and is one of the ultimate products of lipid

Fig. 1. Communication between symbionts and pathogens mediated by *Epichloë* endophytes. The presence of endophytes forms a defensive barrier against initial colonization of the leaf surface (A). Secondary metabolites, including volatile organic compounds (VOC) and alkaloids (ALK), and defense compounds in plant cells are induced due to pathogen infection. The secondary metabolites repel or even kill herbivores, consequently reducing the spread of insect-transmitted disease in grass. After invasion by pathogens (B), the pathogen-associated molecular patterns (PAMPs) are activated, large quantities of reactive oxygen species (ROS) are produced, and the phenylpropanoids are synthesized. The defensive compounds in the plant cell are also mobilized to resist the invasion of pathogens by eliminating all these adverse changes.

Phytohormones. The increasing production of plant hormones may also promote microbial symbiosis and an increase in stress resistance (Saikkonen et al. 2013). Salicylic acid (SA) plays a crucial role in activating plant defense responses to biotic stresses (Edgar et al. 2006; Vlot et al. 2009), and its levels are regarded as closely related to plant disease reaction. The invasion by biotrophic pathogens would primarily induce and activate the SA-dependent defenses of a plant, which would in turn be effective against biotrophic

Phenolic substances. In addition to alkaloids, endophytes induce their host grass to produce phenolic substances to improve their disease resistance. Quinate and shikimate are the precursors of aromatic amino acids and are the compounds necessary for the synthesis of the phenylpropanoids (Herrmann and Weaver 1999) that are involved in plant defense responses (Dixon 2001). Studies have shown that the

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presence of an endophyte increases quinate and shikimate content in E+ perennial ryegrass and tall fescue (Malinowski et al. 1998; Rasmussen et al. 2008), which may further result in an increase in phenylpropanoids in the host grass (Fig. 1B). However, when grasses were infected by pathogens, the production of phenylalanine, which also acts as a major aromatic acid precursor for phenylpropanoid, in E+ grass was lower than in E- grass, but the glutamine content was higher in E+ grass than in E- grass (Wang et al. 2016). Glutamine accumulation can reflect an activation of plant defense systems against pathogen infection (Forde and Lea 2007). This seems to be inconsistent with the change in phenylalanine. However, it is important to note that phenylalanine is the intermediate metabolite for phenylpropanoid metabolism, and thus when plants are attacked by pathogens, the endophyte may exact a cost by depleting the induced phenylalanine to produce other defense compounds, such as lignin (Dixon 2001; Wang et al. 2016). Lignin, as one of the important phenolic compounds, was regarded as a chemical used for reinforcement of cell walls (Farmer 1985). The research on perennial ryegrass found that the presence of an endophyte can promote the lignin production of host grass under normal conditions without pathogen stress (Qawasmeh et al. 2012; Torres et al. 2012). Lignin production was regarded as a potential protective method that barricades the pathogen from invading the plant (Funnell-Harris et al. 2010). Additionally, lignin and total phenolic content were also increased after infection by pathogens, and the content in E+ grass was still much higher than in E- grass (Fig. 1B) (Pańka et al. 2013a, b; Wang et al. 2016). This was regarded as additional strong evidence that lignin positively affected the resistance of plants to pathogens.

Other antifungal activity substances. Furthermore, Niones and Takemoto (2014) reported that endophytes produced a thermostable, low-molecular weight antifungal compound in culture, which reduced the hyphal tip growth and differentiation of the pathogen. Additionally, 17 types of secondary metabolic compounds were isolated from E+ *Elymus tangutorum* grass. One of these, cyclosporin T, strongly inhibits the growth of *A. alternata*, *B. sorokiniana*, *C. lunata*, and *F. avenaceum* in vitro (Song et al. 2015). The volatile oils obtained from E+ drunken horse grass also had a stronger inhibitory effect on pathogen growth than those produced by E- grass in vitro (Zhang et al. 2015), which indicated that volatile oils may directly enhance the pathogen resistance of host grass by inhibiting the growth of pathogens.

Conclusion and Perspectives

There are increasing numbers of researchers focusing on the resistance of the *Epichloë* endophytes to plant pathogens. The present review verified the resistance of *Epichloë* endophytes and their symbiosis with fungal pathogens or plant diseases by summarizing three types of trials, including a dual-culture test, a detached-leaves test, and an *in planta* test. However, the main results obtained from these trials are inconsistent. Therefore, a general conclusion regarding endophyte-mediated grass resistance to pathogens is difficult to formulate. Specific species of endophytes may protect their host grass from pathogenic stress under specific environmental conditions. In other words, the resistance of an *Epichloë* endophyte to a pathogen is affected by multiple factors, such as the genotypes of the *Epichloë* endophyte and host plant and environmental factors. We attempt to understand the multiple effects of *Epichloë* endophytes on plant resistance to pathogenic fungi and highlight our understanding of grass-endophyte symbiosis at the mechanistic level. Thus, further experimental research is needed to enhance our understanding of the disease resistance mechanisms. We may be able to utilize the results from manipulative experiments to identify changes in gene and metabolite levels and protein functions to develop theoretical models regarding the resistance of endophytes and symbioses to pathogens and plant diseases. We should also learn from other symbioses for which more information exists, such as plant-mycorrhizal interactions and plant-bacterial interactions. Only in this way can we learn more about the mechanisms of how endophytic fungi increase the pathogen resistance of host plants and with this beneficial knowledge, breed new disease-resistant varieties of grass using *Epichloë* endophytes in the future.

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