Endophyte-Mediated Suppression of Dollar Spot Disease in Fine Fescues

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ABSTRACT

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In 1989, a close association was found between single-plant progenies of strong creeping red fescue infected with the endophyte *Epichloë festucae* and enhanced suppression of dollar spot, a widespread foliar disease of turfgrass caused by *Sclerotinia homoeocarpa*. From this limited observation, extensive field evaluations were conducted on a wide range of fine fescue germplasm obtained throughout the United States and Europe to determine the frequency and magnitude of this association. In five field trials established between 1985 and 1991, endophyte-infected Chewings, hard, blue, and strong creeping red fescue cultivars, selections, and crosses consistently exhibited endophyte-mediated suppression of dollar spot, when compared with closely related endophyte-free entries. Endophyte-infected Chewings and hard fescue cultivars and selections also had greater turf density and supported less foliar mycelium of *S. homoeocarpa* than endophyte-free entries.

Additional keywords: defensive mutualism, *Neotyphodium*, symbiosis

Many grasses contain endophytic fungi classified in the genera *Epichloë* and *Neotyphodium* of the ascomycete family *Clavicipitaceae* (14,16,22). Endophytes in tall fescue (*Festuca arundinacea*) and perennial ryegrass (*Lolium perenne*) are responsible for causing toxic syndromes in cattle, sheep, and horses (10,16). Because of the toxicosis that develops in animals that consume endophyte-infected forage grasses, endophytes are often considered a liability in forage species. It has become clear, however, that endophytes may also confer benefits in grasses that include insect resistance (3,4,9) and increased drought tolerance (21). This has made the use of endophytes in turfgrass species an attractive alternative to external inputs used to enhance turfgrass performance (5,6,18).

Early cultural studies on endophytes have demonstrated that several endophytes produce compounds that inhibit a range of fungal pathogens of grasses (14,15,23). Tajimi (19) demonstrated that endophyte-infected timothy (*Phleum pratense*) in a

spaced-plant nursery showed less leaf spot disease caused by *Cladosporium phlei* and stem rust caused by *Puccinia graminis* when compared with endophyte-free plants. Greulich et al. (7) showed field protection of timothy from *C. phlei* when infected by the endophyte *Epichloë typhina*. Researchers at the University of Tennessee (1,8) demonstrated that endophyte-infected tall fescue seedlings had reduced disease caused by *Rhizoctonia zeae* in laboratory and greenhouse studies. However, another study by Welty et al. (20) reported no effects of endophytic infection by *Neotyphodium coenophialum* on the susceptibility of tall fescue to rust caused by *P. graminis*.

We conducted research on the possible association between endophyte infection of fine fescues and resistance to fungal diseases. In 1989, several single-plant progenies tracing their maternal origin to a strong creeping red fescue plant (*Festuca rubra* subsp. *rubra*) collected from the Rose City Cemetery in Portland, OR, showed good field resistance to dollar spot, a widespread foliar disease of turfgrasses caused by *Sclerotinia homoeocarpa*. This observation was made at the Rutgers Plant Science Research Farm in Adelphia, NJ, and was considered important because, as a group, strong creeping red fescues are generally considered to be very susceptible to dollar spot (17). Upon verifying the endophyte status of these progenies, a

close association was found between plants infected with *Epichloë festucae* and reduced dollar spot disease. From these limited observations, more extensive field evaluations were conducted on a wide range of fine fescue germplasm obtained from throughout the United States and Europe to determine the frequency of this association.

MATERIALS AND METHODS

This study was conducted on fine fescue turfgrass evaluation trials established in 1985, 1988, 1989, 1990, and 1991 at the Rutgers Plant Science Research Farm, Adelphia, NJ. Each cultivar or selection was seeded by hand in the fall of the year at a rate of 133.7 kg ha⁻¹. Plots were 1.1 × 1.7 m and were replicated at least three times in a randomized block design. The 1985 trial was maintained at a 5.1-cm mowing height and moderate fertility (107.8 kg N ha⁻¹ year⁻¹) until 1989, when fertilizer applications were discontinued. The trials established in 1988 and 1989 were maintained at a height of 4.2 cm and moderate/high fertility (107.8 kg N ha⁻¹ year⁻¹ and 151.9 kg N ha⁻¹ year⁻¹, respectively) throughout the study. The 1991 trial received 117.6 kg N ha⁻¹ year⁻¹, except in 1992, when the trial received 58.8 kg N ha⁻¹ from 15 April to 1 September. In the fall of 1992, plots were equally split into high and low fertility subplots, and the high fertility half of each plot received an additional 46.5 kg N ha⁻¹ on 2 September and 21 September 1992, respectively. Turf in this trial was maintained at a 3.8-cm mowing height. The test area consisted of a sandy loam soil. Soil pH ranged from 5.7 to 6.5. Irrigation was applied during the growing season to prevent severe drought stress. No insecticides or fungicides were used.

The endophyte status of each fine fescue cultivar, selection, or cross was determined microscopically by examining leaf sheaths of 10 randomly selected tillers per entry using the rose bengal staining method described by Saha et al. (12,13). Dollar spot severity was assessed by direct visual estimation of the proportion of foliar area showing necrosis induced by natural infestations of *S. homoeocarpa* to the nearest 1% (0–100%). The pathogen was isolated at each rating date on potato dextrose agar

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(Difco Laboratories, Detroit, MI), and its identity was confirmed microscopically and serologically through the use of immunoassays (Neogen Corp., East Lansing, MI). Turf density was determined by visually estimating the percentage of living grass swards per plot. Turf quality was assessed several times each year on a 1 to 9 scale, where 1 was poorest and 9 was equal to the best-quality turf. This assessment was based on many factors including texture, plant density, color, and damage caused by diseases. Each test was evaluated by two or more individuals to reduce subjective bias. Data were subjected to an arcsine transformation for better approximation to normal distribution prior to statistical analysis by ANOVA and the least significant difference (LSD) multiple comparisons test ($P = 0.05$).

RESULTS

In a 1985 Chewings and hard fescue field trial, an endophyte-infected (E+) Chewings fescue (*F. rubra* subsp. *fallax*) cultivar Longfellow and the progenies of six of its crosses, together with an E+ hard

fescue (*F. brevipila*) cultivar SR 3000 and the progenies of seven crosses with a similar hard fescue, showed significantly higher resistance to dollar spot in comparison with related endophyte-free (E-) entries (Table 1). The average percent turf areas exhibiting dollar spot symptoms for E+ and E- entries were 4.9 and 44.1%, respectively. The E+ entries also had a higher turf density than the E- entries, 98.4% compared with 31.4%, respectively. In the 1988 seeding of strong creeping red fescue, four selections showed significantly less damage from dollar spot disease compared with other strong creeping red fescue entries (Table 2, Fig. 1). One of these selections, Rose City, contained the endophytic fungus *E. festucae* originating from a single plant of strong creeping red fescue collected from the Rose City Cemetery, Portland, OR. The other three dollar spot resistant selections contained endophytes of the same species obtained from 'Ensylva' strong creeping red fescue and a single strong creeping red fescue plant discovered in a plot of 'Kenblue' Kentucky bluegrass seeded at Adelphia. In a 1989

seeding, which contained 12 each of the E+ and E- selections of strong creeping red fescue, the differences in dollar spot susceptibility were striking. The E- plots showed an average of 61.5% turf area damaged by dollar spot, whereas E+ plots showed only 0.3% of the turf area infected (data not shown). In the 1990 field trial, E+ plots of blue fescue (*F. ovina*), Chewings fescue, hard fescue, and strong creeping red fescue showed significantly less dollar spot than E- plots (Table 3). When comparing only E- germplasm, strong creeping red fescue cultivars and selections were consistently more susceptible to dollar spot than were the Chewings, blue, or hard fescue entries.

In a 1991 seeding of Chewings and hard fescue cultivars, E+ plots again demonstrated less dollar spot than E- plots (Table 4). E- entries had more foliar mycelium of *S. homoeocarpa* than E+ entries, 8.0% versus 0.5%, respectively. When turf was evaluated for disease on 7 October 1992, the half of each plot receiving higher nitrogen fertility (105.3 kg N ha⁻¹ year⁻¹) sustained consistently less dollar spot than the low nitrogen fertility (58.8 kg N ha⁻¹ year⁻¹) half. Within each fertility treatment, E- entries were more susceptible to dollar spot than E+ entries.

Table 1. Turf density and disease severity of endophyte-infected and endophyte-free Chewings and hard fescue cultivars, selections, and crosses to dollar spot in a field trial established September 1985 at Adelphia, NJ

Entry ^w	Endophyte ^x	Turf density ^u		Disease severity ^v	
		1991	1991	1992	
Chewings fescue					
Longfellow	E+	98.5	5.7	2.0	
Longfellow 10	E-	27.0	54.2	70.5	
LSD ($P = 0.05$)		5.6	9.1	8.1	
Longfellow ^y × Waldorf	E+	99.3	5.8	1.0	
Longfellow × Longfellow IOBC1 ^z	E+	97.7	6.5	1.2	
Longfellow × Longfellow 10	E+	96.7	6.2	1.2	
Longfellow × Jamestown	E+	95.8	7.1	1.2	
Longfellow × Shadow	E+	98.3	7.0	1.7	
Longfellow × Banner	E+	95.3	9.5	1.8	
Shadow	E-	21.7	38.8	16.7	
Jamestown	E-	21.7	41.3	45.7	
LSD ($P = 0.05$)		4.7	6.7	13.6	
Hard fescue					
SR 3000	E+	98.7	5.6	1.8	
SR 3000	E-	26.7	56.8	18.2	
LSD ($P = 0.05$)		3.7	7.7	2.8	
ST	E+	98.8	3.8	1.0	
ST × Reliant	E+	98.0	5.1	1.0	
ST × Aurora	E+	100.0	1.8	1.3	
ST × Spartan	E+	99.3	2.9	1.5	
ST × Waldina	E+	98.3	2.9	1.5	
ST × TRMR	E+	98.5	4.5	2.8	
TRMR	E-	45.0	29.2	11.0	
Reliant	E-	29.0	48.5	17.1	
Spartan	E-	31.3	38.2	18.5	
Aurora	E-	30.0	48.5	21.4	
ST	E-	40.0	40.6	25.3	
LSD ($P = 0.05$)		10.6	12.9	12.0	

^u Turf density was determined on 3 October 1991 by visually estimating the percentage of living turf per 1.1 × 1.7 m plot.

^v Disease severity was assessed as the percent turf area exhibiting foliar symptoms of dollar spot. Values are means of two and three evaluations made during the 1991 and 1992 growing seasons, respectively.

^w Entries were replicated three times except for cultivars Longfellow (E+) and SR 3000 (E+), which were replicated 15 and 12 times, respectively.

^x Endophyte status was determined microscopically by examining the leaf sheaths of 10 randomly selected tillers per entry stained with rose bengal. Endophyte-infected and endophyte-free entries are represented by E+ and E-, respectively.

^y The first component of each cross in this table was the E+ maternal parent.

^z This represents the first back cross of the F1 hybrid (Longfellow × Longfellow 10) with Longfellow 10.

Table 2. Disease severity of endophyte-infected and endophyte-free strong creeping red fescue cultivars and selections to dollar spot in a field trial established September 1988 at Adelphia, NJ

Entry	Endophyte ^y	Disease severity (%) ^z
Rose City	E+	2.0
PST 43E	E+	3.0
PST 4DD	E+	3.7
PST 4CR	E+	5.3
VDH-7	E-	20.0
VDH-6	E-	21.3
VDH-5	E-	21.3
VDH-4	E-	21.8
VDH-3	E-	22.5
PST 4RD	E-	23.3
PST 43F	E-	25.7
PST 4RE	E-	25.7
VDH-2	E-	26.3
Shademaster	E-	26.7
GS-551	E-	30.0
PST 43E	E-	35.0
PST 4C8	E-	35.0
PST 4NI	E-	35.0
VDH-1	E-	37.5
ZPS 5101	E-	42.5
LSRS	E-	50.0
DS-88	E-	53.3
GW-87	E-	55.0
LSD ($P = 0.05$)		14.1

^y Endophyte status was determined microscopically by examining the leaf sheaths of 10 randomly selected tillers per entry stained with rose bengal. Endophyte-infected and endophyte-free entries are represented by E+ and E-, respectively.

^z Disease severity was assessed as the percent turf area exhibiting foliar symptoms of dollar spot. Values are means of three replicates evaluated on 5 September 1991.

Fig. 1. Strong creeping red fescue selections with and without endophyte. Endophyte-free plot on right shows substantial damage due to dollar spot, whereas endophyte-containing selection on left shows minimal dollar spot damage.

Table 3. Turf quality and disease severity in blue, Chewings, hard, and strong creeping red fescue cultivars and selections (with and without endophyte) established September 1990 in a field trial at Adelphia, NJ

Entry ^z	Endophyte ^z	Turf quality ^y			Disease severity ^x		
		1991	1992	1993	7-24 1992	10-8 1992	9-17 1993
Blue fescue							
SR 3200	E+	5.4	5.7	4.9	1.7	8.7	16.7
SRX 3210	E+	5.3	5.4	4.5	0.0	6.7	21.3
SR 3200	E-	5.2	5.1	4.5	1.7	51.7	32.3
SRX 3210	E-	4.7	4.3	4.4	1.7	46.7	45.0
Chewings fescue							
SR 5100	E+	6.4	6.5	6.4	0.0	1.3	7.0
Banner II	E+	5.6	6.0	4.9	0.0	1.0	9.3
Jamestown II	E+	5.6	5.9	5.3	0.0	1.0	13.7
Banner	E-	5.0	5.0	5.1	0.0	10.0	16.7
Jamestown	E-	4.7	4.9	4.7	0.0	14.7	27.0
SR 5100	E-	6.6	6.9	6.1	1.7	5.3	27.7
Longfellow	E-	5.6	5.7	5.2	0.0	44.3	41.3
Hard fescue							
4HD-90 PST	E+	6.2	6.5	5.9	0.0	2.7	7.0
Nordic	E-	6.0	6.1	6.0	1.7	23.3	32.3
Reliant	E-	5.4	5.8	5.0	0.0	30.0	40.3
Aurora	E-	5.2	5.2	4.8	3.3	38.3	54.0
Strong creeping red fescue							
Syn 4SS	E+	5.7	5.2	5.6	3.3	1.7	11.3
4R3-90 PST	E+	5.5	5.4	4.9	1.7	8.0	13.7
Boreal	E-	3.3	3.7	2.9	32.0	75.0	53.7
Salem	E-	3.7	3.0	3.3	88.0	75.0	59.0
Jasper	E-	4.4	4.5	3.3	92.0	61.7	63.3
Vista	E-	3.9	3.7	3.1	92.0	73.3	68.0
Flyer	E-	3.8	3.8	3.0	95.0	51.7	73.0
Shademaster	E-	3.8	3.7	3.2	97.0	58.3	83.0
LSD ($P = 0.05$)		0.6	1.1	0.7	16.3	24.1	18.4

^x Disease severity was assessed as the percent turf area exhibiting foliar symptoms of dollar spot. Values are means of two and three evaluations made during the 1992 and 1993 growing seasons, respectively. Entries were replicated three times.

^y Turf quality was determined using a visual rating scale of 1 to 9, where 9 is the best quality turf. Values are annual means of multiple evaluations conducted throughout the 1991, 1992, and 1993 growing seasons.

^z Endophyte status was determined microscopically by examining the leaf sheaths of 10 randomly selected tillers per entry stained with rose bengal. Endophyte-infected and endophyte-free entries are represented by E+ and E-, respectively.

The average annual turf quality ratings for E+ and E- cultivars and selections for all trials in the study were similar until 1991, when substantial damage from dollar

spot was observed (Tables 3 and 4). From 1991 to 1993, turf quality ratings for E+ cultivars and selections within the hard and strong creeping red fescues were generally

greater than those of E- entries. However, turf quality ratings for E+ and E- cultivars and selections of blue and Chewings fescues during this period were generally similar.

DISCUSSION

Dollar spot is an important disease of both cool- and warm-season turf. Infections are typically initiated in late spring, summer, and autumn. Once infection foci are established, they are persistent and the disease may redevelop at those sites season after season. Dollar spot is usually controlled with the use of nitrogen fertilizers and fungicide applications throughout the growing season (17). The discovery in the current study that endophytes provide a high degree of suppression of dollar spot in several fine fescue species is important, since the cost of controlling this disease could be reduced considerably through use of endophyte-infected turf. A recent study by Bonos et al. (2) has shown that endophytes in fine fescues increase resistance to red thread disease caused by *Laetisaria fuciformis*. Previous laboratory and greenhouse studies have suggested the potential for enhanced disease resistance in endophyte-infected grasses (8,19,23). Our findings of suppression of dollar spot disease and the results indicating resistance to red thread disease show the potential of endophytes as a strategy for controlling fungus diseases in turfgrasses under field conditions.

The benefits associated with endophytes in grasses are frequently observed only when grasses are grown under certain biological and/or environmental stresses. Intensive cultivation, mowing, low fertility, drought, heat stress, and heavy insect herbivory constitute stresses where the effects of endophytes on plants often become apparent. In some instances, years may pass before significant benefits are noticed. Therefore, it is understandable that some studies (20) may have failed to demonstrate endophyte-mediated improvements in disease suppression, since these grasses were not maintained in the field under the stresses of intensive turf management.

The fine fescues are outcrossing species showing high variation between and within natural populations. The E+ and E- entries that we have employed in these studies are not clones. Thus, host variation is expected to be a consideration in evaluating the source of suppression to dollar spot. However, many of the E+ and E- varieties share parental lines so they are closely related. Some E+ and E- cultivars, including SR 3000 and SR 5100, were developed from the same parental population by selecting for or against the endophyte; otherwise, the two breeding lines are genetically similar. Longfellow hard fescue was developed as a high endophyte containing variety, whereas Longfellow E- was selected from this variety after the loss of endophyte

Table 4. Turf quality, foliar mycelia of *Sclerotinia homoeocarpa*, and dollar spot severity in Chewings and hard fescue cultivars (with and without endophyte) maintained under two nitrogen regimes in a field trial established September 1991 at Adelphia, NJ

Entry ^w	Endophyte ^x	Turf quality ^y	Foliar mycelium ^z	Disease severity ^v		
				Low fertility		High fertility
				10-3	10-7	10-7
Chewings fescue						
Jamestown II '89**	E-	5.6	9.7	11.4	16.3	2.0
Jamestown II '90**	E-	5.6	8.7	9.9	15.6	1.5
Jamestown II '91**	E+	5.2	1.4	0.6	0.3	0.1
LSD (<i>P</i> = 0.05)		0.2	4.5	4.0	7.3	1.4
SR 5000	E+	6.2	0.0	0.3	0.3	0.0
SR 5000	E-	6.1	7.1	14.3	11.6	2.9
SR 5100	E+	6.4	0.0	0.1	0.1	0.0
SR 5100	E-	6.8	5.1	5.7	4.7	1.3
LSD (<i>P</i> = 0.05)		0.3	3.9	5.8	4.4	1.4
Hard fescue						
Reliant M801-CF8*	E+	5.3	1.3	0.4	2.4	0.2
Reliant J09-1**	E-	5.9	8.5	6.7	9.0	2.0
Reliant*	E+	5.4	0.8	0.7	1.5	0.2
LSD (<i>P</i> = 0.05)		0.3	2.6	3.4	3.3	1.1
SR 3000	E+	6.3	0.3	1.3	0.6	0.0
SR 3000	E-	4.4	8.3	9.1	6.7	2.1
SR 3000	E-	4.1	8.3	8.6	5.9	1.9
SR 3100	E-	7.2	7.9	8.3	5.4	1.3
SR 3100	E+	7.4	0.0	0.4	0.1	0.0
LSD (<i>P</i> = 0.05)		0.6	2.4	4.3	4.2	1.5

^v Disease severity was assessed in 1992 as the percentage of turf area exhibiting foliar symptoms of dollar spot. Turf received 58.8 kg N ha⁻¹ from 15 April to 1 September 1992. Plots were then equally split into high- and low-fertility subplots, and the high fertility half of each plot received an additional 46.5 kg N ha⁻¹ on 2 September and 21 September 1992, respectively.

^w Entries were replicated seven times unless identified by an ($n = 10$) or ($n = 20$).

^x Endophyte status was determined microscopically by examining the leaf sheaths of 10 randomly selected tillers per entry stained with rose bengal. Endophyte-infected and endophyte-free entries are represented by E+ and E-, respectively.

^y Turf quality was determined using a visual rating scale of 1 to 9, where 9 = the best quality turf. Values are annual means of multiple evaluations conducted throughout the 1992 growing season.

^z Represents a visual estimate of the percentage of turf foliage covered with the mycelium of *S. homoeocarpa* per plot on 28 September 1992.

viability during seed storage. Although the studies reported here involve diverse varieties and lineages of fine fescues obtained from throughout the United States and Europe, in every comparison to E- turf, the E+ turf showed suppression of dollar spot. It is also interesting to note the uniform abundance of dollar spot mycelium on E- plots compared with the near absence of mycelium on E+ plots, indicating that *E. festucae* was responsible for the disease suppression.

The mechanism of disease resistance in E+ fine fescues is not known and presumably is more complicated than insect resistance. It is widely accepted that alkaloids in E+ plants play a major role in either preventing insects from feeding on grass plants or have an antibiosis effect on the insect pest (9). The mechanism of disease resistance in E+ plants may be due to the presence of similar or related endophyte-produced alkaloids, new compounds, or phytoalexins produced by plants in response to endophyte infection. Alternatively, Moy et al. (11) proposed that a network of epiphyllous mycelium on the surface of leaf blades of many infected fine fescues may exclude pathogens by preventing colonization of grasses by poten-

tial pathogens. Interestingly, perennial ryegrasses possessing the endophyte *Neotyphodium lolii* do not have a comparable epiphyllous stage, and dollar spot suppression was not observed in numerous field trials of E+ and E- perennial ryegrass at our Adelphia research station. To further evaluate endophyte-enhanced disease suppression, we plan to continue observations on grasses with respect to disease incidence and the presence of endophytes in various grass species. We also intend to evaluate the mechanism of enhanced resistance to fungal pathogens so that endophytes may be screened in vitro for their ability to suppress turfgrass diseases. Endophyte strains that show strong disease-suppressive potential will then be used in our turfgrass breeding program to improve turfgrass performance in the field.

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