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Phytoparasitic Nematode Populations in *Festuca arundinacea* Field Plots in Southwestern Missouri[1]

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Abstract: Field plots of tall fescue (*Festuca arundinacea*) at two locations on the same experimental farm in southwestern Missouri were sampled (one in 1987–88, the other in 1988–89) to inventory root-parasitic nematodes and to determine whether cultivars or endophyte (*Acremonium coenophialum*) infection frequencies (EIF) affected nematode population densities within single growing seasons. Plots were planted with seven tall fescue cultivars: Kentucky-31, Kenhy, Johnstone, Martin, Mozark, Missouri-96, and Forager. Kentucky-31 seed with high and low EIF were planted in separate plots. Plant-parasitic nematodes were extracted from soil samples, identified to genus, and enumerated four and three times per year for the 1987–1988 and 1988–1989 studies, respectively. Several plant-parasitic genera were identified from both fields, including *Helicotylenchus, Heterodera, Hoplolaimus, Paratylenchus, Pratylenchus, Tylenchorhynchus,* and members of genera grouped in the family Tylenchidae. Densities of five of these seven groups of nematodes differed among tall fescue cultivars in the 1987–88 study, but only two out of eight groups did so in the 1988–89 study. Irrespective of tall fescue cultivar, EIF had no consistent impact on nematode densities. The putative suppressive effect of endophyte infection on infection by plant-parasitic nematodes is not detectable within single growing seasons and deserves long-term study in field situations.

Key words: Acremonium coenophialum, endophyte, *Festuca arundinacea, Helicotylenchus, Heterodera, Hoplolaimus,* nematode, *Paratylenchus, Pratylenchus,* tall fescue, *Tylenchorhynchus,* Tylenchidae.

Tall fescue (*Festuca arundinacea*), grown on more than 14 million ha, is the predominant cool-season pasture grass in the Eastern United States (4). Despite its popularity as a forage, a major disadvantage exists: cattle grazing tall fescue may develop a set of disorders known collectively as tall fescue toxicosis (22). This toxicosis is caused by an endophytic fungus (*Acremonium coenophialum*) that produces toxic alkaloids in infected plants (2). Tall fescue toxicosis results in annual beef cattle losses of ca. $560 million in reduced calf numbers and ca. $233 million in reduced weaning weights (8).

Although the use of endophyte-free (E−) tall fescue cultivars improves animal health and performance (22), some E− cultivars exhibit decreased insect resistance (13,20). A similar negative effect of endophyte infection on various species of root-parasitic nematodes in tall fescue has also been documented. Numbers of *Helicotylenchus* spp., which are common in southeastern tall fescue pastures, were at least 66% lower in endophyte-infected (E+) tall fescue than in E− (17). Fewer *Helicotylenchus dihystera* and *Paratrichodorus minor* were recovered from E+ 'Kentucky-31' tall fescue than from E− (18). The presence of *A. coenophialum* significantly reduced *Meloidogyne graminis* reproduction in one of four E+ and E− tall fescue clone pairs. Kimmons et al. (10) found that reproduction rates of the endoparasites *Pratylenchus scribneri* and *M. marylandi* were significantly lower on E+ than on E− tall fescue; however, the reproduction of the ectoparasite *H. pseudorobustus* was not affected.

In an Arkansas field trial, West et al. (23) investigated the effects of endophyte infection and irrigation level on tall fescue growth, drought tolerance, and native phytoparasitic nematode populations. Where water deficits occurred, forage yield and leaf area were lower in E− compared with E+ Kentucky-31 tall fescue plots. Numbers of *P. scribneri* and *Tylenchorhynchus acutus* were significantly higher in the E− than in the E+ Kentucky-31 plots. The endophyte apparently conferred drought tolerance to infected Kentucky-31

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tall fescue, an effect that was partially attributable to enhanced nematode resistance.

Few field studies of the effect of E+ tall fescue on phytoparasitic nematodes have been published, and little was known about plant-parasitic nematodes in Missouri tall fescue. Our objectives were: i) to identify the root-parasitic nematodes in experimental tall fescue field plots and ii) to determine whether cultivars or endophyte infection affected nematode population densities.

Materials and Methods

Two field trials of the same set of seven cultivars of tall fescue were established at the University of Missouri Hugo Wurdack Farm located in Crawford and Dent Counties in southwestern Missouri. The first trial was planted in October 1987 and sampled 26 May, 28 July, and 24 September 1988, and 9 May 1989. The second trial was planted in September 1988 and sampled 24 May and 27 September 1989, and 28 June 1990. The 1987–88 trial was located on a Typic Albuqualf soil with a chert layer at a depth of approximately 0.35 m. The 1988–89 trial was located on a Typic Fluvaquent, for which soil particle analyses were conducted for all plots by the pipette extraction method (7).

For both trials, tall fescue was drilled in rows spaced 15.2 cm apart at a seeding rate of 33.6 kg/ha into the residue of 'Pioneer 877F' forage sorghum, *Sorghum bicolor*. Both fields had been continuous Kentucky-31 tall fescue pastures for approximately 25 years before initiation of the study. Site preparation included a spring application of paraquat at a rate of 0.55 kg a.i./ha, a summer competition crop of forage sorghum, and an additional fall application of paraquat (0.55 kg a.i./ha) one day before planting (14). The seven tall fescue cultivars planted at each site were Kentucky-31 (with high or low levels of endophyte infection according to seed labels, thus called Kentucky-31-high and Kentucky-31-low), Kenhy, Johnstone, Martin, Mozark, Missouri-96, and Forager. The latter six cultivars were labeled E−. Separate seed stocks of the seven cultivars were planted in the two sites. For both trials, the presence of *A. coenophialum* in plants was determined by Bacon's method (1). The endophyte infection frequency (EIF) (6) was the percentage frequency of hyphal detection in 10 arbitrarily selected tillers from each plot sampled in August 1988 and September 1989 for the 1987–88 and 1988–89 tests, respectively.

The experimental design for each trial was a split-plot with three replications. Main plots were the eight tall fescue plantings, assigned arbitrarily to sites within the experimental location. Sub-plots were insecticide treatments for a simultaneous study of insect densities, but these treatments had no effect on nematode densities (according to subsequent data analysis) and will not be discussed further. The 1987–88 trial comprised 144 plots (8 tall fescue cultivar main plots × 6 insecticide-treated subplots × 3 replications), with each plot measuring 4.9 m × 7.3 m. The 1988–89 trial comprised 120 plots (8 main plots × 5 subplots × 3 replications), each plot measuring 4.9 m × 4.9 m.

For soil nematode extraction, approximately 20 soil-root cores were collected from the plant rows with a 2.5-cm-d soil probe to a depth of 10–15 cm (16,23). Cores were thoroughly mixed, and a 100-cm^3 subsample was removed for extraction. The nematodes collected during the first three 1987–88 sampling dates were extracted by a modified sieving–sugar flotation–centrifugation method (9), and those collected on the last 1987–88 sampling date and during the 1988–89 study were extracted by elutriation (5) followed by sugar flotation–centrifugation. Because extraction efficiencies were comparable for both methods in our laboratory (ca. 45% for *Heterodera glycines* juveniles), nematode data were not adjusted for extraction efficiency. Population densities were expressed as the number of vermiform nematodes per 100 cm^3 soil. Plant-parasitic nematodes were identified to genus, with the exception of the Tylenchidae, many of which are considered to be facultative fungivores due to their weak stylets, although some are known to be plant-parasitic (12).

Nematode densities were transformed to $\log_{10}(n + 1)$ to reduce correlations between means and variances; transformed data were subjected to analysis of variance. In addition, because the split plot experimental design sacrifices precision in comparing main-plot treatments, analysis of covariance was employed to reduce experimental error by controlling the variance of cultivar means (21). The sources of covariance were EIF for both trials, and the soil particle data (percentages sand, silt, and clay) from the 1988–89 trial.

Mean comparisons were made using the Waller-Duncan k-ratio *t*-test (with a k-ratio of 100, approximately equivalent to $\alpha = 0.05$) when treatments were significant in ANOVA ($P < 0.05$). Single-degree-of-freedom comparisons were constructed to investigate the tall fescue cultivar main effect on the number of nematodes. All statistical analyses were performed with SAS Version 5.0 (SAS Institute, Cary, NC).

Results

A variety of genera of root-parasitic nematodes were identified in both trials, including *Heterodera, Hoplolaimus, Paratylenchus, Pratylenchus,* and *Tylenchorhynchus. Paratylenchus* individuals were counted as either stylet-bearing (adult females, second- and third-stage juveniles) or non-stylet-bearing (adult males and fourth-stage juveniles). The most numerous nematodes were Tylenchidae. In the 1988–89 trial only, *Helicotylenchus* were recovered frequently enough for data analysis. Genera identified infrequently were *Meloidogyne, Paratrichodorus, Tylencholaimellus,* and *Xiphinema.* Three to seven genera (in addition to Tylenchidae) were identified in each plot, with densities ranging from 9–792 total nematodes per 100 cm^3 soil. Because nematode densities did not differ according to sampling dates and variances in nematode densities due to sampling date were homogeneous, data were pooled over sampling dates for analysis of cultivar effects (Table 1). Averages were low for genera other than Tylenchidae. The split-plot ANOVA model explained variability in nematode densities well in most cases (Table 1).

The pre-planned single-degree-of-freedom comparison between Kentucky 31-high and all others for detection of an endophyte effect of nematode densities was insufficient for the 1987–88 trial because staining and microscopic examination of tall fescue leaf sheaths for the presence of *A. coenophialum* showed that many of the E− cultivar plots had detectable levels of infection (Table 2). Thus, for the 1987–88 trial, cultivars with <10% EIF were compared with Kentucky 31-high and Kentucky 31-low (>10% EIF) in addition to the pre-planned comparison (Table 3).

In the 1987–88 trial, tall fescue cultivar had a significant effect on the densities of *Hoplolaimus,* non- and stylet-bearing *Paratylenchus,* Tylenchidae, and *Tylenchorhynchus* (Table 1); however, according to single-degree-of-freedom comparisons (Table 3,C_1 and C_2), the cultivar effect was not related to EIF for the densities of *Tylenchorhynchus,* Tylenchidae, and stylet-bearing *Paratylenchus.* Kentucky-31-high and -low, when compared with the <10% EIF cultivars, had significantly higher densities of non-stylet bearing *Paratylenchus* (Tables 1,3). The contrast of Kentucky-31-high vs. all other cultivars (Table 3,C_2) confirmed that Kentucky-31-high had significantly higher densities of *Hoplolaimus* (Tables 1,3).

In the 1988–89 trial, data were subjected to analysis of covariance to decrease experimental error in cultivar (main plot) comparisons. The covariants were the soil particle data (percentages of sand, silt, and clay) and EIF. The EIF covariant had a significant effect on the numbers of *Helicotylenchus* with all three sampling dates combined. The percentage silt covariant had a significant effect on *Hoplolaimus* den-

TABLE 1. Fescue cultivar effects on soil densities of plant-parasitic nematodes in two different tall fescue (*Festuca arundinacea*) field plots in southwestern Missouri in 1987–88 and 1988–89.

Source of variation	*Helicotylenchus*	*Heterodera*	*Hoplolaimus*	Non-stylet-bearing *Paratylenchus*	Stylet-bearing *Paratylenchus*	*Pratylenchus*	Tylenchidae	*Tylenchorhynchus*
				1987–88				
				$P > F$†				
Model	—	0.0017	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Cultivar	—	0.0803	0.0016	0.0006	0.0101	0.0688	0.0076	0.0189
				Number of nematodes per 100 cm³ soil‡				
Forager	—	3	2 cd	1 d	1 c	<1	196 abc	1 c
Johnstone	—	4	2 bc	2 cd	2 c	0	242 abc	6 bc
Kenhy	—	6	2 cd	1 d	2 c	<1	289 ab	6 bc
Ky-31-high	—	7	6 a	18 a	3 c	<1	153 c	9 ab
Ky-31-low	—	7	<1 d	19 a	9 ab	0	198 abc	4 abc
Martin	—	3	<1 d	10 bc	11 ab	<1	307 a	4 abc
Mo-96	—	4	1 cd	12 ab	12 a	<1	294 ab	1 c
Mozark	—	6	5 ab	9 bc	10 ab	0	141 c	11 a
				1988–89				
				$P > F$†				
Model	0.0001	0.6919	0.0001	0.0002	0.0001	0.0129	0.0037	0.0001
Cultivar	0.1184	0.0144	0.3506	0.0001	0.1148	0.2154	0.2413	0.2757
				Number of nematodes per 100 cm³ soil‡				
Forager	3	2	4	15 b	3	<1	233	6
Johnstone	60	3	2	7 cd	2	<1	319	5
Kenhy	<1	5	3	11 bc	2	<1	176	4
Ky-31-high	23	8	3	4 d	1	<1	332	1
Ky-31-low	6	1	3	24 a	5	0	301	2
Martin	1	4	2	28 a	6	0	159	5
Mo-96	24	4	3	7 c	<1	<1	246	2
Mozark	23	3	1	5 c	1	<1	246	2

† Values are probabilities that variation in soil densities of each nematode were significantly affected by cultivar and the general linear model used in ANOVA. The statistical model was based on the split-plot experimental design with cultivars as main plots, with all sampling dates combined (n = 574 and 358, respectively, for 1987–88 and 1988–89).

‡ Values are antilogs. Data analysis and mean comparisons were performed on data transformed to $\log_{10}(n + 1)$ values. Means followed by the same letter are not significantly different according to the Waller-Duncan k-ratio t-test (k = 100). Apparent discrepancies are due to data conversion and rounding.

TABLE 2. Percentage endophyte (*Acremonium coenophialum*) infection frequency of tall fescue (*Festuca arundinacea*) cultivars grown in field trials in southwestern Missouri in 1987–88 and 1988–89.

Cultivar	EIF† 1987–88	EIF† 1988–89
Kentucky-31-high‡	57	73
Kentucky-31-low‡	30	7
Johnstone	0	0
Mozark	3	0
Martin	5	0
Forager	1	0
Kenhy	1	0
Missouri-96	9	0

† EIF = percentage frequency of hyphal detection in fescue tillers (n = 48/cultivar in the 1987–88 trial; n = 24/cultivar in the 1988–89 trial).

‡ "High" and "low" refer to whether the seedlots were labelled endophyte-infected or endophyte-free, respectively.

sities with all sampling dates combined. Cultivars had a significant impact on the densities only of non-stylet-bearing *Paratylenchus;* the ANOVA model did not explain variability in *Heterodera* densities (Table 1). Comparison of Kentucky-31-high with all other cultivars (Table 3,C_3) confirmed that densities of non-stylet-bearing *Paratylenchus* were significantly lower on Kentucky-31-high (Table 1).

DISCUSSION

We identified several genera of phytoparasitic nematodes in Missouri tall fescue pastures, including *Heterodera, Hoplolaimus, Meloidogyne, Paratrichodorus, Paratylenchus, Pratylenchus, Tylenchorhynchus,* and *Xiphinema.* The most numerous nematodes were Tylenchidae of undetermined genera. Their frequent occurrence, occasionally at high densities, suggests that their relationship with tall fescue should be investigated further.

In the present study, there was no consistent evidence that any of the three E+ Kentucky-31 tall fescue EIF (30, 57, or 73%) suppressed phytoparasitic nematode numbers compared with the essentially E− cultivars, although tall fescue cultivars (irrespective of endophyte infection) differed in their effects on phytonematode densities. For example, densities of non-

TABLE 3. Single-degree-of-freedom comparisons of tall fescue (*Festuca arundinacea*) cultivars for effects on plant-parasitic nematode population densities in 1987–88 and 1988–89 field trials in southwestern Missouri.

	P > F							
Comparison†	*Helicotylenchus*	*Heterodera*	*Hoplolaimus*	Non-stylet-bearing *Paratylenchus*	Stylet-bearing *Paratylenchus*	*Pratylenchus*	Tylenchidae	*Tylenchorhynchus*
C_1	—	0.2922	0.3711	0.0018	0.2602	0.5794	0.4423	0.1244
C_2	—	0.0166	0.0014	0.7260	0.5598	0.6156	0.3143	0.0957
C_3	0.9245	0.0209	0.4388	0.0030	0.1428	0.9950	0.1959	0.9077

Values are probabilities that variation in soil densities of each nematode group was significantly affected by cultivar. Data from all sampling dates were combined, n = 574 and 358, respectively, for 1987–88 and 1988–89.

† C_1 = cultivars with >10% endophyte infection frequency (EIF) vs. cultivars with <10% EIF in 1987–88 trial; C_2 = Kentucky-31-high (high EIF) vs. other cultivars (low EIF) in 1987–88 trial; C_3 = Kentucky-31-high vs. other cultivars in 1988–89 trial.

stylet-bearing *Paratylenchus* in the 1987–88 trial were higher in Kentucky-31-high (57% EIF) plots and Kentucky-31-low (30% EIF) plots than in plots with the six cultivars with <10% EIF, whereas densities in the 1988–89 trial were lower in Kentucky-31-high (73% EIF) plots than in those with the seven essentially E− cultivars. The mechanisms involved in nematode sensitivity to E+ tall fescue have not been elucidated and could be quite complex. Kimmons et al. (10) proposed that variations among nematode genera with respect to response to E+ tall fescue could relate to the degree of endoparasitism of the nematode because endoparasites would be subjected to higher doses of toxic alkaloids for longer periods. We could not test this hypothesis because the methods used were not adequate for endoparasitic nematode populations, but we did note that the cultivar effect was significant (with all sampling dates of the 1987–88 trial combined) for all the ectoparasites, whereas neither *Heterodera* nor *Pratylenchus* was significantly affected.

There could be several reasons for the inconsistent effects we observed of tall fescue endophyte infection on nematode densities. One obvious reason is that tall fescue cultivars represented main plots that, in a split-plot design, could have masked cultivar effects, because edaphic factors influence the reproduction and migration of many plant-parasitic nematodes (15). We attempted to account for this limitation through analysis of covariance. In this analysis, densities of *Hoplolaimus,* the largest nematode consistently found in our study, were significantly affected by percentage silt, but covariance analysis did not reveal any relationships undetected in the initial analysis. Second, population density changes are difficult to examine when densities are low. In an Arkansas field study (23), soil population counts of *Pratylenchus scribneri* (224/100 cm^3 soil) and *Tylenchorhynchus acutus* (306/100 cm^3 soil) in E− Kentucky-31 tall fescue were high. In our study, densities of individual genera were low and could not be easily grouped together for analysis due to varied feeding sites and behaviors (except for the Tylenchidae). Residual effects from either the 25-year monoculture of presumably E+ tall fescue in our experimental fields (if the endophyte had a suppressive effect) or the intervening sorghum crop could explain low densities. Third, tall fescue is a perennial, thus trials of several years' duration will be required to characterize any effect of host endophyte infection status on plant-parasitic nematodes.

Studies of fescue–phytoparasitic nematode interactions will be affected by variation within tall fescue cultivars. One such as Kentucky-31 contains a range of genotypes that promotes adaptability to various environmental conditions independently of endophyte status (3). Another level of complexity is added if interaction between tall fescue genotype and endophyte isolate affects nematode parasitism (11). Conversely, nematode parasitism may affect the tall fescue–*Acremonium* relationship (19). Like mycorrhizal relationships, endophyte associations are complex, and generalizations regarding the effect of E+ tall fescue on nematode response are not yet possible. This assertion is particularly valid when applied to field experiments, where the complexity of the interaction is amplified in an uncontrolled environment. Clearly, these relationships deserve long-term research in the field.

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