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Interactions Among *Pratylenchus penetrans, P. scribneri,* and *Verticillium dahliae* in the Potato Early Dying Disease Complex

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Abstract: Microplots were infested with combinations of the fungus *Verticillium dahliae* and *Pratylenchus penetrans* and *P. scribneri* to test for individual and combined effects of these organisms on potato yield and nematode reproduction. *Verticillium dahliae* alone caused yield losses in all 3 years of the experiment, and the interaction between *P. penetrans* and *V. dahliae* was significant ($P \leq 0.05$) in 2 years. *Pratylenchus penetrans* alone caused yield losses in 2 years and *P. scribneri* alone caused yield losses in 1 year. No two-way or three-way interaction was found involving *P. scribneri.* In 1987, reproduction for low densities of *P. penetrans* was 5 times higher when *P. scribneri* was also present than when it was absent, and 3.5 times higher in 1988. In nematode species mixtures, reproduction of *P. scribneri* was decreased by *V. dahliae* in 1987–88. The final population density of *P. scribneri* was negatively affected by *V. dahliae* and positively related to the initial proportion of *P. scribneri* to *P. penetrans.* In species mixtures with proportions of *P. penetrans* ranging from 0.1 to 0.5, reproduction of *P. penetrans* was negatively affected by *V. dahliae* and decreased linearly in relation to the increase in the initial proportion of *P. penetrans* in both years. The final population density of *P. penetrans* was affected only by *V. dahliae.*

Key words: interaction, lesion nematode, nematode, potato early dying, *Pratylenchus penetrans, P. scribneri, Verticillium dahliae.*

Synergistic yield losses in potato due to the combined effects of the fungus *Verticillium dahliae* Kleb. and the lesion nematode, *Pratylenchus penetrans* (Cobb) Filipjev & Schuur. Stekh., have been characterized using microplot studies (13,14,19,26). Commercial potato fields in the northeastern United States and in Canada are infested with a mixture of *Pratylenchus* spp. (2,11,24). Most abundant in Ohio are *P. penetrans, P. scribneri* (Steiner), and *P. crenatus* (Loof) (2). Microplot studies were performed with each of these *Pratylenchus* species in two-way combinations with *V. dahliae* over 2 years. A definitive interaction occurred only 1 year between *P. penetrans* and *V. dahliae* (18). Other studies failed to detect an interaction with respect to yield losses or symptom development between *P. penetrans* and *V. dahliae* (3,9). Environmental factors such as temperature and soil moisture may limit expression of the interaction (8,25). It is important to test for a *V. dahliae*–nematode interaction over a number of different growing seasons before concluding whether or not an interaction occurs.

Interaction among nematode species may be measured in terms of both nematode reproduction rates and the plant response. Interspecific nematode interactions have been studied with *Pratylenchus* spp. and *Meloidogyne* spp., and in some instances there is a reduction in reproduction or final population densities for each species when both are introduced to a plant, as compared with single-species inoculations (4,6). However, Gay and Bird (10) found an increase in the population densities of *P. brachyurus* when inoculated with *M. arenaria* or *M. incognita* on cotton, although this phenomenon was not seen when tomato, alfalfa, or tobacco was used as the host. Johnson and Nusbaum (12) found a range of responses when tobacco cultivars were inoculated with *M. incognita, M. hapla,* and *P. brachyurus,* including depression of *M. incognita* reproduction in one case, and lower reproduction of *M. hapla* in five of eight cases. Effects on reproduction of *P. brachyurus* were also highly variable. *Tylenchorhynchus agri* and *M. naasi* did not affect reproduction of *P. penetrans,* nor did *P. penetrans* reduce the

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reproduction of *T. agri* (21). While various studies have demonstrated that potato is a good host for *P. penetrans* (1,5,7,16), the population increase of *P. penetrans* may be quite different in the presence of another species with similar feeding habits and a higher rate of reproduction as is the case for *P. scribneri* (18).

Our objective in this study was to determine if a mixture of *P. scribneri* and *V. dahliae* or *P. scribneri* + *V. dahliae* + *P. penetrans* would react synergistically to cause increased yield losses in potato, or if their interaction would affect reproduction of *P. penetrans* and *P. scribneri.*

Materials and Methods

Microplot studies were done in 1986–88 at the Ohio Agricultural Research and Development Center Muck Crops Branch at Celeryville, Ohio. The soil used in the experiments was a Rifle Peat, an euic Typic Borohemists soil (15% silt, 1% fine sand, 9% clay, 75% O.M.; pH 5.4). Details for soil fumigation, soil infestation, and procedures for establishing microplots have been published (19).

Nematode inoculum was produced on alfalfa (*Medicago sativa* L. cv. P545, Pioneer Hi-Bred International, Johnston, IA) callus in monoxenic cultures (17). The contents of the alfalfa callus tubes were removed, blended for ½ second, added to autoclaved Rifle Peat soil (64 tubes/10-liter soil), and gently mixed by hand. After 48 hours, nematodes were extracted from 100-cm^3 subsamples using the pie-pan technique (22) to quantify the inoculum. Appropriate volumes of nematode inoculum were added to 20 liters of fumigated soil in a twin-shell mixer and flipped 10 times. A 100-cm^3 subsample was taken after mixing each 20-liter batch to recheck the nematode population density, and the infested soil was added to appropriate microplots.

Inoculum for *V. dahliae* was produced by growing fungus in the dark at 20–24 C for 6 weeks on minimal medium overlaid with sterile cellophane. Microsclerotia were rubbed from the cellophane and blended for 30 seconds in water. The mixture was poured through nested 230- and 37-μm-pore sieves. The material on the sieve with smaller pore openings was washed repeatedly until few fragments of mycelia and conidia remained. The final suspension (1.5 liters) was slowly added to soil that had been oven dried and passed through an 860-μm mesh sieve. The inoculum was mixed for 0.5 hours in a twin-shell mixer and quantified by dilution plating onto an alcohol-based medium selective for *Verticillium* (15). Soil for the experiment was infested with *V. dahliae* by adding the inoculum to 30 liters of soil in a cement mixer and mixing for 5 minutes.

Treatment combinations used each year are listed in Table 1. Each treatment was replicated 15 times, and a single-eye piece from the potato (*Solanum tuberosum* L.) cv. Superior was planted in each microplot. Total weight of the tubers in a microplot at harvest was defined as the yield. Final nematode population density was estimated from soil samples consisting of four cores taken near the base of the plant at harvest. Nematodes were extracted from 100-cm^3 subsamples of soil over a period

Table 1. Preplant densities of *Verticillium dahliae* (VD), *Pratylenchus penetrans* (PP), and *P. scribneri* (PS) in microplot experiments.

1986			1987			1988		
VD†	PP‡	PS‡	VD	PP	PS	VD	PP	PS
0	0	0	0	0	0	0	0	0
0	10	0	0	0	10	0	0	9
0	50	0	0	0	40	0	0	30
0	0	10	0	4	36	0	3	27
0	0	50	0	10	0	0	9	21
0	10	10	0	10	30	0	9	0
10	0	0	0	20	20	0	15	15
10	10	0	0	40	0	0	30	0
10	50	0	50	0	0	100	0	0
10	0	10	50	0	10	100	0	9
10	0	50	50	0	40	100	0	30
10	10	10	50	4	36	100	3	27
			50	10	0	100	9	21
			50	10	30	100	9	0
			50	20	20	100	15	15
			50	40	0	100	30	0

† Microsclerotia density per cm^3 soil.
‡ Nematodes per 100-cm^3 soil.

of 24 hours using pie pans. The nematodes from each sample were heat relaxed by adding boiling water (1:1 v/v) to each suspension, allowed to cool, and fixed in an equal volume of 10% formalin. Adult *Pratylenchus* was identified to species level and used to estimate the relative percentage of each species at harvest per soil sample. For treatments with mixtures of two *Pratylenchus* spp. and without *V. dahliae,* the ranges of nematodes in 1987 identified for a given plot were 5 to 27, 2 to 26, and 1 to 27 for plots with an initial *P. penetrans* density of 4, 10, and 20 nematodes/100 cm^3 soil, respectively. The mean numbers of specimens examined for these treatments in 1987 were 15, 14, and 11 for plots with an initial *P. penetrans* density of 4, 10, and 20 nematodes/100 cm^3 soil, respectively. With the same nematode density combinations in 1987, but in the presence of *V. dahliae,* the ranges of specimen numbers examined were 5 to 25, 2 to 17, and 4 to 22, respectively. The mean numbers of specimens examined for these treatments were 13, 10, and 11, for initial *P. penetrans* initial densities of 4, 10, and 20 nematodes/100 cm^3 soil, respectively. In 1988, the mean number of specimens examined ranged from 15 to 20 specimens per microplot for the high *P. penetrans* density with *V. dahliae* and 11 to 20 specimens for all other treatments. Nematode identification was based on presence or absence of sperm and number of lip annules.

The yield data were evaluated by analysis of variance (GLM) and regression (RSREG) procedures of SAS (20). Because the experiment was unbalanced, Type IV sums of squares were used for *F*-tests in analysis of variance. The RSREG procedure builds linear and quadratic response-surface regression models for the independent variables (densities of *V. dahliae* [VD], *P. penetrans* [PP], *P. scribneri* [PS]), including interaction terms. Each year's data were subjected to analysis separately.

The population densities for *P. penetrans* and *P. scribneri* at harvest were estimated from the relative percentage of each of the species at harvest and the total *Pratylenchus* count. The dependent terms of interest were reproduction of *P. penetrans* (Rpp) and *P. scribneri* (Rps), and the final population density of *P. penetrans* (PPf) and *P. scribneri* (PSf). Reproduction was calculated by dividing the final population density by the initial population density. Because the experimental design was unbalanced, treatments were separated into two groups and subjected to analysis separately. In group one, Rpp was the dependent variable. The treatments listed below were included in this analysis: 1987: 1) VD = 0, PP = 10, PS = 0; and 2) VD = 0, PP = 10, PS = 30; and 1988: 1) VD = 0, PP = 9, PS = 0; 2) VD = 0, PP = 0, PS = 21; 3) VD = 100, PP = 9, PS = 0; and 4) VD = 100, PP = 9, PS = 21, where VD units are microsclerotia per cm^3 soil and the nematode units are vermiforms per 100 cm^3 soil. This analysis was used to test the effect of presence or absence of *P. scribneri* on the rate of reproduction and final population density of *P. penetrans.* In the second group, the effect of various mixtures of the two nematode species was examined, plus or minus *V. dahliae* on Rpp, Prs, PPf, and PSf. The relative proportion of each nematode preplant density to the total preplant nematode population density, *V. dahliae* (VD), and their interaction were the independent terms in analysis of variance (GLM, with type IV sum of squares). In 1987 and 1988, there were three treatments with different proportions of the two nematode species, in which the total preplant nematode population densities summed to 40/100-cm^3 soil in 1987 and 30/100-cm^3 soil in 1988. Any treatments where the total preplant nematode density did not sum to 40 or 30/100-cm^3 soil were removed from the analysis. If the interaction between nematode proportion and *V. dahliae* was significant ($P = 0.05$), then linear regression was used to estimate the slope with and without *V. dahliae.*

Results

Yield losses were affected by *V. dahliae* alone in all 3 years, and the interaction between *V. dahliae* and *P. penetrans* preplant densities in 2 years, (P = 0.05), based on analysis of variance (Table 2). In 1986 and 1988, the interaction (VD × PP) was demonstrated by fitting a nonlinear model to the VD × PP treatments, while a linear model was fitted to the *P. penetrans* treatments (Fig. 1A,C). In 1987, when there was no VD × PP interaction, a linear model was fitted to the VD × PP treatment, with a slope similar to that fitted to the *P. penetrans*-alone treatment (Fig. 1B). No interaction between *P. scribneri* and *V. dahliae* occurred (Table 2). *Pratylenchus scribneri* alone caused yield losses in 1988 (Fig. 1C), and *P. penetrans* caused yield losses in 1986 and 1988 (Fig. 1A,C; Table 2). There was a nematode–nematode interaction in 1988 (Table 2), but the impact on yield was small (Fig. 1C).

In 1987, reproduction of *P. penetrans* was five times higher in the presence of *P. scribneri* (Rpp = 14.1) than in its absence (Rpp = 2.8), with an initial *P. penetrans* density of 10, and in the absence of *V. dahliae* (Tables 3 and 4). *Verticillium dahliae,* proportion of *P. penetrans* in mixtures of both nematode species (Table 3), and their interaction (P = 0.01) affected Rpp. The reproduction of *P. penetrans* was reduced when *V. dahliae* was present, or when the proportion of *P. penetrans* increased and *P. scribneri* decreased. The interaction occurred because Rpp decreased linearly as the proportion of *P. penetrans* increased from 0.1 to 0.5, with a rate of −31.9 (SE = 8.5) per percentage of *P. penetrans* in the absence of *V. dahliae* and −13.2 (SE = 4.9) in the presence of the fungus.

In 1988, reproduction of *P. penetrans* with an initial density of 9 nematodes/100-cm^3 soil was 3.5 times higher in the presence of *P. scribneri* (Rpp = 14) than in its absence (Rpp = 4) and five times higher in the presence of both *P. scribneri* and *V. dahliae* (Rpp = 5) than in the absence of *P. scribneri* (Rpp = 1) (Tables 3 and 4). The reproduction of *P. penetrans* was affected negatively by the presence of *V. dahliae* (P = 0.04), and positively as the initial proportion of *P. scribneri* increased (P = 0.02). Unlike 1987, there was no interaction between these two factors in 1988. Mean Rpp was 11.5 (SE = 2.0) in the absence of *V. dahliae* and 7.3 (SE = 1.7) in the presence of the fungus. The rate of decrease of Rpp for each percentage that was increased *P. penetrans* was −18.0 (SE = 3.6).

The final population density of *P. penetrans* (PPf) when present in mixtures with *P. scribneri* was negatively affected by *Verticillium dahliae* in both 1987 and 1988. Changes in the ratio of *P. penetrans* to *P. scribneri* had no affect on PPf. The mean PPf was 111 (SE = 14) and 29 (SE = 5) nematodes/100 cm^3 soil in the absence and presence, respectively, of *V. dahliae* in 1987. In 1988, mean PPf was 98 (SE = 13) and 45 (SE = 7) nematodes/100 cm^3

TABLE 2. Comparison of the effects of *Verticillium dahliae* (VD†), *Pratylenchus penetrans* (PP‡), and *P. scribneri* (PS‡) on yield of potato.

1986			1987			1988		
Source	Prob. >F	R^2	Source	Prob. >F	R^2	Source	Prob. >F	R^2
VD	0.00	0.42	VD	0.00	0.36	VD	0.00	0.60
PP	0.00		PP	0.55		PP	0.00	
PS	0.37		PS	0.29		PS	0.00	
VD × PP	0.00		VD × PP	0.87		VD × PP	0.00	
VD × PS	0.17		VD × PS	0.80		VD × PS	0.76	
PP × PS	0.62		PP × PS	0.55		PS × PS‖	0.00	
VD × PP × PS	0.31					PP × PS	0.00	

† Preplant microsclerotia density per cm^3 soil.
‡ Preplant nematode density per 100-cm^3 soil.
‖ PS × PS represents the significant fit of a quadratic model describing yield loss as a function of *P. scribneri* and *P. scribneri* × *P. scribneri*.

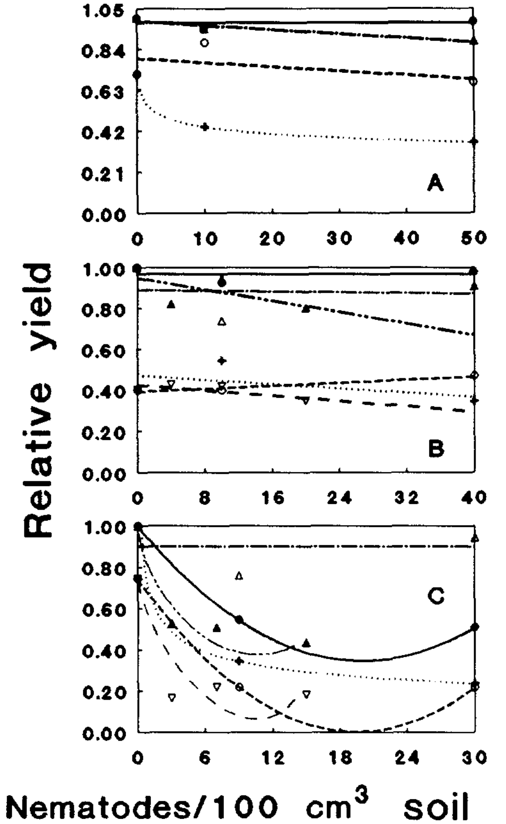

FIG. 1. Relative yield (RY) of potato as affected by *Verticillium dahliae* (VD), *Pratylenchus penetrans* (PP), *P. scribneri* (PS), and their two-way (VD × PP, VD × PS, PP × PS [±VD]) interactions. Linear models (RY = $a + b$(PP)) were fitted to PP (-··-) in all 3 years and VD × PP (······) in 1987, where a and b were estimated parameters. Power models (RY = $a(PP^b)$) were fitted to VD × PP (······) in 1986 and 1988. Linear models were fitted to PS (___) and VD × PS (- - - -) in 1986 and 1987. Quadratic models (RY = $a + b$(PS) + $c(PS^2)$), where c is a parameter to be estimated, were fitted to PS (___) and VD × PS (- - - -) in 1988. Linear models were fitted to PP × PS with VD (- - - -) and PP × PS without VD (—··—··) in 1987, while quadratic models where fitted to PP × PS with VD (- - - -) in 1988. 1A) 1986; 1B) 1987; and 1C) 1988.

soil in the absence and presence, respectively, of *V. dahliae.*

The final population density of *P. scribneri* (PSf) in 1987 was negatively affected by *V. dahliae* and the decrease in the relative proportion of *P. scribneri* to *P. penetrans* (Table 3). The interaction between *V. dahliae* and the initial ratio of *P. scribneri* to *P. penetrans* was significant in 1987, which resulted in a greater increase in population density for *P. scribneri* (while present in mixtures with *P. penetrans*) in the absence of *V. dahliae* than in the presence of the fungus. A rate parameter, estimated using linear regression to predict final population density of *P. scribneri* from the initial proportion of *P. scribneri* to *P. penetrans,* was 1,719 (SE = 442) when *V. dahliae* was absent and 360 (SE = 94) when *V. dahliae* was present. This means that for each percentage that *P. scribneri* increases initially in the relative proportion of the two nematode species, the final population of *P. scribneri* will be 17 or 3.6 nematodes higher, in the absence and presence of *V. dahliae,* respectively. In 1988, the final population density of *P. scribneri* was negatively affected by *V. dahliae* and positively affected by the initial proportion of *P. scribneri.* The rate of increase in the final population of *P. scribneri* was 525 (SE = 157) per initial percentage of *P. scribneri.* In 1987 and 1988, reproduction by *P. scribneri* was affected only by *V. dahliae.* Mean reproduction was 30.7 (SE = 2.3) in the absence of the fungus and 7.0 (SE = 1.0) in its presence, in 1987, and 21.4 (SE = 1.9) and 11.1 (SE = 1.1) in 1988, in the absence and presence, respectively, of *V. dahliae.*

Discussion

Commercial potato fields in Ohio often contain *Pratylenchus* spp., such as *P. scribneri* and *P. penetrans* (2). The synergistic interaction between *V. dahliae* and *P. penetrans* with respect to yield losses has/been described (13,14,19). However, the influence of *P. scribneri* in a mixture with *P. penetrans* on yield losses and *Pratylenchus* spp. reproduction was not known.

In 3 years, no interaction was found between *V. dahliae* and *P. scribneri,* although conditions were conducive for the interaction between *V. dahliae* and *P. penetrans* in 2 of those 3 years. There was no reduction in the final density of *P. penetrans* that could be related to *P. scribneri;* in fact, there was an increase in the net reproduction of *P. penetrans* with increasing proportions of *P.*

TABLE 3. Effects of the relative proportions (Prop) of the preplant densities of *Pratylenchus scribneri* (PS) to *P. penetrans* (PP†) and *Verticillium dahliae* (VD) on the final population density and rate of reproduction (R) of each *Pratylenchus* species on potato.

	1987					1988				
VD	Prop	PS_f‡	PP_f‖	RPS*	RPP§	Prop	PS_f	PP_f	RPS	RPP
0	0.90	1371	119	24	26	0.90	646	78	24	6
+	0.90	237	28	7	7	0.90	377	52	14	17
0	0.75	825	141	28	14	0.70	464	122	22	14
+	0.75	170	31	6	3	0.70	192	43	9	5
0	0.50	489	82	24	4	0.50	278	70	19	5
+	0.50	144	29	7	1	0.50	176	48	12	3

† Nematodes per 100-cm^3 soil.
‡ Population density of PS at harvest per 100-cm^3 soil.
‖ Population density of PP at harvest per 100-cm^3 soil.
* Rate of reproduction of PS calculated as PS_f/PS.
§ Rate of reproduction of PP calculated as PP_f/PP.

scribneri both in the absence and presence of *V. dahliae*. These results are based on the assumption that the relative proportions of *P. penetrans* and *P. scribneri* adults were similar for the juvenile stages as well. If the proportions of the adults were not representative of the juvenile stages, then errors in estimation of reproduction would result.

Gay and Bird (10) found that simultaneous inoculations with *P. brachyurus* and either *Meloidogyne incognita* or *M. arenaria* resulted in an increase in the population of the lesion nematode on cotton. This phenomenon, however, depended on the host species used. No explanation was given for the increase in *P. brachyurus*, just as we cannot explain the increase in *P. penetrans* in our study. One hypothesis is that the early infection by *P. penetrans* may stunt growth of the root system as compared to *P. scribneri*. Mixed-species inoculation, therefore, may permit better growth and, ultimately, a higher equilibrium density for *P. penetrans*. The densities at harvest for both nematode species were lower when *V. dahliae* was present, as would be expected when earlier plant death occurred, and as was observed in earlier studies (18).

The net reproduction of *P. scribneri* in this study was approximately 11 times higher than for *P. penetrans* in single pathogen inoculations, which also corroborates previous work with these nematodes in single-species inoculations of potato and other hosts (18,23). It was surprising, given the high reproductive potential of *P. scribneri*, that competition appeared to favor *P. penetrans*. This finding suggests that reproductive potential is not the primary attribute determine the competitive ability of *Pratylenchus* spp. infecting potato.

Pratylenchus penetrans is the key nematode species in potato early dying. It would be advantageous to devise a rotation that decreases the population of *P. penetrans* below the threshold necessary to interact with *V. dahliae*. Other lesion nematode species (*P. crenatus*, *P. scribneri*) may have competitive attributes that displace populations of *P. penetrans* during the rotation crop. This paper produces evidence that

TABLE 4. Influence of initial population density of *Verticillium dahliae* (VD), *Pratylenchus penetrans* (PP), and *P. scribneri* (PS) on harvest population density (Pf) and reproduction (R) of the *Pratylenchus* species.

	1987				1988			
VD†	PP‡	PS‡	Pf	R‖	PP	PS	Pf	R
0	10	0	28	3	9	0	35	4
50	10	0	—	—	9	0	13	1
0	40	0	80	2	30	0	111	4
50	40	0	—	—	30	0	31	1
0	0	10	499	50	0	9	225	25
50	0	10	119	12	0	9	73	8
0	0	40	1,231	31	0	30	629	21
50	0	40	344	9	0	30	307	10

† Microsclerotia/cm^3 soil.
‡ Nematode density/100-cm^3 soil.
‖ Pf per initial population density.

reproduction of *P. penetrans* can be affected by another species of lesion nematode. However, the effect was to increase the final population of *P. penetrans*. It would be beneficial to find a rotation crop that, combined with *P. scribneri* or *P. crenatus*, would reduce population density of *P. penetrans*.

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