

## Differential Interactions of *Pratylenchus crenatus*, *P. penetrans*, and *P. scribneri* with *Verticillium dahliae* in Potato Early Dying Disease

R. M. Riedel, R. C. Rowe, and M. J. Martin

Professors, Department of Plant Pathology, The Ohio State University (OSU), Columbus 43210, and Ohio Agricultural Research and Development Center (OARDC), Wooster 44691, and research biologist, Agricultural Chemicals Department, E. I. du Pont de Nemours & Co., Inc., P.O. Box 30, Newark, DE 19714.

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### ABSTRACT

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The interaction of *Verticillium dahliae* with *Pratylenchus crenatus*, *P. penetrans*, and *P. scribneri* in plants of potato cultivar Superior was tested in field microplots established on fumigated organic soil. Interactions of lesion nematodes and *V. dahliae* in potato early dying (PED) disease varied with nematode species. In 1982 and 1983, the highest tested population levels of *P. penetrans* and *V. dahliae* reduced tuber fresh weight 20 and 39%,

respectively, and caused severe PED symptoms. *P. crenatus* did not interact with *V. dahliae* in either year of the tests. In 1982, *P. scribneri* did not interact with the fungus, but in 1983, this species and *V. dahliae* at high population levels caused PED symptoms and lowered tuber yield. The interaction of *P. scribneri* and *V. dahliae* in 1983 was correlated with high temperature stress during tuberization.

Early dying disease of potato (*Solanum tuberosum* L.) is a significant factor limiting potato production in the United States. Yield reductions of 11,900 kg/ha (107 cwt/A) have been documented for the susceptible cultivar Superior in Ohio (21). Similar losses have been reported from Long Island, NY (4,23). It has been suggested (22) that several fungi and bacteria, alone or interacting with plant pathogenic nematodes, cause potato early dying (PED).

Martin et al (17), working in microplots, established that PED could result from a synergistic interaction of *Pratylenchus penetrans* [(Cobb) Filipjev & Schuur. Stekh.] and *Verticillium dahliae* (Kleb.) at population levels commonly found in Ohio soils (3,25). Lesion nematode populations in potato soils are seldom monospecific, however. In Ohio, *P. penetrans*, *P. crenatus* (Loof), and *P. scribneri* (Steiner) commonly coexist and, less frequently, they may occur with *P. allenii* (Ferris), *P. thornei* (Sher & Allen), and *P. neglectus* [(Rensch) Filipjev & Schuurmans Stekh.] which are not common species in potato soils (3,4). *P. penetrans* and *P. crenatus* occurred commonly, and *P. neglectus*, *P. thornei*, and *P. vulnus* less frequently, in a Wisconsin survey (7). In a survey of potato soil on Prince Edward Island (13), *P. penetrans*, though predominant, was commonly associated with *P. crenatus* in potato soil (13).

The potential of species other than *P. penetrans* to interact with *V. dahliae* in PED is unknown. This paper reports comparative microplot studies on the interactions of *P. crenatus*, *P. penetrans*, and *P. scribneri* with *V. dahliae* on potato.

### MATERIALS AND METHODS

These studies were done in 1982 and 1983 at the OARDC Muck Crops Branch in north central Ohio (Huron County) in a fine-

textured, organic soil (Rifle peat; 15% silt, 1% fine sand, 9% clay, 75% OM, pH 5.4). The basic replicate in each test was a single, unglazed clay drain tile (25 cm i.d. × 30 cm long) containing a single potato plant cultivar Superior. Tiles were set vertically to plow depth (25 cm) and extended 5 cm above the soil line. Commercial plant spacing of 25 cm in the row and 75 cm between rows was maintained by planting between tiles and establishing guard rows. Each treatment consisted of 15 replicate microplots completely randomized with other treatments among three rows in the field. *Pratylenchus* species were tested in separate blocks to prevent mixing. Planting and harvest dates were 25 May and 25 August 1982 and 26 May and 30 August 1983, respectively. Standard fungicides and non-nematicidal insecticides were applied during both growing seasons to minimize variables caused by other pests. Overhead irrigation provided plants a minimum of 2.5 cm of water per week. Plot soil was preplant fumigated with 465 kg/ha Terro-O-Gas 67® (67% methyl bromide + 31% chloropicrin; Great Lakes Chemical Co., West Lafayette, IN).

Experimental design was a completely randomized factorial with two factors, population levels of *Verticillium* and *Pratylenchus*. After analysis of variance, contrasts of the means were used to evaluate the change in each variable (i.e., yield) with increasing numbers of the populations.

**Seed potato and inoculum production.** Single-eye seed pieces were produced from rooted cuttings of cultivar Superior grown to maturity in steam-disinfested soil in a greenhouse in the winter preceding planting. Rooted cuttings were obtained from pathogen-free tissue cultures (22). *P. penetrans* from W. F. Mai, Plant Pathology Department, Cornell University, Ithaca, NY, and *P. scribneri* and *P. crenatus* (originally from cultivar Superior potato roots from Seneca County and Columbiana County, OH, respectively) were cultured monoxenically on alfalfa callus (*Medicago sativa* L.) according to previously described techniques (16). *V. dahliae* was obtained from laboratory cultures as previously described (22).

Plot establishment, maintenance, and harvest, as well as nematode extraction, have been described previously (16,22). Nematodes in 100-cm<sup>3</sup> soil samples taken after infestation of soil at the time of plot establishment were extracted at 23 C in 1982 and at

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14 C in 1983 because of a mechanical failure. Nematodes were extracted at 23 C from 100-cm<sup>3</sup> soil samples from each microplot taken at harvest in both seasons. Adult and juvenile *Pratylenchus* were counted for each sample in two 5-ml aliquots of stirred, 100-cm<sup>3</sup> suspension containing extracted nematodes.

## RESULTS

Initial populations of nematodes in infested test soils in 1982 and 1983 are given in Table 1. Effects of individual and combined populations of nematodes and *Verticillium* on foliar symptoms and tuber yield are reported in Tables 2 and 3. Each matrix reports results of increasing populations of *Verticillium* from left to right and increasing populations of *Pratylenchus* from top to bottom.

In 1982 and 1983, high population levels of *P. penetrans* and *V. dahliae* in combination resulted in significantly ( $P \leq 0.05$ ) increased symptom expression (Table 2). The highest combined levels also reduced tuber weight 20 and 39%, respectively (Table 3). Either organism alone at tested levels had no significant ( $P \leq 0.05$ ) effect on symptom expression or tuber yield.

In 1982, *P. scribneri* and *P. crenatus*, alone or in combination with *V. dahliae*, had no significant ( $P \leq 0.05$ ) effect on tuber yield or

symptom expression (Tables 2 and 3). In 1983, *P. crenatus*, again, did not interact with *V. dahliae*, but the combination of *P. scribneri* and *V. dahliae* did cause significant ( $P \leq 0.05$ ) PED symptom development (Table 2). Significant ( $P \leq 0.05$ ) yield decreases also occurred as nematode population levels increased (Tables 3).

All three species of *Pratylenchus* reproduced well on potato (Table 4). In terms of maximum populations developed 13 wk after inoculation, *P. crenatus* reproduced least and *P. scribneri* most in both years of the test. Final populations of *P. penetrans* were significantly ( $P \leq 0.01$ ) lower in both years when fungus and nematode combinations caused severe PED symptom development. Final populations of *P. scribneri* were significantly ( $P \leq 0.01$ ) depressed in 1983 when this species and *V. dahliae* interacted to produce PED symptoms (Table 3).

## DISCUSSION

In both years of these tests, the interaction of *P. penetrans* with *V. dahliae* was similar to that described previously (16,22); that is, population levels of nematode and fungus, which alone had little effect, together caused typical symptoms of PED and associated yield reductions.

Data from our studies with *P. crenatus* and *P. scribneri* indicate that the interaction of *Verticillium* and lesion nematode in PED is dependent on the species of *Pratylenchus* involved. Mueller (20) previously reported a similar interaction between *Pratylenchus* and *V. albo-atrum* in balsam (*Impatiens balsamina* L.). He found that *P. penetrans* and *P. vulnus* combinations with *V. albo-atrum* produced wilt, but *P. crenatus*, *P. thornei*, and *P. fallax* combinations did not.

Work previous to ours suggests that nematode species interactions with *V. dahliae* may differ in natural cropping conditions. Field populations of *P. thornei* and occurrence of *Verticillium* wilt of potato were positively correlated in Israel (14,24); and, in Idaho, populations of *P. neglectus* in roots were negatively correlated with *Verticillium* wilt of potato (6). While correlations may indicate differences in interactions of

TABLE 1. Initial population levels<sup>a</sup> of *Pratylenchus* spp. in infested soil in microplots

Population levels	<i>P. penetrans</i>		<i>P. crenatus</i>		<i>P. scribneri</i>	
	1982	1983	1982	1983	1982	1983
Low	23	12	6	10	25	8
Medium	79	15	20	8	47	18
High	249	70	65	20	154	40
LSD ( $P = 0.05$ )	47	32	16	18	46	17

<sup>a</sup> Values are means of 15 soil samples collected immediately following mixing expressed as vermiforms per 100 cm<sup>3</sup> soil. Nematodes were extracted from 100 cm<sup>3</sup> soil samples processed on modified Baermann funnels for 24 hr at 20–23 C in 1982 and, because of mechanical problems, at 14 C in 1983.

TABLE 2. Effects of combined population levels of *Verticillium dahliae* and three *Pratylenchus* species on symptom expression in potato grown in field microplots in Rifle Peat soils in two seasons.

	1982 <i>V. dahliae</i> <sup>a</sup>				P <sup>c</sup>	1983 <i>V. dahliae</i>				P
	0	1	2 <sup>b</sup>	P		0	1	2	P	
<i>P. crenatus</i>	0	0.5 <sup>d</sup>	0.8	0.6	0.78	0	1.3	0.9	0.8	0.15
	1	0.6	0.9	0.2	0.80	1	0.7	0.9	1.0	0.50
	2	0.5	0.7	0.7	0.62	2	0.7	0.9	0.9	0.72
	3 <sup>e</sup>	0.3	0.9	0.9	0.02	3	1.1	1.1	1.4	0.55
P <sup>c</sup>	0.31	0.94	0.23		P	0.64	0.74	0.18		
<i>P. penetrans</i>	0	0.5	0.8	1.1	0.45	0	0.7	1.2	1.0	0.65
	1	0.6	1.4	1.8	0.01	1	0.9	1.5	2.2	0.00
	2	0.5	0.7	1.9	0.01	2	1.0	2.3	2.5	0.00
	3	0.7	1.7	2.4	0.01	3	1.1	2.9	2.8	0.00
P	0.51	0.09	0.01		P	0.25	0.00	0.00		
<i>P. scribneri</i>	0	0.7	0.5	0.7	0.76	0	0.5	0.7	1.6	0.00
	1	0.7	0.5	0.2	0.02	1	0.9	1.1	0.9	0.86
	2	0.9	0.5	0.5	0.15	2	0.8	1.3	2.1	0.00
	3	0.9	0.5	0.6	0.66	3	0.9	2.4	2.5	0.00
P	0.55	0.69	0.84		P	0.64	0.00	0.01		

- <sup>a</sup> Each matrix reports results of increasing *V. dahliae* populations from left to right and increasing *P. penetrans* populations from top to bottom.  
<sup>b</sup> Population levels of *Verticillium dahliae* added to soil at planting: 0=none; 1=ca. 10 propagules per 10 g soil; 2=ca. 100 propagules per 10 g soil.  
<sup>c</sup> Population levels of *Pratylenchus* species added to soil at planting: 0=none; 1=low; 2=medium; 3=high (for exact figures see Table 1).  
<sup>d</sup> Each figure represents the average of 15 microplot plants evaluated visually 90 days after planting on a scale of 0=no visible symptoms; 1=some chlorosis, especially in older leaves; 2=general chlorosis coupled with some necrosis and wilting; 3=severe wilting or death.  
<sup>e</sup> P denotes linear trend significance level, based on contrasts of the data means, for the change in a variable with increasing population levels of one pathogen at a constant population level of the other.

*Pratylenchus* species with *Verticillium* in potato, they also may indicate only differential ability of these species to reproduce in infected potato. In the present work, for example, populations of *P. penetrans* and *P. scribneri* were suppressed when nematode-fungus

combinations caused PED symptom development. Martin et al (17) also reported suppression of *P. penetrans* when PED occurred as a result of interactions with *Verticillium*. Therefore, final populations of these two species would be negatively correlated

TABLE 3. Effects of combined population levels of *Verticillium dahliae* and three *Pratylenchus* species on potato tuber yield in field microplots in Rifle Peat soil in two seasons.

1982					1983						
<i>V. dahliae</i>					<i>V. dahliae</i>						
	0	1	2 <sup>b</sup>	P <sup>c</sup>		0	1	2	P		
<i>P. crenatus</i>	0	608 <sup>d</sup>	862	959	0.01	<i>P. crenatus</i>	0	326	467	385	0.31
	1	764	917	968	0.04		1	426	382	438	0.88
	2	817	847	936	0.30		2	330	447	476	0.04
	3 <sup>c</sup>	749	891	787	0.72		3	297	478	393	0.15
	P <sup>c</sup>	0.09	0.98	0.10			P	0.60	0.60	0.77	
<i>P. penetrans</i>	0	821	941	848	0.76	<i>P. penetrans</i>	0	413	345	350	0.67
	1	878	767	714	0.11		1	365	275	238	0.03
	2	871	824	550	0.01		2	453	240	269	0.01
	3	899	697	659	0.04		3	334	164	252	0.14
	P	0.50	0.05	0.01			P	0.52	0.00	0.10	
<i>P. scribneri</i>	0	610	817	815	0.04	<i>P. scribneri</i>	0	425	394	337	0.16
	1	703	766	784	0.57		1	303	409	555	0.62
	2	596	856	844	0.02		2	388	369	321	0.22
	3	736	780	756	0.82		3	264	344	244	0.20
	P	0.24	0.93	0.75			P	0.06	0.25	0.03	

<sup>a</sup> Each matrix reports results of increasing *V. dahliae* populations from left to right and increasing *P. penetrans* populations from top to bottom.  
<sup>b</sup> Population levels of *Verticillium dahliae* added to soil at planting: 0=none; 1=ca. 10 propagules per 10 g soil; 2=ca. 100 propagules per 10 g soil.  
<sup>c</sup> Population levels of *Pratylenchus* species added to soil at planting: 0=none; 1=low; 2=medium; 3=high (for exact figures see Table 1).  
<sup>d</sup> Each figure represents the average yield in grams per plant of 15 microplot plants at harvest 90 days after planting.  
<sup>e</sup> P denotes linear trend significance level, based on contrasts of the data means, for the change in a variable with increasing population levels of one pathogen at a constant population level of the other.

TABLE 4. Final soil population levels of *Pratylenchus* species in microplots 90 days after inoculation with various initial population levels of *Pratylenchus* species and *Verticillium dahliae* and planting to potato.

1982 <sup>a</sup>					1983						
<i>V. dahliae</i>					<i>V. dahliae</i>						
	0	1	2 <sup>b</sup>	P <sup>c</sup>		0	1	2	P		
<i>P. crenatus</i>	0	3 <sup>d</sup>	0	0	<i>P. crenatus</i>	0	11	0	0		
	1	36	50	17		0.17	1	21	36	138	0.00
	2	119	141	117		0.97	2	95	179	40	0.01
	3 <sup>c</sup>	212	243	207		0.92	3	226	112	204	0.62
	P <sup>c</sup>	0.01	0.01	0.01			P	0.00	0.01	0.09	
<i>P. penetrans</i>	0	0	0	0	<i>P. penetrans</i>	0	33	0	0		
	1	233	197	133		0.01	1	145	101	124	0.58
	2	616	488	293		0.01	2	276	284	44	0.01
	3	1227	1185	327		0.01	3	529	95	225	0.00
	P	0.01	0.01	0.01			P	0.00	0.94	0.01	
<i>P. scribneri</i>	0	18	0	0	<i>P. scribneri</i>	0	67	0	0		
	1	259	692	416		0.29	1	1897	2803	4603	0.00
	2	719	712	585		0.26	2	1999	7794	1032	0.63
	3	2343	1281	1304		0.17	3	5175	1255	1123	0.00
	P	0.01	0.01	0.01			P	0.00	0.67	0.00	

<sup>a</sup> Each matrix reports results of increasing *V. dahliae* populations from left to right and increasing *P. penetrans* populations from top to bottom.  
<sup>b</sup> Population levels of *Verticillium dahliae* added to soil at planting: 0=none; 1=ca. 10 propagules per 10 g soil; 2=ca. 100 propagules per 10 g soil.  
<sup>c</sup> Population levels of *Pratylenchus* species added to soil at planting: 0=none; 1=low; 2=medium; 3=high (for exact figures see Table 1).  
<sup>d</sup> Each figure represents the average of 15 replicates determined from 100-cm<sup>3</sup> soil samples extracted for 24 hr at 23 C by the Baerman funnel technique. Nematodes were counted in two, 5-ml aliquots per 100 cm<sup>3</sup> of stirred suspension containing nematodes extracted from each sample.  
<sup>e</sup> P denotes linear trend significance level, based on contrasts of the data means, for the change in a variable with increasing population levels of one pathogen at a constant population level of the other.

with PED symptoms. Conroy et al (5) also found significant decreases in populations of *P. penetrans* in *Verticillium*-infected tomatoes. Elsewhere, populations of *P. penetrans* are reported to increase in tomato and eggplant (19), and in elm and sugar maple (8), infected by *Verticillium*. Reproduction of *P. neglectus* (= *minyus*) in mint infected by *Verticillium* (10,12), *P. brachyurus* in cotton infected by *Verticillium* (26), and *P. thornei* in potato infected by *Verticillium* (24) also increased. Because of this variability in reproduction, interactions of *Pratylenchus* spp. with *Verticillium* in potato are best evaluated in controlled experiments testing effects of pathogen combinations on yield.

Absolute nematode numbers beyond initial threshold levels apparently have little influence on fungus-nematode interactions in PED, since *P. penetrans*, the most interactive of the species tested, was intermediate between *P. crenatus* and *P. scribneri* in reproduction rates and final population levels. Potato as a host also had little effect on the fecundity of *P. crenatus*, *P. penetrans*, and *P. scribneri* compared to reproduction in alfalfa callus. Alves de Lima (2) found 3-, 6-, and 113-fold increases in populations of *P. crenatus*, *P. penetrans*, and *P. scribneri*, respectively, in 13 wk at 23 C on alfalfa callus. Order of fecundity was the same in both years of our tests and very similar to that of reproduction on callus under controlled conditions. Data in 1983 came very close to these figures and to those of Martin et al (16).

In studies with *P. penetrans*, we have shown that yield reductions due to PED seem to be correlated with high temperature stress (22). High temperature may also have significantly affected the species-dependent reactions with *Verticillium* observed in this study. In 1982 tests, neither *P. crenatus* nor *P. scribneri* interacted with *V. dahliae*, but *P. scribneri* did interact with it in 1983. In contrast to the below-average temperatures of the 1982 season, in 1983, temperatures were substantially above normal with 15 consecutive days exceeding 32 C (22). Although neither species is as interactive with *V. dahliae* as is *P. penetrans*, *P. scribneri* may be a factor in PED if the plants are also stressed by other factors.

While the mechanisms of interaction between lesion nematodes and *Verticillium* in disease complexes are obscure, these data and split-root tests done by Faulkner (11) suggest the interactions in potato may depend on a mechanism more complicated than the wounding theories originally proposed (19).

Nutritional changes in host plants engendered by nematode feeding could be responsible for differential interactions of *Pratylenchus* spp. and *Verticillium*. Emmanouil and Wood (9) induced resistance of tomato, pepper, and eggplant to *V. dahliae* by leaf injections of amino acids, sugars, and growth factors. Nematode feeding causes widespread changes in host nutrition and hormonal balance, and *Pratylenchus* species could induce resistance or susceptibility to *Verticillium* in potato by subtle shifts in host physiology.

Differential elicitation or suppression of antifungal metabolites in potato by the three nematode species we tested also could affect species interaction with *V. dahliae* in PED. *P. penetrans* elicited phaseollin production in *Phaseolus vulgaris* (1) and *P. scribneri* feeding on roots increased resistance of tobacco stems to *Phytophthora* black shank (18). Such examples indicate the potential for *Pratylenchus* species to induce production of phytoalexin-type compounds. Mace et al (15) demonstrated the importance of antifungal compounds in resistance of cotton to *V. dahliae*.

These data indicating differential interaction of *Pratylenchus* species with *Verticillium* also have important implications for control of PED. Predictive systems designed to alert growers to potential PED problems cannot be based solely on preplant populations of *Pratylenchus* identified only to the generic level. Clearly, population levels of species must be determined. This may require additional work and increased training of diagnosticians handling nematode analyses.

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