Role of *Pratylenchus penetrans* in the Potato Early Dying Disease of Russet Burbank Potato

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ABSTRACT

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The interaction of *Pratylenchus penetrans* and *Verticillium dahliae* for symptom expression of potato early dying and yield and quality of tubers of Russet Burbank potato was evaluated in microplots and field plots. Soil was fumigated with metham sodium before being infested with varying population levels of the nematode and/or fungus. In the microplot study, low and high initial populations of *P. penetrans* (about 25 and 75/100 cm^3 of soil) or *V. dahliae* (about 3 and 9 colony-forming units/g of dry soil) had no effect on number and fresh weight of tubers compared to the control. Combined infestations of both organisms reduced yields up to 20% but did not affect number of tubers compared to the control. Dry matter content of tubers was reduced by *V. dahliae* compared to the control regardless of presence or absence of the nematode. Foliar symptoms of potato early dying were caused by *V. dahliae* alone, but were more severe when nematodes were also present with *V. dahliae*. Estimates of percent defoliation at weekly intervals beginning 13 wk after planting until harvest were consistent with rating of symptoms at 13 wk after planting. In field experiments, initial populations of *P. penetrans* ranging from eight to 44 nematodes/100 cm^3 of soil did not affect yield or quality of tubers compared to the control. Initial populations of *V. dahliae* alone reduced yield one year but not another. Regardless of the effect of the fungus alone, the combination of *V. dahliae* and *P. penetrans* reduced yield by as much as 36% and also reduced specific gravity compared to the control. The population dynamics of *P. penetrans* was not consistent among years of experiments; populations of this nematode were either decreased or not affected by *V. dahliae*.

Additional keywords: disease complex, interaction, root-lesion nematode, *Solanum tuberosum*.

Production of potatoes (*Solanum tuberosum* L.) is limited in many regions by a disease syndrome known as potato early dying (22). A major contributor to this syndrome is the wilt fungus, *Verticillium dahliae* Kleb. Several plant parasitic nematode species have been implicated in potato early dying as well.

Pratylenchus penetrans (Cobb) Filipjev & Schuurmans Stekhoven (2,9,17,23), *P. scribneri* (21), *Globodera pallida* (6), and *Meloidogyne hapla* (10) in conjunction with *Verticillium dahliae* Kleb., have been reported to reduce yields by causing plants to senesce prematurely. Recent work has shown that the impact of *M. hapla* on yield is additive with *V. dahliae* and that while plants are stunted, *M. hapla* does not contribute to premature senescence of Russet Burbank potato (16). There can be a synergistic interaction between *P. penetrans* and *V. dahliae* for the development of potato early dying symptoms and yield of Superior potato grown in microplots, even when populations of each are too low to cause potato early dying alone (17,21,23). The effect of combined infection by these pathogens on the quality of tubers has not been studied previously.

Synergistic interactions between *P. penetrans* and *V. dahliae* for Russet Burbank potato have not been reported. This important commercial cultivar is grown in regions of the United States where both organisms are endemic. The relationship between initial populations of *V. dahliae* and development of potato early dying has been determined for some production systems (14) and tactics aimed at reducing populations of the fungus are used to manage this disease (22). If *P. penetrans* interacts synergistically with *V. dahliae* to affect potato early dying and the yield of Russet Burbank potato, then joint thresholds need to be established.

The objective of this study was to determine if there is a synergistic interaction between *P. penetrans* and *V. dahliae* on the yield and quality of Russet Burbank potato. This is the first report of the interaction of *P. penetrans* and *V. dahliae* grown in field plots as well as in microplots, using practices common to the commercial production of potato.

MATERIALS AND METHODS

Microplot experiments. Microplots were established in 1986 at the Hancock Experiment Station on Plainfield loamy sand soil (92% sand, 5% silt, 3% clay, <1% organic matter) under center pivot irrigation. The site was fumigated with 470 L/ha metham sodium (32.7% a.i.) through the center pivot in November 1985 prior to establishing microplots. In April 1986, soil was excavated from 61-cm-diameter by 60-cm-deep holes with an auger attached to the back of a tractor. Holes were lined with 45 × 200 cm by 37-mil thick fiberglass sheets, refilled with soil, and infested with *P. penetrans* and/or *V. dahliae*. Treatments were: two levels of *P. penetrans*, two levels of *V. dahliae*, all possible combinations of the two levels of *P. penetrans* and *V. dahliae*, and pathogen-free controls. Each treatment was replicated eight times in 1986 and six times in 1989, with each replicate consisting of one microplot. Treatment replicates were arranged in a completely randomized design. The site was fumigated again in November 1988. Before fumigation, soil was removed from each microplot and spread on the soil surface outside the microplot. Three weeks after fumigation, the microplots were refilled with the original soil. In December 1988 and April 1989 soil samples were taken to determine the effectiveness of the fumigation treatment. No nematodes or *V. dahliae* were recovered at those times.

Inoculum production and soil infestation. An isolate of *P. penetrans*, recovered from a potato field in Wisconsin, was introduced into the microplots. Nematodes were reared on monoxenic alfalfa callus cultures as described by Riedel et al (20) in 1986 and on corn (I. O. Chief) explants grown on Gamborg's B-5 medium without auxins or cytokinens (7) in 1989.

One week before microplots were infested, nematodes collected by rinsing the agar substrate with water, incubating plant tissue, or macerating plant tissues and agar in water using a Waring blender were concentrated by pouring suspensions over 20-μ sieves. Concentrated nematodes were divided to obtain low and high inoculum levels in equal volumes of water and counted by life stage in 10 0.1-ml aliquots using a stereomicroscope. In 1986,

the low and high inoculum suspensions contained (mean ± standard error) 2,137 ± 43 and 7,013 ± 151 nematodes per milliliter, respectively, with a juvenile to adult ratio of 11:8. Ten milliliters of nematode inoculum was mixed directly into each microplot to a depth of 30 cm with a shovel, resulting in populations of 24 and 79 nematodes per 100 cm^3 of soil. Similar procedures were used in 1989 except that the 10 ml of inoculum for each microplot was first added to 1.5 L of steam-pasteurized soil collected from the microplot site. This soil was incorporated into each microplot to a depth of 30 cm using a shovel. Low and high inoculum levels of 27 and 68 nematodes per 100 cm^3 of soil were established in the microplots.

Inoculum of *V. dahliae*, in 1986, was obtained by growing a virulent isolate of the fungus on 10% potato-dextrose agar for 3 wk. Cultures were suspended in water by macerating the contents of plates in a blender. For the low and high treatment levels, respectively, 125 or 500 ml of the suspension containing 4×10^4 colony-forming units(cfu)/ml was poured on the surface of each microplot and incorporated to a depth of 30 cm with a shovel. Soil samples collected from the microplots 3 wk after planting and processed as described by Nicot and Rouse (13) contained (mean ± standard error) 4.4 ± 0.9 (low) or 5.8 ± 1.3 (high) cfu/g of soil.

In 1989, inoculum was produced by growing the fungus on sterile rye seed for 4–6 wk, and subsequently air drying and grinding the inoculum in a Wiley mill. Soil from the microplot site was steam-pasteurized for 45 min at a minimum of 65 C and infested with inoculum, dried for 4 wk, and assayed for *V. dahliae* by dilution plating. An average of 750 cfu/g of soil were recovered. Infested soil was measured volumetrically to deliver 415 or 1,520 g of infested soil to microplots and incorporated with a shovel, resulting in populations of *V. dahliae* of 2.5 or 9.3 cfu/g of soil (approximately 355 or 1,300 cfu/100 cm^3 of soil) for the low and high treatments, respectively.

Plot establishment. Fertilizer (10-20-20) at 674 kg/ha was broadcast over the surface of the microplots before infestation with *P. penetrans* and/or *V. dahliae* inoculum. After infestation, three seed pieces of cultivar Russet Burbank, each hand cut and weighing 42–56 g, were planted to a depth of 15 cm in each microplot. Planting dates were 7 May 1986 and 15 May 1989. Ammonium nitrate fertilizer (37-0-0) at 243 kg/ha was applied in a split application 3 and 6 wk after planting. Foliar insecticides with no nematicidal properties and fungicides were applied as needed. Weeds were removed within microplots by hand and between microplots by rototilling.

Data collection and analysis. Soil samples for nematode extraction were collected after harvest 30 September 1986 and 13 September 1989. A sample consisting of three cores, 2.5 cm diameter × 30 cm deep, were bulked from each microplot. A 100-cm^3 aliquot from each sample was processed for nematodes by a centrifugal-flotation technique (11) using nested 250 μm-pore and 38 μm-pore sieves. Roots retained on the 250 μm-pore sieve during the soil washing procedure were incubated in Baermann funnels for 2 days. After nematodes were collected, the roots were dried at 80 C for 2 days and weighed. The number of *P. penetrans* were counted with a stereomicroscope. Counts were adjusted to account for the efficiency of the extraction procedures (15) and expressed as nematodes per 100 cm^3 of soil (and roots therein) and nematodes/g dry root weight.

Soil samples were collected 26 July 1986 to assay for *V. dahliae*. Soil was air-dried for 2 wk and assayed as described by Nicot and Rouse (13).

Symptoms of potato early dying were assessed once in 1986, 13 wk after planting, and on eight dates in 1989, beginning 10 wk after planting until harvest, using a scale of 0 = no symptoms, 1 = 1–33% of the foliage showing wilting, necrosis, or chlorosis; 2 = 33–66%, 3 = 66–99%, and 4 = plant dead. Plants were rated individually and the mean for each microplot recorded in 1986. In 1989, one rating was made for each microplot. Percent defoliation was also estimated for each microplot in 1989.

Three stems from each microplot were sampled at random 3 wk before harvest in 1989 and assayed for *V. dahliae*. Two sections, cut approximately 20 cm above the soil line and just above the sixth node from the apical end, were surface-sterilized in 10% NaOCl and plated on Menzies-Griebel medium (8). The number of stems from each microplot infected by *V. dahliae* was recorded 10 days after plating.

Tubers were dug by hand on 30 September 1986 and 13 September 1989. The number and total weight of tubers were recorded for each microplot. In 1989, specific gravity of tubers was calculated for each microplot using the weight-in-air versus weight-in-water technique (18).

Analysis of variance (Statistical Analysis System, Inc., Cary, NC) was conducted for a completely randomized factorial design with two factors, population levels of *P. penetrans* (0, low, and high) and *V. dahliae* (0, low, and high). Analyses of nematode data were performed on transformed ($\log(x + 1)$) counts. Orthogonal contrasts were used to evaluate differences among treatments.

Field experiments. Experiments were conducted in 1987 and 1988 under center pivot irrigation on sites fumigated with 470 L/ha metham sodium in November 1986 and 1987. Planting dates were 30 April 1987 and 3 May 1988. Treatments were four and three levels of *P. penetrans* in 1987 and 1988, respectively, alone and in combination with one level of *V. dahliae*, and a pathogen-free control. Plots were arranged in a randomized block design with each treatment replicated five times in 1987 and four times in 1988. A replicate consisted of one infested row and one noninfested border row each 3 m long in 1987 and one infested row surrounded by two noninfested border rows each 6 m long in 1988. Blocks were separated by a 4.5-m fallow alley.

Inoculum production and soil infestation. Inoculum of *V. dahliae* was grown on rye seed as described for the second microplot experiment. Inoculum was spread evenly over the soil surface in an area 91 cm wide and the length of each plot. Immediately thereafter, the infested surface was rototilled to a depth of 20 cm to mix inoculum into soil. Before incorporation, inoculum was assayed and the amount to be added to each plot was adjusted so that 100 cfu/g of soil were added to each plot to a depth of 20 cm. Soil samples collected after planting and processed as described by Nicot and Rouse (13) contained (mean ± standard error) 11 ± 4 and 17 ± 7 cfu/g of soil in 1987 and 1988, respectively.

Nematodes were reared on alfalfa callus and harvested as described for the microplot experiments. Concentrated nematode suspensions were mixed into 12 L of steam-pasteurized (30 min at 65 C) soil in 1987 and 7 L of soil in 1988, in sufficient water to wet the soil to 10% moisture by weight. In 1987, treatment levels were obtained by mixing 1, 3, 5, and 7 parts of noninfested soil with sufficient pasteurized (30 min at 65 C) soil to make a total volume of 5 L. A 500-cm^3 aliquot of soil from each treatment level was then mixed into 500 cm^3 of pasteurized soil and placed in individual plastic bags (one per plot) for field infestation. Similar procedures were used in 1988 except that the 7 L of infested soil was divided into three treatment levels by combining 1, 2, and 4 parts infested soil with pasteurized soil to a total volume of 5 L and then adding 500 cm^3 of the treated soil with 1 L of noninfested soil to each field plot.

In both years, one 100-cm^3 subsample was removed from each bag of final field inoculum and assayed for *P. penetrans* by incubation on Baermann funnels for 48 hr. Nematode counts were multiplied by 3.33 to account for the efficiency of this recovery procedure. Based on that sample, estimated numbers of nematodes delivered per field plot were 2.7, 5.3, 5.8, and 8.0 $\times 10^4$ for the low, medium, medium-high, and high treatments, respectively, in 1987 and 2.8, 5.0, and 9.3 $\times 10^4$ for the low, medium, and high treatments, respectively, in 1988. Nematode inoculum was removed from the plastic bags and distributed evenly down the row and directly in the furrow after the rows were opened and potatoes delivered using a potato planter with the closing disks removed.

Plot establishment. Seed pieces of cultivar Russet Burbank cut by hand to a size of 42–56 g were planted at a spacing of 30 cm, with 1 m between rows. Following the application of nematode inoculum, rows were closed using a disk coulter. Plots were irri-

TABLE 1. Yield, specific gravity, disease severity, and percent defoliation of Russet Burbank potato grown in microplots noninfested or infested with *Pratylenchus penetrans* and/or *Verticillium dahliae*

Treatment[a]	Yield (kg/plant) 1986	Yield (kg/plant) 1989	Specific gravity 1989	Disease severity[b] 1986	Disease severity[b] 1989	AUDPC—1989[c] Ratings	AUDPC—1989[c] % Def.
1. Control	2.09	1.61	1.0806	0.25	1.50	84	1704
2. Pp-low	2.34	1.59	1.0791	0.17	1.33	89	1879
3. Pp-high	2.43	1.66	1.0827	0.08	1.17	87	1803
4. Vd-low	2.07	1.67	1.0779	0.92	1.50	93	1915
5. Vd-low + Pp-low	1.91	1.50	1.0750	0.96	1.67	109	2375
6. Vd-low + Pp-high	1.85	1.38	1.0765	1.50	2.17	122	2770
7. Vd-high	1.99	1.58	1.0775	1.17	1.33	83	1588
8. Vd-high + Pp-low	1.78	1.23	1.0729	1.33	2.17	124	2946
9. Vd-high + Pp-high	1.66	1.30	1.0758	2.00	2.33	128	3097
Analysis of variance	*P* values						
P. penetrans	0.83	0.04	0.05	0.00	0.15	0.00	0.00
V. dahliae	0.01	0.01	0.01	0.00	0.03	0.00	0.00
Pp × Vd	0.20	0.27	0.70	0.01	0.14	0.14	0.10
Contrasts	*P* values						
Control vs Vd (1 vs 4,7)	0.72	0.94	0.14	0.00	0.81	0.70	0.89
Control vs Pp (1 vs 2,3)	0.11	0.92	0.87	0.55	0.47	0.72	0.69
Vd only vs Pp only (4,7 vs 2,3)	0.02	0.98	0.05	0.00	0.55	0.97	0.75
Vd+Pp vs Vd or Pp (5,6,8,9 vs 2,3,4,7)	0.01	0.01	0.01	0.00	0.00	0.00	0.00
Vd-low vs Vd-low + Pp (4 vs 5,6)	0.30	0.06	0.26	0.85	0.23	0.04	0.06
Vd-high vs Vd-high + Pp (7 vs 8,9)	0.14	0.01	0.11	0.01	0.01	0.00	0.00
Pp-low vs Pp-low + Vd (2 vs 5,8)	0.01	0.06	0.01	0.00	0.09	0.01	0.02
Pp-high vs Pp-high + Vd (3 vs 6,9)	0.01	0.01	0.01	0.00	0.00	0.00	0.00

[a] Vd = *Verticillium dahliae*, Pp = *Pratylenchus penetrans*. Low and high levels of nematodes, respectively, were 24 and 79/100 cm³ of soil in 1986 and 27 and 68/100 cm³ of soil in 1989. Low and high levels of *V. dahliae*, respectively, were 4 and 6 cfu/g of soil in 1986 and 3 and 9 cfu/g of soil in 1989.

[b] Plants were rated for severity of potato early dying symptoms 13 wk after planting on a scale where 0 = no symptoms, 1 = < 33% of foliage with early dying symptoms, 2 = 34–66%, 3 = 67–99%, 4 = plants completely dead.

[c] Area under disease progress curve (AUDPC) for disease severity ratings and percent defoliation in 1989.

gated and managed for fertility, weeds, and pests according to recommendations for the commercial production of potatoes in Wisconsin. Plots received a topdress application of ammonium nitrate fertilizer (37-0-0) 15 May 1987 and 23 May 1988 and were hilled 3 June 1987 and 7 June 1988.

Data collection and analysis. Data were collected as described for the microplot experiments. Soil was sampled 10 June 1987, 22 June 1988, and immediately before harvest in September. Symptoms were assessed once during each season on 13 August 1987 and 10 August 1988; each plant was rated and the mean rating for each plot calculated. Six stems per plot were sampled 2 October 1987 and 6 September 1988 for *V. dahliae*. Tubers were harvested by machine 2 October 1987 and 28 September 1988, graded, and weighed. Specific gravity was measured using a potato hydrometer.

Data were analyzed using regression procedures (SAS) to compare yield data in the presence and absence of *V. dahliae* and analysis of variance procedures to test for differences in nematode reproduction in plots with and without *Verticillium*.

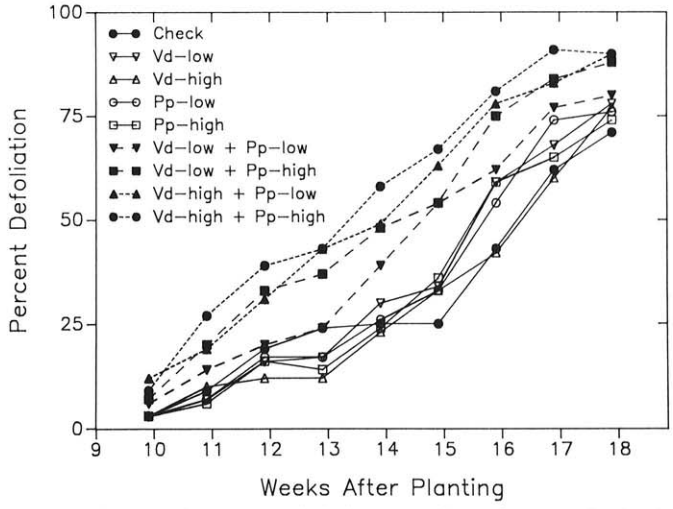

Fig. 1. Estimates of percent defoliation over time of Russet Burbank potatoes grown in microplots in the presence or absence of *Verticillium dahliae* or *Pratylenchus penetrans* or combination of both in 1989.

RESULTS

Microplot experiments. In 1989, combinations of *P. penetrans* and *V. dahliae* reduced the weight of tubers, whereas the nematode or fungus alone had no effect on yield (Table 1). Microplots infested with both nematodes and the low level of *V. dahliae* had 14% less yield than microplots infested with the low level of *V. dahliae* alone (Table 1, contrast of treatment 4 versus treatments 5 and 6). Similarly, microplots infested with both nematodes and the high level of *V. dahliae* had 20% less yield than microplots with the high level of *V. dahliae* alone (Table 1, contrast of treatment 7 versus treatments 8 and 9). In 1986, the effects of both organisms, alone and in combination, were

similar but less pronounced than in 1989 except there was a trend in which treatments with nematodes alone increased yield compared to the control (Table 1, contrast of treatment 1 versus treatments 2 and 3). Mean number of tubers across all treatments ranged from 40.5 to 47.9 and 42.8 to 50.5 in 1986 and 1989, respectively. In both years, the number of tubers produced was not different among treatments ($P = 0.74$).

The specific gravity of tubers, a measure of the dry matter content, was affected by *V. dahliae* and *P. penetrans* as indicated by ANOVA (Table 1). The specific gravity of tubers from microplots infested with both the nematode and fungus was lower than that of tubers from microplots infested with a single pathogen (Table 1, contrast of treatments 5, 6, 8, and 9 versus treatments 2, 3, 4, and 7).

Foliar symptoms of potato early dying occurred when only *V. dahliae* was present in 1986 but not in 1989 (Table 1, contrast of treatment 1 versus treatments 4 and 7). In both years the addition of *P. penetrans* to plots with low population levels of *V. dahliae* did not increase symptoms significantly compared to the low level of *V. dahliae* alone. However, the addition of *P. penetrans* to plots with high population levels of *V. dahliae* resulted in significantly increased symptom expression compared to the treatment with the high level of *V. dahliae* alone (Table 1). *P. penetrans* alone did not affect symptom expression compared with the control. Plots with both the nematode and *V. dahliae* had greater symptom severity then plots with only nematodes present (Table 1, contrast of treatment 2 versus 5 and 8 and contrast of treatment 3 versus 6 and 9). Ratings made 13 wk after planting in 1989 were higher, in general, than ratings collected at the same time in 1986. Progression of symptoms were consistent with the 1986 data, except that *V. dahliae* alone did not increase disease severity or estimates of percent defoliation compared with the control (Fig. 1). Based on the area under the disease progress curve for symptom ratings and percent defoliation, single pathogen treatments did not differ from the control and symptoms were greatest when both pathogens were present together (Table 1).

Assay of potato stems in 1989 revealed the presence of *V. dahliae* in noninfested microplots (data not presented). Mean percentage of infected segments from the basal portion of stems ranged from 55 to 95% in the noninfested microplots and from 84 to 100% in microplots to which *V. dahliae* was added. *V. dahliae* was recovered from an average of 33 to 44% and 33 to 84% of apical segments of stems from noninfested and infested microplots, respectively.

Populations of *P. penetrans* increased 1.3 to 10.4-fold from planting until harvest (Table 2). Differences among the initial treatment levels were still present by harvest in 1986, but not in 1989. In 1989, the presence of *V. dahliae* affected the number of nematodes recovered from soil ($P = 0.06$) when treatments with *P. penetrans* alone were compared against all treatments containing both *P. penetrans* and *V. dahliae* (contrast of treatments 4 and 7 with 5, 6, 8, and 9). Density of nematodes within roots was not affected by *V. dahliae*.

Field experiments. Joint infection of potato by *P. penetrans* and *V. dahliae* reduced tuber yields by as much as 36% in 1988 (Fig. 2). *P. penetrans* alone had no impact on potato yield. Populations of *V. dahliae* alone were insufficient to reduce yields in 1987, but caused losses of 26% in 1988. Mean percentage of cull tubers harvested from each combination of the fungus and nematode and noninfested controls ranged from 7 to 12% in 1987 and from 13 to 19% in 1988 and was not different among treatments. Rejected tubers were misshapen, infected with soft-rot erwinias or *Streptomyces scabies*, or damaged during digging. Neither infection by the nematode or fungus produced noticeable external symptoms on tubers.

Specific gravity of tubers was greater in 1988 than in 1987 (Fig. 3). In both years, specific gravity was reduced in plots infested with *V. dahliae*, regardless of the presence of *P. penetrans*. Except for one treatment in 1988, specific gravity did not vary with initial populations of nematodes.

Symptoms of potato early dying were more severe ($P \leq 0.05$) in plots infested with *V. dahliae* than in noninfested plots in both 1987 and 1988 (data not presented). In 1988, there was a significant

TABLE 2. Number of *Pratylenchus penetrans* recovered from 100 cm³ of soil and the roots therein and from 1 g of dried roots of Russet Burbank potato grown in microplots infested or noninfested with the nematode and/or *Verticillium dahliae*

Treatment[a]	Nematodes/100 cm³ soil		Nematodes/g root	
	1986	1989	1986	1989
1. Control	0	0	0	0
2. Vd-low	0	0	0	0
3. Vd-high	0	0	0	0
4. Pp-low	77	244	164	1168
5. Vd-low + Pp-low	52	157	229	905
6. Vd-high + Pp-low	84	282	191	1305
7. Pp-high	208	446	424	1392
8. Vd-low + Pp-high	101	282	385	1138
9. Vd-high + Pp-high	183	283	652	1118
Analysis of variance $P =$				
P. penetrans	0.00	0.11	0.00	0.42
V. dahliae	0.07	0.17	0.76	0.48
Pp × Vd	0.50	0.87	0.74	0.83
Contrasts $P =$				
Pp-low vs Pp-high (4,5,6 vs 7,8,9)	0.00	0.11	0.03	0.42
Pp vs Pp + Vd (4,7 vs 5,6,8,9)	0.24	0.06	0.76	0.23
Pp-low vs Pp-low + Vd (4 vs 5,6)	0.99	0.11	0.12	0.22
Pp-high vs Pp-high + Vd (7 vs 8,9)	0.10	0.29	0.25	0.63
Pp + Vd-low vs Pp + Vd-high (5,8 vs 6,9)	0.03	0.95	0.01	0.94

[a] Vd = *Verticillium dahliae*, Pp = *Pratylenchus penetrans*. Low and high levels of nematodes, respectively, were 24 and 79/100 cm³ of soil in 1986 and 27 and 68/100 cm³ of soil in 1989. Low and high levels of *V. dahliae*, respectively, were 4 and 6 cfu/g of soil in 1986 and 3 and 9 cfu/g of soil in 1989.

($P \leq 0.05$) linear relationship (symptom rating = 0.22 + 0.0004 initial nematode population [r^2 = 0.90]) between initial populations of *P. penetrans* and disease ratings 13 wk after planting in plots infested with *V. dahliae*.

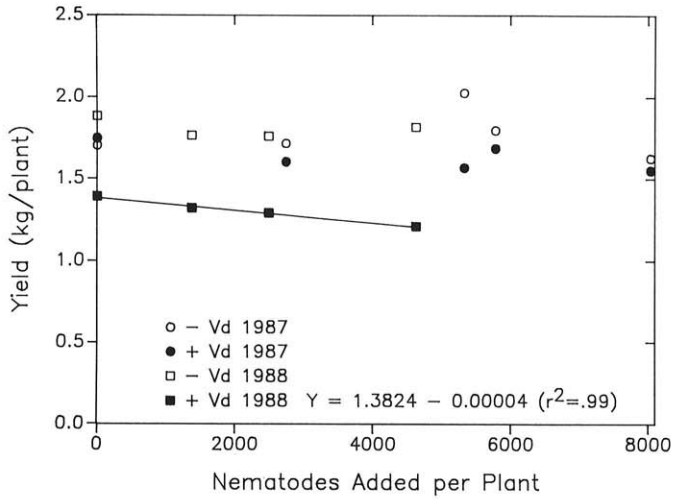

Fig. 2. Relationship between yield and number of *Pratylenchus penetrans* added to soil in field plots in the presence or absence of *Verticillium dahliae*.

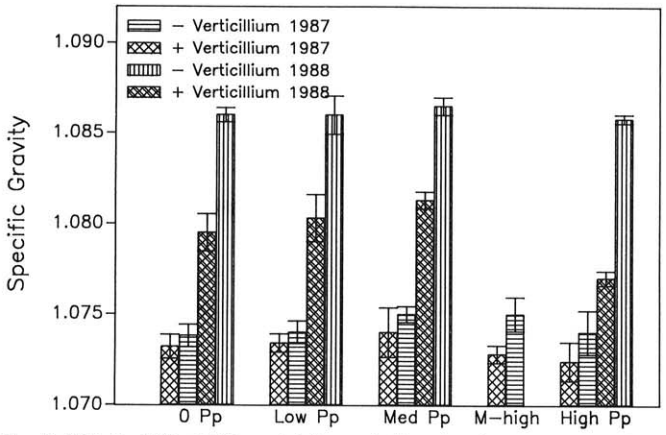

Fig. 3. Effect of *Verticillium dahliae* and *Pratylenchus penetrans*, alone and in combination, on specific gravity of Russet Burbank potatoes. Plots were infested with three population levels of nematodes in 1987 and two population levels of nematodes in 1988.

Colony-forming units of *V. dahliae* in the soil were highly variable, but greater ($P \leq 0.001$) in plots infested with the fungus than in noninfested plots, some of which had very low background populations of *V. dahliae* (Table 3). In 1987, stems were collected too late in the season to reliably assay for *V. dahliae*. In 1988, infection of stems by *V. dahliae* was not influenced by the presence of *P. penetrans*.

Populations of *P. penetrans* increased during the growing season. In June 1987, a mean of eight, two, 26, and 44 nematodes per 100 cm^3 of soil were recovered from the low, medium, medium-high, and high treatments without *V. dahliae*, respectively, and four, 22, 36, and 40 nematodes per 100 cm^3 of soil were recovered for the same treatments with *V. dahliae*. In 1988, initial nematode populations ranged from 1.7 to 8.3/100 cm^3 of soil and did not differ among treatments. Population levels at harvest were greater than at planting, but did not vary among treatments in either year (Table 3). Concomitant infection by *V. dahliae* had no effect on the growth of nematode populations in 1987, and decreased the growth of populations in 1988. Nematode density in roots followed similar trends.

DISCUSSION

The effect of combined plant infection by *P. penetrans* and *V. dahliae* on the symptom expression of potato early dying and yield of Russet Burbank potato can be synergistic. The interaction among treatments was not indicated by the overall analysis of variance but was evident in orthogonal comparisons of the treatment means. However, the data show that populations of the fungus and nematode together can cause foliar symptoms and reductions in yield greater than would be expected from that caused by either organism alone (i.e., synergistic interaction sensu Powell [19]). Synergism occurred between *V. dahliae* and *P. penetrans* when populations of the nematode where lower than those commonly found in commercial potato fields in Wisconsin. This was true whether or not populations of *V. dahliae* were at levels sufficient to reduce yields alone. Similarities among our data from field plots and microplots with other greenhouse (2) and microplot (17,21,23) experiments, strengthen the conclusion that *P. penetrans* can be an important component of the potato early dying disease complex.

Early in the season, after tubers begin bulking, tuber size increases at a faster rate than percent tuber dry weight (5). Since total yield was reduced to a greater extent than dry weight it is possible that the effects of these pathogens occur relatively early in the season when total weight but not proportion dry weight is changing rapidly. Whether this is also the case for other potato systems is not clear, since tuber quality was not measured in earlier experiments (12,17,21,23).

TABLE 3. Occurrence of *Pratylenchus penetrans* and *Verticillium dahliae* in roots, soil, or stems of Russet Burbank potato grown in field plots

Treatment[a]	Pp/100 cm^3 soil[b]		Pp/g root[b]		Vd/g soil[c]		% Stems[d]
	1987	1988	1987	1988	1987	1988	1988
Control	0.0	0.5	0.0	8.2	1.0	0.0	4
Vd	0.0	0.3	0.0	4.0	14.7	32.1	67
Pp-low	55.9	31.6	197.6	208.3	1.7	0.4	0
Pp-med	38.6	134.0	162.4	639.6	3.3	0.4	0
Pp-med high	45.3	nt[e]	89.7	nt	0.3	nt	nt
Pp-high	97.2	157.3	345.7	884.2	2.7	0.0	4
Grand Mean Pp	59.3	107.6	198.9	577.4	2.0	0.3	1
Pp-low + Vd	59.9	18.3	252.3	154.6	24.7	45.0	67
Pp-med + Vd	87.9	21.6	288.5	104.6	11.0	49.6	71
Pp-med high + Vd	55.9	nt	133.9	nt	17.7	nt	nt
Pp-high + Vd	62.6	20.8	180.8	107.4	19.0	64.7	71
Grand Mean Pp+Vd	66.6	20.2	213.9	122.2	18.1	53.1	70

[a] Vd = *Verticillium dahliae*, Pp = *Pratylenchus penetrans*.
[b] Samples taken at harvest each year.
[c] *V. dahliae* cfu/g of soil taken on 10 and 22 June 1987 and 1988, respectively.
[d] Percent stems infected with *V. dahliae* obtained by plating cross sections of stems onto selective medium.
[e] nt = no treatment; in 1988 there were only three treatment levels for *P. penetrans*.

Although a synergistic interaction between *P. penetrans* and *V. dahliae* or trends to that effect were observed in both years of microplot and field tests, the degree of yield loss varied among years. While there may be some minimum initial population level of both the fungus and nematode necessary for synergism to occur, the impact of joint infections was related only slightly to the range of initial population levels of *V. dahliae* and *P. penetrans* used in our study. That similar initial population levels of the nematode and fungus interact differently from year to year is also demonstrated by comparing our results with those of an earlier study in Wisconsin. Using a similar microplot system in 1982, Kotcon et al (12) did not detect a synergistic interaction between *P. penetrans* and *V. dahliae* for symptoms of potato early dying, plant growth, or tuber yield. As seems to be the case in other potato production systems (23), environmental factors appear to greatly influence the relationship of joint infection and yield loss.

Infection of potato by *V. dahliae* can, but does not always, reduce populations of *P. penetrans*. Although the total population of nematodes from microplots with joint infestations tended to be smaller than when no *V. dahliae* was present, the density of nematodes per gram of root was similar among treatments, indicating that the fungus was not competitive or antagonistic to *P. penetrans* in that system. In contrast, populations of nematodes in field plots in 1988 were reduced in the presence of *V. dahliae*, as was the case for *P. penetrans* associated with *V. dahliae* on the cultivars Superior in Ohio (17) and on Kennebec and Katahdin in Pennsylvania (2).

Reciprocal effects of the nematode on soil populations of *V. dahliae* were not measured, but data on the incidence of stem infection by *V. dahliae* at the end of the season was not affected by infection of roots by *P. penetrans*. It may be that, as in other nematode-fungus systems (1,6,19), the primary effect of infection by nematodes is to facilitate the entry of the fungus into roots or expedite its movement from the root cortex into vascular tissue, thereby altering the time course of infection by the fungus.

Data on the interaction of *P. penetrans* and *V. dahliae* for the cultivar Russet Burbank confirm and add to findings for other crops. Synergism between these organisms have been reported for a number of other hosts (3,19) including Superior potato (17,21,23). Up to 50% yield losses of Superior potato can result from initial populations as low as three *P. penetrans* per 100 cm^3 of soil and one microsclerotium of *V. dahliae* per gram of soil (17,21,23). That the combined effect of *P. penetrans* and *V. dahliae* was less than 50% in our study may be due to the moderate resistance of Russet Burbank to *V. dahliae* (4) as compared to the highly susceptible cultivar Superior. Nevertheless, the ability of populations as low as 27 nematodes per 100 cm^3 of soil to interact with *V. dahliae* warrants including *P. penetrans* in plans to manage potato early dying.

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