Interactions of *Verticillium dahliae, Colletotrichum coccodes, Rhizoctonia solani*, and *Pratylenchus penetrans* in the Early Dying Syndrome of Russet Burbank Potatoes

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Portion of a thesis submitted by the senior author in partial fulfillment of the requirements for the Ph.D. degree.

Supported by the University of Wisconsin College of Agriculture and Life Sciences Hatch Project 142-2500 and by funds from the Wisconsin Potato Board.

Accepted for publication 29 June 1984.

ABSTRACT

Kotcon, J. B., Rouse, D. I., and Mitchell, J. E. 1985. Interactions of *Verticillium dahliae*, *Colletotrichum coccodes*, *Rhizoctonia solani*, and *Pratylenchus penetrans* in the early dying syndrome of Russet Burbank potatoes. Phytopathology 75:68-74.

Fumigated microplots were infested with *Verticillium dahliae*, *Colletotrichum coccodes*, *Rhizoctonia solani* (AG-3), and *Pratylenchus penetrans* singly and in all possible combinations in a replicated factorial experiment. Russet Burbank potatoes were used in each experiment. The amount of root colonization by each of the pathogens, stem colonization by *V. dahliae* and *C. coccodes*, visual symptoms of disease, amount of root and foliage growth, and final tuber yield were determined in 1980 and 1982. In 1983, visual symptom and final yield data were collected. Stem colonization by *V. dahliae* was a more sensitive measure of soil infestation by *V. dahliae* than was the amount of root colonization. Symptom severity, scored on a 0–5 scale, was significantly greater in treatments containing *V. dahliae* than in treatments not containing *V. dahliae*. Plants in treatments containing *V. dahliae* had reduced root growth, foliage weight, and tuber yield. *P. penetrans* caused stunting, chlorosis, and premature senescence but did not reduce yield. *C. coccodes* and *R. solani* had no direct effect on disease symptoms, plant growth, or yield. Interactions of *P. penetrans*, *C. coccodes*, or *R. solani* with *V. dahliae* did not result in significant yield reductions. Effects of *P. penetrans* in combination with *V. dahliae* on symptom expression were additive.

Additional key words: disease complex, soilborne plant pathogens, *Solanum tuberosum*.

The potato early dying syndrome (PED) is characterized by stunted growth, chlorotic and necrotic foliage, deterioration of roots, premature senescence, and reduced yields. In Wisconsin, PED has been associated with complexes of soilborne pathogens including *Verticillium dahliae* (VERT), *Colletotrichum coccodes* (COLL), *Rhizoctonia solani* (RHIZ), *Fusarium* spp., *Erwinia carotovora* pv. *atroseptica*, *E. carotovora* pv. *carotovora*, *Pratylenchus penetrans* (PRAT), and *Meloidogyne hapla* (11). Although several workers have assessed the effects of concomitant inoculations with *Verticillium* and some of these pathogens (3,14–16,20,22), most of the work has been done on short-season cultivars, which may differ in susceptibility compared with main crop cultivars. Many factors have been reported to influence the yield loss associated with PED pathogens, eg, climatic conditions (15,22), soil type (14), potato cultivars (1–3), and soil fertility (2).

Nearly two-thirds of the potato production in Wisconsin is in an eight-county area of central Wisconsin on intensively irrigated loamy sand soils (21). Russet Burbank is the most important potato cultivar grown in the United States (4) and also ranks first in total acreage in Wisconsin. The objectives of this study were to assess the effects of *V. dahliae, C. coccodes, R. solani*, and *P. penetrans*, singly and concomitantly, on root and stem colonization of Russet Burbank potatoes; and to determine the relative importance of these four pathogens and their interactions in symptom development, plant growth, and yield loss associated with the PED syndrome in central Wisconsin.

MATERIALS AND METHODS

Microplots were established at the Hancock Experiment Station in April 1980, in a field not previously planted to potatoes. Soil was excavated from 60-cm-diameter by 35-cm-deep holes. These were lined with 45-cm-wide by 37-mil-thick polyester sheets and refilled with soil. Microplots were fumigated with 236 L of methyl isothiocyanate (20%) plus chlorinated C_3 hydrocarbons (80%) per hectare to reduce pathogens or antagonists. The microplots were sealed with plastic covers for 1 wk and then allowed to aerate for 2 wk prior to planting.

Inocula of *V. dahliae* and *C. coccodes* were grown on autoclaved rye seed, air-dried at room temperature for 7 days, and ground in a Wiley mill fitted with a #4 screen. To determine the number of viable propagules per gram of inoculum and as a check for contamination, inocula were assayed by serial dilution in 9-ml sterile distilled water blanks and plating onto potato-dextrose agar (PDA). Inoculum of *R. solani* (AG-3) was grown in soil cultures containing chopped potato (10) for ~1 mo, air-dried, ground with a mortar and pestle, and sieved through a wire mesh with 2-mm openings. This inoculum was assayed by hand-depositing 100-mg samples over PDA. Inocula of at least eight different isolates of each fungus, obtained from infected potato roots and stems the previous year, were combined to increase the genetic heterogeneity of the pathogens.

Immediately prior to planting (9 May 1980), inocula of *V. dahliae, C. coccodes*, and *R. solani* were added to the microplots and mixed into the upper 10 cm of soil, resulting in initial inoculum densities of 6, 14, and 3 propagules per cubic centimeter, respectively. Each fungus was added singly and in all possible combinations to six replicate microplots in a completely randomized factorial design. Three certified seed tubers, cultivar Russet Burbank, were planted in each microplot. Fertilizer, pesticides, and irrigation were applied as needed to control plant stresses and promote normal growth.

Symptoms of PED were assessed on 8 and 22 July and on 5 and 19 August according to a rating scale of 0 = no symptoms, 1 = <25% of the foliage with wilting, chlorosis, necrosis, or stunting typical of Verticillium wilt, 2 = 25–50%, 3 = 50–75%, 4 = 75–100% of the foliage with symptoms, and 5 = stems completely killed. Each stem was rated individually and the mean for each plot was recorded.

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Root samples were taken from midway between plants in three replicate plots of each treatment on 8 July and 5 August with a 10-cm-diameter soil bucket auger. Root samples were taken from all six replicate plots on 19 August. Soil and organic debris were washed from the roots with tap water. Roots were blotted dry with paper towels and weighed. A 1-g sample was surface sterilized for 1 min with 0.5% NaOCl and rinsed for 1 min in sterile distilled water. Twenty randomly selected root segments were cut to ~1 cm in length and plated on modified PDA amended with 50 ppm streptomycin. The remainder of the sample was macerated with 9 ml of sterile distilled water in a Sorval Omnimixer and serial dilutions were plated on Menzies-Griebel (MG) medium (7). Plates were incubated at 22 ± 2 C. The proportion of roots colonized by *C. coccodes* or *R. solani* was determined from PDA plates after 7–9 days of incubation. The number of colony-forming propagules of *V. dahliae* per gram of root tissue was determined from MG plates after 14 days of incubation.

Number and fresh weight of tubers from each microplot was recorded and a sample from the base of the stem was taken from each plant on 30 August. Each stem sample was surface sterilized with 0.5% NaOCl for 1 min, rinsed in sterile distilled water, and a cross section ~2 mm thick was cut from the center and plated on MG. After 14 days of incubation, the stem sections were scored for presence or absence of *V. dahliae* and *C. coccodes*.

The experiment was repeated in 1982 and expanded to include interactions with *P. penetrans*. Inoculum of *P. penetrans* was obtained from greenhouse pot cultures on *Zea mays* by extracting nematodes from roots in flasks on a shaker for 7 days. Inocula of *V. dahliae, C. coccodes*, and *R. solani* were prepared as described above. Microplots were fumigated as described above and inoculated at planting (12 May 1982) with *V. dahliae, C. coccodes*, and *R. solani* at inoculum densities of 55, five, and two propagules, respectively, per cubic centimeter of soil and with 50 *P. penetrans* per 100 cm^3 of soil. Because of variable emergence, plots were thinned to two plants per microplot on 9 June. PED symptoms were assessed 3 August, 17 August, and 7 September. Roots were sampled from three replicates per treatment on 3 August and from all six replicates on 7 September. Length of roots in each sample was estimated by using a modified Newman line intercept method (13,17,23). Root length, density, and root volume were calculated from the root length and estimates of the frequency distribution of root diameters as described previously (12). Root colonization by fungi was assessed as described for 1980. In addition, a 1-g fresh weight root sample was placed in a 125-ml flask and incubated with 50 ml of a 100 ppm streptomycin solution on a reciprocating shaker for 7 days to determine the root population density of *P. penetrans*. Stems were sampled 7 September, and sections from five stems per plant were plated on MG medium. The mean number of vascular bundles from each plant colonized by *V. dahliae* and *C. coccodes* was recorded. In addition, the dry weight of foliage remaining at harvest (7 September) and the number and fresh weight of tubers from each plant was recorded.

The same microplots used in 1980 and 1982 were planted on 2 May 1983 with Russet Burbank potatoes without prior fumigation or addition of inoculum. Disease ratings were taken on 23 August according to the scale described above. The microplots were harvested on 20 September and total yield for each of the microplots was recorded.

The Statistical Package for the Social Sciences (SPSS) (18) was used to perform three-way factorial analysis of variance (AOV) on data collected in 1980 and four-way AOV on data collected in 1982 and 1983. Throughout the remainder of the text the probability of obtaining an *F*-value from the factorial AOV assuming the null hypothesis is correct is given in parentheses. Complete AOV tables are presented elsewhere (11).

RESULTS

Root colonization. To determine the relative levels of effective inoculum present in each of the treatments, the amount of root colonization by each pathogen was assessed several times during each season. Assays of root colonization by *V. dahliae, C. coccodes*, and *R. solani* detected low to moderate levels of contamination in plots not artificially infested with the respective inoculum treatment in both 1980 (Table 1) and 1982 (Table 2).

The proportion of roots colonized by *C. coccodes* was greater in microplots infested with inoculum of *C. coccodes* (hereafter referred to as +COLL) in both years ($P < 0.001$) than in microplots not infested with *C. coccodes* (−COLL) (Tables 1 and 2). The proportion of roots colonized by *R. solani* on the final sample date in both 1980 and 1982 was greater ($P < 0.05$) in microplots infested with *R. solani* (+RHIZ), but differences were not significant in earlier samples. Significantly more colony-forming propagules of *V. dahliae* per gram of root were observed from +VERT microplots than from −VERT microplots on 7 September 1982 (Table 2). In addition, a significant two-way interaction between +COLL and +RHIZ treatments was observed to influence root colonization by *V. dahliae* on 7 September such that the number of colony-forming propagules of *V. dahliae* per gram of root tissue was greatly reduced in microplots concomitantly infested with COLL and RHIZ compared with microplots infested with only one or the other of these fungi. Differences between the +VERT and −VERT treatments were not significant for other dates in 1980 and 1982 (Tables 1 and 2). *P. penetrans* was not detected in noninfested microplots (−PRAT). Nematode population density was significantly influenced by a VERT × RHIZ treatment interaction on 3 August 1982; however, the number of nematodes recovered was low (Table 2).

TABLE 1. Colonization of Russet Burbank potato roots by three fungi on two dates in 1980 in microplots infested with inoculum of those fungi in all possible combinations

Microplot treatment[a]	*V. dahliae*[b]		*C. coccodes*[c]		*R. solani*[c]	
	5 August (cfu)	19 August (cfu)	5 August (%)	19 August (%)	5 August (%)	19 August (%)
Untreated	0 (0)[d]	0 (0)	0 (0)	3 (2)	5 (5)	0 (0)
RHIZ	40 (40)	0 (0)	0 (0)	0 (0)	5 (3)	12 (5)
COLL	0 (0)	0 (0)	23 (8)	51 (12)	7 (7)	0 (0)
COLL+RHIZ	0 (0)	0 (0)	37 (14)	39 (14)	7 (3)	9 (8)
VERT	7,333 (7,333)	227 (131)	3 (3)	2 (1)	7 (7)	5 (4)
VERT+RHIZ	0 (0)	667 (667)	5 (5)	1 (1)	10 (6)	5 (4)
VERT+COLL	0 (0)	33 (33)	43 (4)	49 (9)	5 (5)	2 (2)
VERT+COLL+RHIZ	4,667 (4,667)	700 (700)	48 (9)	42 (13)	5 (2)	6 (3)
Grand mean	1,505	203	20	23.3	6.2	4.8

[a] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), or *Verticillium dahliae* (VERT) prior to planting.

[b] Mean number of colony-forming units of *V. dahliae* per gram of root from three (5 August) or six (19 August) samples per treatment.

[c] Percentage of root segments colonized by the designated fungus. Mean of three (5 August) or six (19 August) samples per treatment with 20 root segments assayed per sample.

[d] Numbers in parentheses are standard errors.

Stem colonization. Stem colonization by *V. dahliae* and *C. coccodes* was assessed as a measure of inoculum potential. The proportion of stems from which *V. dahliae* was isolated in 1980 was greater in +VERT microplots ($P<0.001$) than −VERT microplots, but a two-way interaction between VERT and COLL was observed ($P<0.001$). A lower proportion of stems from microplots concomitantly infested with COLL and VERT was colonized by *V. dahliae* than of stems from microplots infested with VERT but not COLL (Table 3). Although *C. coccodes* was isolated from a large proportion of stems from −COLL microplots (Table 3), stem colonization frequencies were significantly less than in +COLL microplots in 1980 ($P<0.05$).

In 1982, the intensity of stem colonization by *V. dahliae* and *C. coccodes* in each plant was rated from 0 to 3 based on the mean number of vascular bundles colonized by the respective fungus in each of the five stem sections assayed per plant. The amount of stem colonization by *C. coccodes* was significantly increased ($P<0.05$) in the +COLL and the +VERT treatments (compared to the −COLL and −VERT treatments, respectively) and was also influenced by a two-way COLL × VERT interaction ($P<0.05$) and by the three-way VERT × PRAT × COLL interaction ($P<0.001$). The mean level of stem colonization by *V. dahliae* was increased by the main effects of the +VERT ($P<0.001$), +PRAT ($P<0.05$), or +RHIZ ($P<0.05$) treatments. In addition, significant variation in the level of stem colonization by *V. dahliae* was contributed by the treatment interactions of PRAT × RHIZ ($P<0.001$), COLL × RHIZ ($P<0.05$), and PRAT × COLL × RHIZ ($P<0.05$).

Symptom expression. Symptoms of PED were first observed 22 July 1980, 3 August 1982, and 3 August 1983 (respectively, 2,006, 2,134, and 2,240 degree days after planting, base 40 F). AOV showed that symptom ratings were significantly greater in +VERT- than in −VERT-treated microplots on 22 July ($P<0.05$), 5 August and 19 August 1980 ($P<0.001$) (Table 4), on 3 August, 17 August, and 7 September 1982 ($P<0.001$) (Table 5), and 23 August 1983 ($P<0.001$) (Table 6). Increased disease ratings were associated with the +PRAT treatment at all three dates in 1982 ($P<0.05$) and on 23 August 1983 ($P<0.01$). A significant three-way interaction of PRAT × COLL × RHIZ was observed in data from 7 September 1982 ($P<0.05$). No significant main effects on PED symptom ratings could be attributed to +COLL or +RHIZ treatments in any year and no other treatment interactions affecting PED symptoms were found at any other date.

Root growth. Mean root biomass on 8 July 1980 was 1.16 g/L of soil and decreased to 0.64 g/L of soil by 19 August 1980 (Table 7). No significant treatment effects on root biomass were observed on 8 July. Reduced root weights were associated with +VERT treatment on 5 August ($P<0.05$) and a similar trend was observed 19 August ($P<0.08$). Significantly reduced root weights were associated with the +COLL treatment 19 August ($P<0.01$). The +RHIZ treatment did not significantly alter root weights at any date except 5 August for which the data revealed a significant three-way VERT × COLL × RHIZ interaction ($P<0.05$).

In 1982, root growth was assessed as both root length and root volume. Mean root volume decreased from 1.56 cm^3/L of soil on 3 August to 1.37 cm^3/L of soil on 7 September (Table 8). During this period, however, mean root length increased from 1.94 to 2.36 cm/cm^3 of soil. A significant three-way PRAT × COLL × RHIZ treatment interaction was observed to influence root length on 7 September and the two-way interaction of VERT × COLL on root volume was also significant (root volume was less in the +VERT-treated microplots than in −VERT-treated microplots but was not reduced when microplots were concomitantly infested with VERT and COLL) (Table 8). AOV suggested that reduced root length ($P=0.090$) and root volume ($P=0.060$) were associated with +VERT treatments on 3 August. However, increased root length was associated with +PRAT treatments on 7 September ($P=0.085$) and increased root volume was associated with +COLL treatments on 7 September ($P=0.065$).

Tuber yield and foliage growth. In 1980, each microplot yielded an average of 34.4 tubers with a total fresh weight of 3,697 g per microplot. Treatments had no significant effect on either tuber number or fresh weight in 1980.

Foliage dry weight, tuber number, and tuber fresh weight were recorded for each individual plant (two plants per microplot) in 1982. Foliage dry weight averaged 79.2 g per plant at harvest (Table 9) and was significantly reduced ($P<0.01$) in the +VERT treatment. Other treatments or treatment interactions did not significantly affect foliage dry weight. Mean number of tubers per plant was 16.0 and was an average of 9.5% less in +VERT-treated microplots than in −VERT microplots ($P<0.05$). Mean tuber

TABLE 2. Colonization of Russet Burbank potato roots by four soilborne pathogens on two dates in 1982 in microplots infested with inoculum of those pathogens in all possible combinations

Microplot treatment[d]	*V. dahliae*[a]		*C. coccodes*[b]		*R. solani*[b]		*P. penetrans*[c]	
	3 Aug (cfu)	7 Sept (cfu)	3 Aug (%)	7 Sept (%)	3 Aug (%)	7 Sept (%)	3 Aug (no.)	7 Sept (no.)
Untreated	0 (±0)[e]	0 (±0)	10 (±5.8)	10 (±3.4)	7 (±6.7)	1 (±0.8)	0 (±0)	0 (±0)
RHIZ	830 (±830)	25 (±25)	2 (±1.7)	8 (±3.3)	3 (±1.7)	2 (±1.1)	0 (±0)	0 (±0)
COLL	1,200 (±1,200)	700 (±666)	18 (±8.8)	25 (±15.2)	0 (±0)	1 (±0.8)	0 (±0)	0 (±0)
COLL+RHIZ	0 (±0)	0 (±0)	23 (±7.3)	21 (±8.5)	5 (±2.9)	3 (±1.7)	0 (±0)	0 (±0)
VERT	9,000 (±9,000)	5,000 (±4,096)	2 (±1.7)	8 (±2.5)	5 (±5.0)	2 (±1.1)	0 (±0)	0 (±0)
VERT+RHIZ	22 (±22)	30,000 (±29,000)	2 (±1.7)	14 (±5.1)	2 (±1.7)	3 (±1.7)	0 (±0)	0 (±0)
VERT+COLL	1,700 (±1,660)	11,000 (±8,000)	30 (±8.7)	25 (±7.9)	0 (±0)	1 (±0.8)	0 (±0)	0 (±0)
VERT+COLL+RHIZ	2,300 (±1,760)	50 (±50)	29 (±10.3)	39 (±16.5)	6 (±3.1)	5 (±2.2)	0 (±0)	0 (±0)
PRAT	0 (±0)	600 (±583)	0 (±0)	18 (±12.6)	0 (±0)	2 (±1.1)	24 (±15)	56 (±17)
PRAT+RHIZ	70 (±66)	5,200 (±4,958)	5 (±5.0)	6 (±2.4)	3 (±3.3)	3 (±1.7)	2 (±1)	298 (±275)
PRAT+COLL	0 (±0)	0 (±0)	12 (±4.4)	33 (±9.7)	0 (±0)	3 (±2.5)	4 (±4)	56 (±31)
PRAT+COLL+RHIZ	3,200 (±3,200)	0 (±0)	25 (±10.0)	50 (±11.8)	0 (±0)	3 (±1.1)	0 (±0)	221 (±154)
PRAT+VERT	900 (±900)	550 (±348)	7 (±4.4)	6 (±3.0)	2 (±1.7)	0 (±0)	0 (±0)	20 (±13)
PRAT+VERT+RHIZ	430 (±220)	28,000 (±18,000)	0 (±0)	15 (±8.0)	3 (±1.7)	7 (±3.6)	8 (±4)	126 (±91)
PRAT+VERT+COLL	0 (±0)	6,700 (±6,666)	22 (±7.5)	14 (±1.5)	0 (±0)	3 (±2.5)	0 (±0)	15 (±11)
PRAT+VERT+COLL +RHIZ	20,000 (±20,000)	1,100 (±954)	25 (±15.3)	40 (±9.9)	2 (±1.7)	3 (±2.5)	0 (±0)	7 (±4)
Grand mean	2,500	5,600	13.1	20.8	2.6	2.6	2.4	47.3

[a] Mean number of colony-forming units of *V. dahliae* per gram of root from three (3 August) or six (7 September) samples per treatment.
[b] Percentage of root segments colonized by the designated fungus. Mean of three (3 August) or six (7 September) samples per treatment with 20 root segments assayed per sample.
[c] Mean number of *P. penetrans* extracted from roots of three (3 August) or six (7 September) replicates per treatment.
[d] Microplots were fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.
[e] Numbers in parentheses are standard errors.

weight per plant was 2,077 g and was an average of 12.3% less in +VERT-treated microplots than in −VERT microplots ($P < 0.05$) (Table 9). Statistically significant effects on tuber number or fresh weight were not observed with +PRAT, +COLL, or +RHIZ treatments or treatment interactions.

Similar results for tuber yield were observed in 1983 as were observed in 1982. Mean tuber weight was an average of 22% less in +VERT-treated microplots than in −VERT microplots ($P < 0.01$) in 1983 (Table 6). There were no significant effects on tuber yield associated with +PRAT, +COLL or +RHIZ treatments or treatment interactions except that there was a significant PRAT × RHIZ interaction ($P < 0.05$). Yields were lower in microplots infested with both PRAT and RHIZ than in microplots infested with only one of these pathogen treatments.

TABLE 3. Colonization of Russet Burbank potato stems by *Verticillium dahliae* and *Colletotrichum coccodes* in 1980 and 1982 in microplots infested with four soilborne pathogens

Microplot treatment[a]	19 August 1980[b]		7 September 1982[c]	
	V. dahliae (%)	*C. coccodes* (%)	*V. dahliae* (no.)	*C. coccodes* (no.)
Untreated	20 (14)[d]	61 (13)	0.8 (0.28)	0.8 (0.18)
RHIZ	0 (0)	61 (13)	0.7 (0.26)	0.8 (0.28)
COLL	0 (0)	83 (7)	0.6 (0.16)	0.2 (0.08)
COLL+RHIZ	0 (0)	67 (9)	0.4 (0.13)	0.6 (0.22)
VERT	75 (14)	50 (8)	2.3 (0.13)	0.3 (0.12)
VERT+RHIZ	65 (13)	44 (14)	2.1 (0.27)	0.6 (0.24)
VERT+COLL	39 (16)	67 (9)	1.7 (0.30)	1.3 (0.21)
VERT+COLL +RHIZ	28 (13)	77 (11)	1.6 (0.32)	1.2 (0.25)
PRAT	...[e]	...	0.8 (0.31)	0.4 (0.13)
PRAT+RHIZ	...	...	1.0 (0.32)	0.2 (0.11)
PRAT+COLL	...	...	0.4 (0.19)	0.8 (0.31)
PRAT+COLL +RHIZ	...	...	1.7 (0.35)	0.8 (0.30)
PRAT+VERT	...	...	2.1 (0.25)	0.7 (0.25)
PRAT+VERT +RHIZ	...	...	2.3 (0.16)	0.7 (0.17)
PRAT+VERT +COLL	...	...	1.4 (0.22)	1.1 (0.22)
PRAT+VERT +COLL+RHIZ	...	...	2.5 (0.18)	0.6 (0.20)
Grand mean	31	64	1.4	0.7

[a] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.
[b] Percentage of stems colonized. Mean of three stems (one per plant) from each of six replicate microplots per treatment.
[c] Mean number of three vascular bundles of each stem colonized in each of 10 stems (five per plant) from each of six replicate microplots per treatment.
[d] Numbers in parentheses are standard errors.
[e] PRAT treatments were not established in 1980.

TABLE 4. Symptom severity of potato early dying on three dates in Russet Burbank potatoes in microplots infested with three pathogens in 1980[a]

Microplot treatment[b]	Symptom rating on:		
	22 July	5 August	19 August
Untreated	0.00 (±0)	0.05 (±0.03)	0.40 (±0.19)
RHIZ	0.00 (±0)	0.00 (±0)	0.04 (±0.04)
COLL	0.00 (±0)	0.00 (±0)	0.12 (±0.12)
COLL+RHIZ	0.00 (±0)	0.16 (±0.10)	0.32 (±0.21)
VERT	0.01 (±0.01)	0.53 (±0.15)	0.92 (±0.20)
VERT+RHIZ	0.05 (±0.03)	0.36 (±0.12)	1.16 (±0.29)
VERT+COLL	0.11 (±0.11)	0.73 (±0.28)	0.94 (±0.40)
VERT+COLL +RHIZ	0.20 (±0.12)	0.71 (±0.32)	1.11 (±0.44)
Grand mean	0.05	0.32	0.63

[a] Symptom ratings based on a scale of 0 = no symptoms, 1 = <25% of foliage with early dying symptoms, 2 = 25–50%, 3 = 50–75%, 4 = 75–100% of foliage with symptoms, and 5 = plants completely dead. Ratings represent means of all stems from three plants per microplot, six microplots per treatment. Numbers in parentheses are standard errors.
[b] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), or *Verticillium dahliae* (VERT) prior to planting.

DISCUSSION

The results of this study demonstrate the importance of *V. dahliae* as a causal agent of PED in cultivar Russet Burbank potatoes. The characteristic symptoms of PED (ie, wilting, chlorosis, and necrosis of foliage, stunted growth, reduced yield, and premature senescence) were all increased in plots in which the soil was infested with *V. dahliae*. The effect of infestation by *V. dahliae* on symptoms and yield was greater in 1983 (a hot, dry season) than in 1982. The absence of yield reductions in 1980 may be due to weather conditions that year or may simply be attributed to the lower inoculum density of *V. dahliae* used in 1980 (six propagules per cubic centimeter vs 55 propagules per cubic centimeter in 1982). Martin et al (15) found that foliage and root fresh weights of cultivar Superior were reduced in microplots infested with *V. dahliae* at high initial inoculum densities, but not at low inoculum levels. Results of their studies showed that very high initial inoculum densities of *V. dahliae* were needed to significantly reduce tuber yield; however, concomitant infestations of low levels of *V. dahliae* and *P. penetrans* significantly reduced yield. Since low levels of the nematode caused no significant yield loss, they concluded that PED was the result of the interaction of *V. dahliae* and *P. penetrans*. They also showed that this interaction was synergistic at low initial inoculum densities and additive at higher initial inoculum densities.

Bernard and Laughlin (1) and Bird (2) have shown that cultivar Superior is less tolerant of *P. penetrans* than is cultivar Russet Burbank. Olthof (19), however, found significant yield losses due to

TABLE 5. Symptom severity of potato early dying on three dates in Russet Burbank potatoes in microplots infested with four pathogens in 1982

Microplot treatment[a]	Symptom rating on:		
	3 August	17 August	7 September
Untreated	0.17 (±0.17)[b]	0.53 (±0.29)[b]	1.58 (±0.51)[b]
RHIZ	0.08 (±0.08)	0.30 (±0.18)	1.13 (±0.29)
COLL	0.00 (±0.00)	0.20 (±0.07)	1.32 (±0.33)
COLL+RHIZ	0.00 (±0.00)	0.20 (±0.16)	0.89 (±0.24)
VERT	0.33 (±0.21)	1.27 (±0.25)	3.06 (±0.31)
VERT+RHIZ	0.58 (±0.20)	2.07 (±0.25)	3.81 (±0.37)
VERT+COLL	0.33 (±0.21)	1.35 (±0.36)	3.63 (±0.36)
VERT+COLL +RHIZ	0.50 (±0.34)	1.68 (±0.47)	3.67 (±0.28)
PRAT	0.33 (±0.21)	0.50 (±0.29)	1.87 (±0.35)
PRAT+RHIZ	0.08 (±0.08)	0.25 (±0.15)	1.43 (±0.26)
PRAT+COLL	0.00 (±0.00)	0.37 (±0.19)	1.12 (±0.37)
PRAT+COLL +RHIZ	0.17 (±0.17)	0.88 (±0.42)	2.72 (±0.43)
PRAT+VERT	0.75 (±0.25)	2.37 (±0.29)	4.07 (±0.23)
PRAT+VERT +RHIZ	0.83 (±0.11)	2.12 (±0.31)	3.97 (±0.35)
PRAT+VERT +COLL	1.00 (±0.26)	1.93 (±0.24)	3.32 (±0.37)
PRAT+VERT+ COLL+RHIZ	0.33 (±0.17)	1.75 (±0.29)	3.59 (±0.34)
Grand mean	0.34	1.11	2.57

[a] Microplots fumigated with 236 L of methyl isothiocyanate per hectare plus chlorinated C_3 hydrocarbons and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.
[b] Symptom ratings based on a scale of 0 = no symptoms, 1 = <25% of foliage with early dying symptoms, 2 = 25–50%, 3 = 50–75%, 4 = 75–100% of foliage with symptoms, and 5 = plants completely dead. Ratings represent means of all stems from two plants per micorplot, six microplots per treatment. Numbers in parentheses are standard errors.

P. penetrans with Russet Burbank but not with Superior or four other cultivars. He concluded that further studies were needed to resolve the conflict. In the present study, no significant differences in plant growth or yield of Russet Burbank potatoes could be attributed to soil infestation with *P. penetrans*. However, PED symptom development and stem colonization by *V. dahliae* were increased in microplots infested with *P. penetrans*. Further studies incorporating a range of inoculum densities of the nematode and of *V. dahliae* are needed to characterize the disease potential and yield loss of this interaction for Russet Burbank potatoes.

C. coccodes has been associated with PED symptoms in many areas (5). Stevenson et al (22) attributed a significant yield loss in cultivar Superior to this fungus. Thirumalachar (24) reported lesions on roots and stolons of nine cultivars and suggested that these caused significant yield losses of potatoes in India. Otazu et al (20) found that *C. coccodes* was primarily associated with Norgold Russet potatoes that were weakened or predisposed by other factors but concluded that it "definitely is part of the wilt complex." However, Kirkland and Powelson (9) found that the rate of early dying disease progress was lower in Norgold Russet potato plants coinfected with *C. coccodes* and *V. dahliae* compared with that in plants infected with *V. dahliae* alone. Also, Goodell et al (6) found significantly fewer concurrent infections of Russet Burbank stems by *C. coccodes* and other pathogens than would be expected if *C. coccodes* was colonizing plants predisposed by other pathogens. In the present study, roots of Russet Burbank plants grown in microplots infested with *C. coccodes* were colonized at levels greater than normally found in commercial potato fields in Wisconsin (11). The size of the root system was reduced in +COLL-treated microplots in 1980, but not in 1982. Foliage weight and tuber yields were not affected and no influence on PED symptom development was observed in any of the three years. As had been previously described (6,9), colonization of Russet Burbank stems by *V. dahliae* in 1980 was significantly less in +COLL-treated microplots than in −COLL-treated microplots. The same trend was observed in 1982 except in microplots concomitantly infested with PRAT, COLL, and RHIZ (Table 3). Although no direct causal relationship to PED or yield loss in Russet Burbank is evident from the present study, *C. coccodes* may have an important role in the ecology of the root colonizing fungal community and thus may indirectly influence other pathogens and subsequent disease development.

TABLE 6. Symptom severity of potato early dying 23 August 1983 and tuber yield 20 September 1983 in microplots of Russet Burbank potatoes infested singly or concomitantly with four pathogens in 1982

Microplot treatment[a]	Symptom rating[b]	Tuber yields (g/plant)
Untreated	0.23 (±0.06)[c]	1,665 (±429)[c]
RHIZ	0.25 (±0.12)	2,230 (±401)
COLL	0.27 (±0.07)	1,495 (±175)
COLL+RHIZ	0.24 (±0.07)	1,754 (±447)
VERT	0.66 (±0.04)	1,303 (±131)
VERT+RHIZ	0.48 (±0.12)	1,911 (±369)
VERT+COLL	0.61 (±0.09)	1,319 (±114)
VERT+COLL+RHIZ	0.59 (±0.10)	1,789 (±312)
PRAT	0.29 (±0.12)	2,146 (±436)
PRAT+RHIZ	0.62 (±0.14)	1,701 (±410)
PRAT+COLL	0.30 (±0.12)	2,034 (±204)
PRAT+COLL+RHIZ	0.50 (±0.11)	1,597 (±319)
PRAT+VERT	0.64 (±0.04)	1,688 (±318)
PRAT+VERT+RHIZ	0.77 (±0.06)	1,232 (±169)
PRAT+VERT+COLL	0.71 (±0.10)	1,208 (±66)
PRAT+VERT+COLL +RHIZ	0.59 (±0.13)	1,417 (±233)
Grand mean	0.49	1,656

[a] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.
[b] Symptom ratings based on a scale of 0 = no symptoms, 1 = <25% of foliage with early dying symptoms, 2 = 25–50%, 3 = 50–75%, 4 = 75–100% of foliage with symptoms, and 5 = plants completely dead. Ratings represent means of all stems from two plants per microplot, six microplots per treatment.
[c] Numbers in parentheses are standard errors.

TABLE 7. Root density at three dates in 1980 of Russet Burbank potatoes grown in microplots infested with three soilborne fungal pathogens

	Sampling date		
Microplot treatment[a]	8 July (g/L)	5 August (g/L)	19 August (g/L)
Untreated	1.22 (0.42)[b]	1.10 (0.17)[b]	0.72 (0.11)[b]
RHIZ	1.00 (0.13)	1.39 (0.18)	0.84 (0.08)
COLL	1.10 (0.18)	0.96 (0.10)	0.52 (0.06)
COLL+RHIZ	1.36 (0.21)	0.79 (0.16)	0.72 (0.08)
VERT	1.22 (0.10)	1.02 (0.23)	0.71 (0.11)
VERT+RHIZ	1.12 (0.20)	0.57 (0.06)	0.68 (0.11)
VERT+COLL	1.02 (0.22)	0.79 (0.13)	0.45 (0.10)
VERT+COLL +RHIZ	1.10 (0.14)	0.87 (0.20)	0.53 (0.07)
Grand mean	1.16	0.94	0.64

[a] Microplots were fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), or *Verticillium dahliae* (VERT) prior to planting.
[b] Root biomass (g/L soil) based on root fresh weights in a soil core 10 cm in diameter by 15 cm deep from midway between two plants from each of three (8 July and 5 August) or six (19 August) replicate microplots per treatment. Numbers in parentheses are standard errors.

TABLE 8. Mean root length and root volume of Russet Burbank potatoes at two dates in 1982 in microplots infested with four pathogens

	Root length[b]		Root volume[c]	
Microplot treatment[a]	3 August (cm/cm^3)	7 September (cm/cm^3)	3 August (cm^3/L)	7 September (cm^3/L)
Untreated	1.00 (0.06)[d]	1.89 (0.15)	0.64 (0.11)	1.59 (0.54)
RHIZ	2.83 (0.59)	2.14 (0.41)	2.30 (0.88)	1.51 (0.21)
COLL	1.94 (0.75)	2.62 (0.61)	2.19 (1.07)	1.76 (0.37)
COLL+RHIZ	1.94 (0.93)	1.94 (0.33)	1.25 (0.64)	1.18 (0.38)
VERT	1.50 (0.38)	2.41 (0.52)	0.51 (0.19)	1.12 (0.20)
VERT+RHIZ	1.56 (0.20)	1.59 (0.16)	0.50 (0.04)	0.71 (0.11)
VERT+COLL	1.08 (0.22)	2.51 (0.40)	1.15 (0.61)	1.69 (0.42)
VERT+COLL +RHIZ	1.43 (0.28)	2.27 (0.42)	1.06 (0.24)	1.34 (0.29)
PRAT	3.47 (1.97)	3.54 (0.46)	2.26 (1.73)	1.51 (0.37)
PRAT+RHIZ	3.38 (1.60)	2.63 (0.44)	3.91 (2.57)	1.38 (0.29)
PRAT+COLL	2.17 (0.61)	2.13 (0.34)	1.92 (0.40)	1.51 (0.35)
PRAT+COLL +RHIZ	1.35 (0.13)	3.19 (0.97)	1.49 (0.54)	1.38 (0.23)
PRAT+VERT	1.45 (0.19)	2.06 (0.33)	0.56 (0.09)	0.92 (0.15)
PRAT+VERT +RHIZ	1.45 (0.17)	1.76 (0.45)	1.74 (0.85)	1.05 (0.21)
PRAT+VERT +COLL	2.15 (0.37)	1.70 (0.09)	1.90 (0.11)	1.56 (0.27)
PRAT+VERT+ COLL+RHIZ	2.05 (0.77)	3.65 (1.08)	1.36 (0.03)	1.78 (0.46)
Grand mean	1.92	2.38	1.56	1.37

[a] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.
[b] Root length density (cm/cm^3 of soil) based on root length recovered from a soil core 10 cm in diameter by 15-cm deep from midway between two plants in each of three (3 August) or six (7 September) replicate microplots per treatment.
[c] Root volume (cm^3/L soil) calculated from root length and estimates of root diameter frequency distribution from a soil core, 10 cm in diameter by 15-cm deep, from midway between two plants in each of three (3 August) or six (7 September) replicate microplots per treatment.
[d] Numbers in parentheses are standard errors.

R. solani AG-3 is a common pathogen of potatoes and has been shown to cause small, but significant, losses in yield (25). Although it has been associated with PED (24), the role of *R. solani* in relation to PED has not previously been assessed. Field surveys in Wisconsin (11) have shown that *R. solani* AG-3 is a frequent colonist of stems, stolons, and tubers, but usually less than 10% of the roots are colonized. In the present study, *R. solani* colonized a relatively small proportion of roots and had no significant effect on the severity of PED symptoms, plant growth, or tuber yield. Khoury and Alcorn (8) have shown that an isolate of *R. solani* from cotton significantly increased the susceptibility of cotton to *V. albo-atrum* (microsclerotial strain = *V. dahliae*) and that this occurred in both susceptible and resistant cotton cultivars. No effect on potato stem colonization by *V. dahliae* could be attributed to *R. solani* in 1980. In 1982, however, a highly significant interaction between PRAT and RHIZ occurred such that stem colonization by *V. dahliae* was much greater in microplots concomitantly infested with both *P. penetrans* and *R. solani* than in other treatment combinations.

Zambino and Anderson (26) found that the amount of potato stem colonization by *V. dahliae* was related to disease resistance. Our results suggest that the amount of stem colonization by *V. dahliae*, although primarily determined by the presence of inoculum of *V. dahliae* in the soil, is also sensitive to concomitant infection of the host by other pathogens. In addition, the data suggest that the amount of stem colonization by *V. dahliae* is a more sensitive measure of these interactions than is the amount of colonization of root tissues by *V. dahliae*. Interactions with *R. solani* also influenced the population density of *P. penetrans* in roots. This, in turn, may have an indirect impact on colonization by *V. dahliae*.

Interactions among all four pathogens that were studied influence the level of colonization of root and stem tissues of Russet Burbank potatoes with PED. The cumulative effects of these interactions influence pathogen population dynamics and, thereby, may alter disease severity in succeeding potato crops. *V. dahliae* was directly associated with reduced root growth, foliage weight, and tuber yield of Russet Burbank potatoes. *P. penetrans* increased the severity of PED symptoms in plots infested with *V. dahliae*; however, the concomitant effects of *V. dahliae* and *P. penetrans* on symptom development were additive. No effect on growth or final yield could be attributed to the nematode at these population densities. Although differential cultivar responses should be considered, future reseach on yield loss relationships associated with PED should be focused on the inoculum density and population dynamics of these primary pathogens.

TABLE 9. Foliage weight and tuber yields of Russet Burbank potatoes in microplots infested singly or concomitantly with four pathogens in 1982

Microplot treatment[a]	Foliage dry wt[b] (g/plant)	Tuber yields (per plant)[b]	
		Number	Fresh wt (g)
Untreated	79 (±12)	16 (±1.7)	2,027 (±242)
RHIZ	108 (±32)	16 (±1.4)	2,148 (±205)
COLL	96 (±16)	19 (±1.7)	2,332 (±212)
COLL+RHIZ	89 (±14)	15 (±1.9)	2,322 (±310)
VERT	75 (±11)	15 (±1.5)	1,907 (±239)
VERT+RHIZ	63 (±8)	14 (±0.9)	1,760 (±141)
VERT+COLL	61 (±7)	16 (±1.8)	2,032 (±201)
VERT+COLL +RHIZ	71 (±9)	16 (±1.8)	2,081 (±224)
PRAT	83 (±11)	17 (±0.9)	2,204 (±186)
PRAT+RHIZ	85 (±10)	17 (±1.2)	2,225 (±207)
PRAT+COLL	86 (±8)	16 (±1.4)	2.244 (±128)
PRAT+COLL +RHIZ	81 (±8)	18 (±0.9)	2,204 (±137)
PRAT+VERT	65 (±8)	17 (±1.7)	1,980 (±245)
PRAT+VERT +RHIZ	65 (±9)	15 (±1.6)	1,881 (±195)
PRAT+VERT +COLL	71 (±10)	15 (±1.9)	1,869 (±229)
PRAT+VERT+ COLL+RHIZ	89 (±16)	14 (±2.0)	2,022 (±276)
Grand mean	79	16	2,077

[a] Microplots fumigated with 236 L of methyl isothiocyanate plus chlorinated C_3 hydrocarbons per hectare and reinfested with inoculum of *Rhizoctonia solani* (RHIZ), *Colletotrichum coccodes* (COLL), *Verticillium dahliae* (VERT), or *Pratylenchus penetrans* (PRAT) prior to planting.

[b] Mean of 12 plants (two plants from each of six replicate microplots) per treatment harvested 7 September 1982. Numbers in parentheses are standard errors.

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