Effect of *Meloidogyne hapla*, Alone and in Combination with Subthreshold Populations of *Verticillium dahliae*, on Disease Symptomology and Yield of Potato

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We thank Kevin Smith and Timothy Heimerl for technical assistance and Erik Nordheim for statistical advice.
Funded in part by the Wisconsin Potato Industry Board.
Accepted for publication 30 November 1989 (submitted for electronic processing).

ABSTRACT

MacGuidwin, A. E., and Rouse, D. I. 1990. Effect of *Meloidogyne hapla*, alone and in combination with subthreshold populations of *Verticillium dahliae*, on disease symptomology and yield of potato. Phytopathology 80:482-486.

Fumigated microplots on Plainfield loamy sand soil were infested with two levels of *Meloidogyne hapla* and one level of *Verticillium dahliae*, alone and in combination, in 1986. The inoculum density of *V. dahliae* was below the threshold for yield loss in earlier studies. Disease symptoms and yields of potato cultivar Russet Burbank grown in the microplots were evaluated in 1986–1988. There was an increase in populations of nematodes but not *Verticillium* during the 3 yr of the study. Symptoms associated with potato early dying disease were more severe in plots infested with *V. dahliae* in 1986 and 1988. Only *M. hapla* reduced tuber yields. By 1988, yields of plots infested with low and high numbers of nematodes were reduced an average of 48 and 70%, respectively, as compared to noninfested controls. Synergistic interactions between *M. hapla* and subthreshold population levels of *V. dahliae* were not observed for symptom expression or yield reduction.

Additional keywords: disease complex.

Meloidogyne hapla Chitwood occurs in temperate potato production areas. *M. hapla* was found in 25% of the soil samples from potato fields submitted for nematode diagnosis in Wisconsin in 1987 (MacGuidwin, *unpublished*) and in 41% of potato tubers and/or soil samples surveyed in the state of Washington during 1980–1981 (14). Root and tuber infection by *M. hapla* can reduce potato growth, quality, and yields (5,15,19,20).

M. hapla and *Verticillium dahliae* Kleb. often occur together in potato fields. *V. dahliae* alone, at ≥6 propagules/g of soil, causes potato early dying (PED) (12), which can cause significant yield reduction. PED symptoms can develop when population

levels of *Verticillium* are below those necessary to cause disease when the nematodes *Pratylenchus penetrans* (Cobb) Filipj. & Schuur.-Stekh. or *Globodera rostochiensis* (Woll.) Behrens are present (3,10,16,18). Correlations of the density of *M. hapla* with soil populations of *Verticillium*, PED symptoms, and reduced yields in a naturally infested Minnesota field indicate that this nematode also may be involved in the PED disease complex (7).

Populations of *M. hapla* and *Verticillium* are reduced when soil is fumigated with metam-sodium (17). Pesticides with nematicidal properties also can be used to reduce nematode populations and are less expensive and easier to apply than soil fumigants. Using nematicides to manage PED would be economical in some cases if PED can be caused by low populations of *Verticillium* interacting synergistically with nematodes. Although research on interactions between *Pratylenchus* spp. and *G. rostochiensis* with low populations of *Verticillium* has been reported (3,10,16,18), there are no reports on the influence of *M. hapla* on PED at subthreshold population levels of *V. dahliae*.

The objectives of our study were to evaluate the impact of *M. hapla* on the yield of potato cultivar Russet Burbank grown in microplots and to determine if *M. hapla* interacts synergistically with *V. dahliae* when populations of the fungus are too low to cause PED in the absence of contributing pathogens.

MATERIALS AND METHODS

Microplots were established in 1986 at the Hancock Experiment Station on Plainfield loamy sand soil (92% sand, 5% silt, 3% clay, and <1% organic matter) under center pivot irrigation. The site was fumigated November 1985 with 77 L/ha of metam-sodium. In April 1986, soil was excavated from holes 61 cm in diameter × 60 cm deep. The holes were lined with polyester sheets 45 cm wide × 37 ml thick, refilled with soil, and infested with *M. hapla* and/or *V. dahliae*. Treatments were two levels of *M. hapla* (Mh), one level of *V. dahliae* (Vd), all possible combinations of *M. hapla* and *V. dahliae*, and pathogen-free controls. Each treatment was replicated eight times with each replicate consisting of one microplot. The treatment replicates were arranged in a completely randomized design.

Inoculum production and soil infestation. Eggs of *M. hapla* were harvested from tomato (*Lycopersicon esculentum* Miller 'Rutgers') grown in Plainfield loamy sand in the greenhouse (6). The egg inoculum (mean ± standard deviation) was adjusted to 3,256 ± 161 eggs/ml (Mh-low) and 6,735 ± 330 eggs/ml (Mh-high). Nineteen milliliters of inoculum was added to each microplot, resulting in levels of 71 eggs/100 cm^3 of soil and 146 eggs/100 cm^3 of soil distributed to a depth of 30 cm. Cultures of *V. dahliae*, grown on 10% PDA for 3 wk, were macerated in a blender with water and adjusted to 4×10^4 propagules/ml. One hundred twenty-five milliliters of inoculum was added to each microplot, resulting in levels of 41 propagules/g (ppg) of soil distributed to a depth of 30 cm. Based on previous experiments (9,12), this inoculum density of *Verticillium* was below the threshold needed for disease expression. Immediately after the inoculum was poured evenly over the soil surface, the soil was turned and mixed thoroughly with a shovel. Shovels were washed free of soil and disinfected in 5% NaOCl between microplots.

Plot establishment. Fertilizer (10-20-20) at 674 kg/ha and disulfoton at 15.72 kg/ha were incorporated into each microplot before infestation. After infestation, three Russet Burbank certified seed pieces weighing 42–56 g were planted to a depth of 15 cm. Planting dates were 7 May 1986, 7 May 1987, and 3 May 1988. 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. In 1987, it was necessary to replant the microplots after plants were stressed by an accidental overdose of fertilizer applied in June. Foliage and seed pieces from two of the original three plants were removed, but roots were left in the soil when new seed was planted on 1 July 1987. Weeds were removed within microplots by hand and between microplots by rototilling. Tubers were dug by hand and weighed on 30 September 1986, 2 October 1987, and 27 September 1988. Pitchforks used for harvesting were rinsed in 5% NaOCl between plots.

No inoculum was added to the microplots in 1987 and 1988. After harvest, roots were returned to the microplots to encourage the increase of nematodes. Stems were removed to inhibit the increase of *Verticillium*.

Data collection and analysis. Soil samples were collected 27 May 1986, 30 September 1986, and at planting and harvest in 1987 and 1988. Three cores, 2.5 cm in 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 (8) 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. Second-stage juveniles of *M. hapla* were counted, and the counts were adjusted to account for the efficiency of the extraction procedures (33%, MacGuidwin, *unpublished*). Soil was air dried for 2 wk and assayed for *V. dahliae* as described by Nicot and Rouse (12).

Stems were sampled 20 September 1988 for *V. dahliae*. Sections were cut at the sixth node from the apical end from two stems per plant and plated on Menzies-Griebel (MG) medium (4). The percentage of stems and vascular bundles infected by *V. dahliae* was recorded after 10 days.

Symptoms of PED were assessed 13 wk after planting using a scale of 0 = no symptoms, 1 = <33% of the foliage with either wilting, chlorosis, or necrosis typical of Verticillium wilt, 2 = 33–66%, 3 = 66–99%, and 4 = plant dead. Each plant was rated individually, and the mean for each microplot was recorded. Plot labels were removed during the rating to reduce the risk of human bias. Additional ratings were collected at 1-wk intervals if symptoms were not evident after 13 wk.

In June 1988, microplots were reassigned to nematode treatments because samples collected 2 October 1987 and 7 May 1988 indicated no significant ($P \leq 0.05$) differences among microplots

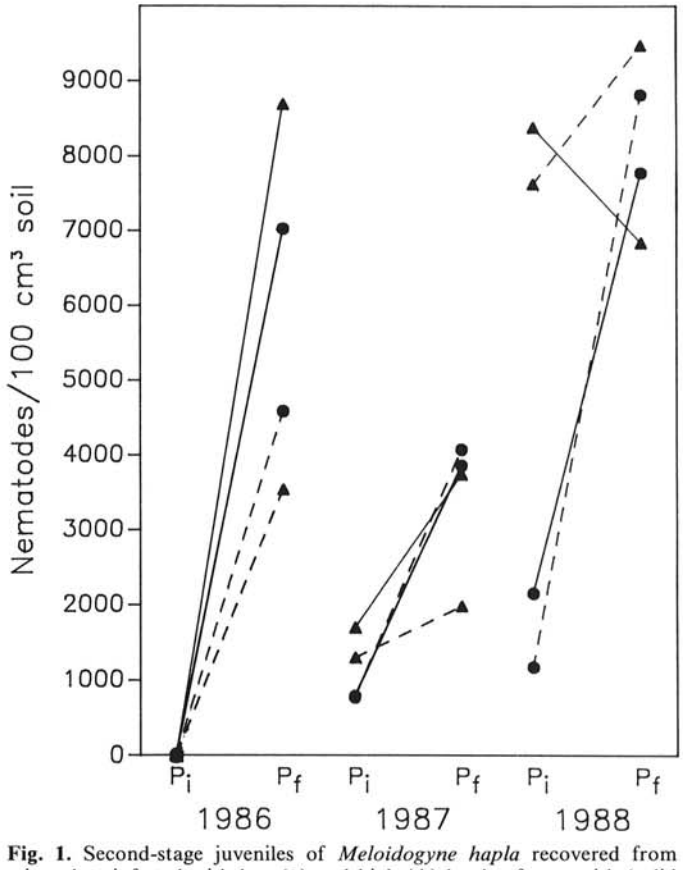

Fig. 1. Second-stage juveniles of *Meloidogyne hapla* recovered from microplots infested with low (●) and high (▲) levels of eggs with (solid line) and without (dashed line) *Verticillium dahliae*. Samples were collected at planting (P_i) and harvest (P_f) from 1986 through 1988.

infested with low and high levels of *M. hapla* in 1986. Microplots were ranked according to counts of nematodes on 7 May 1988. Separate rankings were done for microplots infested with *M. hapla* alone (16 microplots) and microplots infested with *M. hapla* and *V. dahliae* (16 microplots). The six microplots in each ranking containing the lowest number of nematodes were reassigned to the Mh-low treatments; the six microplots containing the highest nematode counts were reassigned to the Mh-high treatments. The four median microplots were not considered in 1988 data analyses. The untreated microplots and those treated with *V. dahliae* alone remained unchanged except that one microplot infested with *V. dahliae* was eliminated from 1988 data analyses because no Verticillium was detected in 1987 and 1988.

Analysis of variance was conducted for a completely randomized factorial with two factors: population levels of *M. hapla* (0, low, and high) and population levels of *V. dahliae* (0 and low). Orthogonal contrasts were used to evaluate differences among treatments. Nematode counts were transformed ($\log_{10}$) for analyses of population levels. There was no difference in the outcome of analyses performed on untransformed and transformed values; therefore, only the untransformed data are presented.

RESULTS

Populations of *M. hapla* established and increased during each of the 3 yr of the study. Few of the eggs had hatched when samples were collected 3 wk after planting in 1986; averages of 7 and 7.5 second-stage juveniles were recovered from microplots infested with 70 and 144 eggs/100 cm^3 of soil, respectively (Fig. 1). By harvest 1986, nematode populations increased 300- to 800-fold but declined during the 1986–1987 winter. Differences between the low and high inoculum levels were not evident until planting in 1987 (Table 1). Populations increased ($P \leq 0.05$) for all treatments except Mh-high + Vd in 1987, but nematode numbers did not differ between the low and high inoculum levels by harvest. Mean populations for the treatments with *M. hapla* on 7 May 1988 were 5,674, 8,159, 7,454, and 9,438 juveniles/100 cm^3 of soil for the Mh-low, Mh-high, Mh-low + Vd, and Mh-high + Vd treatments, respectively. Treatment means after plot reassignment are presented in Figure 1. Mh-low populations increased ($P \leq 0.05$) in 1988, but Mh-high populations did not.

Initial levels of populations of *V. dahliae* recovered from soil samples 3 wk after infestation in 1986 were 2.50 ± 0.59 (mean

TABLE 1. Summary of statistical analyses of the number of second-stage juveniles of *Meloidogyne hapla* per 100 cm^3 of soil recovered from samples collected at planting (P_i) and harvest (P_f) from 1986 through 1988

Source of variation and comparison[a,b]	Degrees of freedom	1986		1987		1988[c]	
		P_i	P_f	P_i	P_f	P_i	P_f
Mh	2	0.10[d]	0.00	0.00	0.00	0.00	0.00
Vd	1	0.89	0.01	0.55	0.55	0.25	0.44
Mh × Vd	2	0.21	0.12	0.76	0.71	0.61	0.19
Mh vs. rest (3, 4, 5, 6 vs. 1, 2)	1	0.03	0.00	0.00	0.00	0.00	0.00
Vd vs. untreated (2 vs. 1)	1	1.00	1.00	1.00	1.00	0.92	0.32
Mh vs. Mh + Vd (3, 4 vs. 5, 6)	1	0.87	0.01	0.46	0.19	0.16	0.13
Mh-low vs. Mh-high (3, 5 vs. 4, 6)	1	0.87	0.31	0.01	0.07	0.00	0.91
Mh vs. Vd (3, 6 vs. 4, 5)	1	0.08	0.81	0.49	0.10	0.86	0.51

[a] Microplots were infested with zero, low (71 eggs/100 cm^3 of soil), or high (146 eggs/100 cm^3 of soil) levels of *M. hapla* (Mh), in combination with zero or low (3 propagules/g of soil) levels of *Verticillium dahliae* (Vd).
[b] Treatments: 1 = untreated, 2 = Vd, 3 = Mh-low, 4 = Mh-high, 5 = Mh-low + Vd, 6 = Mh-high + Vd.
[c] Microplots were reassigned to treatments in 1988 because numbers of *M. hapla* were not different among high and low treatments by 2 October 1987.
[d] *P* values from analysis of variance.

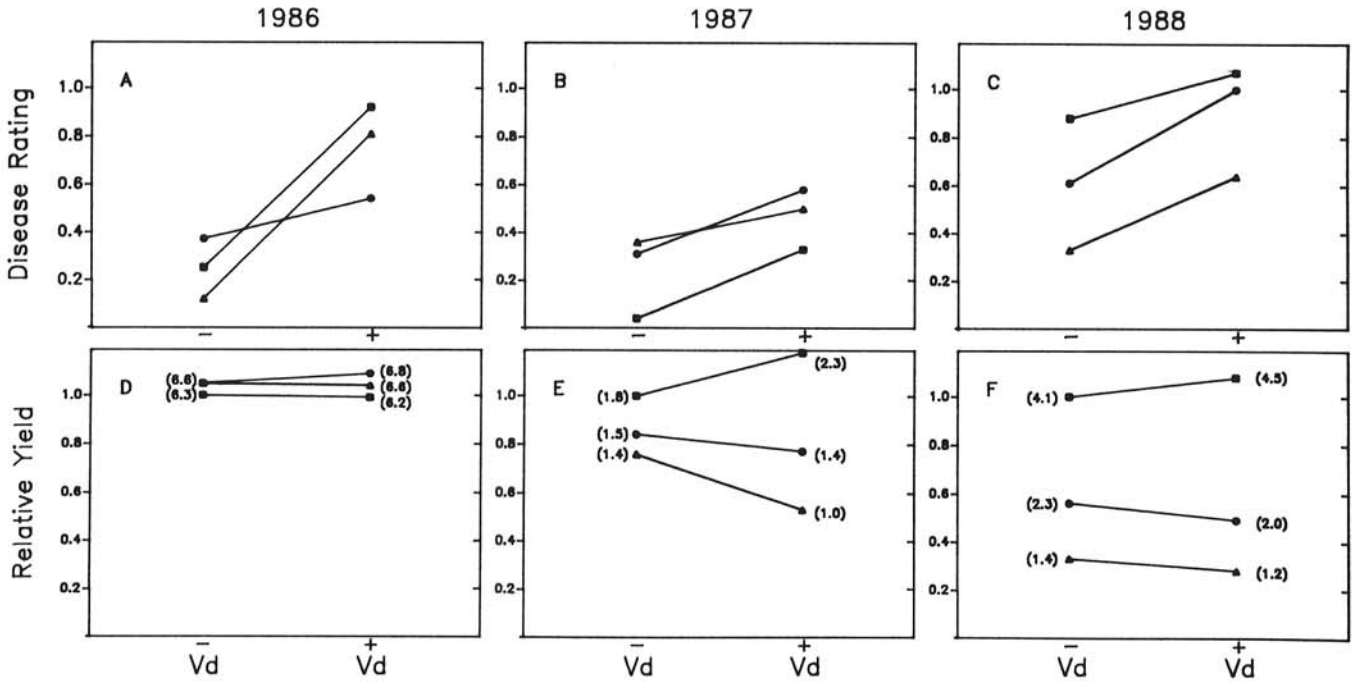

Fig. 2. Disease rating 90 days after planting and relative yield (yield of noninfested plots = 1.00) of microplots infested with zero (■), low (●), or high (▲) levels of *Meloidogyne hapla* with (+) and without (−) *Verticillium dahliae* (Vd). Actual yields (kilograms per microplot) are in parentheses.

and standard error) propagules/g of soil. Populations at planting were 3.64 ± 0.59 in 1987 and 1.48 ± 0.47 in 1988. The presence of *V. dahliae* did not affect *M. hapla* except in 1986, when numbers of *M. hapla* at harvest were three times greater in microplots infested with nematodes alone than in microplots receiving both pathogens (Table 1).

Symptoms of PED were evident 13 wk after planting in only 1 out of 3 yr (Fig. 2, Table 2). In 1987, symptoms were not observed until September. In 1988, PED symptoms were apparent on 10 August, 14 wk after planting. On 17 and 25 August 1988, disease ratings averaged 0.97 and 2.35, respectively, for microplots not infested with *Verticillium* and 1.34 and 2.73, respectively, for microplots infested with *Verticillium*. Symptoms were less ($P \leq 0.05$) severe in microplots containing nematodes than in untreated microplots or in microplots infested with *Verticillium* alone. Although microplots infested with *M. hapla* were visibly stunted, they remained green and erect until harvest, even when *Verticillium* was also present.

Only *M. hapla* decreased tuber yields (Table 3). Yield reductions for the treatments with *M. hapla* averaged 28% in 1987 (Fig. 2). By 1988, yields were reduced an average of 48 and 70% for the Mh-low and Mh-high treatments, respectively. Tubers from microplots infested with nematodes were free from galls but contained all life stages of *M. hapla*. Some eggs recovered from tubers hatched immediately when immersed in tap water.

Stem colonization by *V. dahliae* was greater in microplots infested with *V. dahliae* than in noninfested plots in 1988 (Table 4). *V. dahliae* was detected in an average of 26, 38, 31, 31, 72, and 53% of stems collected from untreated, Vd, Mh-low, Mh-high, Mh-low + Vd, and Mh-high + Vd plots, respectively. Percentage of vascular bundles infected were similar to the percentage of stems infected (data not shown).

DISCUSSION

The rapid increase of populations of *M. hapla* and the severity of yield reductions in nematode-infested microplots indicate the potential threat of this nematode to potato production and support findings of earlier studies (5,15). The yield reductions observed in our study were greater than those previously reported and provide a realistic estimate of crop loss due to this pest because the establishment of nematode populations allowed the timing and extent of infection to approximate field conditions. Although Russet Burbank is considered to be tolerant of infection by *P. penetrans* (1), it is intolerant of *M. hapla*. The differential rate of increase noted for the low and high initial inoculum levels and the failure of nematodes to kill plants suggest that there is a limit to the population of *M. hapla* supported by this cultivar, a phenomenon reported for other *M. hapla*-host systems (13).

There was no evidence of a synergistic interaction between *M. hapla* and *V. dahliae* for symptom expression or crop growth. During the 3 yr of our study, initial populations of *M. hapla* were less than (1986), roughly equivalent to (1987), and greater than (1988) populations commonly recovered in commercial fields in Wisconsin. Populations of *V. dahliae* in all years were less than the threshold of 6–10 ppg established for Russet Burbank

TABLE 2. Summary of statistical analyses of symptom severity of potato early dying for 1986 through 1988 in potato cultivar Russet Burbank grown in microplots infested with two pathogens[a]

Source of variation and comparison[b,c]	Degrees of freedom	1986	1987	1988[d]		
		8 August	5 August	10 August	17 August	25 August
Mh	2	0.70[e]	0.25	0.09	0.01	0.02
Vd	1	0.00	0.10	0.10	0.15	0.04
Mh × Vd	2	0.22	0.90	0.90	0.47	0.30
Mh vs. rest (3, 4, 5, 6 vs. 1, 2)	1	0.41	0.10	0.08	0.00	0.03
Vd vs. untreated (2 vs. 1)	1	0.01	0.23	0.50	0.28	0.49
Mh vs. Mh + Vd (3, 4 vs. 5, 6)	1	0.01	0.24	0.13	0.30	0.04
Mh-low vs. Mh-high (3, 5 vs. 4, 6)	1	0.96	0.91	0.16	0.23	0.07
Mh vs. Vd (3, 6 vs. 4, 5)	1	0.13	0.72	0.86	0.23	0.18

[a] Symptom rating based on a scale of 0 = no symptoms, 1 = < 33% of foilage with early dying symptoms, 2 = 33–66%, 3 = 66–99%, 4 = plants dead.
[b] Microplots were infested with zero, low (71 eggs/100 cm^3 of soil), or high (146 eggs/100 cm^3 of soil) levels of *Meloidogyne hapla* (Mh), in combination with zero or low (3 propagules/g of soil) levels of *Verticillium dahliae* (Vd).
[c] Treatments: 1 = untreated, 2 = Vd, 3 = Mh-low, 4 = Mh-high, 5 = Mh-low + Vd, 6 = Mh-high + Vd.
[d] Microplots were reassigned to treatments in 1988 because numbers of *M. hapla* were not different among high and low treatments by 2 October 1987.
[e] *P* values from analysis of variance.

TABLE 3. Summary of statistical analyses of tuber yields of potato cultivar Russet Burbank infested with two pathogens

Source of variation and comparison[a,b]	Degrees of freedom	Tuber yields (g/microplot)[c]		
		30 Sept 1986	2 Oct 1987	27 Sept 1988[d]
Mh	2	0.51[e]	0.00	0.00
Vd	1	0.91	0.94	0.86
Mh × Vd	2	0.92	0.18	0.68
Mh vs. rest (3, 4, 5, 6 vs. 1, 2)	1	0.26	0.00	0.00
Vd vs. untreated (2 vs. 1)	1	0.90	0.16	0.53
Mh vs. Mh + Vd (3, 4 vs. 5, 6)	1	0.83	0.28	0.55
Mh-low vs. Mh-high (3, 5 vs. 4, 6)	1	0.76	0.23	0.04
Mh vs. Vd (3, 6 vs. 4, 5)	1	0.73	0.57	0.89

[a] Microplots were infested with zero, low (71 eggs/100 cm^3 of soil), or high (146 eggs/100 cm^3 of soil) levels of *Meloidogyne hapla* (Mh), in combination with zero or low (3 propagules/g of soil) levels of *Verticillium dahliae* (Vd).
[b] Treatments: 1 = untreated, 2 = Vd, 3 = Mh-low, 4 = Mh-high, 5 = Mh-low + Vd, 6 = Mh-high + Vd.
[c] Each treatment was represented by eight microplots, three plants per microplot.
[d] Microplots were reassigned to treatments in 1988 because numbers of *M. hapla* were not different among high and low treatments by 2 October 1987.
[e] *P* values from analysis of variance.

potato grown in Wisconsin (12). Even with a range of starting conditions, the outcome of our experiments was similar for all 3 yr. Although it is possible that *M. hapla* and *V. dahliae* interact when populations of the fungus are above threshold levels (6–10 ppg of soil for our system), we consider it unlikely because synergistic interactions occur with *P. penetrans* when populations of *Verticillium* are as low as 1 ppg of soil (10,18).

The severity of disease symptoms present 90 days after planting was not a good indicator of yield in this study. Chlorosis, necrosis, and wilting are not caused exclusively by *Verticillium* but are expected to increase when populations of *Verticillium* are above some threshold level (17). In 1986, *Verticillium* had a significant effect on disease symptoms but not tuber yield. In 1987 and 1988, there were significant differences among treatments for tuber yield but not symptoms. Disease ratings taken later than 90 days after planting in 1988 were confounded further by the fact that nematode infection seemed to delay normal senescence. Unlike the severe symptom expression that results from an interaction between subthreshold populations of *P. penetrans* and *V. dahliae* (18), chlorosis and necrosis were reduced in plants infected with both *M. hapla* and *V. dahliae* in the third year of our study. Whether these findings were due to an unusually dry season or to very high populations of *M. hapla* is not clear.

Recovery of *V. dahliae* from some stems in untreated microplots in 1988 was unexpected. Soil assays did not reveal the presence of *V. dahliae* in the field before the microplots were established or in microplots to which no inoculum of *Verticillium* was added. Other studies using a different microplot system reported a similar problem, with stem infection ranging from 21 to 98% for uninoculated plants (10,18). It is possible that *Verticillium* was always present at levels below the sensitivity of our assay or introduced by infected seed, windblown soil, or cultural practices. The performance of our seed in concurrent experiments and the fact that precautions were taken to avoid the transport of soil between microplots lead us to believe that *Verticillium* was not introduced by these means. Even with low background populations of *Verticillium*, our data were consistent in showing that yields were related to initial populations of *M. hapla* and that synergistic interactions between the nematode and fungus did not occur.

Contrary to our findings, Jacobson et al (7) reported synergism in the interaction of *M. hapla* and *V. dahliae* for yields of Norland and Norgold potatoes. Their conclusions were based on trials conducted at a site naturally infested with both pathogens. Selective reduction of pathogen populations was accomplished with fungicides, nematicides, and fumigant biocides. Yields were less in treatments where nematicides and fungicides were used as compared with fumigated controls, indicating that both pathogens were at densities sufficient to affect potato growth and yield.

The results of our work and those of Jacobson et al indicate that the relationship between *M. hapla* and *Verticillium* may be unique for each potato production system. Studies with *P. penetrans*, another nematode pest of potato, illustrate the variability in host response to concomitant infections. For example, *P. penetrans* and *V. albo-atrum* Reinke & Berthold interacted in causing symptoms of PED but not yield losses in one experiment (2) and in another affected yields but not symptom expression (11). Inconsistencies in the relationship of nematodes and *Verticillium* to PED may be due to differences in experimental approaches, cultivars used, environmental conditions, population levels of pathogens, or edaphic variation. Determining how these factors affect single and joint infestations of nematodes and *Verticillium* may help identify the mechanisms involved in the PED syndrome.

TABLE 4. Summary of statistical analyses of stem colonization of potato cultivar Russet Burbank in 1988 by *Verticillium dahliae* in the presence or absence of *Meloidogyne hapla*

Source of variation and comparison[a,b]	Degrees of freedom	Percent infected	
		Vascular bundles	Stems
Mh	2	0.19[c]	0.25
Vd	1	0.01	0.01
Mh × Vd	2	0.33	0.42
Mh vs. rest (3, 4, 5, 6 vs. 1, 2)	1	0.11	0.14
Vd vs. untreated (2 vs. 1)	1	0.20	0.46
Mh vs. Mh + Vd (3, 4 vs. 5, 6)	1	0.01	0.01
Mh-low vs. Mh-high (3, 5 vs. 4, 6)	1	0.37	0.43
Mh vs. Vd (3, 6 vs. 4, 5)	1	0.18	0.43

[a] Microplots were infested with zero, low (71 eggs/100 cm^3 of soil), or high (146 eggs/100 cm^3 of soil) levels of *Meloidogyne hapla* (Mh), in combination with zero or low (3 propagules/g of soil) levels of *Verticillium dahliae* (Vd).

[b] Treatments: 1 = untreated, 2 = Vd, 3 = Mh-low, 4 = Mh-high, 5 = Mh-low + Vd, 6 = Mh-high + Vd.

[c] *P* values from analysis of variance.

LITERATURE CITED

1. Bernard, E. C., and Laughlin, C. W. 1976. Relative susceptibility of selected cultivars of potatoes to *Pratylenchus penetrans*. J. Nematol. 8:239-242.
2. Burpee, L. L., and Bloom, J. R. 1978. The influence of *Pratylenchus penetrans* on the incidence and severity of Verticillium wilt of potato. J. Nematol. 10:96-99.
3. Corbett, D. C., and Hide, G. A. 1971. Interactions between *Heterodera rostochiensis* Woll. and *Verticillium dahliae* Kleb. on potatoes and the effect of CCC on both. Ann. Appl. Biol. 68:71-80.
4. Green, R. J., Jr., and Papavizas, G. C. 1968. The effect of carbon source, carbon to nitrogen ratios, and organic amendments on survival of progagules of *Verticillium albo-atrum* in soil. Phytopathology 58:567-570.
5. Griffin, G. D., and Jorgenson, E. C. 1969. Pathogenicity of the northern root-knot nematode (*Meloidogyne hapla*) to potato. Proc. Helminthol. Soc. Wash. 36:88-92.
6. Hussey, R. S., and Barker, K. R. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp. including a new technique. Plant Dis. Rep. 57:1025-1028.
7. Jacobson, B. J., MacDonald, D. H., and Bissonette, H. L. 1979. Interaction between *Meloidogyne hapla* and *Verticillium albo-atrum* in the Verticillium wilt disease of potato. Phytopathology 69:288-292.
8. Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for extracting nematodes from soil. Plant Dis. Rep. 48:692.
9. 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.
10. Martin, M. J., Riedel, R. M., and Rowe, R. C. 1982. *Verticillium dahliae* and *Pratylenchus penetrans*: Interactions in the early dying complex of potato in Ohio. Phytopathology 72:640-644.
11. Morsink, F. 1967. *Pratylenchus penetrans*—Its interaction with *Verticillium albo-atrum* in the Verticillium wilt of potatoes and its attraction by various chemicals. Ph.D. thesis, University of New Hampshire, Durham. 68 pp.
12. Nicot, P., and Rouse, D. I. 1987. Relationship between soil inoculum density of *Verticillium dahliae* and systemic colonization of potato stems in commercial fields over time. Phytopathology 77:1346-1355.
13. Noling, J. W., and Ferris, H. 1986. Influence of alfalfa plant growth on the multiplication rates and ceiling population density of *Meloidogyne hapla*. J. Nematol. 18:505-511.
14. Nyczepir, A. P., O'Bannon, J. H., Santo, G. S., and Finley, A. M. 1982. Incidence and distinguishing characteristics of *Meloidogyne chitwoodi* and *M. hapla* in potato from the northwestern United States. J. Nematol. 14:347-353.
15. Olthof, T. H. A., and Potter, J. W. 1972. Relationships between population densities of *Meloidogyne hapla* and crop losses in summer maturing vegetables in Ontario. Phytopathology 62:981-986.
16. Riedel, R. M., Rowe, R. C., and Martin, M. J. 1985. Differential interactions of *Pratylenchus crenatus*, *P. penetrans*, and *P. scribneri* with *Verticillium dahliae* in potato early dying disease. Phytopathology 75:419-422.
17. Rowe, R. C., Davis, J. R., Powelson, M. L., and Rouse, D. I. 1987. Potato early dying: Causal agents and management strategies. Plant Dis. 71:482-489.
18. Rowe, R. C., Riedel, R. M., and Martin, M. J. 1985. Synergistic interactions between *Verticillium dahliae* and *Pratylenchus penetrans* in potato early dying disease. Phytopathology 75:412-418.
19. Santo, G. S., and O'Bannon, J. H. 1981. Effect of soil temperature on the pathogenicity and reproduction of *Meloidogyne chitwoodi* and *M. hapla* on Russet Burbank potato. J. Nematol. 13:483-486.
20. Stirling, G. R., and Wachtel, M. F. 1985. Root-knot nematode (*Meloidogyne hapla*) on potato in south-eastern South Australia. Aust. J. Exp. Agric. 25:455-457.