Interaction Between *Meloidogyne hapla* and *Verticillium albo-atrum* in the Verticillium Wilt Disease of Potato

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ABSTRACT

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In the field and greenhouse, *Meloidogyne hapla* increased the severity of Verticillium wilt of potato. In the greenhouse *Verticillium albo-atrum* was isolated up to 2 wk earlier from petioles of plants grown in soil with both *M. hapla* and *V. albo-atrum* than from plants grown in soil and inoculated with the fungus alone. Nematode populations were higher in root systems of plants infected with the fungus than on plants infected with the nematode alone at 24 C, but they did not differ at 30 C. In fields treated with benomyl (methyl 1-[butylcarbamoyl]-2-benzimidazole carbamate), phenamiphos (ethyl 4-[methylthio]m-tolyl isopropylphosphoramidate), and carbofuran (2,3-dihydro-2,2 dimethyl-7-benzofuranol methylcarbamate) of soils naturally infested with *M. hapla* and *V. albo-atrum*, the correlation was high ($P = 0.05$) among lower yields, disease index, $\log_e$ *M. hapla* soil populations, $\log_e$ *V. albo-atrum* soil populations, and $\log_e$ *M. hapla* $\log_e$ *V. albo-atrum* soil populations for the potato varieties Norland and Norgold when data were analyzed by multiple regression analysis.

There are several reports of the influence of plant parasitic nematodes on the development of wilt caused by *Verticillium albo-atrum* (Reinke & Berth.). *Pratylenchus* spp. have been reported to be involved in the Verticillium wilt of eggplant (14), potato (16), tomato (5), and peppermint (7). However, the relationship of the northern root-knot nematode, *Meloidogyne hapla* (Chitwood), and *V. albo-atrum* in wilt of potato, *Solanum tuberosum L.*, has not been investigated.

In the sand plains area of east central Minnesota, large populations of *M. hapla* were present in some locations where Verticillium wilt of potato was severe. Soil treatments with benomyl (methyl 1-[butylcarbamoyl]-2-benzimidazole carbamate), phenamiphos (ethyl 4-[methylthio]m-tolyl isopropylphosphoramidate), and carbofuran (2,3-dihydro-2,2 dimethyl-7-benzofuranol methylcarbamate), alone and in combination, were applied to a field that was infested with *M. hapla* and that had a history of severe Verticillium wilt. Our objective was to determine the effect of reducing soil populations of one or both pathogens. The results indicated that *M. hapla* enhanced the development of Verticillium wilt. Others (4,10–12) also have reported that systemic insecticides-nematicides applied to the soil controlled Verticillium wilt; however, they only inferred a possible involvement of *M. hapla* in the Verticillium wilt disease of potato. Greenhouse and field experiments were therefore initiated to determine the possible role of *M. hapla* in Verticillium wilt of potato.

MATERIALS AND METHODS

Populations of *M. hapla* were maintained on tomato (*Lycopersicon esculentum* Mill. 'Bonny Best') in a greenhouse at 30 ± 2 C. Cultures of *V. albo-atrum*, both dark mycelial (DM) and microsclerotial (MS) isolates, were maintained on both potato-dextrose agar and sterilized oat straw.

Oat straw inoculum was prepared by inoculating potato-dextrose broth (PDB) with isolates of *V. albo-atrum* and incubating them at 24 C on a reciprocal action shaker. After 30 days, 125 ml of the PDB inoculum was poured over 500 g of sterile, air-dried, blenderized oat straw. Flasks containing the inoculated oat straw were shaken daily and incubated for 14 days. The colonized straw then was air-dried in paper bags and ground in a Wiley mill to pass through a sieve with a mesh of 0.107 cm^2. Inoculum was applied to the soil at 1 g/1,000 cc of steamed greenhouse-mix soil or to seed pieces by shaking the inoculum and seed pieces in a paper bag.

Nematode inoculum was prepared by separating tomato roots from soil 60–90 days after inoculation with fresh egg masses. Infected roots were washed, cut into 2–5 cm segments, placed in water, and shaken vigorously with a wrist action shaker for 30–45 min. Egg masses and small pieces of plant debris were collected on a sieve with a mesh of 0.16 cm^2. Egg masses were removed from root debris with fine tweezers and a dissecting microscope. Egg masses were stored in tap water at 2 C until used, usually within 24 hr of preparation. An average of 296 juveniles hatched in 10 days from the eggs in each egg mass incubated at 21 C. Either 5 or 25 egg masses per pot were mixed with sterile potting soil at the time of planting.

Uniform rooted Kennebec potato plant cuttings and cut Norland seed pieces were used in greenhouse experiments. One cutting or one seed piece was planted in a clay pot 10 or 13 cm in diameter, respectively. Aluminum foil was wrapped around the lower half of each pot to prevent contamination from the greenhouse bench. Plants were watered as necessary and fertilized with Hoagland's solutions biweekly and with soluble 20-10-10 (N-P-K) fertilizer monthly. All greenhouse experiments were carried out at 30 ± 2 C, and one series was replicated at 24 ± 2 C. All stock plants or seed pieces were indexed for the presence of *V. albo-atrum*, and only Verticillium-free stock was used.

Plants were assayed weekly for infection by *V. albo-atrum* by removing the lowermost petiole and placing five segments on either alcohol agar (18) or polygalacturonic acid agar (8). Greenhouse experiments were terminated after 80 days. Root systems were cut into 2–5 cm segments, placed in petri dishes partially filled with water, and agitated on a reciprocal action shaker. After 5–7 days, the roots were rinsed and the *M. hapla* juveniles in the water were counted. The roots were dried for 48 hr at 40 C and dry weights recorded.

Field tests were made in 1972 and 1973 near Cambridge, MN, in a field of Zimmerman sandy loam infested with the *M. hapla* and also with *V. albo-atrum*, DM and MS strains. Benomyl (Benlate 50 W)

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at 270 kg/ha, carbofuran (Furadan 10G) at 16.8 kg/ha, and phenamiphos (Nemacur 15 G) at 16.8 kg/ha were incorporated in the soil in bands 30 cm wide and approximately 15 cm deep with a rotary tiller. To compare residual effects of the treatment, the experimental area was divided in units that received treatments only in 1972, only in 1973, or in both years. An area 3 × 30 m was fumigated with methyl bromide plus 2% chloropicrin at 1 kg/20 m^2 in 1972. Care was taken to avoid subsequent contamination of this area with unfumigated soil.

Certified Norland and Norgold seed pieces cut from disease-free tubers were planted by hand 23 cm apart in rows 76 cm apart. Each treatment was a single 6-m row replicated three times. Plots were fertilized with 910 kg of 8-16-16 (N-P-K)/ha in 1972 and 1,600 kg of 8-10-16/ha in 1973. In addition, the plants were side-dressed with 204 kg of 34-0-0/ha after 30 days of growth in both 1972 and 1973.

One week before planting and harvest in 1972 and 1973, the soil was sampled to a depth of 20 cm with a Hoffer soil tube. Each soil sample was well mixed and subsampled for populations of *M.hapla* and *V. albo-atrum*. A 50 cm^3 portion of sieved soil was assayed for *M. hapla* using the Cornell pie pan technique (13). Populations of *V. albo-atrum* were determined with the Andersen sampler procedure described by Harrison and Livingston (9). The pathogenicity of every colony was not checked, but randomly selected isolates of both MS and DM types were pathogenic on potato.

The plots were rated visually at biweekly intervals in 1973 on a 0 to 6 scale (0 = 0% plants wilted, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, 5 = 100%, 6 = all plants dead). The disease ratings were summed at the end of the season to make a cumulative disease index.

In 1972, both varieties were harvested 95 days after planting when the plants were dead in all but the methyl-bromide treated plot. In 1973, the Norland potatoes were harvested 111 days after planting and the Norgold 126 days after planting. The entire 6 m of each replicate plot was harvested in 1972. In 1973 only the center 3 m of each plot was harvested to minimize the effects of chemicals spread by cultivation. Tubers were dug by hand from each plot and graded over a 4.7-cm diameter grading chain. Both total yield and yield of US No. 1 potatoes were recorded.

The 1972 and 1973 data were statistically analyzed by Duncan's multiple range test (6). Field data from 1973 were pooled regardless of treatment and analyzed by multiple linear regression analysis using the UMST500 computer program (1). The regression equation was of the form $\hat{Y} = b_o + b_1 \log_e N + b_2 \log_e V + b_3 N \log_e V$. $\hat{Y}$ is the dependent variable and is the predicted value for field; $\log_e N$ ($\log_e$ *M. hapla*/ 100 cc of soil) and $\log_e V$ ($\log_e$ *V. albo-atrum*/g of soil) are independent variables; and b_o, b_1, b_2, and b_3 are partial regression coefficients. The level of significance of the multiple correlation coefficient was determined by the F test for n −3 degrees of freedom.

RESULTS

V. albo-atrum, both DM and MS strains, was isolated from a greater percentage of the petioles of Norland potato plants in the greenhouse when *M. hapla* was present than when only fungal inoculum had been added (Fig. 1). The fungus was isolated 28 days sooner from Kennebec plants grown at 30 C than at 24 C when plants were inoculated with *V. albo-atrum* alone. *V. albo-atrum* was isolated 27 and 14 days sooner at 24 C and 30 C, respectively, from plants inoculated with *V. albo-atrum* plus five egg masses of *M. hapla* than from plants inoculated with *V. albo-atrum* alone. *V. albo-atrum* was isolated 22 and 12 days sooner at 24 and 30 C, respectively, when 25 egg masses of *M. hapla* were used in place of five egg masses (Fig. 2). The presence of *V. albo-atrum* greatly increased nematode reproduction on the potato plants at 24 C but not at 30 C (Fig. 3).

In 1973, all fungicide-nematicide treatments except the benomyl-carbofuran treatment significantly increased the yield of US No. 1 potatoes over the untreated plots for both Norgold (Table 1) and Norland (Table 2). Total yields were significantly increased over the untreated plots in all treatments except benomyl-carbofuran and benomyl-phenamiphos for Norgold (Table 1) and benomyl,

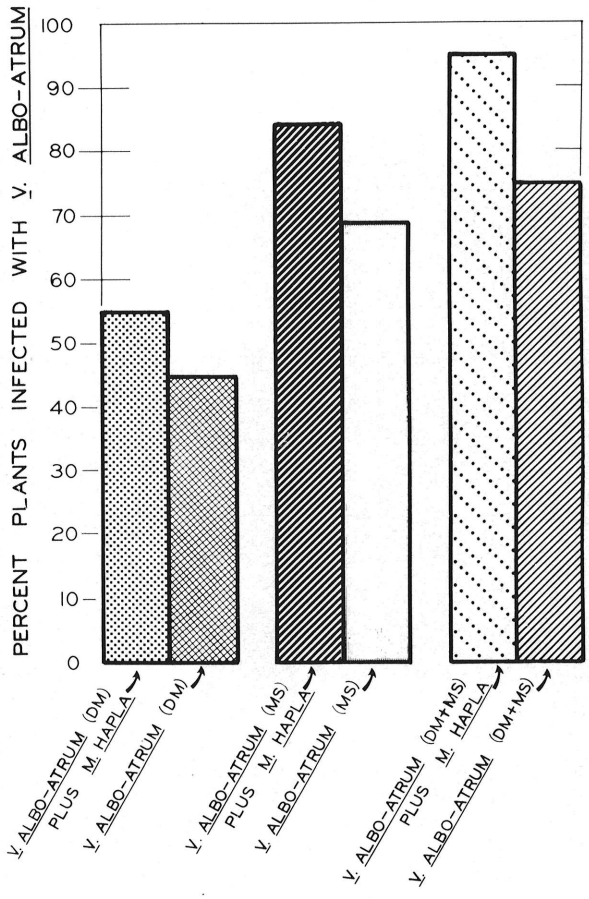

Fig. 1. Percent of Norland potato plants infected with *Verticillium albo-atrum*, dark mycelial and microsclerotial strains, as determined by recovery from petioles when grown in the presence of *Meloidogyne hapla* for 80 days at 24 C.

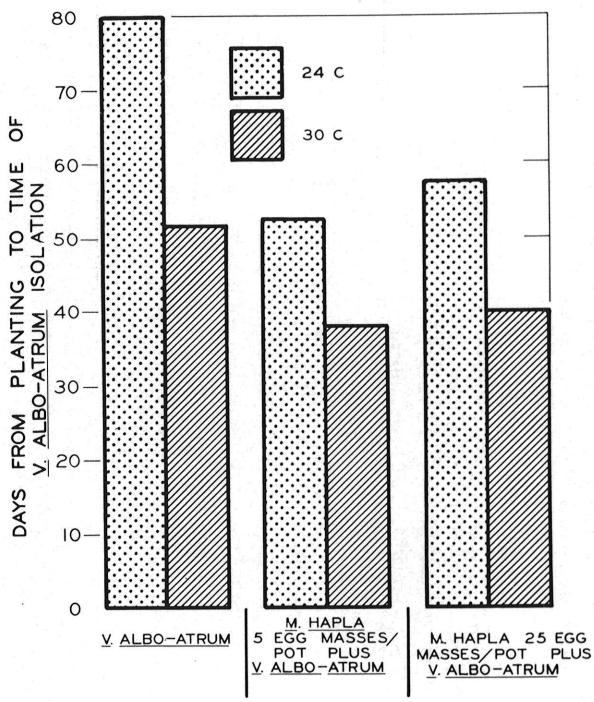

Fig. 2. Average number of days from planting to time of isolation of *Verticillium albo-atrum* from petioles of Kennebec potatoes as affected by temperature and presence of *Meloidogyne hapla*.

carbofuran, benomyl-carbofuran, and carbofuran-phenamiphos for Norland (Table 2). Greatest yield increases were in plots treated with a combination of benomyl-carbofuran-phenamiphos, methyl bromide, methyl bromide-carbofuran, and methyl bromide-phenamiphos-carbofuran-benomyl (Tables 1 and 2).

M. hapla populations were reduced by all treatments (Tables 1 and 2). Treatments that included methyl bromide reduced populations the most and benomyl the least for the variety Norland. Treatments that included methyl bromide reduced populations the most and the benomyl-carbofuran treatment the least for the variety Norgold. *M. hapla* populations were higher on the variety Norland than on the variety Norgold.

V. albo-atrum populations were lowest in treatments that included methyl bromide and highest in benomyl-carbofuran, carbofuran, and phenamiphos-carbofuran treatments. *V. albo-atrum* populations were similar for both varieties.

Total yields of US No. 1 of Norland and Norgold plants were negatively correlated with populations of *M. hapla* and *V. albo-atrum* in soil in the fall and also with disease ratings (Tables 1 and 2). The rankng of treatment yields was the same in 1972 as in 1973.

Yield data were not taken in 1972 from plots fumigated with methyl bromide because plants grown in these plots had little or no tuber set. When plots fumigated with methyl bromide in 1972 were planted in 1973 without further treatment, however, normal tuber set occurred. The only 1973 treatments that resulted in higher yield than methyl bromide in 1972 were the phenamiphos-carbofuran treatments (Tables 1 and 2). This combination did not affect the soil populations of "target organisms" significantly compared with the methyl bromide treatment alone (Table 1 and 2), and no effects on insects were observed that would explain the small but significant yield increases.

Populations of *M. hapla* were larger on Norland than on Norgold (Tables 1 and 2). Phenamiphos and carbofuran were equivalent in control of *M. hapla* on Norland, but phenamiphos

TABLE 1. Yield of Norgold potatoes, disease index, and populations of *Meloidogyne hapla* and *Verticillium albo-atrum* in soil treated with methyl bromide, benomyl, phenamiphos, and carbofuran alone and in combination in 1973

Treatment (kg/h)	Yield (kg/3m)		Disease[x] Index	*M. hapla* per 100 cc	*V. albo-atrum* per gram of soil
	US No. 1	Total			
Benomyl (270)	5.5 cd[y]	8.1 bc[y]	4.5	160 b[y]	352 b[y]
Benomyl and carbofuran (270, 16.8)	2.7 ab	5.1 a	16.4	432 d	809 c
Benomyl and phenamiphos (270, 16.8)	4.9 c	6.4 ab	15.0	113 b	412 b
Benomyl, carbofuran, and phenamiphos (270, 16.8, 16.8)	8.8 f	12.1 e	6.0	140 b	68 a
Carbofuran (16.8)	4.3 c	7.3 b	12.0	259 c	944 c
Carbofuran and phenamiphos (16.8, 16.8)	3.2 b	8.4 c	14.5	248 c	700 c
Phenamiphos (16.8)	4.5 c	7.2 b	14.7	116 b	434 b
Methyl bromide[z] (449)	7.3 e	10.0 d	2.3	52 a	64 a
Methyl bromide[z] and benomyl (449, 270)	8.4 ef	10.0 d	2.0	16 a	100 a
Methyl bromide[z] and carbofuran (449, 16.8)	7.9 e	10.5 d	4.0	25 a	22 a
Methyl bromide[z] and phenamiphos (449, 16.8)	7.5 e	10.0 d	3.0	20 a	34 a
Methyl bromide[z], benomyl, carbofuran, and phenamiphos (449, 270, 16.8, 16.8)	7.5 e	11.4 de	5.5	32 a	46 a
Methyl bromide[z], phenamiphos, and carbofuran (449, 16.8, 16.8)	10.5 g	11.8 e	2.0	43 a	50 a
Untreated	1.3 a	4.0 a	20.0	651 d	2,735 d

[x]Cumulative disease index = sum of eight biweekly ratings where 0 = 0%, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, 5 = 100% plants showing wilt, 6 = all plants dead.
[y]Numbers flanked by the same letter do not differ significantly at $P = 0.05$.
[z]Fumigated in 1972.

TABLE 2. Yield of Norland potatoes, disease index, and population of *Meloidogyne hapla* and *Verticillium albo-atrum* in soil treated with methyl bromide, benomyl, phenamiphos, and carbofuran alone and in combination in 1973

Treatment (kg/h)	Yield (kg/3 m)		Disease[x] Index	*M. hapla* per 100 cc	*V. albo-atrum* per gram of soil
	US No. 1	Total			
Benomyl (270)	4.5 b[y]	6.5 a[y]	13.0	1,710 e[y]	546 b[y]
Benomyl and carbofuran (270, 16.8)	3.4 a	4.7 a	16.5	1,000 d	1,346 c
Benomyl and phenamiphos (270, 16.8)	6.9 cd	8.6 b	9.8	410 c	525 b
Benomyl, carbofuran, and phenamiphos (270, 16.8, 16.8)	9.6 de	11.2 c	8.0	60 a	200 ab
Carbofuran (16.8)	6.1 c	7.9 ab	13.3	190 b	1,540 c
Carbofuran and phenamiphos (16.8, 16.8)	5.5 bc	6.3 a	12.0	136 ab	1,466 c
Phenamiphos (16.8)	8.2 d	10.0 bc	12.1	209 b	230 ab
Methyl bromide[z] (449)	9.6 de	11.1 c	2.5	48 a	57 a
Methyl bromide[z] and benomyl (449, 270)	6.9 cd	8.9 b	5.0	37 a	27 a
Methyl bromide[z] and carbofuran (449, 16.8)	8.4 d	10.2 bc	8.0	88 a	5 a
Methyl bromide[z] and phenamiphos (449, 16.8)	7.2 cd	8.6 b	7.0	90 a	39 a
Methyl bromide[z], benomyl, carbofuran, and phenamiphos (449, 270, 16.8, 16.8)	10.4 e	12.0 cd	8.5	23 a	10 a
Methyl bromide[z], phenamiphos and carbofuran (449, 16.8, 16.8)	10.7 e	12.7 d	3.5	0 a	18 a
Untreated	3.8 a	5.2 a	15.0	6,458 f	2,466 d

[x]Cumulative disease index = sum of six biweekly ratings where 0 = 0%, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, 5 = 100% plants showing wilt, 6 = all plants dead.
[y]Numbers flanked by the same letter do not differ significantly at $P = 0.05$.
[z]Fumigated in 1972.

provided significantly better control than carbofuran on Norgold. Benomyl significantly reduced *M. hapla* populations when compared with the untreated plots (Tables 1 and 2). Populations of *M. hapla* in the fall of 1973 were 41.5% greater in plots treated the previous year with carbofuran than in plots treated with phenamiphos in 1972 but not 1973.

The degree of twisting of the response surface (Fig. 4 and 5) corresponds to the size of the interaction term. Norgold interaction term −0.4220 has a response surface with a greater degree of twist than Norland, interaction term −0.1868. The interaction had its greatest effect at the largest populations of *M. hapla* and *V. albo-atrum* for both cultivars.

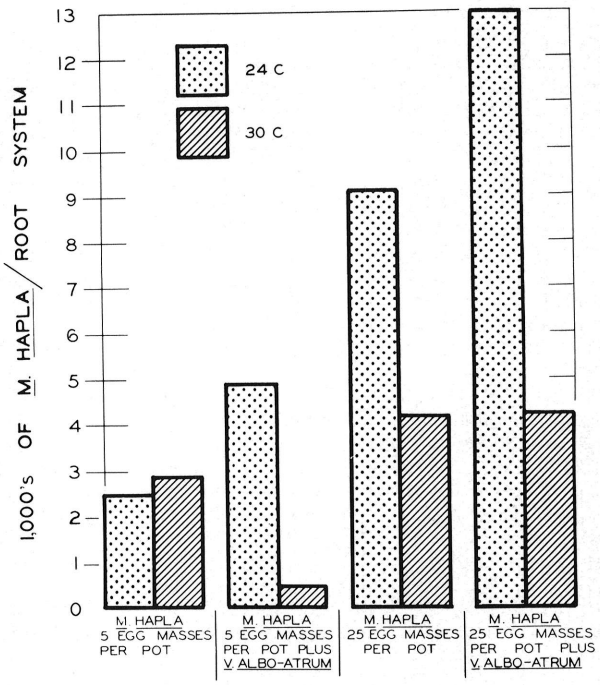

Fig. 3. Populations of *Meloidogyne hapla* on Kennebec potato plants after growth for 80 days as influenced by temperature, presence of *Verticillium albo-atrum*, and primary inoculum concentration.

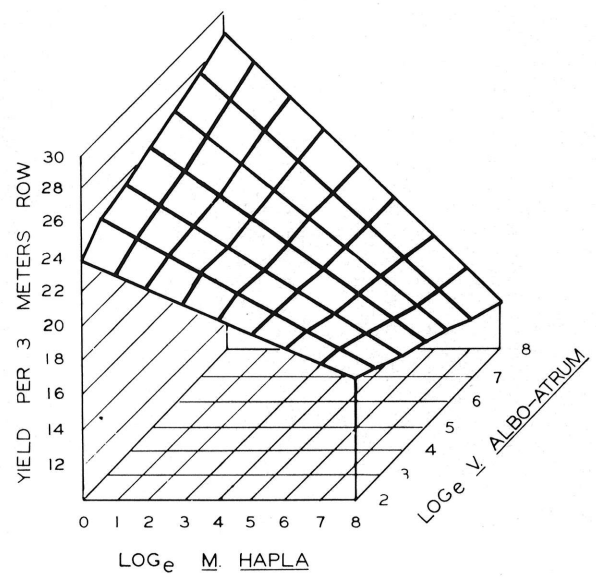

Fig. 4. Response surface developed by substitution of observed population values of *Meloidogyne hapla* and *Verticillium albo-atrum* into the regression equation Yield = $b_o + b_1 \log_e$ *M. hapla*/100 cc + $b_2 \log_e$ *V. albo-atrum*/g + $b_3 \log_e$ *M. hapla*/100 cc *V. albo-atrum*/g for Norland potatoes.

R and R^2 values and range variables used in multiple regression analysis are given in Table 3. High negative correlation −0.73 (Norland) and −0.81 (Norgold) of $\log_e$ *M. hapla* per 100 cc of soil *V. albo-atrum* per 100 g of soil were determined over the range of pathogen density observed in the experiment.

DISCUSSION

Data from glasshouse and field experiments indicate that *V. albo-atrum* was isolated sooner from plants co-infected with *M. hapla* than from plants infected with *V. albo-atrum* alone. The effects of *V. albo-atrum* infection also were more severe, as measured by yield and onset of wilting in the presence of *M. hapla*, than in plants infected with *V. albo-atrum* alone. Therefore, the control of Verticillium wilt of potato achieved by soil treatments with systemic insecticides (11,12) in the presence of *M. hapla* may have resulted from control of the nematode rather than of *V. albo-atrum*.

Larger populations of *M. hapla* developed at 24 C than at 30 C; 24 C was known to be more favorable for the development of *M. hapla* (20). The earlier isolation of *V. albo-atrum* at 30 C, however, possibly reflects the increased transpiration of plants at this temperature. An increase in transpiration may increase the movement of the fungus upward in the plant.

The increase in disease index with increased populations of *M. hapla* and *V. albo-atrum* and the increased *M. hapla* populations on *V. albo-atrum*-infected plants indicates that the relationship

TABLE 3. Correlation coefficient (R and R^2) values and range variable used in multiple regression analysis

Dependent variable	Independent variable[a]	R	% of Variance explained (R^2)	Range[a]	n
Yield	$\log_e$N	−0.73	54	N 0–10,000	46
Norland	$\log_e$V			V 0– 2,800	
Yield	$\log_e$N	−0.81	66	N 0– 3,800	46
Norgold	$\log_e$V			V 0– 2,900	

[a]N = *Meloidogyne hapla* per 100 cc of soil. V = *Verticillium albo-atrum* per gram of soil.

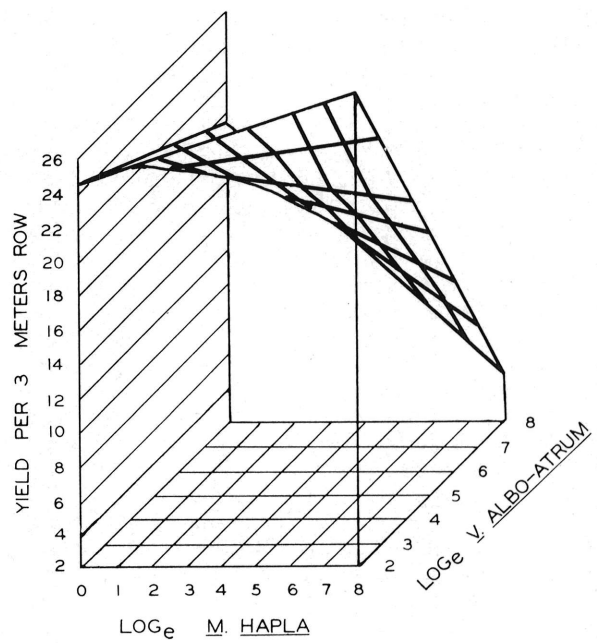

Fig. 5. Response surface developed by substitution of observed population values of *Meloidogyne hapla* and *Verticillium albo-atrum* into the regression equation Yield = $b_o + b_1 \log_e$ *M. hapla*/100 cc + $b_2 \log_e$ *V. albo-atrum*/g + $b_3 \log_e$ *M. hapla*/100 cc $\log_e$, *V. albo-atrum*/g for Norgold potatoes.

between these organisms and the disease is synergistic on both Norgold and Norland potatoes. However, the different interaction terms, −0.4220 (Norgold) and −0.1868 (Norland) derived from multiple regression analysis of field data suggest that the degree of interaction is different between the two organisms and the disease in these two cultivars. The effects of increasing *M. hapla* density and increasing *V. albo-atrum* density were much greater for the Norgold variety than for the Norland variety. The explanation for this may be simple genetic differences or differences in variety maturation. Norland is an early and Norgold a late maturing cultivar.

Increased plant top weights were noted on the greenhouse-grown plants inoculated with *M. hapla* alone. Although tuber weights did not increase in the greenhouse, larger plants might produce greater tuber yields. *M. hapla* is known to stimulate branch root formation; thus, the larger root system might be expected to support more rapid plant development initially, promoting higher yields. Growth stimulation by low populations of plant parasitic nematodes has been observed in potato (7). The increased yield for Norgold predicted by regression may, therefore, be explained on this basis. The increase in plant top weight and potential increase in branch root formation of plants infected with *M.hapla* may have allowed greater water uptake and transpiration, thus speeding the movement of *V. albo-atrum* in the xylem.

The synergistic interaction between *M. hapla* and *V. albo-atrum* in the Verticillium wilt of potato is similar to the synergism of *Pratylenchus penetrans* and *V. albo-atrum* on eggplant (14,17) and the effects of *P. minyus* on Verticillium wilt of peppermint (7), where the presence of the nematode also increased the incidence and severity of Verticillium wilt symptoms and reduced the incubation period for Verticillium wilt. These studies also showed increased nematode populations on plants infected with *V. albo-atrum*. This interaction has now been shown in the greenhouse and in the field with both MS and DM strains of the fungus.

The use of selective pesticides to study a disease complex is not new (3). The technique was useful in evaluating the nematode-fungus relationship studied here and shows potential for use in evaluating other such interactions. The fact that benomyl reduces *M. hapla* populations demonstrates the importance of evaluating the effect of the "selective" pesticide candidate on all potential interactants.

Although not examined in this study, the mechanism by which these organisms interact synergistically may be partially explained by observations of other fungus-*Meloidogyne* interactions. For example, the giant cell has been implicated as a favorable infection court for *Fusarium oxysporum* f. sp. *vasinfectum*, a vascular pathogen of cotton (15). A similar mechanism may be involved with *V. albo-atrum*, which may invade through wounds.

This study suggests, however, that infection by *V. albo-atrum* may not be the site of *M. hapla* interaction, because the difference observed in the presence of the nematode was in the time of isolation of *V. albo-atrum* from the petioles. After 80 days, the fungus could be isolated from plants with and without *M. hapla*, but the fungus was detected earlier and in a greater percentage of plants only in the presence of *M. hapla*. As previously mentioned, the nematode may influence movement of the fungus in the plant after infection. The influence on movement of *V. albo-atrum* in the xylem could be due to increased transpiration and hence speed of upward movement of *V. albo-atrum* or due to interference of nematode infection by the host occlusion reaction that normally slows the upward movement of vascular parasites. These hypotheses were suggested by other researchers (2).

The interaction between *M. hapla* and *V. albo-atrum* may explain, in part, yield reductions more severe than *V. albo-atrum* might cause alone. Robinson et al (19) reported that 20–25% yield reductions of potato attributed to *V. albo-atrum* are common, findings that support our predictions of 0–19% yield reductions due to the fungus alone. Yield decreases greater than 20–25% may reflect the interaction between *V. albo-atrum* and *M. hapla*, *P. penetrans* (16), a combination of *M. hapla* and *P. penetrans*, or other nematodes. Because *M. hapla* is widely distributed throughout areas where potatoes are grown in the USA and Canada, control of this nematode and other nematodes must be considered when attempting to control Verticillium wilt.

The equation $\hat{Y} = b_o + b_1 \log_e N + b_2 \log_e V + b_3 \log_e N \log_e V$, derived from the multiple linear regresion analysis of the field plot data may be useful for predicting yields and pathogen populations.

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