Verticillium dahliae and *Pratylenchus penetrans*: Interactions in the Early Dying Complex of Potato in Ohio

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ABSTRACT

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In 1978, 1979, and 1980, field microplots in fumigated organic soil were used to evaluate the effects of *Pratylenchus penetrans* and *Verticillium dahliae* on growth and yield of potato. Data collected in 1980 established that potato early dying can be caused by a nematode-fungus interaction. All six combinations of low, medium, and high population densities of nematodes ($\sim$15, 50, and 150/100 cm^3 soil) with low and high fungus inoculum densities (6.6 and 17.1 microsclerotia per 10 g dry soil) reduced plant top, root, and tuber weights 75, 60, and 36%, respectively, compared with plants grown in uninfested soil. Top and root weights were not reduced by low levels of either pathogen alone, but were reduced 40 and 36%, respectively, by the medium and high levels. Excepting a 12% reduction with the high nematode treatment, tuber weights were not reduced by any single pathogen treatment. In 1978 and 1979, initial populations of nematodes alone, ranging from 7 to 260/100 cm^3 soil did not reduce tuber yield. In 1979, 75 and 260 nematodes per 100 cm^3 soil reduced root weight $\sim$25%. In 1979, all levels of fungus alone reduced top and root weight, but only high fungus inoculum density reduced tuber weight. Seasonal rainfall was 129 and 104 mm above average in 1979 and 1980, respectively, and 107 mm below average in 1978.

Additional key words: crop loss assessment, *Pratylenchus crenatus*, *Pratylenchus scribneri*, microplots

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Under environmental conditions favorable for continued growth, potato (*Solanum tuberosum* L.) vines can become chlorotic, wilt, and die 4–6 wk prior to expected maturity, often resulting in significant yield loss. This syndrome, called "early dying" or "early maturity wilt" has been reported from most potato-growing regions (7,10,19,25,28–31,34). It is a common problem of intensive potato production in Ohio, particularly with the early market cultivar Superior. Yield losses of this cultivar have exceeded 11 tonnes per hectare (28).

Potato early dying is generally ascribed to an interaction between the lesion nematode *Pratylenchus penetrans* (Cobb) Filipj. and Schuur.-Stekh. and the vascular wilt fungus *Verticillium dahliae* Kleb. (7,10,19,28,29). However, the etiology has not been conclusively determined. In 1978, Burpee and Bloom (4) working under glasshouse conditions could not demonstrate an interaction of *Pratylenchus* and *Verticillium*. In another glasshouse study, Gould (10) demonstrated increased severity of Verticillium wilt symptoms in the presence of *P. penetrans*, but did not reisolate *Verticillium* or report tuber yields. Morsink (19) reported greater suppression in tuber yield in the presence of both organisms than in the presence of the fungus alone; however, results were not reproducible when microsclerotia were used as fungal inoculum and nematode levels were varied. Having used aldicarb in a field infested with the nematode and fungus, Schultz and Cetas (29) reported decreased population densities of *Pratylenchus*, increased yield, but no decrease in Verticillium wilt symptoms. Stem-end browning was considered proof of infection by *Verticillium*. Initial populations of *Pratylenchus* and *Verticillium* were not recorded.

While *P. penetrans* and *V. dahliae* are implicated in potato early dying in Ohio (28), New York (29), and Idaho (7), the etiology may vary in each geographical location (18,25,30,31,34). In Israel, *P. thornei* interacts with *V. dahliae* resulting in earlier incidence and increased severity of Verticillium wilt (30). In Oregon, *Erwinia carotovora* and *V. dahliae* may be the leading causes of early dying (25). Reports from Indiana indicate that the fungus *Colletotrichum*

coccodes may be an additional component (31). In Florida, nematode genera other than *Pratylenchus* may interact with *V. dahliae* to cause early dying (34). In Wisconsin, *V. dahliae*, *E. carotovora* var. *carotovora*, *Fusarium* spp., and *C. coccodes* are considered the components involved in the early dying complex (18).

Whether *Pratylenchus* or *Verticillium* or both are implicated, information is generally lacking concerning their roles separately or in combination on potato yield loss. Specifically lacking are quantitative data, generated in different soil types across many growing seasons, relating pathogen population densities at planting to potato tuber loss at harvest.

Field microplots offer an effective technique to obtain such data. Potatoes grow well in microplots and can be maintained under field conditions while being exposed to defined population densities of the desired pathogens. Field microplots have been used to assess potato crop loss from *P. penetrans* (2,22). Olthof and Potter (22) reported losses of approximately 40% in marketable tuber weight of cv. Sebago from 6,000 to 18,000 nematodes per kilogram of Vineland loam for one season. Bernard and Laughlin (2) reported losses of approximately 28% in fresh weight of cultivar Superior tubers with population densities ranging from 38 to 211 nematodes per 100 cm^3 sandy clay loam in one season. To date, microplots have not been used to assess potato crop loss from *Verticillium*.

Therefore, since conclusive etiological studies on early dying were lacking, and since more quantitative crop loss data concerning *Pratylenchus* species and *V. dahliae* were needed, a long-term study was initiated in 1978 in Ohio to generate these kinds of data. A microplot technique was refined and is being employed on sandy loam, silt loam, and organic (muck) soil; the ultimate goal of the long-term study is to develop a predictive system for crop loss due to *Pratylenchus* species and *V. dahliae* on major Ohio potato soils. This paper describes the microplot system being used, and establishes the etiology of, and extent of crop loss from early dying in organic soil.

MATERIALS AND METHODS

During 1978, 1979, and 1980 the effects of *P. penetrans* and *V. dahliae* alone and in combination on the growth and yield of cultivar Superior potato were assessed in field microplots in Rifle

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peat at the Muck Crops Branch of the Ohio Agricultural Research and Development Center in Huron County, OH. In 1978, the effects of *P. penetrans* alone were evaluated using four population densities of the nematodes and a control soil free of plant parasitic nematodes. This study, with the addition of three inoculum densities of *V. dahliae*, was repeated in 1979. In 1980, the effects of three population densities of *P. penetrans*, two inoculum densities of *V. dahliae*, and all combinations thereof were compared with a pathogen-free soil.

Each year, the basic replicate in the experimental design was a single tile microplot containing one potato plant. Each treatment consisted of 15-replicate microplots completely randomized with other treatments among three rows in the field.

Seed potato and inoculum production. In 1978, "certified" cultivar Superior seed potatoes were indexed for bacteria, *Verticillium*, *Fusarium*, and *Colletotrichum* on potato-dextrose agar (PDA), alcohol agar (21), Komada's medium (15), and Farley's medium (9), respectively, and only *Verticillium*- and *Colletotrichum*-free seed pieces were used in microplot tiles. In the fall and winter of 1979 and 1980, seed tubers free of fungi and bacteria were produced in pots in the greenhouse from stem cuttings indexed on PDA and alcohol agar. If microbial growth was observed from plated stem tissue on either medium, the corresponding stem cutting was discarded. Plants were not indexed for viruses. However any abnormally colored or textured plant was discarded. Insects were carefully controlled by spraying. When plants had grown to maturity, tubers were harvested and stored at 5 C.

Four to six weeks prior to planting, seed tubers were removed from storage, incubated for 10–14 days at room temperature to allow for sprout development, and returned to 5 C. Three to five days prior to planting, tubers were washed and single-sprout seed pieces were made using a 2.54-cm metal scoop. A representative sample of microplot seed pieces was indexed as described above to assure that they were free of fungi and bacteria.

P. penetrans, originally obtained from W. F. Mai, Cornell University, was grown in monoxenic alfalfa callus culture for use as inoculum in the microplots. In preparation for each spring planting, nematodes were subcultured in November and in February according to the methods of Riedel et al (26).

Microsclerotia of *V. dahliae* for use as inoculum in the microplots were grown from a combination of three isolates obtained from Superior potato stems in Champaign, Seneca, and Portage counties, Ohio. Using a modification of Green's technique (11), inoculum was produced each year in February and March in twice sterilized soil amended with dilute (1:10) Czapeck's broth. Amended soil in each of 60 2-L flasks was inoculated with 2 1-cm square blocks of alcohol agar cultures of *V. dahliae*. Twenty flasks were inoculated with one isolate, 20 with another, and 20 with a third. The flasks were sealed with foil, and incubated 4–6 wk in the dark at room temperature. Afterwards, soil was thoroughly air-dried and soil infested with microsclerotia of the three isolates was mixed. Dry soil was stored at room temperature for at least 10 days prior to use.

Plot establishment and maintenance. Each May, when soil temperatures had reached 10 C at 30 cm depth, three 2 × 50 m soil strips were fumigated with methyl bromide (1978) or 66% methyl bromide-34% chloropicrin (1979 and 1980) at 349 kg/hectare to a depth of 30 cm.

Microplots were established on 51 cm centers down the middle of the fumigated strips. Open-ended unglazed, clay drain tiles (30 cm long × 25 cm internal diameter) were placed in holes dug to plow depth (25 cm). Fumigated soil, gathered during the tile sinking process and to be later infested with nematode and/or fungus, was collected in metal bushel baskets. At the same time, each tile was backfilled to one third of its 15 L capacity, with 5 L of fumigated soil.

Twenty-four hours prior to soil infestation, contents of 64 nematode culture tubes were blended for 1 sec in a Waring Blendor and hand-mixed into 10 L of fumigated soil. Similarly, 30 tubes of alfalfa callus without nematodes were mixed into 5 L of fumigated soil as an uninfested control. The soil was incubated overnight at

room temperature in plastic bags to allow the nematodes to redistribute themselves more evenly.

A 28 L capacity twin shell blender (Patterson-Kelly Co., E. Stroudsburg, PA 18301) was used to thoroughly mix quantities of concentrated nematode and/or microsclerotial soil with 20-L volumes of fumigated soil. After mixing each 20-L batch, two soil samples (~200 cm³/sample) were taken and refrigerated in plastic bags at 5 C for later assay of actual initial population densities of *P. penetrans* and *V. dahliae*. Galvanized steel bushel baskets of infested soil were covered with clear plastic and stored overnight at room temperature.

The following day, each microplot tile was filled with 10 L of infested soil and planted with a bacteria- and fungus-free seed piece at 2–3 cm depth. Foundation-grade cultivar Superior seed pieces were planted between each tile and in rows approximately 90 cm from the tile centers on either side of each row of tiles, so that plant spacing would approximate a commercial spacing of 25 cm apart in rows 90 cm apart. Plant dates were: 14 June 1978; 24 May 1979; and 23 May 1980. Maintenance during the growing season followed standard commercial practice, except that no insecticides with nematicidal properties were used.

Assays. Initial population densities of *P. penetrans* and *V. dahliae* were determined from samples taken when fumigated soil was infested. *P. penetrans* was extracted for 24 hr from 100 cm³ of the sample soil using a modified Baermann funnel technique (32). The rest of each sample was air-dried for at least 1 wk prior to assay for *V. dahliae*. Two different techniques were used to quantify microsclerotia of *V. dahliae* in soil. In 1979, a soil dilution plating technique in alcohol agar was used. In 1980, a modified Ashworth-Huisman technique (1,13) was adopted because of dissatisfaction with the previous method. Ten grams of air-dried soil was washed through nested screens with 125-μm and 37-μm openings. The residue on the 37-μm screen was surface sterilized 10 sec in 0.5% NaOCl, rinsed, and washed into a 50-ml beaker where residue and water totaled 15–20 ml. Using a spoon, this was plated onto 10 agar plates prepared as follows: 2 g NaNO₃, 0.5 g KCl, 0.5 g MgSO₄ · 7 H₂O, and 0.015 g of FeSO₄ were dissolved in 400 ml distilled water and set aside. Five grams of polygalacturonic acid and 15 g agar were dissolved in 500 ml of boiling distilled water. The two solutions were mixed and the pH adjusted to 5.0 with 1 M NaOH. The 900 ml of solution and 100 ml of distilled water plus 1.0 ml tergitol NPX were autoclaved separately. After both solutions cooled to 50 C, they were combined, and 200 mg of streptomycin SO₄ was added.

After 7–10 days incubation at room temperature, soil was washed from the agar surface. Each colony of *V. dahliae* in the agar was presumed to have originated from a single microsclerotium. The sum of colonies counted on each set of 10 agar plates equaled the number of microsclerotia in each original 10-g soil sample.

Plot harvest and analysis. Thirteen weeks after planting, microplots were harvested. Disease severity was rated visually in the field on a scale of 0 (healthy) to 3 (dead). Vines were then cut at the soil line and weighed. A 15-cm section was removed from the lower part of the main stem from each plant and saved for isolation of *V. dahliae*. Tiles were then lifted by hand and the contents of each were emptied into a bushel basket. Roots, tubers, and a representative soil sample were collected from each tile. Samples were stored at 5 C until processing.

When processed, tubers and roots were washed and fresh weights recorded separately. All the roots and 100 cm³ of soil from each microplot were extracted separately for nematodes by using modified Baerman funnels as previously described. Potato stems were surface sterilized in 0.5% NaOCl, rinsed in tap water, and a thin section was placed on alcohol agar to check for infection by *V. dahliae*. Plates were incubated at room temperature and evaluated after 1 and 2 wk.

RESULTS

In initial studies in 1978, nematode population densities increased fivefold to 10-fold during the 13-wk growing season, but did not reduce potato growth or yield at any population level tested

TABLE 1. Initial and final population densities of *Pratylenchus penetrans* (P) or *Verticillium dahliae* (V) and their effects on plant top, root, and tuber weights at harvest and disease severity of potatoes grown in microplots on Rifle peat in Ohio in 1978 and 1979

Year and treatments	Populations of P:			Disease severity[w]	Fresh wt (g) per plant:		
	Initial (per cm³ soil)	Final (per cm³ soil)	Final (per g root)		Top	Root	Tuber
1978							
Uninoculated control	...	...	...	...	565 a	6.1 a	907 a
High P	68[x] a[y]	321 a	114.2 a	...	200 a	3.8 a	612 a
Medium high P	33 b	171 b	33.0 b	...	280 a	4.0 a	636 a
Medium P	34 b	212 b	40.7 b	...	578 a	5.0 a	890 a
Low P	7 c	72 c	5.7 b	...	804 a	8.0 a	943 a
1979							
Uninoculated control	...	...	...	2.0 a	574 a	13.1 a	766 abc
High P	260[z] a	1,021 a	231.3 a	1.8 a	489 ab	10.3 b	709 bc
Medium high P	118 b	697 b	92.7 b	2.0 a	575 a	11.4 ab	808 ab
Medium P	75 bc	521 c	83.5 b	2.0 a	517 a	10.0 b	685 bc
Low P	42 c	296 d	30.9 c	1.9 a	585 a	10.9 ab	855 a
High V	...	...	...	2.0 a	239 d	3.4 d	525 d
Medium V	...	...	...	1.5 a	350 cd	5.9 c	630 cd
Low V	...	...	...	1.4 a	381 bc	6.1 c	682 bc

[w] Plants were rated on a scale: 0 (no disease) to 3 (complete necrosis) based on a combination of wilting, chlorosis, and necrosis.
[x] In the 1978 data, values in columns one and two to seven are the means of eight and nine samples, respectively.
[y] Within data for 1 yr, values followed by the same letter are not significantly different according to Duncan's multiple range test, *P* = 0.05.
[z] In the 1979 data, values in columns one and two to seven are the means of eight and 15 samples, respectively.

TABLE 2. Seasonal rainfall at microplot location in Huron County, OH

Month	1978		1979		1980	
	Amount (mm)	Deviation[a] (mm)	Amount (mm)	Deviation (mm)	Amount (mm)	Deviation (mm)
May	76	−12	134	+46	79	− 9
June	66	−42	117	+ 9	166	+58
July	33	−59	117	+25	130	+38
August	95	+ 6	138	+49	108	+19
Total	270	−107	506	+129	483	+104

[a] Deviation from long-term U.S. Weather Bureau average.

(Table 1). In 1979, initial population densities of nematodes fourfold higher than those in 1978 also failed to reduce plant top or tuber weight (Table 1). High and medium populations did, however, significantly reduce root weight approximately 25%. As in 1978, final 1979 soil populations increased fourfold to sevenfold, and high populations were detected in the roots both years (Table 1). Total rainfall in 1979 from May through August was 506 mm, approximately 129 mm above the long-term average, compared to a total of 270 mm in 1978, which was 107 mm below the long-term average (Table 2).

The 1979 initial inoculum levels of *V. dahliae* were 9,000, 900, or 90 microsclerotia per cubic centimeter of dry soil. *V. dahliae* was not detected in uninfested control soil or in potato seed pieces used in the microplots. All three tested inoculum levels of *V. dahliae* significantly reduced plant top and root weight as compared to control plants, however, only the high level significantly decreased tuber weight, causing a 30% yield reduction (Table 1). At harvest, *V. dahliae* was isolated from 67, 93, and 100% of the plants in the low, medium, and high treatments of *V. dahliae*, respectively, and on the average, from 17% of plants in other treatments. Neither *V. dahliae* nor *P. penetrans* increased disease severity as measured by symptoms.

The 1980 initial population densities of *P. penetrans* and initial inoculum levels of *V. dahliae* are given in Table 3. Background microsclerotia of *V. dahliae* were detected in fumigated control soil at 0.2 per 10 g of soil, (0.03 times the lowest treatment), and no plant-parasitic nematodes were detected. *V. dahliae* was detected in 4% of the potato seed pieces used to plant the microplots.

In 1980, in all treatments infested with a *P. penetrans*-*V. dahliae* combination, plant top, root, and tuber weights were reduced an average of 75, 60, and 36%, respectively, over plants grown in uninfested soil (Table 3). Top and root weights were not reduced by

low levels of either pathogen alone, but were reduced 40 and 36%, respectively, by medium and high levels of both combined. With the exception of the high nematode treatment, tuber weight was not reduced by any single-pathogen treatment. At harvest, disease severity in all combination treatments was increased approximately fourfold over the control treatment, while the single pathogen treatments, except for the low inoculum level of *V. dahliae*, increased disease severity approximately two to three times. While 'early dying' symptoms (chlorosis, wilting, and necrosis) were observed in combination treatments but not in single-pathogen or the control treatments as early as 4 wk prior to harvest, a quantitative rating was not done since it would have involved considerable damage to vines and the closed canopy.

In *V. dahliae*-*P. penetrans* combination treatments, final soil and root population densities of *P. penetrans* were approximately 50% less than those in comparable treatments with the nematode alone. *V. dahliae* was recovered from 47–60% of the plants in plots not treated with *Verticillium*, and 73–100% of the plants inoculated with *V. dahliae*. Total May through August rainfall was 483 mm, approximately 104 mm above average (Table 2). On 7 July, 50 mm of rain fell in 30 min. Microplots were under water for 2 hr.

DISCUSSION

In 1980, potato early dying resulted from an interaction between *P. penetrans* and *V. dahliae* at population densities that individually caused no damage. Depending on initial pathogen population densities and the parameters measured, the degree of interaction observed ranged from less than completely additive to synergistic. In 1980, all combination treatments containing one or both of the low population levels of *P. penetrans* or *V. dahliae* caused a synergistic reduction in plant top, root, and tuber weights, and accelerated vine maturity. Similar results have been found with flax (6), where the combined effect of low inoculum levels of *P. penetrans* and *V. dahliae* on stem length and wilting was also synergistic. The synergistic effect was lost however, as inoculum levels increased. This pattern, which occurred in our study as well, is to be expected since the greatest likelihood of synergism exists when the component pathogens are at population levels that independently cause little or no effect.

The potential of *V. dahliae* to interact with other species of *Pratylenchus* found in Ohio fields is unanswered. Müller's (20) report that *P. penetrans* and *P. vulnus*, but not *P. fallax*, *P. thornei*, or *P. crenatus*, interacted with *Verticillium* on *Impatiens balsamina* suggests that interactions may be highly specific. In Ohio, because *P. crenatus*, *P. penetrans*, and *P. scribneri* were detected in 81, 42,

and 31%, respectively, of the cultivar Superior fields (3), work has been initiated to determine the potential of *P. crenatus*, and *P. scribneri* to interact with *V. dahliae*, and these will be the subjects of future reports.

Although it is still too early to predict potato loss from initial population densities of *P. penetrans* and *V. dahliae*, current results suggest that in dry years, a moderate population of the nematode (~75/100 cm³ soil) may cause a yield loss, whereas in wet years, much higher population densities (up to 260/100 cm³ soil) are not damaging. In contrast, Bernard and Laughlin (2) reported a 28% yield reduction of cultivar Superior in microplots on sandy clay loam from as few as 38 nematodes per 100 cm³ soil. Bernard and Laughlin determined at-plant populations using a 30-day bioassay to navy bean. This technique may have resulted in population estimates lower than those in microplot soil. This may account for the yield losses reported at low populations. Olthof and Potter (22) reported a 34% yield reduction of cultivar Sebago in silt loam with 6,000 *Pratylenchus* per kilogram of soil. Comparison of our results to these data, however, is impossible unless nematodes per unit weight of soil can be translated to nematodes per unit volume of soil.

The data collected in 1980 in plots inoculated with *V. dahliae* alone, suggest that in wet years in muck soil, low population densities of the fungus (6.6–17.1 microsclerotia per 10 g of soil) do not cause tuber yield loss. However, in the presence of even low numbers of *P. penetrans*, *V. dahliae* may cause yield losses even in a wet year. This is in contrast to the report that high population densities of *P. thornei* were required to increase severity of Verticillium wilt of potato in Israel (16).

It is difficult to determine if the *V. dahliae* infections in uninoculated treatments occurred from the background microsclerotia or from soil mixing from outside the plot during the July 7 rain. The 4% infection of 1980 microplot seed tubers is not seen as a significant source of inoculum in uninoculated treatments due to Robinson and Ayers' (27) report that only 12–24% of internally infected tubers give rise to wilted plants.

An interesting observation in this study is the suppression of soil and root populations of *P. penetrans* in the presence of *V. dahliae*. Burpee and Bloom (4) reported this also. Siti (30) however, reported that *P. penetrans* population densities were increased in *Verticillium*-infected potato plants. Plants infected with *V. dahliae* may not supply suitable or sufficient food for an obligate parasite like *P. penetrans* to maintain high reproductive levels.

The microplot system used in this study, although laborious, allows for the combination of precise experimental control with commercial growing conditions. This is unobtainable with greenhouse or traditional field work. Experiments based on containerized greenhouse plants have the advantage of the precise inoculum control needed for crop loss prediction, however, they have the disadvantage of artificial growing conditions, poor tuber yield, and potentially exaggerated effects of root and wilt pathogens due to a restricted root system (4,10,14,19,23,33). Studies in naturally infested fields have the advantage of realistic growing conditions and a commercial yield, however control over which pathogens are present and their population sizes is lost, allowing for correlational data at best (24). The common use of fumigants in field studies has the disadvantage of frequently giving yield increases that cannot be adequately explained in terms of control of the target organism since many nontarget organisms may also be controlled (5,8,12,17,29,30,33). The field microplot system used in Ohio combines the advantages of the field and greenhouse. Simulation of commercial spacing and production produces uninfested microplot tuber yields that exceed the expected commercial yield of 2.98 kg per meter of row. Experimental control begins with effective high-volatility fumigation and reinfesting with only the desired pathogens. Because initial population densities are the basis for predicting yield loss from soil pathogens like *P. penetrans* and *V. dahliae*, it is necessary that they be statistically defined so that yield loss can be related to actual differences in initial populations.

Probably the addition of nematodes in standardized monoxenic alfalfa callus culture directly to the microplot soil is the most important step in obtaining statistical definition for the initial *P. penetrans* populations. This standardization, which is difficult with pot cultures and impossible with natural field soil, allows for the replicability of statistically defined populations needed for this work. With both pathogens, standardized inoculum sources, good soil mixing procedures and assays, and adequate replication are all important factors in obtaining statistically significant data suitable for prediction of crop loss.

In summary, the early-dying syndrome in potatoes in Ohio can be caused by a disease complex involving the interaction of *P. penetrans* and *V. dahliae*. Results from 1980 in organic soil show that in a wet year, the combination of singly nondamaging levels of *Pratylenchus* and *Verticillium* cause a synergistic yield loss of 36%. Greater losses may be expected in a normal to dry year, and the work is being repeated to investigate that aspect of the problem. This paper reports only a portion of long-range studies being conducted on organic soil, sand, and silt loam to develop a predictive system for potato crop loss due to *Pratylenchus* species and *V. dahliae*.

TABLE 3. Initial and final populations of *Pratylenchus penetrans* (P) and *Verticillium dahliae* (V) and their effects on plant top, root, and tuber weight and disease severity at harvest of potatoes grown in microplots on Rifle peat in Ohio in 1980

Treatments	Initial V microsclerotia (per 10/g soil)	Populations of P:			Final disease severity[v]	Effects on plants		
		Initial (per 100 cm³ soil)	Final (per 100 cm³ soil)	Final (per g root)		Fresh wt (g) per plant:		
						Top	Root	Tuber
Uninoculated control	⋯	⋯	⋯	⋯	0.8 a	520 ab	9.8 a	746 a
Low P	⋯	18[y] a[z]	229 b	38.4 ab	1.4 b	436 bc	8.4 a	653 ab
Medium P	⋯	56 b	400 c	97.2 cd	1.9 c	330 cd	6.1 b	624 ab
High P	⋯	151 c	860 d	120.9 d	2.1 c	270 d	6.4 b	597 bc
Low V	6.6 a[w]	⋯	⋯	⋯	1.1 ab	603 a	8.3 a	724 ab
High V	17.1 b[x]	⋯	⋯	⋯	2.1 c	308 d	6.0 b	644 ab
Low P/low V	6.6 a	15.a	129 a	14.0 a	2.8 d	121 e	3.6 c	466 d
Low P/high V	17.1 b	14 a	108 a	30.0 ab	2.9 d	127 e	4.4 c	463 d
Medium P/low V	6.6 a	52 b	188 ab	22.6 a	2.9 d	139 e	4.1 c	414 d
Medium P/high V	17.1 b	44 ab	172 ab	20.1 a	2.9 d	121 e	3.8 c	480 cd
High P/low V	6.6 a	147 c	481 c	47.7 ab	3.0 d	140 e	3.6 c	425 d
High P/high V	17.1 b	140 c	437 c	66.6 bc	2.9 d	97 e	3.3 c	366 d

[v] Plants were rated on a scale of 0 (no disease) to 3 (complete necrosis) based on a combination of wilting, chlorosis, and necrosis.

[w,x] Values are the means of 40 10 g soil replicates (ten 10-g soil replicates from each of four high V or four low V treatments).

[y] Values in columns two to eight are the means of 15 samples.

[z] Values followed by the same letter are not significantly different according to Duncan's multiple range test, $P = 0.05$.

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