Distribution and Yield-Loss Relations of *Verticillium dahliae*, *Pratylenchus penetrans*, *P. scribneri*, *P. crenatus*, and *Meloidogyne hapla* in Commercial Potato Fields

T. A. Wheeler, L. V. Madden, R. M. Riedel, and R. C. Rowe

First author: assistant professor, Texas Agricultural Experiment Station, Lubbock 79401; second and fourth authors: professors, Department of Plant Pathology, Ohio Agricultural Research and Development Center, The Ohio State University, Wooster 44691; and third author: professor, Department of Plant Pathology, The Ohio State University, Columbus 43210.

Salaries and research support provided by state and federal funds appropriated to the Ohio Agricultural Research and Development Center, The Ohio State University. Manuscript number 226-93.

Accepted for publication 12 May 1994.

ABSTRACT

Wheeler, T. A., Madden, L. V., Riedel, R. M., and Rowe, R. C. 1994. Distribution and yield-loss relations of *Verticillium dahliae, Pratylenchus penetrans, P. scribneri, P. crenatus,* and *Meloidogyne hapla* in commercial potato fields. Phytopathology 84:843-852.

Potato yields and population densities of organisms that cause or potentially influence the early dying syndrome were measured by sampling along linear transects in commercial potato fields. The distributions of the five organisms were fitted with a negative binomial distribution ($P = 0.05$) in six of 10 fields for *Verticillium dahliae,* six of seven fields for *Meloidogyne hapla,* one of seven fields for *Pratylenchus penetrans,* four of six fields for *P. scribneri,* and six of seven fields for *P. crenatus.* Hill's two-term local quadrat variance method for *V. dahliae* indicated that aggregation generally increased or did not change with plot size, except in two fields where aggregation was highest at or near the smallest plot size (2 m), i.e., the lowest tested spatial scale. With the three species of *Pratylenchus,* aggregation generally increased with plot size; and with *M. hapla,* the peak of aggregation was highly variable from field to field. Taylor's power law was used to estimate a minimum sampling number for each organism. With a coefficient of variation of the mean (C) of 0.50, six to eight samples were necessary for all five species; the required sample number increased dramatically if precision was increased to $C = 0.20$. Significant spatial autocorrelations of low order were observed most frequently for *V. dahliae* and *M. hapla.* Autocorrelation patterns were not clearly evident in most of the fields for *P. penetrans.* No significant covariation was seen between *V. dahliae* and any nematode species density. There was a low degree of positive covariation observed between *M. hapla* and the three species of *Pratylenchus* and a high degree of positive covariation among the three species of *Pratylenchus.* Yields were negatively correlated with preplant densities of *V. dahliae* and *P. penetrans* or their interaction in three of seven fields and with *M. hapla* in three of 10 fields. Yields were also correlated negatively with *V. dahliae* and *P. penetrans* individually, positively with interactions between *M. hapla* and *V. dahliae,* and negatively with *V. dahliae* and *Pratylenchus* spp. (species not identified) and *V. dahliae* and *P. crenatus* in one or two fields each.

Potato early dying, a premature senescence induced by soilborne pathogens, can cause serious yield losses in potatoes (*Solanum tuberosum* L.) (37,45). A number of pathogens have been shown to cause potato early dying, including *Verticillium dahliae* Kleb. (25,30,48), *V. albo-atrum* Reinke & Berthier (25,48), and *Erwinia carotovora* (29,42). Field microplot studies have demonstrated that the combination of *V. dahliae* and the root-lesion nematode *Pratylenchus penetrans* (Cobb) Filipjev & Schuur. can cause an increase in yield loss beyond that anticipated from the additive yield loss attributed to each pathogen alone (33,35,44).

The community of plant-parasitic nematodes found in commercial potato fields in Ohio includes the root-lesion nematodes *P. penetrans, P. scribneri* (Steiner), *P. crenatus* (Loof), and the northern root-knot nematode, *Meloidogyne hapla* (Chitwood) (4). These lesion nematode species also have been reported in potato fields in Maine (21), Wisconsin (9), Prince Edward Island, Canada (28), and throughout the northeastern part of the United States and Upper Great Lakes (52). Potato is a good host for *P. penetrans* (2), and infection by this nematode can cause significant yield losses (40). Microplot experiments with *P. scribneri, P. crenatus,* and *V. dahliae* on potato failed to demonstrate yield-loss interactions (43). *M. hapla* alone can cause significant yield losses on potato (39). Jacobsen et al (26) found a significant negative interaction between the northern root-knot nematode and *V. dahliae* with respect to yield losses in both microplot and field studies. MacGuidwin and Rouse (32) found no interaction between *M. hapla* and low densities of *V. dahliae* in microplot studies.

Although the interaction between *V. dahliae* and *P. penetrans* has been thoroughly demonstrated in controlled studies with fumigated soils, the relative importance of the interaction in commercial potato fields is less clear. The interaction has not been well documented when the nematodes are found in mixed communities of other nematode species. Botseas and Rowe (3), in a study with six isolates, found that the relative magnitude of the interaction between *V. dahliae* and *P. penetrans* could range from none to very high, depending on the isolate of *V. dahliae* used. Variability of the interaction with strains of the nematode *P. penetrans* has not been tested.

Although there is interest in management of potato early dying, simply confirming the presence of *V. dahliae* and *P. penetrans* in soil is not sufficient cause to implement expensive management strategies. Development and implementation of a practical decision aid for potato early dying is limited, in part, by the difficulties in estimating population parameters (mean and variances) for these organisms. To implement a sampling program, one must know the number of samples to collect, the sample unit size where the distribution of the organism becomes random (if at all), and the appropriate time to collect samples (5). Soilborne pathogens are typically distributed in an aggregated pattern (5,6,17,27,38,49). The average cluster size for each organism in a field corresponds to the sample area where the variance of the density of that organism is maximized (7). Many spatial indices can quantify spatial patterns and can be used to decide whether spatial distribution is random, regular, or aggregated for a range of sample unit areas (5). Spatial autocorrelation techniques can also be used to provide information on aggregation (10,20,34).

The objectives of this study were to determine mean density, variance, and spatial pattern of each of these organisms in commercial potato field plots; to determine the degree of aggregation of the organisms and to calculate adequate sample numbers for estimation of preplant population densities; to determine the covariation between densities of the different species

in commercial potato fields; and to determine the additive or synergistic yield responses of potatoes to preplant population densities of *V. dahliae, P. penetrans, P. scribneri, P. crenatus,* and *M. hapla* in commercial potato fields and to compare these fields with microplot studies.

MATERIALS AND METHODS

Commercial field studies. Two commercial potato fields were selected in each of 5 yr (1987–1991). In each field, a four-row transect of the cultivar Superior was planted and maintained by the grower over the season, along with other potatoes in the field. The center two rows were divided into contiguous plots (= sampling units; quadrats) of a length of 2 m (1987–1990) or 8 m (1991). The two outside rows were used only to reduce border effects. The number of plots in any individual field ranged from 22 to 107. In addition, in 1991, three to four plots in each field were fumigated with 67% methyl bromide + 33% chloropicrin at a rate of 392 kg/ha prior to planting. Composite samples, consisting of 10–12 soil cores (2.5 cm in diameter, 20–30 cm deep), were taken from each plot before planting and mixed in a bucket, and 1,000 cm^3 of soil was kept as the sample. Yield was determined by hand harvesting and assessed as the total weight of all tubers in each plot.

The preplant population density of *V. dahliae* was determined by air drying 100 cm^3 of soil for 4–5 wk followed by wet sieving (23) 10 g of dried soil and then plating the concentrated microsclerotia on 20 plates of a sodium polypectate medium selective for *Verticillium* (36). In 1991, the fungal density was determined by directly plating 10 1-ml aliquots of soil onto *Verticillium*-selective media.

Plant-parasitic nematodes were extracted from 100 cm^3 of soil by the pie-pan method (51). All plant-parasitic nematodes were identified to genus. *M. hapla* was assumed to be the only species of *Meloidogyne* present. If 40 or more *Pratylenchus* vermiforms were present in a sample, then the individuals were fixed and adult lesion nematodes later were identified to species. To fix the nematodes in a sample, a volume of boiling water equal to the sample volume was added to the beaker. When the sample had cooled to room temperature, it was concentrated to 10 ml by pipetting the excess water, and an equal volume of 10% Formalin was added. If possible, 20 *Pratylenchus* adults were identified to species in each sample. Previous work (4) has shown that the only species of lesion nematodes common to Ohio potato fields were *P. penetrans, P. scribneri,* and *P. crenatus.* Identification of *P. penetrans* was made on the presence of sperm, three lips, and a smooth tail terminus (18). Identification of *P. scribneri* was based on no sperm, two lips, and a smooth tail terminus (18). Identification of *P. crenatus* was based on a crenate tail, no sperm, and three lips (18). The percentage of adult *P. penetrans, P. scribneri,* and *P. crenatus* was multiplied by the total *Pratylenchus* counted in each plot to obtain an estimate of the density of each species. In plots where there were too few *Pratylenchus* adults to do species identifications, the average percentage of each of the three species determined from the other plots in that field was multiplied by the genus count of *Pratylenchus* for that plot.

Spatial pattern analysis and species correlations. Preplant population densities for *V. dahliae* and the four nematode species in commercial fields were used to construct frequency distributions. The Poisson and negative binomial discrete distributions were fitted to the data from each field (16). A chi-square test was used to determine the goodness of fit of both models to the frequency data.

Hill's two-term local quadrat variance method (TTLQV) was calculated for each species in each field (31). The individual plots were blocked into groups of two, three, etc., and the variance was calculated. With the TTLQV method, the variance of randomly distributed variables fluctuates in a nonsystematic manner for all block sizes or can be nearly constant if the distribution is uniform and tends to peak at a certain block size (which represents the average area occupied by each clump or patch) for an aggregated distribution (31).

Taylor's (50) power model was used to describe the relationship between the variances (σ^2) and means (μ) of each of the pathogen densities over all 10 fields. The REG procedure in SAS (47) was used to fit the model

$$\log(\sigma^2) = \log(a) + b\log(\mu)$$

to the 10 data points. The estimate for b is an index of aggregation across all fields, with <1 representing a regular (uniform) pattern, 1 a random pattern, and >1 a contagious or clustered pattern. The standard error of the estimate for b was used in a t test to determine whether b was significantly ($P < 0.05$) different from 1. Results of the Taylor's power model analysis were used to estimate sample sizes (n), which would ensure that the coefficient of variation of the mean (C), a measure of precision, would be within 10, 20, or 50% (i.e., $C = 0.1$, 0.2, or 0.5) of the value of the mean. Sample size is given by

$$n = (a\mu^{(b-2)})/C^2,$$

in which all terms are as defined previously (5). A graph was generated for each species with the three C values and densities from 10 to 100.

Spearman's rank correlation (31) was used to measure species covariation. All pairwise comparisons were made for each of the 10 commercial potato fields. Because of aggregation of the organisms, P values of the correlations may actually be somewhat larger than calculated (8). To be conservative, a conclusion of significance was based on $P < 0.01$ instead of $P < 0.05$, although all P values are reported.

Spatial autocorrelation was examined by calculating correlograms and partial autocorrelograms with the ARIMA procedure in SAS (46). The density values of each organism (x) were transformed by $x^{[1-(b/2)]}$, where b was calculated from Taylor's power law to produce constant variances. Yield per plot also was analyzed in this manner. Moran's I test was used to determine significant autocorrelations or partial correlations, that is, those significantly different from 0 ($P = 0.05$) (10). These correlations can be used to identify autoregressive and moving-average models (20). The two fields from 1991 were deleted from this analysis since some of the plots were fumigated and there were too few plots (because of the larger size) to use this procedure with confidence.

The relationship between yield and preplant density of *V. dahliae* (*VD*), *P. penetrans* (*PP*), *P. scribneri* (*PS*), *P. crenatus* (*PC*), and *M. hapla* (*MH*), $VD \times PP$, $VD \times PS$, $VD \times PC$, and $VD \times MH$, was examined with regression analysis by using a stepwise variable selection procedure (STEPWISE and RSQUARE [47]). Independent variables were included with and without logarithmic transformations. Square root transformations were also included for *V. dahliae* densities. These transformations have been used successfully to fit yield-loss models to densities of *V. dahliae* and *P. penetrans* previously (14,53). The interactions of nematode species were eliminated from the analyses because they were rarely significant and were highly correlated with other variables. A single model was selected for each field on the basis of two criteria: 1) an overall F statistic significant at $P \leq 0.05$, and 2) estimated parameters for each independent variable (e.g., *VD*) significant (on the basis of t tests) at $P < 0.10$. If multiple models fulfilled these criteria, then the model with the highest coefficient of determination (R^2) and a random residual plot for each independent variable was selected.

Microplot studies. The effect of both *M. hapla* and *V. dahliae* on potato yields was examined for 2 yr in microplots with a randomized complete block design and a factorial arrangement of *V. dahliae* and *M. hapla.* In 1990, a Rifle peat soil (15% silt, 1% sand, 9% clay, and 75% organic matter, pH 5.2) was fumigated with 67% methyl bromide + 33% chloropicrin at a rate of 465 kg/ha and mixed with either 0 or 40 microsclerotia of *V. dahliae* per cubic centimeter of soil in a cement mixer for 5 min. Methods for inoculum production and quantification of *V. dahliae* have

been reported previously (15). The soil was then mixed with 0, 100, 750, or 1,500 eggs of *M. hapla* per 100 cm^3 in a 20-L twin shell mixer (10 rotations). The nematode inoculum had been grown on tomato cultivar Rutgers for 90 days. The roots were chopped into 1- to 2-cm pieces, and the eggs were extracted with 10% NaOCl (24). The infested soil was added to clay tile microplots (30 cm in length, 25 cm inside diameter), and a single-eye seed piece of the potato cultivar Superior was planted in each tile. The procedure was repeated in 1991, except the source of the soil was a nonfumigated Wooster silt loam (65% silt, 20% sand, 15% clay, and 2% organic matter, pH 5.4), which had been found to be free of *V. dahliae, M. hapla,* and *P. penetrans* by assay methods described previously in the paper. The inoculum levels used in 1991 were 0 and 50 microsclerotia of *V. dahliae* per cubic centimeter of soil and 0, 100, 500, 1,000, and 4,000 eggs of *M. hapla* per 100 cm^3 of soil. There were 15 replicates in 1990 and 14 replicates in 1991.

Tubers were hand harvested to determine yield per plant. Effects of the pathogens on yield were assessed by relative yield, which was the total weight of tubers in a microplot divided by the average weight of the tubers in the uninfested control plots. Data sets were analyzed separately with analysis of variance (ANOVA; general linear model [GLM] procedure [47]) to determine whether the interaction term ($VD \times MH$) and main effects (VD, MH) were significant ($P = 0.05$) and then with regression analysis (REG procedure [47]) with and without $\log_{10}$-transformed *M. hapla* densities to develop yield-loss equations.

RESULTS

Spatial analysis of the pathogens. Population densities of *V. dahliae* and some of the nematode species were generally aggregated as indicated by the good fit of the negative binomial, with estimated k mostly <5, and the poor fit of the Poisson distribution to the data. The frequencies of *V. dahliae* propagules were well fitted by the negative binomial distribution in six of 10 fields (Table 1). The parameter k, estimated when the negative binomial was appropriate, ranged from 0.78 to 5.59 (Table 1), indicating high to low aggregation. The frequency of counts of second-stage juveniles (J2) for *M. hapla* was adequately represented by the negative binomial distribution for all fields with more than one J2 per 100 cm^3 of soil (Tables 1 and 2). The parameter k ranged from 0.53 to 2.76 for *M. hapla* (Table 1). The frequency distribution of the vermiform stages of *P. penetrans* was poorly fitted by the negative binomial distribution, with an adequate fit ($k = 0.52$) in only one of seven fields where species were identified (Table 1). In two fields, the null hypothesis of the Poisson model was not rejected, but the average density of *P. penetrans* was four or fewer vermiforms per 100 cm^3 of soil in those fields (Table 2). The frequency distribution of vermiforms of *P. scribneri* was fitted by the negative binomial distribution in four of six fields where that species was identified. Data from one field with a density of *P. scribneri* of more than one vermiform per 100 cm^3 of soil were not fitted by the negative binomial model. The parameter k ranged from 0.72 to 3.99 (Table 1). The frequency distribution of *P. crenatus* was fitted by the negative binomial distribution in six of seven fields where that species was identified, with estimated k values ranging from 0.35 to 5.58 (Table 1).

Taylor's power law model provided an acceptable to excellent fit to the variance-mean data across all fields for *V. dahliae* and the nematode species (Table 3). The parameter b, the index of aggregation, for *V. dahliae, M. hapla, P. penetrans,* and *P. scribneri* was significantly greater than 1.0 for each species,

TABLE 1. Best fitting statistical distribution to frequency of densities of *Verticillium dahliae, Meloidogyne hapla, Pratylenchus penetrans, P. scribneri,* and *P. crenatus* in 10 commercial potato fields

	V. dahliae		*M. hapla*		*P. penetrans*		*P. scribneri*		*P. crenatus*	
Field	Dist.[a]	k[b]	Dist.	k	Dist.	k	Dist.	k	Dist.	k
1	NB	1.49	...[c]		NB	0.52	...		NB	0.71
2	...		NB	0.53	...		...		NB	5.58
3	...		NB	0.53	...		NB	3.99	NB	1.20
4	NB	0.84	NB	2.76	...		NB	1.55	NB	2.37
5	NB	3.38	...		PO		...		...	
6	...		...		PO		NB	0.72	NB	0.35
7	...		NB	1.25	—[d]		—		—	
8	NB	5.59	NB	1.49	...		NB	1.29	NB	1.40
9	NB	2.63	...		—		—		—	
10	NB	0.78	NB	0.60	—		—		—	

[a] The distributions (Dist.) were fitted by a computer program from Gates and Ethridge (16); a chi-square test ($P = 0.05$) was used to determine goodness of fit of the Poisson (PO) or negative binomial (NB) distribution
[b] Negative binomial distribution has a k parameter estimated with the program.
[c] Neither of the distributions could be satisfactorily fitted to the data.
[d] No species identification of *Pratylenchus* was done.

TABLE 2. Average preplant population densities and variances (VAR) of *Verticillium dahliae*,[a] *Pratylenchus penetrans*,[b] *P. crenatus*,[b] and *Meloidogyne hapla*[c] found in 10 commercial potato fields

		V. dahliae		*P. penetrans*		*P. scribneri*		*P. crenatus*		*Pratylenchus*[d]		*M. hapla*	
Field	Year	Mean	VAR	Mean	VAR	Mean	VAR	Mean	VAR	Mean	VAR	Mean	VAR
1	1987	3	6	12	346	25	1,170	11	449	49	2,810	1	49
2	1987	1	27	37	1,584	0	0	167	11,215	205	15,725	57	5,991
3	1988	0.3	0.7	15	404	110	9,197	17	645	142	14,641	22	2,181
4	1988	1	11	11	388	48	2,460	101	8,226	162	13,179	395	100,046
5	1989	23	240	4	85	1	8	17	557	22	847	0	0
6	1989	14	317	1	7	9	310	3	188	13	543	0	0
7	1990	0.3	0.1	...[d]	...	...	...	...	...	371	39,085	112	28,900
8	1990	2	2	13	210	49	1,756	21	640	83	4,251	53	2,540
9	1991	111	12,012	...	...	...	...	...	...	10	458	0	0
10	1991	11	259	...	...	...	...	...	...	45	2,530	26	2,540

[a] Microsclerotia per cubic centimeter of soil, assayed with wet sieving for fields 1–8 and direct plating for fields 9 and 10.
[b] Vermiforms per 100 cm^3 of soil.
[c] Second-stage juveniles per 100 cm^3 of soil.
[d] *Pratylenchus* spp. per 100 cm^3 of soil; all species combined.

indicating aggregation. For *P. crenatus,* however, b was only marginally ($P > 0.10$) greater than 1.0 (Table 3). Estimates of a and b were used to estimate sample number for each of the five species (5). To estimate the mean population density of *V. dahliae* with a standard error of less than 10% of the mean ($C = 0.1$), over 100 samples would be necessary (Fig. 1A). With $b > 2$, the curve increases with mean density because the variance increases faster than the square of the mean (5). For $C = 0.5$, six to eight samples would be needed for 10–100 microsclerotia per cubic centimeter of soil.

To estimate 10–25 vermiforms of *P. penetrans* with a C of 0.1 required 135–192 samples (Fig. 1B). For an estimate within 50% of the mean, six to eight samples would be adequate (Fig. 1B). For *M. hapla* and *P. scribneri,* there was relatively little change in the sample numbers with respect to increases in the mean density (Fig. 1C and D) because b was close to 2. At $b = 2$, n does not change (increasing variance is perfectly balanced by declining 1 per mean squared) (5). For an estimation with $C = 0.5$, four to six samples would have been required for *P. scribneri* and six to eight samples for *M. hapla.* The estimate of mean population density of *P. crenatus* at low densities (10 vermiforms per 100 cm^3 of soil) required 14 samples with a C of 0.5, but at densities ≥50 vermiforms per 100 cm^3 of soil, only four or fewer samples were required with a C of 0.5 (Fig. 1E). With a C of 0.2 for *P. crenatus,* 24–88 samples were necessary for mean estimates of 50–10 vermiforms, and 95–351 samples were necessary for mean estimates of 50–10 vermiforms per 100 cm^3 of soil with a C of 0.1 (Fig. 1E).

TABLE 3. Estimated parameters of Taylor's power law model[a] together with the coefficient of determination (R^2) for preplant population densities of *Verticillium dahliae* (*VD*), *Pratylenchus penetrans* (*PP*), *P. scribneri* (*PS*), *P. crenatus* (*PC*), and *Meloidogyne hapla* (*MH*) from soil collected from commercial potato fields

	Intercept		Slope			
Pathogen	log(a)	SE[b]	b	SE	R^2	Number[c]
VD	−0.06	1.45	2.17	0.43	0.76	10
PP	1.48	0.33	1.64	0.13	0.97	7
PS	0.82	0.43	1.81	0.14	0.97	7
PC	3.12	0.37	1.19	0.11	0.96	7
MH	0.93	0.44	1.90	0.13	0.96	10

[a] Log(variance = log(a) + $b$log(mean).
[b] Standard error.
[c] Number of fields used in the regression.

Hill's TTLQV for *V. dahliae* indicated a uniform or random distribution for field 3 and field 7, which had mean densities of less than 1.0 (Fig. 2A); densities in both fields could not be adequately fitted by the negative binomial distribution. A clustered distribution with a peak around a block size of 1 was found for field 2 (Fig. 2A), while broader peaks were seen with increasing block size for fields 1, 4–6, and 8 (Fig. 2A and B). In general, the variance increased, either slowly or rapidly, with block size for *V. dahliae,* and in only one case (field 2) did aggregation appear to decline with increasing block size. The variance of Hill's TTLQV ranged from 0 to 578 for *V. dahliae.*

Hill's TTLQV for *M. hapla* also showed aggregation at all block sizes, but aggregation increased gradually with block size

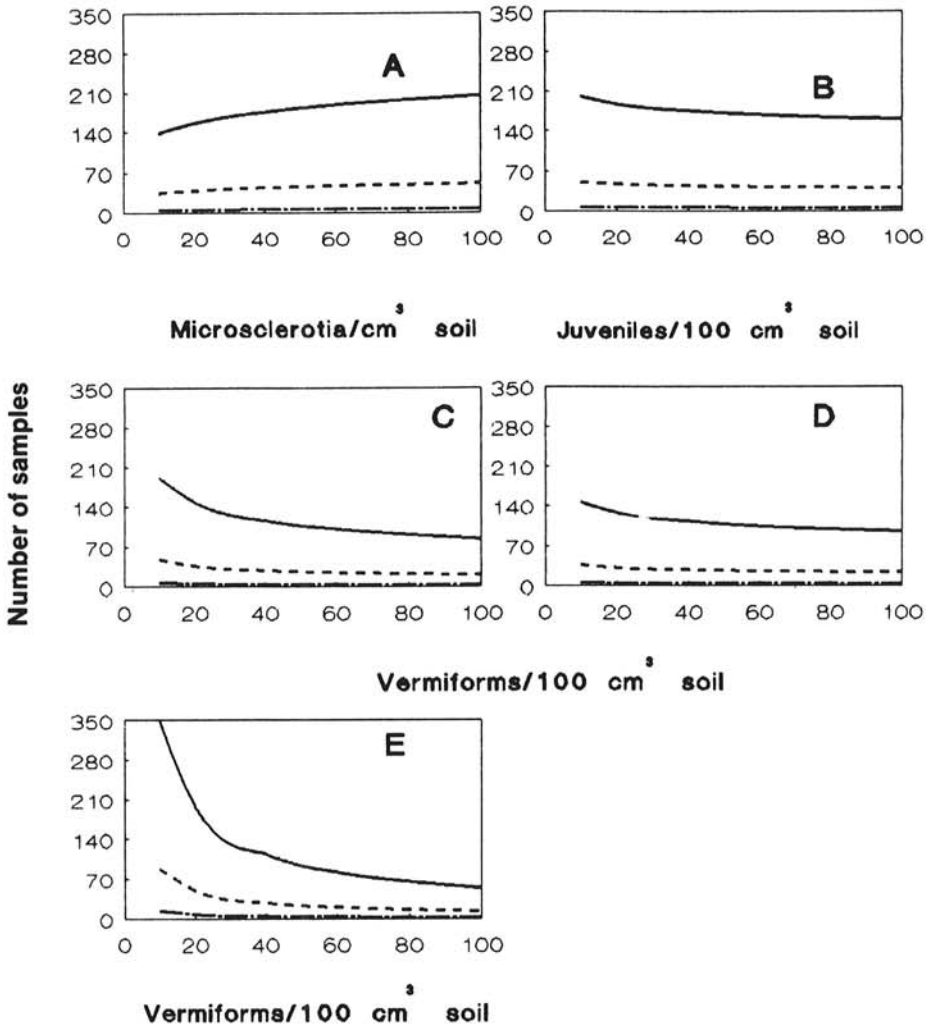

Fig. 1. Predicted minimum sampling number to adequately represent various preplant population densities of **A,** *Verticillium dahliae,* **B,** *Pratylenchus penetrans,* **C,** *Meloidogyne hapla,* **D,** *P. scribneri,* and **E,** *P. crenatus* as a function of coefficient of variation (C) in transects of commercial potato fields. $C = 0.10$ (—), 0.20 (- - -), and 0.50 (-·-).

only in fields 2 and 7 (Fig. 3B and C). Aggregation appeared to decrease with increasing block size in field 1 (Fig. 3A). In field 4, aggregation peaked at a block size of 6. The variance of Hill's TTLQV ranged from 24 to 160,000 for *M. hapla.*

Hill's TTLQV for *P. penetrans* showed similar patterns for fields 4, 6, and 8, with apparently random variations of variance with increasing block size (Fig. 4B). In fields 1, 2, and 5, there was an increase in the variance with increasing block size (Fig. 4A and B). In field 3, there was a broad peak around a block size of 4 to 7 (Fig. 4A). The variance of Hill's TTLQV ranged from 5 to 2,557 for *P. penetrans.*

Hill's TTLQV for *P. scribneri,* in general, increased with increasing block size (fields 1, 3–5, and 8; Fig. 5A). Only in field 6 was there apparently a random fluctuation of variance with increasing block size (Fig. 5B). The variance ranged from 8 to 39,101 for *P. scribneri.*

Hill's TTLQV for *P. crenatus* was similar to that seen for *P. scribneri,* with an increase in variance with increasing block size for fields 1, 2, 5, and 6 (Fig. 6A and B). In fields 3, 4, and 8, there was a broad peak in variance in block sizes of 6 to 10 (Fig. 6A and B). The variance for *P. crenatus* with TTLQV ranged from 182 to 23,168.

Significant and mostly positive spatial autocorrelations and partial autocorrelations of a low order (i.e., two to three plot lengths were correlated) were detected for transformed *V. dahliae* density in three fields; and in two additional fields, higher order spatial autocorrelations (four or more plot lengths were correlated) of this variable also were detected (Table 4). For *P. penetrans*, there were no particular indications of autoregressive or moving-average type models; i.e., no low order autocorrelations or partial autocorrelations were consistently significant. However, with *P. scribneri* and *P. crenatus*, there were significant low order spatial autocorrelations in half of the fields. With *M. hapla,* low order autoregressive models were suggested in four of five fields where the preplant density (J2 per 100 cm^3 of soil) was greater than one.

Potato yields in relation to pathogens. In most fields, individual preplant population densities of *V. dahliae, M. hapla,* and *Pratylenchus* spp. were poorly correlated with potato yields. In three fields, the *VD* × *PP* interactions and in one field, a *VD* × *PC* interaction were negatively correlated with yield (Table 5). There were also two additional fields where an interaction of *VD* and density of *Pratylenchus* spp. (all species combined) was found. *Pratylenchus* species identification was not done in those two fields. In fields where the *VD* × *PP* interaction was significant (and negative), the average preplant densities of *P. penetrans* ranged from 11 to 15 vermiforms per 100 cm^3 of soil, and where only genus counts for the lesion nematode were available, the preplant densities were 45 and 371 vermiforms per 100 cm^3 of soil (Table 2). In fields 1, 2, 5, and 6, where no *VD* × *PP* interaction was observed, the average preplant density of *P. penetrans* was 12, 37, four, and one vermiform per 100 cm^3 of soil, respectively (Table 2). *P. penetrans* alone was negatively related with yield in field 1 (Table 5).

M. hapla was negatively correlated with yields in three fields, while the interaction between *VD* and *MH* was positively related

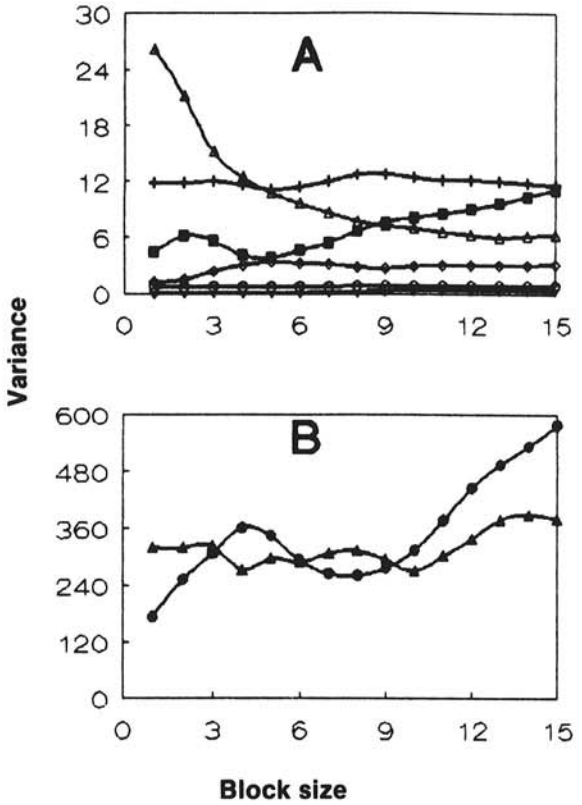

Fig. 2. Hill's two-term local quadrat variance test as applied to densities of *Verticillium dahliae* in transects of commercial potato fields. **A,** Field 1 = ■; field 2 = △; field 3 = ○; field 4 = +; field 7 = ▽; and field 8 = ◇. **B,** Field 5 = ▲, and field 6 = ●. Fields were placed in **A** or **B** on the basis of the magnitude of their variances (e.g., fields with large variances were placed in the same graph).

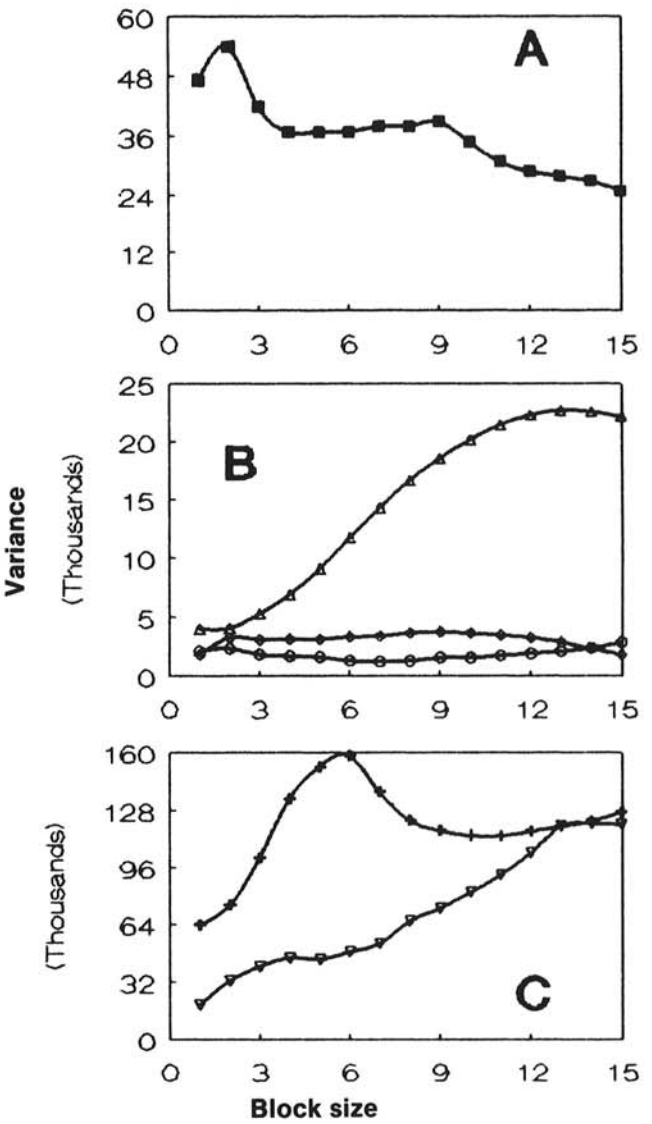

Fig. 3. Hill's two-term local quadrat variance test as applied to densities of *Meloidogyne hapla* in transects of commercial potato fields. **A,** Field 1 = ■. **B,** Field 2 = △; field 3 = ○; and field 8 = ◇. **C,** Field 4 = +, and field 7 = ▽. Fields were placed in **A, B,** or **C** on the basis of the magnitude of their variances (e.g., fields with large variances were placed in the same graph).

to yield in two fields (Table 5). The average preplant densities of *M. hapla* were >100 juveniles per 100 cm^3 of soil in two of the three fields where the root-knot nematodes contributed to yield losses (Table 2). The highest average density of *M. hapla* found in the other fields was 57 juveniles per 100 cm^3 of soil.

V. dahliae alone was the best predictor of yields in only one field (field 9), but 62% of the variation in yield in that field was described by a model with a $\log_{10}$ transformation of the preplant density of the fungus (Table 5). The average density of *V. dahliae* in this field was 111 microsclerotia per cubic centimeter of soil (Table 2). In two fields (fields 2 and 6; Table 5), no relationship between yield and the preplant density of any of the species could be found.

Spatial autocorrelation of yield in each of the 10 fields is presented in Table 6. Significant autocorrelations and partial autocorrelations of low order were found in fields 1, 3, 5–8, and 10. Similar patterns of low order autocorrelations were seen for *V. dahliae* in fields 5 and 7 and for *M. hapla* in field 8 (Table 4). The spatial distribution of *P. penetrans* was not significantly associated with low order spatial autocorrelations, while the distribution of *P. scribneri* and/or *P. crenatus* could in certain fields (fields 1–4) be characterized by low order spatial autocorrelations (Table 4).

Species covariation. *V. dahliae* density was negatively correlated with *M. hapla* in one field (field 7) (Table 7). In the other nine fields, there were no significant correlations between *V. dahliae* and any of the nematode species (Table 7), indicating, in part, that yield-loss analyses were not biased by intercorrelation of the predictors (pathogens). *M. hapla* was positively correlated with *P. crenatus* in fields 2 and 4 ($P = 0.02$ and 0.01, respectively), with *P. scribneri* in field 4 ($P = 0.01$), and with *P. penetrans* in field 8 ($P = 0.05$) (Table 7). *P. penetrans* was positively correlated with *P. scribneri* in five of six fields and with *P. crenatus* in six of seven fields (Table 7). *P. scribneri* was positively correlated with *P. crenatus* in six of the six fields at $P = 0.02$ (Table 7).

Microplot studies of *M. hapla* and *V. dahliae*. In 1990, there was a marginal but significant ($P = 0.05$) relationship between preplant density of eggs of *M. hapla* and yield in microplots on the basis of ANOVA. The effect of *V. dahliae* on yield was significant in ANOVA only at $P = 0.08$. The regression model to 1990 data was

$$RY = 1.00 + 0.38[\log_{10}(MH + 1)] - 0.13[\log_{10}(MH + 1)]^2,$$

with an R^2 of 0.11. RY is the relative yield and equals 1.0 for plots containing no nematode or fungal inoculum. In 1991, only *V. dahliae* caused significant ($P = 0.03$) yield losses in potato according to ANOVA, but both *V. dahliae* and *M. hapla* were found to be significant on the basis of regression analysis ($P = 0.05$). The difference between results in the two types of analysis was likely the result of proper choice of transformations in the regression analysis. With either analysis, the effect of either pathogen was slight on average. The yield model for 1991 was

$$RY = 1.00 - 0.0022(VD) + 0.057[\log_{10}(MH + 1)],$$

with an R^2 of only 0.08. In neither year was there any statistical interaction between *V. dahliae* and *M. hapla* with yield ($P \geq 0.3$) in the ANOVA.

DISCUSSION

Aggregation of the soilborne pathogens in commercial potato fields was characterized here with the k parameter from the

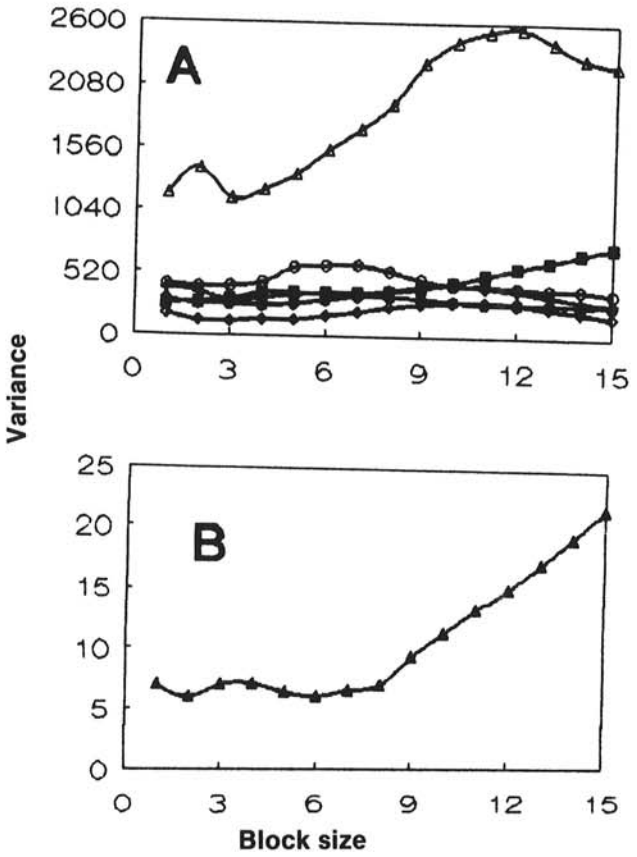

Fig. 4. Hill's two-term local quadrat variance test as applied to densities of *Pratylenchus penetrans* in transects of commercial potato fields. **A,** Field 1 = ■; field 2 = △; field 3 = ○; field 4 = +; field 6 = •; and field 8 = ◇. **B,** Field 5 = ▲. Fields were placed in **A** or **B** on the basis of the magnitude of their variances (e.g., fields with large variances were placed in the same graph).

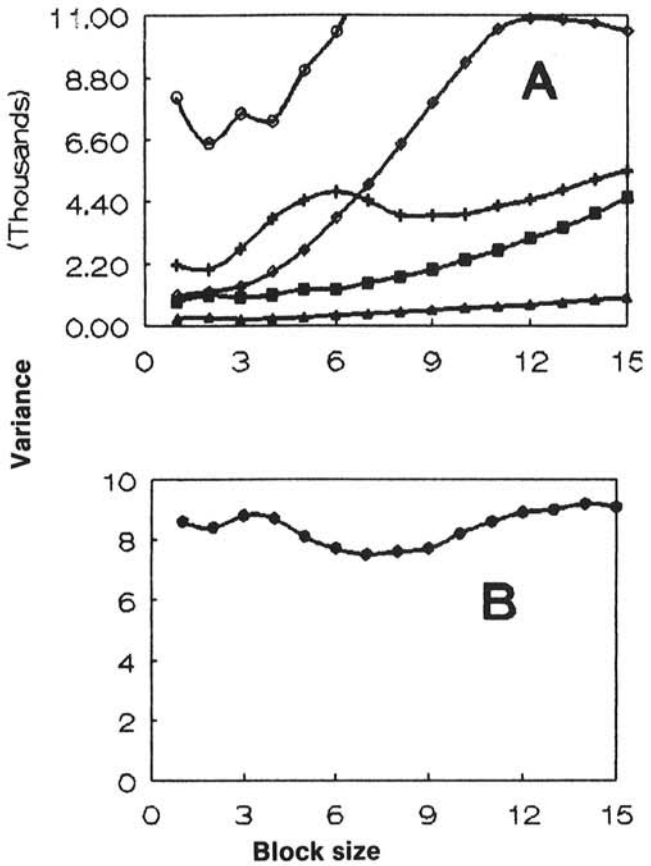

Fig. 5. Hill's two-term local quadrat variance test as applied to densities of *Pratylenchus scribneri* in transects of commercial potato fields. **A,** Field 1 = ■; field 3 = ○; field 4 = +; field 5 = ▲; and field 8 = ◇. **B,** Field 6 = •. Fields were placed in **A** or **B** on the basis of the magnitude of their variances (e.g., fields with large variances were placed in the same graph).

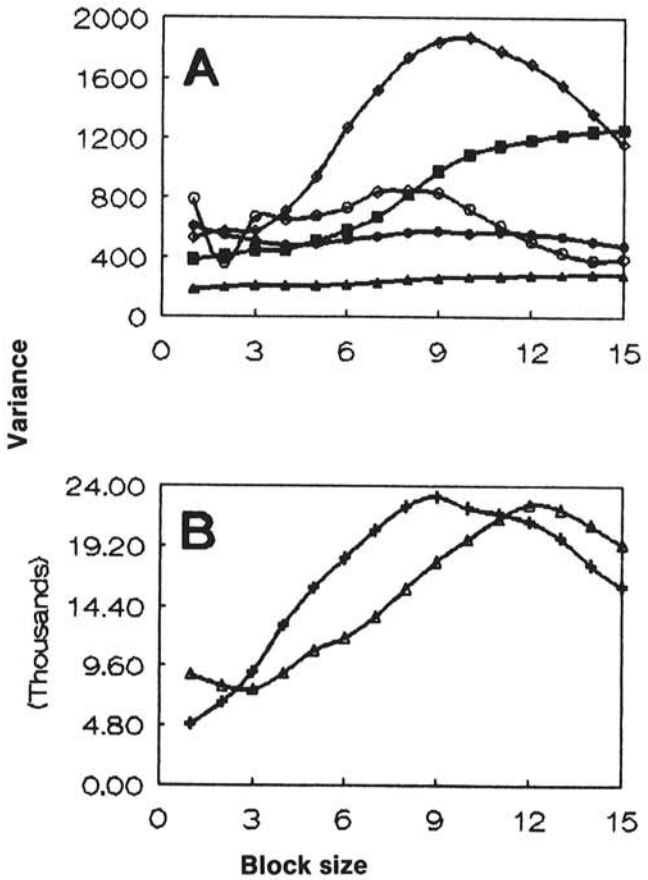

Fig. 6. Hill's two-term local quadrat variance test as applied to densities of *Pratylenchus crenatus* in transects of commercial potato fields. **A,** Field 1 = ■; field 3 = ○; field 5 = ▲; field 6 = ●; and field 8 = ◇. **B,** Field 2 = △, and field 4 = +. Fields were placed in **A** or **B** on the basis of the magnitude of their variances (e.g., fields with large variances were placed in the same graph).

negative binomial distribution, Taylor's power law, Hill's TTLQV, and spatial autocorrelation coefficients. A wide range of patterns was found for these organisms over the 5 yr and 10 fields. Results for aggregation of an organism vary between tests, because the tests measure different aspects of the complicated phenomenon of aggregation. Pielou (41) describes spatial pattern as a continuum in intensity and grain. Intensity of pattern refers to the extent that density varies from location to location, i.e., the differences between patches of high or low magnitude. Indices based on the variance and the mean or statistical distribution parameters (k) reflect the intensity of the patterns, at least at one spatial scale. The grain of a pattern refers to the spacing between patches, i.e., widely spaced (coarse grained) or a range of densities encompassed in a small space (fine grained) (41). Statistical methods that use several spatial scales (TTLQV) or comparisons of variables separated by various distances (autocorrelation) are needed to assess grains. With a coarse grain, there will be wider fluctuations in the variances and correlations over various spatial scales compared with a fine grain (7).

Aggregation can also be attributed to true or apparent contagion (34). True contagion can be characterized by the following: patches are small relative to the quadrat size; Taylor's power law $b > 1.0$; the negative binomial provides an adequate fit at some scale; Hill's TTLQV shows one or more sharp peaks; and there are few or no significant autocorrelation or partial autocorrelation coefficients. Apparent contagion can be characterized by large patches; Taylor's $b > 1.0$; adequate fit of the negative binomial at some scale; Hill's TTLQV showing one or more broad peaks; and an autoregressive model adequately describing the data. The intensity-grain concept of pattern describes the appearance of the patches of density, while the contagion concept is related to the mechanism that generates a certain pattern of densities. In reality, spatial data alone do not prove specific mechanisms, but the contagion concept can be useful for categorizing results. A given data set, however, can show elements of several categories, that is, intensity, grain, and contagion. There are no absolute measures to distinguish these characteristics.

The uses to which aggregation can be put include determining the minimum number of samples that should be taken to estimate

TABLE 4. Significant spatial autocorrelations and partial correlations of the preplant population densities of *Verticillium dahliae, Pratylenchus penetrans, P. scribneri, P. crenatus,* and *Meloidogyne hapla* from soil taken in 10 commercial potato fields

Field	Pathogen	Lag number[a] (autocorrelation, partial autocorrelation)
1	*V. dahliae*	4 (. . .[c], 0.23)
($r = 15$)[b]	*P. scribneri*	1 (0.25, 0.25), 3 (0.24, . . .)
2	*V. dahliae*	1 (0.24, 0.24), 2 (0.23, . . .)
($r = 15$)	*P. penetrans*	3 (. . ., 0.24)
	P. crenatus	2 (0.23, . . .), 3 (0.28, . . .), 4 (0.29, . . .), 13 (. . ., −0.26))
	M. hapla	1 (0.32, 0.32), 2 (0.36, 0.28)
3	*P. penetrans*	8 (. . ., −0.30)
($r = 10$)	*P. scribneri*	2 (0.31, 0.30)
	P. crenatus	2 (0.51, 0.49)
	M. hapla	7 (0.34, 0.30)
4	*P. scribneri*	8 (. . ., 0.39)
($r = 15$)	*P. crenatus*	1 (0.38, 0.38), 2 (0.24, . . .)
	M. hapla	1 (0.35, 0.35)
5	*V. dahliae*	1 (0.29, 0.29), 9 (0.29, 0.24)
($r = 20$)		
6	*V. dahliae*	10 (0.33, 0.34), 15 (0.29, 0.34), 20 (. . ., −0.25)
($r = 20$)	*P. penetrans*	10 (0.58, 0.56), 12 (. . ., −0.30), 18 (. . ., −0.27), 20 (. . ., −0.55)
	P. scribneri	3 (0.24, 0.23), 5 (0.33, 0.32), 11 (. . ., −0.23), 13 (0.30, 0.31), 16 (−0.28, −0.41), 18 (. . ., −0.27), 19 (. . ., 0.44)
7	*V. dahliae*	1 (0.51, 0.51)
($r = 5$)	*PRAT*[d]	1 (0.52, 0.52), 2 (0.47, . . .), 3 (0.54, . . .)
	M. hapla	1 (0.38, 0.38)
8	*P. scribneri*	1 (0.28, 0.28), 2 (0.40, 0.35), 5 (0.40, 0.31)
($r = 10$)	*M. hapla*	1 (0.29, 0.29)

[a] Lag number is the number of plots in which there was a consistent, significant, negative or positive correlation between the densities of the pathogens.
[b] Number of partial autocorrelations tested based on total number of plots in each field.
[c] Not significant at $P = 0.05$.
[d] *Pratylenchus* spp. per 100 cm^3 of soil; all species combined.

mean density with a given level of precision (5) as well as improving yield-loss predictions when yield-loss models are nonlinear (1,13,22,38,54). When field population densities are determined in order to assess treatment differences, (e.g., cultivar effects), typically the responses to mean densities are compared in ANOVA. With densities of organisms, the variance increases with the mean, which violates an ANOVA assumption. Information on aggregation can be used to transform data to stabilize variances so that ANOVA is properly utilized (11,12). Furthermore, treatments may affect the distribution of the organisms, or cluster size, rather than just the mean density.

Results for *V. dahliae* in individual fields where the mean density was >1.0 microsclerotia per cubic centimeter of soil included 1) adequate fit of the negative binomial distribution in most fields; 2) Hill's TTLQV variance usually fluctuating with somewhat of

TABLE 5. Regression models relating yield in commercial potato fields as a function of preplant densities of *Verticillium dahliae* (*VD*), *Pratylenchus penetrans* (*PP*), *P. scribneri*, *P. crenatus* (*PC*), and *Meloidogyne hapla* (*MH*), together with the coefficient of determination (R^2)

Field	Significant[a] independent variables and coefficients for multiple regression	R^2
1	$-0.019(PP)$	0.08
2	No variables were significant	
3	$-0.087\,(VD \times PP) - 0.95(\log_{10}(MH + 1)$	0.28
4	$-0.00016(VD \times PP) - 0.0012(MH) + 2 \times 10^{-5}(VD \times MH)$	0.11
5	$0.026(PC) - 0.0012(VD \times PC)$	0.18
6	No variables were significant	
7	$-1.7[\log_{10}(MH + 1)] + 0.32(VD \times PRAT$[b]$)$	0.29
8	$-0.00093(VD + PP) + 0.00031(VD \times MH)$	0.10
9	$-6.5[\log_{10}(VD + 1)]$	0.62
10	$-0.00060(VD \times PRAT)$	0.18

[a]Estimated significant parameter ($P = 0.10$); overall model was significant at $P = 0.05$.
[b]*PRAT* are the genus counts of *Pratylenchus*, where no species identifications were done.

TABLE 6. Significant yield autocorrelations and partial autocorrelations

Field	Lag number[a] (autocorrelations, partial autocorrelations)
1	1 (0.49, 0.49), 2 (0.45, 0.28), 3 (0.44, ...[b]), 13 (..., 0.27)
2	5 (..., −0.23)
3	1 (0.61, 0.61), 2 (0.44, ...), 3 (0.44,...)
4	None
5	1 (0.53, 0.53), 2 (0.37, ...), 3 (0.33, ...)
6	1 (0.29, 0.29), 2 (0.36, 0.30), 3 (0.28, ...), 5 (0.29, ...), 6 (0.23, ...)
7	1 (0.75, 0.75)
8	1 (0.79, 0.79), 2 (0.74, 0.29), 3 (0.65, ...), 4 (0.58, ...)
9	None
10	1 (0.69, 0.69)

[a]Lag number is the number of plots in which there was a consistent, significant, negative or positive correlation between the densities of the pathogens.
[b]Not significant at $P = 0.05$.

TABLE 7. Spearman's correlation coefficients and significance levels (in parentheses) for covariation in densities of *Verticillium dahliae* (*VD*), *Pratylenchus penetrans* (*PP*), *P. scribneri* (*PS*), *P. crenatus* (*PC*), and *Meloidogyne hapla* (*MH*) in 10 commercial potato fields

	PP	*PS*	*PC*	*MH*	*Pratylenchus*[a]
Field 1					
VD	0.12 (0.22)	0.02 (0.86)	0.07 (0.47)	−0.10 (0.31)	...
PP	...	0.57 (0.01)	0.64 (0.01)	0.11 (0.27)	...
PS	...	...	0.52 (0.01)	−0.07 (0.48)	...
PC	...	...	...	0.10 (0.34)	...
Field 2					
VD	0.08 (0.39)	...	0.03 (0.74)	0.12 (0.21)	...
PP	...	...	0.39 (0.01)	−0.04 (0.69)	...
PC	...	...	...	0.23 (0.02)	...
Field 3					
VD	−0.05 (0.71)	0.21 (0.12)	−0.04 (0.74)	0.13 (0.32)	...
PP	...	0.38 (0.01)	0.37 (0.01)	0.17 (0.22)	...
PS	...	...	0.35 (0.01)	0.13 (0.34)	...
PC	...	...	...	−0.06 (0.67)	...
Field 4					
VD	0.03 (0.78)	−0.01 (0.93)	−0.14 (0.24)	−0.12 (0.28)	...
PP	...	0.05 (0.67)	0.15 (0.19)	0.18 (0.11)	...
PS	...	...	0.26 (0.02)	0.30 (0.01)	...
PC	...	...	...	0.42 (0.01)	...
Field 5					
VD	−0.09 (0.37)	−0.12 (0.25)	−0.04 (0.70)	...	...
PP	...	0.72 (0.01)	0.62 (0.01)	...	...
PS	...	...	0.49 (0.01)	...	...
Field 6					
VD	−0.09 (0.40)	−0.14 (0.19)	−0.01 (0.90)	...	...
PP	...	0.73 (0.01)	0.81 (0.01)	...	...
PS	...	...	0.57 (0.01)	...	...
Field 7					
VD	...	...	...	−0.43 (0.01)	0.40 (0.02)
MH	...	...	...	...	−0.41 (0.02)
Field 8					
VD	0.03 (0.81)	0.06 (0.62)	0.04 (0.75)	−0.03 (0.81)	...
PP	...	0.53 (0.01)	0.66 (0.01)	0.25 (0.05)	...
PS	...	...	0.71 (0.01)	0.13 (0.31)	...
PC	...	...	...	0.20 (0.13)	...
Field 9					
VD	...	...	...	−0.12 (0.59)	−0.26 (0.25)
MH	...	...	...	...	0.13 (0.56)
Field 10					
VD	...	...	...	−0.17 (0.35)	0.24 (0.20)
MH	...	...	...	...	−0.17 (0.35)

[a]All species combined.

an upward trend for all block sizes, with no particular pattern; and 3) a few significant autocorrelations or partial autocorrelations, signifying, in some cases, a low order autoregressive process. Apparent contagion is consistent with results 1 and 3, while 2 indicates a pattern of low intensity and poorly defined clusters, that is, a variable grain. The exception, where a sharp peak occurred in one field, indicates a high intensity and coarse grain, also consistent with apparent aggregation. The aggregation patterns of *M. hapla* were similar to those of *V. dahliae* and were also described as apparent contagion with generally low intensity and poorly defined clusters.

The results for *P. penetrans, P. scribneri,* and *P. crenatus* all differed in some manner between the different measures of aggregation. Apparent aggregation was indicated by density being fitted with the negative binomial distribution, low order spatial autocorrelations, and large patches, as indicated by Hills TTLQV for *P. crenatus* and *P. scribneri.* However, when Taylor's power law model was used to assess aggregation as a measure of all of the fields, *P. crenatus* was not significantly aggregated, while *P. scribneri* was aggregated. The results for *P. penetrans* demonstrated some of the attributes of true contagion, i.e., Taylor's power law $b > 1.0$ and few significant autocorrelation coefficients. However, there was no adequate fit to the negative binomial distribution at any scale examined and no consistent sharp peaks with Hill's TTLQV. The lesion nematodes can all be characterized generally as coarse grained from Hill's TTLQV, but intensity differed greatly from field to field.

Providing potato yield-loss estimates caused by early dying on the basis of sampling aggregated pathogen populations is impacted by the intensity of the densities of clusters, the grain of the clusters, and whether the yield-loss model involves linear or nonlinear relationships. When the grain of the clusters is coarse, then all the bulked cores for a sample may be taken from a single cluster, resulting in a realistic estimate for the yield-loss modeling. Even with a fine grain, when the intensity between clusters is low, the averaging that occurs when soil cores are bulked may still give meaningful results in a yield-loss model, especially if the yield relationship is linear or close to linear. A nonlinear yield-loss model is particularly sensitive to averaging of densities between clusters, when grain of a pattern is fine and intensity is high. In the situation where an interaction may occur between *V. dahliae* and *P. penetrans* or *M. hapla,* bulking of soil cores to achieve an average density in a sample is even more sensitive to intensity and grain pattern of the organisms.

One or more of the soilborne plant pathogens, *V. dahliae, P. penetrans, P. scribneri, P. crenatus,* and *M. hapla,* were related to potato yield in eight of 10 commercial fields. An interaction between *V. dahliae* and *P. penetrans* ($VD \times PP$) was the most common factor associated with yield, although there was substantial variation among fields. This interaction occurred even when low populations of both organisms were present. These findings confirm results from studies done in microplots with the two pathogens (15,44,53). It is the first demonstration of the interaction between *V. dahliae* and *P. penetrans* in commercial potato fields with no experimental intervention.

The interaction between *V. dahliae* and *M. hapla* was positively associated with yield in several of the fields in this study. This interaction term occurred only when another *V. dahliae* interaction was present (*P. crenatus* in one field and *P. penetrans* in another). Since these variables were not independent, it is difficult to interpret the importance of the *V. dahliae* × *M. hapla* interaction. These organisms were shown not to interact in our microplot studies nor in those of MacGuidwin and Rouse (32). Hoyman (19) found no indication of an interaction between these two organisms in field trials with different *Solanum* species. Jacobsen et al (26), however, found an interaction between *V. dahliae* and *M. hapla* in both microplot and field studies with potatoes. These differences may be the result of isolates of the nematode or the fungus involved (3). Variation in the isolate of the fungus has recently been shown to have a large effect on the interaction.

The aggregation parameters for both *V. dahliae* and *P. penetrans* were determined, although only Taylor's power law permitted a somewhat similar parameter estimate (b) for both organisms, possibly because b is a single measure over all fields. All other methods to characterize aggregation showed dramatically different patterns for *V. dahliae* and *P. penetrans.* Aggregation parameters can be used to improve yield-loss models, but in this case, the disparity in aggregation patterns between *V. dahliae* and *P. penetrans* may affect our ability to predict when a synergistic interaction with respect to yield losses occurs between the two organisms in commercial fields.

LITERATURE CITED

1. Bélair, G., and Boivin, G. 1988. Spatial pattern and sequential sampling plan for *Meloidogyne hapla* in muck-grown carrots. Phytopathology 78:604-607.
2. Bernard, E. C., and Laughlin, C. W. 1976. Relative susceptibility of selected cultivars of potato to *Pratylenchus penetrans.* J. Nematol. 8:239-242.
3. Botseas, D. D., and Rowe, R. C. 1994. Development of potato early dying in response to infection by two pathotypes of *Verticillium dahliae* and co-infection by *Pratylenchus penetrans.* Phytopathology 84:275-282.
4. Brown, M. J., Riedel, R. M., and Rowe, R. C. 1980. Species of *Pratylenchus* associated with *Solanum tuberosum* cv. Superior in Ohio. J. Nematol. 12:189-192.
5. Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. John Wiley & Sons, New York.
6. Campbell, C. L., and Noe, J. P. 1985. The spatial analysis of soilborne pathogens and root diseases. Annu. Rev. Phytopathol. 23:129-148.
7. Cliff, A. D., and Ord, J. K. 1981. Spatial Processes: Models and Applications. Pion, London.
8. Clifford, P., Richardson, S., and Hemon, D. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45:123-134.
9. Dickerson, O. J., Darling, H. M., and Griffin, G. D. 1964. Pathogenicity and population trends of *Pratylenchus penetrans* on potato and corn. Phytopathology 54:317-322.
10. Diggle, P. J. 1990. Time Series, A Biostatistical Introduction. Oxford University Press, Oxford.
11. Elliott, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, no. 25. The Ferry House, Ambleside, England.
12. Evans, G., and Gleeson, A. C. 1980. An evaluation of the sampling variation when estimating the population of *Verticillium dahliae* in field soil. Ann. Appl. Biology 95:177-184.
13. Ferrandino, F. J. 1989. A distribution-free method for estimating the effect of aggregated plant damage on crop yield. Phytopathology 79:1229-1232.
14. Francl, L. J., Madden, L. V., Rowe, R. C., and Riedel, R. M. 1987. Potato yield loss prediction and discrimination using preplant population densities of *Verticillium dahliae* and *Pratylenchus penetrans.* Phytopathology 77:579-584.
15. Francl, L. J., Rowe, R. C., Riedel, R. M., and Madden, L. V. 1988. Effects of three soil types on potato early dying disease and associated yield reduction. Phytopathology 78:159-166.
16. Gates, C. E., and Ethridge, F. G. 1970. A generalized set of discrete frequency distributions with FORTRAN program. Math. Geol. 4:1-24.
17. Goodell, P., and Ferris, H. 1980. Plant parasitic nematode distributions in an alfalfa field. J. Nematol. 12:136-141.
18. Handoo, Z. A., and Golden, A. M. 1989. A key and diagnostic compendium to the species of the genus *Pratylenchus* Filipjev, 1936 (lesion nematodes). J. Nematol. 21:202-218.
19. Hoyman, W. G. 1974. Reaction of *Solanum tuberosum* and *Solanum* species to *Meloidogyne hapla.* Am. Potato J. 51:281-286.
20. Hudelson, B. D., Clayton, M. K., Smith, K. P., Rouse, D. I., and Upper, C. D. 1989. Nonrandom patterns of bacterial brown spot in snap bean row segments. Phytopathology 79:674-681.
21. Huettel, R. N., Francl, L. J., Henn, A., and Bourgoin, T. 1990. Plant parasitic nematodes in Maine agricultural soils. J. Nematol. 22:745-749.
22. Hughes, G. 1990. Characterizing crop responses to patchy pathogen attack. Plant Pathol. 39:2-4.
23. Huisman, O. C., and Ashworth, L. J., Jr. 1974. Quantitative assessment of *Verticillium albo-atrum* in field soils: Procedural and substrate improvements. Phytopathology 64:1043-1044.
24. 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.
25. Isaac, I., and Harrison, J. A. C. 1968. The symptoms and causal agents of early-dying disease (Verticillium wilt) of potatoes. Ann. Appl. Biol. 61:231-244.
26. Jacobsen, B. J., MacDonald, D. H., and Bissonnette, H. L. 1979. Interaction between *Meloidogyne hapla* and *Verticillium albo-atrum* in the Verticillium wilt disease of potato. Phytopathology 69:288-292.
27. Johnson, K. B., Apple, J. D., and Powelson, M. L. 1988. Spatial patterns of *Verticillium dahliae* propagules in potato field soils of Oregon's Columbia Basin. Plant Dis. 72:484-488.
28. Kimpinski, J. 1979. Root lesion nematodes in potatoes. Am. Potato J. 56:79-86.
29. Kirkland, M. L. 1982. The roles of *Verticillium dahliae, Colletotrichum atramentarium, Erwinia carotovora* subs. *carotovora* and *E.* subsp. *carotovora atroseptica* in "early dying" disease of potatoes. M.S. thesis. Oregon State University, Corvallis.
30. 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.
31. Ludwid, J. A., and Reynolds, J. F. 1988. Statistical Ecology. John Wiley & Sons, New York.
32. 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.
33. MacGuidwin, A. E., and Rouse, D. I. 1990. Role of *Pratylenchus penetrans* in the potato early dying disease of Russet Burbank potato. Phytopathology 80:1077-1082.
34. Madden, L. V. 1989. Dynamic nature of within-field disease and pathogen distributions. Pages 96-126 in: Spatial Components of Plant Disease Epidemics. M. J. Jeger, ed. Prentice Hall, Englewood Cliffs, NJ.
35. 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.
36. Nicot, P. C., and Rouse, D. I. 1987. Precision and bias of three quantitative soil assays for *Verticillium dahliae.* Phytopathology 77:875-881.
37. Nnudo, E. C., and Harrison, M. D. 1979. The relationship between *Verticillium albo-atrum* inoculum density and potato yield. Am. Potato J. 56:11-25.
38. Noe, J. P., and Barker, K. R. 1985. Overestimation of yield loss of tobacco caused by the aggregated spatial pattern of *Meloidogyne incognita.* J. Nematol. 17:245-251.
39. Olthof, T. H. A., and Potter, J. W. 1972. Relationship between population densities of *Meloidogyne hapla* and crop losses in summer-maturing vegetables in Ontario. Phytopathology 62:981-986.
40. Olthof, T. H. A., and Potter, J. W. 1973. The relationship between population densities of *Pratylenchus penetrans* and crop losses in summer-maturing vegetables in Ontario. Phytopathology 63:577-582.
41. Pielou, E. C. 1977. Mathematical Ecology. John Wiley & Sons, New York.
42. Rahimian, M. K., and Mitchell, J. E. 1984. Relationships of *Verticillium dahliae* and *Erwinia carotovora* pv. *carotovora* in the early dying disease of potato. Phytopathology 74:327-332.
43. 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.
44. 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.
45. 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.
46. SAS Institute. 1984. SAS-ETS User's Guide. Version 5 ed. SAS Institute, Cary, NC.
47. SAS Institute. 1986. SAS-STAT User's Guide. Version 6 ed. SAS Institute, Cary, NC.
48. Slattery, R. J. 1981. Inoculum potential of *Verticillium*-infested potato cultivars. Am. Pot. J. 58:135-142.
49. Smith, V. L., and Rowe, R. C. 1984. Characteristics and distribution of propagules of *Verticillium dahliae* in Ohio potato field soils and assessment of two assay methods. Phytopathology 74:553-556.
50. Taylor, L. R. 1961. Aggregation, variance and the mean. Nature (London) 189:732-735.
51. Thistlethwayte, B. 1970. Reproduction of *Pratylenchus penetrans* (Nematoda: Tylenchida). J. Nematol. 2:101-105.
52. Townshend, J. L., Potter, J. W., and Willis, C. B. 1978. Ranges of distribution of species of *Pratylenchus* in Northeastern United States. Can. Plant Dis. Surv. 58:80-82.
53. Wheeler, T. A., Madden, L. V., Rowe, R. C., and Riedel, R. M. 1992. Modeling of yield loss in potato early dying caused by *Pratylenchus penetrans* and *Verticillium dahliae.* J. Nematol. 24:99-102.
54. Yang, X. B., Snow, J. P., and Berggren, G. T. 1991. Patterns of Rhizoctonia foliar blight on soybean and effect of aggregation on disease development. Phytopathology 81:287-293.