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Spatial Pattern Analysis of Plant-Parasitic Nematodes[1]

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Abstract: Spatial patterns of *Meloidogyne incognita, Tylenchorhynchus claytoni, Helicotylenchus dihystera,* and *Criconemella ornata* were analyzed using Hill's two-term local quadrat variance method (TTLQV), spectral analysis, and spatial correlation. Data were collected according to a systematic grid sampling plan from seven tobacco fields in North Carolina. Different estimates of nematode cluster size were obtained through TTLQV and spectral analysis. No relationship was observed between either estimate and nematode species, time of sampling (spring vs. fall), or mean density. Cluster size estimates obtained from spectral analysis depended on sampling block size. For each species examined, spatial correlations among nematode population densities were greater within plant rows than across rows, indicating that clusters were ellipsoidal with long axes oriented along plant rows. Analysis of mean square errors indicated that significant gains in sampling efficiency resulted from orienting the long axis of sampling blocks across plant rows. Spatial correlation was greater in the fall than in spring and was greater among 1 × 1-m quadrats than among 3 × 3-m quadrats.

Key words: nematode distribution, spatial pattern, sampling design.

Understanding the spatial distribution patterns of plant-parasitic nematodes is essential for the formulation of efficient sampling plans and for the design and interpretation of field experiments. Spatial distribution affects the accuracy and precision of population density measurements, because intense clustering of individuals results in high sample variance.

Previous work related to the spatial distribution of nematodes has been concerned primarily with fitting a negative binomial distribution to frequency distributions of nematode sample counts (7,12,14). The parameter k of the negative binomial was then used as an index of aggregation (5,20), with the assumption that small k values indicated a clumped spatial distribution (1,2,15). It has not been established, however, that k values are related to the physical size of clusters in a field. One report (19) indicated that k was not suitable for use as an index of aggregation, because it was not directly related to spatial pattern. Analysis of frequency distributions indicates whether nematodes have clustered spatial patterns but offers little information on the precise nature and scale of clustering. A more direct analysis of spatial distribution is necessary to define efficient sampling plans.

Various methods have been devised for the analysis of spatial patterns in biological populations. The most common methods were derived from quadrat variance techniques proposed by Greig-Smith (8). Ludwig and Goodall (11) compared available quadrat variance methods and determined that Hill's (9) two-term local quadrat variance technique (TTLQV) most accurately detected known scales of spatial patterning. This method also has the advantage of allowing the detection of spatial patterns at any multiple of unit quadrat size, whereas most methods are restricted to multiples that are powers of two.

Another method for analyzing spatial patterns is spectral analysis. It is used in the physical sciences to measure periodicity in spatially or temporally sequential data (10) and has been used to analyze spatial patterns in botanical ecology (4).

A third approach to analyzing spatial patterns is spatial correlation. Spatial correlation methods detect clustering by examining the change that occurs in the degree of correlation between paired density measurements as the physical distance between measurements changes. They are available for the analysis of biological count data from a systematic grid sampling plan (13). This approach has been used to analyze the spatial distribution of soilborne plant-pathogenic fungi (18). If nematodes have a clustered distribution, then spatially proximal measures of population density should show a strong degree of autocorrelation.

Spatial correlations may also be used to derive standardized mean square errors

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(STMSE) in two dimensions (13). The STMSE may be used to calculate the relative efficiency of various plot sizes and shapes with respect to nematode population variation.

The spatial patterns of four plant-parasitic nematode species in tobacco fields are analyzed in this paper. A quadrat variance method, spectral analysis, and spatial correlation are compared. The relationship of negative binomial k values to cluster sizes of plant-parasitic nematodes is considered. The relative efficiencies of various experimental plot sizes and shapes are compared.

Materials and Methods

Seven fields were sampled for population densities of plant-parasitic nematodes with a systematic-grid sampling plan. Four of the fields were sampled twice, once after harvest in the fall and again in March. Four fields were sampled with quadrats measuring 1 m on a side (referred to as 1-m quadrats), and three fields were sampled with quadrats measuring 3 m on a side (referred to as 3-m quadrats). Sampling grids were arranged so that one axis of the grid was parallel to the direction of plant rows and the other axis was perpendicular. One-meter grids were sampled within adjacent plant rows, and 3-m grids were sampled within every third plant row. Samples were then located down plant rows at a distance equal to that taken across plant rows.

Ten soil cores (2.5 × 20 cm) were removed from each quadrat in a systematic pattern within the plant row and bulked for analysis. Nematodes were separated from the soil by elutriation and centrifugation (3) and identified.

Data sets used in the analyses are described in Table 1. All the fields had been planted in tobacco (*Nicotiana tabacum* L. various cultivars).

A negative binomial distribution was fitted to the frequency distribution of nematode counts in each data set in order to derive a maximum likelihood estimate of k (6).

Cluster size analysis: Hill's TTLQV (9) was used to estimate average cluster size for each nematode species in each field. The variance in population density among quadrats was computed for successively larger groupings of quadrats up to N/2, where N was the number of unit quadrats. The variance among blocks of quadrats increased until the area of grouped quadrats was approximately equal to the average cluster area of the target organism. Cluster size was considered to be the area of peak variance, which was determined by plotting variance against area.

Next, spectral analysis was used to estimate cluster size. Spectral analysis measures periodicity in a sequence of observations by fitting a Fourier series (16). Analysis of the Fourier series leads to the determination of periodic densities, which can be used to determine cluster size in a spatially sequential data set. Spectral analysis was done with the Statistical Analysis System (SAS) (17).

A linear correlation procedure compared cluster sizes derived by Hill's TTLQV and spectral analysis. A *t*-test procedure was used to detect differences in cluster size due to time of sampling (fall vs. spring) and sampling quadrat size (1 m vs. 3 m), and analysis of variance tested for differences among nematode species. All analyses were done with SAS, and differences reported were significant at the 0.05 level.

Spatial correlation analysis: Spatial lag correlations analyzed the relationships of nematode counts among quadrats (13). Correlations were calculated between each quadrat of each grid row and its nearest neighbor, and next nearest neighbor, . . . , and n^{th} nearest neighbor, where n is the number of quadrats in one axis of the grid. The process was repeated for the other grid axis. Correlation terms were calculated as previously described (13) to yield a matrix of correlations in which the (x,y) element represented the correlation coefficient between all quadrat pairs that were x units apart in one dimension and y units apart in the other dimension. A significant correlation value indicated that the nematode counts were spatially autocorrelated. Because sampling grids were aligned with plant rows, it was possible to compare spatial correlations within plant rows to coefficients across plant rows.

To compare the relative efficiencies of various experimental plot sizes and shapes, covariances were calculated and from them a matrix of mean square errors (MSE) was derived (13). This matrix represented vari-

TABLE 1. Estimated cluster sizes from Hill's two-term local quadrat method (TTLQV) and spectral analysis (SA), with mean densities, standard deviations (SD), and negative binomial k values, by sampling site.

Data set	Location (county)	Month of sampling	Grid size/ shape	Quadrat length (m)	Nematode species†	Density/500 cm³ soil		k	Cluster diameter (m)	
						Mean	SD		Hill's TTLQV‡	SA
A	Johnston #1	October	8 × 8	1	*M. incognita*	1,890	1,430	2.6	6	4.9
B	Johnston #1	October	8 × 8	1	*T. claytoni*	137	108	2.6	np	4.9
C	Johnston #1	October	8 × 8	1	*H. dihystera*	143	199	0.4	np	3.8
D	Johnston #1	March	8 × 8	1	*M. incognita*	1,173	891	3.5	3	6.4
E	Johnston #1	March	8 × 8	1	*T. claytoni*	79	48	10.7	np	2.9
F	Johnston #1	March	8 × 8	1	*H. dihystera*	91	149	0.3	2	2.1
G	Wilson	October	8 × 8	1	*M. incognita*	8,153	5,391	3.1	28	4.0
H	Wilson	October	8 × 8	1	*T. claytoni*	196	194	1.1	8	2.1
I	Wilson	October	8 × 8	1	*H. dihystera*	52	101	0.2	27	5.3
J	Wilson	March	8 × 8	1	*M. incognita*	5,619	3,738	5.0	12	4.0
K	Wilson	March	8 × 8	1	*T. claytoni*	277	148	3.5	3	2.8
L	Wilson	March	8 × 8	1	*H. dihystera*	61	86	0.3	25	2.8
M	Franklin	October	10 × 10	3	*M. incognita*	2,298	3,548	0.3	15	8.7
N	Franklin	October	10 × 10	3	*T. claytoni*	457	538	0.7	9	7.8
O	Franklin	October	10 × 10	3	*H. dihystera*	51	103	0.2	3	6.3
P	Franklin	March	10 × 10	3	*M. incognita*	895	2,260	0.2	12	12.6
Q	Franklin	March	10 × 10	3	*T. claytoni*	353	429	0.7	6	7.8
R	Franklin	March	10 × 10	3	*H. dihystera*	31	63	0.2	6	12.9
S	Johnston #2	October	10 × 10	3	*M. incognita*	114	200	0.3	6	9.0
T	Johnston #2	October	10 × 10	3	*T. claytoni*	79	101	0.6	9	20.1
U	Johnston #2	March	10 × 10	3	*M. incognita*	39	68	0.2	3	8.4
V	Johnston #2	March	10 × 10	3	*T. claytoni*	45	44	1.1	12	8.7
W	Columbus #1	September	8 × 8	1	*M. incognita*	467	383	2.5	7	2.8
X	Columbus #1	September	8 × 8	1	*T. claytoni*	289	274	1.2	15	2.4
Y	Columbus #1	September	8 × 8	1	*C. ornata*	564	608	1.0	16	3.2
Z	Columbus #2	September	8 × 8	1	*M. incognita*	1,164	767	4.4	6	2.8
AA	Columbus #2	September	8 × 8	1	*T. claytoni*	227	154	5.4	10	3.6
BB	Columbus #2	September	8 × 8	1	*C. ornata*	71	63	1.1	np	2.8
CC	Columbus #3	September	8 × 8	3	*M. incognita*	338	406	0.3	32	10.8
DD	Columbus #3	September	8 × 8	3	*T. claytoni*	234	223	1.3	12	8.1
EE	Columbus #3	September	8 × 8	3	*H. dihystera*	140	151	1.0	12	8.4
FF	Columbus #3	September	8 × 8	3	*C. ornata*	199	194	1.7	np	9.0

† *Meloidogyne incognita, Tylenchorhynchus claytoni, Helicotylenchus dihystera,* and *Criconemella ornata.*
‡ np = no peak in the variance to block size relationship. Cluster size could not be estimated.

TABLE 2. Spatial correlations of *Meloidogyne incognita* population densities, data set A.

Distance across rows (m)	Lag quadrat distance (m) within plant rows						
	0	1	2	3	4	5	6
0	1.00	0.56*	0.50*	0.47*	0.43*	0.53*	0.04
1	0.39*	0.23	0.18	0.17	0.15	0.29	0.03
2	0.18	0.18	0.18	0.20	0.13	0.16	0.15
3	−0.19	0.01	−0.06	−0.07	−0.24	−0.09	−0.05
4	−0.35*	−0.17	−0.20	−0.32	−0.19	−0.20	−0.03
5	−0.11	0.05	0.14	0.08	0.25	−0.10	0.16
6	−0.14	−0.16	−0.20	−0.28	0.11	−0.52	−0.66

* Correlation significantly different from zero at the 0.05 level. Degrees of freedom = [(8 − L)(8 − K)] − 2, where L is the distance across columns and K is the distance across rows.

ability among hypothetical sampling blocks of all possible sizes and shapes that could be made by combining original quadrats. For each set of sampling data, the MSE matrices were standardized by dividing each MSE by the MSE calculated among blocks consisting of exactly one quadrat (i.e., the sample MSE). The resulting values are referred to as standardized mean square errors (STMSE). The comparison of STMSE within plant rows with STMSE across plant rows provided a measure of the relative efficiency, with respect to variation in nematode counts, of orienting the long axis of sampling blocks within rather than across plant rows.

A *t*-test procedure compared spatial correlations within and across plant rows and the spatial correlations at two different quadrat sizes (1 m vs. 3 m). A paired *t*-test compared spatial correlations in the fall and spring, using only data sets with two sampling dates, and analysis of variance tested for differences among nematode species. All analyses were done with SAS, and differences reported were significant at the 0.05 level.

RESULTS

Meloidogyne incognita (Kofoid and White) Chitwood and *Tylenchorhynchus claytoni* Steiner were found in all seven fields, *Helicotylenchus dihystera* (Cobb) Sher was detected in four fields, and *Criconemella ornata* (Raski) Luc & Raski was found in three fields (Table 1).

Cluster size analysis: Cluster diameter, as calculated by Hill's TTLQV and spectral analysis, was variable among fields and had no apparent relationship to nematode species or time of sampling (fall vs. spring) (Table 1). Average cluster diameters estimated from spectral analysis were smaller than those obtained from Hill's TTLQV (6.3 m vs. 11.4 m). A larger quadrat size (3 m vs. 1 m) resulted in a larger estimate of cluster diameter with spectral analysis (9.9 m vs. 3.5 m); Hill's TTLQV was unaffected by quadrat size. Neither estimate of cluster diameter was related to mean density.

Negative binomial k values had no detectable relationship to estimates of cluster size. There was, however, a significant interaction among k values, quadrat size, and spectral analysis estimates. At the larger quadrat size, k values were smaller and cluster size estimates were larger, resulting in a negative relationship between k and spectral cluster size. No relationship between k and spectral cluster size was detected when the quadrat size effect was removed.

Spatial correlation analysis: Table 2 is an example of a spatial correlation matrix derived for one species in one field (data set A). Matrix element (0,1) (0.56) represents the correlation of all possible adjacent quadrat pairs within plant rows, whereas matrix element (1,0) (0.39) represents the correlation of all possible adjacent quadrat pairs across plant rows. Similar matrices were derived for the remaining 31 data sets. For data set A, correlations were significant up to five quadrats distant within the same row (first row of the matrix); however, a lag of only one quadrat was significant across plant rows (first column of the matrix). The correlations within rows stayed uniformly high, but the correlations across rows decreased rapidly until a negative correlation was reached at four rows

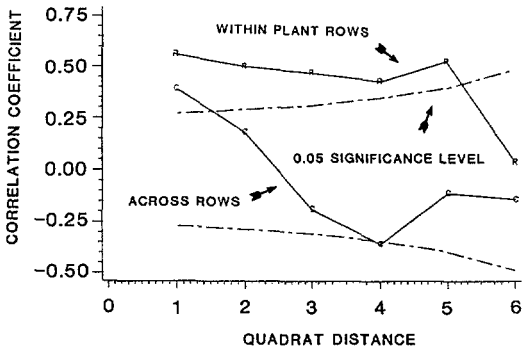

FIG. 1. Spatial correlation among *Meloidogyne incognita* population counts versus quadrat distance (m) for data set A. Correlation is within and among plant rows, with significance level ($P = 0.05$). Correlation remains positive among quadrats within plant rows, but drops rapidly across rows, becoming negative at a distance of 4 meters.

(Fig. 1). The negative correlation at lag four indicated the completion of an average cycle in population densities.

Table 2 and the other correlation matrices were combined to generate average lag correlations for different nematode species, grid sizes, grid orientations, and times of sampling. There were no significant differences by nematode species in the average lag-one spatial autocorrelations. The average lag-one correlation within plant rows was greater than the lag-one correlation across rows (0.30 vs. 0.09).

In a paired comparison of data sets with fall and spring sampling dates, spatial lag-one correlation was greater in the fall than in spring (0.28 vs. 0.17). When the correlations within and across plant rows were analyzed separately, the correlation within plant rows decreased from fall to spring (0.38 to 0.20) but the correlation across rows did not decrease. The average lag-one correlation was greater among 1-m quadrats, than among 3-m quadrats (0.26 vs. 0.12).

The average lag distance over which quadrats were significantly correlated was greater within plant rows than across rows (2.2 quadrats distant vs. 0.5). There were no differences among nematode species in average significant lag distances. Grids with 1-m quadrats had an average significant lag distance of 2.9 quadrats within rows, indicating that density levels of plant-parasitic nematodes were spatially correlated within 3-m sections of plant rows. Analysis of 3-m quadrats was in agreement with this estimate, where the average number of adjacent correlated quadrats within rows was 1.2.

For data set A, STMSE increased more rapidly within plant rows than across (Table 3). The first row represented lag STMSE within plant rows, and the first column represented lag STMSE across plant rows. Comparison of a one-row by four-quadrat block (STMSE = 2.42) to a four-row by one-quadrat block (STMSE = 1.73) showed a 40% increase in STMSE (2.42/1.73 = 1.40) if blocks were oriented in the direction of plant rows. A 2 × 2 block (STMSE = 2.17) increased mean square error by 25% over a 4 × 1 block. Thus, optimal orientation of a four-quadrat sampling block was one-quadrat wide across four plant rows.

Standard mean square errors were greater among quadrats within rows than across plant rows in matrices calculated for all 32 data sets. The average gain in efficiency (decrease in sampling error) by orienting four quadrat sampling blocks across

TABLE 3. Standardized mean square errors on a per unit basis for plots r × c units in size, *Meloidogyne incognita*, data set A.

Number of unit plots across rows, c	Number of unit plots within plant rows, r						
	1	2	3	4	5	6	7
1	1.00	1.53	1.98	2.42	2.84	3.31	3.67
2	1.41	2.17	2.81	3.41	4.01	4.70	5.23
3	1.66	2.62	3.43	4.21	4.96	5.85	6.56
4	1.73	2.81	3.69	4.54	5.34	6.29	7.09
5	1.70	2.80	3.68	4.52	5.30	6.25	7.07
6	1.65	2.77	3.67	4.52	5.30	6.24	7.08
7	1.59	2.70	3.58	4.41	5.19	6.10	6.93

TABLE 4. Summary of spatial statistics by nematode species.

	Density/ 500 cm³ soil	k	Cluster diameter (m)		Lag-one correlation		Correlated quadrats (av. no.)		% decrease MSE‡
			TTLQV†	SA	WPR	APR	WPR	APR	
Meloidogyne incognita									
(N = 11)									
Mean	2,014	2.04	11.8	6.8	0.28	0.04	1.7	0.5	71
Standard error of mean	148	0.56	2.9	1.0	0.05	0.06	0.5	0.2	21
Tylenchorhynchus claytoni									
(N = 11)									
Mean	216	1.91	9.6	6.5	0.32	0.13	2.2	0.5	69
Standard error of mean	38	0.46	1.2	1.6	0.05	0.06	0.7	0.2	23
Helicotylenchus dihystera									
(N = 7)									
Mean	81	0.37	12.5	5.9	0.28	0.13	1.6	0.4	31
Standard error of mean	17	0.11	4.5	1.4	0.13	0.09	0.6	0.3	14
Criconemella ornata									
(N = 3)									
Mean	256	1.27	16.0	5.0	0.31	0.09	2.0	0.7	90
Standard error of mean	148	0.22	0.0	2.0	0.01	0.15	0.6	0.3	45

TTLQV = Hill's TTLQV.
SA = Spectral analysis.
WPR = Within plant rows.
APR = Across plant rows.
MSE = Mean square error.
† Actual number of observations varies. Variance to block size curve did not peak for some data sets. See Table 1.
‡ Blocks oriented across plant rows.

plant rows was 63%. No differences were detected among the nematode species in lag-one STMSE or in the ratio of 4 × 1 blocks to 1 × 4 blocks. The gain in efficiency due to block orientation was greater at the 1-m scale of quadrats than at the 3-m scale (75% vs. 48%). This relationship was consistent with the previously noted decrease in spatial correlation with increasing quadrat size. The gain in sampling precision decreased from fall to spring (82% to 28%) as the previous years' host plant distribution became less important.

Population density levels, negative binomial k values, and spatial statistics for each nematode species are presented in Table 4. There were no significant differences among the species in any of the spatial parameters.

Discussion

Average cluster sizes of *M. incognita, T. claytoni, H. dihystera,* and *C. ornata* appear to be field-specific characteristics. Cluster sizes were not related to time of sampling, mean population density, or nematode species. Of the two methods tested for spatial analysis, Hill's TTLQV offered a more useful tool. This method has been tested against known spatial patterns (11), and was found to be accurate. In our TTLQV analyses, cluster size did not depend on sampling quadrat size, as it did with spectral analysis.

The negative binomial parameter k was of limited value as an index of spatial dispersion, since it was not related to either measure of physical cluster size. According to previous reports (1,20), k should decrease as cluster size decreases, indicating that the spatial distribution is more compactly clustered. In our analyses, spectral estimates of cluster size increased and k values decreased as sampling quadrat size increased. The dependence of k values on quadrat size for nematode counts has been reported previously (7,12). Ideally, an indicator of aggregation should not depend on sampling quadrat size.

Lag correlation analysis was useful for relating spatial pattern to factors that may impact the distribution of nematodes. Levels of autocorrelation were related to the orientation of sampling grids with respect to plant rows and changes during the overwintering process. Clusters of plant-parasitic nematodes in tobacco fields are ellipsoidal, with long axes oriented in the direction of plant rows. Higher spatial correlation of nematode densities within plant rows is probably the result of cultural practices. Most management activities were oriented in the direction of plant rows (planting, cultivating, chemical application), and plants were closer together within rows, than between rows.

Differences in mean square error terms within and across rows have practical implications in sampling and experimental design. The best orientation of research plots depends on the purpose of an experiment. If minimum variation among plots with respect to nematode densities is required, as in variety trials or nematicide evaluation, blocks should be oriented with the long axis across previous plant rows. Counts obtained from sampling across plant rows tend to average the densities within various rows, leading to more uniform sample population densities. The opposite orientation is optimal in experiments aimed at determining yield–loss relationships. Establishing plots in the direction of previous plant rows maximizes variation in nematode counts, thus providing a greater range of densities for yield-loss curves.

Gains in efficiency due to plot orientation decrease as blocks become larger. The effects of local correlations among quadrats became insignificant at larger block sizes. Also, the relative efficiency (ratio of mean square errors) decreased over winter, as the effect of the previous seasons' plant rows was decreased.

Spatial pattern analysis should become an important tool in nematological research. Variability in nematode population estimates is a serious problem in the analysis and interpretation of experimental data. Information obtained on the spatial distribution of a nematode species in a particular field is useful in maximizing precision in experimental design. Estimates of nematode cluster size provide a guide to the selection of optimum plot sizes, and spatial correlation analyses are useful in determining the optimum shape and orientation of plots and sampling blocks.

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