Relation of Within-Field Spatial Variation of Plant-Parasitic Nematode Population Densities and Edaphic Factors

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ABSTRACT

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Variations among total nematode population densities, and overwinter changes in population densities of *Meloidogyne incognita, Tylenchorhynchus claytoni* and *Helicotylenchus dihystera*, were related to soil parameters in 64 1-m^2 contiguous quadrats at two sites. Discriminant functions composed of 26 edaphic variables correctly classified 70% of the quadrats into high, medium, and low categories of nematode density. Optimum discrimination was provided by six to eight soil parameters in stepwise-discriminant analyses. Different subsets of the 26 edaphic variables were useful with different species and sites for the discrimination of quadrats according to nematode densities. Quadrats were separated into clusters of high, medium, and low nematode densities along edaphic canonical axes. Variation in soil parameters accounted for over 50% of the spatial variation in nematode counts. Clay content and sodium and copper concentrations were particularly useful in explaining spatial variation among population densities of *M. incognita, T. claytoni*, and *H. dihystera*.

Additional key words: nematode ecology, spatial distribution.

Plant-parasitic nematodes typically have a patchy distribution within infested fields (1,10,13). This characteristic affects the precision of sample estimates of nematode population densities (1,13) (hereafter called "nematode densities" or, more simply, "densities") and the accuracy of resulting yield-loss estimates in management-advisory systems (15). Analysis of the relationships between variation in soil parameters and the irregular spatial patterns of plant-parasitic nematodes should lead to an improved understanding of how these organisms interact with the soil environment. This information may also be used to improve precision in nematode assay methods by allowing compensation for soil-parameter effects.

To some extent, densities of nematodes represent a response to the soil environment. Soil micro-sites with varying physical and chemical parameters may have differential effects on the nematode or host plant. Densities of plant-parasitic nematodes have been correlated with a visual index of soil texture in an alfalfa field (10). Differences in soil pH (8,17,18), cation-exchange capacity (18), percent organic matter (17,18), soil texture (3,8,17,18,22), and soil moisture (17,22,23) have been related to the relative abundance of nematode species in studies comparing soil samples from different fields.

Many soil parameters are strongly correlated (2). The impact of a single parameter cannot be isolated if only a few edaphic factors are observed. Measured effects may be due to an observed variable or may be the result of another correlated variable. Multivariate statistical methods have been developed for the analysis of intercorrelated data sets (25). Canonical variate analysis has been recommended as an appropriate technique for the analysis of several data sets related to the same biological phenomenon (5).

This study was designed to relate variations in 26 edaphic components to the patchy field distribution of *Meloidogyne incognita* (Kofoid and White) Chitwood, *Tylenchorhynchus claytoni* Steiner, and *Helicotylenchus dihystera* (Cobb) Sher. Changes in nematode densities from fall to spring also were analyzed in relation to soil components as an indication of how spatial patterns change in response to differing soil environments. Quantification of the effects of specific soil structural and chemical parameters was needed to gain greater understanding of how the patchy distribution of plant-parasitic nematodes may arise.

MATERIALS AND METHODS

Data collection. Areas shown by previous assays to be infested with *M. incognita* were selected in two fields in North Carolina. The soils in both fields were loamy sands (Site 1—Johnston County, 88% sand, 9% silt, and 3% clay; Site 2—Wilson County, 85% sand, 12% silt, and 3% clay) with no visible differences in color. One site was selected in each field and divided into a grid of 64 contiguous 1-m^2 quadrats. Fifteen cores of soil (2.5 cm in diameter, 15 cm deep) were removed from each quadrat and bulked for nematode assay and soil analysis. Plant-parasitic nematodes were extracted by elutriation and centrifugation (4) from 500 cm^3 of soil per sample and identified. After the fields were disked in the fall, permanent sampling grids were established. Samples were collected on four sampling dates (October 1981, November 1981, February 1982, and March, 1982). Both sites had been planted with *Nicotiana tabacum* L., and were left fallow for the duration of the experiment.

Soil texture (percent sand, silt, and clay) was determined for each quadrat by hydrometric particle-size analysis (7). Acidity, base saturation, cation-exchange capacity, percent organic matter, pH, bulk density, and levels of exchangeable and extractable anions and cations (calcium, copper, magnesium, manganese, nitrate, total nitrogen, phosphorus, potassium, and zinc) were determined by the Agronomic Division, North Carolina Department of Agriculture, Raleigh.

Oxidation/reduction potential was measured in each quadrat at site 1 with a platinum electrode resistance measuring device (12). The other field was too uniformly aerated to obtain meaningful data. Percentage moisture content on an oven-dry-weight basis was determined for each quadrat on each of the sampling dates. Change in percent moisture was then calculated for each quadrat as an indication of the differential rates of wetting and drying over sampling dates.

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Data analysis. Population density estimates for individual quadrats were averaged across dates to establish the levels of *M. incognita, T. claytoni*, and *H. dihystera*. Relative changes in nematode densities were calculated as the percent difference between fall and spring density estimates in each quadrat. Fall nematode density was used as a covariate in the analysis of overwinter changes in nematode numbers. Changes in numbers of plant-parasitic nematodes were found to be related to initial density, so the effect of this component was considered important when assessing the impact of soil physical and chemical components. In one sense, this component was a "biotic" soil parameter, ie, the density of other species' members in the immediate soil environment.

Discriminant analysis was used to determine the suitability of edaphic variables for discriminating among the quadrats according to nematode density levels. Discriminant analysis requires that observations be categorized according to a single variable, which is used as a basis for discrimination. For this purpose, quadrats were grouped into three equal-size categories according to the density of each species of nematode (high, medium, and low density). Initially, quadrats were ranked from lowest to highest by average density for each species. Then, the lowest third of the ranked quadrats was categorized as low density, the middle third was considered medium density, and the highest third was high density. A similar ranking process was performed on the quadrats by relative changes in nematode densities (fall to spring). High, medium, and low category ranges are given in Table 1. After discriminant analysis, posterior probabilities of cluster membership were calculated and compared to the rank-derived a priori classifications.

The results of discriminant analysis provided an indication that variation in nematode densities among quadrats was related to edaphic variation, but this information could not be used to determine the effects of specific variables (24). A stepwise-discriminant analysis was done (24) to reduce the number of variables and to select variables that were most important for discriminating differences. After the stepwise process, canonical-discriminant analysis was used to determine the precise relationships of selected variables to densities of plant-parasitic nematodes. As the name implies, canonical-discriminant analysis combines elements of canonical correlation and discriminant analysis. The canonical correlations were a measure of the strength of association between edaphic variables and nematode densities (6). Wilks'-Lambda (11) statistic was used to determine the significance levels of the correlation values. The canonical loadings derived from corresponding discriminant functions were used to assess the relative effect and importance of individual edaphic variables (20). Variables with loadings greater than 0.30 accounted for at least 10% of the variation in the canonical variate scores, a level considered sufficient for interpretation in this procedure (24). Analyses were done for each nematode species, at each site, and for both sites combined.

Mahalanobis distances were calculated among categories of quadrats, based on the canonical-discriminant variate scores (14,24). Significance of the Mahalanobis distances were used as an indication of the overall significance of discrimination among quadrat nematode densities by edaphic variables. Quadrat canonical variate scores were plotted with 95% confidence intervals and Mahalanobis distances. Category scores showed the central tendency of clusters of quadrats along each canonical variate axis, weighted for the importance of individual edaphic components in the analysis. Confidence areas indicated the region within which the true cluster centers would fall with a 95% probability based on single-sample statistics.

Statistical analyses were done with the Statistical Analysis System (SAS) (21). Three-dimensional contour maps of nematode densities and edaphic variables were drawn using a contour-mapping procedure of SAS. The maps were used to cross-validate spatial covariations indicated in the statistical analyses. Negative binomial and Poisson distributions were fitted to nematode counts, and certain edaphic measurements, by using a FORTRAN program (9). Distribution parameters and indices of spatial aggregation were compared among population densities and edaphic variables, as another means of cross-validating the spatial covariation.

RESULTS

M. incognita, T. claytoni, and *H. dihystera* were found at both sites with sufficient frequency and density for spatial analysis. Nematode densities in more than 70% of the quadrats were correctly categorized as high, medium, or low by edaphic discriminant functions. In similar analyses, edaphic discriminant functions correctly categorized more than 67% of the quadrats according to relative changes in nematode densities (fall to spring).

Correlations between nematode density levels and canonical variates composed of edaphic variables were uniformly high (Table 2) for *M. incognita, T. claytoni*, and *H. dihystera*. The canonical r^2 values showed that 40–50% of the spatial variation in nematode population density levels was accounted for by canonical variates

TABLE 1. Nematode population densities and relative changes in density levels used to categorize quadrats as high, medium, or low for discriminant analysis[a]

	Category ranges		
Category	*Meloidogyne incognita*	*Tylenchorhynchus claytoni*	*Helicotylenchus dihystera*
Density/500 cm^3 of soil			
Site 1			
Low	300–830	23–70	0–20
Medium	831–1,240	71–130	21–80
High	1,241–3,390	131–270	81–670
Site 2			
Low	490–3,970	60–180	0–20
Medium	3,971–6,820	181–320	21–40
High	6,821–16,060	321–570	41–370
Change in density (%)[b]			
Site 1			
Low	65–91	51–92	72–100
Medium	35–64	20–50	30–71
High	−2–34	−3–19	−10–29
Site 2			
Low	53–78	−42–71	20–100
Medium	23–52	−130–−41	−100–19
High	−7–22	−170–−129	−147–−99

[a] Sixty-four 1-m^2 quadrats per site.

[b] Calculated as ([fall density − spring density]/fall density) × 100. Negative numbers indicate net increase in nematode density.

composed of relatively few soil components (three to eight variables). Wilks'-Lambda was significant ($P < 0.001$) for all canonical analyses.

Optimum discrimination was obtained by three to eight soil parameters in stepwise-discriminant analyses (Table 3). Canonical variate scores were useful for placing individual quadrats into clusters of low, medium, and high densities (Fig. 1). The placement of individual quadrats along the two axes was solely on the basis of edaphic measurements, but it was observed that clusters were formed according to relative nematode densities.

Although Mahalanobis distances between quadrat clusters were significant ($P < 0.05$) in all the analyses (Fig. 2), differing soil parameters were related to different nematode species. Percent clay, copper, change in percent moisture, and percent organic matter had adequate loadings for interpretation in the analysis of *M. incognita* density variation (Table 3). The loadings for clay and organic matter were negative. Since the cluster centers were arranged on the axis in inverse order (high, medium, to low—Fig. 2), the effects of clay and organic matter were positive. Higher densities of *M. incognita* were associated with higher levels of clay and organic matter in this loamy-sand soil. Likewise, since the loadings were positive for the other two variables, higher densities were associated with lower concentrations of copper and smaller changes in percent moisture (slower wetting and drying). The first canonical function accounted for most of the variance among quadrats in nematode densities. The second function was useful, however, in discriminating the medium density quadrats from the high and low quadrats. The interaction of population density of *M. incognita* and percent clay was not important in the second function (as it was in the first function) (Table 3), whereas the other three variables were more important, with additional effects from sodium and zinc concentrations. Thus, exchangeable cations were useful in the fine discrimination of medium level quadrats from low and high.

Interpretation of canonical variates in the analysis of overwinter changes in nematode densities proceeded similarly. Fall population density was the only variable in the first canonical function with a loading greater than 0.30 in the analysis of the change in density of *M. incognita* (Table 3). This variable alone accounted for 81% of the variation in the first canonical variate scores. The other three variables, cation-exchange capacity, magnesium, and phosphorus all had adequate loadings in the second canonical function. The loading for fall population density was positive. Since the cluster centers were arranged along the first axis in inverse order (Fig. 2), the effect of this variable was negative. Higher percent survival was

TABLE 2. Relationships of edaphic variables to population density and change in population density (fall to spring) of *Meloidogyne incognita, Tylenchorhynchus claytoni,* and *Helicotylenchus dihystera*

Site and nematode species	Population density		Change in density	
	Canonical correlation[a]	$P>F$	Canonical correlation	$P>F$
Site 1				
M. incognita	0.67	0.0001	0.63	0.0001
T. claytoni	0.74	0.0001	0.45	0.003
H. dihystera	0.79	0.0001	0.68	0.0001
Site 2				
M. incognita	0.64	0.0002	0.77	0.0001
T. claytoni	0.75	0.0001	0.60	0.0004
H. dihystera	0.51	0.002	0.49	0.0001

[a] Canonical analysis based on variables selected by stepwise-discriminant analysis. $N = 64$ quadrats per site.

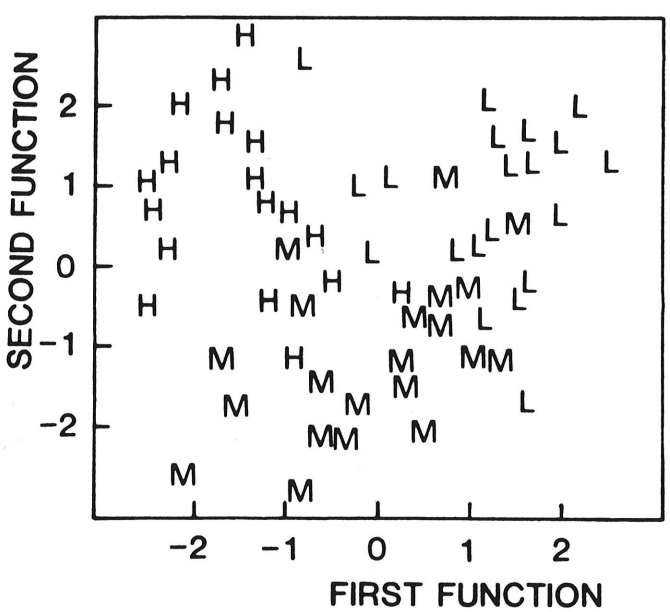

Fig. 1. Plot of individual quadrat scores on first and second canonical functions, showing clustering of quadrats by population density categories along edaphic axes. Discrimination of population density of *Meloidogyne incognita* at site 1, by functions composed of copper, calcium, total cations, percent clay, percent silt, and change in percent moisture. Individual quadrat scores ($N = 64$) are labeled according to high (H), medium (M), or low (L) relative population density levels.

TABLE 3. Edaphic variables used in canonical-discriminant analysis of population density and change in population density (fall to spring) of *Meloidogyne incognita, Tylenchorhynchus claytoni,* and *Helicotylenchus dihystera,* with canonical loadings in discriminant functions

Edaphic variables[a]	Significance of Wilks'-Lambda[b]	Canonical loadings	
		First function	Second function
Population density			
M. incognita			
Copper	0.0017	0.53	0.57
Percent clay	0.0003	−0.55	−0.02
Change-percent-moisture	0.0001	0.37	−0.41
Sodium	0.0001	0.19	0.56
Zinc	0.0001	−0.11	0.35
Organic matter	0.0001	−0.32	0.58
T. claytoni			
Sodium	0.0001	0.58	0.10
Percent clay	0.0001	0.27	−0.11
Magnesium	0.0001	0.31	−0.14
Phosphorus	0.0001	−0.19	0.31
Bulk density	0.0001	−0.37	0.05
H. dihystera			
Sodium	0.0001	−0.29	−0.34
Percent moisture	0.0001	−0.16	0.33
pH	0.0001	0.36	−0.10
Percent silt	0.0001	0.13	0.38
Percent sand	0.0001	0.31	−0.36
Magnesium	0.0001	0.16	−0.30
Copper	0.0001	0.06	0.38
Phosphorus	0.0001	0.42	−0.12
Change in population density			
M. incognita			
Fall population density	0.0001	0.90	−0.15
Phosphorus	0.0001	−0.17	0.90
Cation-exchange-capacity	0.0001	0.28	0.52
Magnesium	0.0001	0.24	0.54
T. claytoni			
Fall population density	0.0001	0.99	−0.05
Organic matter	0.0001	−0.02	0.66
Percent moisture	0.0001	−0.02	0.54
H. dihystera			
Percent clay	0.0055	0.41	−0.46
Fall population density	0.0006	0.49	0.26
Buffer acidity	0.0002	0.08	0.54
Zinc	0.0001	0.16	0.31
Change-percent-moisture	0.0001	0.31	−0.01
Sodium	0.0001	0.28	0.33

[a] Variables listed in order of selection by stepwise-discriminant analysis.
[b] Both sites combined, $N = 128$.

associated with lower fall densities. In the other canonical function, all three variables were related to host nutrition (cation-exchange capacity, phosphorus, and magnesium). Fall population density was important in analysis of changes in densities of *T. claytoni* and *H. dihystera*, but components related to host nutrition were not (Table 3). Variables related to suitability of the soil as a nematode habitat, such as texture, percent moisture, percent organic matter, and acidity affected these ectoparasitic species more than they did the sedentary endoparasite, *M. incognita*.

Three soil parameters had high loadings for all nematode species (Table 4). Copper had a canonical loading greater than 0.30 in all analyses of nematode densities, and sodium had a similarly high loading in all except one analysis. Percent clay had sufficient loadings at one site for all three nematode species but did not have a sufficient loading for any of the species at the other site. Thus, there were both species and site differences in the relative importance of individual edaphic components.

Contour mapping confirmed that greater densities of *M. incognita* occurred where there were greater percentages of clay and lower concentrations of copper (Fig. 3). This physical representation validated the configuration of canonical loadings for discrimination among quadrats according to densities of *M. incognita* (Table 3). A positive relationship of density of *M. incognita* to soil sodium concentration was also observed (Fig. 4), as expected from the canonical variate loading. All three major clusters in the test site coincided spatially between the two variables.

Frequency distributions for counts of *M. incognita* and for percent clay were similar at site 1 (Fig. 5). The frequency categories contained nearly identical numbers of quadrats. An association was observed among nematode densities and edaphic variables with high canonical loadings, in the type of distribution fitted, and in estimated parameter values (Table 5). At site 1, both counts of *M. incognita* and edaphic parameters had small negative binomial k parameter estimates, and the associated frequency distributions were significantly different from the Poisson, but not from the negative binomial. At site 2, however, with high k estimates, the Poisson was also a valid description for frequency distributions of counts of *M. incognita* and associated soil variables.

DISCUSSION

A large portion of quadrat-to-quadrat spatial variation was shared between nematode densities and edaphic variables, but

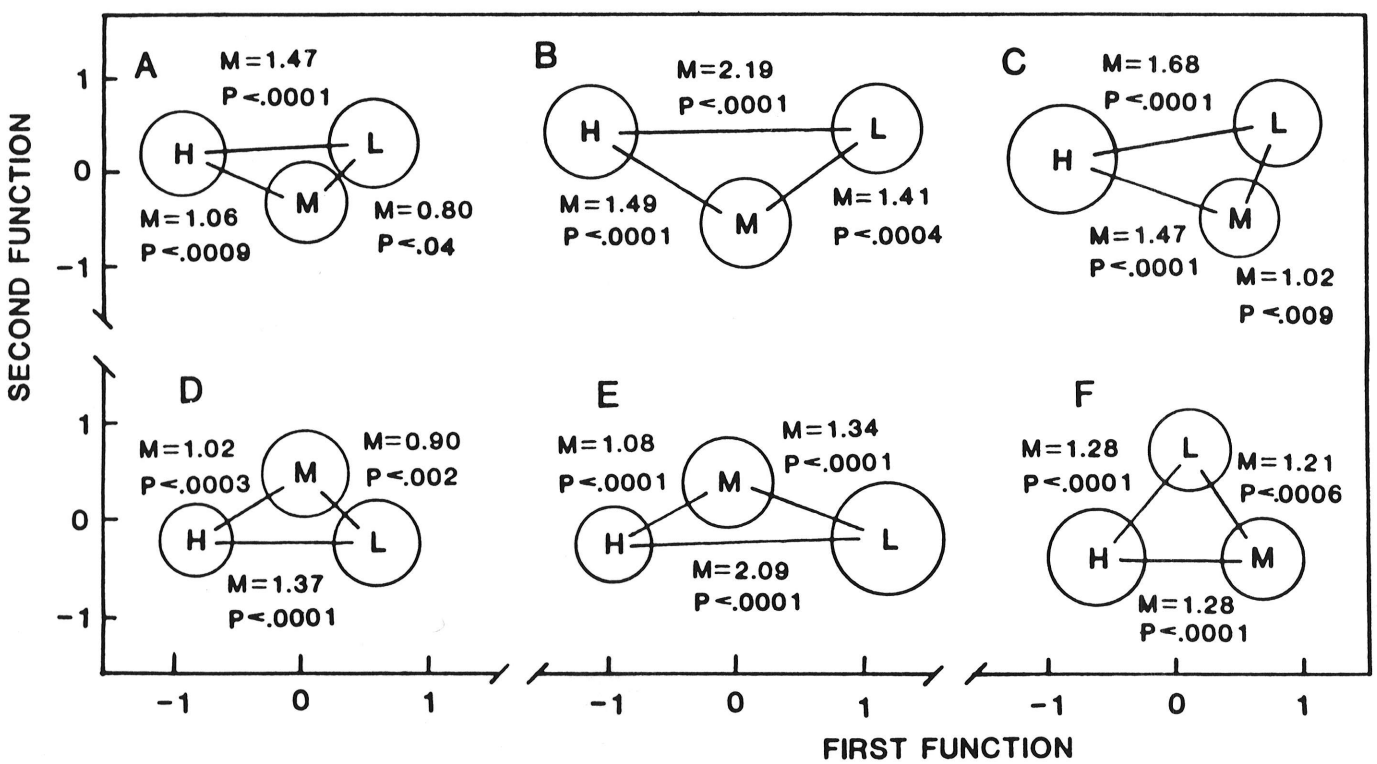

Fig. 2. Plot of cluster centers and 95% confidence areas, showing discrimination of nematode population densities, and overwinter changes in population densities by edaphic canonical functions. Centers of clusters of sampling quadrats which were ranked as having high (H), medium (M), or low (L) levels of population density or changes in density (fall to spring) are encircled by 95% confidence areas, indicating the region that contains the true center of quadrat clusters, with a 95% probability. Mahalanobis distances (M), with associated probability levels (P), are a measure of the significance of discrimination between two cluster centers, along canonical function axes. Population density: **A,** *Meloidogyne incognita;* **B,** *Tylenchorhynchus claytoni*; and **C,** *Helicotylenchus dihystera*. Change in density: **D,** *Meloidogyne incognita;* **E,** *Tylenchorhynchus claytoni*; and **F,** *Helicotylenchus dihystera.*

TABLE 4. Canonical loadings for discrimination of nematode population density with selected edaphic components, by site and nematode species[a]

Edaphic component	Site 1			Site 2		
	Meloidogyne incognita	*Tylenchorhynchus claytoni*	*Helicotylenchus dihystera*	*Meloidogyne incognita*	*Tylenchorhynchus claytoni*	*Helicotylenchus dihystera*
Copper	0.43	0.60	0.45	0.38	0.36	0.39
Sodium	0.31	0.38	0.26	0.51	0.64	0.30
Clay	0.36	0.65	0.79	0.08	0.20	0.28

[a]Canonical loadings are an indication of correlation between the edaphic variable and the canonical variate.

differences in the relative importance of individual soil parameters to the plant-parasitic species were apparent in the analyses. Soil components interact in many ways, and there is compensation among biologically limiting variables. The edaphic variables that occur at or near biologically limiting levels for a given host-pathogen system will be important at any particular site. If clay is scarce in the soil matrix, then percent clay may determine the location of nematode clusters. In other fields there may be ample clay, and other variables will relate to nematode distributions.

Soil components may have interacted with nematode clusters indirectly, through effects on the host plant, or directly through physiological activity on the nematode species. Percent clay, which was related to variation among quadrats in nematode densities, may influence water relationships of the host plant, increase cation-exchange capacity, and affect nematode movement through the soil pores. Soil sodium concentration had a positive relationship to nematode density. A significant positive correlation between soil sodium and density of *Meloidogyne* spp. has been reported among samples collected from 64 different countries (25). Since leaching of cations from the soil is a function of cation-exchange capacity (2), soils with a high capacity tend to hold cations more tightly. This greater retention of cations may have resulted in higher residual levels of sodium after the addition of sodium nitrate fertilizer, and the effect on nematode densities is a result of improved host-plant nutrition during the growing season. Also, soil sodium may be acting directly on the nematode chemotactic response. A functional model has been described (26) for the operation of nematode chemosensilla in which available sodium cations are necessary to activate the nerve processes. Greater concentrations of sodium cations may improve the host-finding ability of plant-parasitic nematodes. Copper concentration in the soil had a negative

TABLE 5. Discrete frequency distributions fitted to counts of *Meloidogyne incognita* and selected edaphic variables

	Negative binomial			Poisson		
Variable	k[a]	χ^2	$P>\chi^2$	m[b]	χ^2	$P>\chi^2$
Site 1						
M. incognita counts	2.4	6.1	NS[c]	2.0	33.9	0.0001
Percent clay	2.0	6.9	NS	1.8	27.7	0.0001
Nitrogen	1.4	4.4	NS	1.3	14.2	0.003
Zinc	3.6	10.4	NS	3.0	28.4	0.0001
Site 2						
M. incognita counts	10.4	2.5	NS	2.3	4.4	NS
Cation exch. capacity	12.1	7.0	NS	2.1	9.1	NS
Bulk density	15.0	8.5	NS	3.8	8.5	NS
Sodium	10.6	6.0	NS	1.9	6.0	NS

[a] Negative binomial k-parameter.
[b] Poisson mean.
[c] NS = not significantly different from the tested distribution at $P = 0.05$.

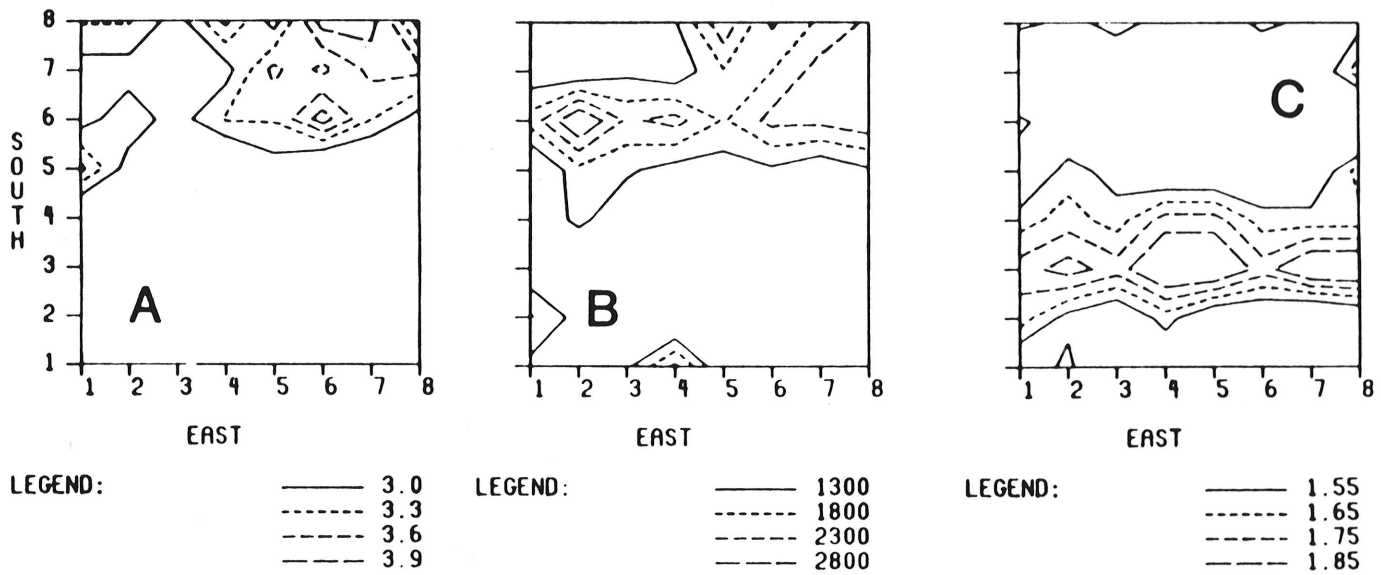

Fig. 3. Contour maps of relative levels of **A,** clay (percent/volume); **B,** *Meloidogyne incognita* population density (juveniles per 500 cm^3 of soil); and **C,** copper (mg/dm^3 of soil) at site 1. Higher levels of *Meloidogyne incognita* are found associated with higher levels of clay and lower levels of copper.

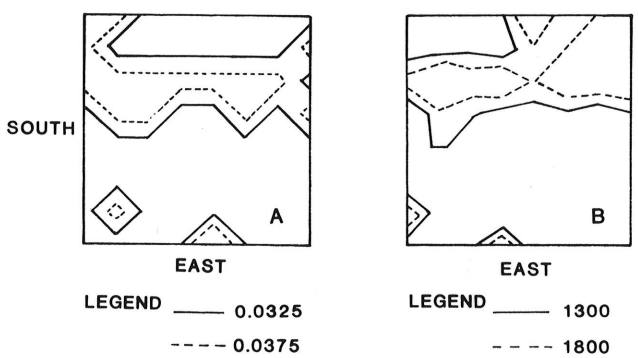

Fig. 4. Contour maps of relative levels of **A,** sodium (MEQ/100 cm^3 of soil); and **B,** *Meloidogyne incognita* population density (juvenile per 500 cm^3 of soil) at site 1. All three primary clusters of *Meloidogyne incognita* are associated with higher levels of sodium.

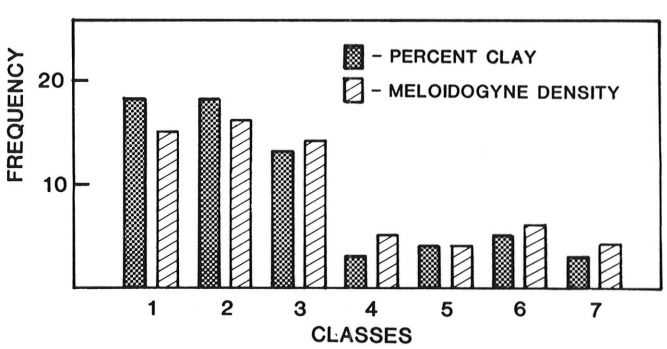

Fig. 5. Frequency distributions of sample counts for population density of *Meloidogyne incognita*, and percent clay, across relative classes (classes 1–7), at site 1 ($N = 64$). Frequency distributions are similar in shape, and can be fitted by similar discrete models (Table 4).

relationship to nematode density, which may indicate that increases measured in the availability of this cation were toxic to plant-parasitic nematodes.

Since specific variables which were important in accounting for variation in nematode spatial distributions varied from site-to-site, and among differing nematode species, it is unlikely that a general predictive model can be formulated for nematode density variation. Differences among the analyses in the significance of specific soil parameters may represent the selection of different variables from among groups of highly correlated soil components. An example was the selection of either phosphorus or potassium from the N-P-K group, or the selection of clay or sand from the soil texture group. Examples of the selection of each of these variables were observed throughout the analyses, as well as the selection of representative variables of other groups such as exchangeable cations. The selection of one of these variables precluded the selection of others in a correlated set.

Contour maps showed that there were clusters, or aggregations, of unique soil physical and chemical micro-sites that coincided well with clusters of plant-parasitic nematodes. This evidence of coinciding clusters was an effective means of cross-validating the interpretation of relationships derived from canonical analyses. Further validation resulted from analysis of frequency distributions. Smaller negative binomial k parameter estimates indicated an aggregated, or more clumped, spatial pattern (19). Larger k values were associated with a more random spatial dispersion. Since this parameter was similar for nematode densities and related soil variables within sites, information derived from sampling fields for soil fertility could be applied to the design of nematode sampling plans. If no other a priori information was available, parameters from the frequency distributions of soil fertility components could be used in appropriate formulas (13) to calculate the number of samples necessary to obtain an estimate of nematode population density at a given level of precision.

Variation in soil micro-sites accounted for over half of the spatial variation in the plant-parasitic nematodes. Remaining variation can be attributed to experimental error, biological parameters of the host-pathogen system, and associated flora and fauna. The distribution of host-plant roots also has a significant impact on the spatial distribution of plant-parasitic nematodes (16). The distribution of host roots is a function of plant species, cultural practices, and soil components.

The stepwise-discriminant process was an important step in establishing spatial covariation between edaphic variables and nematode densities. By starting with many variables, and reducing to a key subset for discriminatory ability, important edaphic variables were selected, accounting for their intercorrelations. Canonical techniques were preferred to other multivariate analyses for a number of reasons. Canonical-discriminant methods divided the data set into two groups of variables, preserving a dependent/independent type of relationship (11). The discriminant aspect required forming one group of variables into categories, which removed difficulties associated with the non-normal distribution of nematode population counts. Finally, significance testing with canonical techniques had a sounder theoretical basis than factor analytical methods (11).

Within-field aggregations of selected soil parameters were useful in explaining the clustered spatial patterns of *M. incognita, T. claytoni,* and *H. dihystera.* Increased understanding of how these patterns are developed in a field should provide practical methods of adjusting research designs to account for spatial covariation among nematode densities and soil parameters. Quantification of effects due to specific soil components provided an indication for areas of research that may show direct physiological activity of certain exchangeable cations.

LITERATURE CITED

1. Barker, K. R., and Campbell, C. L. 1981. Sampling nematode populations. Pages 451-472 in: Plant-Parasitic Nematodes. Vol. 3. B. M. Zuckerman and R. A. Rhode, eds. Academic Press, New York. 508 pp.
2. Brady, N. C. 1974. The Nature and Property of Soils. MacMillan, New York. 639 pp.
3. Brodie, B. B. 1975. Vertical distribution of three nematode species in relation to certain soil properties. J. Nematol. 8:243-247.
4. Byrd, D. W., Jr., Barker, K. R., Ferris, H., Nusbaum, C. J., Griffen, W. E., Small, R. H., and Stone, C. A. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. J. Nematol. 8:206-212.
5. Campbell, N. A., and Tomenson, J. A. 1983. Canonical variate analysis for several sets of data. Biometrics 39:425-435.
6. Cooley, W. W., and Lohnes, P. R. 1971. Multivariate Data Analysis. John Wiley & Sons, New York. 364 pp.
7. Day, P. R. 1965. Particle fractionation and particle-size analysis. Pages 545-567 in: Methods of Soil Analysis. C. A. Black, ed. American Society of Agronomy, Madison, WI. 770 pp.
8. Ferris, V. R., Ferris, J. M., Bernard, R. L., and Probst, A. H. 1971. Community structure of plant-parasitic nematodes related to soil types in Illinois and Indiana soybean fields. J. Nematol. 3:399-408.
9. Gates, C. E., and Ethridge, F. G. 1970. A generalized set of discrete frequency distributions with FORTRAN program. Math. Geol. 4:1-24.
10. Goodell, P. B., and Ferris, H. 1980. Plant-parasitic nematode distributions in an alfalfa field. J. Nematol. 12:136-141.
11. Kshirsagar, A. M. 1972. Multivariate Analysis. Marcel Dekker, New York. 534 pp.
12. Lemon, E. R., and Erickson, A. E. 1955. Principle of the platinum microelectrode as a method of characterizing soil aeration. Soil Sci. 79:383-392.
13. McSorley, R., and Parrado, J. L. 1982. Estimating relative error in nematode numbers from single soil samples composed of multiple cores. J. Nematol. 14:522-529.
14. Morrison, D. F. 1976. Multivariate Statistical Methods. McGraw-Hill, New York. 415 pp.
15. Noe, J. P., and Barker, K. R. 1985. Overestimation of yield loss due to the clustered spatial distribution of *Meloidogyne incognita.* J. Nematol. 17:(In press).
16. Noe, J. P., and Campbell, C. L. 1985. Spatial pattern analysis of plant-parasitic nematodes. J. Nematol. 17:(In press).
17. Norton, D. C., and Schmitt, D. P. 1974. Distribution of selected plant-parasitic nematodes relative to vegetation and edaphic factors. J. Nematol. 6:81-86.
18. Norton, D. C., Frederick, L. R., Ponchillia, D. E., and Nyhan, J. W. 1971. Correlations of nematodes and soil properties in soybean fields. J. Nematol. 3:154-163.
19. Pielou, E. C. 1977. Mathematical Ecology. John Wiley & Sons, New York. 385 pp.
20. Rao, C. R. 1973. Linear Statistical Inference and Its Applications. John Wiley & Sons, New York. 625 pp.
21. SAS Institute Inc. 1982. SAS User's Guide: Statistics. 1982 Edition. SAS Institute Inc., Cary, NC. 584 pp.
22. Schmitt, D. P. 1973. Soil property influences of *Xiphinema americanum* populations as related to maturity of loess-derived soils. J. Nematol. 5:234-240.
23. Schmitt, D. P., and Norton, D. C. 1972. Relationships of plant-parasitic nematodes to sites in native Iowa prairies. J. Nematol. 4:200-206.
24. Tabachnik, B. G., and Fidell, L. S. 1983. Using Multivariate Statistics. Harper & Row, New York. 509 pp.
25. Taylor, A. L., Sasser, J. N., and Nelson, L. A. 1982. Relationship of Climate and Soil Characteristics to Geographical Distribution of *Meloidogyne* spp. in Agricultural Soils. Cooperative publication of the Department of Plant Pathology, North Carolina State University, and the United States Agency for International Development, Raleigh, NC. 65 pp.
26. Wright, K. A. 1983. Nematode chemosensilla: Form and function. J. Nematol. 15:151-158.