

Correlation of Edaphic Factors with Plant-parasitic Nematode Population Densities in a Forage Field

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Abstract: Two hundred soil samples from the A_p horizon of a reed canarygrass field overlaying several different but related soils in northern Minnesota were analyzed for plant-parasitic nematodes and 22 edaphic factors. *Pratylenchus penetrans* was the predominant nematode taxon. Others were *Aglenchus agricola*, *Tylenchorhynchus* spp., *Heterodera trifolii*, *Paratylenchus* spp., *Tylenchus maius*, and *Criconemella* sp. Five nematode taxa, *P. penetrans*, *A. agricola*, *Tylenchorhynchus* spp., *H. trifolii*, and *Paratylenchus* spp., were correlated with particle size. *Tylenchus maius* and *Criconemella* sp. were correlated with effective cation exchange capacity. Nematode field spatial arrangements were related to a combination of statistically significant positive and negative soil factor effects on the nematode populations. Contour maps derived by geostatistical techniques were used to visually validate statistically significant correlations of nematode and soil data. Contour mapping to supplement traditional statistical techniques can be used to achieve a more holistic approach to studies of nematode-soil interrelationships.

Key words: *Aglenchus agricola*, contour mapping, *Criconemella*, edaphic factor, effective cation exchange capacity, forage, geostatistics, *Heterodera trifolii*, nematode, *Paratylenchus*, particle size, *Phalaris arundinacea*, *Pratylenchus penetrans*, soil, *Tylenchorhynchus*, *Tylenchus maius*.

It is widely accepted that the host plant is the major influence in plant-parasitic nematode community dynamics (20). However, the soil environment undoubtedly affects nematode population growth and species survival by physical and physiological impact on the nematode and through positive and negative effects on the host plant. Many attempts have been made to determine relationships between abiotic soil parameters and plant-parasitic nematode populations. Associations of plant-parasitic nematode populations with soil type (6,7,23,25,32), texture (10,12,19,21,22,29), moisture content (7,19,21,22), pH (7,19,21,22,29), cation exchange capacity (19,21,25,29), organic matter content (7,19,21,22,29), and levels of ions present in the soil solution (7,19,21,29) have been explored. Methodologies for soil analyses vary widely, and questions still arise as to which methods yield the most meaningful results (20). Some soil parameters, e.g., soil texture and cation exchange capacity, are not independent and compli-

cate interpretation of results. Correlations of plant-parasitic nematodes with observed soil factors may be due to chance or to some variable not measured.

This study was undertaken to relate variations in 22 edaphic components with variations in population densities of seven nematode taxa in a forage field. The taxa were *Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans Stekhoven, *Aglenchus agricola* (de Man) Meyl, *Tylenchorhynchus* spp., *Heterodera trifolii* Goffart, *Paratylenchus* spp., *Tylenchus maius* Andr assy, and *Criconemella* sp.

MATERIALS AND METHODS

A 1.56-ha portion of a forage field at the University of Minnesota's North Central Experiment Station at Grand Rapids was selected for study. The field overlaid several different but related soils (Fig. 1) (5). Soils included Spooner very fine sandy loam (fine-silty, mixed, frigid Typic Ochraqulf), Cowhorn loamy very fine sand (coarse-loamy, mixed, nonacid, frigid Aeric Haplaquept), Hiwood loamy fine sand (mixed, frigid Aquic Udipsament), Morph loam (fine-loamy, mixed, frigid Typic Glossaqualf), and Rosy silt loam (coarse-loamy, mixed Aquic Eutroboralf). Preliminary sampling in the fall

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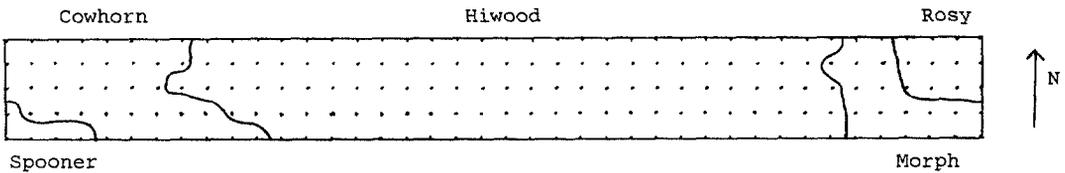


FIG. 1. Detailed soil map of the study site at the North Central Experiment Station in Grand Rapids, Minnesota. Dimensions of the site are 390×40 m, with a total area of 1.56 ha. Dots indicate sampling points. Predominant surface particle size is very fine sand for Spooner and Cowhorn series soil, fine sand for Hiwood series soil, and silt for Morph and Rosy series soil.

of 1988 indicated that *P. penetrans* was ubiquitous throughout the site. Reed canarygrass (*Phalaris arundinacea* L.) was the predominant agronomic plant species. Other species present at the time of sampling included smooth bromegrass (*Bromus inermis* Leysser), timothy (*Phleum pratense* L.), quackgrass (*Elytrigia repens* (L.) Nevski), and white clover (*Trifolium repens* L.). Total plant cover was uniform. Because of the fibrous and relatively homogeneous nature of graminaceous root systems and their habit of rhizome production, plant species distribution in the field was not determined.

Management history of the forage field was as follows. The area was plowed in 1985 and oat (*Avena sativa* L.) with red clover (*Trifolium pratense* L.) and reed canarygrass as a companion crops were planted. A 12-6-30 (N:P:K) fertilizer was applied at 336 kg/ha. In 1987, 74,765 liters/ha of liquid hog manure were applied to the surface. No other fertilizer was applied during the period from 1985 through 1989. The forage was harvested twice per year. In 1986 and 1987, red clover and reed canarygrass were the predominant plant species. In 1988 and 1989, reed canarygrass predominated, with no red clover remaining.

In late June 1989, the forage field was divided into a 10×10 -m network of grid-lines by laying out five east-west transects of 40 points each. A single soil core was removed from the A_p horizon at each of the 200 grid intersections using a truck-mounted hydraulic corer with a 7.5-cm-d sampling tube. The A_p horizon (and sampling depth) varied from approximately

20 to 35 cm. Each core was placed in a separate plastic bag and labeled. Samples were transported in an air-conditioned vehicle to St. Paul and stored at 5 C until they were processed.

Plant-parasitic nematodes were extracted from 116 cm^3 soil using the modified Baermann pan technique (13), identified, and counted. Counts were adjusted before statistical analysis to reflect numbers of nematodes per 100 cm^3 soil. Soil parameters were determined as follows. Particle size analyses (PSA) were effected for each sample by the pipet method (26). PSA yielded percentages of total sand and its components (very coarse, coarse, medium 1, medium 2, fine, very fine 1, and very fine 2), total silt and its components (coarse and fine), and clay. Effective cation exchange capacity and levels of exchangeable cations (Ca, Mg, K, Na) were measured by the ammonium acetate method (28). Extractable acidity was determined by using a modification of the potassium chloride method (28). Loss-on-ignition was used to estimate organic matter content of the soil samples (1,3,17,18). The pH of each soil sample was determined in water and 0.01 M CaCl_2 (16). Field moisture content was measured by drying preweighed samples in a forced air oven at 34 C for 24 hours, cooling, and re-weighing.

Statistical analysis to determine correlation of soil properties with nematode taxa was made using Generalised Linear Interactive Modelling (GLIM) (24), which has the capability of approximating a negative binomial model. To determine the relationship between soil characteristic variables and nematode counts, seven separate

models were fitted, one for each taxon. The nematode data followed a negative binomial distribution. To calculate appropriate statistics using GLIM, a Poisson distribution with a scale factor was used to approximate the negative binomial distribution. The model was of the form $\ln(y) = a + b_1x_1 + \dots + b_kx_k$, where y is the response variable (= nematode taxa), $x_1 \dots x_k$ are the explanatory variables (= soil properties), a is the intercept of the generalized linear model, and $b_1 \dots b_k$ are the regression coefficients of $x_1 \dots x_k$. A stepwise procedure was used to determine which, if any, of the soil variables were associated with variation in nematode counts. The difference in the scaled deviance (DELTA G2) between the model without a variable and the model with the variable was used to test whether a variable should be entered or removed. DELTA

G2 follows a chi-square distribution with one degree of freedom. The scaled deviance is the negative logarithm of the maximized likelihood of the fitted model divided by the negative logarithm of the maximized likelihood of the full model. A significance level of $P = 0.05$ was used to enter a variable and $P = 0.1$ to remove a variable.

Geostatistical analyses of soil and nematode data were made to produce contour maps of each variable for visual validation of statistically significant GLIM correlations. Several computer programs were used to complete the geostatistical analyses. Initial data entry was made using Lotus 1-2-3 (14). Geostatistical Environmental Assessment Software was used to model semi-variograms for each variable (30). Contour maps were constructed and plotted using the program Surfer 4.04 (9).

TABLE 1. Results of Generalized Linear Interactive Modelling to show significant correlations between nematode species and soil factors.

Nematode	Soil factor	Estimate	Standard error	z value†
<i>Pratylenchus penetrans</i>	Fine silt	0.0329	0.0095	3.45
	Calcium	-0.0292	0.0199	-1.47
<i>Aglenchus agricola</i>	Potassium	0.6339	0.2380	2.66
	Coarse sand	0.6521	0.2903	2.25
	Very fine 1 sand	-0.0308	0.0074	-4.16
	Medium 1 sand	-1.8550	0.5555	-3.34
<i>Tylenchorhynchus</i> spp.	Coarse silt	0.2151	0.0331	6.50
	Medium 1 sand	-1.5160	0.4973	-3.05
	Moisture content	-0.2262	0.0814	-2.78
	Acidity	-32.3100	16.1100	-2.01
	Potassium	-1.6960	0.9337	-1.82
<i>Heterodera trifolii</i>	Moisture content	0.4370	0.1346	3.25
	Very coarse sand	-3.8390	1.6340	-2.35
	Total silt	-0.2546	0.1205	-2.11
	pH in water	-1.2830	0.7066	-1.82
<i>Paratylenchus</i> spp.	Potassium	-1.8980	1.3180	-1.44
	Sodium	24.2100	8.3110	2.91
	Fine silt	0.1340	0.0466	2.88
	Moisture content	0.3485	0.1352	2.58
	Calcium	-0.2333	0.0865	-2.70
	Potassium	-9.0520	3.8000	-2.38
	Acidity	-49.1700	28.0200	-1.75
<i>Tylenchus maius</i>	ECEC‡	0.2347	0.0609	3.86
	Magnesium	-0.5792	0.2981	-1.94
<i>Criconebella</i> sp.	Sodium	29.1600	13.6500	2.14
	ECEC	-0.4362	0.1801	-2.42
	pH in CaCl ₂	-2.2900	1.0910	-2.10

† The z value is the estimate/standard error, which is compared to critical values of $z = 1.96$ and $-z = -1.96$ (4). A large z value indicates a strong correlation, with + being a positive correlation and - a negative correlation.

‡ ECEC = effective cation exchange capacity.

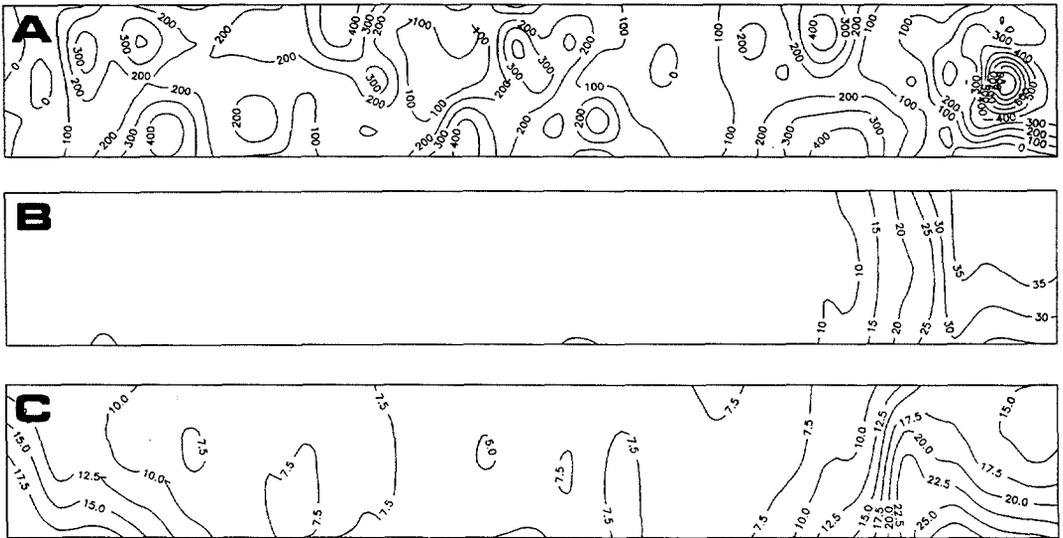


FIG. 2. Contour maps of *Pratylenchus penetrans* and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390×40 m, with a total area of 1.56 ha. A) *P. penetrans*. Contour units are numbers of nematodes per 100 cm^3 soil. B) Fine silt (+). Contour units are percent. Particle size is $0.02\text{--}0.002$ mm. C) Calcium (-). Contour units are cmol/kg .

RESULTS AND DISCUSSION

Eight nematode taxa were extracted from soil samples. Frequencies of nematode taxa present were 89.5% for *P. penetrans*, 81.5% for *A. agricola*, 55.0% for *Tylenchorhynchus* spp., 46.0% for *H. trifolii*, 44.0% for *Paratylenchus* spp., 41.5% for *T. maius*, 11.0% for *Criconemella* sp., and 1.0% for *Hoplolaimus* sp. *Hoplolaimus* sp. was considered to occur too infrequently for further statistical analysis.

Sand or silt particle size classes were significantly correlated with population densities of five nematode taxa (Table 1). Effective cation exchange capacity correlated significantly with the two nematode taxa (*Tylenchus maius*, *Criconemella* sp.) that were not correlated with particle size. Concentrations of individual exchangeable cations, most frequently potassium, were significantly correlated with population densities of all nematode taxa. Moisture content and pH correlated with densities of several taxa. No significant correlations were found with organic matter or clay content.

Nematode field spatial arrangements were related to a combination of statisti-

cally significant positive and negative soil factor effects on the nematode populations (Table 1). By utilizing GLIM to model nematode distribution, essentially all soil variables that improved the fit of a nematode's model were retained, and these included negative as well as positive soil influences on nematode population density. Some soil factors had a stronger influence than others.

To visualize the soil-nematode interactions, the contour map for each nematode taxon was compared with maps of significantly correlated soil factors (Figs. 2-8). Delimitations of areas with high nematode population density can be made by looking for closely spaced contour intervals on the nematode map (which indicate sharp increases in nematode density in an area) and comparing those areas to the magnitude of soil values from the same areas on the soil maps. If the soil value is high relative to values elsewhere on the soil map, the correlation between soil and nematode population density is positive; if the soil value is high but nematode density is low, correlation is negative.

Pratylenchus penetrans was ubiquitous in the site, but its highest densities occurred

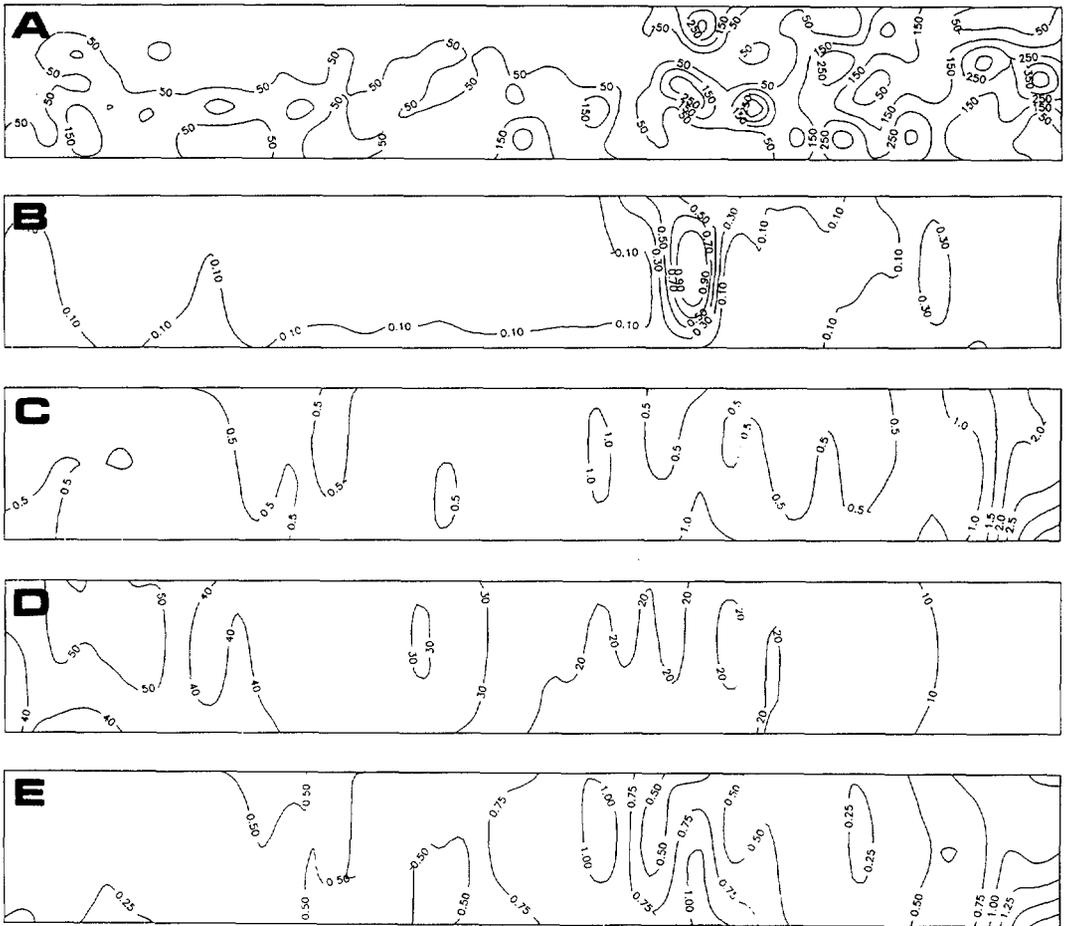


FIG. 3. Contour maps of *Aglenchus agricola* and significantly correlated soil factors. Positive correlation is indicated by (+) negative correlation by (-). Dimensions of the site are 390 × 40 m, with a total area of 1.56 ha. A) *A. agricola*. Contour units are numbers of nematodes per 100 cm³ soil. B) Potassium (+). Contour units are cmol/kg. C) Coarse sand (+). Contour units are percent. Particle size is 1–0.5 mm. D) Very fine sand (-). Contour units are percent. Particle size is 0.1–0.074 mm. E) Medium sand (-). Contour units are percent. Particle size is 0.5–0.42 mm.

in areas with a high fine silt content. This contrasts with earlier work reporting a higher incidence of *P. penetrans* in sandy soils (7,12). Within the area of high fine silt content, densities of *P. penetrans* were negatively related to calcium concentration. Where calcium concentration exceeded 20 cmol/kg, nematode densities were low. Although *P. penetrans* can inhabit a wide variety of soil textures, it was silt content rather than sand that most favored high densities. Because silt has more surface area and a faster weathering rate than sand, it contains more water and soluble nutrients for plant growth. The positive

effect of silt on *P. penetrans* density may have been due to improved host health rather than direct physiological or physical impact on the nematode.

Densities of *A. agricola* were high in areas of coarse sand but low in areas of very fine and medium sand, except where potassium was concentrated. There is little or no information regarding soils favorable to this nematode species. Coarse sand particle size was limited to the eastern portion of the site (Morph/Rosy series). Other characteristics of this area were higher concentrations of clay, silt, and organic matter than in the rest of the site, all of

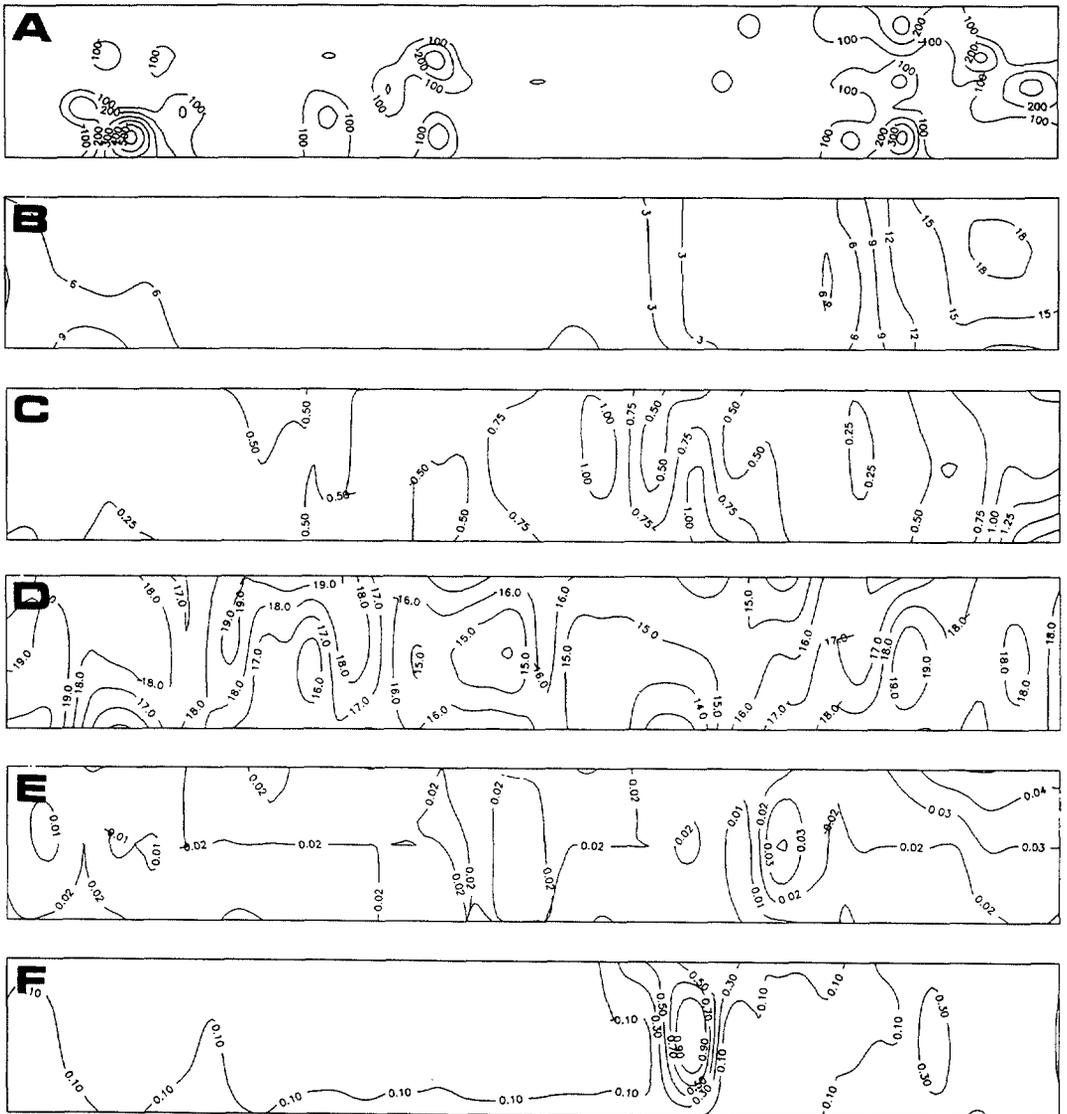


FIG. 4. Contour maps of *Tylenchorhynchus* spp. and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390×40 m, with a total area of 1.56 ha. A) *Tylenchorhynchus* spp. Contour units are numbers of nematodes per 100 cm^3 soil. B) Coarse silt (+). Contour units are percent. Particle size is 0.05–0.02 mm. C) Medium 1 sand (-). Contour units are percent. Particle size is 0.5–0.42 mm. D) Moisture content (-). Contour units are percent. E) Acidity (-). Contour units are cmol/kg. F) Potassium (-). Contour units are cmol/kg.

which can improve host health through increased nutrient availability and water holding capacity. Potassium, another mineral contributing to plant health, altered the distribution of *A. agricola* with respect to medium sand particle size.

Tylenchorhynchus spp. were abundant in areas high in coarse silt but not medium sand. Goodell and Ferris (10) found that

Merlinius brevidens, a species in a genus closely related to *Tylenchorhynchus*, was strongly associated with fine textured areas in an alfalfa field. Other workers have found population development of *Tylenchorhynchus* spp. to be favored in a dark-colored silty clay loam (6) or by clay percentage (19). At the Grand Rapids site, other soil factors in addition to medium

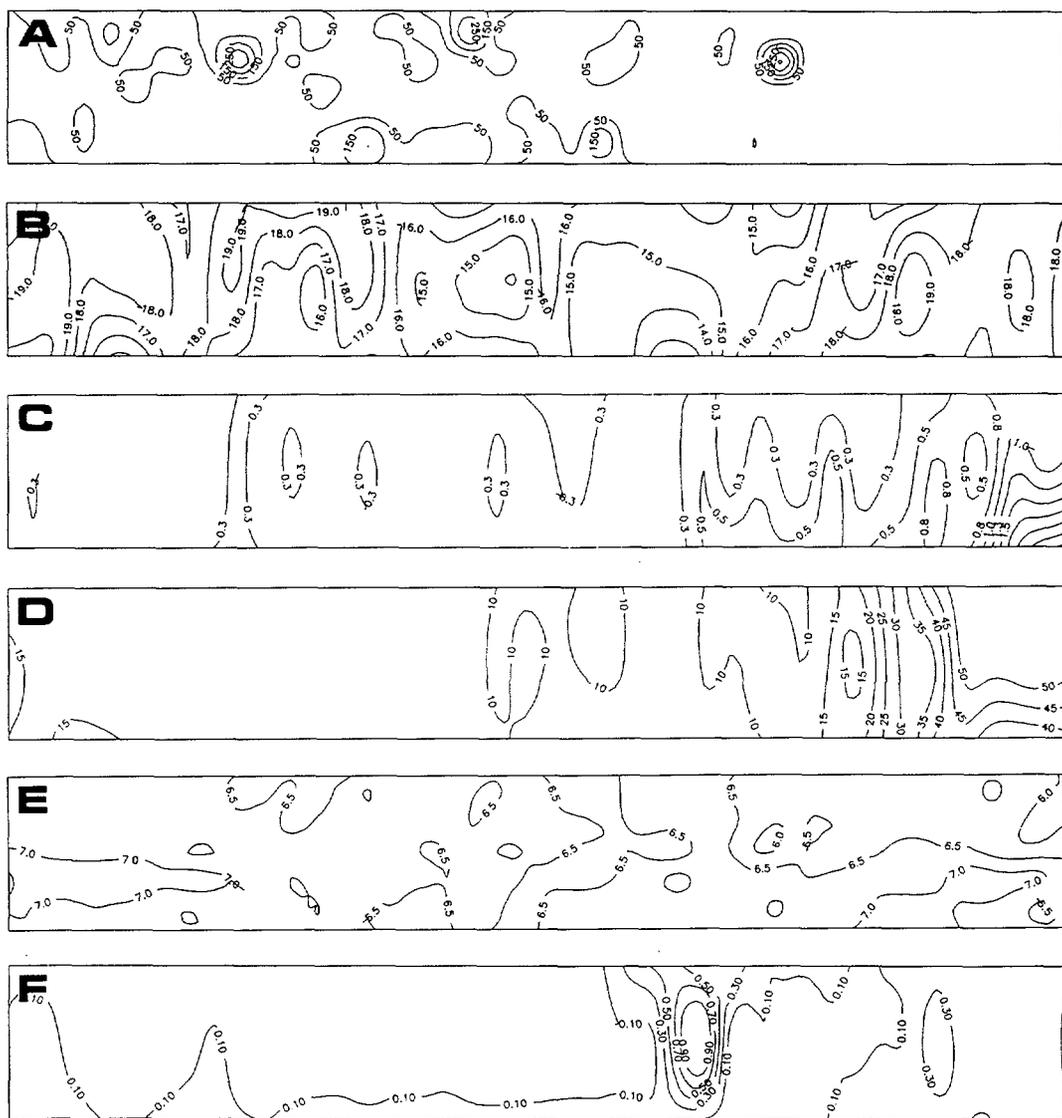


FIG. 5. Contour maps of *Heterodera trifolii* and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390 × 40 m, with a total area of 1.56 ha. A) *H. trifolii*. Contour units are numbers of nematodes per 100 cm³ soil. B) Moisture content (+). Contour units are percent. C) Very coarse sand (-). Contour units are percent. Particle size is 2–1 mm. D) Total silt (-). Contour units are percent. Particle size is 0.05–0.002 mm. E) pH as determined in water (-). F) Potassium (-). Contour units are cmol/kg.

sand had a negative impact on *Tylencho-rhynchus* spp. densities. Nematode densities were low in areas where moisture content was 19% or more, where extractable acidity was 0.03 cmol/kg or more, and where potassium was concentrated. The areas of negative association appeared to be additive in some instances (e.g., medium sand and potassium concentration).

Densities of *Heterodera trifolii* juveniles were negatively correlated with areas high in very coarse sand and total silt, i.e., juveniles were not found in the Morph loam and Rosy silt loam but were present in the sands of the Cowhorn and Hiwood series. High populations of *H. trifolii* have been reported to occur in sandy soils in the Netherlands (15). Highest numbers of ju-

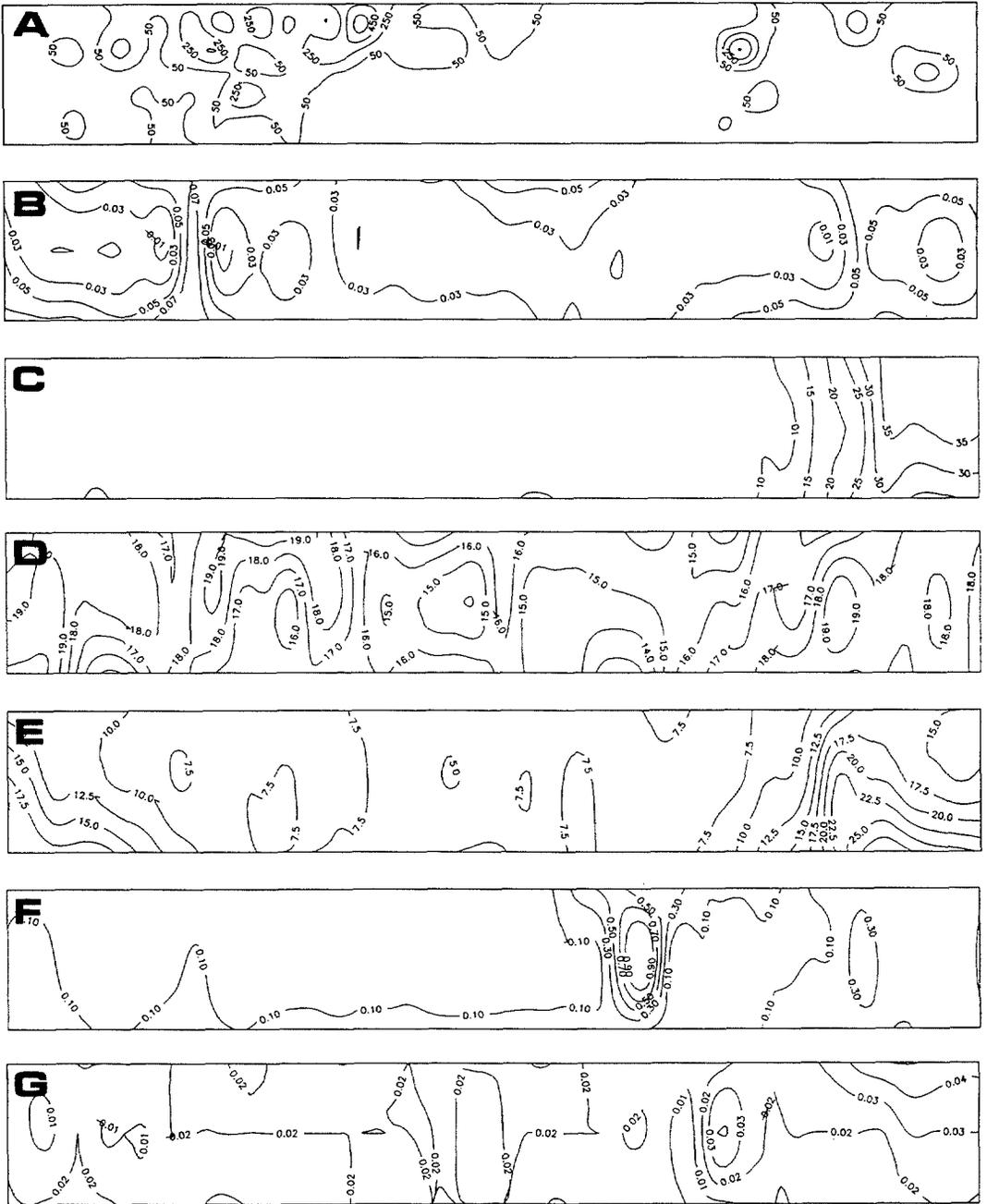


FIG. 6. Contour maps of *Paratylenchus* spp. and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390 × 40 m, with a total area of 1.56 ha. A) *Paratylenchus* spp. Contour units are numbers of nematodes per 100 cm³ soil. B) Sodium (+). Contour units are cmol/kg. C) Fine silt (+). Contour units are percent. Particle size is 0.02–0.002 mm. D) Moisture content (+). Contour units are percent. E) Calcium (-). Contour units are cmol/kg. F) Potassium (-). Contour units are cmol/kg. G) Acidity (-). Contour units are cmol/kg.

veniles at the Grand Rapids site were present where the sand was the wettest (18–19% moisture content). Juveniles were scarce or absent in sandy areas where pH was 7.0 or greater (Spooner series) and where potassium was concentrated. White

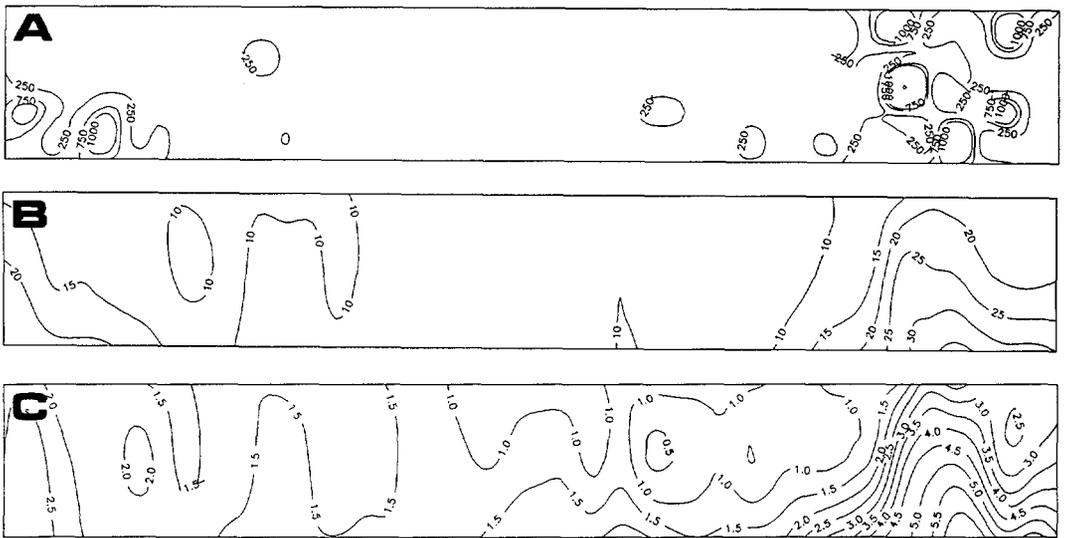


FIG. 7. Contour maps of *Tylenchus maius* and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390 × 40 m, with a total area of 1.56 ha. A) *T. maius*. Contour units are numbers of nematodes per 100 cm³ soil. B) Effective cation exchange capacity (+). Contour units are cmol/kg. C) Magnesium (-). Contour intervals are cmol/kg.

clover, the only plant present at sampling on which *H. trifolii* could reproduce (Wallace, unpubl.) was scarce and unlikely to contribute to juvenile population density. Juvenile presence was probably due to spontaneous hatch from eggs in cysts, and hatching may have been more favorable under relatively wetter conditions.

Paratylenchus spp. population densities were positively correlated with fine silt, and it has been reported that *P. projectus* was favored by light-colored silt loams (6). Sodium concentration and moisture content also favored *Paratylenchus* spp. Areas where calcium, potassium, and extractable acidity were high were negatively associated with nematode densities. Relationships between positive and negative soil factor effects on *Paratylenchus* spp. and possible underlying mechanisms are not as clear as for other nematode taxa present at the site. Although *Paratylenchus* occurred frequently in samples, densities were low. Sampling at another time during the growing season may have revealed more striking associations of nematode densities and soil factor effects.

The two nematode taxa (*T. maius* and *Criconebella* sp.) that were not correlated

with particle size were apparently influenced by effective cation exchange capacity (ECEC), a soil parameter that has not been examined previously in soil-nematode studies. In previous work, the effect of cation exchange capacity (CEC) on nematode population densities was examined but no significant correlations were found (19,21,25,29). There is a fundamental difference in analytical methodology for determining CEC and ECEC. Exchangeable cations are determined in similar ways for both methods. However, to determine exchangeable acidity (used in calculating CEC), the pH of a soil sample is adjusted to 8.2, whereas to determine extractable acidity (used for calculating ECEC), the pH is not adjusted. Because the soil solution that nematodes at the Grand Rapids site encountered was not at pH 8.2, determining ECEC was considered to be a more realistic analytical tool.

Tylenchus maius was abundant in soils with high ECEC (15–30 cmol/kg). Areas of high ECEC included the east portion of the site (Morph/Rosy series), which was high in both clay and organic matter, and the southwest portion of the site (Spoooner series), which had little clay but an average

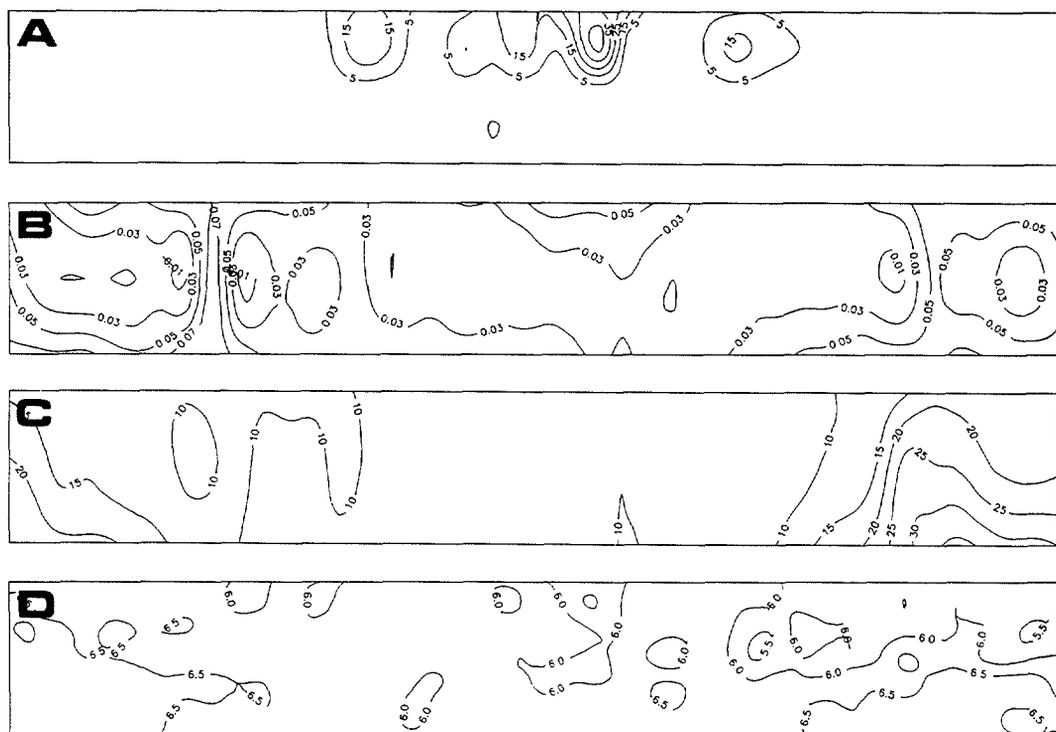


FIG. 8. Contour maps of *Criconebella* sp. and significantly correlated soil factors. Positive correlation is indicated by (+) and negative correlation by (-). Dimensions of the site are 390 × 40 m, with a total area of 1.56 ha. A) *Criconebella* sp. Contour units are numbers of nematodes per 100 cm³ soil. B) Sodium (+). Contour units are cmol/kg. C) Effective cation exchange capacity (-). Contour units are cmol/kg. D) pH as determined in CaCl₂ (-).

organic matter content of 3.4% (range 1.7–5.8%). Organic matter can contribute up to 80% of the cation exchange capacity of a soil (27). *Tylenchus* spp. are considered to be polyphagous and can feed on fungi and mosses as well as plant roots (8). Organic matter can provide a substrate suitable for fungal colonization and growth, thus providing an abundant food source for *T. maius*. Underlying differences in soil texture and organic matter content at a sample point directly influenced the ECEC and may have indirectly influenced distribution of *T. maius*.

Densities of *Criconebella* sp. were highest in sandy areas where sodium concentrations were high but ECEC and pH in CaCl₂ were low, i.e., populations appeared to be favored in areas where sodium and aluminum were measurable, but overall chemical activity of the soil was low. Aluminum ions in various forms on the exchange

complex become more prevalent as pH drops below 6.0 (2). At the Grand Rapids site, pH in CaCl₂ was frequently below 6.0. Aluminum may not be deleterious to plant-parasitic nematodes, as has been found for soil copper levels (19). The positive influence of sodium on host plant nutrition and the necessary presence of sodium cations to activate the nerve processes in nematode chemosensilla (31) may enable *Criconebella* sp. to find healthy host roots more efficiently. The sensitivity of *Criconebella* sp. to soil chemistry may be a function of its sedentary ectoparasitic feeding behavior (11). The sluggish movements and habit of feeding from the same cell for many days would not allow them to move quickly from chemically deleterious soil microsites.

Separating soil and plant influences on population density and distribution of nematodes is not feasible. Soil components

may be correlated with plant-parasitic nematode densities through effects on the host plant or by physically or physiologically affecting the nematode itself. Edaphic components present at biologically limiting levels for a given host-pathogen system will be important at any particular site (19). The spatial arrangement of plant-parasitic nematodes in a field is a net result of positive and negative soil factor effects on the population, coupled with food source preferences and macroclimatological considerations. A holistic approach to nematode-soil studies can be approximated through the use of contour mapping to supplement traditional statistical techniques.

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