

Journal of Nematology 21(3):299-307. 1989.
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Abiotic Soil Factors and Plant-parasitic Nematode Communities¹

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Abstract: A natural community of plant-parasitic nematodes is usually polyspecific. The host plant is the most important driving force in nematode populations, but abiotic factors are important in maintaining the steady state. Nematode communities often separate by abiotic soil factors. In any continuous habitat, including crop plants, generally there is a consistency of the most abundant species, which are largely predictable. Data on single species provide little information about community patterns. Although certain nematode species might be indicators of certain environments, only when we discuss such aspects as diversity and ordination do we relate to communities irrespective of any interactions among component species. Only if plant-parasitic nematodes act independently of each other do autecological studies have validity in polyspecific communities.

Key words: community, diversity, abiotic factor, ecology.

A natural community of plant-parasitic nematodes is usually polyspecific. Species have different niche dimensions. The same species may be present in different proportions in different environments and at different times (2,38). The host affects populations of plant-parasitic nematodes more than do soil factors (22,30,40,45). Even though the host-parasite associations are often strong and overshadow other interrelationships, the living part of a community cannot be separated from the physical part. When a plant supports a polyspecific nematode community, niche differentiation is usually evident because of different feeding habits and different tissues being parasitized. If the species composition of communities is largely fortuitous, then density dependent factors are weak. (A discussion of herbivore community organization appears in Lawton [18]). Perhaps the most difficult problem with nematode communities is to separate the factors such as soils, host, and competition,

among others, that influence community composition and structure. Although much descriptive work needs to be done to ascertain whether general patterns exist, descriptive patterns do not relate cause and effect except by inference. Nematode communities result from a continuous series of events, often making community composition a fortuitous one in that the nematodes have little control in their occurrence.

Much has been written about single nematode species populations as correlated with different abiotic soil factors (23,30,47,48,52), and an extensive review is not necessary. In spite of a wealth of information on individual species and soil factors, little information is available on polyspecific communities. In this paper, I am interested in communities of nematodes. Because data on single species provide little information about the community patterns, we must look for patterns, correlations, and cause and effect. A mere listing of species does not provide much information about the dynamics of a community. Only if plant-parasitic nematodes act independently of each other do autecological studies have validity relative to polyspecific communities. Interactions of nematodes with biota other than their

Received for publication 15 August 1988.

¹ Symposium paper presented at the annual meeting of the Society of Nematologists, 12-16 June 1988, Raleigh, North Carolina. Journal Paper No. J-13079 of the Iowa Agriculture and Home Economics Experiment Station, Ames; Project 2382.

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hosts, including interactions among plant-parasitic nematodes themselves, have been studied little. Until biotic interactions are clarified, possible interactions of nematode communities with abiotic edaphic factors will be difficult to recognize and interpret.

Nematode–nematode interactions have been divided by Eisenback and Griffin (10) into ecological and etiological types. Included in the former are antagonistic interactions resulting from spatial competition, physical alteration and destruction of feeding sites, and a decrease in host suitability by physiological change. But, are the nematode–nematode “interactions” that operate indirectly, such as physiological change in the host, really host–parasite interactions that result in nematode succession by a decrease or increase of populations of other species? Artificial environments, as in the greenhouse, can force artificial interactions (42); however, these are not discussed here.

TERMINOLOGY

Abiotic, as used here, refers to purely physical and chemical factors, such as particle size, structure, gases, and chemicals in the soil, as well as to organic matter from decaying plants and animals. Although the terms population changes and population dynamics are often used interchangeably, I prefer to keep them separate. A description of a population change does not provide much information on the dynamics or on the driving forces behind those changes.

Holmes (16) made a plea for better communication between persons working on parasitological communities and ecologists in other areas. This also applies to plant nematologists. The need for a unified ecological terminology has long been advocated, but little progress has been made. Some terms, such as climax, that are commonly used in plant ecology probably cannot be applied properly to the short-term life cycles of nematodes. The terms competition, interaction, inhibit, and population dynamics are examples. As Wallace (49) noted, the word interaction has often been used imprecisely in nematology. Sta-

tistical and biological use of interaction can have different connotations. Pielou (33) states that most people think a community without interactions is not structured. The many references to community structure without indications of interactions, however, seem to contradict her statement, although there might be a tacit assumption that interactions occur as the host–parasite relationship dictates. Excluding this host–parasite relationship, interactions among plant-parasitic nematodes are more nebulous. The ambiguous term strategy as commonly used in ecology would best be stricken from much of the ecological vocabulary because of its frequent purposeful teleological implications. Loose use of terms such as antagonize, compete, and inhibit without reasonable proof confuses issues. Nematologists need to arrive at common definitions and concepts in general ecological contexts, not just a nematological one.

COMPETITION

When interactions among nematodes are discussed, competition often is mentioned. Competition has been discussed elsewhere (21,25), and I will not belabor the issues here. We cannot define clearly the role of abiotic factors in nematode communities, however, without being cognizant of other possible regulating factors. There are two schools of thought on the importance of competition and interaction, and one places greater importance on competition (19) than the other (3,25,31,35). To have competition, there must be a shortage of substrate and niche overlap (32). An observation that one nematode species increases while another decreases does not necessarily indicate antagonism, interaction, or competition between the species, as is often stated or implied in the literature. Population changes may be merely a matter of natural life cycles or of abiotic changes in niche dimensions that have nothing to do with interactions among nematodes. Herbivores are seldom resource limited and therefore are not likely to compete for common resources (15). But when there is resource competition among plant-para-

sitic nematodes, it is usually of the exploitative type. Competition among plant-parasitic nematodes is probably not as great as is sometimes thought. A plant usually can support a far greater nematode population than it does; therefore, there is not the great resource competition that we sometimes like to imagine. The host is the dominating regulating factor in the establishment of a population. After nematodes become associated with an efficient host, then primarily environmental factors govern populations. What probably is more important than competition among the plant parasites are the interactions of plant-parasitic nematodes with other biotic associates. In plant nematology, we are often dealing with ephemeral substrates resulting in changes in nematode communities that may have nothing to do with direct interactions among the nematodes themselves.

ABIOTIC SOIL FACTORS

In describing soil environments, often only the relatively easy-to-measure factors such as pH, texture, and organic matter are given. Other parameters whose methodology is more difficult, more time consuming, or even unknown, but which may be highly important to a nematode, are omitted. Questions still arise as to the best method for measuring pH or other parameters so that truly accurate and meaningful results can be obtained. Soil is complex, and simple heuristic models to explain nematode population or community behavior, however informative, are not very satisfying, and more complicated models may be necessary (17).

Sometimes differences in environmental factors seem small, but, as with soil texture, large variations may occur in the components of a soil designation. For example, according to the USDA classification of soil textures, a clay soil can have up to 45% sand, which results in different-sized pores, which in turn allows different sizes of nematodes to inhabit the soil. Small differences to us may be large to the nematode. Abiotic factors may be operative

where a soil favoring nematode increase and survival allows a greater nematode increase compared with areas where smaller increases occur in seemingly homogeneous soils as found by Alby et al. (1) and, in part, may explain the patchy distribution of nematode populations.

Other than when the environment limits survival, the critical time that the environment controls nematode populations is during the reproductive stage, which may be short. Favorable edaphic conditions, including temperature and moisture, may exist for considerable periods, but the nematode may not have reached the reproductive stage or may have passed it. Little is known about the length of the post-reproductive period of plant-parasitic nematodes. Whether nematodes can reproduce as long as resources and the environment are favorable is not known. Undoubtedly, physiological aging occurs, but many nematodes probably fail to reach maturity because of adverse environmental factors. Most plant-parasitic nematodes probably have a type III survivorship curve; that is, most mortality in a population occurs early in life. Some nematode populations peak early in the season and then are difficult to find later in spite of abundant resources and seemingly favorable environments. The life cycle of some species of *Longidorus* and *Xiphinema* is a year or more (14,20,27). Can adult female nematodes resume reproduction after a quiescent winter? Survival adaptations might be more important in large species such as *Longidorus* and *Xiphinema*, which probably produce fewer eggs than nematodes with shorter life cycles. The nematodes with long life cycles often must survive several periods of unfavorable environment, whereas species with shorter life cycles and higher reproductive rates produce many more offspring. As a result, the latter may not survive as well as species with long life cycles but they persist through survival of offspring. Survivorship varies with developmental stages of the species.

The two abiotic factors most difficult to predict are moisture, unless irrigation is

used, and temperature. As vegetation, both natural and cultivated, grows where moisture and temperature favor the extant taxa, so do the nematode parasites. Mathematical equations projecting population growth as geometric progressions are often criticized because resultant assumptions frequently are not biologically realistic. Cole (8) has attempted to show that those scientists who make assumptions not compatible with the biological data often come to the same conclusions as those who consider as many variables as possible in studies of population growth. Indeed, Ferris (11) has shown that predicted numbers of *Meloidogyne* spp. eggs and juveniles are similar, except late in the season, to actual data even though growth parameters such as fecundity, natality, and mortality were not known.

Differences in pH have been associated with certain nematode responses and may be important in formation of the community components. *Helicotylenchus platyurus*, *Xiphinema chambersi*, and *X. rivesi* are relatively common in Iowa woodlands (26, unpubl.) but are rare in the low pH duff soils in the boreal forest-hemlock hardwood forest in the northeastern United States. Correlations of pH with nematodes in Iowa woodlands have been shown (26), but the added variable of duff soils in an Adirondack Mountains study (29) versus the mineral soils in Iowa woodlands must also be considered.

Regional distribution: According to my tabulation in 1985, 172 species of plant-parasitic nematodes had been reported in association with maize in the world. As the geographical area was restricted, the numbers of species present decreased; 78 species were reported in the 48 contiguous United States, 27 in Iowa, and in any Iowa field, 4-8 species were known. Holmes (16) indicated that various factors can act as screens that prevent establishment or limit reproduction of species, thereby exerting control on community composition. Potential species occurrences are limited by lack of nematode availability due to geographical isolation or other historical factors,

temperature or moisture limitations, immune or resistant plants, changes in substrate caused by cultural practices, and nematode genomes that affect ability to reproduce sufficiently to maintain the population. Habitats are not static but change with time, slowly or instantaneously. The nematode species present at any particular time were able to survive many changes or have evolved as a result of isolation in changing environments. Thus, historical factors are highly important in community composition. Assuming that these and other events had resulted in a polyspecific community, how then do the physical and chemical properties of the soil govern the size and composition of a population?

On a large geographical scale, percentages of plant-parasitic nematode species associations were tabulated for the British Isles (6) and later expanded to a comparison of the British Isles and Belgium (46). Certain species were associated in greater frequencies than others. When trichodorid nematodes in the British Isles and Belgium were compared, the associations of species were generally similar except that *Trichodorus viruliferus* and *Paratrichodorus teres* had different affinities with other nematodes in the two countries. Also, associations of *Xiphinema diversicaudatum*, *Longidorus goodeyi*, and *L. leptcephalus* were similar in the two countries, but *L. elongatus* and *L. caespiticola* differed. Causes of similarities and differences are not known, but both host and edaphic factors must be considered.

Local distribution: Examples of species distribution along environmental gradients are provided by Burkhalter (7), Egunjobi (9), Norton and Oard (29), and Weaver and Smolik (51) in mountainous areas and by Norton and Oard (28), Nyhan et al. (30), and Procter (36) in areas of small relief. Even in areas of small relief, generalities cannot be made about populations in toposequences. In an Iowa clay-loam soil, the greatest number of individuals were usually found at the summit position (30), whereas in a highly silty soil (28), most plant-parasitic nematodes, except for *Paratylenchus* sp., were below the summit. Sim-

ilarly, Procter (36) found that free-living nematodes in the Arctic increased from the summit position down the backslope to the lowland transition of a toposequence. He speculated that these changes in numbers were due to changes in vegetation and the drier conditions at the upper parts of the toposequence. Besides heterogeneity of soils, coexistence may result from small differences in a given soil property, such as pH, soil texture, temperature, moisture, gas content, or other factors. Even when one species of plant is studied, the nematode species often separate on the basis of edaphic factors (24,39). Ferris et al. (13) found that similarity indices of plant-parasitic nematode species and numbers in 14 soybean fields in Illinois and Indiana frequently separated by soil factors.

With crop plants, there generally is a consistency in occurrence of the most abundant nematode species. The species found in a crop are generally the same from one decade to the next and are largely predictable for an area, assuming no major alterations in habitats. For example, comparisons of selected nematodes in the lower Rio Grande Valley of Texas were essentially the same between 1978 and 1987 as they were in 1965–66 (39). In polyspecific plant communities in the Lower Rio Grande Valley of Texas when distribution cannot be attributed to hosts, *Meloidogyne incognita* and *Rotylenchulus reniformis* separate by soil texture (39). Abiotic environmental resistance certainly contributes to maintaining established populations in a flexible steady state. Unless one examines markedly different soils, one usually learns by experience which nematodes to expect around a crop or habitat in a given area. What is true for maize in Iowa, however, is not always the same for maize in Asia or even in the southern United States. Part of this is due to major climatic differences in which some species cannot survive, and historical factors may be important.

When species cluster by habitat, such as in native prairies (41), the clustering due to host relationships cannot be separated from that due to edaphic factors. Edaphic

factors seem paramount in many instances because of the almost constant association of certain species with given soil conditions. Unknown causes and effects aside, such studies are valuable in making predictions within broad limits.

Nematode diversity and soils: Diversity is a measure of community composition, and the diversity index H' is based on the proportions of species in a community (34). Variations in local conditions usually are the determining factors (38). Few data exist on the diversity (H') of nematodes in different soils or soil perturbations. Yeates (53), while acknowledging that more data are needed, suggested that topographic, soil, and climatic factors are likely to be as important in determining H' as are vegetation and cultivation.

There are few studies in which polyspecific nematode communities are monitored around the same crop species in different soils. In an Illinois rotation study (12), trends in H' containing six nematodes at four different locations varied with the crop and soil (Table 1). Maize generally supported the highest diversities when only maize, soybeans, and wheat were considered. Maize in rotation had a higher H' than continuous maize at the only site where this cropping system was used. The H' s were higher in the clay loams than in the silt loams.

Results of studies in Montana (51), Poland (50), Switzerland (7), and New Zealand (9) indicate that nematode numbers or diversities, either of genera or species, are greatest in grasslands and least in forests or cultivated areas. Unfortunately, extraction techniques favorable for recovery of the criconematids (5) were not used in early studies. In a study in Poland covering nematode genera in all trophic groups, the H' s were 4.0–4.9 for grasslands, 3.2–4.3 for forests, and 3.1–4.2 for cropfield habitats (50). Part of these differences in H' probably is due to the diversity of hosts, but diverse soil factors may also be important because many woodlands are too dissected to be suitable for cultivation and some prairies are also unsuitable for agri-

TABLE 1. Diversity (H')† of six nematodes‡ in soybean rotation plots sampled in midsummer in Illinois.

Soil type and crop rotation	Nematodes/ 473 cm ² soil	H'
Urbana-Proctor silt loam		
Maize	1,055	0.95
Soybeans	858	0.87
Wheat	601	0.79
Forage§	2,259	0.44
Toledo-Cisne silt loam		
Maize	1,530	0.83
Soybeans	1,694	0.43
Wheat	1,321	0.39
Forage§	2,114	0.60
Urbana-Drummer silty clay loam		
Maize	973	1.06
Soybeans	1,574	0.94
Wheat	537	0.87
Forage§	518	1.24
Hartsburg-Illiopolis silty clay loam		
Maize	1,947	1.04
Soybeans	1,300	1.02
Wheat	807	1.17
Maize (continuous)	1,434	0.86
Soybeans (continuous)	1,219	1.00

† Calculated from table 1 in Ferris and Bernard (12).

‡ *Helicotylenchus pseudorobustus*, *Paratylenchus projectus*, *Pratylenchus* spp., *Quinisulcius acutus*, *Tylenchorhynchus martini*, *Xiphinema americanum*.

§ Alfalfa, red clover, bromegrass.

culture because of drainage problems. Drainage problems often indicate diverse topography and, in all probability, different soil conditions.

Stinner and Crossley (43) found that in a rotation of sorghum (July–November) and rye (December–June), diversity of plant-parasitic nematodes tended to be greater under conventional tillage than under no-till from July to November. There was generally little difference after that. The influence of the season or the crops was not measured.

Calculation of H' s for the four extreme tillage practices from population studies of seven different tillage systems in a maize field (44) resulted in discernable trends. For all trophic groups combined, the fall-pow treatment consistently had higher H' s than did the no-till ridge treatment (Fig. 1A). The H' s of both generally declined over time largely because of the increase in the proportion of bacterial feeders rel-

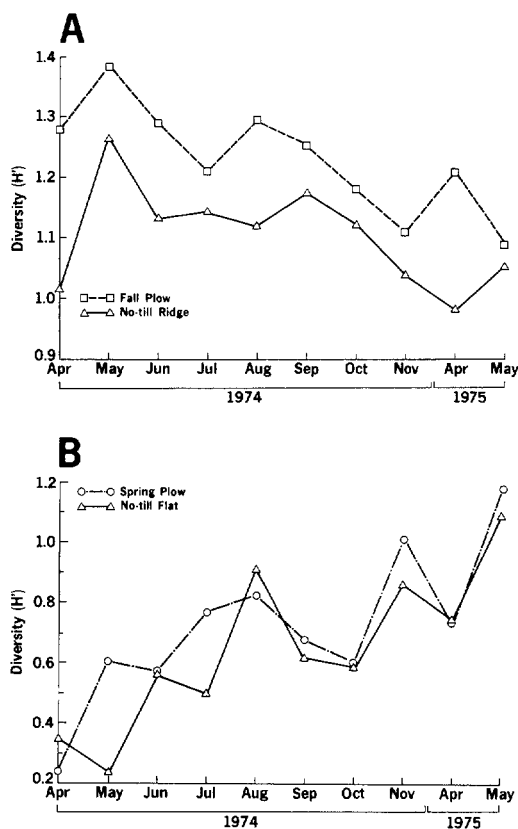


FIG. 1. Diversity (H') in nematodes. A) All nematode trophic groups in fall-pow and no-till ridge maize tillage plots. B) Plant-parasitic nematodes in spring-pow and no-till flat maize tillage plots. Calculated from raw data of Thomas (44).

ative to the plant-parasitic forms. The no-till flat and spring-pow treatments had similar trends, but they were not as strong. When only the plant-parasitic nematodes were considered, the H' s in the spring-pow and no-till flat treatments tended to increase over time (Fig. 1B), mainly because of increases in proportions of *Pratylenchus* spp. and *Xiphinema americanum* relative to *Helicotylenchus pseudorobustus*. When the seasonal H' s were compared among the treatments, the no-till ridge treatments generally had the lowest H' in the various trophic groups. Baird and Bernard (4) found "no significant differences in species dominance or species diversity" while studying cropping and tillage systems in Tennessee.

H' and elevation. The H' s are expected to change with changes in elevation. When

elevation changes are small, H' changes are likely to be caused by local edaphic conditions such as soil texture or moisture. Where there are major elevation changes, such as going through vegetational zones, changes in H' might be caused by host changes and edaphic factors such as changes in the climate. In a toposequence planted to maize, H' was generally highest at the backslope (28). The spread in amplitude, however, was greater on the north-facing than on the west-facing slope, and the general trends were different on the two slopes. The soils at all sites were deep loess of 60–84% silt. The greatest amount of organic matter, up to 4.6%, was at the toeslope. Because the same maize germplasm was used, the differences were presumed to be caused by environmental variations.

Where major changes in elevation occur, as in mountainous areas, the reduction in nematode diversity at higher elevations is thought to be caused mainly by the climate at higher elevations (7,29,51). Whereas a moisture gradient was most evident in the maize toposequence, temperature gradients were the most plausible causes for the lower diversity at higher elevations in the mountain studies. In a Swiss alpine study (7), the richness of genera and species, mostly those that are not plant parasitic, became less as height increased but the number of individuals remained approximately the same. In an Adirondack Mountain study (29), the lesser H' 's with increasing elevation probably were due to the more rigorous climate at the higher elevations, until mainly *Criconea sphagni* and *Ogma menzeli* were obtained as the alpine tundra was approached. This was true whether a single plant species (*Abies balsamea*) was sampled in the vegetational zones (hemlock–hardwood, boreal forest, tundra) or whether mixed vegetations were sampled. This might indicate that climate and soil factors are more important than the host.

Diversity and stability: The concept that a diverse community, based on many species and an abundance of interactions, leads to

community and even environmental stability (37) has lost favor in recent years. More consideration is being given to the concept that environmental stability leads to community stability, which in turn, allows community diversity (21,34). Although information about nematode diversities and community structure is not sufficient to test these hypotheses, most plant-parasitic nematodes probably are r-selected species, especially those in the simple and changeable cultivated agroecosystems. The K-selected species usually occur in the more stable natural environments, are biologically more complex, and probably cannot recover after severe perturbations as well as r-selected species (21).

FUTURE

A better understanding of nematode ecology is needed. We need a much clearer idea of a community, to define our terms clearly, to document mechanisms (dynamics) of population changes in a community, and to look for cause-and-effect relationships. After the host, abiotic factors can be the most important. We need to know the meaning of competition, and how much is operative. What role do abiotic soil factors have in maintaining the steady state of populations? Only when we know all we can about the driving forces behind nematode populations can we predict composition and diversity. Plant-parasitic nematodes probably have a type III survivorship curve or close to it. To what degree do abiotic factors govern this? How can we alter the abiotic factors when it is desirable to reduce survivorship further? How can we differentially reduce survivorship or reproductive of the individuals in a community? A study of abiotic factors in the composition and structure of nematode communities is necessary, but only when we can understand the dynamics with the biological associates will we be able to be sure of cause-and-effect relationships. More work involving two or more variables are necessary. Obviously, many more studies are needed to discern relationships.

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