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Soil Nematode Assemblages: Regulators of Ecosystem Productivity

Undoubtedly the most well-known and studied genera of soil nematodes are those directly dependent (‘parasitic’) on plants and which have been associated with obvious economic crop loss; *Anguina, Ditylenchus, Globodera, Heterodera, Meloidogyne, Longidorus, Pratylenchus, Trichodorus* and *Xiphinema* are among the more important. However, the single most intensively studied soil nematode species is the bacterial-feeding *Caenorhabditis elegans.* In addition to a series of scientific meetings concerning this species, there are several home pages on the World Wide Web devoted to its morphology, physiology and genome. Generally, ecological studies of soil nematode assemblages have not been the focus of such intensive research.

One factor impeding intensive study is the sheer diversity of nematodes. The soil nematode faunae of ecosystems (*i.e.* α-diversity) have been found to encompass over 200 morphological species (5) and recent classifications have included the following feeding groups: bacterial-feeding, fungal-feeding, predacious, plant-feeding (species with direct plant dependency), plant-associated, and omnivorous (15). In addition, dispersal phases of nematodes dependent on invertebrates and vertebrates may be present; such transients presumably do not contribute significantly to soil processes.

The nematode assemblage in a soil includes representatives of these feeding groups and the net effect of the nematode assemblage on soil processes reflects its contribution to a wide range of ecosystem processes. Traditionally ‘nematode’ has been taken to refer to plant-feeding forms and a negative relation to yield inferred. However, when the whole nematode assemblage is considered, a positive relationship between yield ($\sim$ ecosystem productivity) and total nematodes has been demonstrated (11) – at least in grasslands, where turnover of shoots and roots is more rapid than, for example, in a forest.

In most cases soil nematodes are but one of the phyla utilizing a particular food resource. In addition to nematodes there are, for example, insects feeding on above- and below-ground parts of plants; mites and tardigrades preying on nematodes; enchytraeids, collembola and mites feeding on fungi; and protozoa and rotifers feeding on bacteria in soil water.

Feeding or grazing by microbial-feeding and predacious nematodes and other invertebrates may have positive effects on ecosystem productivity. Laboratory experiments demonstrated dramatically that microbial grazing by bacterial-feeding (*Pelodera, Acrobeloides*) and fungal-feeding (*Aphelenchus avenae*) nematodes increased growth of blue grama grass *(Bouteloua gracilis)* (4). Analysis of field populations showed that predation by both nematodes and microarthropods is an important form of regulation of nitrogen fluxes and litter decomposition under the Chihuahuan desert annual *Lepidium lasiocarpum* (6).

Regular monitoring of soil microbial populations and nematode trophic groups has brought together information showing that microbial populations grazed by soil microfauna (especially nematodes) have greater turnover and thus greater flux of plant nutrients (10). However, the standing crop of soil bacteria and fungi may be lowered, and the nematodes grazing the microflora may themselves be grazed by (predated upon) predacious nematodes resulting in lower populations of bacterial-feeding and fungal-feeding nematodes. Thus the measured, instantaneous populations of microbes and their grazers do not necessarily indicate the contributions of the populations to ecosystem processes; population turnover is the key to fluxes of energy and nutrients through them. Furthermore, recent work in which white clover (*Trifolium repens*) was infested with clover cyst nematode (*Heterodera trifolii*) showed a significant increase in soil microbial biomass compared with uninfested plants (14). These findings suggest that root feeding by nematodes increases the ‘leakage’ of nutrients from roots into the rhizosphere and, if this is found to be widespread, it will significantly advance our understanding of rhizosphere processes.

Classic studies, such as those on the migration of *Heterodera schachtii* juveniles through substrates of various textures and moisture contents (8), and the reproduction of *Rhabditis*, *Caenorhabditis, Pelodera* and *Mesodiplogaster* on agar plates at temperatures from 5 to 40°C (1), have demonstrated the importance of moisture and temperature in controlling the activity of nematodes. However, we are largely ignorant about the impact of these simple factors on resource utilization by nematodes in the field. These and other factors (*e.g.* salinity, pH, heavy metal contents, trace elements, soil parent material) remain to be studied and quantified. Until the critical limits for activity of each stage of a range of nematode species in each soil have been determined, it is not feasible to assess the effect of the nematode assemblage on soil processes (13). The activity of ecologically related soil organisms is part of this picture. The filtering of bacteria from soil water by rotifers presumably has an effect on the availability of the resource for bacterial-feeding nematodes. Such bacterial-feeding nematodes also exhibit various cephalic specializations which allow several species to coexist while utilizing a single food resource; the ‘pine-cone hypothesis’ of De Ley (2) represents an important insight to both the functional morphology of the cephalobid head and the feeding mechanisms used by bacterial-feeding nematodes.

An example of how these various interactions may be integrated and related to agricultural production has been given by Ferris *et al.* (3). During the tomato (*Lycopersicon esculentum*) growing season, *r*-selected bacterial-feeding nematodes were most responsive to inputs of organic matter and related increases in soil microbial biomass. When the bacterial-feeding nematode population was lowest, early in the growing season, the crop evinced symptoms of nitrogen deficiency. The authors hypothesized that increased abundance, biomass and activity of these nematodes in spring following incorporation of residue from the previous crop, would reduce the observed nitrogen stress.

Nematode species lists published for various ecosystem types average 49 species, with the greatest diversity (228 species) being found in Kansas prairie soils (5). While the species can be allocated to the six feeding groups listed above, the species populations within a feeding group have often been found to be complementary. There may be a range of plant-dependent nematodes with great host-specificity: several plant-dependent nematodes may show a sequence of invasion of a given plant (11); Rhabditidae may occur under more eutrophic conditions than Cephalobidae; various species of Plectidae and Mononchidae may have different dimensions, life-cycles and generation times and so utilize differing segments of a single resource (12). Such apparent 'ecological redundancy' within a functional group is considered by many to increase the resilience of ecosystems to short- and long-term changes and stresses. There is ongoing debate about the relationship between diversity and productivity in communities as well as the relative importance of above- and below-ground diversity (7,10).

Some workers believe that 'ecological redundancy' is dependent on the level of resolution. In soils many key processes, and nematodes, occur on a microscopic scale reflecting soil mineralogy, site relief and the organic regime. Therefore to understand soil processes, and the contribution of nematode assemblages, investigation must be based on samples reflecting the contribution of each land unit to the whole area; the only alternative is sufficiently detailed understanding of processes and populations such that their contributions to each land unit can be incorporated in an adequate model. Both approaches require an improved understanding of the relationships and roles of nematode assemblages.

For decades, pre-plant populations of plant-dependent nematodes such as *Anguina* and *Heterodera* have been used as indicators of potential economic crop loss. In the last decade there have been attempts to assess soil nematode assemblages as a whole and to define nematode taxa or indices which may indicate soil conditions generally favorable for crop production or the less well-defined concepts of 'environmental health' and 'soil quality'. As we work towards an holistic approach to understanding natural and managed ecosystems, soil nematode assemblages should be seen as an essential part of the soil and soil processes. All the species should be considered as components of various food, energy and nutrient webs, rather than treated in isolation.

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