

# Nematodes: Ecology

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## INTRODUCTION

Nematodes are among the most successful of multicellular organisms. They inhabit every environment imaginable. Although less diverse in number of species than some other phyla, they are incredibly abundant in number of individuals. An estimated four out of every five multicellular organisms on the planet are nematodes,<sup>[1]</sup> surely a testament to their success and their ability to adapt physiologically and behaviorally to diverse habitats and niches. Cobb<sup>[2]</sup> asserted that if all matter other than nematodes were removed, the outlines of geographic features, vegetation, and centers of habitation would be recognizable by the abundance and characteristics of nematode communities. That understanding has grown, and nematode community structure is now recognized as a powerful tool in the biomonitoring of soil history and condition.<sup>[3]</sup> The ecology of plant and soil nematodes can be considered at several levels of resolution, for example, the physiological and behavioral response of individuals to environmental conditions; the reaction of life history traits to environmental resources, and the resulting consequences to abundance and spatial patterns; and the structural positions and functional roles of the organisms in the ecosystems that they inhabit.

## PHYSIOLOGICAL ECOLOGY OF PLANT AND SOIL NEMATODES

Like all nematodes, those in plants and soil respond both physiologically and behaviorally to environmental conditions and cues. As poikilotherms, their metabolic activity is modified by temperature; the efficiency of energy release for cellular and organismal function approaches a maximum when they are exposed to favorable temperature ranges. Nematodes are aquatic organisms. In soil, they inhabit water surrounding soil particles, and their permeable cuticle provides direct contact with their microenvironment. They do not rapidly migrate from stressful conditions, and many species survive dehydration, freezing, or oxygen stress; others are more sensitive. Metabolic activity becomes constrained by limiting factors, including availability of moisture in the soil or plant material in which the nematodes live, or the availability of

oxygen to drive metabolic processes. They are also affected physiologically by the osmotic condition and pH of the milieu. Such factors vary considerably as concentrations of the soil solution are affected by rainfall, percolation, and evapotranspiration. The amplitude of tolerance to such varying conditions determines the habitats occupied by different species.<sup>[4]</sup>

It seems reasonable to assert that population levels or aggregations of nematodes in soil or plant material will be greatest where the integral affect of environmental conditions is optimal for their metabolism. In such locations they should feed more effectively, move most efficiently, reproduce most rapidly, and survive longest. Aggregations of nematodes are also enhanced by kinetic effects (movement). Movement is most rapid in favorable zones and less rapid, or even prevented, in unfavorable zones. Of course, the overriding determinant of population aggregates is the presence of food and the ability of nematodes to detect and access it while potentially constrained by the top-down effects of density-dependent predation by natural enemies.

## BEHAVIORAL ECOLOGY OF PLANT AND SOIL NEMATODES

Nematodes respond to environmental (and other organismal) cues through taxes and kineses. Kineses are alterations in rate of activity; taxes are directional responses to stimuli. Chemosensory signals are detected by the amphids, which may be relatively small in environments where signal strength changes slowly (e.g., soil), or elaborate where signal strength is more dilute or changes rapidly (e.g., freshwater or marine environments). Even where amphids are small, as in most soil nematodes, expansions of the neuronal endings and the presence of mucoidal material may enhance their sensitivity. In those nematodes (e.g., *Caenorhabditis elegans*) where the nervous system has been studied intensively, cell bodies of amphidial neurons are aggregated in the nerve ring, which may allow some integration of signal strength from the amphids on either side of the head—or between amphids and the posterior phasmids—and allow generation of a signal for muscular responses.<sup>[5,6]</sup>

Chemosensory communication between individuals is evident in taxis responses of males to females in sexually reproducing species and in the apparently tactile determination of the location of reproductive structures during mating. Response to host signals is generally strongest in plant-feeding nematodes that have a narrow host range and less obvious in those species with wide host ranges. Nevertheless, coordination of life history events with host availability is very important in species that have evolved sophisticated host-parasite relationships, for example, the root-knot nematodes, *Meloidogyne* spp.<sup>[7]</sup> In those cases, the food reserves packaged into the egg by the female nematode must be sufficient to drive the embryo through several hundred cell divisions, a molting event from the first to the second juvenile stage, hatch from the egg, detection and migration to a host root, penetration of the root tissues through a complex migration pathway, and induction of a feeding site. All of those energy-intensive activities are necessary before the nematode is able to independently obtain new resources. Clearly, there are many opportunities for disaster, including inability to find a root, a nonhost response by the root, and insufficient residual energy to complete the penetration process.

## POPULATION ECOLOGY OF PLANT AND SOIL NEMATODES

Population processes are, of course, regulated by physiological responses to the environment. The dynamics of increase and decrease in nematode populations are the integral of birth and death rates as constrained by environmental conditions, resource availability, and community regulatory pressures. Birth rates are affected by the intrinsic capacity of female nematodes to produce eggs and the duration of the life course over which those eggs are produced. Birth rates may be influenced by availability of males where fertilization is necessary, but not where parthenogenesis occurs.<sup>[8]</sup> Hermaphroditism occurs in some bacterial-feeding nematodes (e.g., *C. elegans*). In those cases, the number of viable eggs produced is greater when cross- rather than self-fertilization occurs, apparently because the hermaphrodite does not produce and store enough sperm to fertilize all the eggs it is capable of producing.<sup>[9]</sup>

Most plant and soil nematodes seem to produce eggs for the duration of their adult life course. Induced mutants of *C. elegans* may have extended survival beyond the reproductive period, with possible competitive consequences for food. The occurrence of such variants in nature is unknown and, arguably, there would be strong selection pressure against them, as there does not appear to be any social contribution to the population on the part of elderly nematodes.

The life course of plant and soil nematodes may be as short as a week in opportunistic bacterial-feeding species; is often in the 4–8 week range in plant-feeding species; but may be as long as several years in long-lived, large-bodied plant-feeders, predators, and omnivores inhabiting undisturbed and stable environments.<sup>[3]</sup> The distribution of death expectancy around the mean life duration is generally not known except in some model systems.<sup>[10]</sup>

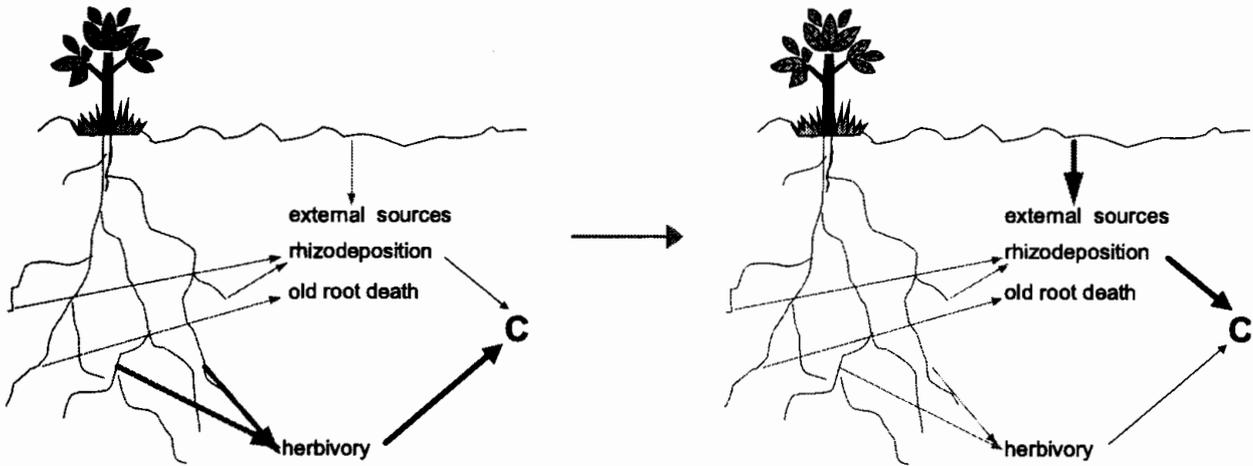
Resource availability in an environment determines its carrying capacity for a nematode population. In closed systems, that carrying capacity may be fixed by the total amount of carbon available. But in dynamic systems, such as those generated by a growing plant that is continually fixing carbon, producing roots, and depositing and leaking materials into the rhizosphere, the carrying capacity changes with time. For a plant-feeding nematode species, there is a delicate balance between the amount of damage or pressure a successful parasite applies to the growth of its host plant and the rate and amount of food that the host can make available to the parasite. At higher starting population levels, the damage to the host may be so great that growth and development of the plant is impaired, total photosynthetic input is compromised, and the nematode population is limited to a lower level than it might have been if initial population pressure were lower.<sup>[11,12]</sup>

## COMMUNITY ECOLOGY OF PLANT AND SOIL NEMATODES

Nematodes in any environment are components of communities of organisms and, depending on their feeding habits and life history attributes, fit into their communities in various functional roles. The essential feature of a community is that the participating organisms are interdependent as food resources or interact in some way in the acquisition of resources.

The community of interacting soil organisms is sometimes known as the soil food web. The primary sources of carbon and energy from soil organisms stem from the photosynthetic activity of plants. The flow of carbon from plant material into the soil food web is influenced by nematodes in various ways. Some nematodes are herbivores that channel carbon and energy into the soil food web by direct herbivory on the plant. Others feed on fungi and bacteria and so constitute important bridges between primary decomposers of organic material and detritus and the balance of the food web. Still others are predators and omnivores consuming a range of higher soil organisms. These exert pressure on the abundance of their prey and potentially regulate or even suppress prey populations. Structure of the community is maintained as the integral of the population ecology of various taxa and the regulatory effects of predation across and within





**Fig. 1** A management goal in sustainable agricultural production: to maximize the flow of carbon (C) into the soil food web through detritivore rather than herbivore channels.

trophic levels, but ultimately the size and activity of the food web must depend on the amount of carbon entering the soil. A major goal of sustainable production systems that are reliant on the functional roles of soil food webs is to increase carbon flow into the system through detrital channels while minimizing carbon flow resulting from herbivory (Fig. 1).

Besides predation, mechanisms of interaction at the community level include interspecies competition and mutualism. Certainly, nematodes with the same feeding habits compete for resources, but in some situations, competition is mitigated by adaptation of the nematodes to different environmental conditions. Predominance of species in the communities varies with their thermal adaptation; competition is reduced by spatial and seasonal variations in temperature and its diurnal amplitude.<sup>[13]</sup> One interesting example of mutualism in soil nematodes is exhibited by the so-called entomopathogenic nematodes. These bacterial-feeding nematodes transport mutualistic bacteria into the intestinal tract of insects. There the bacteria are released, which kills the insect and provides an abundance of food for the nematode.<sup>[14]</sup>

Communities of organisms tend to be centered on sources of food. In the soil, such foci may occur at the interface of organic litter layers and the mineral layers of the soil. They also occur at the metabolically active parts of the root system, the root tips. Because of the multiplicity and dispersion of the various organic matter sources that drive the soil food web (Fig. 1), coupled with the physical heterogeneity of the soil environment, the soil community tends to exist in patches. It might be considered a metacommunity, a series of borderless communities with opportunities for migration of organisms among the patches, depending on their motility and sensory capabilities.

Both resource availability and predation pressure affect soil nematodes, and the interplay between these forces affects the dynamics of the participating populations. Bacterial-feeding nematodes may enter inactive "dauer" states, which allows them to conserve resources and, perhaps, renders them less accessible or attractive to predators. Nevertheless, the predators require food, and both they and the prey nematode populations must decline in the absence of resources entering the system.

## SUCCESS OF NEMATODE ECOLOGICAL STRATEGIES

Nematodes are found in every habitat, from frozen tundra to hot springs, and from marine sediments to alpine peaks. They obtain sustenance from every form of fixed carbon imaginable, from algae and bacteria to humans. Recent classification systems recognize around 19 orders that constitute the phylum Nematoda. Plant-feeding species occur in three of those orders and are most prevalent in one, the Tylenchida. This relatively small sector of the phylum has developed strategies for feeding on perhaps every species of higher plant and for coexisting with other species on the same plant. Most species feed on root tissues and so avoid the dry conditions of the aboveground habitat, but some species have become behaviorally and physiologically adapted to feeding in stem, leaf, and seed tissues. Enormous diversity exists among root-feeding strategies, from root tip feeders to root hair piercers, and from migratory ectoparasites that withdraw contents of individual cells to sedentary endoparasites that elicit highly specialized feeding-site responses from the host.

## ARTICLES OF FURTHER INTEREST

- Agriculture and Biodiversity*, p. 1  
*Biological Control of Nematodes*, p. 134  
*Classification and Identification of Nematodes*, p. 283  
*Ecology and Agricultural Sciences*, p. 401  
*Ecology: Functions, Patterns, and Evolution*, p. 404  
*Ecophysiology*, p. 410  
*Nematode Biology, Morphology, and Physiology*, p. 781  
*Nematode Feeding Strategies*, p. 784  
*Nematode Population Dynamics*, p. 797  
*Organic Agriculture As a Form of Sustainable Agriculture*, p. 846  
*Sustainable Agriculture: Ecological Indicators*, p. 1191

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