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Author: McSorley, Robert

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ADAPTATIONS OF NEMATODES TO ENVIRONMENTAL EXTREMES

ROBERT MCSORLEY
Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611-0620

ABSTRACT

Nematodes are a highly diverse group of organisms that show a variety of adaptations to extremes in soil and plant environments. Developmental dormancy and diapause are important for seasonal survival and long-term longevity of eggs in some species, whereas changing sex ratios may improve survival chances of the next generation in some instances. More direct and immediate responses to environmental conditions include aggregation or the formation of relatively resistant dauer larvae. Many nematodes can undergo temporary quiescence in response to environmental stress, and entry into anhydrobiosis or other extreme states allows long-term survival in unusually stressful environments. These inactive survival stages may make up a substantial proportion of the nematode population in some terrestrial environments.

Key Words: anhydrobiosis, dormancy, nematode survival, plant-parasitic nematodes, soil ecology

RESUMEN

Los nemátodos son un grupo de organismos sumamente diverso que demuestra una variedad de adaptaciones a los ambientes extremos de suelo y plantas. La latencia desarrollada y la diapausa son importantes para la sobrevivencia estacional y la larga longevidad de huevos en algunas especies, mientras que cambiando la proporción de sexos puede mejorar la probabilidad para sobrevivir de la proxima generación en algunos casos. Las respuestas más directas e inmediatas a la condiciones ambientales incluyen la agregación o la formación de larvas del estadio "dauer" (etapa alternativa adaptada para su supervivencia) relativamente resistentes. Muchos nemátodos pueden pasar por una quiescencia temporaria en respuesta al estres ambiental, y entrar a la anhidrobiosis u otros estados extremos permite la sobrevivencia de largo plazo en ambientes extraordinariamente severos. Estos estadios inactivos de sobrevivencia pueden representar una proporción substancial de la población de nemátodos en algunos ambientes terrestres.

Nematodes are a diverse group of invertebrates abundant as parasites or free-living forms in soil, freshwater, and marine environments. The more than 15,000 described species probably represent only a small portion of the total members in the Phylum Nematoda (Barker 1998). The soil is a particularly rich habitat for nematodes, with about 26% of described genera inhabiting soil as bacterivores, fungivores, omnivores, predators, or plant parasites (Wharton 1986). Added to this are soil-dwelling stages of parasites on insects or other animals, as well as freshwater genera that colonize soil to varying degrees. A moisture film is necessary for normal nematode activity (Wallace 1973), and therefore soil moisture, relative humidity, and related environmental factors directly affect nematode survival.

The soil environment offers varying degrees of protection for nematodes from dehydration. Parasites that are inside plant roots or insects enjoy optimal moisture and protection from desiccation as long as the health of the host persists. Life stages or species that do not live inside a host find protection in moist soil, but risk increasing exposure to dehydration as soils dry. Hazards increase as the soil-air interface is approached (Womersley 1987). A few unusual genera of plant parasites, such as *Anguina*, *Ditylenchus*, and *Aphelenchoides*, risk exposure in air as they climb (under humid conditions) to infect aerial plant parts. Risk may increase further as above-ground plant parts (leaves, seeds, etc.) dry up or die along with the nematode parasite inside. This overview introduces some of the strategies that soil-inhabiting nematodes use to cope with deteriorating environmental conditions and with particularly severe conditions.

ADAPTATIONS IN THE LIFE CYCLE

The most generalized life cycle of a nematode involves an egg, four juvenile stages (referred to as J1 to J4), and the adult. In many species, the appearance of juveniles and adults are similar, but great diversity exists in the life cycles of this large group (Wharton 1986). The life cycle of some nematodes offers built-in opportunities for resisting environmental stresses, such as a protective cyst that covers the eggs of some species. Many nematodes undergo the first molt in the egg, retaining the protection of the eggshell for the developing J2.

Developmental Dormancy and Diapause

Diapause and other delays in development that are common in insects (Chapman 1971; Romoser & Stoffolano 1998) occur in some nematodes as well (Evans & Perry 1976; Wharton 1986). Although diapause is not necessarily a result of adverse environmental conditions nor ended by favorable conditions (Chapman 1971; Evans & Perry 1976; Wharton 1986), it is nonetheless a critical survival mechanism during cold seasons and in the absence of a host. The stimulation of egg hatching in *Meloidogyne naasi* Franklin by chilling is a well-known example of diapause in a nematode (Van Gundy 1985). In some species of root-knot (*Meloidogyne* spp.) and cyst (*Heterodera* spp., *Globodera* spp.) nematodes, a portion of the eggs hatch quickly while others hatch slowly over time (DeGuiran 1979; Zheng & Ferris 1991; Huang & Pereira 1994). The distribution of egg hatch over time may be quite complex. Zheng & Ferris (1991) recognized four types of dormancy in eggs of *Heterodera schachtii* Schmidt. Some eggs hatched rapidly in water, some required host-root diffusate for rapid hatch, while others hatched slowly in water or in host-root diffusate. Stimuli for hatching and ending of dormancy in various species include such factors as temperature (Van Gundy 1985) or the presence of host plant or root leachate (Huang & Pereira 1994; Sikora & Noel 1996). The quality of the latter depended on crop cultivar, phenology, and other factors (Sikora & Noel 1996). Interpretation of dormancy and diapause in nematode eggs is further complicated in that the induction of dormancy in cyst nematodes varies seasonally, and may be dependent on temperature or host phenology (Yen et al. 1995; Sikora & Noel 1996). Diapause and developmental dormancy seem to apply mostly to the egg stage and to juvenile stages within eggs, although instances of diapause in later juvenile stages or adults are known, mainly in a few animal-parasitic nematodes (Evans & Perry 1976).

Sex Ratios

Sex ratios are environmentally determined in many nematodes, including amphimictic species and those that are primarily parthenogenetic (Triantaphyllou 1973). The production of males has been especially well-studied in the root-knot nematodes. In this group, the nematode hatches from the egg as a mobile J2, which migrates through soil and into plant root tissue, where it establishes a permanent feeding site. Once the J2 begins to feed, it becomes immobile, increases its body size, and progresses through subsequent molts, developing into a female that can reproduce parthenogenetically. Males can be very rare in root-knot nematode populations, but in some instances may comprise more than 60% of the population (Papadopoulou & Triantaphyllou 1982). A variety of stresses may lead to increased production of males. These include nutritional deficiency or reduced photosynthesis in the host plant, age of the host plant, plant growth regulators or inhibitors, increased nematode population density, presence of plant pathogens, level of host plant resistance, and even temperature or irradiation (Bird 1971; Triantaphyllou 1973). If stress is imposed during development, second-stage juveniles developing as females can undergo sex reversal, producing intersexes or males (Triantaphyllou 1973; Papadopoulou & Triantaphyllou 1982). Aside from the obvious advantage of producing fertilized eggs with perhaps a better chance of surviving adverse conditions, increased male production in root-knot nematodes results in the production of a mobile form that can leave an area or plant under stress (Bird 1971).

RAPID RESPONSES TO ENVIRONMENTAL STRESS

Protective strategies built into the life cycles of nematodes help to ensure survival of the current or subsequent generation. Some physiological and behavioral responses allow nematodes to react more quickly to environmental stresses. For example, *Steinernema carpocapsae* (Weiser) Wouts, Mracek, Gerdin, & Bedding can cope with changing levels in soil O_2 by alternating between aerobic and anaerobic metabolism (Shih et al. 1996). Many species of nematodes will coil in response to drying (Bird & Bird 1991).

Dauer Larvae

Many nematodes form a temporary stage called a "dauer larva" in response to various types of environmental or nutritional stresses. Depending on the nematode species, dauer larvae can be formed in J2, J3, or J4 stages (Bird & Bird 1991). They undergo modifications in the cuticle structure to decrease permeability (Bird & Bird 1991), and some forms retain the cuticle from the previous molt as additional protection (Evans & Perry 1976). Dauer larvae are relatively inactive, but can react if stimulated, and revert to the normal juvenile stage if conditions improve. Desiccation, depletion of food supply, crowding, or deterioration of an insect host are factors that can stimulate formation of dauer larvae (Wharton 1986; Bird & Bird 1991; Womersley 1993). The formation of dauer larvae in *Caenorhabditis elegans* (Maupas) Dougherty as the food supply declines is mediated by pheromones (Huettel 1986).

The abilities of dauer larvae to resist environmental stress and to recover quickly to normal stages vary from species to species. The J4, or preadult, of *Ditylenchus dipsaci* (Kuhn) Filipjev as well as the J3 can control water loss to such an extent that both stages could be considered as forms of dauer larvae (Bird & Bird 1991). The J3 of *S. carpocapsae* is a relatively resistant infective stage that may be exposed on vegetation or the soil surface as it actively searches for insect hosts (Poinar 1979).

Aggregation

Occasionally, individuals of some nematode species will mass together forming large aggregations. Probably the best known example is the accumulation of large numbers of *D. dipsaci* on the surface of stored flower bulbs (Christie 1959). The nematode clumps may be so large that they are actually visible to the naked eye as whitish masses referred to as "nema wool." The masses probably offer some protection against desiccation (Cooper et al. 1971), and nematodes in the masses may exhibit other low moisture adaptations such as coiling and anhydrobiosis. In contrast, swarming, which refers to large coordinated population movements of nematodes, is believed to function more in dispersal and migration than in moisture conservation (Croll 1970). Nematode aggregation is difficult to study since large masses of nematodes building up in laboratory culture may not be typical of those found in nature.

RESPONSES TO EXTREME ENVIRONMENTS

Quiescence refers to a dormant state in which metabolism and activity are slowed down in response to environmental stress. Unlike diapause, the dormant state ends when the environmental stress is relieved, and nematodes then return to normal activity. A variety of environmental stresses may trigger quiescent states (Table 1). In extreme cases of prolonged quiescence, the metabolic rate may fall below detectable levels and appear to cease. This extreme dormant condition is referred to as anabiosis (Wharton 1986) or alternatively as cryptobiosis (Cooper et al. 1971). The term "anhydrobiosis" is used most often to refer to quiescent and anabiotic states, probably because desiccation is the most frequent and most studied cause of quiescence. The degree of quiescence observed among nematodes varies along a continuum from mild quiescence to anabiosis, depending on the nematode species involved and even within the same species (Wharton 1986). Most nematodes can show quiescence at some point, but relatively fewer species are capable of anabiosis. Anabiosis is not restricted to nematodes, but is common in some other invertebrate groups such as rotifers and tardigrades (Barnes 1980).

TABLE 1. TERMINOLOGY APPLIED TO QUIESCENT STATES OF NEMATODES.

Environmental stress	Quiescent state in response to stress[1]
Desiccation	Anhydrobiosis
Low temperature	Cryobiosis
Osmotic stress	Osmobiosis
Low oxygen	Anoxybiosis

[1] These terms used in response to specific environmental stresses. The terms quiescence (least extreme) and anabiosis (most extreme) refer to the intensity of the quiescent state. Cryptobiosis is a synonym for anabiosis.

Nematodes in anhydrobiosis (including extreme anabiosis) can survive under remarkably severe conditions (Table 2). *Filenchus polyhypnus* (Steiner & Albin) Meyl was revived from a dry herbarium specimen after 39 years (Steiner & Albin 1946). Important observations and insights into the unusual phenomenon of anhydrobiosis have been provided by several reviews (Cooper et al. 1971; Demeure & Freckman 1981; Wharton 1986; Womersley 1987; Barrett 1991). During entry into anhydrobiosis, a gradual water loss occurs over time, as water content falls from 75-80% in active nematodes to 2-5% in anhydrobiotic forms (Demeure & Freckman 1981). Survival is best if nematodes dry slowly; most species are killed if drying occurs too quickly (Barrett 1991; Demeure & Freckman 1981). Anhydrobiotic nematodes will rehydrate in water, but there is a lag time between immersion and their return to normal activity (Barrett 1991). The lag time is normally a few hours, but can vary from less than an hour to several days, increasing with the intensity of anhydrobiosis (Cooper et al. 1971; Wharton 1986; Barrett 1991). Recovery is improved if rehydration is slow, and if nematodes are exposed to high relative humidity before being immersed in water. Repeated cycles of drying and rehydration decrease viability (Barrett 1991).

The mechanisms responsible for anhydrobiosis are not well understood, but decreased cuticular permeability and the condensation or packing together of tissues and organelles are often observed, and in some species, increased levels of glycerol or trehalose are noted (Demeure & Freckman 1981; Wharton 1986; Womersley 1987; Barrett 1991). Coiling is a typical behavioral response observed in anhydrobiotic nematodes, and in most anabiotic forms since they enter anabiosis through anhydrobiosis. However, the behaviorial response seems to depend on the factor inducing anabiosis, since *Aphelenchus avenae* Bastian coils in response to drying but relaxes in a straight position in response to low O_2 (Cooper et al. 1971).

Many of the extreme examples of anhydrobiosis (Table 1) are foliar nematodes that venture above ground or bacterivorous and fungivorous nematodes from dry soils. But anhydrobiosis is probably common in many types of nematodes, including plant parasites living in soil (Womersley 1987), entomopathogenic nematodes (Womersley 1990), and possibly even freshwater forms inhabiting temporary ponds (Wharton 1986; Womers-

TABLE 2. EXAMPLES OF NEMATODE SURVIVAL AFTER LENGTHY TIME IN ANHYDROBIOSIS.

Nematode	Normal active habits	Anhydrobiosis conditions[1]	Time in anhydrobiosis	Reference
Anguina agrostis	Foliar plant parasite	Dried plant material	4 yr	Fielding 1951
A. tritici	Foliar plant parasite	Dried plant material	9-30 yr	Fielding 1951
Ditylenchus dipsaci	Foliar plant parasite	Dried plant material	16-23 yr	Fielding 1951
D. dipsaci	Foliar plant parasite	-80°C	5 yr	Cooper et al. 1971
Filenchus polyhypnus	Foliar in moss	Dried plant material	39 yr	Steiner & Albin 1946
Acrobeloides nanus	Bacterivore in soil	Dry soil	6.5 yr	Nicholas & Stewart 1989
Panagrolaimus sp.	Bacterivore in soil	Dry soil	8.7 yr	Aroian et al. 1993
Plectus sp.	Bacterivore in soil	-190°C	125 hr	Cooper et al. 1971
Plectus sp.	Bacterivore in soil	-270°C	8 hr	Cooper et al. 1971
Dorylaimus keilini	Freshwater nematode	Dry mud	10 yr	Cooper et al. 1971
Helicotylenchus dihystera	Plant parasite in soil	Dry soil	250 d	Aroian et al. 1993
Pratylenchus penetrans	Plant parasite in soil, roots	Dry soil	770 d	Townshend 1984

[1]Most at room temperature except as noted. Subzero exposures in laboratory, free of dry plant material or soil.

ley & Ching 1989). Plant-parasitic nematodes living in soil or roots, such as *Rotylenchulus reniformis* Linford & Oliveira or *Pratylenchus penetrans* (Cobb) Filipjev & Schuurmans Stekhoven, are able to undergo rather extreme states of anhydrobiosis, but in general are not considered as successful at this strategy (e.g., less extreme anhydrobiosis, shorter time in anhydrobiosis) as some of the more extreme examples such as *D. dipsaci* (Townshend 1984; Womersley & Ching 1989), and their long-term survival under anhydrobiosis is lower (Wharton 1986).

CONCLUSIONS

Varying degrees of quiescence, particularly anhydrobiosis, enable nematodes to survive a variety of extreme conditions, including desert soils (Freckman et al. 1977), Antarctic climates (Pickup & Rothery 1991), dry fallow soils without hosts (Womersley & Ching 1989), or dispersal in dry seed, plant debris, or dust (Barrett 1991). The phenomenon may be more common in nature than formerly thought, if we consider that many common soil nematodes may use this strategy to some extent (Womersley 1987). In the plant parasite *P. penetrans*, for example, 22-31% of the population was in an anhydrobiotic state in soils dried quickly, while 58-70% of the population was in anhydrobiosis in soils dried slowly (Townshend 1984). It is likely that substantial portions of a nematode population in soil may be overlooked, since commonly used methods for extracting nematodes from soil may miss anhydrobiotic forms (McSorley 1987), for which specialized extraction methods are required (Freckman et al. 1977). Extreme states of anhydrobiosis appear to be more common in nematodes in water-stressed environments such as drying, above-ground plant parts, but nematodes active at the soil-air interface are also vulnerable to desiccation and would benefit from such strategies (Womersley 1987). The fungivorous genus *Aphelenchoides* comprised 65-75% of the nematode fauna in pine litter in Florida (McSorley 1993), and the capability of *Aphelenchoides* spp. and the closely related *Aphelenchus* spp. for anhydrobiosis is well known (Demeure & Freckman 1981; Wharton 1986). The bacterivores and fungivores living in litter environments are relatively unstudied compared to economically important plant parasites. However, it is possible that anhydrobiosis is a common phenomenon and that a high proportion of the nematode population may be in an anhydrobiotic state in extreme environments such as those at the soil-air interface, litter, above ground, or in very cold or dry climates. Anhydrobiosis is fairly typical among Antarctic nematodes, for example (Pickup & Rothery 1991; Wharton & Barclay 1993). Our ability to investigate and understand nematode ecology in these environments will remain limited unless the anhydrobiotic portion of the community is considered. Studies of such marginal and stressful environments have and will continue to yield more information on anhydrobiosis and other nematode survival strategies.

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