

BIOLOGY AND MANAGEMENT OF
SOYBEAN CYST NEMATODE

SECOND EDITION

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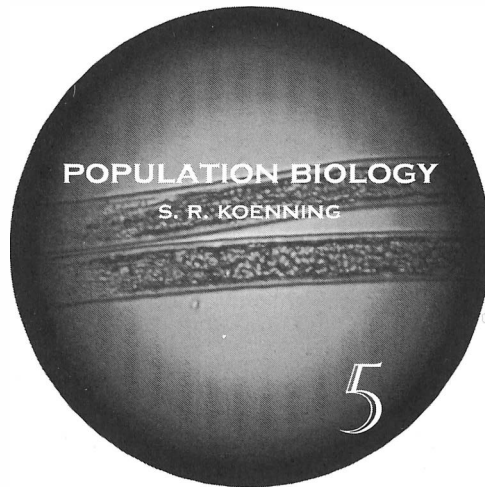
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Predicting the behavior of soybean cyst nematode, or any other nematode, is a challenge and will continue to be so. For predictions to be successful, a detailed, factual database about the organism and a sound synthesis and interpretation of that data is required. Developing technologies in statistics, ecology and molecular biology will be helpful tools for nematologists who attempt to unravel the factors governing populations of soybean cyst nematode.

Cyst nematodes, in general, and certain species in particular, exhibit a high level of specialization for a parasitic life style. Some of the specialization includes: a narrow host range, variation in virulence, synchronization of host and parasite-life cycle and the evolution of strategies for survival. Adaptations for survival, such as the cyst stage and diapause, have allowed this nematode to spread to many diverse habitats.

In 1978, D. C. Norton posed the question, “when we speak of a population, what do we mean?”, in his book “Ecology of Plant-

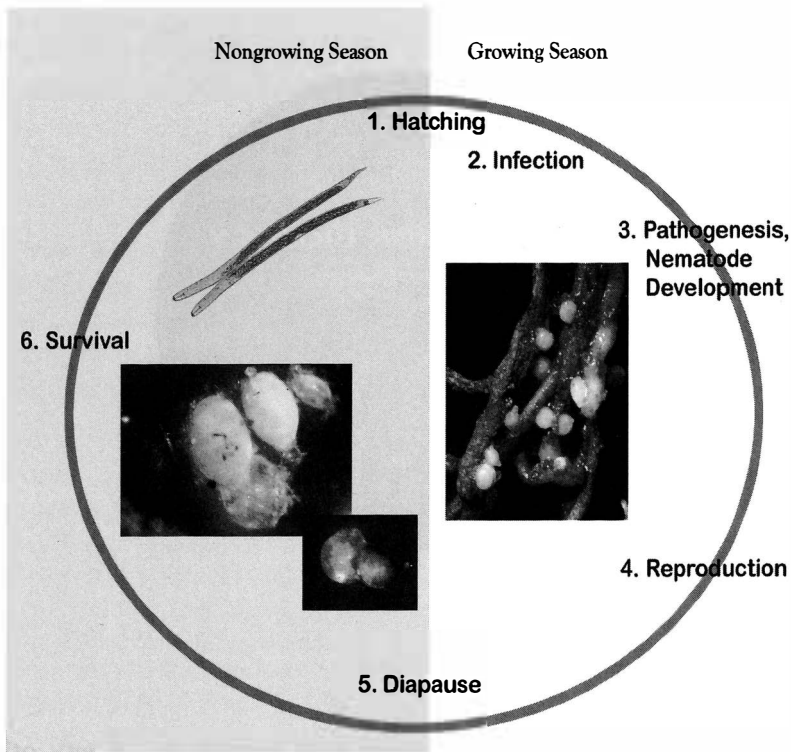


Figure 1. Key aspects in the life cycle of soybean cyst nematode.

Parasitic Nematodes”. The same question applies to population biology. When speaking of population biology, what is meant? In this chapter, population biology of the soybean cyst nematode will be restricted to factors affecting its life stages, including development and survival (Fig. 1).

LIFE HISTORY

Life cycle

The life cycle of soybean cyst nematode has the typical developmental stages exhibited by most plant-parasitic nematodes. This

Table 1. Life history of soybean cyst nematode. (Source: Lauritis *et al.*, 1983.)

Days after inoculation	Male	Female
0-1	Penetration	Penetration
1-3	Second-stage juvenile	Second-stage juvenile
3-4	Second molt	Second molt
4-5	Third-stage juvenile	Third-stage juvenile
5-6	Sexual differentiation	Sexual differentiation
6-7	Third molt	Third molt
7-8	Fourth-stage juvenile	Fourth-stage juvenile
8-9	Fourth molt	Fourth-stage juvenile
9-10	Ensheathed adult	Fourth molt
10-11	Ensheathed adult	Adult with sac formation
11-12	Exsheathing	Adult with sac formation
12	Mating	Mating
12-17	Free adult	Embryogenesis
17-18	Free adult	First-stage juvenile
18-19	Free adult	First molt
19-21	Free adult	Second-stage juvenile in egg
21-22	Free adult	Hatching

cycle has been characterized in monoxenic culture on soybean roots at 25°C (Lauritis *et al.*, 1983) (Table 1). Upon fertilization of eggs by males, embryogenesis proceeds to the first-stage juvenile, which molts to form the second-stage juvenile. The juvenile then hatches and infects a host-plant root to establish a feeding site. Postembryonic development continues with three additional molts before adulthood is reached and reproduction occurs. Each stage of development to reproductive maturity is described in greater detail in the following sections. Although many references are to other species of *Heterodera* or *Globodera*, development of soybean cyst nematode is assumed to be the same for all nematodes within these taxa.

Oogenesis and embryogenesis

Most of the oogonial divisions in soybean cyst nematode are completed in the fourth-stage juvenile and the fourth molt (Triantaphyllou and Hirschmann, 1962). Very few divisions of the oogonia occur in the adult female. In young, recently molted adult females, the oogonia move from the germinal zone of the ovary to the growth zone where they become oocytes. The oocytes, arranged in a single row in the growth zone, are fully grown at this point. The first division of the oocytes will occur as they approach the oviduct. The oocytes then migrate through the spermatheca, and while migrating, one spermatozoan enters at one pole of each oocyte. The sperm and egg pronuclei fuse to form a zygote. The first cleavage of the zygote nucleus then follows. The second cleavage division is not simultaneous in the two daughter cells (Triantaphyllou and Hirschmann, 1962). Cell differentiation continues with organ formation occurring during the later stages of embryogenesis and ends with the production of a first-stage juvenile (Wood, 1988).

The first-stage juvenile has fully formed exoskeleton (or cuticle), somatic musculature, digestive, nervous and excretory systems (Wood, 1988). The cell number is fixed at this stage, except for new cells associated with reproduction. The reproductive system is the only system that remains to be developed after embryogenesis (Hirschmann, 1971), although the organism grows in size. Growth is enabled by molts, the first of which occurs within the egg yielding a second-stage juvenile. This juvenile is developmentally prepared for hatching and emergence from the cyst and/or egg mass.

Hatching

Hatching of soybean cyst nematode involves a complex array of ecological adaptations. Some eggs hatch soon after they are pro-

duced and provide the inoculum for the current year. Most of these are from the egg sac (gelatinous matrix) and they hatch at a higher rate than those from the cyst (Ishibashi *et al.*, 1973; Thompson and Tylka, 1997). On the other hand, hatching of juveniles from eggs within cysts may be delayed for months or several years due to inhibitors in the cyst wall (Okada, 1972) or diapause (Evans, 1987; Ross, 1963; Slack *et al.*, 1972).

Diapause is an important aspect of the population biology of soybean cyst nematode as it facilitates survival under adverse conditions and limits physiological activity in the absence of a host (Clarke and Perry, 1977; Koenning and Sipes, 1998; Yen *et al.*, 1995). It is induced by soil temperature and may be influenced by host phenology (Hill and Schmitt, 1989). It may also be time mediated (Yen *et al.*, 1995). Diapause begins with a reduction in hatching during mid-summer in central Missouri (Yen *et al.*, 1995) and late fall in North Carolina when soils temperatures fall below 22°C (Hill and Schmitt, 1989; Ross, 1963). This temperature mediated dormancy is broken in the spring. Hatching of juveniles from eggs in Missouri and North Carolina remains low until May or June (Koenning and Anand, 1991; Koenning and Schmitt, 1985; Yen *et al.*, 1995).

Although hatching of some eggs occurs without stimulants present in exudates from host roots, hatching is stimulated by the secretions from the plant (Clark and Perry, 1977; Evans, 1987; Koenning and Sipes, 1998; Sharma and Sharma, 1998). The effects of these stimulants vary by plant age and cultivar. Root diffusates from younger vegetative soybeans are generally more stimulatory than those from older plants (Hill and Schmitt, 1989; Sikora and Noel, 1996; Teft and Bone, 1985; Yen *et al.*, 1995). Apparently, soybean cultivars vary in the production of a hatching factor, either in concentration or type of factor, since the amount of hatching differs with cultivars (Schmitt and Riggs, 1991; Sikora and Noel, 1996).

Some insight has been gained about factors that stimulate hatching of soybean cyst nematode. Glycinoeclepin A, a hatching

factor isolated from roots of kidney beans, shows striking activity in stimulating hatching of soybean cyst nematode at very low concentrations (Fukuzawa *et al.*, 1985; Masamune *et al.*, 1982). Egg hatching is also known to be a zinc-mediated process (Teft and Bone, 1984). A gene possibly involved in the regulation of egg hatching in soybean cyst nematode is homologous to *hch-1* (Bolla and Kay, 1997). This gene encodes products involved in regulation of hatching and specific cell movement during embryogenesis in *Caenorhabditis elegans* (Sharma and Sharma, 1998) and may behave similarly in soybean cyst nematode.

Environmental factors also affect the amount of hatching. Among the multitude of edaphic factors that are believed to alter hatching rates, water and oxygen concentration in the soil surely have a major influence on the hatching of soybean cyst nematode eggs. This conclusion is based on the changes observed in the hatching behavior of sugar beet cyst nematode (Wallace, 1955). For example, hatching of this latter nematode in three grades of sand was greatest at or near field capacity (-33 kPa). When the soil medium was saturated (water tension less than -33 kPa), hatching was inhibited. Evidently, under saturated conditions, hatching is inhibited by a lack of oxygen, whereas dry conditions prevent hatching because of limited water availability (Koenning and Sipes, 1998). Further support of the soil-water relationship to hatching of eggs comes from Wallace (1956) and Clarke *et al.* (1978). They demonstrated that solutions of organic or inorganic materials that inhibit the uptake of water by eggs and juveniles of sugar beet cyst nematode or golden potato cyst nematode would prevent hatching. The role of water may be related to oxygen since the greatest amount of hatching occurred at soil moisture tensions with high oxygen content. Since oxygen consumption of golden potato cyst nematode increased prior to hatching (Atkinson and Ballantyne, 1977), the oxygen content around the nematode would presumably be critical for the hatching process.

Hatching (eclosion), aided by enzymatic activity that softens the eggshell (Perry and Clarke, 1981), will occur at temperatures

from 16°C to 36°C (Slack and Hamblen, 1961). The softened eggshell is punctured with the stylet, creating a slit through which it emerges from the egg (Doncaster and Shepherd, 1967).

Movement to the penetration site

Upon hatching, the parasitic life phase of the soybean cyst nematode must be initiated for its continued existence. During the interval between hatching and penetration of a root, the juvenile is exposed to the soil environment. Its success in getting to the root depends on how effectively it moves from the site of hatching to the site of the root where it will penetrate. Some environmental resistance factors to movement include various attractants, soil physical factors, soil water content and oxygen.

Attraction of motile second-stage juveniles to host roots may involve carbon dioxide gradients, thermal gradients or host leachates (Dusenbery, 1987; von Mende *et al.*, 1998). Soybean cyst nematode is attracted to soybean leachates (Papademetriou and Bone, 1983). While specific products of the host root system are surely among the most important stimuli for their movement and attraction to a host, there are other factors that may serve to orient the juvenile to specific sites on the root. Such factors could be gradients in sugars, pH and amino acids. Second-stage juveniles of sugar beet cyst nematode are attracted by carbon dioxide (Johnson and Viglierchio, 1961). Juveniles of golden potato cyst nematode respond to thermal gradients (Rode, 1962). Even though experiments designed to critically test and evaluate nematode attraction to hosts have been scarce in recent years, information about nematode nervous systems and chemoreception is becoming available (Dusenbery, 1987; Perry, 1996) and may provide insight into this area of nematode biology.

The principal physical characteristic of soil that affects the juvenile's ability to migrate is pore space. The pore has to be large enough for the nematode to move through it but not so large that

it does not have leverage. Soils with a pore space provided by particles ranging from 150-250 μm in diameter resulted in the best movement of the sugar beet cyst nematode (Wallace, 1958). This soil condition should be the same for movement of second-stage juveniles of soybean cyst nematode since they are similar in size to those of sugar beet cyst nematode. In addition to soil particle size, aggregation of soil particles also affects pore spaces that may influence migration.

Water is an important medium for the active migration of the second-stage juveniles in the soil. The optimal soil moisture content for movement of golden potato cyst nematode in several soils was approximately field capacity (-33 kPa). Since reproductive behavior of soybean cyst nematode was favored at moisture levels slightly below field capacity (Young, 1992) and because this species is similar in size to golden potato cyst nematode, the movement behavior of the two species should be similar.

Penetration of the root and nematode development

The individuals that successfully make contact with a host root penetrate it and initiate the formation of a feeding site (syncytium) (Ross, 1958). Syncytia usually forms in the stele, but with high moisture levels, it may be formed in the cortex (See Chapter 6). Syncytia are transfer cells that sustain the now sedentary life style of the nematode as its body swells and develops to reproductive maturity. Their development involves signal exchanges between the nematode and the plant cells (Hussey and Grundler, 1998).

In a compatible host (susceptible plant), the nematode swells and loses its mobility (Acedo *et al.*, 1984; Kim *et al.*, 1987). With incompatibility (resistant soybean), the plant will fail to form a functional syncytium. If the juvenile is still vermiform, it may exit and penetrate another root or a different point on the same root. In some resistant hosts, the juvenile may die.

After the nematode has successfully incited the formation of the

syncytium and begun to feed, development proceeds with the formation of the next two juveniles stages (third and fourth) (Lauritis *et al.*, 1983). The third juvenile stage lasts 48-hours or less. Likewise, the fourth-stage is brief, lasting about 24-hours for the male and approximately 48-hours for the female. It is during the third-stage that sexual differentiation is detectible. The genital primordium begins to divide and elongate. Males have a single unbranched primordium, whereas females have a branched primordium that will form the two ovaries (Raski, 1950). By the fourth-stage, males become vermiform and are coiled within the fourth-stage cuticle; females continue to swell. Males exsheath the fourth-stage juvenile cuticle, exit the roots and seek sedentary females for copulation. Spermatogenesis occurs in the adult male testis and several thousand sperm are produced (Shepherd and Clark, 1983).

The mature lemon-shaped female ruptures the root epidermis with her posterior end, exposing her vulva to the rhizosphere, facilitating mating (Raski, 1950). The female is white at this time and receptive to copulation. Females appear to remain in this receptive state for a long period, at least for 2 months if they are not inseminated (Triantaphyllou and Hirschmann, 1962). After insemination, females begin to produce fertilized eggs. Some of the eggs are deposited in a gelatinous matrix and others retained inside her body (Niblack and Karr, 1994). The female body wall eventually senescences and tans to become the cyst. This cyst provides some protection from desiccation and predation by soil microorganisms (Ishibashi *et al.*, 1973). Some eggs in cysts survive at least nine years (Inagaki and Tsutsumi, 1971; R. D. Riggs, personal communication).

Because the soybean cyst nematode is a poikilothermic organism, embryogenesis and post-infection development are influenced by temperature. The rate of egg development is linear between 15°C and 30°C (Alston and Schmitt, 1988). The thermal optimum for development (that which minimizes mortality while maximizing rate of development) is 25°C (Alston and Schmitt,

1988; Ross, 1964). High and low temperature extremes are lethal, although the second-stage juveniles in cysts are resistant to low temperatures (Alston and Schmitt, 1988; Ross, 1964). The time to complete the life cycle of a cyst nematode will vary depending upon the temperature at which the nematode lives. At 25°C, it takes 21 days for soybean cyst nematode to develop into egg laying adults after it hatches (Lauritis *et al.*, 1983). Under field conditions with a range of soil temperatures, adults were observed as soon as 14-days (D. P. Schmitt, personal communication) and as late as 28-days after soybean planting (Alston and Schmitt, 1988).

Reproduction and mating

Sexual reproduction (amphimixis) is required for the production of fertile eggs (Triantaphyllou and Hirschmann, 1964). Without fertilization, oocytes will not develop beyond metaphase I, nor will eggshells be formed (Triantaphyllou and Hirschmann, 1962). Males are attracted to female produced sex pheromones (Perry and Aumann, 1998), such as vanillic acid (Jaffe *et al.*, 1989). The copulation process begins with the male coiling around the female, ultimately inseminating her. During copulation, sufficient sperm are ejaculated into the female to fertilize all oocytes that she has produced.

The mating behavior in soybean cyst nematode is sure to have an affect on gene flow in the population. A given female may mate with one or more males, some being sibling-matings (Triantaphyllou and Esbenshade, 1990). In the case of multiple matings, most of the matings probably occur within 24-hours and are not random (Triantaphyllou and Esbenshade, 1990). Males are not likely to move long distances, increasing the probability of sibling-matings and half-sibling matings. This inbreeding serves to fix alleles and decrease the proportion of heterozygotes in the population. Although inbreeding is deleterious in many organisms, soybean cyst nematode is adapted to and tolerant of inbreeding, as

demonstrated by little change in its reproduction on several soybean lines (Luedders, 1985).

Egg production depends upon several factors including host nutrition, host status and environment. Although under optimal conditions, an individual female can produce up to 600 eggs (Sipes *et al.*, 1992), the average number actually developed per female in the field is much less. The mean number of eggs per female from field samples tended to be near 100 in North Carolina (D. P. Schmitt, personal communication), near 200 in Missouri and about 65 in Tennessee (P. Donald, personal communication).

Sex in soybean cyst nematode is genetically determined and is not altered by embryological or post-embryological factors (Goldstein, 1981; Triantaphyllou, 1971). The ratio of males to females is approximately 1:1. Variations from this equal ratio occur when there is differential death of one sex. If males are more abundant, females have probably failed to develop because of stressful conditions such as over-crowding, water-stress or resistant host plants (Koliopanos and Triantaphyllou, 1972). Males develop in such situations because they require less time (9-days) and nutrients to reach adulthood than females (11-days) (Lauritis *et al.*, 1983). Furthermore, females must continue to feed after maturation, placing additional nutritional demands upon the host and therefore, they are more likely to die under stress than males. It is common, however, to find many females and cysts, but few males, in soil samples collected from the field. In this situation, the females are assumed to survive longer than males.

FUTURE DIRECTIONS IN POPULATION BIOLOGY

Advances in population biology will depend on knowledge gained through the study of fundamental ecological processes that link individuals, populations and whole communities of plants, animals and microorganisms. The ultimate goal is to apply this knowledge to management of soybean cyst nematode with a concomitant

rational management of the environment.

Molecular techniques and computer enhancement technology will undoubtedly aid in advancing our understanding of the population biology of soybean cyst nematode. Certainly, the new knowledge garnered through molecular analysis of the host-parasite relationships will provide new insights and tools for management of these parasites. Molecular tools, improved methods for culturing, greater power of computerized statistics for ecology and improvements in microscopy may permit us to more fully comprehend the genetics, population ecology and other aspects of cyst nematode biology that are, at present, beyond human understanding. Ultimately, the field of biology will be enriched and our ability to manage this parasite and its negative impacts on soybean will be improved.

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