

Adaptive biology of plant-parasitic nematodes-a review

Abstract:

Nematodes are highly diverse group of organisms in many ecosystems. The biology of nematodes is a sum total of adaptations in relation to the host and the environment. Nematodes show a variety of adaptations throughout their life-cycle. Under adverse condition such as extreme temperature, lack of oxygen, lack of food, crowded population, they adopted some mechanism which is known as adaptive mechanism. Some physiological or behavioral responses allow nematodes to react more quickly to environmental stresses. The degree of dormancy or hypobiosis observed among nematodes varies along a continuum from mild quiescence to anabiosis, depending on the nematode species involved and even within the same species.

Keywords: Adaptive biology, life-cycle of plant parasitic nematodes, Dormancy, Diapause, Survival.

1. Introduction

Nematodes also referred to as roundworms, play an important role in many ecosystems. Nematodes can be subdivided based on their trophic behavior as free-living, obligate parasitic and facultative parasite. Obligate parasitic nematodes feed on plant, invertebrate or vertebrate hosts. Facultative parasitic nematodes are usually more flexible in their food source; in a free-living cycle they feed on microbes, whereas in a parasitic cycle they parasitize a host organism. Plant-parasitic nematodes are obligate, biotrophic pathogens of many plant species. In agriculture, plant-parasitic nematodes cause estimated annual global economic losses of USD 173 billion (Elling, 2013). They cause dramatic changes in the morphology and physiology of their host and effect on the yield. Nematodes have a similar basic pattern of life cycle that consist six stages, viz., egg, J₁, J₂, J₃, J₄ (with a moult between each stage) and adult. For their growth, development and reproduction require a favorable environment. The different stages of the life cycle are adapted for survival under unfavorable environmental conditions as occur in their natural habitats. A moisture film is necessary for normal activity and therefore soil moisture, relative humidity, and related environmental factors directly affect nematode survival. The soil environment offers varying degrees of protection for nematodes. Parasites that are inside plant roots enjoy optimal moisture and protection from desiccation as long as the health of the hosts persists. Life stages or species that do not live inside a host find protection in moist soil, but in dried soil risk increases. Risk may increase further in some nematode such as *Ditylenchus*, *Anguina*, and *Aphelenchoides* spp. as they climb to infect aerial plant parts. These microscopic round worms are widely distributed even in extreme [environmentenvironments](#) where water availability is limited. Survival strategies enable nematodes to persist in soil where their activity may be limited. To overcome unfavorable environmental conditions during growth and development, a resting stage have evolved by depressing their metabolic activity in the life cycle of many nematodes. Nematode with different mode of parasitism has to live in discontinuous environment. The instability of their environment increases with increasing host specificity. ~~Thus~~ Thus, the adaptive biological features are among the factors responsible for the diversity in simplicity and numerical abundance of nematodes on earth. Understanding the nematode ecology

in terms of adaptation will help in implementation of management packages in the field situation. Their diverse morphological, physiological, and behavioral adaptations enable them to thrive in various environments by evading predators, utilizing a multitude of food sources, and withstanding environmental stress. The absence of food resources, temperature, humidity and soil oxygenation ~~is considered to be~~ is the main limiting factor of nematode survivorship (McSorley, 2003). In addition, the biotic environment may modify nematode survivorship. The effect of environmental conditions on the development and survival of parasitic nematodes varies depending on stage-specific adaptations of eggs and/or larval stages and their interactions with intermediate hosts and the environment (Molnár et al., 2013).

2. Life cycle of plant-parasitic nematodes

Plant-parasitic nematodes basically have separate male and female sexes and reproduction is amphimictic. However, reproduction may be mitotic or meiotic parthenogenesis or may be hermaphroditism. The eggs are deposited singly or into a gelatinous egg matrix into the soil or on the surface or within the host tissue, or retained inside the female nematode body. After embryogenesis, the first stage juvenile (J1) is formed which is similar to the other stages in general morphology. The J1 is ready to hatch out of the egg in adenophoreans, but in secernentians the first moult occurs within the egg and the J2 hatches out of the egg shell either simply or in the presence of specific host root diffusate. The second, third and fourth moults occur each time giving rise to a fresh cuticle to cover the body of the J₃, J₄ and adult stages that are formed. The sexes can be differentiated by observing the genital primordium in the J₂ or J₃, but the fully developed sex organs are visible only in the adults. In stressful environment many nematodes can undergo various adaptive mechanisms to ensure survival of the current or subsequent generation.

3. Plant-parasitic nematodes' adaptation mechanisms

(A). Behavioral and physiological strategies: PPNs use a combination of behavioral and physiological strategies to survive, such as coiled or shrunken body or clumping, injecting effectors into the host's tissues or sucking food from the host. A coiled or shrunken body, with a reduced surface area exposed to the environment is better adapted to reduce the rate of water loss and it may also be useful in avoiding predators and wounding of the body. Coiling has been observed in *Pratylenchus penetrans* (Townshend 1984) and *P. thornei* (Glazer and Orion 1983). Shrinking is a reversible process, leading to a controlled narrowing of the grooves between the transverse annulations in *Rotylenchus robustus* (Rössner and Perry, 1975). Individuals of some nematode species mass together to form large aggregations or clump. Clumping and sticking together conserves water, and is used by many nematode species to aid survival in dry conditions. All stages of the life cycle of *D. myceliophagus* could survive for 3 to 4 years in dried aggregations ('curds') (Grewal, 1993), the 4th stage juveniles of *D. dipsaci* were found in dry aggregations ('eelworm wool') surviving for at least 23 years (Fielding, 1951). Both J₃ and J₄ of *D. dipsaci* showed evidence of an intrinsic ability to control water loss. The nematode clumps may be so large so large that they are visible to the naked eye as whitish masses as 'nema wool' which offer some protection against desiccation with morphological adaptation as coiling. Increasing parasitic specialization is related to the oesophageal gland development and establishment of modified cellular or syncytial feeding sites leads to morphological changes in feeding site. Endoparasitic nematodes establish their feeding site in the host tissue where from they take nutrients. *Meloidogyne* spp. produce giant cell, *Heterodera* spp. produce syncytia and *Tylenchulus semipenetrans* produce nurse cell in the root tissue.

(B).Morphological adaptations viz., specialized cuticle, modification of feeding structure, metacarpus and posterior oesophageal glands, sexual dimorphy etc. Specialized cuticle (*Hemicycliophora arenaria*) retains extracuticle. Some of the dauer larvae form second cuticle layer to protect them from stress environment. Many of the plant-parasitic nematodes have different structures of feeding apparatus as per mode of parasitism, include a hollow, protrusible stylet (feeding spear) connected to three esophageal gland cells that express products secreted into plant tissues through the stylet. In anhydrobiotic *Anguinatritici*, the composition of external cortical layer and spatial arrangement of the muscle filaments are different from the active form. Similarly, anhydrobiotic *A. agrostis* J2 were longer and thicker cuticle and showed differences in the shape of the lateral alae (Bird and Stynes, 1981). The desiccated J2 of *Ditylenchus dipsaci* reduced thickness of various layers of the cuticle (Wharton et al., 1985). *Meloidoderacharis* developed an extracuticular subcrystalline layer to aid in survival during desiccation (Demeure and Freckman, 1981).

(C).Egg production: In stressful environments like high population, lack of oxygen, lack of food, nematode produces mass of egg. A low survival rate or the difficulty in reaching the host is compensated by large number of eggs. *Meloidogyne* sp. produce 100-500 eggs per female, survival rates relatively high, varying from 20 to 80%. *Rotylenchulus reniformis* has a high reproductive rate combined with a very low survival rate. On good hosts female can lay 75-120 eggs per day. The immature ~~proceed~~proceeds through molts without feeding. This expenditure of energy may be a contributing factor to low survival.

(D).Protective site: Some nematode species use the previous juvenile cuticles, the gelatinous matrix or the female body as aids to reduce water loss. Egg matrix produced by rectal gland in *Meloidogyne* spp., *Heterodera* spp., *Rotylenchulus* spp., and excretory pore in *Tylenchulus semipenetrans*. *M. javanica* egg masses had no water retention properties; on drying, the gelatinous matrix exerted a mechanical pressure on the enclosed eggs which inhibited water uptake by the eggs thus preventing hatching. Formation of protective cyst from dead female hard cuticle in heteroderids in which dormant juveniles remain inside for many years. Some nematode ~~induce~~induces the host plant to produce protective gall from floral parts by *Anguinasp.* and vegetative parts produced by *Fergusobiasp.* The strategy adopted in each case depends on the mode of life of the species and on the hazards it is faced with.

(E).Migratory response: PPNs can move away from stressful conditions to a more favorable environment. There are multiple means of active and passive dispersal. Dispersal of inseminated females in many amphimictic nematodes, e.g. *Tylenchorhynchus* spp., *Hoplolaimus* spp. In case of passive dispersal, use of other animals in dispersal, e.g. *Rhadinaphelenchus cocophilus* using the palm weevil, *Rhynchophorus palmarum* and *Bursaphelenchus xylophilus* using the cerambycid beetle, *Monochamus alternatus*. Similarly, *Fergusobiasp.* having two separate life cycles, one as an insect parasite in gall fly, *Fergusoniasp.* and the other as a plant parasite in plant shoot galls. Swarming refers to large coordinated population movements of nematode is believed to function in dispersal and migration.

(F).Timing mechanism: PPNs can synchronize their life-cycle with their host to avoid stressful conditions. Some plant-parasitic nematodes like *A. besseyi* and *R. cocophilus* can complete life-cycle in 11-13 days and 9-10 days, respectively. There seem to be a correlation between the duration of life cycle and environmental stability, i.e. those occurring in an unstable environment have a shorter life-cycle than those in a more stable ecosystem. Moreover, there is a tendency to shorten intermediate moulting periods, e.g., in more specialized parasites like *Meloidogyne* spp.

where J2 is the infective stage, the J3 and J4 stages are completed in a very short period and without feeding.

(G).Changing sex ratios: Changing sex ratios can improve the survival chances of the next generation. Sex ratios are environmentally determined in many nematodes including amphimictic species and parthenogenetic species. In root-knot nematode, 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, but in some instances may comprise more than 60% of the population. A variety of stresses, viz., 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 may lead to increased production of male. If stress is imposed during development, second-stage juveniles developing as females can undergo sex reversal, producing intersexes or males. 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).

(H).Mode of reproduction: Parthenogenesis is a reproduction process where males are not involved. Many nematodes can reproduce by meiotic, facultative meiotic, or mitotic parthenogenesis, so that when isolated in very small numbers, even a single parthenogenetic disseminule can establish a population. Endoparasitic nematodes, *Meloidogyne* spp. and *Heterodera* spp. can reproduce by parthenogenetically. Their males are not plant parasitic, so they come out from root and live as a free living. Parthenogenesis can lead to polyploidy and thus different phenotypes and eventually even different species evolved e.g., *H.trifolii* is a parthenogenetic triploid of *H.schachtii*.

(I).Capacity adaptation: Plant parasitic nematodes can adapt to adverse conditions so that they can grow and reproduce. Some species can use developmental dormancy and diapause to survive seasonally and for long-term longevity. Dormancy is a general term applied to the condition of lowered metabolism and various categories, viz., diapauses, quiescence, cryptobiosis etc. (Evan, 1987).

Diapause: To overcome cyclic (seasonal), long term and extreme environmental conditions, nematodes have evolved a specific stage in their life cycle preconditioned to arrest their development is termed as diapause. Organisms in diapause are dormant according to season, under influence of temperature, and remain in this state for a set time, even if favourable circumstances return (Perry and Moens, 2011). Endogenous factors are responsible for the initiation of the arrest, and a specific signal must act for a minimum period of time on the receptive stage before activity is resumed. It is considered to be a physiological state of dormancy with very specific initiating and inhibiting conditions. Diapause seem to apply mostly to the egg stage and to juvenile stages within eggs in plant-parasitic nematodes. The important factor to break diapauses is temperature, type of host plant, day length at which host is growing, and strain of the nematode parasite. An example of diapause in nematodes is the *Bursaphelenchus xylophilus* dispersal stage J3 and J4 that stay dormant in winter (Wang et al., 2017). Similar features are seen in cyst nematodes of the genera *Globodera* and *Heterodera*; pre-parasitic second stage juveniles (pre-J2) go into a seasonal diapause in winter or summer, while still inside the egg (Banyer and Fisher,

1971; Perry 1989). During diapause *G. rostochiensis* eggs are insensitive to external host cues that otherwise would induce hatching. Once diapause is lifted by the increasing temperatures of spring, they are perceptive to hatching stimuli again (Palomares-Rius et al. 2016). In case of obligate diapause, dormancy is initiated by endogenous factors with delayed resumption of development under favorable conditions after specific requirements are satisfied. 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 overtime. Zheng and Ferris (1991) recognized four types of dormancy in eggs of *Heterodera schachtii*. 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). Diapause might be lifted by a certain temperature sum, i.e. rising spring temperature, 5-10°C require for egg hatching in *Meloidogyne naasi*, 10°C for *H. avenae*, 5°C for *Ditylenchus dipsaci*. In facultative diapauses, dormancy is initiated by environmental factors with delayed resumption of development under favorable conditions, is believed to be initiated by environmental factors which act as signals on the receptive stage and ended by spontaneous endogenous factors acting after a minimum period of time. Species exhibiting facultative diapauses will arrest their development only if environmental conditions become unfavorable, providing the necessary signals to the receptive stage. To be biologically active, diapauses must be initiated and terminated at the right time of the year. Spontaneous factors acting after a minimum period of time will result in the resumption of activity. e.g. Scottish population of *G. rostochiensis* and a French population of *H. avenae* where host root diffusate stimulus aided in the synchronization of the nematode's life-cycle with that of its host.

Quiescence refers to a dormant state in which metabolism and activity are slowed down caused by unfavourable environmental conditions. To overcome unanticipated, non-cyclic deviations of one or more environmental factors (lack of water-anhydrobiosis); high salt concentration (osmobiosis), lack of oxygen (anoxybiosis), low temperature (cryobiosis), high temperature (thermobiosis), most plant parasitic nematodes are believed to react spontaneously by arresting their development. A combination of these factors may act to induce dormancy or quiescence. Quiescence is not associated with a type of morphogenesis and does not affect ontogenic development. During quiescence, somatic development is affected only ~~as a result of~~ [because of](#) slowed metabolic rate (Evans, 1982). The dormant state ends when the environmental stress is relieved, and nematodes then return to normal activity. In facultative quiescence, dormancy under unfavorable conditions with development readily resumed as conditions become favorable. It can occur at any time of the year and may be experienced by some or all the stages in the nematode's life-cycle. It is readily reversible and ends as soon as favourable conditions return. In case of obligate quiescence, is induced by unfavourable environmental conditions acting on a specific stage in the life cycle. To end, it requires specific environmental signals which indicate that favourable conditions have returned. Required dormancy for a life stage with development readily resumed under favorable conditions. The absence of a resting stage in *R. similis* could explain the low survivorship

of this nematode (Gowen et al., 2005). In undisturbed soils, *R. similis* survived longer in dry soils with half-lives 57 days (Christian et al., 2009). *Pratylenchus* species able to survive soil desiccation, and after prolonged storage they are able to successfully reproduce on host plants. *Paratylenchus*, *Helicotylenchus*, *Rotylenchus* and Criconematidae also showed an ability to survive in soil for a shorter period of time.

Cryptobiosis: 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 or cryptobiosis is an ametabolic state of life entered by an organism in response to adverse environmental conditions such as desiccation, freezing, and oxygen deficiency. In the cryptobiotic state, all metabolic processes stop, preventing reproduction, development and repair. An organism in a cryptobiotic state can essentially live indefinitely until environmental conditions return to being hospitable. When this occurs, the organism will return to its metabolic state of life as it was prior to the cryptobiosis. The presence or absence of metabolism as criteria to distinguish cryptobiosis. Nematodes enter a state of cryptobiosis when they lose contact with water or when exposed to other unfavorable environmental conditions accompanied by suspension of all life process for considerable period of time ([reference](#)).

Anhydrobiosis: Anhydrobiosis facilitates survival in some nematode species, and is accompanied by cessation of movement and feeding (Evans and Perry, 1976). is used to refer quiescent and anabiotic states in terms of environmental stress like desiccation. is a process in which an organism becomes almost completely dry and dormant until living conditions improve. During the process, all of the organisms' tissues and cells become stable and they are able to avoid what could be the lethal damage to their bodies caused by the extreme condition. The anhydrobiosis process is a gradual release of the moisture from the nematode body to a level. This process enhances the survival chances of the juveniles for longer duration without a host. An increasing degree of desiccation tolerance is afforded to organisms as they progress from quiescence to cryptobiotic anhydrobiosis. At the extreme end of the continuum, anhydrobiosis is characterized by a radical loss of body water (greater than 99% in some cases) and termination of metabolic activity that is reversed by rehydration (Crowe et al., 1992). 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). Anhydrobiotes are unique in that they are capable of losing essentially all their body water, their metabolism falling to an undetectable level, without apparent damage to their cellular structure. 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 responseobserved in anhydrobiotic nematodes, andin most anabiotic forms since they enter anabiosissthrough anhydrobiosis. However, the behavioralresponse seems to depend on the factor inducinganabiosis, since*Aphelenchusavenae* coils in response to drying but relaxes in a straight positionin response to low O₂(Cooper et al. 1971). Many of the examples of anhydrobiosis are foliar nematodes that ventureabove ground or bacterivorous and fungivorousnematodes from dry soils. But anhydrobiosis isprobably common in many types of nematodes, includingplant parasites living in soil (Womersley,1987), Anhydrobiotic nematodes can revive following exposure to 0% relative humidity and freezing temperature. Anhydrobiotic nematodes are known to survive in this [statestate for](#) 30 years or more (Womersley et al.,1998).Anhydrobiosis is common in plant parasites living in soil or roots, such as *Rotylenchulusreniformisor Pratylenchus penetrans* 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) and their long-term survival under anhydrobiosis is lower (Wharton 1986). The first report of anhydrobiosis was that of *Anguina tritici* on wheat in 1743 by Needham. Anhydrobiosis is a common attribute of nematodes that are successful in habitats that are subject to seasonal drying and to those that feed on the aboveground parts of plants. Fourth stage juveniles of *Ditylenchus dipsaci* enter anhydrobiosis, usually in large masses, on or below the surface of plant tissue. The term ‘eelworm wool’ is coined to describe the appearance of the dried nematodes.The last juvenile stage arrested and showed variation from the normal juveniles.The arrested stage was found to be larger in size with a higher amount of lipid reserves Similarly, the second stage juveniles of *Aphelenchoidesbesseyi* enter anhydrobiosis under rice hulls.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.

Table.1..Anhydrobiotic stages of different nematodes

Nematode Species	Anhydrobiotic stages	Longevity	Reference
<i>Ditylenchus dipsaci</i>	J4	16-23 Year	Fielding, 1951;Perry,1977
<i>Ditylenchus myceliophagus</i>	J4		Perry, 1977
<i>Heteroderaavenae</i>	J2	4.5 Year	Meagher,1974
<i>Anguina tritici</i>	J2	9-30 Year	Fielding,1951
<i>Anguinaagrostis</i>	J2	3-6 Year	Courtney and Howell,1952
<i>Meloidogyne javanica</i>	J2 or egg	6 months	MCSorley,2003
<i>Tylenchulussemipenetrans</i>	J2 or egg	3-10 Years	Baines etal.1959
<i>Hemicycliophora arenaria</i>	Adult	6 months	Gundy et al,1961
<i>Paratylenchus dianthus</i>	J4	5 Years	MCSorley,2003
<i>Helicotylenchusdihystera</i>		250 days	MCSorley,2003
<i>Pratylenchus penetrans</i>		770 days	Townshend,1984

Cryobiosis is a form of dormancy that takes place in low temperature. Cryobiosis initiates when the water surrounding the organism’s cell has been frozen, stopping

molecule mobility and allowing the organism to endure the freezing temperature until more hospitable conditions return. If a nematode is adapted to withstand water shortage, then it is able to survive freezing at least for short periods of time. Some nematodes have been reported to survive after exposure to temperature as low as -196°C . *A. tritici* J2 maintained viability over a range of -190°C to $+105^{\circ}\text{C}$ for short periods of time. Anhydrobiotic *A. avenae* were relatively unaffected by exposure to -196°C for 15 minutes. Low temperature was found to slow down or stop embryonation in *M. naasi* eggs, which resumed normally as soon as the eggs were transferred to 20°C . In contact with water at -20°C , over 50% survival was obtained in unhatched juveniles of *G. rostochiensis*. It is likely that the egg-shell acts by preventing ice seeding across from the medium to the juvenile.

Table.2.. Cryobiosis in plant-parasitic nematodes

Nematode species	Stage	Temperature	Time	Reference
<i>Meloidogyne hapla</i>	J2 or egg	-4°C	10 Days	Vrain et al.,1978
<i>Bursaphelenchus xylophilus</i>	J3	-80°C	30 days	Pan et al.2021
<i>Heterodera tabacum</i>	J2 or egg	-27°C	14 days	Miller,1986

Anerobiosis or anoxybiosis: Activity and development in nematodes require oxygen but some species can survive periods of anoxia in an inactive, anabiotic state. The oxygen tension required for activity may be further reduced by elaborations of the cuticle and by the long body shape of nematodes, which ensure a high surface to volume ratio. Many nematodes are thus able to remain active under relatively low oxygen tensions. Growth and reproduction may be more susceptible to anerobiosis. Flooding may bring about a condition in the soil. *A. avenae* was reported to survive for more than 30 days in anoxybiotic condition. In many *Meloidogyne* species, low oxygen concentrations reduced hatching and suspended embryonic development without killing the eggs.

Osmobiosis occurs in response to increased solute concentration in the solution of the organism. High osmotic pressure results in dehydration of the body. Nematodes may experience high osmotic pressure in drying soils after the application of fertilizers, which may induce them to enter dormancy. High osmotic pressure has been reported to cause suspension of embryonic development and hatch in many *Meloidogyne* species. *M. javanica* J2 became quiescent in 0.3 M NaCl (Reversat, 1981). *Rotylenchus robustus* placed in a solution of 1M glucose were observed to shrink in the same way as the slowly dried specimens (Rossner and Porstendorfer, 1973).

Thermobiosis: High temperature can denature proteins and thus reduce enzyme activity and thus slowed or stop metabolism and ultimately caused death. Most of the nematodes may die at certain higher lethal temperature $30-45^{\circ}\text{C}$, being different in different species and population. However, some species have protein stabilization system while some other produces stress protein or chaperons. As the temperature rises within the higher non lethal zone, the nematode shows uncoordinated movement and further stopped movement. Some nematodes survive at temperature above the heat coma but below the instant lethal temperature. The juveniles of *Anguina* sp. withstand the temperature extremities until it finds the host. Brief heat treatment (46°C for 10 minutes) suppressed embryogenesis and egg hatch in *M. javanica*. Embryonation of *M. naasi* eggs was also slowed down or

stopped at temperature between 25°C and 30°C and resumed at 10°C (Antoniou and Evans, 1987).

Dauer larva: Many nematodes form a temporary stage called a 'dauer stage' 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 and Bird, 1991; Vlaar et al. 2021). They undergo modifications in the cuticle structure to decrease permeability, and some forms retain the cuticle from the previous molt as additional protection (Evans and Perry, 1976). In hypobiosis, 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 are factors that can stimulate formation of dauer larvae. Many of the nematodes that have phoretic relationship with insects are in a dauer stage during the phoresy. The abilities of dauer larvae to resist environmental stress and to recover quickly to normal stages vary from species to species. The J3, J4, or preadult of *D. dipsaci* can control water loss to such an extent that both stages could be considered as forms of dauer larvae.

(K). Biochemical adaptations: Wharton (2004) found no evidence for metabolism of lipid, protein or glycogen in anhydrobiotic *A. tritici* J2. *Aphelenchus avenae* was reported to utilize lipid and glycogen during the induction of anhydrobiosis and to synthesize glycerol and trehalose (Madin and Crowe, 1975). Anhydrobiotic *A. tritici*, *D. dipsaci*, and *D. myceliophagus* also stored trehalose in preference to glycogen and only small amounts of glucose were detected (Womersley and Higa, 1998). High lipid contents in anhydrobiotic nematodes are believed to be essentially used as food reserves although the morphological distribution of such lipids may be important in maintaining the spatial distribution of body tissues in the absence of bulk water (Womersley, 1981). Although organisms appear to lose most of their water during severe periods of desiccation, those capable of anhydrobiotic survival are able to withstand such a loss without structural impairment. *D. dipsaci* juveniles, when desiccated, contain 1-2% water by weight. This water may be sufficient to maintain the structure of macromolecules. Desiccation was found not to result in a significant increase in DNA breaks or in any appreciable denaturation of proteins in this nematode. The adenylate charge was found to be greatly reduced in the desiccated juveniles of *D. dipsaci* but ATP level was found to be present in normal amounts after several hours (Barrett, 1982). *A. avenae* in anoxybiotic condition, glycogen catabolism yielded lactic acid during first phase, while during longer periods ethanol was produced (Cooper and Van Gundy, 1971).

4. Conclusion:

Understanding stage-specific adaptations is the key to understanding the persistence and dynamics of parasites under changing environmental conditions (Brooks et al., 2020). It is believed that nematodes in the desiccated form are more resistant to extremes of many environmental factors, as well as nematicides (Riddle and Bird, 1985). However, dormancy does not always guarantee the survival of the individual, but in most cases, it ensures the survival of the population. Knowledge regarding biology of nematode, especially dormancy is essential for population studies and modeling, and for timing of control measures in the field. Knowledge of the biochemical adaptation might lead to the development of artificial ways of either extending the arrest or breaking it sooner. Similarly, knowing the survival strategies of *R. similis* help banana growers optimize their cropping system by improving the intercrop period, and by evaluating if it can be reduced in length with one year host-free period. 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). Specialized extraction methods are required as substantial portions of anematode population in anhydrobiotic state in soil may be overlooked (Freckman et al. 1977). It has been observed that *Pratylenchus-crenatus*, *P. penetrans* and *P. thornei* can also survive prolonged periods of desiccation and are regulated pests for at least one country globally (Lee et al. 2017) their status as a biosecurity risk is increased. Having a better understanding of plant parasitic nematode survival in soil inadvertently transported with commodities, freight, used machinery or humans (e.g. footwear) is important in the development of both scientifically valid pest risk analysis as well as cost-effective management strategies (McNeill et al. 2017).

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