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Role of Predeceous nematodes in plant disease management

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Abstract

Nematodes inhabit most environments and play a important role in managing plant disease in the form of beneficial nematodes (predeceous nematode and EPNs) due to their cosmopolitan distribution. Predeceous nematode reduce population of plant parasitic nematodes and also release nutrients in plant available forms, which enable plants to better withstand nematode burden on the roots. Biocontrol potential of predatory nematode depends on the rate of predation, prey searching abilities, strike rate, resistance to environmental conditions. The predators feed by puncturing the cuticle of the prey and then sucking its body contents, after penetrating the body of prey the predators move their feeding apparatus sideway. Stylet bearing predators show density dependent predation (Khan *et al.*, 1991) similar to other group of predators. More predator-prey encounters at higher prey densities always result in the increased rate of predation.

Keywords: Feeding behavior, predeceous nematode, phytophagous, omnivores, mycophagous

Introduction

This topic is dealing with role nematodes play in managing plant disease. Nematodes directly do not help in controlling plant diseases instead they help by killing plant parasitic nematodes which are smaller in size. There are a lot number of microorganisms live freely in the soil, including beneficial species of bacteria, fungi, nematodes, and protozoa that make interactions among them. They give contribution to ecosystem with decomposing soil organic matter and mineralizing nutrients that depend on the population size, rate of energy use, and their ability to affect the functioning of the organisms (de Ruyter and Neutel, 1997). Nematodes, microorganisms like-worms that live freely in the soil environment, marine and fresh water, are one of the soil microorganisms which have important role in the soil habitat. In the soil, nematodes have a function to decrease the remains of larger animals and plant tissues (Dropkin, 1980). Nematodes contribute to a variety of functions within the soil system. In agricultural systems, nematodes can enhance nutrient mineralization and act as biological control agents. Based on feeding habits, nematodes, which are recognized as the major consumer group in the soil and can be divided into five categories, namely:

1. Plant-feeding nematodes (root-feeding nematodes; phytophages; plant parasites)
2. Fungal-feeding nematodes (fungivores; mycophages)
3. Bacterial-feeding nematodes (microbivores; bacterivores)
4. Predatory nematodes
5. Omnivorous nematodes (Zunke and Perry 1997; Norton and Niblack 1991; and Ingham 1996) ^[36]

Plant-feeding nematodes which feed on higher plant usually have stylets to suck the nutrients from the plants which have a wide diversity of size and structure. This group of nematodes have an ability to cause plant disease and reduce crop yield (Yeates 1971 in Ingham, 1996) ^[11]. Fungal-feeding nematodes, which feed on fungal mycellium, hyphae, conidia, including plant pathogenic fungi, have "protusible hollow stylets". For example, *Aphelenchus sp.*, *Aphelenchoides hamatus* (Zunke & Perry 1997; Ingham 1996) ^[36]. Bacterial-feeding nematodes which feed on bacteria and other microflora have "a simple, open and unarmed stoma in the form of cylindrical or tringulartube, terminating in a teeth valve-like apparatus" (Nicholas 1975 in Ingham 1996) ^[37]. For example, *Acrobelus spp.* which are mainly live in sandy soil, *Bunonema sp.* which is found in moss, decaying vegetable matter, cow dung and rotting wood of bark beetle tunnels, *Rhabditis sp.*, *Acrobeliodes tricornis*, *Caenorhabditis elegans*, *Panagrolaimus subelongatus* (Zunke & Perry 1997; Laakso & Setala 1999) ^[36, 31].

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Predatory nematodes that feed on other nematodes have “a large stylet or a wide cup-shaped cuticular line stoma armed with powerful teeth” (Nicholas 1975 in Ingham, 1996)^[37]. For instance, *Mononchus spp.*, *Parazercon radiatus*. Omnivorous nematodes feed on algae, bacteria, fungi, protozoas, rotiferas, tardigrads, etc. For instance, *Dorylaimus spp.*, *Lysigamasus lapponicus* which feed on microarthropods (Laakso & Setala, 1999)^[31].

Role of nematodes in plant disease management

There has been widespread interest in using predatory nematodes to control populations of plant parasitic nematodes (Khan and Kim, 2007; Stirling 2014). Yeates and Wardle (1996) introduced the dual function of predation by nematodes: Potential control of plant parasitic nematodes, and their important role in stimulating cycling of plant nutrients, which may enable plants to better withstand any nematode burden on their roots. The majority of predatory nematodes belong to the orders *Mononchida*, *Dorylaimida*, *Diplogasterida* and *Aphelenchida* and super families, Actinolaimoidea, Dorylaimoidea, Nygolaimoidea and families Ironidae, Monhystridae, Oncholaimidae and Thalassogeneridae etc. The commonly occurring mononchids feed extensively, though not exclusively, on plant parasitic. They may swallow their prey whole if it is of smaller size, or at times feed by cutting larger prey into pieces. Significant reductions in the population densities of potato cyst nematode, *Globodera rostochiensis* and root-knot nematode, *Meloidogyne incognita* in the presence of a mononchid predatory nematode, *Prionchulus punctatus*, have been reported. Predator-prey relationship existed between plant parasitic nematodes, *Tylenchulus semipenetrans* and *Helicotylenchus dihystra* with mononchid predator, *Iotonchus tenuicaudatus* in mandarin orange orchards. These reports indicated that mononchids are providing natural control of plant parasitic nematodes in soil. If their population can be manipulated in the field then they can be used as successful biocontrol candidates.

Dorylaimids possess a hollow stylet, properly called as odontostyle with which they puncture the prey organisms suck food. The most advantageous and encouraging aspect of dorylaimids is that it is easy to maintain their populations simply by adding organic matter to agricultural fields. The diplogasterid predators possess a small buccal cavity which armed with a dorsal tooth. They feed on nematodes, bacteria and other soil microorganisms. Diplogasterids are generally found abundantly in decomposing organic manure. They are the most readily cultured nematodes, being easily maintained on simple nutrient media containing bacteria. Fauzia *et al.* (1998)^[23] demonstrated the ability of *Mononchoides longicaudatus* to reduce root galling by root-knot nematodes, resulting in improved vegetative growth and increased root mass. Further Khan and Kim (2005)^[7] reported that a pre-planting application of *M. fortidens* in potted field soil infested with root-knot nematode reduced the root galling on tomato plants and suppressed the nematode population. The hyphal feeder nematodes' belong to the orders *Tylenchida*, *Dorylaimida*, and *Aphelenchida*. They have weak, hollow stylet for piercing the fungal hyphae and sucking the contents. The feeding habits of these nematodes sometimes protect plants from pathogenic fungi. For example, *Aphelenchoides hamatus* and *A. hylurgi* feed on plant pathogenic fungi and damping off disease of cucumber (*Cucumis sativus*) by *Rhizoctonia solani* is less severe in the presence of

Aphelenchus avenae. In nature, the hyphal feeder nematode may be responsible for significant natural control of fungal pathogens. Likewise, bacterial feeder nematodes may reduce soilborne bacterial diseases by lowering the primary bacterial inoculum. Addition of organic matter to agricultural soils increases the populations of hyphal and bacterial feeder nematodes (Ishibashi and Kondo, 1986)^[38].

Role of Nematodes as Predators

The soil-inhabiting nematodes dominate over all other animals, both in numbers and species. They mainly fall under four groups based on their feeding types—the microphagous which feed on microorganisms, the saprophagous obtaining food from the dead and decaying organic matter, the phytophagous feeding on plants and the predaceous which kill other organisms for food. Predatory nematodes generally feed on smaller organisms like protozoa and other nematodes and help moderate population growth of bacterial-and fungal-feeding nematodes and protozoa, and help regulate populations of plant-parasitic nematodes. The predatory nematodes fall under three categories depending upon their mode of feeding and the type of feeding apparatus. The first type are those which feed by cutting the body of prey and then sucking its body contents as they are unable to engulf intact preys. These predators possess small but well developed buccal cavities and belong mainly to the order Diplogasterida. The second type of predators are those which feed by a combined action of cutting and sucking as well as at times, engulfing a prey whole. The latter group of nematode predators which belong to the Order Mononchida possesses a strong and comparatively larger buccal cavity provided with teeth, tooth and denticles. The third group is of those which feed only by puncturing the cuticle of prey and then suck their body contents. The feeding apparatus of this latter group belonging to the Suborders *Dorylaimina*, *Aphelenchina* and *Nygolaimina* is of piercing and sucking type (stylet/spear/mural tooth). The possibility of using predatory nematodes specially the mononchs for checking populations of plant parasitic nematodes in soil was speculated by Cobb (1917)^[5] while making observations on their biology and predatory ability.

Mononchida, *Diplogasterida*, *Aphelenchida*, *Enoplida* and *Rhabditida* are classified into three categories depending on their feeding apparatus, food and feeding habits. Predators commonly known as *mononchus* possess highly sclerotised feeding apparatus with a large pointed dorsal teeth, small teeth or denticles. Thin feeding apparatus is a cutting and engulfing type (*Mononchus*, *Mylonchus*) where they engulf prey whole and intact (Bilgram *et al.*, 1986).

Dorylaimids is referred to as the stylet-bearing predators' e.g. *Dorylaimids*, *Nygolaim* and *Aphelenchid*. These predators puncture the prey with their needle-like feeding apparatus that sucks the prey body contents. Feeding apparatus in dorylaimids predatory (*Labronema*) is axial in position but in *nygolaimus* (*Aquatides*) it is non-axial. The former has dorsal aperture and a groove but the latter does not have any such structures. Feeding apparatus of *Aphelenchid* predator (*Seinura*) is narrow and pointed (Jijapuri and Bilgrami, 1920). In *Diplogasterida* feeding type is cutting and sucking type eg *Mononchoides*. Their feeding apparatus commonly known as the strong the buccal cavity is small but well armed with a strong claw like movable dorsal tooth. Teeth or denticles may also be present to help cut prey cuticle and grind food particles (Jijapuri and Balgrami, 1990). The feeding apparatus

and feeding mechanism of *Actinilaimus* (*Actinilaimus*), *Enoplid*, (*Ironus*) predators are similar to those of diplogasterids. In *Actinolaim* predators, the vestibule is reinforced with plate like or ribbed basket like structures accompanied by large onchia with or without denticles. Onchia help predators slit open the prey's cuticle. The *Enoplid* predators (*Ironus*) have three sharply pointed teeth to tear open the prey (Van der Heiden, 1976) [46]. The action of buccal aperture is supported by the feeding apparatus muscles and the oesophageal suction. Cobb (1917) [5] first suggested the use of predatory nematode, *Mononchus* spp. for *Tylenchulus semipenetrans* biocontrol. Steiner and Heinly (1922) [39] suggested the use of *Clarkus papillatus* in controlling *Heterodera radicola* in sugar-beet fields. Cassidy (1931) concluded that under suitable conditions *Leptonchus brachylaimus* might partially control populations of pest nematodes. Thorne and Swanger (1936) and Linford and Oliviera (1937) [30] reported several species of *Aporcelaimus*, *Nygolaimus*, *Sectonema*, *Labronema*, *Dorylaimus*, *Dorylaimoides* and *Actinolaimus* as predaceous. Yeates (1969) [33] first evaluated the predatory ability of *Diplenteron colobocercus* (*Mononchoides potohikus*) on plant-parasitic nematodes. Investigations were made on their life cycle predatory behavior, ultrastructure and function of feeding apparatus, predation abilities, effect of mechanical stimulation and crowding on predation, factors influencing predation, cannibalistic tendency and intra-specific interactions. Two new species of *Seinura*, *S. pinusa* n. sp. and *S. pointa* n. sp., inhabiting bark of *Pinus roxburghii*, and one *S. albizica* sp. from *Albizia lebbek* twigs have been described from India (Bajaj, 2015).

Feeding mechanism of predatory nematodes vary with the type of nematode feeding apparatus and habitat. Prey capturing and feeding mechanisms of the predatory nematodes are divided into five phases-

1. Encounter with prey
2. Attack response
3. Attack
4. Extracorporeal digestion
5. Ingestion

Encounter with the prey may be by chance contact (*Mononchus*) or by willful movements in response to prey emitted kairomones (e.g- *diplogasterids*, *dorylaims* or *nygolaims* predators) (Bilgrami and Jairajpuri, 1988a, Bilgrami *et al.*, 2000, 2001) [2]. Positive attraction towards prey and during and post feeding aggregation activities of the predators at the feeding site suggest more than a casual role of chemoattractants in establishing predator prey contacts. The diplogasterids predators are attractants towards bacteria besides prey nematodes (Bilgrami and Jairajpuri, 1988). Predator attraction towards prey and aggregation around the feeding sites suggest an important role of prey secretions in establishing predator-prey contacts. Head probing, feeding apparatus movements and oesophageal pulsations generate an attack response predatory nematodes. Probing with head (with the help of papillae and amphid) and pharyngeal pulsations helps the predators identify their prey, locate suitable spot on the prey initiating an attack with a convenient posture at right angles. Probing by diplogasterid is quite aggressive, rapid and consists of side-to-side rubbing for a varying duration and in different times. Probing in *Mononchus aquaticus* is rapid side to side lip rubbing for short durations.

Moreover, predators initiate side to side lip rubbing over the

body of prey simultaneously with few feeding apparatus movements that cut or penetrate prey cuticle. Prey is attacked by the stylet (e.g *Mesodorylaimus*, *Discolaimus*, *Seinura*), mural tooth (e.g *Aquatides*), dorsal tooth (e.g *Mylonchulus*), teeth (e.g *Ironus*), or combined actions of movable dorsal tooth and high oesophageal suction (*Mononchoides*, *Butleries*). *Labronema vulvapapillatum* puncture prey with quick feeding apparatus movements (Wyss and Grootaert, 1977) [25], whereas *Aquatides* and *Dorylaimus* achieve perforation by gradual and intermittent thrusting of their feeding apparatus. The prey catching and attack is instant and only one or two attacks are enough to puncture the cuticle of prey. *Mononchoides* (Bilgrami and Jairajpuri, 1976) use their movable dorsal tooth and oesophageal suction to slit open the prey cuticle. *Butlerius* species show attack response by head shaking and lip rubbing against the prey's body. *Mononchoides aquaticus* attacks its prey by moving the lips backward resulting in the mouth opening wide and dorsal tooth coming in close contact with the prey. *M. dentatus* initiates attack by widely opening its vestibule with the help of labial muscles and exposing the dorsal tooth and denticles to bite the prey. The cuticle of the prey is ripped upon or punctured. *Seinura* injects toxic oesophageal secretions to paralyse prey to feed (Hechler, 1963) [26]. Other stylet bearing predators diagnose internal body organs of prey structures to make them immobile, whereas mononchus inactive their prey by holding them firmly with buccal armature and high oesophageal suction. In nematodes, extracorporeal digestion takes place through pharyngeal gland secretion. Complex food globules are broken down into small particles that are ingested through the feeding apparatus lumen to the intestine. The feeding apparatus lumen of piercing and sucking types of predator is too narrow to ingest large food molecules. Therefore, the food is partially digested outside the oesophagus before ingestion. Such phenomenon is known as extracorporeal digestion. Predatory mononchus do not predigest food since they can swallow a prey whole or ingest its pieces through the wide oral aperture whereas, diplogasterids predators partially digest food molecules before the ingestion by releasing oesophageal gland secretions. The ingestion of prey contents is intermittent with brief sucking periods. Swallowing of prey is supported by the oesophageal muscle contraction that pulls into the buccal cavity through vertically positional plates. Prey contents are ingested by the feeding apparatus that pass into the intestine through oesophago-intestinal junction (cardia) by simultaneous relaxation and contraction of oesophageal bulb. Once the contents are ingested predators detach their lips from the prey and move in search of another prey. *Dorylaim* and *Nygolaim* predator also feed on the eggs of other nematode species but not conspecific egg. When in contact with conspecific egg these predators probe in an exploratory fashion by making side to side lip rubbing but cause no harm to the egg. An injured prey attack predators to aggregate at the feeding site. Predator struggle among themselves to feed if their number exceeds more than two at a feeding site. Group feeding allows predators to finish their prey rather quickly and then continue hunting. All diplogasterid predators' viz., *Mononchoides longicaudatus*, *M. fortidens*, *Butlerius degrissei* and *Diplenteron colobocercus* get hold of their prey with the help of high suction force created by their oesophagus. *M. fortidens* devour intact first and second stage juveniles of small-sized prey nematodes, *Acrobeloides* sp., and *Cephalobus* sp., and also cut larger prey into pieces for feeding purposes.

Biocontrol potential of predaceous nematode

Predatory nematodes belong to order *Mononchida*, *Diplogasterids*, *Aphelenchida*, *Enoplida* and *Rhabditida* and are most suited for biocontrol of nematodes, because of their short life cycles, easy culture, prey-specificity, chemotaxis sense and resistance to adverse condition. As a biocontrol agent the predaceous nematodes offer an ecologically safe alternative to chemical nematicides. *Mononchus* which possess a well developed buccal cavity with strong buccal musculature tooth feed by cutting and engulfing an intact prey. As a result of their inability to perceive prey secretions, their contacts with prey depend on chance encounters. Small (1977) [44] reported significant reduction in the population of *Heterodera rostochiensis* in the presence of *Prionchulus punctatus* and partial control of *Meloidogyne incognita* was resulted in considerable reduction in root galling in the presence of *Prionchulus punctatus*. Azmi (1983) [12], reported the increase in population of *Iotonchus monhystera* have a gradual reduction in the population of *Helicotylenchus dihystra*. Availability of wide prey range, short life cycle, high rate of reproduction leads to the biocontrol potential of *Diplogasterid* predator. Bilgrami (1997) [15] reported that *Depelenteron* and *Butlerius* switch to feeding on bacteria in the absence of prey strongly suggest enhanced capability to persists when prey population are reduced. *Mononchoides* are able to reduce galling by root knot nematodes resulting in improved vegetative growth and increased root mass. Similarly, Bilgrami *et al.*, (2008) [20] reported that *M. gaugleri* have significant control of plant-parasitic nematodes although the rate of predator persistence was low in a turf grass. Grootaert and Jaques (1979) [41] reported that *Butlerius degriisei* infect the juveniles of *G. rostochiensis* and causes significant reduction in its population. *Dorylaim* and *Nygolaim* predator occurs in all soil type, climate and habitat. They can switch to feeding on bacteria and fungi which presumably enhances their survival when prey nematodes are scarce (Bilgrami & Gaugler, 2004) [18]. Predation rate, feeding and prey search activities in Dorylaims are governed by biotic and abiotic factor like temperature, starvation, incubation etc. Starvation of 14 days did not alter predation by *Dorylaimus stagnalis* but short term food deprivation enhanced predation. Maximal predation in 6 days starved predators (Bilgrami and Gaugler, 2005) because food deprivation increased predator ability to detect more prey individuals to kill. Starved nematodes could perceive weaker stimuli much faster than when they are well fed. (Doncaster and Seymour, 1973) [22]. Yeates (1967) [43] reported that *Discolaimus arenicolus* reduces population of juveniles of *M. incognita* in many crop. Mankau (1982) [42] reported that *A. amylovorus* able to reduce population of in mandarin *T. semipenetrans*.

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