

Predatory Nematodes and Their Potential in Biological Control of Plant Parasitic Nematodes in Soil

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포식선충의 토양중 식물기생선충의 생물학적 방제 이용 가능성

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ABSTRACT

Predatory nematodes are ubiquitous and feed on soil microorganisms including plant parasitic nematodes. They reduce populations of plant parasitic nematodes in virtually all soils because of their constant association with plant parasitic nematodes in the rhizosphere. Predatory potential of several species of predacious nematodes, belonging to the orders Mononchida, Diplogasterida, Dorylaimida and Aphelenchida, have been studied in detail on plant parasitic nematodes but most of the studies were based on *in vitro* experiments. A review of progress on the use of predatory nematodes as biological control agents of plant parasitic nematodes reveals that advocacy for predatory nematodes dates back to the early 20th century; nevertheless, their potential has begun to be studied in recent years. Information on the efficacy of predatory nematodes under field conditions is lacking; however, some predatory nematodes have given very promising results against plant parasitic nematodes. This article summarizes research progress to date on predatory nematodes and discusses about their possible use in the management of plant parasitic nematodes.

Key words : Biological control, plant parasitic nematodes, predatory nematodes

INTRODUCTION

Soil inhabiting nematodes predominate over all other animals, both in numbers and species (Jairajpuri and Bilgrami 1990). On the basis of their feeding habits, nematodes are known as plant feeder, bacterial feeder, fungal feeder, algal feeder, animal predator, and omnivore (Yeates *et al.* 1993). Several types of organism, including fungi, bacteria, viruses, protists, nematodes and other invertebrates, have been found to parasitize or prey upon plant parasitic nematodes (Stirling 1991). Biological control of plant parasitic nematodes has been oriented almost exclusively to microbial pathogens (Kerry 2000). While pathogens have received significant research emphasis for biological control of plant parasitic

nematodes, predatory nematodes have been largely ignored. However, in recent years predatory nematodes have shown biological control potential against plant parasitic nematodes and established themselves as an important entity of the soil food web.

Biological control advocacy of predatory nematodes dates back to the early 20th century when Cobb (1917) speculated on their possible role in management of plant parasitic nematodes. Nevertheless, their potential has only begun to be studied in recent years. There has been widespread interest in using predatory nematodes to control populations of plant parasitic nematodes (Mankau 1980, Jairajpuri and Bilgrami 1990, Stirling 1991). 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. Sometimes biological control measures are used alone; more often

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they are combined with cultural methods in systems of integrated pest management (IPM). When used as a part of an IPM program, biopesticides (bacteria, fungi, nematodes, protozoa, viruses) offer viable, safer and ecologically sound alternatives to chemical nematicides (Hom 1996).

This paper reviews the status of progress made up till present time, and discusses future directions that may be followed to enhance the use of predatory nematodes as biological agents in the management of plant parasitic nematodes.

TYPES OF PREDATORY NEMATODES

The majority of predatory nematodes belonging to the orders Mononchida, Dorylaimida, Diplogasterida, Aphelenchida, Enoplida and Rhabditida are classified into three categories depending on their feeding apparatus, feeding mechanisms and food preferences. They feed on plant parasitic nematodes when they come in physical contact.

The first type of predators commonly known as mononchs (Mononchida) possess a strongly sclerotized buccal cavity, which is often armed with one or more large puncturing tooth or numerous small grasping teeth or both. Their feeding apparatus is a cutting and engulfing type. Several of commonly occurring mononchids feed extensively, though not exclusively, on plant parasitic and other nematodes. They may swallow their prey whole if it is of smaller size, or at times feed by cutting larger prey into pieces. The second type is referred to as the stylet-bearing predators, e.i. dorylaims, nygolaims and aphelenchs (Dorylaimida and Aphelenchida). They possess piercing and sucking type of feeding apparatus. These predators puncture the prey with their needle-like feeding apparatus that sucks the prey body contents. Feeding apparatus in dorylaim predators (*Dorylaimus*, *Labronema*) is axial in position but in nygolaims (*Aquatides*) it is nonaxial. The former has a hollow stylet with a dorsal aperture but later has a slender, protrusible mural tooth with which they pierce or slit their prey. This tooth is not hollow and food is sucked up through the oral aperture. The feeding apparatus of aphelenchs is narrow and pointed with fine lumen and aperture. They penetrate the cuticle of prey nematodes with their fine needle-like stylet and inject digestive enzymes into the prey body, which paralyse the prey almost instantly (Hechler 1963, Wood 1974). Ingestion of the body contents then takes place. The third types are those which feed by cutting the body of prey and then sucking its body contents. These predators

belong to the order Diplogasterida (*Mononchoïdes*, *Butleriūs*), they possess small but well developed buccal cavity armed with a claw-like movable dorsal tooth. Teeth or denticles may also be present to help cut prey cuticle and grind food particles (Jairajpuri and Bilgrami 1990).

BIOLOGICAL CONTROL POTENTIAL

Mononch, dorylaim, nygolaim, diplogaster and aphelench predators show different predatory potential, depend on their rate of predation, prey searching abilities and resistance to adverse conditions.

1. Mononch predators

The possibility of using mononchs to check populations of plant parasitic nematodes in soil was first speculated by Cobb (1917) while making observations on their biology and predatory ability. Steiner and Heinly (1922) observed feeding by *Clarkus papillatus* on *Meloidogyne* sp. and suggested the use of *C. papillatus* for controlling populations of plant parasitic nematodes in sugar-beet fields. However, observations by Thorne (1927) regarding the behavior and habits of various species of mononchs, including *C. papillatus* present in sugar-beet fields were not encouraging. He found that soil population of mononchs tended to be unstable and to change rather abruptly, sometimes disappearing or becoming drastically reduced; some species of mononchs were subjected to infection by an Apicomplexa parasite, which may have been a factor in reducing their numbers.

Cassidy (1931) concluded that, under suitable conditions, *Iotonchus brachylaimus* might partially control populations of pest nematodes. Not much work had been done on these aspects until 1970's when several workers recorded observations on the predatory abilities of mononchs but most of these experiments limited to laboratory conditions. Christie (1960) suggested that the use of predatory nematodes should be assessed for determining the practicability of their use in control of plant parasitic nematodes. Further studies in this direction were made by Mulvey (1961), Esser (1963), Esser and Sobers (1964), Ritter and Laumont (1975). According to Webster (1972) and Jones (1974), non-specific predators like mononchs exert only partial control of plant parasitic nematodes. However, studies have shown that they have reduced *Tylenchulus semipenetrans*, *Globodera rostochiensis* and *Meloidogyne incognita* populations in pots (Cohn and

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Table 1. List of predatory mononchs and their prey nematodes (plant parasitic)

Predatory nematodes	Plant parasitic nematodes preyed upon	References
<i>Anatonchus</i> spp.	Aphelenchs, tylenchs, <i>Paratylenchus vulnus</i>	Szczygiel (1971) Ritter & Laumond (1975)
<i>A. amiciae</i>	Tylenchs, <i>Xiphinema</i>	Coomans & Lima (1965)
<i>A. ginglymodontus</i>	<i>Meloidogyne hapla</i> , tylenchs	Szczygiel (1966, 1971)
<i>A. tridentatus</i>	<i>Aglenchus agricola</i> , aphelenchs, <i>Globodera rostochiensis</i> , <i>Paratylenchus macrophallus</i> , <i>Longidorus</i> , <i>Pratylenchus</i>	Mulvey (1961); Ritter & Laumond (1975) Small & Grootaert (1983)
<i>Clarkus mulveyi</i>	<i>Helicotylenchus multicinctus</i> , <i>M. incognita</i> , <i>Rotylenchulus reniformis</i> , <i>Tylenchorhynchus nudus</i>	Mohandas & Prabhoo (1980)
<i>C. papillatus</i>	<i>Aphelenchoïdes</i> , <i>Hemicriconemoides</i> , <i>Heterodera schachtii</i> , <i>M. hapla</i> , <i>Tylenchus</i> , <i>Tylenchulus semipenetrans</i> , <i>Subanguina radicicola</i>	Cobb (1917); Menzel (1920) Steiner & Heinly (1922) Thorne (1927); Szczygiel (1966, 1971)
<i>C. sheri</i>	<i>Tylenchorhynchus</i>	Bilgrami <i>et al.</i> (1986)
<i>C. venezolanus</i>	<i>Helicotylenchus</i>	Loof (1964)
<i>Coomansus indicus</i>	<i>Hemicriconemoides</i> , <i>Pratylenchus</i> , <i>Tylenchorhynchus</i> , <i>Xiphinema</i>	Bilgrami <i>et al.</i> (1986)
<i>Iotonchus acutus</i>	<i>Rotylenchus robustus</i> , <i>Trichodorus obtusus</i> , <i>X. americanum</i>	Thorne (1932)
<i>I. amphigonicus</i>	<i>H. schachtii</i>	Thorne (1924)
<i>I. antedontus</i>	<i>Tylenchorhynchus</i>	Bilgrami <i>et al.</i> (1986)
<i>I. basidontus</i>	Tylenchs	Clark (1960)
<i>I. brachylaimus</i>	<i>Radopholus similis</i> , <i>S. radicicola</i>	Cassidy (1931)
<i>I. kheri</i>	<i>H. multicinctus</i> , <i>Hirschmanniella oryzae</i> , <i>M. incognita</i> , <i>R. reniformis</i> , <i>Scutellonema curvata</i> , <i>T. nudus</i> , <i>X. elongatum</i>	Mohandas & Prabhoo (1980)
<i>I. longicaudatus</i>	<i>Hirschmanniella</i> , <i>Hoplolaimus</i>	Bilgrami <i>et al.</i> (1986)
<i>I. monhystrera</i>	<i>H. multicinctus</i> , <i>H. dihystera</i> , <i>H. oryzae</i> , <i>Hoplolaimus</i> , <i>M. incognita</i> , <i>Pratylenchus</i> , <i>T. nudus</i> , <i>R. reniformis</i>	Mohandas & Prabhoo (1980) Azmi (1983)
<i>I. nayari</i>	<i>H. multicinctus</i> , <i>H. oryzae</i> , <i>M. incognita</i> , <i>R. reniformis</i> , <i>X. elongatum</i>	Mohandas & Prabhoo (1980)
<i>I. parabasidontus</i>	<i>H. oryzae</i>	Bilgrami <i>et al.</i> (1986)
<i>I. prabhooi</i>	<i>M. incognita</i> , <i>R. reniformis</i>	Mohandas & Prabhoo (1980)
<i>I. risoceiae</i>	<i>Pratylenchus</i>	Bilgrami <i>et al.</i> (1986)
<i>I. shafi</i>	<i>Hoplolaimus</i>	Bilgrami <i>et al.</i> (1986)
<i>I. tenuicaudatus</i>	<i>T. semipenetrans</i> , <i>H. dihystera</i>	Rama & Dasgupta (1998)
<i>I. trichurus</i>	<i>Hoplolaimus</i> , <i>Pratylenchus</i> , <i>Tylenchorhynchus</i> , <i>Xiphinema</i>	Bilgrami <i>et al.</i> (1986)
<i>I. vulvapapillatus</i>	<i>Tylenchorhynchus</i>	Andrássy (1964)
<i>Miconchus aquaticus</i>	<i>Hoplolaimus</i> , <i>Hemicycliophora</i> , <i>Xiphinema</i>	Bilgrami <i>et al.</i> (1986)
<i>M. citri</i>	<i>Pratylenchus</i> , <i>Tylenchorhynchus</i>	Bilgrami <i>et al.</i> (1986)
<i>M. dalhousiensis</i>	<i>Aphelenchoïdes</i> , <i>Diphtherophora</i>	Bilgrami <i>et al.</i> (1986)
<i>Mononchus</i> spp.	<i>Aphelenchoïdes</i> , <i>Heterodera</i> eggs, <i>M. marioni</i>	Linford & Oliveira (1938) Banage (1963); Arpin (1980)
<i>M. aquaticus</i>	<i>Aglenchus parvus</i> , <i>Anguina tritici</i> , <i>Globodera rostochiensis</i> , <i>H. oryzae</i> , <i>H. indicus</i> , <i>Heterodera motti</i> , <i>Hoplolaimus indicus</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>M. naasi</i> , <i>Paralongidorus citri</i> , <i>Paratrichodorus</i> , <i>Rotylenchus fallorobustus</i> , <i>Trichodorus</i> , <i>Tylenchorhynchus mashhoodi</i> , <i>X. americanum</i>	Grootaert & Maertens (1976) Grootaert <i>et al.</i> (1977) Grootaert & Wayss (1979) Small & Grootaert (1983) Bilgrami <i>et al.</i> (1984) Bilgrami (1992)
<i>M. truncatus</i>	<i>Heterodera schachtii</i> , tylenchs	Thorne (1927); Szczygiel (1971)
<i>M. tunbridgensis</i>	<i>Hemicriconemoides</i> , <i>Hoplolaimus</i> , <i>Tylenchorhynchus</i>	Mankau (1980); Bilgrami <i>et al.</i> (1986)
<i>Mylonchulus agilis</i>	<i>Helicotylenchus vulgaris</i> , <i>Longidorus caespiticola</i> , <i>Rotylenchus fallorobustus</i>	Doucet (1980)
<i>M. brachyuris</i>	<i>S. radicicola</i> , <i>R. similis</i>	Cassidy (1931)
<i>M. dentatus</i>	<i>A. tritici</i> , <i>Basiria</i> , <i>Helicotylenchus indicus</i> , <i>H. oryzae</i> , <i>H. indicus</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>P. citri</i> , <i>T. mashhoodi</i> , <i>T. semipenetrans</i> , <i>X. basiri</i>	Jairajpuri & Azmi (1978) Bilgrami & Kulshreshtha (1994)

Table 1. To be continued.

Predatory nematodes	Plant parasitic nematodes preyed upon	References
<i>M. hawaiiensis</i>	<i>H. oryzae</i> , <i>M. incognita</i> , <i>T. nudus</i> , <i>R. reniformis</i>	Mohandas & Prabhoo (1980)
<i>M. minor</i>	<i>A. tritici</i> , <i>M. incognita</i> , <i>T. semipenetrans</i> , <i>X. americanum</i>	Kulshreshtha et al. (1993)
<i>M. parabrachyurus</i>	<i>H. schachtii</i>	Thorne (1927)
<i>M. signaturus</i>	<i>H. schachtii</i> (eggs), <i>M. javanica</i> , <i>R. similis</i> , <i>S. radicicola</i> , <i>T. semipenetrans</i>	Thorne (1927); Cassidy (1931) Cohn & Mordechai (1973, 1974)
<i>Prionchulus</i> spp.	<i>Aphelenchoïdes</i>	Arpin (1980)
<i>P. muscorum</i>	<i>Aphelenchs</i> , <i>Hemicriconemoides</i> , <i>Hoplolaimus</i> , <i>Tylenchorhynchus</i> , tylenchs	Altherr (1950); Szczygiel (1971) Arpin (1976); Bilgrami et al. (1986)
<i>P. punctatus</i>	<i>A. tritici</i> , <i>G. rostochiensis</i> , <i>H. dihystera</i> , <i>M. naasi</i> , <i>R. fallorobustus</i>	Nelmes (1974); Grootaert et al. (1977) Small & Evans (1981) Small & Grootaert (1983)
<i>Sporonchulus ibitensis</i>	<i>Aphelenchoïdes</i>	Carvalho (1951)
<i>S. vagabundus</i>	<i>Aphelenchoïdes</i> , <i>Pratylenchus</i> , <i>Hemicyclophora</i> , <i>Trichodorus</i>	Bilgrami et al. (1986)

Mordechai 1974, Small 1979). They also decreased *Trichodorus*, *Hemicriconemoides*, *Helicotylenchus* and *Tylenchulus* populations under field conditions (Ahmad and Jairajpuri 1982, Azmi 1983, Rama and Dasgupta 1998).

Mononchs do have efficient predatory capabilities and are able to prey on a wide range of prey. However, mononchs have some flaws from a practical biological control point of view. The main drawback lies in their poor adaptability to environmental fluctuations. They can hardly survive drought or flooded conditions. Besides, their low rate of reproduction and longer life cycle and cannibalistic behavior are other hindering factors. The duration of the life cycle varies from species to species. To complete one generation, *Prionchulus punctatus* takes 45 days while *Mononchus aquaticus* takes only 15 days at 25°C (Maertens 1975, Grootaert and Maertens 1976). The possibility of using mononchs in biological control program can not be ruled out on the basis of above mentioned rather limited studies. This is an explored area and it may be surmised that an extensive research on life cycle, predator-prey interactions in terms to biotic and abiotic factors, population dynamics, etc. may result in more information which could prove very vital in the use of mononchs as promising biological control agents. The species of mononch predators and their prey nematodes are listed in Table 1.

2. Stylet-bearing predators

Substantial information is available on the predatory potential of dorylaim nematodes but mostly based on *in vitro* studies. Feeding by *Eudorylaimus obtusicaudatus* on eggs inside the cysts of *Heterodera schachtii* and an increase in the

population of *Thornia* sp. in the presence of citrus nematodes but a decrease in their absence in pot trials suggested more than a casual role of stylet bearing predators in nematode biological control under natural conditions and generated optimism in using these predators as biological control agents (Boosalis and Mankau 1965). Dorylaim and nygolaim predators are the most ubiquitous group of predatory nematodes, occurring in all types of soils, climates and habitats. The presence of two, three or more genera of dorylaims in one place/field is quite common and their abundance has been estimated at 200-500 million/acre (Thorne 1930). These predators may be maintained and established under field conditions by making slight modifications in their environment. In addition to nematodes, they also feed on algae, fungi and protozoa (Ferris 1968). Consequently, these predators can also be cultured on algae and fungi. Generally dorylaims take 3-6 months to complete one life cycle, while *Labronema vulvapapillatum* completes life cycle in 36 days (Ferris 1968, Wood 1973). The efficient rate of predation and prey preference (Khan et al. 1991, 1994, 1995a, b) and wide range of predation on nematode species have established their credentials as efficient biological control agents. The most advantageous and encouraging aspect of dorylaims is that it is easy to maintain their populations simply by adding organic matter to agricultural fields; as they are polyphagous in nature, they will remain abundant in soil without prey nematodes (Webster 1972). *In vitro* studies on dorylaim predators, viz. *Aporcelaimellus nivalis*, *Allodorylaimus americanus*, *Discolaimus silvicolus*, *Neoactinolaimus agilis*, *Paractinolaimus elongatus*, *Mesodorylaimus bastiani* and *Dorylaimus stagnalis* exhibited preference to prey upon second stage

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Table 2. List of stylet-bearing predatory nematodes and their prey nematodes (plant parasitic)

Predatory nematodes	Plant parasitic nematodes preyed upon	References
<i>Dorylaimus</i>	<i>Belonolaimus longicaudatus</i> , <i>Criconemoides</i> , <i>M. marioni</i>	Linford & Oliviera (1938); Esser (1963)
<i>Actinolaimus</i>	<i>M. marioni</i>	Linford & Oliviera (1937)
<i>Allodorylaimus americanus</i> and <i>Discolaimus silviculus</i>	<i>A. tritici</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>Helicotylenchus indicus</i> , <i>Hemicyclophora dhirenderi</i> , <i>H. mothi</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>Trichodorus</i> , <i>T. mashhoodi</i> , <i>T. semipenetrans</i> , <i>X. basiri</i>	Khan <i>et al.</i> (1995a)
<i>Aporcelaimellus nivalis</i>	<i>A. tritici</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>H. indicus</i> , <i>Hemicriconemoides mangiferae</i> , <i>H. dhirendri</i> , <i>H. mothi</i> , <i>H. oryzae</i> , <i>Hoplolaimus indicus</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>P. citri</i> , <i>Scutellonema</i> , <i>T. mashhoodi</i> , <i>T. semipenetrans</i> , <i>Trichodorus</i> , <i>X. americanum</i> , <i>X. insigne</i>	Khan <i>et al.</i> (1991); Bilgrami (1993)
<i>A. obscurus</i>	<i>H. schachtii</i> (eggs)	Thorne & Swanger (1936)
<i>A. obtusicaudatus</i>	<i>H. schachtii</i> (eggs)	Thorne (1928)
<i>Aporcelaimus</i> spp.	<i>Heterodera trifolii</i> , <i>Meloidogyne</i>	Doncaster (1962); Esser (1987)
<i>Aquatides thornei</i>	<i>A. tritici</i> , <i>H. indicus</i> , <i>H. mothi</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>P. citri</i> , <i>T. mashhoodi</i> , <i>Paratrichodorus</i> , <i>X. americanum</i>	Bilgrami <i>et al.</i> (1985); Bilgrami (1992)
<i>Cchararolaimus</i> spp.	<i>Meloidogyne</i> , <i>Rotylenchulus reniformis</i>	Linford & Oliviera (1937); Esser (1963)
<i>Discolaimus</i> spp.	<i>Hemicyclophora</i> , <i>M. marioni</i>	Linford & Oliviera (1937); Esser (1963)
<i>D. areniculus</i>	<i>M. incognita</i>	Esser (1963, 1987)
<i>Dorylaimus</i> spp.	<i>M. marioni</i>	Linford & Oliviera (1937)
<i>D. obscurus</i>	<i>H. schachtii</i> (eggs)	Thorne & Swanger (1936)
<i>D. stagnalis</i>	<i>A. tritici</i> , <i>H. indicus</i> , <i>H. mothi</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>P. citri</i> , <i>Paratrichodorus</i> , <i>T. mashhoodi</i> , <i>X. americanum</i>	Shafqat <i>et al.</i> (1987) Bilgrami (1992)
<i>Eudorylaimus</i> spp.	<i>Bursaphelenchus xylophilus</i> , <i>M. incognita</i>	Boosalis & Mankau (1965); Esser (1987)
<i>E. obtusicaudatus</i>	<i>H. schachtii</i> (eggs)	Cobb (1929); Esser (1987)
<i>Labronema vulvapapillatus</i>	<i>A. tritici</i> , <i>G. rostochiensis</i> , <i>M. naasi</i> , <i>X. index</i>	Wyss & Grootaert (1977) Grootaert & Small (1982) Small & Grootaert (1983)
<i>Mesodorylaimus</i> spp.	<i>M. incognita</i>	Spaul (1973)
<i>M. bastiani</i>	<i>A. tritici</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>H. indicus</i> , <i>H. dhirenderi</i> , <i>H. mothi</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>P. citri</i> , <i>Paratrichodorus</i> , <i>T. mashhoodi</i> , <i>X. americanum</i> , <i>X. basiri</i>	Bilgrami (1992)
<i>Neoactinolaimus agilis</i>	<i>A. tritici</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>H. indicus</i> , <i>H. oryzae</i> , <i>H. mothi</i> , <i>M. incognita</i> , <i>R. robustus</i> , <i>P. citri</i> , <i>Paratrichodorus</i> , <i>T. mashhoodi</i> , <i>T. semipenetrans</i> , <i>X. americanum</i>	Khan <i>et al.</i> (1995b)
<i>Paractinolaimus elongatus</i>	<i>A. tritici</i> , <i>H. indicus</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>T. mashhoodi</i> , <i>X. basiri</i>	Khan & Jairajpuri (1997)
<i>Thornia</i> spp.	<i>Criconemoides</i> , <i>M. floridensis</i> , <i>P. curvitatus</i> , <i>P. penetrans</i> , <i>P. vulnus</i> , <i>T. semipenetrans</i>	Boosalis & Mankau (1965) Esser (1987)
<i>Westindicus rapax</i>	<i>Xiphinema</i>	Hunt (1978)
<i>Aphelenchoides</i> spp.	<i>M. marioni</i>	Linford & Oliveira (1938)
<i>Seinura</i> spp.	<i>Ditylenchus dipsaci</i> , <i>H. trifolii</i> , <i>G. rostochiensis</i> , <i>Neotylenchus linfordi</i> , <i>M. hapla</i>	Vinciguerra (1979) Small & Grootaert (1983)
<i>S. demani</i>	<i>Aphelenchoides bicaudatus</i> , <i>Tylenchus</i>	Wood (1974)
<i>S. oxyura</i>	<i>Ditylenchus myceliophagus</i>	Cayrol (1970)
<i>S. tenuicaudatus</i>	<i>Aphelenchoides parietinus</i> , <i>D. dipsaci</i> , <i>H. trifolii</i> , <i>M. hapla</i> , <i>M. marioni</i> , <i>N. linfordi</i> , <i>Pratylenchus pratensis</i>	Linford (1937); Hechler (1963)

Table. 3. List of predatory diplogasters and their prey nematodes (plant parasitic)

Predatory nematodes	Plant parasitic nematodes preyed upon	References
<i>Butlerius degrissei</i>	<i>Aphelenchoides fragariae</i> , <i>Pratylenchus</i> , <i>G. rostochiensis</i> , <i>M. naasi</i> , <i>R. robustus</i>	Grootaert <i>et al.</i> (1977) Small & Grootaert (1983)
<i>Diplogaster</i> spp.	<i>M. marioni</i>	Linford (1937)
<i>Mononchoides fortidens</i> and <i>M. longicaudatus</i>	<i>A. tritici</i> , <i>H. indicus</i> , <i>H. oryzae</i> , <i>Longidorus</i> , <i>M. incognita</i> , <i>Trichodorus</i> , <i>T. mashhoodi</i> , <i>X. americanum</i>	Bilgrami & Jairajpuri (1988, 1989b)
<i>M. gaugleri</i>	<i>A. tritici</i> , <i>H. indicus</i> , <i>H. mangiferae</i> , <i>H. oryzae</i> , <i>Hoplolaimus indicus</i> , <i>Longidorus attenuatus</i> , <i>M. incognita</i> , <i>Paratrichodorus christiei</i> , <i>T. mashhoodi</i> , <i>X. americanum</i>	Bilgrami <i>et al.</i> (2005)
<i>Odontopharynx longicaudata</i>	<i>A. amsinckiae</i> , <i>A. pacifica</i> , <i>Aphelenchoides fragariae</i> , <i>Criconemella xenoplax</i> , <i>M. hapla</i> , <i>M. incognita</i> , <i>M. javanica</i> , <i>P. vulnus</i> , <i>Trichodorus</i> , <i>T. semipenetrans</i> , <i>X. index</i>	Chitambar & Noffsinger (1989)

juveniles of endoparasitic nematodes viz. *Anguina tritici*, *M. incognita*, *Heterodera mothi* and *T. semipenetrans* over other prey nematodes used in the experiments (Khan *et al.* 1991, 1994, 1995a, b, Bilgrami 1992, 1993, 1995, Khan and Jairajpuri 1997). The aggregation of some of these dorylaimid predators around injured prey at the feeding site and their subsequent feeding together on that prey is an indication of the positive response of predators towards prey secretions. Widespread and abundant presence of these predators in fields, and their omnivorous feeding habits, chemotaxis sense and inverse relationship with prey nematode are certainly encouraging phenomenon, to explore their biocontrol potentials.

Aphelenchs in spite of their smaller body size and slender stylet, these predators are able to cope successfully with prey many times larger than their own size by injecting enzymes into prey body (Linford and Oliveira 1937). Some of the members of the order Aphelenchida have been observed feeding on plant parasitic nematodes. *Seinura* spp. complete their life cycles in 3-6 days (Hechler 1963, Hechler and Taylor 1966), have a high reproductive potential and can be easily and rapidly cultured on fungivorous nematodes under laboratory conditions. The species of stylet-bearing predators and their prey nematodes are listed in Table 2.

3. Diplogaster predators

The diplogasters feed on nematodes, bacteria and other soil microorganisms. They complete their life cycles in 8~15 days and are the most readily cultured nematodes, being easily maintained on simple nutrient media containing bacteria (Yeates 1969). This group of predators was largely neglected until Yeates (1969) evaluated the predatory abilities of *Diplenteron colobocerus* (= *Mononchoides potohikus*), which

feed on bacteria in the absence of prey nematodes, whereas Grootaert *et al.* (1977) examined feeding habits of *Butlerius degrissei*. Both studies suggested that future use of diplogasters in biological control of plant parasitic nematodes. Diplogasterid predators appear to be more prey-selective than other groups. *Odontopharynx longicaudata* attacked and killed six out of 17 prey species presented in the laboratory study and 100% of individuals of *Anguina pacifica* were killed (Chitambar and Noffsinger 1989). They also reported that its ability to eliminate a population of *Anguina pacifica* is of particular interest because it suggests that a target prey-predator relationship exists in the field habitat from where the two species were collected. A strong degree of prey preference was reported for *Mononchoides fortidens*, *M. longicaudatus* and *M. gaugleri*: they preferred juveniles of endoparasitic over ectoparasitic nematodes (Bilgrami and Jairajpuri 1989a, Bilgrami *et al.* 2005). The main advantages of using diplogasterid predators lie in their chemotaxis sense and high rates of predation, short life cycles, high fecundity and easy culture. In addition, they form dauer larvae under adverse conditions (Bilgrami and Jairajpuri 1990). Because of these characteristics, diplogasterid predators certainly deserve the attention to explore their potential. A list of diplogasterid predators and their prey nematodes is given in Table 3.

EFFICACY OF PREDATORY NEMATODES

Interests in predatory nematodes for biological control of plant parasitic nematodes is long standing, yet remarkably few efficacy experiments have been reported while these have been restricted to petridish or pot studies. Cohn and Mordechai (1974) found *Mylonchulus* suppressed the population of the reniform nemtodes in pot experiments. Small (1979) subse-

quently reported a significant reduction in the population of potato cyst nematode, *Globodera rostochiensis* and root-knot nematode, *Meloidogyne incognita* in the presence of *Prionchulus punctatus*, also in pots. Root-knot development caused by *M. incognita* on chilli (*Capsicum annuum*) significantly declined in the presence of *Mononchus aquaticus*. The severity of root-knot infection was reduced when chipped leaves of neem (*Azadirachta indica*) and castor (*Ricinus communis*) were incorporated into the soil and improvement in plant growth was positively correlated with the level of nematode control (Akhtar and Mahmood 1993).

The efficacy of diplogaster predators has been suggested from a handful of pot experiments. Osman (1988) showed *Diplogaster* reduced population of *Meloidogyne javanica* and *Tylenchulus semipenetrans* in pots. Fauzia *et al.* (1998) demonstrated the ability of *Mononchoides longicaudatus* to reduce root galling caused by root-knot nematodes, resulting in improved vegetative growth and increased root masses. Further Khan and Kim (2005) reported that a pre-plant application of *M. fortidens* in potted field soil infested with root-knot nematode, *M. arenaria* reduced the root galling on tomato plants and suppressed the *M. arenaria* population, and the final population density of *M. fortidens* increased by about 2-folds compared to initially added density. Thus, the diplogasterid predators may prove promising as biological control agents, but only further studies will confirm their utility at commercial level.

CULTURE AND CONSERVATION OF PREDATORY NEMATODES

A huge population of predators is required to execute biological control programs successfully against a plant parasitic nematode species population in the field. The better understanding and advanced knowledge to elevate population of predators both under *in vitro* and *in vivo* conditions is therefore required. With a few exceptions, predators are reared using *in vivo* methods, which require maintaining concurrent prey cultures, thereby reducing efficacy. Esser (1963) cultured predatory mononchs, Pillai and Tailor (1968) cultured diplogasters on a dixenic culture of bacteria and *Aphelenchus avenae*, Yeates (1969) cultivated *D. colobocerus* on agar plates using a bacterium, *Bacillus cereus* var *mycoides*. Nelmes (1974) reared *P. punctatus* on *Aphelenchus avenae* and *Panagrellus redivivus* in soil extract agar medium and reported that *A. avenae* appear to be more suitable prey

for many mononchs. Grootaert and Maertens (1976) and Small (1977) used the same technique to raise the populations of *Mononchus aquaticus* and *P. punctatus* using *P. redivivus* as prey. Small and Evans (1981) cultured sufficient *P. punctatus* on *A. avenae* and *P. redivivus* in soil extract agar at pH 7 to use as a biological control agent in pot trials. Allen-Morley and Coleman (1989) reported that larger populations of *Mononchus tunbridgensis* were supported by *A. avenae* but also that mononchs could be cultivated on 'thick lawns' of bacteria. Shafqat *et al.* (1987) and Bilgrami and Jairajpuri (1988) cultivated predators, *D. stagnalis* and *M. fortidens* and *M. longicaudatus*, respectively using *Rhabditis* sp. in agar plates supplemented with infant milk powder (Lactogen) under *in vitro* conditions. Addition of milk powder boosted bacterial growth in maintaining their culture for long duration. Khan *et al.* (1991, 1994, 1995a, b) and Khan and Jairajpuri (1997) have also used the same technique to elevate population of dorylaim predators.

The conservation of predatory nematodes appears to be simple and cost effective. With relatively little efforts their activity may be stimulated and density elevated to counter populations of target pest nematode. Lal *et al.* (1983) recorded a two-fold increase in the population of predatory nematodes, such as species of *Dorylaimus*, *Discolaimus* and *Mononchus*, when green manure was added to the soil. Few studies on soil nematodes with neem (*A. indica*) products such as leaf powder, sawdust and oil seed cake showed encouraging results in maintaining and conserving predatory nematode populations in the field (Akhtar 1995). Winter mulching could be another option to improve predatory nematodes preservation in the field. This technique has been found to be effective in stabilizing the population of *Iotonchus tenuicaudatus* that feeds on *T. semipenetrans* and *Helicotylenchus dihystera* in orange orchards (Rama and Dasgupta 1988). Further studies are warranted on the role of organic matter in predatory nematode conservation. Prey nematodes and bacteria have supported growth and development of diplogasters predators.

CONCLUSION AND PROSPECTS

Many studies have shown predatory nematodes to be effective at killing plant parasitic nematodes. Much of the information on predatory nematodes is based on agar plate experiments; limited data are available on predation in soil. Small and Grootaert (1983) emphasized that studies on predatory nematodes as biocontrol agents should concentrate on

the migratory stages of endoparasitic nematodes as these are more susceptible to predation. This view was also supported by the findings of Khan *et al.* (1991, 1994, 1995a, b), Bilgrami (1992, 1993), and Bilgrami *et al.* (2005). Predation rate often depends on chance encounter and thus density dependent (Yeates 1969, Osman 1989, Bilgrami 1993). It may be assumed that impact of predatory nematodes as biocontrol agent may increase during the peak season of hatching/ emergence of plant parasitic nematodes, especially of endoparasitic nematodes under field conditions.

Biological control potential and efficacy of predatory nematodes vary with their groups. Mononchs because of their long life cycle, low fecundity, susceptibility to changing environmental conditions and cannibalistic behavior do not fulfill the requirements of an efficient biological control agent. On the other hand, the advantage of dorylaim, nygolaim and other stylet-bearing predators lied in their wide spread natural occurrence and easy mass culturing due to their polyphagous feeding habits. Also, their population may be elevated in the field by adding organic materials. However, more field studies are needed to confirm this hypothesis. Their long life cycle and low rate of fecundity are also causes of concern.

The real possibility of using predatory nematodes in biological control of nematodes lies in diplogasterid predators, due to their chemotaxis sense and high rates of predation, short life cycles, high fecundity and easy culture. In addition, they are polyphagous and form dauer larvae under adverse conditions (Bilgrami and Jairajpuri 1990). These groups of predators are likely to offer the most promising as augmentative agents in colonization efforts in combination with cultural practices, such as cover crop, green manuring or organic amendment and plant resistance. The immediate need is to assess the diversity of predacious species present in different agro-climatic regions. The efforts should include identification of the predatory nematode species that are well adapted to local climates and develop sustainable techniques for their mass culturing, formulation, and time and mode of application. The effectiveness of predatory nematodes can be tested on migratory stages of endoparasitic nematodes. After testing predation potential in pot experiments, field experiments need to be conducted and, if results are encouraging, properly designed multi-location trials should be initiated. Greater research and development and extension efforts are required to identify and popularize this environmentally friendly nematode pest management approach.

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