ANADOLU ÜNİVERSİTESİ BİLİM VE TEKNOLOJİ DERGİSİ ANADOLU UNIVERSITY JOURNAL OF SCIENCE AND TECHNOLOGY

Cilt/Vol.:8-Sayı/No: 1 : 1-12 (2007)

REVIEW / DERLEME

BIOLOGICAL CONTROL OF PLANT PARASITIC NEMATODES

Mehmet KARAKAŞ¹

ABSTRACT

Many different bacteria and fungi have been able to reduce population density of some kinds of plant parasitic nematodes under laboratory conditions but successes at field scale are rare. Most organisms recognized to be promising for biological control of plant parasitic nematodes are quite specific in which nematodes they will attack or have been very diffucult to culture in sufficient quantities to be useful for field application or both. The conditions under which each is most effective are often quite specific and limited. In all, then, commercially effective biological control as a means to reduce the effects of plant parasitic nematodes on laws still appears to be many years away.

Keywords: Biological control, Plant parasitic Nematodes, Feeding

BİTKİ PARAZİTİ NEMATODLARIN BİYOLOJİK KONTROLÜ

ÖZ

Farklı birçok bakteri ve mantar, laboratuvar koşullarında, bazı bitki paraziti nematodların populasyon yoğunluğunu azaltabilmektedir. Fakat tarla denemelerinde bu başarı oldukça düşüktür. Bitki paraziti nematodların biyolojik kontrolü için tanımlanmış birçok organizma, oldukça spesifik olup, bunların nematodları sınırlayıcı etkisi ya da verimli bir tarla uygulaması için kültürlerinin yapılması oldukça zordur. Bu şartlar etkin bir biyolojik kontrol için de tamamen spesifik ve sınırlayıcıdır. Bunlara ilaveten, kanunlar kapsamında ticari açıdan etkin bir biyolojik kontrolün uygulamaya geçmesi de, birkaç yıl daha alacak gibi gözükmektedir.

Anahtar Kelimeler: Biyolojik kontrol, Bitki paraziti, Nematodlar, Beslenme

Geliş: 03 Mayıs 2004; Düzeltme: 05 Eylül 2006; Kabul: 03 Nisan 2007

¹, A.Ü. Fen Fakültesi Biyoloji Bölümü 06100 Tandoğan-ANKARA **E-posta:** mkarakas@science.ankara.edu.tr.

1. INTRODUCTION

For many reasons, nematode management is not and should not be a matter of simply identifying a specific pest and then applying a chemical nematicide that is effective against it. There are many situations for which no safe, effective chemical nematicide is available. Most chemical nematicides are relatively toxic, so they are hazardous to people, pets and other animals if handled carelessly (Thomason, 1987). Most nematicides are environmentally risky because of their toxicity. Unfavorable environmental conditions and events can make all nematicides less effective than expected (Eddaoudi and Bourijate, 1998). Nematicides are expensive. Many cultural practices can effect how seriously nematodes affect a planting and how effective nematicides are if they must be used (Bridge, 1987).

Carefully combining many of the practices into an integrated nematode management program often will help keen nematodes below damaging levels and improve effectiveness of nematicides if they are available and must be used (Reddy et.al., 1997; Rao et.al., 1998; Abou-Jawdah et.al., 2000; Bulluck and Ristaino 2002).

Many different bacteria and fungi that are nematodes-natural enemies have been isolated from nematode populations apparently being kept a low levels by the bacteria and fungi. Nematologists have been able to use some bacteria and fungi to reduce populations of some kinds of nematodes under laboratory conditions but successes at the full-scale field level have been few (Liu and Chang, 2000a; 2000b; Galper et.al., 1995).

Various aspects of biological control of plant parasitic nematodes have been reviewed a number of times (Christie, 1960; Esser and Sobers, 1964; Boosalis and Mankau, 1965; Sayre, 1971; Mankau, 1972; Webster,1972; Mankau,1980; Spiegel, 2005). But the numerous recent developments in this area and the impending loss of several of the most widely used nematicides for reasons of hazards to human health have prompted this examination of the status of natural enemies for control of nematode pests.

Many natural enemies attack plant parasitic nematodes in soil and reduce their populations (Deacon, 1991). It is important to determine the nature and extent of such constraints on nematode multiplication in order to establish whether these enemies can be exploited to reduce damage and increase crop yields. Detailed studies on biological control of nematodes are few but some general principles have emerged and there are well documented cases where effective biological control has been established (Sayre and Walter, 1991).

The term "biological control" in the classical sense is defined by De Bach (1964) as the action of parasites, predators or pathogens in maintaining other

organism's population density at a lower average than would occur in their absence. Commonly more than one microorganism occurs with plant parasitic or saprozoic nematodes in a particular rhizosphere (Sikora, 1992). Constant association of these organisms in a given ecological niche undoubtedly has a greater impact on the establishment of such nematodes than would be caused by each microorganism alone (Kerry, 1990). Such association results in a biological balance that may manifest itself in the form of direct parasitism by attachment and penetration by one or more pathogenic microorganisms in the eggs, juveniles or adult nematodes, causing death and possibly allowing subsequent invasion by many or selected saprophytic microorganisms (Stirling, 1991). Egg masses, sedentary females or cysts may be directly invaded by pathogenic or some opportunistic organisms that draw their nutrients from the mucilaginosus compounds present in the invaded body or indirectly invaded by the action of toxic, diffisuble metabolites produces by one or more organisms on various developmental stages of nematodes. These toxins often render nematodes (particularly eggs and juveniles) more vulnerable to infection or to the activities of organisms that are either nonvirulent, slightly pathogenic or basically saprophytic in nature (Spiegel et.al., 1991).

Soil fauna includes diverse groups of microorganisms in constant association with similarly diverse genera and species of free living and plant parasitic nematodes (Hussey, 1990). Free living nematodes, in general, are the more numerous of the two and play very important roles in soil biology. Many of the soil microorganisms, such as fungi are specialized to infect only the free living nematodes (Kerry, 1987). Spores of these organisms must be ingested by the nematode hosts prior to their germination in the esophagus and their eventual consumption of the nematode (Aschnar and Kohn, 1958). These organisms are generally excluded as potential biocontrol agents of plant parasitic nematodes.

2. BIOCONTROL AGENTS

2.1 Viruses

Our knowledge of viral diseases of nematodes is limited, partly owing to our imperfect methods of nematode recovery, which rarely allow the isolation of inactive or virus infected nematodes. Some viruses are commonly associated with the stylets and the esophagi of several species of *Xiphinema*, *Longidorus*, *Trichodorus* and *Paratrichidorus* for short periods of time. But no pathogenic activities by these viruses have been observed (Mankau, 1980).

Loewenberg et. al. (1959), reported sluggishness of *Meloidogyne incognita*, presumably caused by a virus that had passed through the bacteriological filter. Juveniles of this nematode were incapable of forming galls. However no virus particles were found in the

diseased nematodes. The phenomenon of the nematode swarming in *Tylenchorhynchus martini* was attributed to the virus particles found on the surface of the cuticle in the hypodermis and muscle layers, and in the digestive and reproductive systems (Mc Bride and Hollis, 1966; Ibrahim et.el., 1973). The same authors suggested that the virus renders the swarming nematode more susceptible to chemicals and other adverse conditions. Nematod pathogenic viruses might be operative but have escaped our detection.

2.2 Rickettsias

Rickettsias are intracellular bacteriumlike microorganisms that have been reported in *Heterodera* goettingina, Globedera roctochiensis and Heterodera glycines (Ibrahim and Hollis, 1973; Endo, 1979; Shepherd et.al., 1973; Walsh, 1979; Walsh et.al., 1983). These microorganisms appear identical and they resemble a companion symbiont of leafhoppers. They have been reported to be transmitted transovarially from generation to generation (Walsh, 1979). Despite their presence in the sperm cells they cannot be transmitted from one generation to the next (Walsh, 1979; Walsh et.al., 1983). Some rickettsias are pathogenic to insects and multiply in specialized cellular structures called mycetomes which are not found in *Heterodera*. The role of *Xiphinema* index as a possible vector of these microorganisms has been (Rumbos et.al.. 1977). Additional information is needed to define the role of these microorganisms in the control of nematodes.

2.3 Bacteria

Reports of bacterial diseases of nematodes are largely records of the observation of bacteria within the body cavity, gut and gonads of individual nematodes (Dollfus, 1946). These observations, however did not distinguish between the parasitic and saprophytic forms. Mankau (1981) observed what appeared to be a bacterial symbiont in the ovaries of Xiphinema Trichidorus sp., americanum Xiphinema silvaticum. These mycetomes are apparently bacterial aggregates, behaving as an individual organism enclosed in the host cell or mycetocyte. The role of these organism in preventing egg production is yet to be determined. Infection of Xiphinema americanum juveniles by Pseudomonas denitrificans was reported by Adams and Eichenmuller (1963). Although these authors suggested the possibility of transovarian transmission, their findings on the status of ovarian abnormalities are inconclusive. Others reported the association of some bacteria with the nematode cuticle (Dollfus, 1946; Ketznelson et.al., 1964; Banage, 1965; Mankau and Das, 1974). However, the role these bacteria may play in reducing the population of plant parasitic nematodes is unknown.

The bacterial parasite of nematodes, *Pasteuria* penetrans probably received the most attention and research effort in recent years (Pembroke et.al., 1998;

Regina et.al., 1999; Hallmann, 2001; Burelle and Samac, 2003). It was first described by Thorne (1940) as a sporozoan, Duboscqia penetrans. Its procaryotic and bacterial affinities were established later and the name Bacillus penetrans was adopted (Mankau, 1975; Imbriani and Mankau, 1977; Sayre and Wergin, 1977). Pasteuria penetrans is probably the most specific obligate parasite of nematodes, with a life cycle remarkably well adopted to parasitism of certain plant nematodes (Mankau and Imbriani, 1975). Apparently there is a synchronization of this organism with the development and physiology of its host, Meloidogyne species (Netscher and Duponnois, 1998; Samaliev, 1997). Spores attach to the cuticle of the juveniles with germination occuring approximately eight days after the infected nematodes penetrate the root system (Sayre and Wergin, 1977). Approximately % 30 of the attached spores germinate (Stirling, 1984). The germ tubes penetrate the cuticle, giving rise to spherical dichotomously branched thalli or microcolonies that eventually fragment to daughter colonies. These continue to poliferate in the pseudocoelum, eventually filling the body cavity of the developing female (Mankau, 1980). Upon the decomposition of the dead females, spores are liberated in the soil and remain there for long periods of time until contacted by another nematode.

Pasteuria penetrans exerts various degrees of nematode biocontrol under greenhouse and field conditions (Mankau, 1975; Mankau, 1981; Nishizawa, 1984; Sayre, 1980; Stirling, 1984; Stirling and Wachtel, 1980; Williams, 1967; Devappa et.al., 1997). Repeated cultivations of susceptible annual of perennial crops tend to increase the bacterial inoculum (Nishizawa, 1984; Stirling and White, 1982; Williams, 1967). The mass production method of this organism was greatly improved by Stirling and Wachtel (1980). Its ability to attack important parasitic nematodes of several crops, to persist in soil for long periods of time, to resist desiccation and temperature extremes, as well as its compatibility with several pesticides, are ideal characteristics for its candidacy as successful biocontrol agent. Recent developments in genetic engineering research and tissue culture practices provide interesting possibilities for the commercial mass production of this organism (Oostendorp and Sikora, 1989; Esnard et.al., 1997; Chen et.al., 1997; Orui, 1997; Pembroke et.al., 1998; Regina et.al., 1999; Duponnois et.al., 1999; Reitz et.al., 2000; Wei et.al., 2003).

2.4 Fungi

The fungal antagonists of nematodes consist of a great variety of organisms which include the nematode trapping or predacious fungi, endoparasitic fungi, parasites of nematode eggs, parasites of nematode cysts and fungi that produce metabolites toxic to nematodes (Wheeler et.al., 1992). Is is remarkable that fungi belonging to widely divergent orders and families occur in each of the above groups. Predacious, parasitic and biochemical relationships with nematodes

have evolved among almost all major groups of soil fungi from the *Phycomycetes* to the *Basidomycetes*. Considering the long coevolution of nematodes and fungi which obviously occurred in the close confines of the soil habitat, it is not surprising that a great variety of interrelationships have developed between the two groups. A very complete and readable account of these interesting organisms was published in a small book on the nematode destroying fungi by Barron (1975).

In nature, fungi continuously destroy nematodes in virtually all soils. Microbial and fungal control of nematodes is very important biologically and in some circumstances economically (Kerry and de leij, 1992). However, there are great technical problems in observing and assessing the importance of these organisms; these include the complexities of the soil habitat, the specialized techniques required to extract, count and isolate the fungal antagonists and the fact that many of these organisms are obligate parasites or do not sporulate readily.

Some fungus species, for example, have spores that must be ingested by the nematod host (Kerry, 1988). These spores then germinate in the esophagus and eventually develop and consume the nematode (Aschner and Kohn, 1958). Such fungi generally do not infect plant parasitic nematodes which feed through a stylet with a relatively minute aperture that is far smaller than even the minutest fungal spores.

The spores inject the infective cell particle through the cuticle of passing nematodes upon mechanostimulation. Davidson and Barron (1973), have described the process in detail.

The unique hyphal adaptations which make up the traps of predacious fungi are quite familiar and there is no need to redescribe them here but some studies have revealed the interesting fact that in many species the traps or infection pegs which penetrate captured nematodes give off a substance or toxin which immobilizes a nematode almost immediately (Olthof and Estey, 1963; Balan and Gerber, 1972; Krizkova et.al., 1976; Duponnois et.al., 2001; Sharon et.al., 2001; 2003). There are also fungi which apparently immobilize or intoxicate nematodes without any direct contact with the hyphae (Giuma and Cooke, 1971; 1973). In addition, some predacious fungi have trapping organs which give off substances attractive to nematodes (Balan and Gerber, 1972; Field and Webster, 1977; Jansson and Nordbring-Hertz, 1979). There are also appears to be good evidence that the assimilative or haustorial hyphae of a trapping fungus found within the nematode release an antibiotic which prevents the development of competing microorganisms in the captured nematode (Barron, 1975). There are a number of natural openings such as the buccal cavity, excretory pore, vulva and anus through which secondary microorganisms can enter moribund nematodes; however in nematodes captured in the hyphal traps of most species of predacious fungi,

competing organisms seldom or never develop. The body contents of captured nematodes are consumed until only an empty cuticle remains that is filled with the assimilative hyphae which eventually lyse. No enter organisms develop in the victim. Most attempts to produce inoculum on a commercial scale or for experimental soil colonization have concentrated on the production of mycelia and conidia but these may have very limited survival when introduced into soil (Abu-Laban and Saleh, 1992). Some soils are very fungistatic towards predacious fungi (Mankau, 1962). In general the entire group is considered to be rather poor saprophytic competitors in the soil habitat.

Catenaria auxiliaris was first described in 1877 by Kühn in the females of beet cyst nematode Heterodera schachtii. It was not that reduction of the population of cereal cyst nematode Heterodera avenae to a nondamaging level was attributed to the infection of females by Nematophthora gynophila (Kerry, 1974; Kerry and Crump, 1977). Catenaria auxiliaris can also parasitize females of Heterodera avenae and Globodera rostochiensis (Kerry, 1975; Kerry et.al., 1976). Nematophthora gynophila infected Heterodera carotae, Heterodera cruciferae, Heterodera goettingiana, Heterodera schachtii and Heterodera trifolii but did not infect Globodera rostochiensis under glasshouse conditions (Kerry and Crump, 1977).

Verticillum chlamydosporium was found to parasitize the developing females of Heterodera avenae prior to their egg production stages (Kerry, 1980; Irving and Kerry, 1986; de leij and Kerry, 1991; Kerry, 1991; de leij, 1992; de leij et al., 1992; 1992)

Morgan-Jones et.al. (1981), reported *Verticillum chlamydosporium* as an effective parasite of maturing females and eggs of *Meloidogyne arenaria*.

Chaetomium cochloides, Exophiala pisciphila, Fusarium oxysporum, Fusarium solani, Phytophthora cinnomomi, Trichosporon beigelii, Pythium sp. and a sterile mycelium were found to be associated with females and precyst stages of Heterodera glycines (Gintis et.al., 1983).

Jatala et. al. (1979), reported that the penetration of *Meloidogyne incognita* females by *Paecilomyces lilacinus* is generally through the anal or vulval openings. *Paecilomyces lilacinus* was also found in the females of *Tylenchulus semipenetrans* and in adult females of *Nacobbus aberrans* (Bansal et al., 1988). *Dactylella oviparasitica*, an egg parasite, can occasionally parasitize *Meloidogyne* females, particularly on hosts where the egg production is relatively slow (Mankau, 1981).

Destruction of nematode eggs by Fusarium and Cephalosporium species was first noted by Lysek (1963). Later he reported that Verticillum chlamydosporium, Verticillum bulbillosum, Mortierella nana, Paecilomyces lilacinus, Acremonium bacillosporum

and *Helicoon farinosum* were able to perforate eggshells and enter eggs of nematodes (Lysek, 1966).

The discovery of fungi parasitic on the eggs of plant parasitic nematodes has been very recent. Several organisms have been reported to parasitize eggs of plant parasitic nematodes (Tribe, 1977; 1979; Stirling and Mankau, 1978; Nigh et.al., 1980; Morgan-Jones et.al., 1981; Godoy et.al., 1982). Although the majority of these organisms are associated with the eggs and cysts of important plant parasitic nematodes, their efficiency in and adaptability to different soil environmental conditions vary (Jatala, 1985).

2.5 Predacious Nematodes

Predacious nematodes are probably very important influences in the population dynamics of numerous species of soil nematodes since their biomass in some soils is substantial but their role in biological control of plant parasitic nematodes is virtually unknown (Grewal and Lewis, 1999). Nematodes in the Mononchida, Dorylaimida and Diplogasteroidea are largely predacious although the actual feeding habits of most species is unknown. An obligatory predatory genus Seinura, occurs in the Aphelenchoidea. Predacious nematodes are characterized by either a large open stoma armed with teeth or dendicles which are used in seizing and ripping open prey or swallowing them whole or a pharynx equipped with an onchiostyle, stomatostyle or mural tooth for piercing prey. These features and certain lip region characters are modified into an amazing number of variations for which the specialized functions are almost completely unknown. Small Seinura spp. can kill nematodes much larger than themselves because of their ability to paralyze the prey. The prey is inactivated almost immediately after the stylet is inserted. Repeated secretions of the dorsal esophagal gland pass into the victim during feeding and digest the body contents (Hechler, 1963). Earlier reviewers have presented highly variable views about the importance of predacious nematodes but all have generally lamented lack of imformation about their biology (Boosalis and Mankau, 1965; Christie, 1960; Esser and Sobers, 1964; Sayre, 1971; Webster, 1972; Shapiro and Lewis, 2000).

Nematodes are often observed in the gut contents of mononchs and are presumed to be the principal feed of many species. The *Diplogasteroidea* can be both microbial feeders and predators (Yeates, 1969).

Selective predation may be releated more to a relative abundance of alternative food sources than to the presence of prey nematodes. When nematodes are preyed upon, the prey species consumed are probably determined by such factors as prey size and mobility (Nelmes, 1974).

As possible biocontrol agents for plant parasitic nematodes, the *Mononchida* have attracted more attention than any of the other soil inhabiting

predators. Steiner and Heinly (1922) observed that Clarkus papillatus fed voraciously on Meloidogyne sp. in vitro, survived well in dry soil and is a hermaphrodite which may faciliate the rapid build up of its populations in soil. Thorne (1927) also studied Clarkus papillatus and recorded voracious feeding on Heterodera schachtii larvae and observed that it and three other mononchid species often occurred in large populations in sugar beet fields. Nelmes (1974) observed that larvae of Aphelenchus avenae appears to be a suitable prey for many mononchs. Cohn and Mordechai (1974) noted that Mylonchulus sigmaturus, a cosmopolitan species, interfered with a routine culture of the citrus nematode, Tylenchulus semipenetrans. In laboratory tests the nematode fed on Tylenchulus semipenetrans and Meloidogyne javanica but not on Helicotylenchus multicinctus or Longidorus africanus and in pot tests small populations of Tylenchulus semipenetrans were always associated with large populations of Mylonchulus sigmaturus, although the predation was insufficient to reduce damage to sour orange seedlings. Small (1979) also obtained evidence of predation by Prionchulus punctatus on Meloidogyne incognita in pot tests and partial control as evidenced by a significant reduction in galling of tomato roots in treatments where the predator was added but no significant difference in overall growth of the plants.

The *Dorylaimida* are frequently abundant in soils although their numbers and species diversity appears to decline in soils disturbed by frequent agricultural operations. Stirling and Mankau (1977) recorded and species of dorylaims which had common or moderately occurrence in citrus orchard soils. One of these species *Thornia sp.* had been studied earlier (Boosalis and Mankau, 1965) for its effect as a biological control agents of the citrus nematode, *Tylenchulus semipenetrans*. Predacious nematodes may contribute towards natural control in some situations (Azmi, 1983). But as with other predators, problems in their mass production an application to soil would prevent their use as induced biological control agents.

2.6 Tardigrates, Turbellarians, Collembola, Mites, Enchytraeids, Protozoa

These are a complex group of naturally occuring organisms that are found in varying densities in many agricultural soils. Because of their active mobility in the soil, their capability to search for prey is significantly higher than that of predacious fungi. Predation of plant parasitic nematodes by tardigrates was observed by several investigators (Hutchinson and Streu, 1960; Doncaster and Hooper, 1961; Sayre, 1971).

Turbellarians are carnivorous flatworms that feed on nematodes and other soil organisms. The feeding of *Meloidogyne incognita* by *Adenoplea sp.* was observed by Sayre and Powers (1966). They concluded that although addition of *Adenoplea sp.* decreased the root-

galling index, it was insufficient to be of practical value

Collembola and mites are probably the most numerous arthropods around plant roots and in decaying organic material. Feeding of plant parasitic nematodes by these organisms is reported by various investigators (Sharma, 1971; Muraoka and Ishibashi, 1976; Mankau and Imbriani, 1978; Inserna and Davis, 1983). The collembola *Onychiurus armatus* were observed to perforate the cysts of *Heterodera cruciferae*, enter them and devour the nematodes within them (Muraoka and Ishibashi, 1976).

Mites were also observed to damage the *Heterodera sp.* cysts (Murphy and Doncaster, 1957). Apparently mites exhibit density dependent traits of effective and specific predators. There are an increase of nematode prey (Imbriani and Mankau, 1983) The ability of mites to use fungi as alternative food sources in the absence of nematodes is an advantageous characteristic. However, their role as effective biocontrol organisms for limiting the population of plant parasitic nematodes is yet to be understood.

Although enchytraeids are reportedly possible antagonists of nematodes, their role in actual predation of plant parasitic nematodes has not yet been determined. Similarly, some predacious amoeboid protozoans are reported to prey on several plant parasitic nematodes (Winslow and Williams, 1957; Doncaster and Hooper, 1961; Esser and Sobers, 1964; Webster, 1972). The extent to which these organisms can be efficient and economically imported is not known.

3. CONCLUSION

Although the potential for biological control of plant parasitic nematodes is great, it has yet to be widely exploited. Perhaps one of the main reason why the use of biological control agents in the nematode management system has not been received with much enthusiasm is its lack of spectacular results, compared to the results of the nematicides. Investigators hesitations and limitations for field applications of the organisms due to bureaucratic regulations, have limited the exploitation of the biocontrol agents in the nematode management practices (Jairajpuri et.al., 1990; Duncan, 1991).

The biological control of plant parasitic nematodes has largely followed the classical approach utilizing pathogens and predators to kill particular pest species. This approach will probably continue to form the basis of future research, particularly if successes can be achieved by using other treatments to stress nematodes, making them more susceptible to attack by biological agents (Wei et.al., 2003). However, other means already explored by plant pathologists (Cook, 1985) seem worthy of consideration. The biological protection of plant surfaces, preventing pathogen invasion of the host, has been used to protect leaves,

pruning wounds and roots from bacterial and fungal diseases. But their potential as a biological control agents is not clear.

Opportunities in genetic engineering may extend to producing more effective biological control agents for plant parasitic nematodes (Piotte et.al., 1992). Already, a genetically manipulated agent has been produced in the United States of America to protect frost sensitive plants from damage by ice-nucleating bacteria (Cook, 1985) and the toxin gene from the insect pathogen Bacillus thuringiensis has been transferred to the root-colonizing bacterium Pseudomonas fluorescens (Beardsley, 1984). Also ultraviolet radiation has been used to produce fungicide-tolerant mutants of some fungi and coincidentally increase their efficacy as biological control agents over that of the wild strains (Papavizas et.al., 1982; Gaspard and Mankau, 1985).

Given such enlightened support biological control could play an important part in the future management of many of major plant parasitic nematodes (Roberts, 1993). All told, the proper and efficient utilization of biocontrol agents in suppressing nematode populations is a great challenge. Removal of the obstacles in achieving our goals can only be attained by dedication, persistence and hard work.

REFERENCES

- Abou-Jawdah, Y., Melki, K., Hafez, S.L., Sobh, H., El-Masri, Y. and Sundararj, P. (2000). Alternatives to methyl bromide for root-knot nematode management on cucumber in Lebanon. *Nematropica* 30, 41-45.
- Abu-Laban, A.Z. and Saleh, H.M. (1992). Evaluation of animal manures for mass production, storage and application of some nematode egg-parasitic fungi. *Nematologica* 38, 237-244.
- Adams, R.E. and Eichenmuller, J.J. (1963). A bacterial infection of *Xiphinema americanum*. *Phytopathology* 53, 745.
- Aschner, M. and Kohn, S. (1958). The biology of *Harposporium anguillulae. Gen. Microbiol.* 19, 182-189.
- Azmi, M.I. (1983). Predatory behavior of nematodes. I. Biological control of *Helicotylenchus dihyste-ra* through the predacious nematodes, *Iotonchus monhystera*. *Indian J. Nematol.* 13, 1-8.
- Balan, J. and Gerber, N.N. (1972). Attraction and killing of the nematode *Panagrellus redivivus* by the predaceous fungus *Arthrobotrys dactyloides*. *Nematologica* 18, 163-173.
- Banage, W.B. (1965). Notes on the bacterium *Clostridium pasteurianum* affecting a free living nematode. *E. Afr. Agric. For. J.* 30, 311-313.

- Bansal, R.K., Walia, R.K. and Bhatti, D.S. (1988). Evaluation of some agro-industrial wastes for mass propagation of the nematode parasitic fungus *Paecilomyces lilacinus*. *Nematol. Medit.* 16, 135-136.
- Barron, G.L. (1975). The nematode destroying fungi: Guelph, Canada: *Can. Biol. Publ.* 140p.
- Beardsley, T. (1984). Genetic pesticides. *Nature* 312, 686
- Boosalis, M.G. and Mankau, R. (1965). Parasitism and predation of soil microorganisms. *In Ecology of Soil Borne Plant Pathogens* 6, Eds. K.F. Baker and W.C. Snyder, Univ. Calif. Press. 571 p, ss.374-389, Barkeley
- Bridge, J. (1987). Control strategies in subsistence. *Principles and practice of nematode control in crops*, Eds. R.H. Brown and B.R. Kerry, pp. 389-420, Academic Press, Sydney, Australia.
- Bulluck, L.R, Ristaino, J.B. (2002). Effect of synthetic and organic fertility amendments on southern blight, soil microbial communities, and yield of processing tomatoes. *Phytopathology* 92, 181-189.
- Burelle, N.K. and Samac, D.A. (2003). Use of grampositive bacteria as biological control agents for plant parasitic nematodes. *J. Nematol.* 35, 347-348
- Chen, Z.X., Dickson, D.W., Mitchell, D.J., McSorley, R. and Hewlett, T.E. (1997). Suppression mechanisms of *Meloidogyne arenaria* race 1 by *Pasteuria penetrans. J. Nematol.* 29, 1-8.
- Christie, J.R. (1960). Biological control-predacious nematodes. *Nematology.Fundamentals and Recent Advances with Emphasis on Plant Parasitic and Soil Forms* 46, pp. 466-468, Eds. J.H. Sasser and W.R. Jenkins, Chapel Hill, NC, Univ.North Carolina Press.
- Cohn, E. and Mordechai, M. (1974). Experiments in suppressing citrus nematode populations bt use of a marigold and a predacious nematode. *Nematol. Mediterr.* 2, 43-53.
- Cook, R.J. (1985). Biological control of plant pathogens: Theory to application. *Phytopathology* 75, 25-29.
- Davidson, J.G.N. and Barron, G.L. (1973). Nematophagous fungi: *Hoptoglossa. Can. J. Bot.* 51, 1317-1323.
- Deacon, J.W. (1991). Significance of ecology in the development of biocontrol agents against soilborne plant pathogens. *Biocon. Sci. Technol.* 1, 5-10.

- De Bach, P. (1964). *Biological control of insect pests and weeds*. London: Chapman and Hall, 213 p.
- de Leij, F.A.A.M. (1992). Significance of ecology in the development of *Verticillium chlamydosporium* as a biological control agent against rootknot nematodes (*Meloidogyne* spp.). University of Wageningen, the Netherlands. (Ph.D. thesis)
- de Leij, F.A.A.M. and Kerry, B.R. (1991). The nematophagous fungus, *Verticillium chlamydosporium* as a potential biological control agent for *Meloidogyne arenaria*. *Revue Nematol*. 14, 157-164.
- de Leij, F.A.A.M., Davies, K.G. and Kerry, B.R. (1992). The use of *Verticillium chlamydosporium* and *Pasteuria penetrans* alone and in combination to control *Meloidogyne incognita* on tomato plants. *Fund. Applied Nematol.* 15, 235-242.
- de Leij, F.A.A.M., Dennehy, J.A. and Kerry, B.R. (1992). The effect of temperature and nematode species on interaction between the nematophagous fungus *Verticillium chlamydosporium* and root-knot nematodes (*Meloidogyne* spp.). *Nematologica* 38, 65-79.
- Devappa, V., Krishnappa, K. and Reddy, B.M.R. (1997). Management of root-knot nematode *Meloidogyne incognita* in sunflower. *Mysore Journal of Agricultural Sciences* 31, 155-158.
- Dollfus, R.P. (1946). Parasites des Helminthes. In Encyclopedie Biologique, ed. P. Lechevalier, Paris Vol. 27, 482 p.
- Doncaster, C.C. and Hooper, D.J. (1961). Nematodes attacked by protozoa and tardigrades. *Nematologica* 6, 333-335.
- Duncan, L.W. (1991). Current options for nematode management. *Annu. Rev. Phytopathol.* 29, 469-490.
- Duponnois, R., Amadou, M. and Thierry, M. (1999). Beneficial effects of Enterobacter cloacae and *Pseudomonas mendocina* for biocontrol of *Meloidogyne incognita* with the endospore-forming bacterium *Pasteuria penetrans. Nematology* 1, 95-101.
- Duponnois, R., Chotte, J.L. and Sall, S. (2001). The effect of organic amendments on the interactions between a nematophagous fungus *Arthrobotrys oligospora* and the root-knot nematode, *Meloidogyne mayaguensis* parasitizing tomato plants. *Biological Fertilization Soils* 34, 1-6.
- Eddaoudi, M. and Bourijate, M. (1998). Comparative assessment of *Pasteuria penetrans* and three nematicides for *Meloidogyne javanica* and their

- effect on yields of successive crops of tomato and melon. *Fundamental and Applied Nematology* 21, 113-118.
- Endo, B.Y. (1979). The ultrastructure and distribution of an intracellular bacterium-like microorganisms in tissues of larvae of the soybean cyst nematode, *Heterodera glycines*. *J. Ultrastruct*. *Res.* 67, 1-14.
- Esnard, J., McClure, M.A., Dickson, D.W., Hewlett, T.E. and Zuckerman, B.M. (1997). Effects of monoclonal antibodies cationized ferritin and other organic molecules with *Pasteuria penetrans* endospores to *Meloidogyne incognita*. *J. Nematol.* 29, 556-564.
- Esser, R.P. and Sobers, E.K. (1964). Natural enemies of nematodes. *Soil Crop. Sci. Soc. Pla. Proc.* 24, 326-352.
- Field, J.I. and Webster, J. (1977). Traps of predacious fungi attract nematodes. *Trans. Br. Mycol. Soc.* 68, 467-469.
- Galper, S., Eden, L.M., Stirling, G.R. and Smith, L.J. (1995). Simple screening methods for assessing the predacious activity of nematode-trapping fungi. *Nematologica* 41, 130-140.
- Gaspard, J.T. and Mankau, R. (1985). Induced benomyl resistance in *Paecilomyces lilacinus* and *Verticillium chlamydosporium*. *J. Nematol*. 17, 496.
- Gintis, B.O., Morgan-Jones, G. and Rodriquez-Kabana, R. (1983). Fungi associated with several developmental stages of *Heterodera glycines* from an Alabama soybean field soil. *Nematropica* 13, 181-200.
- Giuma, A.Y. and Cooke, R.C. (1971). Nematoxin production by *Nematoctonus haptocladus* and N. concurrens. *Trans. Br. Mycol. Soc.* 56, 89-94.
- Giuma, A.Y. and Cooke, R.C. (1973). Thermostable nematoxins produced by germinating conidia of some endozoic fungi. *Trans. Br. Mycol. Soc.* 60, 49-56.
- Godoy, G., Rodriquez-Kabana, R. and Morgan-Jones, G. (1982). Parasitism of eggs of *Heterodera glycines* and *Meloidogyne arenaria* by fungi isolated from cysts of *H. glycines. Nematropica* 12, 111-119.
- Grewal, P.S., Lewis, E.E. and Venkatachari, S. (1999). Allelopathy: A possible mechanism of suppression of plant parasitic nematodes by entomopathogenic nematodes. *Nematology* 1, 735-743.
- Grewal, P.S., Miller, R., Martin, R. and Lewis, E.E. (1997). Summary of field trials for entomopa-

- thogenic nematodes as biological control agents of plant parasitic nematodes. *Biological Control Science and Technology* 7, 393-399.
- Hallmann, J. (2001). Plant interactions with endophytic bacteria. *Biotic interactions in plant-pathogen interactions*, Eds. Jeger, M.G.and Spence N.J., Pb. 87-119, CAB International, Wallingford, UK.
- Hechler, H.C. (1963). Description developmental biology and feeding habits of *Seinura tenuicaudata* (de Man) J.B. Goodey, 1960 (Nematoda: Aphelenchoididae) a nematode predator. *Proc. Helminthol. Soc. Wash.* 30, 182-195.
- Hussey, N.W. (1990). Agricultural production in the third world a challenge for natural pest control. *Exp. Agric*. 26, 171-183.
- Hutchinson, M.T. and Streu, H.T. (1960). Tardigrades attacking nematodes. *Nematologica* 5, 149.
- Ibrahim, I.K.A. and Hollis, J.P. (1973). Electron microscope studies on the cuticle of swarming and non-swarming *Tylenchorhynchus martini*. *J. Nematol.* 5, 275-281.
- Ibrahim, I.K.A., Joshi, M.M. and Hollis, J.P. (1973). The swarming virus disease of *Tylenchorhynchus martini*. *Int. Congr. Plant Pathol*. Minneapolis, Minn. Abstr., 555 p.
- Imbriani, J.L. and Mankau, R. (1977). Ultrastructure of the nematode pathogen, *Bacillus penetrans*. *J. Invertebr. Pathol.* 30, 337-347.
- Imbriani, J.L. and Mankau, R. (1983). Studies on *Lasioseius scapulatus*: A Mesostigmatid mite predacious on nematodes. *J. Nematol.* 15, 523-528.
- Inserra, R.N. and Davis, D.W. (1983). Hypoaspis nr. aculeifer: A mite predacious on root knot and cyst nematodes. *J. Nematol.* 15, 324-325.
- Irving, F. and Kerry, B.R. (1986). Variation between strains of the nematophagous fungus, *Verticillium chlamydosporium* Goddard. II. Factors affecting parasitism of cyst nematode eggs. *Nematologica* 32, 474-485.
- Jairajpuri, M.S., Alam, M.M. and Ahmad, I. (1990). *Nematode bio-control*. CBS Publ. and Distr. Pvt. Ltd., 152 p., Delhi, India
- Jansson, H.B. and Nordbring-Hertz, B. (1979). Attraction of nematodes to living mycelium of nematophagous fungi. *J. Gen. Microbiol.* 112, 89-93.
- Jatala, P. (1985). Biological control of nematodes. An Advanced Treatise on Meloidogyne, *Biology* and control 1, Eds. J.N. Sasser and C. Carter. North Carolina State Graphics, pp. 303-308.

- Jatala, P., Kaltenbach, R. and Bocangel, M. (1979). Biological control of *Meloidogyne incognita* acrita and *Globodera pallida* on potatoes. *J. Nematol.* 11, 303.
- Kerry, B.R. (1974). A fungus associated with young females of the cereal cyst nematode, *Heterodera* avenae. Nematologica 20, 259-260.
- Kerry, B.R. (1975). Fungi and the decrease of cereal cyst nematode population in cereal monoculture. *EPPO Bull.* 5, 353-361.
- Kerry, B.R. (1980). Biocontrol; fungal parasites of female cyst nematodes. *J. Nematol.* 12, 253-259.
- Kerry, B.R. (1987). Biological control, Eds. R.H. Brown and B.R. Kerry. Biological control of nematodes: Prospects and opportunities. Principles and practice of nematode control in crops, 92 pp. 233-263, Academic Press, Sydney, Australia.
- Kerry, B.R. (1988). Fungal parasites of cyst nematodes. *Agric. Ecosys. Environ.* 24, 293-305.
- Kerry, B.R. (1990). An assessment of progress towards microbial control of plant parasitic nematodes. *J. Nematol.* 22, 621-631.
- Kerry, B.R. (1991). Methods for studying the growth and survival of the nematophagous fungus, *Verticillium chlamydosporium* Goddard, in soil. In B.R. Kerry & D.H. Crump, eds. *Methods for studying nematophagous fungi*. IOBC/WPPRS Bulletin XIV/2: 34-38.
- Kerry, B.R. and Crump, D.H. (1977). Observation on fungal parasites of females and eggs of the cereal cyst nematode, *Heterodera avenae* and other cyst nematodes. *Nematologica* 23, 193-201.
- Kerry, B.R. and de Leij, F.A.A.M. (1992). Key factors in the development of fungal agents for the control of cyst and root-knot nematodes. *Biological control of plant diseases*. p. 139-144, London, Plenum
- Kerry, B.R., Jenkinson, S.C. and Crump, D.H. (1976). Fungal parasites of cyst nematodes. Rothamsted *Exp. Stn. Rep.* Part I, p: 201-202.
- Ketznelson, H., Gillespie, D.C. and Cook, F.D. (1964). Studies on the relationship between nematodes and other soil organisms. *Can. J. Microbiol.* 10, 699-704.
- Krizkova, L., Balan, J., Nemec, P. and Kolozsvary, A. (1976). Predacious fungi *Dactylaria pyriformis* and *D. thaumasia* and nematicides. *Fol. Microbiol.* 21, 493-494.

- Lackey, L.A. (2001). Book Review: Formulation of microbial biopesticides: Beneficial microorganisms, nematodes and seed treatments. Ed: H.D. Burgers. Kluwer Academic Publishers, Dordrecht, The Netherlands, 412 p.
- Liu, X.Z. and Chen, S.Y. (2000a). Parasitism of *Hete-rodera glycines* by *Hirsutella* spp. in Minnesota soybean fields. *Biological Control* 19, 161-166.
- Liu, X.Z. and Chen, S.Y. (2000b). Screening isolates of *Hirsutella* species for biocontrol of *Heterodera glycines*. *Biocontrol and Technology* 1, 23-29.
- Loewenberg, J.R., Sullivan, T. and Schuster, M.L. (1959). A virus disease of *Meloidogyne incognita*, the southern root-knot nematode. *Nature* 184, 1896.
- Lysek, H. (1963). Effect of certain soil organisms on the eggs of parasitic roundworms. *Nature* 199, 925.
- Lysek, H. (1966). Study of biology of geohelminths. II. The importance of some soil microorganisms for the viability of geohelminth eggs in the soil. *Acta Univ. Palacki: Olomuc.* 40, 83-90.
- Mankau, R. (1962). Soil fungistasis and nematophagous fungi. *Phytopathology* 52, 611-615.
- Mankau, R. (1972). Utilization of parasites and predators in nematode pest management ecology. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manag.* 4, 129-143.
- Mankau, R. (1975). Bacillus penetrans n. comb. Causing a virulent disease of plant parasitic nematodes. *J. Invertebr. Pathol.* 26, 333-339.
- Mankau, R. (1975). Procaryotic affinities of Duboscqia penetrans, Thorne. *J. Protozool.* 21, 31-34.
- Mankau, R. (1980). Biological control of nematodes pests by natural enemies. *Ann. Rev. Phytopathol.* 18, 415-440.
- Mankau, R. (1981). Microbial control of nematodes. In Plant Parasitic Nematodes 3, Eds. B.M. Zuckerman and R.A. Rohde, pp. 475-494, Academik, New York
- Mankau, R. and Das, S. (1974). Effect of organic materials on nematode bionomics in citrus and root-knot nematode infested soil. *Indian J. Nematol.* 4, 138-151.
- Mankau, R. and Imbriani, J.L. (1975). The life cycle of an endoparasite in some Tylenchid nematodes. *Nematologica* 21, 89-94.

- Mankau, R. and Imbriani, J.L. (1978). Studies on the mite Lasioseius scapulatus- a predator on soil nematodes. *Nematropica* 8, 15.
- Mc Bride, J.M. and Hollis, J.P. (1966). Phenomenon of swarming in nematodes. *Nature* 211, 545-546.
- Morgan-Jones, G., Gintis, B.O. and Rodriquez-Kabana, R. (1981). Fungal colonisation of Heterodera glycines cysts in Arkansas, Florida, Mississippi and Missouri soils. *Nematropica* 11, 155-163.
- Morgan-Jones, G., Godoy, G. and Rodriquez-Kabana, R. (1981). Verticillium chlamydosporium, fungal parasite of Meloidogyne arenaria females. *Nematropica* 11, 115-120.
- Muraoka, M. and Ishibashi, N. (1976). Nematode feeding mites and their feeding behavior. *Appl. Entomol. Zool.* 11, 1-7.
- Murphy, P.W. and Doncaster, C.C. (1957). A culture method for soil meiofauna and its application to the study of nematode predators. *Nematologica* 2, 202-214.
- Nelmes, A.J. (1974). Evaluation of the feeding behavior of Prionchulus punctatus (Cobb), a nematode predator. *J. Anim. Ecol.* 43, 553-565.
- Netscher, C. and Duponnois, R. (1998). Use of aqueous suspensions for storing and inoculating spores of Pasteuria penetrans to Meloidogyne spp. *Nematologica* 44, 91-94.
- Nigh, E.A., Thomason, I.J. and Van Gundy, S.D. (1980). Identification and distribution of fungal parasites of Heterodera schachtii eggs in California. *Phytopathology* 70, 884-889.
- Nishizawa, T. (1984). Effects of two isolates of Bacillus penetrans for control of root-knot nematodes and cyst nematodes. *Proc. 1st. Ins. Congr. Nematol.* Guelph, Canada, p: 60-61.
- Oka, Y., Nacar, S., Putievsky, E., Ravid, U., Yaniv, Z. and Spiegel, Y. (2000). Nematicidal activity of essential oils and their components against the root-knot nematode. *Phytopathology* 90, 710-715
- Olthof, H.A. and Estey, R.H. (1963). A nematoxin produced by the nematophagus fungus Arthrobotrys oligospora. Fresenius. *Nature* 197, 514-515.
- Oostendorp, M. and Sikora, R.A. (1989). Seed treatment with antagonistic rhizobacteria for the suppression of Heterodera schachtii early root infection of sugar beet. *Revue Nematol*. 12, 77-83.

- Orui, Y. (1997). Effect of spore sonication on attachment range of Pasteurella penetrans to the root-knot nematode. *Applied Entomology and Zoology* 32, 101-107.
- Papavizas, G.C., Dunn, M.T., Lewis, J.A. and Beagle-Ristaino, J. (1982). Liquid fermentation technology for experimental predation of biocontrol fungi. *Phytopathology* 74, 1171-1175.
- Pembroke, B., Gowen, S.R. and Giannakoue, I. (1998). Advanced of ideas for the use of Pasteuria penetrans for the biological control of root-knot nematodes, Meloidogyne spp. *Bringhton Crop Protection Pests and Diseases* 3, 555-560.
- Piotte, C., Castegnone-Sereno, P., Uijthof, J., Abad, P., Bongiovanni, M. and Dalmasso, A. (1992). Molecular characterization of species and populations of Meloidogyne from various geographic origins with repeated DNA homologous probes. *Fundam. Appl. Nematol.* 15, 271-276.
- Rao, M.S., Reddy, P.P. and Nagesh, M. (1998). Integrated management of Meloidogyne incognita on tomato using Verticillium chlamydosporium and Pasteuria penetrans. *Pest Management in Horticultural Ecosystems* 4, 32-35.
- Reddy, P.P., Nagesh, M. and Devappa, V. (1997). Effect of integration of Pasteuria penetrans, Paecilomyces lilacinus and neem seed cake management of root-knot nematodes infecting tomato. *Pest Management in Horticultural Ecosystems* 3, 100-104.
- Regina, M.D.G., Onivaldo, R., Freitas, L.G. and Dickson, D.W. (1999). Attachment of endospores of Pasteuria penetrans to males and juveniles of Meloidogyne spp. *Nematology* 1, 267-271
- Reitz, M., Rudolph, K., Schröder, I., Hoffmann-Hergarten, D., Hallmann, J. and Sikora, R.A. (2000). Lipopolysaccharides of Rhizobium etli strain G12 act as including agent of systemic resistance in potato towards infection by the cyst nematode Globodera pallida. *Applied and Environmental Microbiology* 66, 3515-3518.
- Roberts, P.A. (1993). Future of nematology integration of new and improved management strategies. *J. Nematol.* 25.
- Rumbos, I., Sikora, R.A. and Nienhaus, F. (1977). Rickettsia-like organisms in Xiphinema index Thorne and Allen found associated with yellow disease of grapevines. *Z. Pflanzenkr. Pflanzenschutz* 84, 240-243.
- Samaliev, H. (1997). Observations on spore attachment of Pasteuria penetrans to Meloidogyne species from vineyards in Bulgaria. *Bulgarian Journal of Agricultural Science* 3, 357-362.

- Sayre, R.M. (1971). Biotic influences in soil environment. *Plant Parasitic Nematodes* 9(I), Eds. B.M. Zuckerman, W.F. Mai and R.A. Rohde. pp. 235-266, Academic, New York:
- Sayre, R.M. (1980). Biocontrol: *Bacillus penetrans* and related parasites of nematodes. *J. Nematol*. 12, 260-270.
- Sayre, R.M. and Powers, E.M. (1966). A predacious soil turbellarian that feeds on free living and plant parasitic nematodes. *Nematologica* 12, 619-629.
- Sayre, R.M. and Walter, D.E. (1991). Factors affecting the efficacy of natural enemies of nematodes. *Ann. Rev. Phytopathol.* 29, 149-166.
- Sayre, R.M. and Wergin, W.P. (1977). Bacterial parasite of a plant nematode; morphology and ultrastructure. *J. Bacteriol.* 129, 1091-1101.
- Shapiro, D.I., Lewis, E.E., Paramasivam, X. and McCoy, C.W. (2000). Nitrogen partitioning in Heterorhabditis bacteriophora infected hosts and the effects of nitrogen on attraction/repulsion. *J. Invertebr. Pathol.* 76, 43-48.
- Sharma, R.D. (1971). Studies on the plant parasitic nematode Tylenchorhynchus dubius. Meded. Landbauwhogesch. Wageningen 71-1, 150 p.
- Sharon, E., Bar-Eyal, M., Chet, I., Herrera-Estrella, A., Kleifeld, O. and Spiegel, Y. (2001). Biocontrol of the root-knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. *Phytopathology* 91, 687-693.
- Sharon, E., Chet, I. and Spiegel, Y. (2003). Attachment of the fungus *Trichoderma harzianum* to the root-knot nematode *Meloidogyne javanica* for improved biocontrol activity. *Phytoparasitica* 31, 414-415.
- Shepherd, A.M., Clark, S.A. and Kempton, A. (1973). An intracellular microorganism associated with tissues of *Heterodera* spp. *Nematologica* 19, 31-34.
- Sikora, R.A. (1992). Management of the antagonistic potential in agricultural ecosystems for the biological control of plant parasitic nematodes. *Ann. Rev. Phytopathol.* 30, 245-270.
- Small, R.W. (1979). The effects of predatory nematodes on populations of plant parasitic nematodes in pots. *Nematologica* 25, 94-103.
- Spiegel, Y., Cohn, E., Galper, S., Sharon, E. and Chet, I. (1991). Graduation of a newly isolated bacterium Pseudomonas chitinolytica sp.nov., for

- controlling the root-knot nematode Meloidogyne javanica. Biocon. Sci. Technol., 1, 115-125.
- Spiegel, Y. (2005). Nematology: Advances and Perspectives. Vol. II Nematode Management and Utilization. Eds. Z.X., Chen, S.Y., Chen and D.W., Dickson. 608 pp. CABI Publishing, U.K. Eur. J. Pl. Pathol.
- Steiner, G. and Heinly, H. (1922). Possibility of control of Heterodera by means of predatory nemas. *J. Wash. Acad. Sci.* 12, 367-368.
- Stirling, G.R. (1984). Biological control of *Meloido-gyne javanica* with *Bacillus penetrans*. *Phytopathology* 74, 55-60.
- Stirling, G.R. (1991). *Biological control of plant parasitic nematodes*. 282 pp., CAB International, Walllingford, UK.
- Stirling, G.R. and Mankau, R. (1977). Biological control of nematode parasites of citrus by natural enemies. *Proc. Int. Soc. Citriculture* 3, 843-847.
- Stirling, G.R. and Mankau, R. (1978). Dactylella oviparasitica, a new fungal parasite of Meloidogyne eggs. *Mycologia* 70, 774-783.
- Stirling, G.R. and Wachtel, F.M. (1980). Mass production of Bacillus penetrans for the biological control of root-knot nematodes. *Nematologica* 26, 308-312.
- Stirling, G.R. and White, A.M. (1982). Distribution of a parasitic of root-knot nematodes in South Australian vineyards. *Plant Dis.* 66, 52-53.
- Thomason, I.J. (1987). Challenges facing nematology: Environmental risks with nematicides and the need for new approaches. Eds. J.A. Veech and D.W. Dickson, Hyattsville, USA. Society of Nematologists. Vistas on nematology, p. 469-476.
- Thorne, G. (1927). The life history, habits and economic importance of some Monochs. *J. Agric. Res.* 34, 265-286.
- Thorne, G. (1940). *Duboscqia penetrans*, n.sp. (Sporozoa: Microsporidia, Nosematidae) a parasite of the nematode Pratylenchus pratensis (de Man) *Filipjev. Proc. Helminthol. Soc.* (Wash.) 7, 51-53.
- Tribe, H.T. (1977). Pathology of cyst nematodes. *Biol. Rev. Cambridge Philos. Soc.* 52, 477-508.
- Tribe, H.T. (1979). Extent of disease in populations of *Heterodera*, with special reference to *H. schachtii. Ann. Appl. Biol.* 92, 61-72.

- Walsh, J.A. (1979). An intracellular microorganism in tissues of the potato cyst nematode Globodera rostochiensis and the pea cyst nematode Heterodera goettingiana. *J. Nematol.*, 11, 317.
- Walsh, J.A., Lee, D.L. and Shepherd, A.M. (1983). The distribution and effect of intracellular rickettsia-like microorganisms infecting adult males of the potato cyst nematode *Globodera rostochiensis*. *Nematologica* 29, 227-239.
- Walsh, J.A., Shepherd, A.M. and Lee, D.L. (1983). The distribution and effect of intracellular rickettsia-like microorganisms infecting second stage juveniles of the potato cyst nematode *Globodera rostochiensis*. *J. Zool*. 199, 395-419.
- Webster, J.M. (1972). Nematodes and biological control. In *Economic Entomology*, ed. J.M. Webster. *London: Academic* 19, 469-496, 563 p.
- Wei, J.Z., Hale, K., Carta, L., Platzer, E., Wong, C., Fang, S.C. and Aroian, R.V. (2003). *Bacillus thuringiensis* crystal proteins that target nematodes. *PNAS* 100, 2760-2765.
- Wheeler, T.A., Madden, L.V., Rowe, R.C. and Riedel, R.M. (1992). Modelling of yield loss in potato early dying caused by *Pratylenchus penetrans* and *Verticillium dahliae*. *J. Nematol.* 24, 99-102.
- Williams, J.R. (1967). Observations on parasitic protozoa in plant parasitic and free living nematodes. *Nematologica* 13, 336-342.
- Winslow, R.D. and Williams, T.D. (1957). Amoeboid organisms attacking larvae of the potato eelworm (*Heterodera rostochiensis* Woll.) in England and the beet eelworm (H. schachtii Schm.) in Canada. *Tijdschr. Plantenziekten* 63, 242-243.
- Yeates, G.W. (1969). Predation by *Mononchoides potohikus* (Nematoda: Diplogasteridae) in laboratory culture. *Nematologica* 15, 1-9.