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Management of Plant Parasitic Nematodes

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1.0 INTRODUCTION

Plant parasitic nematodes are among the major soil-borne crop pests that cause significant economic losses to a wide variety of crops. They cause an estimated annual crop-yield loss of US$78 billion worldwide which warrants for effective control strategies (Sasser and Freckman, 1987). Nematodes have the greatest impact on crop productivity when they attack the roots of seedlings or young plantlets (Ploeg, 2001). Nematode feeding also creates open wounds that provide entry to a wide variety of plant-pathogenic fungi and bacteria. These microbial infections are often more economically damaging than the direct effects of nematode feeding.

Plant-parasitic nematodes—the majority of which are root feeders, completing their life cycles in the root zone—are found in association with most plants. About 66 species of plant parasitic nematodes belonging to 27 genera are reported on ten major spices (Koshy *et al.*, 2005). A list of economically important ones and the symptoms they cause on some important spice crops are given in Table 1. The most predominant and widely distributed among these are root knot nematodes (*Meloidogyne* spp.). Tremendous diversity is observed in the nematode fauna present in the rhizosphere of tropical spices like black pepper, ginger and turmeric.

2.0 NEMATODE CONTROL

Among all the options for plant-parasitic nematode control, chemical control is widely used, due to its non-selective nature in controlling nematodes.

Chemical nematicides have been the primary management tool for over fifty years. Chemicals are effective but the application rates needed to kill nematodes in soil are quite high and they are highly expensive. However, the use of these chemicals is increasingly restricted because inappropriate application may

Table 1. Economically important nematode problems of major spices

Crop	Nematode species	Symptoms
Black pepper	*Radopholus similis*	Yellowing of leaves, defoliation and dieback and 'slow decline' leading to death of vines Lesions, necrosis and rotting of roots, especially of feeder roots
	Meloidogyne spp.	Yellowing of leaves (inter-veinal chlorosis), unthrifty growth and gradual decline of vines Presence of moderate to large galls on roots, root rotting
Cardamom	*Meloidogyne* spp.	Poor germination of seeds in nurseries; stunted growth, reduced tillering, narrowing, yellowing and drying of leaf tips and margins Severe galling of roots in seedlings; galls not prominent in mature plants but unusual branching of roots is common
Ginger	*Meloidogyne* spp.	Chlorosis and marginal necrosis of leaves; stunted and patchy growth, poor tillering; early maturing of plants Galling and rotting of roots and underground rhizomes
	Radopholus similis	Stunting, reduced vigour and tillering; chorotic leaves with scorched tips; infested plants mature and dry out faster Small, shallow, water soaked lesions on rhizomes
	Pratylenchus spp.	Yellowing of leaves and dry rot symptoms on rhizomes Dark brown necrotic lesions within rhizomes
Turmeric	*Meloidogyne* spp.	Stunted growth; yellowing, drying of leaf tips and margins, poor tillering; wilting and pre-mature death of plants Heavy galling and rotting in roots; infested rhizomes have dull colour
	Radopholus similis	Infested plants dry faster Shallow, water-soaked brown areas on rhizomes; extensive rotting in roots
	Pratylenchus spp.	Rhizomes less turgid and wrinkled with dark brown necrotic lesions and dry rot symptoms

have negative environmental impacts and risks to human health. The non-target effects of nematicides are too great that have an impact on the environment and the whole soil community. The chemical nematicides are now being *reappraised* in respect of environmental hazard, high costs, limited availability in many developing countries or their diminished effectiveness following repeated applications. In recent years, continuing environmental problems associated with the use of nematicides have introduced a sense of urgency into the search for alternative methods of nematode management (Kerry, 2000).

Nematode control is essentially *prevention*, because once a plant is parasitized it is impossible to kill the nematode without also destroying the host (Guerena, 2006). This warrants a sustainable approach to nematode control integrating several tools and strategies, including cover crops, crop rotation, soil solarization, least toxic pesticides, biological control and plant varieties resistant to nematode damage (Barker and Koenning, 1998).

2.1 Preventive measures

Preventing nematodes from entering uninfested areas is important. Use of certified planting material, use of soil-less growing media in greenhouses/nurseries, good agricultural practices and phytosanitation can reduce nematode spread to a greater extent. Sanitation covers a wide range of cultural practices such as weed control, crop-residue destruction, use of selective crops as mixed or companion crops, use of nematode-free planting materials etc. Though not very powerful, these tactics, when used along with other techniques, can bring down the nematode incidence significantly.

Excellent reduction in populations of plant parasitic nematodes can be achieved through use of various heat treatments like steam, hot water and sunlight. Soil solarization, a method of pasteurization, can effectively suppress most species of nematode wherever summers are predictably sunny and warm. It has been successfully employed in many crops, as a pre-sowing treatment to bring down the initial nematode population in a field. Solarization is more detrimental to plant parasitic than saprophytic nematodes (Ostrec and Grubisic, 2003). Biofumigation by incorporating brassica or cabbage residues under plastic mulches increases the fumigation-like effect (Gamliel and Stapleton, 1993; Chellami *et al.*, 1997). Fallowing and flooding are also being used to manage nematode problems in some crops. But all these techniques are employed only under special conditions and are not reliable for economic control of nematodes when used in isolation.

2.2 Resistant crops

The use of resistant or tolerant cultivars is an economically attractive and effective means of nematode management. Resistant cultivar is more effective against sedentary endoparasitic species such as root-knot and cyst nematodes. Most of these are narrow resistance governed by dominant R genes that trigger hypersensitive reactions in host plants (Dangl and Jones, 2001). Nematode-resistant rootstocks are used in perennial crops like apple, citrus and grapes to ensure protection against these unseen pests. Resistant varieties have been developed for only a few crops and are not widely used in practice (Starr *et al.*, 2002). These must be used judiciously to reduce the selection pressure for races that are able to break down the nematode resistance. Present-day research aims at introgression of polygenic resistance (gene pyramiding) for more reliable results. Application of chemicals like DL-b-amino-n-butyric acid (BABA) acid and salicyclic acid triggered genetic resistance response and suppressed root knot nematodes (Oka *et al.*, 1999; Vasyukova *et al.*, 2003). Transgenic crop resistance to nematodes and other pests is being developed for numerous crops by various companies worldwide. But the use of genetically modified organisms is not accepted in organic production systems.

2.3 Cropping practices

Crop rotation or planting crops in special sequences is an old but effective management practice to reduce nematode populations in the soil. A general rule of thumb is to rotate crops not related to each other or broad leaf to a grass. Researchers have observed that sesame, soybean and brassicas have a nematode-suppressive effect that benefits the following crop in a rotation. Crop rotation is effective, provided crops that are resistant or non-hosts for the target nematode are rotated with susceptible crops. The usefulness of crop rotation depends on the longevity of survival stages of the nematode (van der Putten *et al.*, 2006). Rotations like these not only help prevent nematode populations from reaching economic levels, they also help control other plant diseases and insect pests. Intercropping, on the other hand, not only controls plant parasitic nematodes but also a range of other pests and diseases. The mechanisms involved are release of nematicidal compounds by some component crops and limited availability of food resources for host-specific nematodes. Allelochemicals such as polythienyls, glucosinolates, cyanogenic glycosides, alkaloids, lipids, terpenoids, steroids, triterpenoids, and phenolics, produced by certain cover crops like sudan grass, marigolds exhibit nematode suppressive characteristics. But both these methods do not fit the intensive agricultural practices but are good options in subsistence agriculture.

2.4 Botanical nematicides

Extracts or essential oils of certain plants are able to kill or repel pests, disrupt their life cycle, or discourage them from feeding. A classical example is neem and its derivatives like neem cake that are toxic to plant parasitic nematodes and is not as detrimental to beneficial free-living soil organisms (Riga and Lazarovits, 2001; Abbasi *et al.*, 2005). Higher plants have yielded a broad spectrum of active compounds (Table 2). The development of nematicidal phytochemicals has not yet reached maturity but their agricultural utilization, although currently uneconomic in many situations, offers tremendous potential.

2.5 Soil amendments

There is substantial evidence that the addition of organic matter in the form of compost or manure will decrease nematode pest populations and associated damage to crops (Stirling, 1991; Akhtar and Alam, 1993; Oka and Yermiyahu, 2002; Walker, 2004). Some sources of organic matter known to be nematode-suppressive include oilcakes, sawdust, sugarcane bagasse, bone meal, horn meal, manures, compost, and certain green manures. Reduced nematode damage from increased organic matter in soil is likely a combination of improved soil structure and fertility, alteration of the level of plant resistance, release of nemato-toxins, or increased populations of fungal and bacterial parasites and other nematode-antagonistic agents. Most nematode species can be significantly reduced by tilling in chitinous materials such as crushed shells of crustaceans (Hallmann *et al.*, 1999; Guerena, 2006). To be effective against nematodes, the organic amendments should possess low C:N ratios and have a high protein or amine-type content (Rodriguez-Kabana *et al.*, 1987). Moreover, they should be applied at high rates (>1 ton ha^{-1}) in order to have significant effect on nematodes (van der Putten *et al.*, 2006).

3.0 BIOLOGICAL CONTROL

Suppression of plant-parasitic nematodes with nematode predators, parasites or disease agents is a desirable alternative to chemicals. This emerging area is called biological control. In a nematological perspective, biological control is the reduction of nematode populations, which is accomplished through the action of living organisms other than nematode-resistant host plants, which occur naturally or through the manipulation of the environment or the introduction of antagonists. The mechanisms involved in biological control of nematodes are mainly hyper-parasitism, predation, competition and antibiosis.

Tal le 2. A list of phytochemicals, their source and mode of action on nematodes

Her	Family	Nematicidal compound	Mode of action	Reference
Mar gold (*Tagetes* spp.)	Asteracea	Polythienyls	Causes mortality of nematodes; inhibits host finding	Uhlenbroek and Bijloo (1958)
Mus ard (*Brassica* and *Sinapsis* spp.)	Brassicaceae	Isothiocyanates Glucosinolates	Inhibits egg hatching by reacting with the sulfhydryl groups of proteins	Brown and Morra (1997)
Sud in grass (*Sorghum sudanense*)	Poaceae	Glycosides	On hydrolysis releases cyanide that is toxic to nematodes	Widmer and Abawi (2000)
Blac -eyed Susan (*Rudbeckia hirta*), *Cart amus tinctorius, Heleniumsp., Cirsi im japonicum, Solidago canadensis* etc.	Asteracea	Polyacetylenes	Broad spectrum nematicidal activity	Kogiso *et al.* (1976); Kawazu*et al.* (1980); Gommers (1981)
Cala ar bean (*Physostigma venenosum*), *Crot laria spectabilis*, Mad gascar periwinkle (*Catharanthus rose s*) etc.	Fabaceae and other families	Alkaloids like physostigmine, Monocrotaline, Serpentine etc.	Acetylcholinesterase inhibitor that affects nematode movements, hatching of eggs etc.	Bijloo (1965); Fassuliotis and Skucas (1969); Chandravadana *et al.* (1994) etc.
Basil (*Ocimum basilicum*), tulsi (*O. sanc um*), peppermint (*Mentha piper itum*), bottle brush (*Callistemon lance olatus*), clove (*Eugenia caryc phyllata*), *Lantana camara*, neem (*Aza irachta indica*) etc.	Lamiaceae, Myrtaceae, Geraniaceae etc.	Terpenoids, diterpenoids, triterpenoids, sesquiterpenoids etc.	Direct toxicity, hatching stimulants etc.	Malik *et al.* (1987); Oka *et al.* (2000); Shakil *et al.* (2004) and several others
Knen a hookeriana, betel vine (*Piper betle*) *Rhyncholacis penicillata* etc.	Myristicaceae, Piperaceae, Podostemaceae etc.	Phenolics such as lignans, chromenes, tannins, flavanoids etc.	Different mode of actions	Evans *et al.* (1984); Mahajan *et al.* (1992); Alen *et al.*, (2000) etc.
Aspa agus (*Asparagus officinalis*)	Liliaceae	Asparagusic acid	Inhibition of hatching and mortality	Takasugi *et al.* (1975)
Garlic (*Allium sativum*)	Liliaceae	Allicin	Inhibition of hatching	Gupta and Sharma (1993)
Jackb ean (*Canavalia ensiformis*)	Fabaceae	Concanavalin A	Blocks nematode's chemoreceptors	Marban-Mendoza *et al.* (1987)

Hundreds of organisms, which parasitize or prey on nematodes, are reported and they belong to diverse taxa including nematode trapping or endoparasitic fungi, predatory nematodes, arthropods (e.g. mites and collembola), bacterial parasites, and predatory protozoa. A number of such organisms have been identified from spice based cropping systems and further evaluated in greenhouse and field trials for managing nematode pests of spices (Table 3). Deploying and managing biocontrol agents will likely become increasingly important components of integrated pest management programs and sustainable agricultural systems.

3.1 Fungi

Interest in biological control of nematodes was elicited as soon as plant parasitic nematodes were recognized as pests. Fungi belonging to widely divergent orders and families, from Phycomycetes to Basidomycetes, were reported as antagonists of nematodes (Mankau, 1980). Nematophagous fungi are those fungi with the capacity to capture parasitise or paralyse nematodes at all stages of their life cycles. They are divided into groups depending on their mode of infection: nematode-trapping, endoparasitic, egg and female-parasitic and toxin-producing fungi (Jansson *et al.*, 1997).

The existence of fungi that trap and prey on nematodes was noticed in 19th century. Almost after one decade, the use of predacious or nematode-trapping fungi to control root-knot nematodes of pineapple was first attempted in Hawaii (Linford *et al.*, 1938), which stimulated interest among several workers in nematode-trapping fungi. Several reviews were published accounting apparently, over 100 species of these fungi that attack nematodes and the major genera were *Arthrobotrys, Dactylaria, Dactylella,* and *Monacrosporium* (Duddington, 1954; Christie, 1960; Sayre, 1971; Barron, 1977; Mankau, 1980; Gray, 1987). Majority of nematode-trapping species were reported to be fairly ubiquitous, but their population levels in soil were quite low, as they exist in soil as mycelium rather than as spores (Gray, 1987). Nematode-trapping fungi appear to have little host specificity and can also live at varying degrees of saprophytism in soil (Persmark *et al.*, 1995).

Another group was fungal endoparasites of vermiform nematodes belonging to Chitridiomycete (*Catenaria anguillulae*), Oomycetes (*Myzocytium humicola*), Zygomycete (*Meristacrum asterospermum*), Deuteromycete (*Harposporium anguillulae*), and Basidiomycete (*Nematoctonus* sp.) (Jatala, 1986). Two obligate parasites of females of cyst nematodes viz. *C. auxiliaries* (Tribe, 1979) and *Nematophthora gynophila* (Kerry and Crump, 1980) were isolated. Several isolates of *Hirsutella rhossiliensis* were screened and most of them showed parasitization of soybean cyst nematode (Liu and Chen, 2001).

Table 3. Potential microbial agents for biological control of plant parasitic nematodes infesting spices.

Crop	Nematode	Biocontrol organism	Result obtained	Reference
Black pepper	Root knot nematodes (*Meloidogyne* spp.)	*Pochonia chlamydosporia*	Reduction in nematode population and >70 per cent increase in yield	Eapen (2003)
		Pseudomonas fluorescens	Growth promotion from 26.7 to 55.6% and nematode suppression in greenhouse trials and in nurseries	Eapen *et al.* (1997); Beena *et al.* (2001)
	Burrowing nematode (*Radopholus similis*)	*Pseudomonas fluorescens*	More than 80% suppression of nematodes in greenhouse evaluation	Beena *et al.* (2003)
		Curtobacterium luteum	*More than 70% suppression in greenhouse trails*	*Eapen (2007)*
		Bacillus megaterium	-do-	*Eapen (2007)*
Cardamom	Root knot nematodes (*Meloidogyne* spp.)	*Trichoderma harzianum*	Reduction in nematode population and higher number of quality seedlings	Eapen (2003); Eapen *et al.* (2000)
		Paecilomyces lilacinus	-do-	Eapen (2003)
		Pochonia chlamydosporia	-do-	Eapen (2003)
Ginger	Root knot nematodes (*Meloidogyne* spp.)	*Pochonia chlamydosporia*	Significant reduction in nematodes and increase in yield under field conditions	Ramana *et al.* (2002)
Turmeric	Root knot nematodes (*Meloidogyne* spp.)	*Fusarium oxysporum*	Significant reduction in rematodes and increase in yield under field conditions	Ramana *et al.* (2002)

The endoparasites are obligate parasites that do not form trapping organs, but use their spores that are either motile or non-motile, to infect the nematode hosts. Many of these fungi spend their vegetative lives inside infected nematodes, and in the soil, they mainly exist as spores. They generally have a more restricted host range than nematode-trapping fungi (Jansson and Lopez-Llorca, 2001). Eggs and females that are sedentary stages in the life cycle of nematodes are also vulnerable to the infection by several fungi. Some of them produce toxins which are nematicidal or nematistatic in nature (Dong and Zhang, 2006). Nematophagous fungi have long been considered promising biological agents for control of plant-parasitic nematodes (Jansson *et al.* 1985; Duponnois *et al.* 1995; Sorbo *et al.* 2003).

A large number of species have been recorded as facultative parasites of root-knot nematode females and eggs (Stirling and Mankau, 1978; Godoy *et al.*, 1982; Morgan-Jones and Rodriguez-Kabana, 1988; Stirling, 1991). The first report on the natural occurrence of *Pochonia chlamydosporia* (formerly *Verticillium chlamydosporium*) was from England (Kerry, 1974). Natural parasitism of *Meloidogyne* females and eggs by this fungus has been reported from several crops cultivated in tropical and subtropical soils across the world. Many species of *Verticillium* have been recorded from eggs of *Meloidogyne* (Godoy *et al.*, 1982; Morgan Jones and Rodriguez-Kabana, 1988). The genus *Paecilomyces*, a close relative of *Penicillium*, was first observed to be associated with nematode eggs in 1976 (Lysek, 1976). Later *P. lilacinus* was found parasitizing eggs of *M. incognita* and *M. arenari* in several countries. Two other species, *P. marquandii* from 'chinampa' soils (Marban-Mendoza *et al.*, 1992) and *P. fumosoroseus* from Cuba (Cuadra *et al.*, 2000), were equally suppressive of root-knot nematodes. *Dactylella oviparasitica* has been the first parasite of *Meloidogyne* eggs to be described (Stirling and Mankau, 1978). Some isolates of *Trichoderma* spp., widely used as antagonists of many fungal diseases in several crops, were found to have good potential as a nematophagous fungus (Saifullah and Thomas, 1996; Spiegel and Chet, 1998; Sharon *et al.*, 2001; Eapen *et al.*, 2005). *Cylindrocarpon destructans* was frequently found in association with nematode eggs (Freitas *et al.*, 1995). A hyphomycete similar to the genus *Scytalidium* was isolated from black-coloured egg masses of *M. javanica* (Oka *et al.*, 1997). *Beauveria bassiana*, a known insect pathogen, parasitized eggs of *M. incognita* (Saikia, 1998). *Phoma glomerata* and *Curvularia* species were also reported to be parasitic on juveniles of *M. javanica* (Varaprasad *et al.*, 1998). *Aspergillus niger*, *A. terreus*, *Cladosporium oxysporum*, *Fusarium oxysporum* and *F. dimerum* (*Microdochium dimerum*) were observed inhibitory to nematodes (Goswami *et al.*, 1998). Among these, *C. oxysporum* parasitized root-knot nematode larvae and eggs.

A survey for fungi associated with root-knot nematode egg masses in India showed the highest frequency of occurrence of *F. oxysporum* followed by *F. solani, F. pallidoroseum* and *F. moniliforme* (Goswami and Uma, 1996).

Many plants harbor endosymbiotic microorganisms within their tissues and some of them viz. *F. oxysporum* (Hallman and Sikora, 1996), *Lecanicillium lecanii* (Monfort *et al.*, 2005), *Melanconium betulinum* (Schwarz *et al.*, 2004) and *Phomopsis phaseoli* (Schwarz *et al.*, 2004) are nematophagous. Antagonism of endophytic fungi is by making the plant hosts more resistant and putting the nematodes at a disadvantage. Among endophytic fungi, mycorrhizal fungi constitute an important component of the agricultural and forestry ecosystems. Arbuscular mycorrhizal fungi (AMF) have a protective role and mechanisms like improved plant nutrition, competition with pathogens for photosynthates and infection sites, local elicitation of plant defense mechanisms etc. are reported. *Glomus* species are the most diverse of the arbuscular mycorrhizal fungi and are found in many soils all over the world (Talavera *et al.*, 2002). AMF would be more effective against endoparasitic nematodes than ectoparasites (van der Putten *et al.*, 2006).

Commercially available fungal formulations include *T. harzianum, Hirsutella rhossiliensis, H. minnesotensis, Pochonia chlamydosporia, A. dactyloides,* and *P. lilacinus. P. lilacinus*, a common soil hyphomycete with a cosmopolitan distribution (Dube and Smart, 1987), is the one in which the largest number of formulated biological nematicides has been reported.

3.2 Actinomycetes

Actinomycetes like *Streptomyces* spp. are antagonistic towards plant parasitic nematodes (Dicklow *et al.*, 1993). The natural and semi-synthetic derivatives of avermectins, produced by them, are potent anthelmintic and insecticidal compounds. One such compound, Abamectin, has been commercialized to be used as a prophylactic treatment for the control of *M. incognita* (El-Nagdi and Youssef, 2004).

3.3 Bacteria

Bacteria antagonistic towards plant-parasitic nematodes include rhizobacteria, endophytic bacteria, rhizobia and bacterial symbiont of entomopathogenic nematodes. But species belonging to *Pasteuria* are the only obligate parasites of nematodes (Poinar and Hansen, 1986; Sayre and Starr, 1988). This was first described as a protozoan namely *Duboscqia penetrans* (Thorne, 1940) and was subsequently related to bacteria through electron microscopic studies and was named as *Bacillus penetrans* (Mankau, 1975).

because of the resemblance of *B. penetrans* with *Pasteuria ramosa*, a parasite of water fleas, it was renamed as *P. penetrans* (Sayre and Starr, 1985). Soon it became apparent that the bacterium constituted an assemblage of numerous pathotypes and those that parasitized primarily root-knot nematodes were called *P. penetrans*. Members of the *P. penetrans* group were found to infest 323 nematode species in about 116 genera from 80 countries (Sturhan, 1988; Chen and Dickson, 1998). However, the inability to mass-produce this fastidious bacterium *in vitro* used to be the barrier to making *P. penetrans* a marketable product.

Several root-colonizing bacteria were reported to inhibit the development of plant parasitic nematodes (Zavaleta-Mejia and van Gundy, 1982; Becker *et al.*, 1988). These included several coryneform and Gram-negative bacteria like *Serratia* (Zavaleta-Mejia and vanGundy, 1989), *Pseudomonas* spp. (Oostendorp and Sikora, 1989; Spiegel *et al.*, 1991; Kloepper *et al.*, 1992; Kluepfel *et al.*, 1993), *Bacillus* spp. (Becker *et al.*, 1988), *Enterobacter cloacae* (Duponnois *et al.*, 1999), *Agrobacterium radiobacter* (Jonathan *et al.*, 2000), and many others from egg masses of *M. incognita* (El-Sherif *et al.*, 1995).

Second stage juveniles of *M. javanica* were disorientated in the presence of the bacterial symbiont, *P. oryzihabitans* of the entomopathogenic nematode, *Steinernema abbasi* (Samaliev *et al.*, 2000). The control mechanisms include suppression of root-gall development (Chen *et al.* 2000; Jonathan *et al.* 2000), nematode reproduction (Al-Rehiayani *et al.*, 1999; Duponnois *et al.*, 1999; Hackenberg *et al.*, 2000; Jonathan *et al.*, 2000), egg hatching (Cronin *et al.*, 1997; Neipp and Becker, 1999; Insunza *et al.*, 2002; El-Nagdi and Youssef, 2004) or juvenile survival (Neipp and Becker, 1999; El-Nagdi and Youssef, 2004), nematode killing (Huang *et al.*, 2005), toxin production (e.g., Jacq and Fortuner, 1979; Ali *et al.*, 2002; Jagdale and Grewal, 2002) or endoparasitism (Davies *et al.*, 2001; Talavera *et al.*, 2002).

Several endophytic bacteria that exist in a variety of tissue types within numerous plant species, also have been found antagonistic towards nematodes like root lesion nematodes (Sturz and Kimpinski, 2004). Apart from their nitrogen fixing capabilities, some rhizobia also benefit economically important crops by protecting them from various soil-borne plant pathogens including root-knot nematodes (Siddiqui and Shaukat, 2002). Further, two genera of symbiotic bacteria, *Photorhabdus* (Hu *et al.*, 1999) and *Xenorhabdus* (Grewal *et al.*, 1999), have been reported antagonistic towards plant-parasitic nematodes. Commercial formulations of *P. penetrans*, *Bacillus thuringiensis* (available in insecticidal for mulations) and *Burkholderia cepacia* are currently available.

One limiting factor of biological control is the inconsistent performance of microbial biocontrol agents under field conditions, especially in tropical and subtropical countries, due to a range of complex, integrated, intrinsic (microbial) and external (host and environmental) factors. Lack of adequate understanding of these has hampered the development of effective biocontrol agents (Kerry, 1987). For fine tuning microbial control of nematodes, the five party interactions naturally occurring among 'host plant-nematode-soil-microbial biocontrol agent-environment' have to be studied and anlysed (Dong and Zhang, 2006). The consistency and efficacy of biological control can be increased by the proper handling of the above intrinsic and external factors and by the careful integration of different control measures. For example, crop rotation (Roberts *et al.*, 1981; Chen and Reese, 1999) and organic amendment (Jaffee *et al.*, 1994) can also affect performance of biocontrol agents (Woodward *et al.*, 2005). Nematode-trapping or closely related endoparasitic fungi have been reported being stimulated by organic amendments (Cooke, 1962; Eren and Pramer, 1978; van den Boogert *et al.*, 1994). In another experiment, soil application of *Paecilomyces lilacinus* with oil cake of neem (*Azadirachta indica*) showed synergistic effect with respect to nematode management and improvement in plant growth parameters (Anver *et al.*, 2001). By combining two or more microbial enemies the success of biological control can be improved (Meyer and Roberts, 2002).

4.0 MANAGING SOIL BIOLOGY AND SOIL HEALTH

The ultimate goal of plant-parasitic nematode control is to improve soil health and gain economic benefits. Soil health is the capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health (Doran *et al.*, 1996). A healthy soil is a biologically or chemically buffering and equilibrium system, possessing high biological diversity and providing resilience to disturbance (short-term) or stress (long-term) by pests or pathogens and most importantly, improving plant health. The basis of sustainable nematode control is the maintenance of a healthy soil food-web which can be achieved with routine application of organic matter. Organic amendments lead to improved soil structure and fertility, alteration of the level of plant resistance, release of nemato-toxins, or increased populations of indigenous fungal and bacterial parasites and other nematode-antagonistic agents (Akhtar and Malik, 2000). Natural enemy communities tend to build up relatively slowly over a period of 3-4 years under perennial crops or crops grown in monocultures (van der Putten *et al.*, 2006). Higher organic matter content increases soil's water-holding capacity, and supports thriving communities of the decomposers and predators. Nematodes regulate mineralization processes in the soil and are important participants in this underground energy-transfer system. Evidence suggests that between 30 and 50 percent of the nitrogen present in crop plants was made available by the activity of bacteria-consuming nematodes (Ingham, 1996; Ferris *et al.*, 2004). More diversity in nematode communities is observed in relatively undisturbed soil. Higher biodiversity and thus supposedly a higher soil health is observed in organic soil due to the lower plow depth and especially the use of the organic amendments and the absence of artificial fertilizer (van Diepeningen *et al.*, 2006). Agricultural intensification disrupts the biological equilibrium in the soil and the stable food-web that results in build up of pests and plant parasites (Giller *et al.*, 1997). Therefore, the presence of large populations of plant parasitic nematodes is an indication of poor ecosystem health (Berkelmans *et al.*, 2003). Therefore, it is important to actively manage soil biology using minimum-tillage practices, compost, animal manures, green manures, cover crops, and crop rotations.

5.0 CONCLUSION

Complex agro-ecosystems involving mixed cropping, rotations etc. are common in developing countries of the tropics. Biodiversity of plant-parasitic nematodes in tropical agro-ecosystems is greater than in temperate regions. Control methods targeting specific nematodes are then not very effective in reducing nematode damage in such locations. Such complex agro-ecosystems are more similar to natural ecosystems that may enhance competitive interactions, thereby preventing outbreaks of individual plant parasitic nematode species (Brinkman *et al.*, 2005). Such systems are more resilient and therefore, by monitoring the soil diversity in such systems more sustainable ways of nematode management can be identified.

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