CHAPTER 9

THE SOIL AS A RESERVOIR FOR NATURAL ENEMIES OF PEST INSECTS AND MITES WITH EMPHASIS ON FUNGI AND NEMATODES

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1. Introduction

The soil is the home of innumerable forms of plants, animals and microbes, and life in the soil is highly diverse, ranging from microscopic single-celled organisms to large burrowing animals. As in above ground environments, there are well-defined food chains and competition for survival in the soil environment (Foth & Turk, 1990). Biotic and abiotic interactions in soil ecosystems may enhance or reduce populations of pest arthropods (defined here as insects and mites). Ninety percent of arthropod pest species spend at least part of their life cycle in soil (Gaugler, 1988; Villani & Wright, 1990; Kaya & Gaugler, 1993). Soil dwelling pest arthropods have natural enemies among soil organisms, but also pests that occasionally come into contact with soil might be consumed by predators or become infected with pathogenic propagules (Sunderland 1975; Purvis & Curry, 1984, Tanada & Kaya 1993; Hajek, 1997; Eilenberg & Meadow, 2002).

Soil ecologists often work with single groups of minute organisms in the cryptic soil environment. In this cryptic environment it is not easy to conduct studies that reveal the effect of specific factors on natural enemies of pest arthropods. "Acts" in what can be called the "ecological theatre" are played out on various scales of space and time. To understand the drama, it must be viewed in the appropriate scale (Wiens, 1989). In soil ecological studies it is therefore important to define the scale of the organism and ecosystem. The scale of a soil ecosystem might vary between a few cubic mm of soil to an entire landscape unit extending for several hundred km^2 (Coleman, 1986). To use the appropriate scale there is a need for knowledge about the size, fragmentation and duration of organism's habitat. Moore *et al*. (1988) also emphasise the importance of using the functional scale to identify the mechanisms controlling the ecosystem. They suggest that the use of groups based solely on taxonomy, such as nematodes or microarthropods, is misleading because function rather than taxon should be the focus of ecosystem research.

In this chapter we will try to give an overview of different organisms, physical soil factors and management systems that might be important to natural enemies of pest insects and mites. We will focus on insect and mite pathogenic fungi and insect parasitic nematodes, but other pathogens and arthropod natural enemies are mentioned briefly. At the end of the chapter we present a few examples of successful use of the soil as a reservoir for these natural enemies.

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2. Epizootiology of insect and mite pathogenic fungi and insect parasitic nematodes in the soil ecosystem

Epizootiology is defined as the science of causes and forms of mass phenomena of diseases at all levels of intensity in an animal host population. The study of insect epizootiology, linked to the broader science of ecology, includes diseases caused by non-infectious (amicrobial) and infectious (microbial) agents (Tanada & Kaya, 1993). For a more thorough coverage of different aspects of epizootiology we refer the reader to many excellent studies conducted within this field (Bovien, 1937; Dutky, 1959; Poinar, 1975; Fuxa & Tanada, 1987; Keller & Zimmermann, 1989; Tanada & Kaya, 1993; Hajek, 1997; Pell *et al.* 2001). In this section we will briefly mention some of the most important factors influencing the epidemic development of insect pathogens and insect parasitic nematodes in the soil ecosystem.

The development of a disease in an insect or mite population involves a complex interaction of factors associated with the pathogen, host, environment, and time. Humans also occupy a special position with respect to these systems by affecting and managing the ecosystem in which these interactions occur. Plant pathologists have long recognized this five-way interaction, and it has been illustrated as the disease tetrahedron, which is also used to understand insect and mite disease epizootics (Agrios, 1997) (Fig.1). The practical use of insect pathology for the control of pest arthropods demands a full understanding of the interactions described by the disease tetrahedron (Carruthers & Soper, 1987; Hajek & Leger, 1994). To study epizootic development, it is critical to study the habitat in which the arthropod pathogen interactions take place. It is microenvironmental rather than ambient conditions that influence disease dynamics, however, spatial aspects of epizootic development have rarely been addressed (Hajek, 1997). In the soil, the microenvironment is the scale most pertinent to the survival and activity of individual microorganisms such as insect and mite pathogens and insect parasitic nematodes, because ultimately it is at this scale the microbes interact with their environment (Buckley & Schmidt, 2002). The scale of relevance to the study of the epizootic development of a pathogen in a larger soil dwelling insect might, however, be very different, all depending on the question asked. In the cryptic soil environment it may be difficult to define exactly the scale of the system one would like to study since the different processes are hidden within the soil matrix. The time scale of an epizootic study is also of importance, and long-term investigations over numerous host generations are needed (Keller & Zimmermann 1989). Such investigations are rare, especially on naturally occurring pathogens in the soil. The different factors and interactions influencing patterns of insect and mite diseases over place and time are complex and differ between pathogens. Fungi, protozoa, and nematodes require close contact for their transmission, but viruses can cause epizootics in less dense populations (Weiser, 1987).

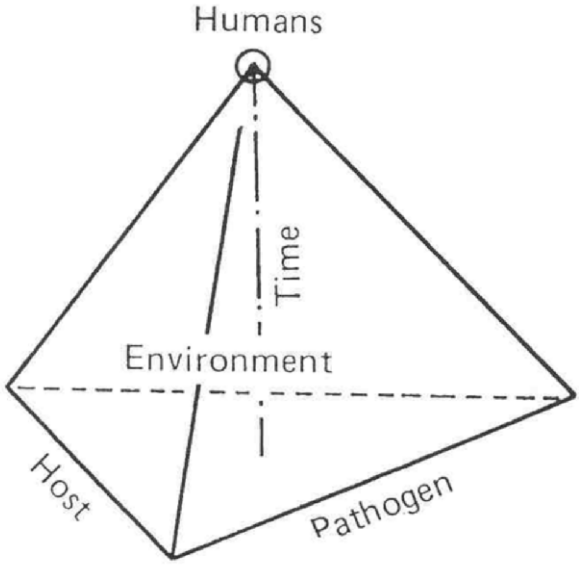

Figure 1: Agrios´ (1997) schematic diagram of the interrelationships of factors involved in plant disease epidemics is also representative for insect and mite disease development

3. Natural enemies of pest insects and mites and some soil organisms important to them

All ecosystems have two types of organisms based on carbon sources, namely autotrophs (the producers), that use inorganic carbon (principally CO^2) and heterotrophs (the consumers and decomposers) that use organic carbon (Foth & Turk, 1990). Plants belong to the autotrophs and can affect pest arthropods and their natural enemies in many ways in the soil. Among the heterotrophs belonging to the soil ecosystem, both microorganisms and soil animals affect pest arthropods and their natural enemies. Among the soil organisms; the host population, host plants of target insects or mites, predators and antagonists of the natural enemies and alternate hosts all influence natural enemies in soil (Barbercheck, 1992). To exploit the natural populations of insect parasitic nematodes and arthropod pathogenic fungi for controlling pest populations, further knowledge is required to understand their ecology. In this section we will give a short presentation of plants, microorganisms and soil animals that are present in the soil ecosystem, and how these might affect pest arthropods and their natural enemies.

3.1. Plants

Plants belong to the autotrophs and constitute the principal biochemical motive force for all subsequent activities of heterotrophs in soils. The inputs come from two directions: (1) from aboveground onto the soil surface as litter and (2) from belowground, as roots, which constitute exudates and exfoliated cells while the root is alive, and root litter when the root dies. The root-fungus mutualistic association, mycorrhiza, is equally important to the above mentioned inputs. This symbiotic association has a significant effect on soil microbes and fauna (Coleman *et al*., 2004). The rhizosphere is the area immediately surrounded and influenced by plant roots (Foth & Turk, 1990), and the great majority of organisms in the rhizosphere are microorganisms, including the major groups: bacteria, fungi and protozoa. It is also well known that nematodes and mites are found in higher concentrations in the rhizosphere than in root-free soil (Lynch, 1990).

Plants may inhibit or stimulate soil organisms in many different ways, for example through the release of plant root exudates. The main part of root exudates consists of carbohydrates. Free amino acids and organic acids are also commonly reported root exudates. Numerous other substances found include nucleotides, phenolic compounds and vitamins (Sundin, 1990). Root exudates release important host signals for soil dwelling plant pathogens, nematodes and herbivorous insects and mites. Among the cyst forming plant-parasitic nematodes, *Globodera rostochiensis* and *G. pallida*, show sophisticated hatching mechanisms that ensure host invasion. Root exudates from the host plant stimulate hatching of the cysts. This reliance on root exudates to stimulate hatching favours persistence of the nematode in the soil (in cysts) in the absence of host plants. Large numbers of infective juveniles from the cysts may therefore be present to invade when host plants are introduced (Perry, 2002). Van Tol *et al*. (2001) showed that the roots of a conifer plant, attacked by vine weevil larvae, release chemicals that attracted the entomopathogenic nematode *Heterorhabditis megidis*. Root exudates have also been suggested as the cause of enhanced germination and survival of the insect pathogenic fungi *Metarhizium anisopliae* in the soil around plant roots (Klingen *et al*., 2002b).

Secondary plant compounds are released in root exudates or upon wounding of plant roots. Brassica plants for example produce isothiocyanates, a group of secondary plant compounds, upon wounding of roots (e.g. pest insect attack). Isothiocyanates are used by pest insects specializing on Brassica plants to localize the plant. This has been shown for the soil dwelling larvae of the dipteran *Delia floralis* which is a Brassica specialist (Ross & Anderson, 1992). It is also known that isothiocyanates affect insect pathogenic fungi, and several laboratory studies not including soil have shown that isothiocyanates may inhibit insect pathogenic fungal species in the class Hyphomycetes (Vega *et al.*, 1997, Inyang *et al.*, 1999, Klingen *et al*., 2002b). No such effects were, however, observed in a more realistic fungus/plant/soil microcosm study (Klingen *et al.*, 2002b).

3.2. Heterotrophic microorganisms

Fungi, bacteria, viruses and protozoa may be beneficial to pest arthropods or they may be pathogenic and hence behave as natural enemies. They may also be pathogenic to other natural enemies such as predators and parasitoids of pest arthropods (Steenberg *et al.*, 1995; Lacey *et al.* 1997; Howarth, 2000; Vestergaard *et al.*, 2003). Soil is a natural reservoir for many insect pathogens, and many arthropod species are hosts to a wide number of pathogens. Jackson *et al.* (2000) report that at least 30 different pathogen species belonging to fungi, bacteria, viruses or protozoa are commonly associated with soil-dwelling insects. Scarab beetles appear to be host

to the widest numbers of pathogens. The soil can be inoculated with insect and mite pathogens either by an infected insect or mite entering into the soil and subsequently dying, or by deposition of pathogenic propagules on the soil surface. For some pathogens, the soil environment also provides a medium for growth and potential dispersal (Hajek 1997). Since most pest arthropod populations come into contact with the soil at some point in their life cycle, the soil is important for the introduction of pathogens into pest arthropod populations. Despite a wide range of known pathogens for soil-dwelling insects, natural epizootics of disease are not frequently observed. This is due, in part, to the difficulty of observing diseased insects within the soil and the rapid decomposition of cadavers. It may, however, also reflect natural resistance to pathogens. Moreover, microbial competition is intense and the presence of other soil microbes may limit the efficacy of pathogens against pest arthropods (e.g. Popowska-Nowak *et al*., 2003). Soilborne pathogens such as nematophagous fungi and bacteria may have quite a significant effect on nematode populations and has been reviewed by Timper & Davies (2004) for nematodes in general and by Kaya (2002) for entomopathogenic nematodes. Timper & Davies (2004) describe four types of interactions where other organisms harm nematodes: predation, parasitism, amensalism and competition. A comprehensive review by Stirling (1991) on the range of antagonists involved is recommended reading.

3.2.1. Fungi

Traditionally, living organisms have been divided into two Kingdoms: Plantae and Animalia, and fungi have been placed in the Kingdom Plantae. However, many biologists now recognize five Kingdoms: Procaryotae, Protoctista, Fungi, Plantae and Animalia. The fungi are placed in the separate Kingdom Fungi, primarily on the basis of their simple eukaryotic thallus with heterothrophic and absorptive nutrition. They are divided in two groups; the Myxomycota in which the vegetative phase lacks a cell wall, and the Eumycota that are typically filamentous or unicellular with a well-defined cell wall (Tsuneda, 1983; Ingold & Hudson, 1993). Assessing the total number of fungal species worldwide is problematic, but three different arguments have led to an estimate of 1.5 million species. The arguments are: (1) only about 5% of the fungi on earth have been identified, (2) there are around six times as many fungi as vascular plants; and (3) the fungi are the largest major group of organisms apart from arthropods (Hawksworth, 1991). The estimate of fungal species is, however, constantly under revision, ranging from 500 000 to 9.9 million species (Hawksworth, 2001). Fungi play many roles in different ecosystems, but the most significant of these is decomposition of organic matter (Cannon, 1996). Probably around two thirds of all fungi on earth are associated with soil or leaf litter for at least part of their life cycles (Cannon & Kinsey, 1996). Fungi can be divided in ecological terms into those that complete their life cycles within the soil, or those with a more complex system involving infection of aerial parts of plants, or animals. Fungi that do not complete their life cycle in soil may either exist as dormant propagules, or live saprobically on decaying host matter (Cannon, 1996). Fungi are food sources for a wide variety of vertebrates such as mice and squirrels that use fungal fruit bodies as a significant part of their diet. Fungi are also a major food source for soil invertebrates such as collembolans and nematodes. However, fungi themselves can exploit insects, mites, nematodes, rotifers etc. as a food source (Cannon & Kinsey, 1996).

Insect pathogenic fungi are natural enemies of pest insects and mites. The most important groups are, Deuteromycetes and Entomophthorales and the soil is the main reservoir of

infective propagules of many species within these groups. Deuteromycetous fungi is well known to grow and disperse in or in very close connection with the soil, and this fungal group causes natural epizootics in soil dwelling pest insects. Fungi in the order Entomophthorales cause epizootics mainly in foliar insects and mites (Pell *et al.*, 2001), but some species are also found to cause epizootics in soil dwelling arthropods. For some examples of fungi causing epizootics in pest arthropods that spend some time on or in the soil see table 1. Even though the soil is not the most common habitat for epizootics caused by Entomophthorales, the soil is an important reservoir for resting stages of fungi in this order. Insects or mites infected with Entomophthorales produce cadavers with resting propagules under unfavourable conditions. These drop down onto the soil where they contribute to the soil reservoir of insect pathogenic fungi. Several studies have shown that Entomophthoralean fungi can survive long periods at low temperatures and still be infective (Klubberttanz *et al.,* 1991; Odour *et al.,* 1995; Hajek & Humber, 1997; Nielsen *et al.,* 2003; Hajek *et al.,* 2004). One example is the aphid pathogenic fungus *Pandora neoaphidis* where the fungal inoculum retains the ability to initiate infections in aphids after storage on the soil for at least 95 days at 5^{o} C (Nielsen *et al.*, 2003). Also the fungus *Entomophaga maimaiga* that is pathogenic to the gypsy moth *(Lymantria dispar*) retains the ability to initiate infections up to 8 months after storage at 4^{o} C (Hajek *et al.,* 2004).

Nematophagous fungi are well known parasites of nematodes e.g. fungi in the genera *Arthrobotrys*, *Dactylella*, *Duddingtonia* and *Monocrosporium* (Timper & Davies, 2004). Nematode trapping fungi and entomopathogenic nematodes occur naturally in many soils, and observations in the laboratory have shown that these fungi trap entomopathogenic nematodes on agar (e.g. Koppenhofer *et al*., 1996). Observations on their interactions in soil is rather limited, however Koppenhofer *et al*. (1997) conducted a study where it was found that the fungus *Arthrobotrys oligospora* competes well against other nematode trapping fungi.

Table 1: Reports on epizootics caused by insect pathogenic fungi on pest insects that spend some time on or in the soil

Scientific name of host insect or mite (Order: Family)	**Fungal species (Hyphomycetes/ Entomophthorales)**	**Host and fungi in the soil ecosystem**	**References**
Costelytra zealandica (Coleoptera: Scarabaeidae)	*Beauveria bassiana* *Beauveria brongniartii* (Hyphomycetes)	*B. bassiana* caused an epizootic with prevalence reaching up to 99% in *C. zealandica* larvae sampled from soil. *B. brongniartii* caused an epizootic with prevalence reaching up to 30% in *C. zealandica* larvae sampled from soil.	Townsend *et al.,* 1995
Tipula paludosa (Diptera: Tipuloidea: Tipulidae)	*Conidiobolus osmodes* (Entomophthorales)	The fungus caused an epizootic with prevalences reaching about 40% in *T. paludosa* larvae extracted from the soil. Several mummified larvae were also found on the soil surface.	Gökce & Er, 2003
Ostrinia nubilalis (Lepidoptera: Pyralidae)	*B. bassiana* (Hyphomycetes)	The fungus caused up to 84% mortality in overwintering larvae of *O. nubilalis* in corn residues. Corn residues were laying or standing on the soil surface.	Bing & Lewis, 1993
Cydia pomonella= Laspeyresia pomonella (Lepidoptera: Tortricoidea: Tortricidae)	*B. bassiana* *Paecilomyces farinosus* (Hyphomycetes)	*B. bassiana* and *P. farinosus* caused 34.4% and 29.5% mortality respectively, in *C. pomonella* larvae overwintering beneath the bark at the base of apple trees. The larvae come in contact with soil after emerging from apples, dropping on the ground, before crawling up a tree trunk.	Subinprasert, 1987

Scientific name of host insect or mite (Order: Family)	**Fungal species (Hyphomycetes/ Entomophthorales)**	**Host and fungi in the soil ecosystem**	**References**
Agrotis segetum (Lepidoptera: Noctuidae)	*Tolypocladium cylindrosporum* (Hyphomycetes)	The fungus was found to severely reduce populations of *A. segetum* larvae hibernating in the soil.	Steenberg & Øgaard, 2000
Pseudoplusia includens Anticarsia gemmatalis (Lepidoptera: Noctuidae)	*Nomuraea riley* (Hyphomycetes)	This fungus often causes natural epizootics in populations of noctuids. *N. riley* overwinter in the soil and the level of overwintering inoculum is probably one of the key factors in the development of epizootics.	Carruthers & Soper, 1987
Pemphigus penax (Homoptera: Aphidoidea: Pemphigidae)	*Erynia (Pandora) neoaphidis Conidiobolus coronatus* (Entomophthorales)	These fungi cause about 70% mortality in nymphs and adults on carrots in the soil. *E. neoaphidis* being the most prevalent.	Pers. obs.

3.2.2. Bacteria

Bacteria are numerous in the soil, and a gram of soil may contain over one billion bacteria (Foth & Turk 1990). In adequately aerated soils, both bacteria and fungi dominate, whereas bacteria alone account for almost all the biological and chemical changes in environments containing little or no oxygen. Bacteria isolated from soil can be placed into two broad divisions: the indigenous species that are true residents, and the invaders. Indigenous bacteria may have resistant stages and endure long periods without being active metabolically, but under favourable conditions they become active. Invaders, however, do not participate in a significant way in community activities. They enter the soil with precipitation, diseased tissues, animal manure or sewage sludge, and they may persist for some time in a resting form and sometimes even grow for short periods (Alexander, 1977).

Several soil dwelling bacteria are pathogenic to arthropods. Some of these are obligate pathogens, but the majority are facultative and a few are potential pathogens that may show a certain degree of pathogenicity. Under conditions of stress, non-pathogenic bacteria present in the digestive track of organisms (e.g. insects, nematodes) may exhibit pathogenicity (Tanada & Kaya, 1993). Other bacteria have a close association with insects, but are not pathogenic. One such example is soil dwelling insects such as *Delia* spp. that have a close association with plant soft-rot bacteria (*Erwinia* spp.). The *Delia* larvae transmit decay-causing bacteria to healthy plant tissues, aiding in the development and spread of the plant rot. The association of the larvae and the bacteria is coincidental and not obligatory (Coaker & Finch, 1971). *Delia* larvae are known to have a very low susceptibility to insect pathogenic fungi (Vänninen *et al*., 1999a;

Vänninen *et al*., 1999b; Klingen *et al*., 2002c), which has led to speculations that the bacteria present on *Delia* compete with insect pathogenic fungi. Other factors such as plant metabolites seem, also, to affect the fungal infection of *Delia* spp. (see section 3.1). Volatiles emitted by some bacteria, e.g. *Bacillus subtilis*, *B. pumilus* and *Pseudomonas aurantiaca,* are also known to have a fungistatic effect on insect pathogenic fungi important in the soil ecosystem (Popowska-Nowak *et al.*, 2003), and bacteria are also known to lyse fungi (Ekesi *et al*., 2003).

Enright *et al*. (2003, pers. comm.) found endospore-forming bacteria in the genus *Paenibacillus* associated with entomopathogenic nematodes. These bacteria were found to inhibit nematode movement, thus contributing to the regulation of nematode populations. For details on effects of bacteria on nematodes in general we refer to the excellent reviews by Stirling (1991) and Hominick & Kerry (2002). A unique association between bacteria and nematodes, in which bacteria (*Xenorhabdus* and *Photorhabdus*) require nematodes to gain entry into host insects is mentioned later in section 3.3.3.

3.2.3. Viruses

Viruses are of considerable economic and medical importance because they cause diseases of plants, animals and humans. Each viral particle requires the presence of a viable metabolic organism for its reproduction. In the absence of the host, little activity and no reproduction or duplication is possible. Many viruses are limited in their host range and are often species specific (Alexander, 1977). Exceptions do exist, for example the family Reoviridae comprise viruses that infect vertebrates, invertebrates and plants (Hunter-Fujita *et al.*, 1998; Hull, 2002). The classification of viruses is without a natural base, primarily because there is no time-related information on their evolution and on relationships between virus species and genera. An effective system for classifying viruses has been developed by Hull (2002). Insect viruses belong to at least 13 families, some of which occur exclusively in arthropods and some of which include vertebrates and/or plants. Occlusion is a feature of many arthropod viruses, which does not occur in plant or vertebrate viruses. Occlusion means that the virons are embedded within a proteinaceous body. Occlusion bodies (OBs) vary in size but are visible under the light microscope (Hunter-Fujita *et al.*, 1998).

Viral diseases are among the most widely investigated infections in insects, and there are several examples of viral diseases causing death in pest arthropod populations living in, on or in close contact with the soil. An example is the *Wiseana* spp (Lepidoptera: Hepalidae), which are important pests in pastures in New Zealand. Larvae in this genus live on or in the soil and become infected with Nuclear Polyhedrosis virus (NPV) as young larvae by ingesting viral occlusions present on the soil surface, on the underside of grass leaves, or in pasture debris. Infected larvae usually die outside their burrows, where they are consumed by birds or become part of the soil reservoir (Tanada & Kaya, 1993). The ultimate deposition for viruses, particularly the occluded viruses, is the soil, which can protect the inoculum for many years. Viable viruses will remain close to the surface, provided that the soil is undisturbed (Evans, 2000). The high occurrence of viruses in the soil reservoir increases the competition with other soil natural enemies for susceptible arthropod hosts. Many viruses are, as mentioned earlier, quite host specific and will therefore not compete for a wide range of arthropod hosts. This applies for example for the family Baculoviridae that is also widely used in microbial control (Hunter-Fujita *et al.,* 1998).

3.3. Animals

Animals, the other group of major heterotrophs in soil systems, exist in elaborate food webs containing several trophic levels. Animal members of the soil biota are numerous and diverse, and are often divided into the microfauna, the mesofauna and the macrofauna based on their size, and the method for collection of these animals. The micro, meso and macrofauna are linked to each other through food webs. The animals, especially the small ones, are also linked to soil microorganisms through food webs. Representatives of the microfauna are protozoans (Flagellates, Naked Amoeba, Testacea, Ciliates). The mesofauna is represented by Rotifera, Nematoda, Tardigrada and microarthropods such as Collembola, Mites, Protura, Diplura, Microcoryphia, Pseudoscorpionidae, Symphyla and Pauropoda. Representatives of the macrofauna are Isopoda, Diplopoda, Chilopoda, Scorpionidae, Areanae, Insects, Spiders, Gastropoda and Earthworms (Coleman *et al*., 2004). Only the animal groups most numerous or relevant to the subject discussed in this chapter will be mentioned below. They will be presented according to their systematic position, and not according to their size as indicated above.

3.3.1. Protozoa

Protozoa are single-celled organisms and are the smallest of the soil animals. They live in the films of water surrounding soil particles and are in a sense aquatic animals. Soil protozoa are largely predators, feeding on soil bacteria. Some also feed on fungi, algae or dead organic matter (Foth & Turk, 1990). Most of the insect pathogenic protozoa occur in the phyla Apicomplexa and Microspora. The microsporidia (Microspora) are the most important protozoan pathogens of insects, and they are the most promising candidates for use in microbial control. Insects in nearly all taxonomic orders are susceptible to microsporidia but more than half of the hosts are registered in two orders, Lepidoptera and Diptera (Tanada & Kaja, 1993). Very few reports show that microsporidia have been isolated from nematodes, and it is possible that many infections are missed (Kaya, 2002).

3.3.2. Rotifers and tardigrades

Soil rotifers are considered to be aquatic organisms and more than 90% are in the order Bdelloidea, or wormlike rotifers. The importance of these organisms is largely unknown, and is often not listed in major compendia of soil biota even though they might be very numerous in soil (Coleman *et al.*, 2004). Tardigrades are essentially aquatic and these interesting animals, also called “water bears”, range in size from 50 µm to 1200 µm, rarely exceeding 500 µm. Soil inhabiting tardigrades are found in the upper porous strata where oxygen concentration is high. The degree of compaction of the soil is probably one of the most important factors affecting their distribution. Soil tardigrades feed on algae, fungi, bacteria, protozoa, rotifers, nematodes, organic debris, and other tardigrades (Nelson & Higgins, 1990; Coleman *et al.*, 2004).

3.3.3. Nematodes

Nematodes, or roundworms, are among the most numerous of the multicellular organisms in ecosystems, and have adapted to almost every environment wherever there is moisture available (Wallace, 1963; Freckman & Baldwin, 1990; De Ley, 2000; Coleman *et al.*, 2004; Lee, 2002). The soil offers an excellent site for insect-nematode interactions. Previous and current work on the ecology of nematodes in soil related to plant and soil health can give valuable information for further studies on the ecology of insect parasitic nematodes.

De Man is considered as one of the pioneers of nematode ecology based on his studies in the late 1800's (Filipjev & Schuurmans-Stekhoven, 1941). He divided the soil nematodes into 5 groups: (1) the ubiquitous species, (2) the meadow and forest forms which live in a soil rich in humus, (3) the nematode fauna of sandy soil and dunes, (4) species living in soil, soaked in brackish water and (5) fresh-water species. A number of reviews concerning aspects on the ecology of nematodes have been published since that time, (Overgaard Nielsen, 1949; Goodey, 1951; Winslow, 1960; Overgaard Nielsen, 1967; Wallace, 1973; Norton, 1978; Yeates, 1971; 1979, 1981, 2004; Kaya, 1990; Norton & Niblack, 1991; Ferris, 1993; Lewis, 2002,). As with other soil fauna, taxonomy, sampling and extraction procedures and the difficulty of *in vivo* observations, are some of the limitations imposed on the study of nematode ecology. Nevertheless research into nematode ecology has progressed increasingly in the past couple of decades. The recognition of different feeding groups, i.e. the functional role of soil nematodes, forms a basis for ecological classification. It distinguished, rather broadly at first, between plant feeders, predators, fungivores, microbial-feeders and omnivores (Yeates, 1971). Yeates *et al*., (1993) published the first comprehensive overview of nematode feeding habits presenting 8 essential feeding types (table 2).

Much work has been done on studying differences between species at the molecular level. It is becoming clear that there is a need to develop molecular methods for classifying whole nematode communities in soil (Adams & Nguyen, 2000; De Ley & Blaxter, 2002). The application of molecular techniques for studying animal communities in soil will greatly improve our knowledge regarding many aspects of their life in soil.

Table 2: Ecological classification of soil nematodes based on feeding types, adapted from Yeates et al., (1993)

Feeding type	**Nematode orders**	**Description of feeding group**
1. Plant feeding	Dorylaimida Tylenchida	Most of these are plant parasitic and many are quite well studied. Presence of a stylet (spear). Sub-divided further into 6 groups: Sedentary parasites, migratory endoparasites, semi endoparasites, ectoparasites. Plant feeders may be polyphagous or show host specificity. Epidermal cell and root feeders, algal, lichen or moss feeders.
2. Hyphal feeding	Dorylaimida Tylenchida	Penetration of fungal hyphae using a stylet (spear). Includes alternate cycles of some invertebrate parasites. Not known whether the same nematode species can feed on both saprophytic and mycorrhizal fungi.
3. Bacterial feeding	Araeolaimida Chromadorida Diplogasterida Enoplida Isolaimida Monhysterida Rhabditida	Includes species that feed on a prokaryote food source, through a narrow or broad mouth part. The soil stages of certain nematode parasites of vertebrates and invertebrates that feed on bacteria should be included. Some may use insects as a phoretic host.
4. Substrate ingester	Diplogasterida Monhysterida	More than one pure food source is ingested, but it is unknown whether nematodes can digest complex organic substrates.
5. Predatory	Chromadorida Diplogasterida Dorylaimida Monhysterida Mononchida Tylenchida	Nematode species in this group may feed on protozoa, other nematodes, rotifers and/or enchytraeids either as “ingesters” or “piercers”.
6. Unicellular eukaryote feeding	Chromadorida Diplogasterida Enoplida Monhysterida Tylenchida	Reported to feed on algae, but difficult to prove, includes ingestion of fungal spores and whole yeast cells.
7. Dispersal stage or infective stage of animal parasites	Rhabditida Stichosomida Tylenchida	The entomogenous species included here, life cycle with stages in the soil.
8. Omnivore	Dorylaimida Enoplida	Restricted to certain groups, but when possible nematodes should be classified in types 1-7.

Bongers (1990) proposed an ecological measure based on nematode species composition defined as the maturity index (MI). This index weighs nematode species mean abundance by a colonizer-persister (c-p) scale, related to r and K life strategies, and reflects the maturation of communities. The MI index, or faunal nematode analysis, has been enhanced and refined by Ferris *et al*. (2001). Faunal nematode analysis may be employed for investigating the effect of entomopathogenic nematodes to the soil nematode community, although few studies have been conducted so far. In one study, the application of entomopathogenic nematodes significantly reduced the number of genera and abundance of plant-parasitic, but not free-living, nematodes (Somasekhar *et al*., 2002).

Insect parasitic nematodes comprise several different groups of nematodes and it is beyond the scope of this chapter to give a detailed review on all of them. The main emphasis will be on Steinernematidae and Heterorhabditidae (Gaugler, 2002), but the terrestrial Mermithidae and Sphaerularioid nematodes will also be mentioned at the end of this section. Nematodes in the families Steinernematidae and Heterorhabditidae, commonly known as entomopathogenic nematodes, are the most studied nematodes for biological control of insects, and currently comprise the genera *Steinernema*, *Neosteinernema* and *Heterorhabditis* (Gaugler & Kaya, 1990; Bedding *et al*., 1993; Gaugler, 2002). Entomopathogenic nematodes are characterized by having a unique mutualistic relationship with bacteria (*Xenorhabdus* and *Photorhabdus*). The infective stage of the nematodes (also known as the dauer stage) provides protection and transportation for their bacterial symbionts, this is the only stage in the life cycle of these nematodes that can disperse and survive outside the host. The bacterial symbionts contribute to the relationship by killing the insect host, establishing and maintaining suitable conditions for nematode reproduction, and providing nutrients and antimicrobial substances that inhibit growth of a wide range of microorganisms. Understanding these multitrophic interactions among the nematodes their symbiotic bacteria, and insect hosts is of fundamental importance for nematode infectivity, survival and use in biocontrol. Some species are produced commercially, and much research has gone into production and formulation of these nematodes (Ehlers, 1996; Grewal, 2002; Gaugler & Han, 2002).

Entomopathogenic nematode species exhibit differences in habitat preferences, host range, infectivity, environmental tolerances and suitability for commercial production. For example Sturhan (1999) revealed that some species like *Steinernema affine* is a species characteristic of grasslands, whereas *S. kraussei* appears to be characteristic of woodlands in lowland parts of Europe (Spiridinov *et al*., 2004). *S. carpocapsae* has shown to be relatively tolerant to desiccation (Womersley 1990). The great diversity of habitats exploited by entomopathogenic nematodes is demonstrated in the numerous isolation records published (Kaya & Gaugler, 1993; Hominick 2002). The genus *Steinernema* is the most intensively studied of the entomopathogenic nematodes. Spiridinov *et al*. (2004) have recently published a comprehensive study on the phylogenetic relationships within the genus, including ecological patterns. The patterns reveal possible habitat preferences for *Steinernema* species, as mentioned above. The major factors determining these habitat preferences are likely to involve both soil physical factors and availability of hosts, although further studies are required to reveal this. To increase our dearth of knowledge on the ecology of entomopathogenic nematodes, Koppenhofer & Kaya (1999) presented a number of simple experiments that can be conducted on any new nematode species that is described, which could serve as a model for ecological outlines of entomopathogenic nematodes.

Few studies have been conducted on the population dynamics of naturally occurring entomopathogenic nematodes (Kaya, 1990; Lewis *et al*., 1998), although some interesting models have been developed recently (Dugaw *et al*., 2004; Fenton & Sands, 2004). A review on the population dynamics of nematodes has recently been published by Boag & Yeates (2004). They show that no long-term studies have been conducted on soil nematodes, except for some economically important plant-parasitic nematodes. Epizootic outbreaks have been reported for entomopathogenic nematodes for example in bibionids (Bovien, 1937; Mráčzek & Sturhan, 2000), scarabs (Akhurst *et al*., 1991), and sawflies (Mráčzek & Bečvář, 2000). Mráčzek (1982) investigated the horizontal distribution of *Steinernema kraussei* in two localities with an outbreak of the sawfly *Cephalcia abietis*; he found that 24-27% of the pest (diapausing larvae) was killed by *S. kraussei* annually. Peters (1996, pers. comm.) has collected useful data of known natural occurrence of entomopathogenic nematodes in insects, (Table 3).

Table 3: Reports of naturally occurring infections of insects with entomopathogenic nematodes (adapted from Peters, 1996 and pers. comm.; Adams & Nguyen, 2002.)

Nematode species	**Host Insect order**	**Host species**	**Reference**
Steinernema affine	Diptera	*Bibio* sp.	Peters, 1996
		Helina duplicata	Peters, 1996
	Coleoptera	*Cantharis* sp.	Nielsen & Philipsen, 2003
		Phyllopertha horticola	Nielsen & Philipsen, 2003
		Pterostichus nigrita	Nielsen & Philipsen, 2003
S. arenarium	Coleoptera	*Anomala dubia*	Peters, 1996
		Melolontha hippocastani	Poinar, 1992
S. bicornutum	Coleoptera	Curculionidae (Carabidae) *Harpalus* sp.	Gradinarov, 2003
S. carpocapsae	Coleoptera	*Agriotes lineatus*	Peters, 1996
		Cleonus mendicus	Peters, 1996
		Diaprepes abbreviatus	Peters, pers. comm.
		Graphognathus leucoloma	Peters, 1996
		Hylobius pales	Peters, 1996
		Otiorhynchus sulcatus	Peters, 1996
		Popillia japonica	Peters, 1996
	Hymenoptera	*Cephalcia arvensis*	Peters, pers. comm.
		C. lariciphila	Peters, 1996
		Vespula sp.	Ehlers *et al*., 1991
	Diptera	*Rhagoletis pomonella*	Peters, 1996
	Lepidoptera	*Cydia pomonella*	Peters, 1996
		Heliothis armigera	Peters, 1996
		Mamestra brassicae	Peters, pers. comm.
		Pieris brassicae	Peters, 1996

Nematode species	**Host Insect order**	**Host species**	**Reference**
S. carpocapsae (continued)	Lepidoptera	*Scotia segetum* *Semiothisa pumila* *Vitacea polistiformis*	Peters, 1996 Peters, pers. comm. Peters, 1996
S. feltiae	Coleoptera	*Amphimallon solstitiale* *Bothynoderes punctiventris* *Capnodis tenebrionis* Curculionidae *Graphognathus leucoloma* *Hylobius abietis* *Onitis alexis* *Otiorhynchus sulcatus* *O. ovatus* *O. dubius* *Pentodon algerinum* *Phyllobius urticae* *Phyllopertha horticola* *Pytho depressus* *Rhagium inquisitor* *Selatosomus melancholicus*	Peters, 1996 Peters, 1996 Peters, 1996 Nielsen & Philipsen, 2003 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Nielsen & Philipsen, 2003 Peters, 1996 Peters, 1996 Peters, 1996
	Diptera	*Bibio hortulans* *B. ferruginatus* *Delia radicum* *Dilophus vulgaris* *Mycetophila fungorum*	Bovien, 1937 Peters, pers. comm. Nielsen & Philipsen, 2003 Peters, pers. comm. Poinar, 1992
	Lepidoptera	*Agrotinae* gen.sp. *Agrotis ipsilon* *A. lineatus* *Crambus simplex* *Heliothis armigera* *Hepialus lupulinus* *Leucania acontistis* *Scotia segetum*	Peters, 1996 Peters, 1996 Nielsen & Philipsen, 2003 Peters, 1996 Peters, 1996 Nielsen & Philipsen, 2003 Peters, pers. comm. Peters, 1996
S. glaseri	Coleoptera	*Anomala flavipennis* *Migdolus fryanus* *Popillia japonica* *Strigoderma arboricola*	Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996
S. intermedium	Coleoptera	*Cantharis* sp.	Nielsen & Philipsen, 2003,

Nematode species	**Host Insect order**	**Host species**	**Reference**
S. intermedium (continued)	Diptera	*Bibio marci*	Gradinarov *et al*., 2000 Mráčzek & Sturhan, 2000
S. kraussei	Hymenoptera Coleoptera	*Cephalcia abietis* *C. falleni* Curculionidae	Peters, 1996 Peters, 1996 Gradinarov, 2003
S. kushidai	Coleoptera	*Anomala cupre*	Peters, 1996
S. rarum	Lepidoptera	*Heliothis sp.*	Peters, 1996
S. riobravis	Lepidoptera	*Helicoverpa zea* *Spodoptera frugiperda*	Peters, 1996 Peters, 1996
S. scapterisci	Saltatoria	*Scapteriscus* *S. borelli* *S. vicinus*	Peters, 1996 Peters, 1996 Peters, 1996
S. scarabaei	Coleoptera	*Anomala(=Exomala) orientalis* *Popillia japonica*	Koppenhofer & Fuzy, 2003 Stock & Koppenhofer, 2003
S. neocurtillae	Saltatoria	*Neocurtilla hexadactyla*	Peters, 1996
Steinernema sp.	Coleoptera Lepidoptera Diptera	*Acantholyda nemoralis* *Adoryphorus couloni* *Amphimallon solstitiale* *Melolontha hippocastani* *M. afflicta* *Phyllopertha horticola* *Scitala sericans* *Graphognathus* sp. *Agrotis ipsilon* *Scotia segetum* *Sesamia nonagrioides* Asilidae	Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Gradinarov, 2003
Neosteinernema longicurvicaudum	Isoptera	*Reticulitermes flavipes*	Peters, 1996
Heterorhabditis bacteriophora	Coleoptera	*Amphimallon solstitiale* *Curculio caryae* *Cyclocephala hirta* *Diabrotica balteata* *Diaprepes abbreviatus* *Drasterius bimaculatus* *Hoplia philanthus* *Popillia japonica* *Phyllophaga* sp.	Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Gradinarov, 2003 Ansari *et al*., 2003 Peters, 1996 Peters, 1996

Nematode species	Host Insect order	Host species	Reference
Heterorhabditis bacteriophora (continued)	Lepidoptera	*Diatrea grandiosella* *Heliothis punctigera* *Helicoverpa zea*	Peters, 1996 Peters, 1996 Peters, 1996
H. indica	Lepidoptera	*Scirpophaga excerptalis*	Poinar *et al*., 1992
H. megidis	Coleoptera	*Amphimallon solstitiale* *Otiorhynchus sulcatus* *Phyllopertha horticola* *Popillia japonica*	Peters, 1996 Peters, 1996 Klingen *et al*., 2002d Peters, 1996
H. marelata	Lepidoptera	*Hepialus lupulinus*	Strong *et al*., 1995
H. zealandica	Coleoptera	*Heteronychus arator*	Peters, 1996
Heterorhabditis sp.	Coleoptera	*Agriotes ponticus* *Antitrogus consanguineus* *Cylas formicarius* *Graphognathus leucoloma* *Lepidiota crinita* *L. negatoria* *L. picticollis* *Pachneus litus* *Phyllopertha horticola*	Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996 Peters, 1996

The effect of entomopathogenic nematodes on non-target hosts when used in biological control has been investigated, but few long-term studies have been conducted. Most of the early work involved laboratory tests with a wide range of animal species (Georgis *et al*., 1991). Bathon (1996) has conducted an excellent review and field study on the impact of entomopathogenic nematodes on non-target hosts. The release of entomopathogenic nematodes can cause mortality to non-target arthropod populations but it was found that the effect was spatially restricted and temporary only affecting part of the population. It is important to monitor entomopathogenic nematode populations and their effect on non-target organisms in the field after their release. This should become an important recommendation in experimental and practical work with entomopathogenic nematodes.

Predatory nematodes may have a negative effect on entomopathogenic nematodes, although this is not well documented (Kaya, 2002). Duncan *et al*. (2003) showed the apparent importance of competitors such as free-living bactivorous nematodes as potential significant regulators of entomopathogenic nematodes

In sections, 4.2., 5.2, and some parts of section 6, we refer to nematodes in general and more specifically to entomopathogenic nematodes (Steinernematidae and Heterorhabditidae), the other two important groups of nematodes parasitic in insects are briefly described below.

Terrestrial mermithids include species ranging from a few millimetres to 405 mm, where most are between 50 and 150mm long. Kaiser (1991) gives an excellent review on the terrestrial and semiterrestrial Mermithidae, which is briefly summarized here. Reports on infections with mermithids are found for virtually all insect orders, and Poinar (1975) has compiled an extensive host list. Many of the mermithids reported in insect hosts are not identified to species, because these parasitic stages lack distinguishing characters for identification. Three phases of parasitic development are described, (1) penetration into the

host, only slight growth, and important changes in the cuticle take place for uptake of food, (2) the growth phase, the nematode grows rapidly in length almost filling the hemocoel, the cuticle is still a thin membrane that can burst easily, (3) the end of the growth phase is signalled by the increasing thickness of the cuticle, and this stage bores its way out of the host, enters the soil for further free-living development. The diversity of mermithids depends on the host diversity and on the nature and moisture of the soil. The most studied insect order with respect to mermithids is grasshoppers in which the evidence for moisture dependence has been shown. Mermithids are considered common parasitoids of agricultural pests, and they have a significant impact on for example regulating the population dynamics of grasshoppers; however their potential as biological control agents has yet to be realized.

Nematodes in the superfamily Sphaerularioidea, and the Allantonematidae represent the basic type of Sphaerularioidea. The complex host-parasite relationships of Sphaerularioid nematodes are not well known (Remillet & Laumond, 1991). In brief, survival and reproduction is ensured by annual parasitism, the host's fecundity reduction, dissemination of juvenile nematodes by living adult insects, adaption of the length of the free-living period of infective females, and the synchronization of the host larval development. Free-living or plant parasitic generations allow the survival of the nematodes in the absence of hosts. These highly specialized adaptions lead to a high degree of specificity between the nematode and insect species. This specificity and the complex balance maintained between hosts and parasites are limiting factors in the use of Sphaerularioids in biological control. Anderson & Skorping (1991) found that levels of parasitism by *Heterotylenchus autumnalis* (Allantonematidae) to carabid beetles was significantly enhanced in certain protected microhabitats (silty, more or less vegetated, often shady sites) compared to more open microhabitats. This difference was not attributed to the differences in micro-climate but to the differences in soil type and location. The open sites were close to a river, with a coarser soil type and were subject to flooding and erosion.

3.3.4. Earthworms

Earthworms are the most familiar, and with respect to soil processes often the most important group of soil fauna. They play an important role in influencing soil structure and in the breakdown of organic matter in soil (Coleman *et al*., 2004). Soil fungi are considered to be an important food source for earthworms (Bonkowski *et al*., 2000); however, fungi and bacteria are also known to be pathogenic to earthworms. Many soil animals such as protozoa, rotifers, platyhelminths, mites, dipterous larvae, beetles and centipedes prey on earthworms (Wallwork, 1970; Grewal & Grewal, 2003; Shah *et al.*, 2003). Nematodes belonging to the genera *Rhabditis* and *Cephalobus* have been found to naturally infect between 7 and 13% of earthworm cocoons (Kraglund & Ekelund, 2002). None of these nematode genera are, however, used in biological control of insects or slugs. Studies show that biological control agents such as entomopathogenic nematodes and insect pathogenic fungi do not appear to have negative effects on earthworms (Capinera *et al.*, 1982; Iglesias *et al.*, 2003; De Nardo *et al.,* 2004; Hozzank *et al.*, 2003a). The ecology and host range of *Phasmarhabditis*, a nematode parasite of slugs, needs to be better understood before it can be claimed completely safe for earthworms, even though laboratory studies so far indicate that there is no negative effect (Grewal & Grewal, 2003; Morand *et al*., 2004).

It has been suggested that earthworms might work as a vector of insect pathogenic fungi in the soil (Milner *et al.*, 2003). Shapiro *et al*. (1995) reported that upward dispersal of two species

of entomopathogenic nematodes increased in the presence of earthworms, they also suggested that nematodes may have a phoretic association with earthworms.

3.3.5. Arthropods

Many arthropods have one or several stages of their life cycle associated with the soil environment. Some are permanent soil inhabitants, where all life stages are found in or on the soil. Immature stages of other species are soil dwellers whereas the adult stages live and feed in aboveground food chains (see Fig. 2). A high proportion of soil animals are arthropods, and the most abundant are collembolans (springtails) and mites (Coleman *et al.*, 2004). Many soil dwelling arthropods are pests of plants, but several of them, such as predators and parasites, are also important natural enemies of pest arthropods. Centipedes, mites, spiders, beetles, and wasps are all common predators in or on the soil. Predatory mites in the orders Mesostigmata and Prostigmata feed on a variety of soil animals such as Collembola, Protura, Pauropoda, nematodes, enchytraeids and eggs, larvae and pupae of insects. The predatory mites *Hypoaspis aculeifer* and *H. miles* (Mesostigmata) are used in inundative biological control against thrips, fungus gnats and bulb mites in greenhouses (Walter & Proctor, 1999). Spiders are another familiar group of carnivores. Many species are found in above ground habitats, but some are cryptozoans in litter and on the soil surface (Coleman *et al*., 2004). Even though many spiders are not true soil-dwellers the families Lycosidae, Linyphiidae, Gnaphosidae, Tetragnathidae, Clubionidae, Thereidiidae and Agelenidae can establish a close association with the soil community and prey on other arthropods (Wallwork, 1970; Coleman *et al*., 2004). Two of the most widespread beetle families in soil are carnivorous Carabidae and the Staphylinidae, which includes both predatory and saprophagous forms (Wallwork, 1970). Recent studies with monoclonal antibodies have revealed the importance of earthworms and slugs as prey sources for ground beetles (Shah *et al.*, 2003). Some Dipteran larvae such as the Brachycera may prey on other insect larvae, small molluscs and annelids, and nematodes. Several Brachycera species in the families Tachinidae, Phoridae and Calliphoridae are parasites of earthworms, molluscs, and soil-inhabiting arthropods (Wallwork, 1970). *Ormia depleata* (Tachinidae), for example, is well known as a classical biological control agent against mole crickets, *Scapteriscus* in USA (Parkman *et al.*, 1996). Many Hymenoptera in the families Mutilidae, Scoliidae, Chalcididae, Proctotrupidae, Tiphiidae and Sphecidae parasitize soil-dwelling insect larvae. *Larra bicolor* (Sphecidae) is known as a classical biological control agent against mole crickets in USA (Wallwork, 1970; Frank *et al.*, 1995). Parasitoids from other families and even other orders are also known as parasites of soil dwelling pupae of pest insects. Pupae of the soil dwelling pests *Delia radicum* and *D. floralis,* for example, are parasitized by the following: *Trybliographa rapae* (=*Cothonaspis rapae*) (Eucolidae: Hymenoptera), *Aleochara bilineata, A. sufussa* (Staphylinidae: Coleoptera) and *Phygadeuon trichops* (Ichneumonidae: Hymenopthera) (Sundby & Taksdal, 1969; Jonasson *et al*., 1995). High levels of parasitism have been observed, and *T. rapae* has been shown to parasitize up to 50% of *D. radicum* and *D. floralis* pupae in Norway (Sundby & Taksdal, 1969). The soil environment also functions as a reservoir for insect parasitoids that attack insect pests above ground since many of these parasitoids spend their diapausing or over wintering stage in the litter or the upper layer of the soil (Stary, 1988).

Predators and parasites in the soil environment can interact antagonistically with insect and mite pathogens and insect parasitic nematodes by decreasing host density and by competing for

hosts and vice versa (Bathon, 1996). Insect and mite pathogens and insect parasitic nematodes might also directly decrease soil arthropod natural enemy populations. Steenberg *et al.* (1995) and Vestergaard *et al.* (2003) for example report that insect pathogenic fungi can infect soil dwelling arthropod natural enemies. Several studies of epigeal systems show that arthropod natural enemies change their behaviour and often avoid hosts that are infected with a pathogen (Hajek, 1997; Pell *et al.*, 2001). Behavioural studies are difficult to conduct in a soil ecosystem and to our knowledge no studies on avoidance by predators and parasitoids to infected hosts have been conducted. Competition between pathogens and parasitoids inside an insect or mite host after infection and parasitation is also known to occur, and most pathogens kill the host faster than a coidiobiont parasitoid. Parasitation therefore affects the pathogen development only when the host is parasitized before it is infected (Hajek, 1997; Pell *et al.*, 2001; Lacey *et al*., 2003). Natural enemies of pest arthropods and other non-target arthropods can also interact synergistically with insect and mite pathogens and insect parasitic nematodes, by for example enhancing transmission and dispersal. Studies conducted with predators and parasitoids in epigeal systems show that the presence and activity of these natural enemies resulted in a substantial increase of pathogen transmission, both because the natural enemy vectors the pathogen and because it increases the movement of the host (e.g. Roy & Pell, 2000). Evans (2000) also shows that predators and parasitoids have a role to play in dispersal of insect pathogenic viruses from the soil inoculum to the host. Microbes can be disseminated by soil microarthropods, where microarthropods can passively transport bacteria, fungi, and protozoa in the gut or on the cuticle across regions of soil that are impenetrable to the microbiota. Microphytophages such as collembolans are well known to feed on fungi (Moore *et al.*, 1988), and they are non-susceptible to insect pathogens (Broza *et al.*, 2001). Considerable amounts of viable conidia of insect pathogenic fungi can be carried on the cuticle and in the gut of collembolans (Broza *et al.,* 2001; Dromph, 2001). Dromph (2003) also showed that insect pathogenic fungi like *Beauveria bassiana*, *B. brongniartii* and *Metarhizium anisopliae* can be vectored by collembolans and as a result cause mortality in susceptible host insects in the soil. Little work has been done on dispersal of entomopathogenic nematodes by arthropods, (Kaya, 1990), although phoretic relationships between other nematodes and insects is well known. Hosts that have become infected with entomopathogenic nematodes may disperse nematodes in the soil before they die.

Insects and mites are hosts of arthropod pathogens and insect parasitic nematodes, and the presence of a host affects the persistence and abundance of arthropod pathogens and insect parasitic nematodes in the soil. A soil ecosystem with a high density of host arthropods will therefore also support a high abundance of insect and mite pathogens and insect parasitic nematodes. Although saprophytic growth of some arthropod pathogens are known (Hajek, 1997), the growth is often limited and primarily restricted to host insects or mites in native soils (Kessler *et al*., 2004). Entomopathogenic nematodes are obligate pathogens of insects, and in order to persist they need to reproduce (recycle) within a host (Kaya 1990). Kowalska (2000) reported on the presence of an alternative host, the curculionid *Strophosoma faber* that could enhance the effect of entomopathogenic nematodes against the turf pest *Amphimallon solstitiale* (Scarabaeidae). An interesting study investigating the recycling of entomopathogenic nematodes in cruciferous crops showed that relatively small and abundant insects that only pupate in the soil can contribute to maintaining entomopathogenic nematode populations in soil (Nielsen & Philipsen, 2004).

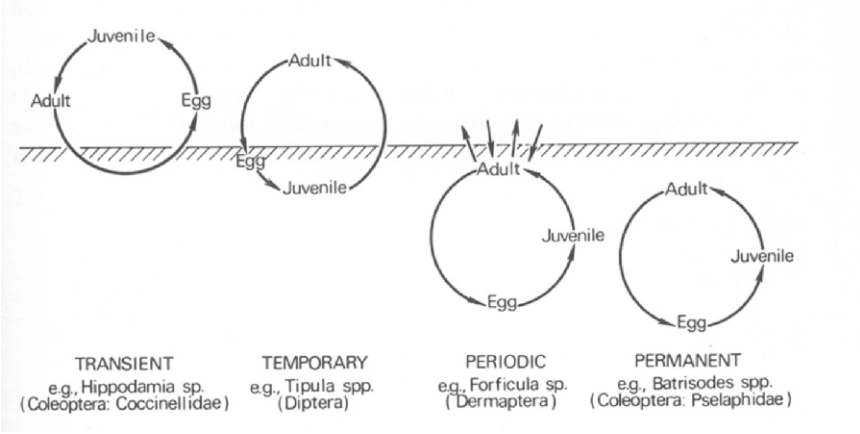

Figure 2: Categories of soil animals defined according to degree of presence in the soil, as illustrated by some insect groups (from Wallwork, 1970)

3.3.6. Slugs and snails

Terrestrial gastropods (snails and slugs) are important herbivores and several species are important pests in agroecosystems (Barker, 2002). The majority of species, however, feed on decaying tissue as well as numerous Basidomycetes, facilitating decomposition on soils and return of plant litter to the soil (Dallinger *et al.*, 2001; Coleman *et al.*, 2004). There is a wide range of natural enemies of slugs and snails, including predators, parasites and diseases, recently reviewed by Barker (2004). Important predators are vertebrates such as birds and mammals (Allen 2004). Among the predatory arthropods, Coleoptera are important, especially carabid beetles. Sciomyzid fly larvae (Marsh flies) are also well studied predators of slugs and snails (Symondson, 2004; Barker *et al.,* 2004). The trombidiform "slug mite" *Riccardoella limacum* is an ectoparasite of slugs, Fain (2004) gives an update on predaceous and parasitic mites. Nematodes have been recorded as parasites of slugs and snails on a number of occasions (Grewal *et al.*, 2003), but are not well studied. Morand *et al.* (2004) have listed 8 families and 27 described species of nematodes parasitic in terrestrial gastropods, it is likely that there are several more nematode species that have yet to be discovered. In recent years one particular nematode, the rhabditid *Phasmarhabditis hermaphrodita*, has been developed as a biological control agent of slugs, (Wilson *et al.*, 1993; Morand *et al*., 2004).

3.3.7. Vertebrates

Vertebrates have a great influence on the soil community through an impressing diversity of interactions. It is difficult, however, to make a rigid definition of the vertebrate soil fauna, and several species may be mentioned that influence the soil. Animals that burrow or make nests in the soil, animals that feed on other soil animals (moles, rodents and birds) and animals that graze and deposit dung on the soil surface all affect the soil community in one way or the other. One example is the mole that can consume between 18 and 36 kg earthworms and insects each year over an area of 0.1 acre (Wallwork, 1970). It is also known that birds or grazing sheep can disperse a NPV virus pathogenic to the lepidopteran pasture pest complex *Wiseana* spp (Tanada & Kaya, 1993).

4. Soil physical factors important to natural enemies of pest arthropods

Several physical soil factors are important to natural enemies of pest arthropods, and in this section we will review some of them. Soil texture (the relative proportions of sand, silt and clay particles) and soil structure (the combination and arrangement of primary soil particles into secondary particles, aggregates) has a strong impact on the accessibility of food, shelter, water, oxygen and nutrients to the soil biota (Coleman, 1986; Foth & Turk, 1990). Different sized organisms have different amounts of space available to them depending on soil texture. Smaller particle size and finer soil texture results in reduced pore size and increased tortuosity that can impede the movement of soil organisms. Structure is strongly affected by climate, biological activity, density and continuity of surface cover, and soil management practices. Most research on effects on biological control, however, has been concerned with texture (Barbercheck, 1992). Soil pH can have some impact on insect and mite pathogens and insect parasitic nematodes (Smith, 1999; Kessler *et al.*, 2003). Soil climatic conditions such as temperature, gases, water status and humidity are also important factors (Barbercheck, 1992). Soil temperature will vary depending on the geographical location, aspect and gradient of surface slopes, exposure, soil colour, soil cover and the nature and density of plant cover (Keller & Zimmermann, 1989). Water status and humidity are dependent on soil texture, structure, organic matter and the climatic conditions (Foth & Turk, 1990). At the surface, moisture is frequently in equilibrium with the atmosphere, and under dry climatic conditions, growth of many soil organisms might be restricted or inhibited. In the deeper soil layers and in temperate climatic zones the moisture content is higher. Rainfall influences the vertical movement of soil organisms (Keller & Zimmermann 1989; Inglis *et al.*, 2001).

4.1. Pathogens of insects and mites

Soil can provide favourable physical conditions for survival of insect and mite pathogens. In comparison to the epigeal environment, pathogens in soil are not subject to destruction by solar radiation, and humidity is relatively high and stable (Barbercheck, 1992).

4.1.1. Soil texture, structure and organic matter

The activity and location of the host insect or mite are important for the contact between the pathogen and the host. Contact between soilborne pathogens and their hosts in the soil are also determined largely by soil factors affecting passive percolation into the soil profile (texture, structure and organic matter) (Storey & Gardner, 1987; Barbercheck, 1992). Several studies have been conducted on the distribution, abundance, persistence and percolation of arthropod pathogens in the soil (e.g. Rath *et al*., 1992). Many studies suggest that a high clay content of soil enhances the abundance and persistence of many insect pathogenic fungi because clay particles adsorb conidia (Kessler *et al.*, 2003; Vänninen *et al.,* 1989; Studdert *et al*., 1990). The mechanisms responsible for the high retention of conidia in clay soils are unknown, but may be related to their high cation exchange capacity (the capacity of soils to adsorb ions) and/or its reduced pore size (Inglis *et al*., 2001). Ignoffo *et al.* (1977) further hypothesize that electrical differentials between conidia and clay particles might be responsible. Conidia adsorbed in this way in clay are retained where they were originally produced (from a host cadaver) or where they were artificially applied (as a microbial control agent), and not washed away by rainwater. This could be an advantage or a disadvantage depending on where the host is located or whether other soil organisms or water are able to spread the fungal propagules to the sites where the host is located. The movement of soil during cultivation (ploughing, harrowing and hoeing) can also disperse microorganisms within 20-30 cm of the plough depth and several meters horizontally. Ploughing and harrowing increases porosity of the soil, but heavy traffic during cultivation causes compaction of the soil destroying macropores. The former thus aids dispersal and the latter hinders it (Dighton *et al.*, 1997).

Soil with high organic matter content can affect arthropod pathogenic fungi. Whether the net effect is positive or negative for their occurrence and persistence is not clear. Several authors suggest that arthropod pathogenic fungi have low persistence in soil high in organic matter (Studdert *et al.*, 1990; Vänninen *et al.*, 2000; Kessler *et al.*, 2003). They explain this by the high biological activity and presence of numerous antagonistic organisms. On the other hand, soil high in organic matter has a greater diversity and density of arthropods, which are possible pathogen hosts. It has been suggested that soil low in organic matter tends to retain fewer fungal propagules than soils high in organic matter, explained by the fact that the latter has a higher cation exchange capacity, that helps adsorb fungal conidia (Ignoffo *et al.*, 1977; Inglis *et al*., 2001). This means that although it is suggested that soils high in organic matter adsorb conidia of several insect pathogenic fungi, the conidia that are present in the soil are probably killed or degraded faster. An increase in new fungal propagules produced in soil high in organic matter, due to the high density of arthropod hosts, should also be taken into account.

Differing water content and temperature of the soil studied may confuse the results obtained. In several of the soil type studies, water content and temperature were not measured and hence the differences observed could be due to these other factors rather than the properties of the soil. Studdert *et al*. (1990) report for example that conidia half-lifes were significantly longer in Yolo fine sand loam (<1% organic matter) than in peat (62% organic matter) in the middle range of water potentials (-0,3 to –15 bars) and at temperatures up to 20^{o}C. At the more extreme water potentials and at the higher temperatures, these differences were no longer significant. According to Keller & Zimmermann (1989), it also appears that the structure of the

fungal spores, their formulation and probably the addition of a wetting agent may interfere with how easily fungal propagules percolate through the soil. Some of the soil type studies are conducted with formulated fungi and some with clean spores. This may confuse what the actual effect of a specific soil type is. For example in a study conducted by Storey & Gardner (1987) they were not able to show that high clay composition in soil restricted vertical movement of formulated *B. bassiana* conidia even though studies with clean spores show restricted movement in clay soils.

4.1.2. Temperature

Differences in the geographical distribution of insect and mite pathogenic fungi may partly be explained by their average temperature requirements. Vänninen *et al.* (1989) and Vänninen (1995) found that *M. anisopliae* and *Paecilomyces fumosoroseus* were more prevalent in the south of Finland than for example *P. farinosus* and *B. bassiana* which were more prevalent in northern locations. Vänninen (1995) also suggest that the frequency of insect pathogenic fungi in general appears to decline northwards in Europe. In Norwegian studies, *M. anisopliae* has been found further north ($67^{o}16^{l}$N, $14^{o}27^{l}$E) than in the Finnish study, but the location was close to the coast where the temperatures are generally higher than inland (Klingen *et al.* 2002a). Several studies confirm that *P. farinosus* and *B. bassiana* can tolerate a wider range of climatic conditions and that *M. anisopliae* is more thermophilic. Laboratory studies conducted by Mietkiewski *et al.* (1994) and Tkaczuk *et* al. (2000) for example show that *M. anisopliae* was the most thermophilic of the fungi tested while *P. farinosus* show best growth at the lowest temperature (5^{o} C). It is important to mention, however, that in a study conducted by De Croos & Bidochka (1999), *M. anisopliae* isolates have also been deemed cold-active (grow at 8^{o} C). In this study, all the cold-active isolates were isolated from the more northern sites, and no isolate originating below 43.5^{o} N showed cold activity. Both *B. bassiana* and *P. farinosus* are known to tolerate a wide range of climatic conditions and *B. bassiana* has been found as far north as 75^{o} N in Canada (Widden & Parkinson, 1979). The insect pathogenic fungi *Tolypocladium cylindrosporum* is also known from northern locations and has been found in Norway at $69^{o}20^{l}$N, $19^{o}19^{l}$E (Klingen *et al.*, 2002a).

Several authors have focused on finding cold-active strains of insect pathogenic fungi for use as microbial pesticides, and as suggested above the influence of temperature on the activity of these fungi has shown to be linked to the provenance of the isolates. Indigenous strains are therefore often regarded as the best candidates for biocontrol agents. Considerable intraspecific variation with respect to temperature tolerance among isolates or strains originating from the same geographical location does exist, however, and sometimes isolates originating from warm areas outperform more northern isolates, even under cool conditions (Vänninen, 1999). It is also suggested that the habitat type decides the temperature requirements for an isolate and Bidochka *et al.* (2001) found that fungal isolates collected from forested areas show an ability for cold-active growth (at 8^{o} C), while fungal isolates from agricultural areas showed ability for growth at high temperature (37^{o} C).

As mentioned in the introduction to this section, the soil temperature might be modified by other factors than geographic location, soil cover being one of them. Hummel *et al.* (2002) observed that insect pathogenic fungi were negatively affected when soil temperatures were artificially raised due to the presence of black plastic mulch or bare ground. They suggest that these fungi are adapted to lower temperature ranges and that the increase in soil temperature

reduce their survival. The negative effects of high temperature on insect pathogenic fungi have been shown by several authors (e.g. Mietkiewski *et al*., 1994).

4.1.3. Water potential and moisture

Water potential is the primary factor determining the availability of soil water to plants and animals. In general nematodes, protozoans and bacteria often require a water film for activity, whereas fungi do not. It is known that free water can adversely affect fungal propagules (Barbercheck, 1992). There might be several explanations for this. One is the lack of oxygen and hence the production of carbon dioxide that harms fungal propagules in water saturated soil (Keller & Zimmermann 1989). The other is that bacterial activity and movement is positively related to soil moisture. Active bacteria lyse fungi and reduce the number of fungal propagules under humid or wet soil conditions (Ekesi *et al.*, 2003). Drier soil has been suggested to benefit fungi for the opposite reasons. Fungi are known to survive as resting propagules under very dry conditions (Keller & Zimmermann, 1989). Little is known about optimal field moisture conditions for entomopathogens, but several studies have identified critical parameters in the laboratory (Barbercheck, 1992). One of these studies shows that *B. bassiana* conidia half-lives were longest in non-sterile soil at –15 bars, and decreased as soil became moister or drier (Studdert *et al.*, 1990). Another microcosm study demonstrated that both soil temperature and moisture influence the survival and infectivity of *M. anisopliae* to four fruit fly species. It also showed that the effect of soil moisture is dependent on temperature. At 20-30^{o} C, fungal induced mortality in puparia of the fruit fly, *Ceratitis capitata*, was highest at water potential of -0.1 and -0.001 mega Pascal (Mpa) and lowest at water potential of –0.0055 and –0.0035 Mpa, but infection across all soil moisture levels was similar at 15^{o} C (Ekesi *et al*., 2003).

Water in the form of rain might influence the vertical movement of insect and mite pathogens. It is shown that conidia of insect and mite pathogenic fungi deposited on the surface of soil become washed into the soil at varying degrees depending on soil type (Hajek, 1997). Soil texture and organic matter appear to be the most important factors determining vertical movement of fungal propagules in water. The ratio of polar to neutral lipids in the fungal conidia also determines the relative miscibility of the conidia in water and thus influences their vertical percolation in soil (Storey & Gardner, 1987). Sandy-textured soil low in organic matter tend to retain fewer propagules than clayey and organic soils (Inglis *et al.*, 2001). Many studies show that fungal propagules tend to remain very close to the soil surface (Hajek, 1997), although some surveys show that insect pathogenic fungi can be found at depths down to 30 cm (Mietkiewski *et al.*, 1995). The occurrence of insect pathogenic fungi in deeper soil layers may be due to the vertical saprophytic growth of the fungi. For pathogens that are able to grow as saprophytes, fungal growth can extend far beyond cadavers in the soil environment (Hajek, 1997). To our knowledge, however, no studies have been conducted on how deep naturally occurring fungal infected cadavers can be found. Soil dwelling insect or mite hosts are known to move down to 45 cm undercertain conditions (Colemanet *al.,* 2004). It should be expected that insect pathogens inhabiting these hosts could be found at these soil depths as well. Infected insects or mites might, however, alter their behaviour and move to abnormal soil depths. This has been shown for the common armyworm *Pseudaletia separata* infected with either the fungus *Entomophaga aulicae* or the virus PsNPV. Healthy larvae exhibited a daily rhythmic pattern of movement, feeding on plants above ground during the night and burrowing into the soil during the day. When infected with either *E. aulicae* or PsNPV the pattern of move-

ment was disturbed: larvae crawled out of soil during the day and died near the top of the plant (Ohbayashi & Iwabuchi, 1991). The third-instar larvae of the masked chafer grub (Scarabaeidae) parasitized by the fungus *Tiphia pygidialis* is another similar example, where infected grubs burrowed to depths of 12-16 cm whereas healthy grubs remained in the upper 4 cm soil (Rogers *et al.*, 2003).

4.1.4. pH

The soil microflora is highly influenced by the soil pH. In general, high acidity decreases the growth of bacteria and increases that of soil fungi (Keller & Zimmermann, 1989). Fungi are important in all soils, and their tolerance of acidity makes them particularly important in acid forest soils (Foth, 1984). The influence of soil pH and ionic conductivity is not well understood (Inglis *et al.*, 2001). This might be due to the fact that in most studies, the average pH of bulk soil is used, which may vary considerably from the pH of the microenvironment (Barbercheck 1992). Since the microenvironment is the scale most pertinent to the survival and activity of individual microorganisms (Buckley & Schmidt, 2002), studies at this level might clarify the effect of pH on insect and mite pathogens further. A number of studies using the average pH of bulk soil have demonstrated, however, no or minimal effects of soil pH on the distribution and abundance of insect and mite pathogenic fungi (e.g. Rath *et al*., 1992; Kessler *et al.*, 2003). Laboratory studies also show that 29 different isolates of *B. bassiana* tolerated quite a wide range of pH from 5 - 13, but that pH 3 was toxic to all isolates, and the pH optimum varied between isolates (Padmavati *et al.*, 2003). Rath *et al*. (1992) also found that a specific isolate of *M. anisopliae* was able to grow across a wide range of pH (from 4.0 - 7.8). To our knowledge, little is known about the mechanisms of aluminium toxicity to insect pathogens in soil, even though aluminium may be a major factor limiting microbial growth and activity in acid soils. Some insect pathogenic fungi, like for example *P. fumosoroseus* are frequently found in natural habitats, particularly in hedges and forest soils (Vänninen, 1995; Chandler *et al.*, 1997). There is as yet no good explanation for this, but it might be that *P. fumosoroseus* thrives in more acid forest soil or is more tolerant of aluminium than e.g. *M. anisopliae*.

4.2. Insect parasitic nematodes

Several studies have investigated the physical factors in soil that affect nematodes in general; (Wallace, 1971; Jones, 1978; Norton, 1978; Norton, 1989; Kaya, 1990; Baur & Kaya, 2001). Nematode behavioural response to environmental factors (physical, chemical, mechanical and energy) has recently been reviewed by Barbercheck & Duncan (2004). Several decades ago Wallace (1968) stated that the principal soil factors affecting nematodes are pore size (soil texture), water (moisture and water potential), aeration, temperature and the chemistry of the soil solution, which still holds true today, although some more knowledge has been acquired (Kaya, 1990; Barbercheck, 1992). With respect to entomopathogenic nematodes, studies on physical factors have been conducted with emphasis on trying to understand their efficacy as biological control agents in the field (Gaugler & Kaya, 1990; Gaugler, 2002). Entomopathogenic nematodes require an insect host to complete their life cycle, hence during periods when hosts are scares or unavailable they must possess mechanisms that enable them to persist for long periods in the soil. Some studies on soil physical factors that affect entomopathogenic nematodes are presented in table 4. Most of these studies are controlled laboratory experiments.

Table 4: Selected reports on soil physical factors affecting entomopathogenic nematodes

Nematode species	**Abiotic factor studied**	**Brief comments**	**References**
Heterorhabditis bacteriophora *Steinernema feltiae* *S. carpocapsae* *S. glaseri* *S. kraussei* *Steinernema* sp.	Temperature	Detailed study on behaviour and infectivity at different temperatures	Molyneux; 1986
S. carpocapsae *S. glaseri*	Soil type	Persistence in different soil types	Kung & Gaugler, 1990
S. carpocapsae *S. glaseri*	Soil pH and oxygen	Persistence at different pH and oxygen levels	Kung *et al*., 1990
S. carpocapsae *S. glaseri*	Soil temperature and moisture	Persistence and infectivity at different temperatures and moisture	Kung & Gaugler, 1991
H. bacteriophora *S. carpocapsae*	Soil texture	Host finding and soil texture	Barbercheck & Kaya, 1991
H. bacteriophora *H. megidis* *H. zealandica* *Heterorhabditis* sp *S. feltiae* *S. carpocapsae*	Soil temperature	Reproduction at 10^{o}C	Wright, 1992
S. carpocapsae *S. glaseri*	Soil moisture and depth	Infectivity at different soil depths and moisture	Koppenhofer *et al.,* 1995
S. carpocapsae *S. glaseri* *S. riobravis*	Temperature	Survival under freezing conditions	Brown & Gaugler, 1998
S. kraussei	Soil temperature	Rate of infection at 10^{o}C	Mráčzek *et al*., 1999
S. riobravis	Soil depth and moisture	Distribution at different moisture levels and depths	Gouge *et al*., 2000
S. feltiae *S. kraussei* *H. megidis*	Soil temperature	Infectivity at low temperatures	Long *et al*., 2000

Nematode species	Abiotic factor studied	Brief comments	References
S. riobravis	Soil moisture	Persistence and infectivity in the root zone under dry conditions	Duncan & McCoy, 2001
S. arenarium *S. carpocapsae* *S. feltiae* *H. bacteriophora* *H. megidis*	Soil temperature	Infectivity against *Delia radicum* at different temperatures	Chen *et al*., 2003
S. carpocapsae *S. feltiae* *S. glaseri* *H. bacteriophora*	Soil moisture	Effect on virulence under fluctuating moisture conditions	Grant & Villani, 2003a,b

4.2.1. Soil texture, structure and organic matter

The efficiency with which nematodes can explore their physical environment is important for their ability to locate a host, mate and avoid predators. Wallace (1968) gives an extensive account on nematode movement in soil, describing how they predominately propel themselves through the soil using the surface tension in the water films surrounding soil grains. The movement of nematodes is significantly affected by many factors like chemical gradients in soil, temperature (see 4.2.3.) and the size of the nematode, but to enable movement through soil, soil texture, soil structure and soil moisture (see 4.2.2.) are critical. Soil pore space is related to particle size (soil texture); an increase in particle size gives an increase in width of pores and pore necks. The elongate cylindrical shape of nematodes appears to be an adaption for migration through narrow spaces. Wallace (1968, 1971) describes the importance of nematode size with respect to pore size and moisture, as the length and diameter of the nematode increase, the optimum pore and particle size also increase. Most studies focus on soil texture rather that soil structure, where structural pore space is determined by size and arrangement of aggregates and affects movement of water, air, chemicals and organisms. Soil compaction greatly impedes movement in fine-textured soils, but has little effect in sandy soils. Models for nematode movement in soil have been conducted where it was found that slower movement in fine textured soils would be expected to increase isolation among local populations, and increase the number of species that can co-exist in a given area. (Hunt *et al.*, 2001).

Portillo-Aguilar *et al*. (1999) showed the importance of soil structure for entomopathogenic nematodes by examining the influence of bulk density, (degree of soil compaction), on survival and movement of *H. bacteriophora*, *S. glaseri* and *S. carpocapsae*. The data indicated that the relative compaction of a sandy loam soil strongly affected the survival of the 3 species, but that the effects differed among the species. High bulk densities reduced survival in *H. bacteriophora* whereas *S. glaseri* survived well. It was suggested that the larger nematode *S. glaseri* (diameter 45μm) was restricted in movement thus conserving metabolic reserves, whereas the smaller *H. bacteriophora* (diameter 25 μm) was not restricted in movement resulting in a depletion of energy reserves.

There is evidence of differences in the active dispersal behaviour among entomopathogenic nematodes (Lewis, 2002). Understanding dispersal abilities has practical importance for biological control of pest species. As indicated by several authors (Kung & Gaugler, 1990; Portillo-Aguilar *et al*., 1999), soil texture and structure influences survival and pathogenicity of nematodes. The non-feeding infective juveniles of *Steinernema* and *Heterorhabditis* must rely on their stored reserves for survival and pathogenicity and soil texture can affect nematode energy reserves indirectly by regulating their movement.

Organic matter is an essential component of all soils and its influence on the general microbial population of the soil has been well studied. Less is known about specific relationships between nematodes and organic matter. The effect of organic amendments on plant parasitic nematodes has been studied mostly with respect to reducing crop damage. Soil organic matter contains predaceous fungi and other potential agents for the biological control of nematodes (Duddington, 1965). However ecological studies also show that the bacterial feeding nematodes increase with the content of organic matter. For entomopathogenic nematodes it can be expected that soils high in organic matter might be detrimental due to the presence of predators and pathogens, on the other hand, the increased abundance of possible arthropod hosts in organic soils may sustain or increase entomopathogenic nematode populations (Kaya 1990). Bednarek & Gaugler (1997) found that increased organic matter (organic manure) appeared to encourage nematode establishment and recycling. With regard to nematode movement, Barbercheck & Kaya (1991) found that *H. bacteriophora* was more motile in organic soil than *S. carpocapsae*. In Scotland and Ireland entomopathogenic nematodes (*S. carpocapsae*, *H. downesii* respectively) have been tested in the field against large pine weevil larvae (*Hylobius abietis*), with promising results (Kenis *et al*., 2004). In this case, the nematodes have to move through soil with high organic matter content to reach the pine weevil larvae. Dillon (2003) reported that *S. carpocapsae*, *S. feltiae*, *H. downesii* and *H. megidis* were capable of infecting *H. abietis* larvae at least 40 cm from the zone of application when nematodes were applied to pine stumps. Nematodes migrated further under natural conditions than in containerised peat (Aiofe Dillon pers. comm.). These studies support the hypothesis that the presence of roots plays an important role in the migration of nematodes through soil (van Tol *et al*., 1998, see also 4.2.4.).

Torr *et al*. (2004) demonstrated for the first time that entomopathogenic nematodes (*S. carpocapsae*, *S. feltiae* and *H. megidis*) responded positively to seismic vibrations in peat soil, hypothetically responding to noises made by host larvae feeding on roots.

4.2.2. Water potential and moisture

Soil moisture is one of the main factors affecting nematode activity in soil (Wallace, 1968, 1971). Moisture is critical for movement because nematodes need a water film in the interstitial spaces of soil for effective propulsion. The moisture content, (grams water per 100g dry soil), for different soil types gives little indication of the percentage of pores that contain water or air (moisture characteristic), for example sandy soils have large pore spaces but less total pore space than clay soils. When the soil becomes dry, nematode movement is inhibited because there is no water film available. Oxygen becomes the limiting factor for nematodes in clay soils, water saturated soils, or soil with high organic content. Temperature is also affected by moisture, since solar heat penetrates deeper in wet soil but produces a smaller rise in temperature than in dry soil (Kaya, 1990).

It has been shown that some nematodes are able to survive extremely low moisture levels and enter into a state of anhydrobiosis in which metabolism comes reversibly to a standstill (Womersley, 1987; Wharton, 2002; McSorely, 2003). Inactivity caused by abiotic factors, such as dehydration, that induce these physiological changes increases nematode persistence and often reflects the habitat and life cycle of the nematode. The plant parasitic nematodes *Ditylenchus dipsaci* ("stem nematode") and *Anguina tritici* ("wheat nematode") are well known to be capable of anhydrobiosis (Norton, 1978; Sturhan & Brzeski, 1991; Krall, 1991).

Effects of soil moisture on entomopathogenic nematodes have been studied in relation to behavioural strategies, virulence and survival (Koppenhofer *et al*., 1995; Grant & Villani, 2003a; Grant & Villani, 2003b). Koppenhofer *et al*. (1995) hypothesized that differences in nematode establishment (numbers of nematodes entering a host) observed between *S. glaseri* and *S. carpocapsae* at different moisture levels was due in part to the size difference between the two nematodes. *S. glaseri* the larger of the two, requires a thicker film of water (ie. higher soil moisture) for optimal movement compared to *S. carpocapsae*. In wet soil, however, *S. carpocapsae* will not find enough surface tension to enable movement, and will be affected earlier than *S. glaseri*. Thus nematode species, soil texture and moisture interact to affect the nematodes ability to infect a host. The possibility for nematode infection is better over a wide range of water potentials in a sandy soil containing some silt and clay than in clay soil (Kaya, 1990). It has also been shown that the optimum moisture level required for survival is much lower than the optimum required for infection of a host (Womersley, 1990; Gouge *et al*., 2000).

The effect of desiccation on entomopathogenic nematodes has been reviewed by Womersley (1990). There are essentially two basic groups of anhydrobiotes, slow-dehydration and fast-dehydration strategists. This realization has helped to explain why different nematode species appear to require completely different conditions to induce anhydrobiosis (Womersley, 1987). Studies on entomopathogenic nematodes so far show that they require slow dehydration and that they cannot become fully anhydrobiotic, but enter a quiescent phase. These studies have mainly focussed on the commercial aspects of entomopathogenic nematodes with the aim to improve long-term storage of the infective stages. Womersley (1990) presumes that it is highly unlikely that for example *Steinernema* spp. have evolved strategies for tolerating rapid dehydration stress, as their natural habitat is in the upper soil profile where they are subjected to slow rates of evaporation.

Until now we have discussed the physical factors that can affect the infective stages of entomopathogenic nematodes directly in soil, however factors affecting the host, especially after infection, are also important to consider. Studies on the effect of host desiccation on entomopathogenic nematodes have been conducted (Koppenhofer *et al*., 1997; Serwe-Rodriques *et* al., 2004). In both studies implications for nematode survival and infectivity in desiccated hosts are discussed. Interestingly, an increased infectivity of emerging infective juveniles was observed in the latter study. It appears that for *S. carpocapsae*, originating from Wisconsin, the "in host desiccation process" selects for populations that enhance survival under environmental conditions native to the United States mid-west (e.g. Wisconsin).

4.2.3. Temperature

Responses to temperature extremes may be inactivity (quiescence), or behavioural. Variations in temperature affect nematode development, reproduction and the length of the life cycle (Freckman & Baldwin, 1990; Wharton, 2002; Barbercheck & Duncan, 2004). There will be an

optimum temperature at which nematode life cycles can proceed at their fastest rate. As temperatures increase or decrease from the optimum, these rates will decrease until normal processes are disrupted. The optimum temperature and rates of decrease in activity or development will vary from species to species and is likely to occur over a range of temperatures (Wharton, 2002).

Entomopathogenic nematodes have been isolated from many different habitats including temperate (cold climate) areas, indicating that they are adapted to low temperatures, as well as hot arid regions indicating their tolerance to high temperatures (Hominick *et al.*, 1996; Hominick, 2002). Several studies, mostly laboratory experiments, have investigated the effect of temperature on entomopathogenic nematodes. Temperature is one of the important factors limiting the success of entomopathogenic nematodes. Low temperature restricts use of some species in temperate regions of the world, and similarly, high temperatures are a constraint for their use in tropical countries. Exposure to extremes of temperature is damaging for nematodes, but the extent of damage depends on the duration of the exposure and on the nematode strain (Griffin, 1993). New *Heterorhabditis* isolates from arid regions or tropical climates have been shown to be heat tolerant the tolerance involving the presence of Heat-shock proteins (Glaser, 2002).

Thermal preferences were investigated by Grewal *et al*. (1994) for several species and strains of entomopathogenic nematodes at a range of temperatures between 8 ^{o}C and 39 ^{o}C (Table 5).

Table 5: Thermal preferences for some entomopathogenic nematodes adapted from Grewal et al. (1994)

Species	**Thermal niche breadths for different development stages in the life cycle**		
	Infection (mortality)	Establishment (number of nematodes entering a host)	Reproduction (nematode reproduction within a host)
Steinernema riobravis	10 – 39 ^{o}C	12 – 37 ^{o}C	20 – 35 ^{o}C
S. feltiae	8 – 30 ^{o}C	8 – 30 ^{o}C	10 – 25 ^{o}C
S. glaseri	10 – 37 ^{o}C	10 – 37 ^{o}C	12 – 32 ^{o}C
S. carpocapsae	10 – 32 ^{o}C	12 – 32 ^{o}C	20 – 30 ^{o}C
S. anomaly (arenaria)	10 – 35 ^{o}C	10 –32 ^{o}C	12 – 32 ^{o}C
S. scapterisci	10 – 35 ^{o}C	20 – 32 ^{o}C	20 – 32 ^{o}C
Heterorhabditis bacteriophora	10 – 32 ^{o}C	15 – 32 ^{o}C	15 – 30 ^{o}C
H. megidis	10 – 35 ^{o}C	12 – 35 ^{o}C	20 – 32 ^{o}C

Nematodes which survive low temperatures in their natural habitat are said to be cold tolerant. In cold habitats the free-living stages of nematodes are exposed to, and must be able to survive, sub-zero temperatures for shorter or longer periods. Cold tolerance strategies for nematodes in general are discussed by Wharton (2002) and for entomopathogenic nematodes by Brown & Gaugler (1996). Brown *et al*. (2002) discuss the possibilities of latent infection in hosts as a strategy for overwintering, and suggests it is a rare event but of great advantage to those nematodes that successfully overwinter in their host. Sturhan & Reuss (1999) isolated

Steinernema sp."E" from subarctic heath soil in Sweden (68°20'N, 51'E). Surveys in Norway and Finland have also revealed the presence of *Steinernema* spp. in the northernmost areas (Vänninen *et al*., 1989; Haukeland, 1993; Salinas, 1996; Klingen *et al*., 2002d). In the Norwegian survey, *Heterorhabditis* sp. was isolated for the first time in the coastal southern part of the country, and a *Steinernema* sp. was isolated far north of the arctic circle, near the Russian border, at 69°27'N, 30°02'E (Haukeland pers. obs.). *S. kraussei* is commercially sold as a cold-active nematode, although there are few published reports on the biology and thermal preferences of this nematode (Willmott *et al*., 2002). *S. feltiae* is also considered to be a cold-active nematode (Grewal *et al*., 1994; Hazir *et al*., 2001).

4.2.4. Soil solution

Soil nematodes are affected by a wide range of chemicals in soil, and soil water acts as a medium for transport of, for example, host exudates that can trigger specific responses. A model has been reported for nematode migration through soil in response to a chemical gradient (Feltham *et al*., 2002).

The importance of plant roots for host-finding by entomopathogenic nematodes has been shown by several authors (Lei *et al*., 1992; van Tol *et al*., 1998; van Tol *et al*., 2001; Boff *et al*., 2002; Cutler & Webster, 2003). These nematodes are highly dependant on finding a suitable host and have shown to be attracted to host related chemicals such as root exudates, host faeces, and CO2 gradients (Schmidt & All, 1978, 1979; Gaugler *et al*., 1980; Pye & Burman, 1981; Kaya, 1990; O'Halloran & Burnell, 2003) Torr *et al*. (2004) suggest that with increasing content of soil organic matter, the utility of host chemical cues will decline, necessitating alternative host cues.

In most soils pH ranges from 4 to 8 and probably has little effect on nematode activity. Studies have shown that pH above or below this range can have negative effects on nematode survival (Kaya, 1990; Kung *et al*., 1990).

5. The effect of agroecosystems on the diversity and abundance of natural enemies

As mentioned in sections 3 and 4 both soil organisms and soil physical factors influence natural enemies such as arthropod pathogens and insect parasitic nematodes in soil. The action of man and activities such as frequency and type of pesticide application, the use of inorganic fertilizer or manure, the plant species grown, cultural practices and tilling also affect the diversity and abundance of different natural enemies in the soil. Management practices aimed at improving soil health frequently enhance or stimulate the natural enemies of plant pests. Magdoff (2001) discusses strategies for improving soil health in which the addition of soil organic matter, use of cover crops and reduced tillage, are some of the suggested strategies. Field boundaries, and the more diverse ecosystem they represent, are also known to influence the survival and propagation of natural enemies. More studies have been conducted on the effect of cropping systems and cultural practices on predatory and parasitoid arthropods than studies on arthropod pathogens and insect parasitic nematodes (e.g. Dritschilo & Wanner, 1980; Purvis & Curry, 1984; Hokkanen & Holopainen, 1986; Andersen, 1997; Fadl *et al*., 1996; Andersen, 1999; Wardle *et al*., 1999; Andersen & Eltun, 2000; Hummel *et al*., 2002; Shah *et al*., 2003; Andersen *et al*., 2004). Predators and parasitoids will not be treated thoroughly in this section, but will

only be mentioned in connection with the implications they have on insect and mite pathogens and insect parasitic nematodes.

5.1. Insect and mite pathogens

A positive relationship between the presence of insect pathogenic fungi and organically farmed fields has been shown in some studies (Kleespies *et al.,* 1989; Klingen *et al.*, 2002a; Hozzank *et al*., 2003b). This could be explained by the absence of synthetic pesticides in organically farmed soil, and the use of organic instead of mineral fertilizers.

The absence of pesticides, especially fungicides could to have a positive effect on the natural occurrence of arthropod pathogenic fungi. Numerous papers have been published on the effect of pesticides to arthropod pathogenic fungi (see Table 6), and very different conclusions are reached. A pattern appears to exist however. There is a strong tendency for insecticides not to be very harmful and herbicides to be moderately harmful, mostly affecting vegetative growth. The fungicides are most harmful but vary greatly depending on their active ingredient and fungal species. This is probably explained by the fungicides mode of action and the biology and response of each fungal species.

In a field experiment conducted by Hummel *et al.* (2002) it was found that several pesticides significantly reduced the presence of naturally occurring insect and mite pathogenic fungi in the soil. Laboratory studies also confirm the negative effect of pesticides (Vänninen & Hokkanen, 1988; Majchrowicz & Poprawski, 1993; Poprawski & Majchrowicz, 1995; Todorva *et al*., 1998; Li *et al.* 2004). Results from laboratory experiments and field conditions might differ, however Mietkiewski *et al.* (1997) examined the effect of several pesticides on naturally occurring insect and mite pathogenic fungi in field and laboratory experiments. In some cases the results obtained in the field were confirmed in the corresponding laboratory experiment, in other cases not (see table 6 for details). They suggested that several factors may be responsible for these results; including biotic and abiotic factors, the uneven distribution, different concentration and degradation rate of pesticides in a dynamic soil micro-environment. Keller *et al.* (1993) suggested that the non-target effect of chemical pesticides to arthropod pathogenic fungi applied as a microbial control agent might not be significant under practical conditions. For the use of *B. brongniartii* in orchards, for example, the fungus is applied at a soil depth of some centimetres so that direct contact with fungicides is avoided thereby avoiding adverse effects. For naturally occurring arthropod pathogenic fungi, the effect of fungicides will also depend on where they are located, which again depends on the movement of infected hosts in the soil profile (see section 4.1.3.). Studies also show that although several fungicides seem to be incompatible with the use of arthropod pathogenic fungi as microbial agents, the proper evaluation and timing of application can increase compatibility (Anderson & Roberts, 1983; Kouassi *et al.*, 2003). Several studies also suggest that some fungal species are more tolerant to pesticides than others, and *M. anisopliae* for example is considered to be tolerant to pesticides. It is shown, however, that the tolerance to pesticides varies between isolates within one single species (Mietkiewski *et al.*, 1997). Another complicating factor is that the application of insecticides in crop management systems, that causes insect host mortality, will indirectly reduce host density and fungal inoculum in the soil.

The use of organic fertilizers, could possibly provide arthropod pathogenic fungi with favourable conditions in organically farmed soil. This has been found to be the case in field studies of insect pathogenic nematodes, where organic manure resulted in increased densities

of a native population of *S. feltiae* while inorganic fertilizers suppressed nematode densities (Bednarek & Gaugler, 1997). Many of the mechanisms found in their study, such as the positive response of soil inhabiting insects to manure, could also be relevant to insect pathogenic fungi, because soil inhabiting insects are potential hosts and contribute to their spread and survival (Keller & Zimmermann, 1989).

In the few studies where the occurrence of insect and mite pathogenic fungi from organic and conventionally managed soil are compared there appears to be a weak dominance for fungal species other than *M. anisopliae* in organically managed soil (Klingen *et al*., 2002a; Hozzank *et al*., 2003b). *B. bassiana* is known to be associated with undisturbed habitats high in organic matter (Mietkiewski *et al.*, 1997). Soil high in organic matter is typical for organically managed soil and one could therefore possibly expect increased prevalence of *B. bassiana* in these soils compared to conventionally managed soils. There is a tendency for this in one study conducted by Klingen *et al*. (2002a). More studies are, however, needed to confirm this.

Minimal tillage can benefit the accumulation of pathogens and it has been shown that maximum benefit is obtained from arthropod pathogens by maintaining and restoring older pastures rather than engaging in regular cultivation for pasture renewal (Jackson *et al.*, 2000). Hummel *et al.* (2002) found that arthropod pathogenic fungi (*B. bassiana* and *M. anisopliae*) were more abundant in conservation tillage compared to conventional tillage systems. Keller *et al.* (2003) also found that meadows contained higher densities of *M. anisopliae* than in adjacent arable land, probably due to the scarcity of hosts as a result of control measures, soil cultivation and the application of fungicides. Sosa-Gomez & Moscardi (1994) showed that the density of entomopathogenic fungi were higher in no-tillage soy bean crops compared to tilled crops. In a study conducted by Bing & Lewis (1993), the greatest number of *B. bassiana* Colony Forming Units (CFUs) were observed in no-till systems. They also found that numbers of CFUs from soils varied greatly depending on the sample date, and suggested that *B. bassiana* inoculum in soil is probably influenced more by environmental conditions than by tillage practices. They do not specify, however, what they mean by environmental conditions. The success and survival of insect pathogens in soil is strongly dependent on stable environmental conditions, including the continuous, or at least frequent, presence of host insects. Vänninen *et al.* (1989) therefore suggested that the high occurrence of insect pathogenic fungi found under rowan trees was partly due to the continuous presence of larvae or pupae of the apple fruit moth (*Argyresthia conjugella*) and the absence of pesticides. Similar studies have also found an increased abundance of insect pathogenic fungi in more permanent habitats compared to arable fields (Chandler *et al.*, 1997).

Table 6: Reports on the effect of pesticides on insect- and mite pathogenic fungi that are known from the soil environment

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
Propiconazole Thiram Vinclozolin	Fungicides	*Metarhizium anisopliae* *Beauveria bassiana* *Paecilomyces fumosoroseus* *Paecilomyces farinosus*	Propiconazole, thiram and vinclozolin: Inhibited the linear growth of the fungi in petri dishes. Propiconazol and thiram: Also inhibited sporulation. (Laboratory study, *in vitro*).	Vänninen & Hokkanen, 1988
Benomyl Metalaxyl+ mancozeb	Fungicides	*M. anisopliae* *B. bassiana* *P. fumosoroseus* *P. farinosus*	Benomyl and metalaxyl+ mancozeb: No effect on *B. bassiana*, but the other species was inhibited up to three days after treatment. Metalaxyl+ Mancozeb: *P. fumosoroseus* was sensitive. (Laboratory study, *in vitro*).	Vänninen & Hokkanen, 1988
Captan+ Penconazole (Topas) Captan +Pyrifenox (Rondo) Copper-oxychloride (Recop) Triforine (Funginex)	Fungicides	*Beauveria brongniartii*	All fungicides completely inhibited mycelial growth *in vitro*. "Semi field" study on growth of fungus on barley kernels (commercial preparation) on soils sprayed with fungicides showed smaller differences. (Laboratory, *in vitro* and "semi field" study).	Keller *et al.,* 1993

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
Copper oxychloride (Miedizan 50) Hymexazol (Tachigaren) Mancozeb (Dithane M-45) Metalaxyl (Ridomil) Sulfur (Siarkol Extra) Sulfur +nitrothal-isopropyl (Siarkol N) Triadimefon (Bayleton) Zineb +copper oxychloride (Cynkomedzian)	Fungicides	*B. bassiana* *Conidiobolus coronatus* *Conidiobolus thromboides* *M. anisopliae* *P. farinosus* *P. fumosoroseus* *Scopulariopsis brevicaulis* *Verticillium lecanii*	Zineb+ copper oxychloride and mancozeb: Completely inhibited germination of *C. coronatus, C. thromboides, B. bassiana, P. farinosus, M. anisopliae* and *V. lecanii in vitro.* Triadimefon, copper oxychloride, metalaxyl, Sulfur, sulphur +nitrothal-isopropyl and hymexazol: Exhibited various effects on the fungi *in vitro*. Generally, adverse effects were much greater against the Entomophthorales than against the Hyphomycetes *in vitro*. (Laboratory study, *in vitro*)	Majchrowicz & Poprawski, 1993
Carbendazim (Bavistin) Flusilazole (Nustar) Prochloraz (Sportak) Propiconazole (Cane sett treatment)	Fungicides	*M. anisopliae*	Carbendazim, flusilazole, prochloraz and propiconazole: Inhibited mycelial growth and sporulation. (Laboratory study, *in vitro*).	Li & Holdom, 1994
Anilazine Benomyl Chinomethionat Copper hydroxide Dithianon	Fungicides	*V. lecanii* (*Trialeurodes vaporariorum*)	Chinomethionat, dithianon, triflumizole and zineb: Highly toxic to conidial germination *in vitro*. From some to no inhibition of the fungal killing	Saito & Yabuta, 1996

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
(study continued) Mepronil Polyoxin Procymidone Sulfur Triflumizole Zineb			capacity of *T. vaporariorum* larvae when treated (39%, 54%, 72% and 100% *T. vaporariorum* mortality respectively). Copper hydroxide, dithianon, mepronil, polyoxin, procymidone, sulphur and zineb: No negative effect on mycelial growth. Anilazine, benomyl, chinomethionat and triflumizole: Inhibited mycelial growth. (Laboratory study: *in vitro* and insect bioassay).	
Benomyl Triadimefon	Fungicides	*B. bassiana* (*Galleria mellonella*, bait insect)	Benomyl: Significantly fewer *G. mellonella* became infected in field soil treated with benomyl. Confirmed in *in vitro* experiments. Triadimefon: Significantly more *G. mellonella* became infected in field soil treated with Triadimefon. *In vitro* experiments showed inhibition rather than stimulation. (Laboratory study *in vitro* and field studies with *G. mellonella* as bait insect).	Mietkiewski *et al*., 1997

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
Chlorothalonil Mancozeb Maneb Metalaxyl +mancozeb Thiophanate-methyl Zineb	Fungicides	*B. bassiana*	Chlorothalonil, mancozeb, maneb, metalaxyl +mancozeb, thiophanate-methyl, zineb: Inhibition of mycelial growth and sporulation *in vitro*. (Laboratory study, *in vitro*).	Todorova *et al.,* 1998
Copper oxide Mancozeb Metalaxyl	Fungicides	*B. bassiana*	Copper oxide, mancozeb, metalaxyl: Strongly fungistatic and inhibited the fungal radial growth *in vitro.* (Laboratory study, *in vitro*).	Kouassi *et al*., 2003
Penycuron Quintozene	Fungicides	*B. bassiana*	Quintozene: Affected the *B. bassiana* conidial germination negatively *in vitro*. It also significantly impacted vegetative growth and sporulation of *B. bassiana in vitro.* Penycuron: Compatible with *B. bassiana.* (Laboratory study, *in vitro*).	Andalo *et al.,* 2004
Trifluralin	Herbicide	*M. anisopliae* *B. bassiana* *P. fumosoroseus* *P. farinosus*	Trifluralin: Inhibited the linear growth of the fungi in Petri dishes (Laboratory study, *in vitro*).	Vänninen & Hokkanen, 1988
Glyphosate MCPA	Herbicides	*M. anisopliae* *B. bassiana*	Glyphosate and MCPA: Only *B. bassiana* was sensitive.	Vänninen & Hokkanen, 1988

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
(study continued) Simazine		*P. fumosoroseus* *P. farinosus*	Simazine: Affected only the two *Paecilomyces* species. (Laboratory study, *in vitro*).	
Atrazine (Atrazine) 2-4-D amine (Amicide) Diuron (Diuron) Glyphosate (Glyphose) Paraquat dichloride (Gramoxone) Pendimethalin (Stomp) Trifluralin (Treflan)	Herbicides	*M. anisopliae*	Atrazine, 2-4-D amine, diuron, glyphosate, paraquat dichloride, pendimethalin and trifluralin: The negative effect of mycelial growth and sporulation were not very pronounced, but it varied between isolates. As the concentrations became lower the negative effect was less pronounced or not pronounced at all. Diuron, paraquat dichloride and pendimethalin seemed to have the most pronounced negative effect. (Laboratory study, *in vitro*).	Li & Holdom, 1994
Chloridazon Lenacil Metolachlor Phenmedipham +desmedipham	Herbicides	*C. thromboides* *C. coronatus* *B. bassiana* *M. anisopliae* *P. farinosus* *V. lecanii*	All herbicides except from lenacil had pronounced adverse effects on all fungi. Lenacil temporary stimulated *C. thromboides* at low concentrations (0.1X). (Laboratory study, *in vitro*).	Poprawski & Majchrowicz, 1995
Glyphosate	Herbicide	*B. bassiana*	Glyphosate: No significant difference compared to control for	Mietkiewski *et al*., 1997

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
(study continued)			infection of *G. mellonella. In vitro* experiments showed inhibition of fungal growth at increasing glyphosate concentrations. (Laboratory study: *in vitro* and insect bioassay)	
Acetochlor Azafenidin 2,4-D Dimethylurea Glyphosate Oxyfluorfen Simazine +Ametryne	Herbicides	*B. bassiana*	Acetochlor, azafenidin, 2,4-D, oxyfluorfen and simazine +ametryne: Affected the conidial germination negatively. Acetochlor, azafenidin, 2,4-D, dimethylurea, glyphosate, oxyfluorfen and simazine +ametryne: Significantly impacted vegetative growth and sporulation of *B. bassiana* negatively. (Laboratory study, *in vitro*).	Andalo *et al.,* 2004
Azinphos-methyl (Gusathion 50WP & 2F) Carbaryl (Servin 50WP) Carbofuran (Furadan 4F) Diflubenzuron (Dimilin 25WP) Endosulfan (Thiodan 3EC & 50WP) Fenvalerate (Pydrin 2EC)	Insecticides	*B. bassiana*	The formulation of the insecticide was often more significant than the active ingredient on *B. bassiana* inhibition. Permethrin and fenvalerat caused significant inhibition of *B. bassiana (in vitro).* Separate application of *B. bassiana* and insecticides greatly mitigated *B. bassiana* inhibition (microcosm study).	Andersen & Roberts, 1983

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
(study continued) Permethrin (Ambush 2EC & Ectiban 25WP) Piperonyl butoxide (PBO 8EC, Prentox) Oxamyl (Vydate 2EC)			(Laboratory: *in vitro* and microcosm studies).	
Diazinon Cypermethrin Pirimicarb	Insecticides	*M. anisopliae* *B. bassiana* *P. fumosoroseus* *P. farinosus*	Cypermethrin, diazinon and pirimicarb: No effect on growth and sporulation. (Laboratory study).	Vänninen & Hokkanen, 1988
Abamectin Thuringiensin Triflumuron	Insecticides	*B. bassiana* *(Leptinotarsa decemlineata)*	Abamectin, thuringiensin and triflumuron: No significant inhibition of *B. bassiana in vitro.* In field cage test: Extremely variable, but *B. bassiana* +insecticide caused generally higher *L. decemlineata* mortality than one agent alone. (Laboratory *in vitro* and semi field studies).	Anderson *et al.,* 1989
Aldicarb (Temik) Carbofuran (Furadan) Chlorpyrifos (Lorsban) Ethoprophos (Mocap) Fenamiphos (Nemacur)	Insecticides	*M. anisopliae*	Aldicarb, carbofuran, chlorpyrifos, ethoprophos and fenamiphos: The negative effect of mycelial growth and sporulation were very weak, but it was some variation between isolates. (Laboratory study).	Li & Holdom, 1994

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
Aldicarb Chlorfenvinphos	Insecticides	*B. bassiana* (*G. mellonella*, bait insect)	Clorfenvinfos: fewer *G. mellonella* (but not significantly) became infected in field soil treated with clorfenvinfos Confirmed in *in vitro* experiments. Aldicarb: No significant difference compared to control for infection of *G. mellonella* in field soil. *In vitro* experiments showed stimulation of fungal growth. (Laboratory, *in vitro* and field studies with G. *mellonella* as bait insect).	Mietkiewski *et al*., 1997
Triflumuron (Alsystin)	Insecticide/ acaricide	*B. bassiana* *(Tetranychus urticae)*	Triflumuron: Reduced mycelial growth, but not conidial germination of *B. bassiana* (*in vitro*). When *B. bassiana* and triflumuron were sprayed in combination against *T. urticae* the effect was less than with *B. bassiana* alone (bioassay). (Laboratory study: *In vitro* and mite bioassay).	Irigaray *et al.,* 2003
Abamectin (Vertimec 18) Acrinathrin (Rufast 50) Amitraz (Parsec) Chlorfenapyr (Citrex) Cyhexatin (Sipcatin 500)	Acaricides/ insecticides	*B. bassiana*	All acaricides/ insecticides tested caused different levels of inhibition on germination, vegetative growth and sporulation on *B. bassiana*.	De Olivera & Neves, 2004

Active ingredient/common name (Trade name)	**Pesticide group**	**Fungal species (host species if relevant)**	**Effect on insect and mite pathogenic fungi (type of study)**	**References**
(study continued) Dimethoate (Dimetoato) Fenbutatin oxide (Partner) Fenpyroximate (Kendo) Hexythiazox (Savey) Pyridaphethion (Ofunack 400) Pyridine (Sanmite)			The acaricides: Amitraz, clorfenapyr, cyhexatin, dimethoate, fenbutatin oxide, fenpyroximate, hexythiazox, pyridaphethion, and pyridine belonging to the organophosphate and organostatic groups drastically affected conidial germination as well as vegetative growth and sporulation. Abamectin and acrinathrin belonging to the Avermectins and pyrethroids were more compatible with *B. bassiana.* (Laboratory study, *in vitro).*	
Imidacloprid	Insecticide	*B. bassiana*	Imidacloprid was compatible with *B. bassiana.* (Laboratory study, *in vitro*).	Andalo *et al.,* 2004
Carbofuran Thiamethoxam	Nematicide	*B. bassiana*	Thiamethoxam, and carbofuran were compatible with *B. bassiana.* (Laboratory study, *in vitro*).	Andalo *et al.,* 2004
Endosulfan Esfenvalerat Imidacloprid	Insecticides	*B. bassiana* *M. anisopliae*	Detection of *B. bassiana* and *M. anisopliae* was significantly lower in plots treated with chemical versus biological pesticides. Synthetic herbicides, fungicides	Hummel *et al.,* 2002

Active ingredient/common name (Trade name)	Pesticide group	Fungal species (host species if relevant)	Effect on insect and mite pathogenic fungi (type of study)	References
(study continued) Chlorothalonil Copper hydroxide Atrazine Ethalfluralin Metolachlor Metribuzin Napropamide Paraquat	Fungicides Herbicides		and insecticides were used as recommended for the area and the crop. (Field study).	

5.2. Insect parasitic nematodes

Bardgett & Cook (1998) reviewed extensively the factors influencing the abundance of important soil animals, including naturally occurring nematodes in grassland, and concluded that organically managed low-input farming systems are optimal for an increase in soil biotic diversity. They did however stress that future studies are necessary to prove that soil biodiversity is positively associated with stability and productivity of the ecosystem. There have been several short-term studies of effects of various crop management systems on plant and soil nematodes. The economically important cyst nematodes (*Globodera rostochiensis* and *G. pallida*) are the most studied in long-term experiments (Whitehead, 1997). Yeates *et al*. (1999) studied soil nematode communities over a 7 year period in different agroecosystems: an annual and a perennial crop using three weed management practices (cultivation, herbicide application and mulching). The greatest long-term effects were from sawdust mulching, where total nematode populations initially increased, but subsequently declined, co-inciding with an increase in predatory nematodes. Herbicide use did not result in any consistent effects on the nematode communities. Their work revealed that some of these effects were only apparent after 3 years, underlining the importance of long-term studies. Nematode faunal analyses have been conducted with respect to changes in the soil, mainly for bioindicator purposes (Neher, 2001; Yeates & Bongers, 1999; Yeates, 2004).

Entomopathogenic nematodes are mostly used as biopesticides, applied as a drench to the soil surface to target the susceptible insect pest in the soil. With some exceptions, entomopathogenic nematodes are generally applied against insect pests in high value crops such as ornamentals and strawberries. There are numerous reports on the application of nematodes against different insect pests (Gaugler & Kaya, 1990; Bedding *et al.*, 1993; Ehlers, 1996; Gaugler, 2002). The effect of different agroecosystems regarding entomopathogenic nematodes has not been well studied until fairly recently. In a review by Lewis *et al*. (1998), it is stated that the requirements and limitations for field use of entomopathogenic nematodes are quite well understood, whereas the requirements for population level survival are poorly known. Millar & Barbercheck (2002) reported on the effect of tillage practices in no-till and conventional-till maize (corn) on entomopathogenic nematodes. The study involved two endemic nematode species (*S. carpocapsae* and *H. bacteriophora*) and one inundatively applied nematode (*S. riobravis*), where the objective was to evaluate the effect of tillage on all three nematodes. Interestingly the study suggested that the three nematode species had different sensitivities to the conditions created by tillage. *H. bacteriophora* did not appear to be affected by tillage, *S. carpocapsae* appeared to be negatively affected by tillage, and in contrast the inundatively applied *S. riobravis* was favoured by tillage. The effect of tillage on abiotic and biotic factors could have contributed to these effects, as well as the differences in dispersal behaviour of the nematodes themselves.

The compatibility of entomopathogenic nematodes with agrochemicals has been reviewed by Grewal (2002). Entomopathogenic nematodes are tolerant of short exposures to many agrochemicals. Some pesticides can reduce nematode activity, but it has also been shown that low rates of insecticides combined with entomopathogenic nematodes can give strong synergistic effects against target pests (Koppenhofer & Kaya, 1998; Nishimatsu & Jackson, 1998). In general Heterorhabditidae tend to be more sensitive to pesticides than the Steinernematidae. In a laboratory study, Bednarek & Gaugler (1997) also found that heterorhabditids were more sensitive to inorganic fertilizers.

6. Successful use of the soil as a reservoir of natural enemies

A few examples of the successful use of soil as a reservoir in classical, inoculation, inundation and conservation microbial control as defined by Eilenberg *et al*. (2001) will be given in this section. For practical purposes the term microbial control includes entomopathogenic nematodes in this section. The ultimate indicator of successful microbial control is a reduction in crop damage to an acceptable level. Success also depends on avoiding adverse effects on health and environment. Aspects of health and environment in microbial control have been covered thoroughly elsewhere by Howarth (2000), Strasser *et al*. (2000), Wajnberg *et al*. (2001), Goettel *et al*. (2001) and Hokkanen & Hajek (2003).

Soil-dwelling pests have always been difficult to manage, and inexpensive persistent chemicals, applied prophylactically, were long considered as ideal for their control. These chemicals no longer meet environmental standards and have been withdrawn from most markets. The challenge for microbial control is to fill this niche. Many microbial control agents can persist in soil and provide long-term pest control so that their costs may be spread over several years. Production and application costs of most microbial control agents are often too high for control of soil-dwelling pests in extensive agricultural systems. Thus it is no surprise that many applications are made through inoculation, baiting and strategic application methods (Jackson *et al*., 2000). In our examples we will therefore focus on these strategies.

6.1. Classical biological control

Classical biological control is considered successful when the non-indigenous biological control agent controls and becomes established in the targeted host pest population. In addition the control agent should not have any detrimental long or short-term effects on non-target organisms. It is in the nature of this definition that we will never know for certain whether a classical biological control agent is truly successful. It is not possible to monitor every single organism in space and time that may be affected by the introduction of an exotic biological control agent. To enable evaluation of possible non-target impacts it is important to develop methods for identifying the introduced pathogen or nematode (Hajek *et al.*, 2003). The introduction of parasitoids and predators is most common in classical biological control and out of 5500 programs, less than 50 involve the introduction of exotic insect and mite pathogens (Hajek *et al*., 2000). Among these, only a few have been on soil dwelling insects or mites, but as the soil is an important environment in most organisms' life cyc1e, the soil plays an important role in the establishment of several exotic agents. According to a model developed by Fenton *et al*. (2001) entomopathogenic nematodes were shown not to be particularly suitable for classical biological control. Among the relatively few programs conducted only some have been successful. See table 7 for examples.

Table 7: Examples of classical biological control where the soil is an important reservoir for the natural enemy

Exotic agent introduced (pathogen or nematode)	**Host species (common name)**	**Type of introduction**	**Role of the soil environment (reference)**
Entomophaga maimaiga (fungi)	*Lymantria dispar* (Gypsy moth)	Accidental introduction and subsequent redistribution.	The soil is an important reservoir of resting spores for this insect pathogenic fungus, and hence is important for the survival and establishment of this exotic control agent (Hajek *et al*., 2003).
Oryctes virus, OrV (virus)	*Oryctes rhinoceros* (Rhinoceros beetle)	Introduction.	*O. rhinoceros* larva develop in separate breeding sites witch includes compost heaps, rubbish pits and decaying logs. In these sites the OrV inoculum can be available to many larvae (Hunter-Fujita *et al*., 1998).
Steinernema scapterisci (nematode)	*Scapteriscus* spp. (Mole cricket)	Initial introduction into a limited area. Has been isolated as far as 23 km from the original release site.	Mole crickets spend nearly all their life cycle underground. Eggs are deposited in underground chambers. Nymphs tunnel to the surface and feed in the upper soil layer and litter. Juveniles and adults make and occupy extensive gallery and tunnel systems (Adjei *et al.*, 2003). *S. scapterisci* is applied to pasture or incorporated into sand below mole cricket traps (Jackson *et al.* 2000).

6.2. Inoculation and inundation biological control

In inoculation biological control the long-term effect of the beneficial organism released into the environment is essential for the control efficacy of the target pest arthropod. The long-term effect may be considered a problem when it comes to the environmental risk from the released organism due to possible non-target effects. This risk is much reduced if the natural enemy is highly host specific. Long-term effects of insect pathogenic fungi in soil have been studied by several authors (Enkerli *et al.*, 2004; Vänninen *et al.*, 2000; Keller *et al*., 2003; Kessler *et al.*, 2004). Persistence of up to 40 years for *B. brongniartii* is reported (Keller *et al*., 2003). In another study, a field trial with inoculation of different *B. brongniartii* strains showed that all strains were detected at all test sites up to 14 years after the application (Enkerli *et al.*, 2004). This is the first time that applied fungal strains have successfully been re-isolated after such a long time in the field. *M. anisopliae* is also known to persist for at least three years post-application. After three years fungal propagule levels caused up to 80% infection in the bait insect *Tenebrio molitor* (Vänninen *et al.*, 2000). High persistence of *B. brongniartii* is considered desirable because of its narrow host range. In contrast *M. anisopliae* has a much wider host range, and persistence is not desirable. It is however, important to remember that the host range is much more restricted for a specific isolate (Vestergaard *et al*., 2003). *B. brongniartii* is considered a successful inoculative control agent for the long term control of cockchafer *M. melolontha* and *M. hippocastani* due to the narrow host range and long persistence. A method based on sterilized barley kernels colonized by *B. brongniartii* is used to apply the fungi (Keller, 1992). By the use of an adapted seed-drilling machine, the fungus colonized barley kernels are directly applied into soil of *M. melolontha* infested sites. Based on this technique, a successful commercial product (*Beauveria* Scweizer, Eric Schweizer Seeds Ltd., Switzerland) has been available in Switzerland since 1991 (Enkerli *et al.*, 2004). *B. brongniartii* was also registered as the product Melocont©-Pilzgerste in Austria in 2000 (Bipesco Midterm Report, Interim-Report 3). No other EU countries have at present registered *B. brongniartii* as an active ingredient of any product (http://europa.eu.int/comm/food/plant/protection/evaluation/stat_active_subs_3010_en.xls). *B. brongniartii* is, however, registered as the active ingredient of products in several non-European countries.

Entomopathogenic nematodes have been commercially available in several countries in Europe, USA and Australia for a number of years. As far as we are aware there are no reports to date of successful inoculation biological control for entomopathogenic nematodes and most studies indicate poor long-term resistance. Apart from the fact that long-term studies are rare, there is growing evidence that under certain conditions, such as the presence of suitable hosts, persistence can be improved. A major limitation with the inoculative approach in microbial control is the time taken for the pathogen or nematode to spread from the site of application to other sites of the pest population. This limitation can be overcome with an inundative release where the organism is applied to the whole population within a defined area. Selection for an appropriate species, biotype or strain of the control organism is a key factor for inundation biological control of soil-dwelling pests. Appropriate biological properties, pathogenicity and environmental competence, however, are not enough to ensure success. The agent must also be easy and cheap to mass-produce and distribute. Friedman (1990) provides an excellent early account on the techniques and factors involved for mass-production of entomopathogenic nematodes. For a more recent update on production technology, a review is published by Gaugler & Han (2002). Microbial control products are often applied with propagule densities sufficient to initiate an epizootic of disease. This usually mimics the level found during natural

epizootics (Jackson *et al*., 2000). Many pest managers focus on the deposition of large quantities of virulent propagules on to the target host. This approach has often resulted in inadequate suppression of insect and mite pests, since the inoculum threshold is not static and is influenced by many aspects of the disease tetrahedron described in section 2. A thorough understanding of the epizootiology of the specific host pathogen or host nematode combination is therefore required to be able to develop an agent that may be used successfully (Inglis *et al*., 2001). Competition with other soil organisms is one factor that affects the epidemic development of a microbial control product applied to the soil (section 3.2.). Persistence of applied microbial control agents is therefore a major challenge. Microbial control agents are also susceptible to desiccation and ultra violet (UV) radiation and avoidance of these conditions during application has been a major hurdle. Since soil is an environment that may protect the applied microbial product from desiccation and UV radiation, subsurface applications have often been used to overcome these problems.

Unlike leaf and stem feeding pests, where generalist strains of insect pathogens, such as B.t. var *kurstaki*, have been used to control a wide range of target insects, there are few agents or products that have proven successful against more than one species of soil-dwelling insect. It has been reported that at least 13 different microorganisms or nematodes are used as biological control agents against at least 16 different soil dwelling pest insect species. Some of them are used for inundative biological control and some for inoculation biological control (Jackson *et al.*, 2000).

6.3. Conservation biological control

Eilenberg *et al*. (2001) proposed that conservation biological control is distinguished from other strategies in that natural enemies are not released. Whereas Fuxa (1998) has suggested that research on conservation biological control falls into two categories: (1) to enhance natural epizootics, (2) in conjunction with, but not simultaneous with, releases of the biocontrol agent. In this section we will only discuss enhancement of natural epizootics and not enhancement of released or applied agents. As viewed by Gurr *et al.* (2000), conservation biological control is based on a two-stage strategy: (1) reduced pesticide induced natural enemy mortality, (2) habitat manipulation to provide key ecological recourses. There has been a growing level of international research on conservation biological control in the last 10 years, but there are few documented applications of this biological control strategy (Gurr *et al.* 2000; Pell *et al.* 2001; Eilenberg *et al.*, 2001). The conservation approach has until recently been dominated by entomologists aiming to control arthropod pests by enhancing activity of arthropod agents. Recently, however, some attention has focused on conservation of entomopathogens (Gurr *et al*., 2000). The research has largely focused on viruses and fungi, probably because these groups have the best ability to produce disease epizootics with a high case fatality rate. There have also been attempts, however, at conservation approaches with entomopathogenic nematodes. Lewis *et al.* (1998) suggests three conditions that should be met to enhance or sustain biological control by entomopathogenic nematodes with special reference to turf: (1) moderately susceptible pests should be present throughout most of the year, (2) pests should have a high economic threshold level, and (3) soil conditions should be favourable for nematode survival.

Research on environmental manipulation of insect and mite pathogens and insect parasitic nematodes has mainly focused on four areas: (1) improved transport of the pathogen from the

reservoir, usually the soil, to a site where the insect or mite host can come into contact with the pathogen or the nematode, (2) improvement in persistence of the pathogen or the nematode at the site where it contacts the insect or mite host, (3) overall growth of the pathogen or nematode population, (4) activation of latent infections (especially for viruses) (Fuxa 1998). The success of conservation biological control is very difficult to measure since it is based on a hierarchy of different criteria involving several trophic levels. It is apparent that reduced pesticide-induced natural enemy mortality has been successful in making a contribution to IPM (e.g. Steinkraus *et al.*, 1996). According to Gurr *et al.* (2000), evidence for the success of conservation biological control through habitat manipulation is less clear-cut than the effect of pesticides.

In section 5.1. we have mentioned several effects of pesticides, and other human manipulation of the agro-ecosystem on natural enemies belonging to insect and mite pathogenic fungi. Most of these studies have been conducted in the laboratory or in semi-field trials, and few practical solutions for arthropod fungal pathogen systems have to our knowledge been achieved. Carruthers (1981) and Carruthers *et al*. (1985) developed a model where a combination of adapted pesticide use and habitat manipulation was used to enhance the prevalence of *Entomophthora muscae* in an onion maggot (*Delia antiqua*) population. This conservation approach affects the prevalence of *E. muscae* in adult (not soil dwelling) onion maggot flies by reducing the negative effect of pesticides to the beneficial fungi. The model also suggests enhancing spore germination and host infection by grassy boarder areas and strip planting onion with other crops. *E. muscae* attacks the adult fly stage and not the soil dwelling larval and pupal stage of the onion maggot. The soil is probably an important reservoir for the resting spores of this fungus and hence also for the initial infection in the spring. In the onion maggot/*E. muscae* system it was revealed that primary infection in the spring was much higher in adults emerging from pupae in the border areas than in adults emerging in the field. Due to the comparable biology of the cabbage root fly and the turnip root fly (*D. radicum* and D. *floralis*) with the onion maggot there are reasons to believe that this also applies for the *D. radicum*/ *D. floralis*/*E. muscae* host pathogen system (Klingen, 2000). Systems have also been suggested to enhance the natural occurrence of the more typical arthropod pathogenic soil fungi. Bing & Lewis (1993) for example, suggested that epizootics of *B. bassiana*, in overwintering larvae of the European corn borer (*Ostrinia nubilalis*) in maize residues, could be enhanced by modifying agronomic practices, such as no-till or reduced tillage systems. Similar suggestions were also made by Hummel *et al*. (2002) who conducted a field experiment on effects of different production practices on soil born entomopathogens in vegetable systems.

There are quite a few examples of enhancement of insect pathogenic viruses by the use of conservation control strategies. One fascinating example involving soil or soil litter is the blowing of NPV contaminated forest litter up into trees for the initiation of a viral epizootic in larvae of *Lymantria dispar* (Fuxa, 1998).

According to Fuxa (1998) there has been only one attempt to enhance natural epizootics of nematodes. In that study tillage, weed management, and irrigation were investigated for enhancement of *Heterorhabditis bacteriophora* (*heliothidis*) in *Diabrotica undecimpunctata howardi* infesting maize. No-till and the presence of weeds significantly increased the numbers of nematodes in soil bioassays, but irrigation had no effect (Fuxa, 1998). Lewis *et al*. (1998) discuss a conservation approach to using entomopathogenic nematodes, and emphasise the need to understand the requirements and structure of natural populations before this approach can be recommended for practical use.

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