Chapter 1
Biological Control of Plant-Parasitic Nematodes: An Ecological Perspective, a Review of Progress and Opportunities for Further Research

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Abstract Plant-parasitic nematodes are important pests, causing billions of dollars damage to the world's food and fibre crops. However, from an ecological perspective, this group of nematodes is simply one component in a vast array of organisms that live in soil. All these organisms interact with nematodes and with each other, and during that process, contribute to regulatory mechanisms that maintain the stability of the soil food-web. Populations of individual species do not increase indefinitely but are subject to a constant series of checks and balances, which more or less stabilises their population densities. Thus, biological control is a normal part of a properly functioning soil ecosystem, with plant-parasitic nematodes only becoming pests when they are no longer constrained by the biological buffering mechanisms that normally keep them in check. This chapter therefore focuses on approaches that can be used to restore, maintain or enhance the natural nematode-suppressive mechanisms that should operate in all agricultural soils. The positive impact of organic matter and the negative effects of tillage, biocides, fertilisers and other management practices on suppressiveness are discussed, together with examples of suppression due to host-specific natural enemies. The problems associated with replacing soil fumigants and nematicides with biological alternatives, and the ecological issues likely to affect the efficacy of such products, are also considered.

Keywords Soil food web • Organic matter • Soil health • Organic amendments • Nematode-suppressive soil • Minimum tillage • Egg parasites • Predatory nematodes • Nematode-trapping fungi • *Pasteuria* • *Brachyphoris* • *Pochonia* • *Paecilomyces*

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1.1 Introduction

The relatively stable behaviour of animal populations in natural environments should serve as a constant reminder that in nature, all organisms are subject to a constant series of checks and balances. Populations of individual species do not increase indefinitely but are constrained by the physical environment and by the community of organisms within which they co-exist. Cyclic changes in populations will occur, but provided there is no major change in the physical or biotic environment, populations will fluctuate between certain upper and lower limits. This phenomenon, commonly referred to as ‘biological balance’ or the ‘balance of nature’, more or less stabilises animal population densities and applies to all organisms, including plant-parasitic nematodes. The action of soil organisms in maintaining nematode population densities at lower average levels than would occur in their absence is generally termed ‘biological control’.

These words, which were included on the first page of my book on biological control of nematodes (Stirling 1991) define the general area of biological control, indicate that it operates wherever nematodes occur, and remind us that plant-parasitic nematodes only reach unacceptably high population densities (i.e. become pests of economic concern) when they are no longer constrained by the biological mechanisms that normally keep them in check. Phrases such as ‘the balance of nature’ also provide a focus for this chapter, because the aim is to discuss biological control of nematodes within an ecological framework. Thus the chapter begins with a discussion of the soil environment and the regulatory forces that operate within the soil food web and then considers how these natural regulatory mechanisms can be exploited in various farming systems to improve the level of nematode control achievable by biological means.

1.2 Fundamentals of Soil Ecology

It is only in the last few decades that ecologists have undertaken detailed studies of belowground soil processes, and this has led to a better understanding of the nature of the soil environment and the complex biological communities that live in soil. Bacteria and fungi have always been recognised as the most numerically abundant members of the soil biota, but culture-independent molecular tools are now indicating that they are far more numerous and diverse than previously thought (Coleman 2008; Buée et al. 2009a, b). Our knowledge of the feeding habits of the microfauna (e.g. protozoa), mesofauna (e.g. rotifers, nematodes, tardigrades, collembolans, mites and enchytraeids) and macrofauna (e.g. earthworms, termites and millipedes) is also improving, and this is giving us a better insight into the numerous biotic interactions that occur within the soil environment, and how these interactions influence major ecosystem processes such as organic matter turnover and nutrient cycling. These issues are only covered briefly here, but further information is available in several comprehensive textbooks in soil microbiology (e.g. Tate 2000;

Davet 2004; Sylvia et al. 2005; Paul 2007; van Elsas et al. 2007) and in recent books on soil biology and ecology (e.g. Wardle 2002; Coleman and Crossley 2003; Bardgett 2005).

1.2.1 The Soil Food Web

The reason for interest in biological control of nematodes is that some plant-feeding nematodes are important pests, causing billions of dollars damage to the world's food and fibre crops. However, from an ecological perspective, this group of nematodes is simply one component of a large community of organisms that make up what is known as the soil food web. This community is sustained by the photosynthetic activity of plants, its food supply coming from roots, root exudates and plant-derived materials that either accumulate on the soil surface or become available when roots die. The primary consumers within the food web are bacteria, fungi, plant-feeding nematodes and root-grazing insects that feed directly on living plant roots, and the bacteria and fungi that decompose detritus. However, bacteria and fungi are by far the most important component of the soil food-web: they comprise most of the living biomass in soil and are primarily responsible for breaking down and mineralising organic compounds from plant tissue.

The resources transferred from plants and detritus to primary consumers do not remain locked up for very long because these organisms soon become food and energy sources for secondary consumers. Thus bacteria are consumed by nematodes and protozoa, fungal hyphae are pierced by stylet-bearing nematodes and then plant-feeding and free-living nematodes are parasitised by fungi or eaten by predators. These secondary consumers are eventually utilised by organisms at higher levels in the soil food web, while nutrients that are defecated, excreted or contained in dead bodies are also a resource for other organisms. Thus the soil food-web contains a complex array of interacting organisms with numerous pathways that transfer energy from producers (plants) to primary and secondary consumers. Since some of the resources available to the food web are lost at each trophic interchange due to respiration, detrital food chains do not continue indefinitely. They are generally limited in length to about five members (Coleman and Crossley 2003).

1.2.2 Functions of the Soil Food Web

The two most important functions of the soil food-web are to decompose plant material that enters the soil as litter and dead roots, and to mineralise the nutrients contained within that organic matter so that they can be re-used by plants. The decomposition process is mainly the result of microbial activity, but the soil fauna plays a role by fragmenting and ingesting organic matter, thereby increasing the surface area available for microbial colonisation. As plant material is decomposed, elements are converted from organic to inorganic forms that can be taken up by plants or used by microbes. This process is of critical importance in natural ecosystems (e.g. forests and grasslands), as almost all the nutrients required to sustain primary productivity are derived from mineralisation of soil humus and indigenous biomass. The soil food web also has many other important functions, as it regulates populations of plant pests and pathogens (discussed in the following section), immobilises nutrients within microbial biomass, sequesters carbon, detoxifies pollutants and stabilises soil aggregates.

1.2.3 Biotic Interactions Within the Soil Food-Web

The soil food-web contains huge populations of innumerable species and these populations are continually interacting with each other. These interactions become more complex as the diversity within the soil food-web increases, with multiple forces exerting pressures that prevent the uncontrolled proliferation of particular populations. Interactions between populations therefore have the effect of stabilising the community that makes up the food-web.

Given the complexity of the soil food-web, it is not surprising that populations interact in many different ways. Davet (2004) gives examples of the types of interaction that can occur, and most are relevant to a discussion of biological control.

Antibiosis is the inhibition of one organism by the metabolic product of another. It usually involves interactions where the adversary is killed or inhibited but is not consumed. The metabolic products (usually soluble or volatile antibiotics) are produced in such small quantities by bacteria or fungi that it is difficult to prove conclusively that they are present in the natural environment. Nevertheless, they are known to play a role in interactions between various plant pathogens and the soil biota, with one well-studied example being inhibition of the take-all pathogen *Gaeumannomyces graminis* var. *tritici* by two antibiotics (2,4-diacetylphloroglucinol and phenazine-1-carboxylic acid) produced by fluorescent pseudomonads on wheat roots (Weller et al. 2002).

Lysis is similar to antibiosis in that its effects are manifested at a distance from the organism responsible for lytic activity, but differs in that the adversary is exploited. It occurs when an organism produces extracellular enzymes (e.g. chitinases, cellulases and glucanases) that digest the cell wall or cuticle of another organism. Sometimes the process is accompanied by the production of toxins that immobilise or kill the prey. Bacteria, and more particularly actinobacteria, are significant producers of lytic enzymes and toxins, and important agents in the lysis of fungi.

Predation is generally characterised by the consumption or assimilation of one organism (the prey) by a larger organism (the predator). It requires intimate contact between the two organisms and usually involves an active search for the prey by the predator. Protozoans, nematodes and microarthropods all have the capacity to consume other soil organisms, some feeding indiscriminately on a wide range of organisms and others having quite specific food preferences. With respect to nematodes, predators of bacteria and fungi can be differentiated from predators of organisms further along the food chain by referring to the latter as ‘top predators’.

Parasitism occurs when an organism (the parasite) lives in or on another organism (the host) and obtains all or part of its nutritional resources from that host. Bacteria and viruses are known to parasitise some soil organisms (e.g. protozoans and nematodes), but fungi are probably the most important parasitic organisms in soil. Numerous fungal parasites of arthropods and nematodes are known, and mycoparasitism (parasitism of one fungus by another) is also commonly observed.

Competition between organisms occurs when the amount of an essential substrate or nutrient is insufficient to satisfy the needs of both organisms. The organism most adept at accessing the limiting element, making it inaccessible to others or eliminating those trying to obtain it, will prosper relative to its competitors. Competition is a universal phenomenon within the soil food web, but becomes particularly intense when organisms in the same ecological niche are attempting to access the same scarce resource.

The word **antagonism** is often used instead of antibiosis to describe the situation where one organism inhibits another through antibiotic production. However, the term is used in a more general sense in this chapter to cover all situations where one organism (the pest) is detrimentally affected by the actions of other organisms. Such a definition is commonly used in the literature on biological pest control, as it is useful for describing the general suppressive effects of an organism on a pest, regardless of whether the antagonist is acting through parasitism, predation, antibiosis, competition or some other process.

Although the above mechanisms depict the types of interaction that occur between organisms in the soil food web, outcomes from these interactions are not easy to predict. Environmental factors have marked effects on relationships between organisms, while the interactions between two organisms will be modified by the introduction of a third organism. Thus the structure of a microbial community is the result of environmental effects and multiple interactions that are often quite difficult to comprehend.

1.2.4 Biotic Interactions in the Root Zone

The principal means by which plant roots impact on soil food webs is through the quality and quantity of organic matter that they return to soil. These carbon inputs are derived from fine roots (which have a relatively short life span and rapid turnover times), from cells that slough off as roots move through the soil, and from root exudates. Exfoliation and exudation from roots are particularly important processes because they contribute sugars, amino acids, mucilage and other materials that are high quality nutrient sources for rhizosphere microorganisms. Thus the area in the immediate vicinity of roots is a zone of intense biological activity and complexity

(Buée et al. 2009a). Since herbivores such as arthropods, plant-parasitic nematodes and pathogenic fungi also live in this zone, their activities are most likely to be influenced by organisms that are able to establish and maintain themselves in this extremely competitive ecological niche.

The surface of the root (often referred to as the rhizoplane) is a particularly important niche for soil microorganisms. Some of these organisms thrive in regions where exudation is most intense and protective mucilage is thickest, others survive saprophytically on senescent epidermal and cortical cells, and others are endophytes, colonising root cortical tissue and living in a symbiotic association with the plant. Mycorrhizal fungi are a well-known example of the latter association, as they receive carbon substrates from the plant and provide fungal-acquired nutrients to the plant. Since ramifying mycelial filaments affect soil structure and the mycorrhizal colonisation process improves plant growth, alters root morphology, changes exudation patterns and provides some protection against root pathogens, mycorrhizae influence the biotic interactions that occur in and near roots. Other symbiotic associations also add complexity to the soil-root interface. Examples include rhizobia and other bacteria that fix nitrogen in nodules on plant roots; plant growth promoting rhizobacteria that enhance seed germination and plant growth; and endophytic fungi that deter pests from feeding on plants or improve the plant's capacity to adapt to stress conditions.

1.3 Soil Ecology and Biological Control

The preceding discussion demonstrates that plant-parasitic nematodes cannot be considered in isolation from other components of the soil biological community. Their root-feeding habit brings them into contact with a vast number of root and rhizosphere-associated microorganisms and they also interact with numerous organisms in the detritus food web (Fig. 1.1). Additionally, the activities of plant-parasitic nematodes and other soil organisms are influenced, directly and indirectly, by various soil physical and chemical properties and by environmental factors such as temperature and moisture. These ecological realities must be recognised in any discussion of biological control.

One reason for opening this chapter with a general discussion of soil biology and ecology is to make the point that biological control is a normal part of a properly functioning soil ecosystem. Numerous soil organisms interact with nematodes and with each other and in that process they contribute to the regulatory mechanisms that maintain the stability of the soil food-web. Since plant-feeding nematodes become pests when these biological buffering processes are inadequate, biological control should be thought of as maintaining, restoring or enhancing the natural suppressive mechanisms that exist in all soils. Given that it may take months or years to arrive at a new 'balance' of interactions, the difficulties involved in shifting a stabilised system to a new equilibrium should not be underestimated.

Although most nematologists have some understanding of soil ecology, many fail to view biological control from an ecological perspective. Instead, biological

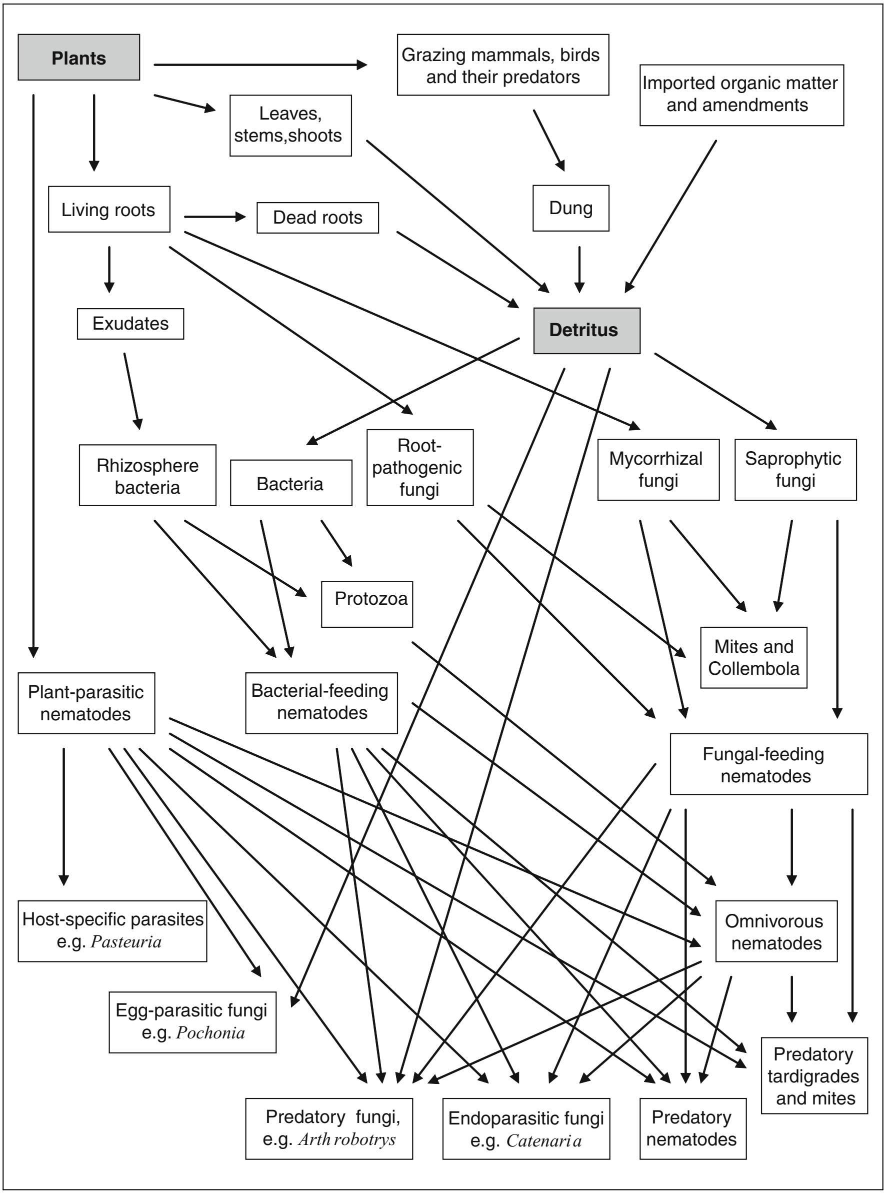

Fig. 1.1 Representation of a soil food web, showing the main interactions between plant-parasitic nematodes, some other primary consumers, and the detrital food web

control is thought of, in relatively simplistic terms, as the introduction of beneficial organisms to control a pest. Most farmers are no different. Having depended on soil fumigants and nematicides for many years, they consider that biological control is about replacing relatively toxic chemicals with safe biological products. Thus there is a common perception amongst both professionals and growers that given time and an appropriate amount of research, we will eventually be able to reduce nematode populations to non-damaging levels by adding a biological pesticide to soil. I suggest that given the likely cost of producing and distributing such products and the ecological complexity of soil, this approach is unlikely to be successful, except perhaps in specific and quite limited circumstances (discussed later). This chapter, therefore, focuses on other approaches to biological control.

1.3.1 What Is Biological Control?

As pointed out by Stirling (1991), there are a wide range of opinions on what constitutes biological control, with plant pathologists and entomologists often differing on the meaning of the term. The definition used by Baker and Cook (1974) has been adopted here because of its relevance to all plant pathogens, including plant-parasitic nematodes. Thus biological control is considered to:

- Involve the action of one or more organisms
- Result in a reduction in nematode populations or the capacity of nematodes to feed on the plant or cause damage
- Be accomplished in a number of possible ways:
  - Naturally
  - By manipulating the environment, the host plant or the soil food web
  - By introducing one or more antagonists

As mentioned previously, the last-mentioned approach has tended to dominate biological control thinking for many years, whereas the attraction of the above definition is that it takes a more holistic view of the topic. Mass introduction of fungal and bacterial parasites of nematodes is still an option, but is only one of many possible ways of maintaining nematode populations below damaging levels through the action of parasites, predators and other antagonists. Such a definition encourages us to think about how a suite of organisms might act together to regulate a nematode population, to consider why natural suppressive forces are effective in one environment but not another, and to consider how a farming system might be modified to enhance the level of biological control that will already be occurring.

1.4 Suppressive Soils

Soilborne pathogens debilitate roots or cause wilt, root-rot and damping-off diseases in most of the world's crops. Although these pathogens are widely distributed, there are situations where disease severity is lower than expected, given the prevailing environment and the level of disease in surrounding areas. In some of these cases, the indigenous microflora is the reason plants are effectively protected from the pathogen, a phenomenon that is known as disease-suppression. Books by Baker and

Cook (1974), Cook and Baker (1983), Hornby (1990) and Stirling (1991) summarise much of the early work in this area and discuss many examples of suppressiveness to nematodes and other soilborne pathogens.

Two types of disease suppressiveness can occur in agricultural soils. The most common (often referred to as 'general' or 'non-specific' suppressiveness) is found in all soils and provides varying degrees of biological buffering against most soil-borne pests and pathogens. Since the level of suppressive activity is broadly related to total soil microbial biomass and is therefore enhanced by practices that conserve or enhance soil organic matter, the term 'organic matter-mediated general suppression' is also commonly used (Hoitink and Boehm 1999; Stone et al. 2004). This type of suppression can be removed by sterilising the soil and is due to the combined effects of numerous soil organisms.

A second form of suppression (usually known as 'specific' suppressiveness) is also eliminated by sterilisation and other biocidal treatments but differs from general suppressiveness in that it results from the action of a limited number of antagonists. This type of suppression relies on the activity of relatively host-specific pathogens and can be transferred by adding small amounts of the suppressive soil to a conducive soil (Westphal 2005). Since specific suppression operates against a background of general suppressiveness (Cook and Baker 1983), the actual level of suppressiveness in a soil will depend on the combined effects of both forms of suppression.

1.4.1 Broad-Spectrum, Organic Matter-Mediated Suppression

The role of organic matter in enhancing suppression of soilborne diseases caused by fungi, Oomycetes, bacteria and nematodes has been known for many years and there are now well-documented examples in many quite different agricultural systems. These include suppression of *Pythium* in Mexican fields following the application of large quantities of organic matter over many years (Lumsden et al. 1987); broad-spectrum control of *Pythium*, *Phytophthora* and *Rhizoctonia* in peat and compost-based soilless container media (Hoitink and Boehm 1999); the use of cover crops, organic amendments and mulches to suppress *Phytophthora* root rot of avocado in Australia (Broadbent and Baker 1974; Malajczuk 1983; You and Sivasithamparan 1994, 1995); suppression of the same disease with eucalyptus mulch in California, USA (Downer et al. 2001); the management of a fungal, bacterial and nematode-induced root disease complex of potato in Canada with chicken, swine and cattle manures (Conn and Lazarovits 1999; Lazarovits et al. 1999, 2001), and the use of crop residues, animal manures and organic waste materials to reduce damage caused by plant-parasitic nematodes (reviewed by Muller and Gooch 1982; Stirling 1991; Akhtar and Malik 2000; Oka 2010).

It is obvious from the above examples that a wide range of types and sources of organic matter can be used to enhance suppressiveness and that they are effective in many different situations. However, studies (summarised by Hoitink and Boehm

1999 and Stone et al. 2004) in relatively simple nursery potting media have given us a much better understanding of the mechanisms involved. Suppression is generated soon after an amendment is added to soil and is associated with the activity of indigenous microorganisms that colonise organic material during the decomposition process. Development of suppression is associated with high levels of microbial activity, with many studies showing that the rate of hydrolysis of fluorescein diacetate (FDA) is a relatively good indicator of suppressiveness. Since microbial activity must remain high to maintain suppressiveness, the quantity and quality of the organic inputs have a major impact on the duration of suppressiveness. The labile constituents of organic matter (e.g. sugars, proteins and hemicelluloses) are degraded relatively quickly and suppression is then sustained by the subsequent decomposition of more recalcitrant materials in the coarse and mid-sized particulate fraction (Stone et al. 2001).

Perhaps the most important feature of organic-matter mediated general suppression is its capacity to act against most, if not all, major soilborne pathogens of food and fibre crops. Since root disease problems in the field rarely involve a single pathogen, enhancing the suppressive potential of a soil with organic matter is one of the only non-chemical techniques available to control a suite of pathogens. This does not mean that manipulating organic matter to manage several pathogens is a simple matter. When pathogens which are good primary saprophytes but poor competitors are involved (e.g. *Pythium* and *Fusarium*), the fact that they may multiply on fresh organic matter before being suppressed must be taken into account when designing application strategies. In the case of *Rhizoctonia*, which has a high competitive saprophytic ability due to its capacity to degrade cellulose as well as simple sugars, organic-matter mediated general suppression is often insufficient to achieve control and specific antagonists may also be required (Stone et al. 2004).

1.4.2 Suppressing Nematodes with Organic Amendments

It has been known for many years that animal manures, oil-cakes, residues from leguminous crops and other materials with a low C/N ratio can be added to soil to control plant-parasitic nematodes (see reviews by Muller and Gooch 1982; Rodriguez-Kabana 1986; Stirling 1991). Although there is some evidence that such amendments increase populations of microorganisms antagonistic to nematodes, the main mechanism is thought to be the release of nematicidal compounds such as ammonia during the decomposition process. Since relatively high concentrations of ammonia are needed to achieve control, there is a direct relationship between the amount of N in an amendment and its effectiveness (Rodriguez-Kabana 1986). Thus amendments with N contents greater than 2% are usually used and application rates are typically greater than 10 t/ha.

Although the nematicidal effects of ammonia are well established (Eno et al. 1955; Rodriguez-Kabana et al. 1982; Oka and Pivonia 2002; Tenuta and Ferris 2004) and lethal concentrations are achievable with nitrogenous amendments, the commercial use of such amendments is limited by cost and by concerns about the environmental impact of large quantities of nitrogen. Most recent studies have therefore sought to achieve efficacy at lower application rates. One successful approach involved adding a nitrification inhibitor (nitrpyrin) with the amendment to slow the oxidation of ammonia to nitrite and nitrate, therefore allowing ammonia concentrations to build up for an extended period. When the inhibitor was applied with chitin or cottonseed amendments, ammonia levels were higher for longer periods than in amended soils without the inhibitor, and this was associated with reduced egg production and galling from *Meloidogyne javanica* (Oka and Pivonia 2002). Alkaline additives have also improved the effectiveness of nitrogenous amendments by increasing soil pH and therefore shifting the equilibrium between the NH_4^+ and NH_3 to the latter form, which is nematicidal (Oka et al. 2006a).

Other work in the USA and Israel has shown that specially formulated organic amendments can cause nematode mortality through mechanisms other than ammonia production. De-watered municipal biosolids applied at 1.1% w/w did not affect *Heterodera glycines*, but the nematode was killed when the biosolids were stabilised with alkaline materials such as cement kiln dust, fly ash or quicklime (Zasada 2005). Nematode mortality was associated with a rapid increase in the pH of the soil solution (to a $pH > 10$), and this occurred when CaO in the amendment reacted with water to form $Ca(OH)_2$ (Zasada and Tenuta 2004; Zasada 2005). The contribution of ammonia production to the nematicidal effect was unclear in the American studies, but work with similar products in Israel suggested that it was important there (Oka et al. 2006b). However, the mechanism is clearly chemical rather than biological, as experiments with autoclaved materials indicated that microbes associated with the amendment were not involved (Zasada 2005).

Whether it will eventually be possible to use nitrogenous amendments in nematode management programs remains a moot point. Enormous quantities of organic and inorganic wastes and industrial by-products are available in most countries and there is a need to find uses for them as commercial fertilisers and soil conditioners. Alkaline-stabilised organic amendments are effective against plant-parasitic nematodes, but fine tuning will be needed before they can be used routinely in nematode management. Thus there is a need to determine the application rates required to achieve consistent nematode control; develop methodologies to prevent over-production of ammonia and ensure that pH does not increase excessively; understand the long-term effects of these amendments on soil physical properties, soil chemistry and soil microbial ecology; and find ways of integrating the practice into the soil and crop management programs used for specific nematode-susceptible crops.

Although most recent research on organic amendments for nematode control has focused on nitrogenous materials, the possibility of using materials with a much higher C/N ratio has also received attention. McSorley and Gallaher (1995) used a composted mixture of sticks, leaves, branches, grass clippings and wood chips from the urban environment (C/N ratio = 36) as an amendment or mulch and found that it had little effect on plant-parasitic nematodes in vegetable crops planted immediately after the amendment was applied. However, in another study that continued for 3 years, population densities of plant-parasitic nematodes on maize were reduced in the third season, once the woody compost material had broken down and levels of soil organic matter had increased in amended plots (McSorley and Gallaher 1996).

Three studies in Australia have also shown that amendments with minimal amounts of N have suppressive effects on nematodes. In the first of these studies, apple trees mulched with sawdust for 5 years had much lower populations of *Pratylenchus jordanensis* in years 2–5 than non-mulched trees or trees growing in fumigated or nematicide-treated plots. In years 4 and 5, yields from mulched trees were as good as those obtained with methyl bromide fumigation (Stirling et al. 1995). A second study in which tomato was planted into field plots that had been amended over the previous 2 years with sawdust and urea showed that the amended soil was highly suppressive to *M. javanica* and that the level of nematode control was significantly better than that obtained with the nematicide fenamiphos. Plants in amended plots were almost free of galls, whereas the untreated controls were heavily galled (Vawdrey and Stirling 1997). The third study involved an amendment of sugarcane residue (the tops and leaves remaining in the field after sugarcane is mechanically harvested). Sugarcane was planted 23 weeks after the residue was incorporated into soil, and 24 weeks after planting there were 95% fewer lesion nematodes (*Pratylenchus zeae*) in roots growing in amended soil than in roots from the non-amended control (Stirling et al. 2005).

Results from these studies indicate that amendments with a high C/N ratio act much more slowly than nitrogenous amendments. When soil is amended with materials such as yard waste, sawdust or sugarcane residue, suppressiveness may take months or years to develop whereas it develops almost immediately when the amendment has a relatively high N content. Interestingly however, suppressiveness is soon lost with nitrogenous amendments. Thus when soil was assessed 4 and 7 months after it was amended with N-rich materials (e.g. lucerne hay, feedlot manure, poultry manure, chitin and a waste product from sugar mills known as mill mud), it was not suppressive to *M. javanica* or *P. zeae* (Stirling et al. 2003). In contrast, materials with a much higher C/N ratio (e.g. sawdust, sugarcane residue and grass hay) were suppressive to both nematodes.

Although the suppressiveness generated by high C/N amendments has not been studied in detail, the evidence currently available suggests that physical or biological rather than chemical mechanisms are responsible. Relatively large predators (e.g. nematodes and arthropods) may be able to operate more effectively when soil structure is improved with organic matter, while in the Australian studies discussed previously, one common observation was that fungi appeared to be associated in some way with suppressiveness. For example, a suppressive, sawdust-amended soil had high numbers of fungal-feeding nematodes (Vawdrey and Stirling 1997), while low concentrations of nitrate nitrogen, a fungal-dominant soil biology and high numbers of omnivorous nematodes were associated with suppression in one of the other experiments (Stirling et al. 2003). In an experiment where *P. zeae* was suppressed after soil was amended with sugarcane residue, an unidentified predatory fungus was found in the amended but not the non-amended soil (Stirling et al. 2005). It is therefore possible that fungal predation on nematodes was responsible for these suppressive effects. The predatory hyphomycetes and several genera of wood-decaying basidiomycetes are commonly found in habitats that are rich in cellulose and lignin and are thought to have evolved the capacity to scavenge for additional N in low N environments by preying on nematodes (Barron 1992; Tzean and Liou 1993). Thus when high C/N amendments are added to soil, these fungi may utilise free-living nematodes as a food source and coincidently capture plant-parasitic species.

1.4.3 Farming Systems to Enhance General Suppressiveness

Although amending soil with high rates of organic matter can generate suppressiveness to nematodes and other soilborne pathogens and maintain it for some time after the amendment is applied, it is important to recognise that this approach to disease control is likely to be most useful in high value horticultural production systems. Nurseries where plants are grown in containers, glasshouses producing vegetable or ornamental crops and intensive in-field production of crops with a high monetary value are perhaps the only situations where it is realistic to use amendments in this way to manage nematodes. In all other agricultural systems, applying organic matter at rates of 10–100 t/ha/annum is never likely to be economically feasible. Importation of organic matter will generally be expensive relative to the income derived from most crops, largely because transportation costs are high and non-agricultural markets compete for the resource. Since high application rates are required to achieve the desired effects, there is also the potential for environmental problems from the nitrogen, heavy metals and other potential pollutants that may be present in the amendment. Thus for all the world's staple food and fibre crops, organic-matter mediated general suppression will mainly be achieved by developing farming systems that increase C inputs and conserve soil organic matter. Almost all soil and crop management practices affect the levels of soil organic matter, but perhaps the most important are crop rotation, cover cropping, crop residue management, organic amendments and tillage (Magdoff and Weil 2004). They are therefore the main tools that can be used to improve a soil's physical, chemical and biological status and therefore influence its capacity to suppress soilborne pests and pathogens.

Since accumulation of organic matter is directly related to C inputs (Paustian et al. 1997), reducing the frequency and duration of bare fallow periods and including perennial forages, high residue crops and cover crops within the farming system are the most practical ways of minimising the decline in soil organic C that occurs in all cropping systems. Careful management of above and below-ground plant residues also has a place, particularly in cropping systems where most of the above-ground material is harvested. Organic amendments may also be useful, but successive inputs at low application rates are likely to be more economically, agronomically and environmentally desirable than occasional inputs at high application rates. When used collectively, these practices are the first step towards increasing levels of soil organic matter and enhancing the suppressiveness of field soils to nematodes and soilborne diseases.

The second step involves reducing tillage, as conventional tillage arguably causes greater losses of soil organic matter than any other farm management practice (Magdoff and Weil 2004). In comparison to cultivated soils, non-tilled soils are less susceptible to erosion losses caused by water or wind, and decomposition also proceeds more slowly because crop residues remain on the soil surface rather than being mixed with the soil. Non-tilled soils are also cooler and subject to less pronounced wetting and drying cycles, both of which reduce rates of microbial respiration and organic matter decomposition. A compilation of studies from the literature (Franzluebbers 2004) indicates that soil under no tillage accumulates organic C to a greater extent than under inversion tillage, and that this effect is seen for both particulate organic matter and the more labile C fractions on which heterotrophic soil organisms depend. It is therefore not surprising that reducing tillage produces profound changes in the detritus food web, the most obvious impact being favourable effects on larger organisms such as predatory and omnivorous nematodes, mites, enchytraeids, earthworms, beetles and spiders (Wardle 1995).

When appropriate crop rotations, reduced tillage, residue retention, more frequent cover cropping and regular inputs of animal manures and organic wastes are integrated into a farming system, they are a powerful combination of practices that will result in improved soil and ecosystem health. Their widespread adoption in many industries in recent years is testimony to the benefits obtained. Although enhanced suppression of plant-parasitic nematodes will never be the primary reason for such improvements to a farming system, recent work on sugarcane in Australia suggests that it is one of the benefits that will accrue. Damage caused by *M. javanica* and *P. zeae*, the most important nematode pests of sugarcane, has been reduced by introducing a rotation crop and implementing residue retention and minimum tillage to enhance natural biological control mechanisms that suppress these pests (Stirling 2008). Although such suppressiveness is likely to take years to reach its full potential, particularly in farming systems where biomass production is limited by low rainfall, it is nevertheless worth pursuing because it comes with numerous other soil health benefits (e.g. improved nutrient cycling, better soil structure, increased water and nutrient holding capacity and broad-spectrum disease suppression) that are crucial for the long-term sustainability of a cropping system (Weil and Magdoff 2004). From the perspective of nematodes, future studies within improved farming systems should concentrate on establishing the levels of soil organic matter required to achieve suppression, understanding the regulatory mechanisms involved, and determining how the quality, quantity and timing of organic inputs influences the development of suppressiveness.

1.4.4 Specific Suppression of Soilborne Pathogens

There are many situations where soilborne diseases caused by fungi, bacteria or nematodes are suppressed by pathogen-specific agents. Historically, the best-documented examples for nematodes are the suppression of *Heterodera avenae* in a cereal monoculture by two fungi, *Nematophthora gynophila* and *Pochonia chlamydosporia*, and the multiplication of *Pasteuria penetrans* in some cropping systems to levels that suppress root-knot nematodes. Both examples were discussed in detail by Stirling (1991).

In the last two decades, other examples of natural suppression due to *P. penetrans* have been reported (Weibelzahl-Fulton et al. 1996) and suppressiveness has been transferred from one field to another (Kariuki and Dickson 2007). The role of other *Pasteuria* species as suppressive agents has also been recognized, with Noel et al. (2010) demonstrating that when *P. nishizawae* is introduced into a non-suppressive field soil, it induces suppressiveness to soybean cyst nematode (*H. glycines*).

Another important contribution to our understanding of nematode-suppressive soils has been a decade-long investigation (reviewed by Borneman et al. 2004 and Borneman and Becker 2007) on the development of suppressiveness to *H. schachtii* in a field that had been cropped intensively with hosts of the nematode. After a period when populations of *H. schachtii* were high and disease incidence was severe, nematode populations declined to such an extent that studies commenced on the causes of the phenomenon. Work with various biocides (Westphal and Becker 1999) and experiments in which suppression was transferred to a conducive soil using either soil or cysts (Westphal and Becker 2000, 2001) showed that the suppressiveness was biological in nature and prompted studies of the microflora associated with nematode cysts and eggs. This work showed that eggs from the field were frequently parasitised by fungi and that *Brachyphoris* (syn. *Dactylella*) *oviparasitica*, *Fusarium oxysporum*, other *Fusarium* spp., *Paecilomyces lilacinus* and various unidentified fungi could be isolated on agar media (Westphal and Becker 2001).

The above investigations showed that fungi were associated with suppressiveness and subsequent studies demonstrated that modern technologies were useful for identifying the key suppressive organisms. Soils with different levels of suppressiveness were created with biocides or by combining different amounts of suppressive and conducive soil and oligonucleotide fingerprinting of rRNA genes (OFRG) was used to identify the main fungal phylotypes associated with different levels of suppression (Yin et al. 2003). The main phylotype in the most suppressive treatments had high sequence identity to rRNA genes from various nematode destroying fungi. Subsequent analyses indicated that the fungus represented by this phylotype was most closely related to *Brachyphoris oviparasitica*, a parasite of *Meloidogyne* eggs that had previously been found to suppress this nematode in California peach orchards (Stirling and Mankau 1978; Stirling et al. 1979). A second phase of the study validated this result, with sequence-selective quantitative PCR assays showing that the largest amounts of *B. oviparasitica* PCR product came from soils possessing the highest levels of suppressiveness to *H. schachtii* (Yin et al. 2003). In phase three of the study, *B. oviparasitica* was added to fumigated soil and produced the same high level and long-term suppressiveness that was observed in the naturally suppressive soil (Olatinwo et al. 2006a, b, c).

Other recent studies indicate that when field soils are surveyed systematically for suppression using appropriate techniques, examples of specific suppressiveness to plant-parasitic nematodes are often found. Thus suppressiveness to *Rotylenchulus reniformis* was detected in cotton fields in Texas and Louisiana USA (Robinson et al. 2008), while another study showed that one of six California soils was suppressive to *M. incognita* (Bent et al. 2008). In the latter work, a negative correlation between *P. chlamydosporia* rRNA genes and nematode population densities suggested that this fungus may have been one of the major factors responsible for suppressiveness.

There are many examples of specific suppressiveness to fungal and bacterial pathogens, and work in this area has been discussed by numerous authors, including Baker and Cook 1974; Cook and Baker 1983; Hornby 1990; Schippers 1992; Whipps 1997; Alabouvette 1999; Weller et al. 2002 and Mazzola 2004, 2007. As in the examples cited for nematodes, suppression develops in situations where a pathogen increases to high population densities, causes severe disease and then declines spontaneously to levels that do not cause damage. Take-all decline of wheat is perhaps the best-known example and it is encouraging to note that after years of research on the microbial antagonists involved, there are now situations where growers can be confident that suppressiveness will be maintained and disease losses will be negligible (Weller et al. 2002).

1.5 Mass Release of Biological Control Agents

The possibility of introducing mass-produced antagonists into soil or establishing them on seeds or roots has been a major component of research on biological control of soilborne pathogens for several decades. However, any objective review of that research would have to conclude that there have been relatively few practical outcomes. By 2005, only nine bacteria and five fungi were registered with the United States Environment Protection Agency for control of soilborne diseases (Fravel 2005). Of these organisms, strains of *Agrobacterium* are known to be effective against crown gall, but it is not known whether the others are efficacious in the hands of the consumer. Worldwide, the number of biological products is greater, but as in the United States, most are formulations of the fungi *Gliocladium* and *Trichoderma* or the bacteria *Pseudomonas* and *Bacillus*, and many are marketed as plant growth promoters, plant strengtheners or soil conditioners rather than as biocontrol agents (Paulitz and Belanger 2001). The only organism listed by Fravel (2005) as registered in the USA for nematode control was a non-biological product consisting of killed mycelium and fermentation materials from *Myrothecium verrucaria*. However, since that time, a strain of *Paecilomyces lilacinus* (Melancon®, Bioact®) has been commercialised in the USA, some parts of Europe and several other countries for use against cyst and root-knot nematodes.

In considering the types of organism most likely to have potential for development as biocontrol agents, Deacon (1991) pointed out that host specificity and the capacity to operate in the same ecological niche as the target pathogen were attributes that were required to achieve success. With regard to antagonists of nematodes, endospore-forming bacteria in the genus *Pasteuria* fit these criteria, as they are specific parasites of most economically important plant-parasitic nematodes (Sturhan 1988; Sayre and Starr 1988; Ciancio et al. 1994; Chen and Dickson 1998). Recent advances in the *in vitro* culture of some members of the genus (Hewlett et al. 2004; Gerber et al. 2006) indicate that mass production by liquid fermentation is possible, thereby opening opportunities for commercial exploitation of the parasite. Initial work is being done with Candidatus *Pasteuria usgae* (Giblin-Davis et al. 2003), a parasite of sting nematode (*Belonolaimus longicaudatus*) and is focused on control of the nematode on golf courses and athletic fields in southeastern USA (Hewlett et al. 2008).

Although host specificity is clearly advantageous to a biological control agent and also limits impacts on non-target organisms, it remains to be seen whether the extreme specificity of *Pasteuria* will limit its commercial usefulness. Thus in *P. penetrans*, for example, spores do not attach to all populations of the *Meloidogyne* species from which they are obtained, indicating that host preference is determined at a population rather than species level (Stirling 1985). Later studies have shown that *P. penetrans* produces heterogeneous sub-populations of endospores that show preferences for particular nematode populations (Davies et al. 1994; Davies and Redden 1997). Thus variability in *P. penetrans* may be a host-adaptive process that allows endospores to attach to and infect the nematodes present in a given environment. Any biological control program involving the mass culture of *P. penetrans* will therefore have to consider host specificity issues when deciding which bacterial strains are to be produced for a particular market.

Pasteuria clearly has potential as a mass-produced biological control agent but another host-related issue that requires consideration is whether it will be equally effective against all its known hosts. Examples of long-term natural suppression due *Pasteuria* have largely been confined to root-knot and cyst nematodes, presumably because millions of spores are produced in saccate females and inputs from these infected nematodes are sufficient to maintain relatively high spore concentrations in an environment where losses are always occurring due to predation and percolation. Thus, when sedentary endoparasitic nematodes are being targeted, spore populations should increase naturally, and this will limit the number mass-produced spores needed, or the number of applications required, to achieve satisfactory control. However, the same level of natural increase may not occur with vermiform nematodes, as fewer spores are produced and this limits the spore population densities achievable in soil. Low spore production in infected nematodes may have been one of the reasons that *P. usgae* did not always suppress populations of sting nematode (*Belonolaimus longicaudatus*) to acceptable levels, despite relatively high levels of parasitism (Giblin-Davis et al. 1990). Thus, when *Pasteuria* is used against ectoparasitic and migratory endoparasitic nematodes, it may be necessary to regularly supplement natural populations of the parasite with spores produced *in vitro*.

One way of ensuring that a biocontrol agent is capable of operating in the same ecological niche as the target nematode is to concentrate on organisms that naturally inhabit the rhizosphere. Initial studies with rhizosphere-inhabiting bacteria showed that some isolates were antagonistic to plant-parasitic nematodes (Becker et al. 1988; Kloepper et al. 1991, 1992; Kluepfel et al. 1993; Oka et al. 1993), while more recent work has focused on fluorescent pseudomonads and strains of *Bacillus* that have the capacity to enhance plant growth and induce disease resistance (Weller et al. 2002; Haas and Keel 2003; Kloepper et al. 2004). Some of these bacteria have given broad-spectrum protection against soilborne pathogens (Jetiyanon et al. 2003) and in tests on vegetable crops, they consistently increased plant growth and sometimes reduced galling caused by root-knot nematode (Kokalis-Burelle et al. 2002a, b). Since bacteria are relatively easy to apply to transplants, they may eventually find a place in the vegetable industry within integrated management programs for nematodes and other soilborne pathogens.

Given that fungi capable of parasitising females and eggs of endoparasitic nematodes must come into intimate contact with the target nematode to utilise them as a food source, it is hardly surprising that they are commonly found in the rhizosphere (Stirling 1979; Bourne et al. 1996). However, there have been relatively few behavioural studies of this group of fungi in this intensely competitive environment. In the case of *P. chlamydosporia*, root colonising ability is known to be important in bringing the fungus in contact with nematode eggs (DeLeij and Kerry 1991), but a capacity to colonise sites where nematodes are present may be an even more important attribute. *P. chlamydosporia* is abundant on roots infected by root-knot nematodes (De Leij et al. 1992; Bourne et al. 1996; Atkins et al. 2009) and populations increase markedly when egg masses are extruded on the galled root surface (Bourne et al. 1996), suggesting that specificity towards sedentary endoparasitic nematodes is associated in some way with a capacity to recognise the quantitative and qualitative changes in root exudation patterns that occur following nematode infection (Wang and Bergeson 1974).

Although Gaspard and Mankau (1986) were able to isolate several species of nematode-trapping fungi from the root surface, little is known about the capacity of these fungi to form traps and prey on nematodes in the rhizosphere. Persson and Jansson (1999) found that differences in the root colonising ability of nematode-trapping fungi did not explain differences in their capacity to reduce damage caused by root-knot nematode. However, it may be premature to conclude that these fungi do not prey on nematodes in the rhizosphere, as some species probably perform better in this environment than others. Also, we know little about where traps are produced in relation to the root surface, and we lack the tools required to monitor the intensity and timing of trap production. If we are to ever understand the predatory behaviour of this group of fungi at the soil/root interface, these issues must be addressed.

Given the difficulties involved in establishing an introduced organism in the extremely competitive rhizosphere environment, one approach that has received increasing attention in recent years is the possibility of using endophytic organisms for biocontrol purposes. The advantage of endophytes is that they occur in the same ecological niche as endoparasitic nematodes but are not subject to competition from microorganisms in the soil and rhizosphere. With regard to endophytic organisms for nematode control, most recent work with fungi has focused on strains of *Fusarium oxysporum* that reduce infection and reproduction of *Radopholus similis* (Athman et al. 2007) and *M. incognita* (Hallman and Sikora 1994; Dababat and Sikora 2007). Endophytic bacteria have received less attention but are of interest because they act in much the same way as the plant growth-promoting rhizobacteria mentioned previously (Compant et al. 2005). Their suppressive mechanisms have not been fully elucidated, but those commonly proposed include competition with the pathogen for an ecological niche or substrate, production of inhibitory allelochemicals and induction of systemic resistance (Hallman and Sikora 1996; Compant et al. 2005; Vu et al. 2006; Franco et al. 2007).

Since endophytic microorganisms enable plants to adapt to stress conditions and are a potential source of metabolites for the pharmaceutical industry (Maheshwari 2006), they will be the subject of increasing attention in coming years. From the perspective of biological control of nematodes, endophytes should be relatively easy to apply as inoculants to seed or seedlings and can therefore be established in the root system before nematodes are attracted to roots and begin to feed. The future challenge is to find strains that are active against nematodes, show that these organisms can be established in appropriate niches within roots, and demonstrate that they are efficacious enough to warrant inclusion in integrated management programs for nematodes.

Mononchids and stylet-bearing dorylaimids are often observed in the soil environment, but their usefulness as mass-produced biological control agents is limited by their long life cycles and low fecundity, and an inability to culture them in large quantities. Predatory nematodes in the Diplogastrida are not seen as frequently but may be a better alternative. Diplogastrid predators are much easier to mass produce, they show some specificity towards their prey and can survive periods of low prey density by feeding on bacteria (Bilgrami et al. 2005); all useful attributes for a biological control agent. Recent work with two diplogastrids in the genus *Mononchoides* has shown that *M. fortidens* reduces damage caused by root-knot nematode in pots while *M. gaugleri* decreases total populations of plant-parasitic nematodes in turf grass (Khan and Kim 2005; Bilgrami et al. 2008).

1.6 Directions for Future Research

It should be apparent from the preceding discussion that our understanding of biological control systems as they apply to nematodes has improved markedly in the last 30 years. However, biological control has still not taken the step from ‘potentially useful management option’ to ‘reliable and effective control measure’. The following is a personal opinion of what needs to be done to ensure that in future, biological control contributes in a much greater way to integrated management systems for nematodes.

1.6.1 Developing More Sustainable Farming Systems

One of the biggest changes to world agriculture in the last 30 years has been the development of no-till farming. Various forms of conservation tillage are now applied to many millions of hectares of cropped land, and when combined with practices such as crop rotation and cover cropping, it has resulted in farming systems that are much more profitable and sustainable than they were in the past. One of the benefits from this change will be an increase in the suppressiveness of soils to soilborne disease (Stone et al. 2004).

Given the economics of broad-scale agriculture and the cropping area involved, enhancing general suppressiveness through the farming system is probably the only realistic way of improving the level of biological control in most of the world's agricultural land. The role of farming systems in enhancing suppressiveness should therefore be a major focus of future research. We need to know how the main soil management practices available to farmers (e.g. tillage, fallowing, rotation crops, cover cropping and organic inputs from crop residues and amendments) influence the physical, chemical and biological properties of soil and in turn affect the development of suppressiveness to various pathogens, including nematodes.

A comprehensive review by Wardle (1995) demonstrates that tillage practices have a major impact on the detritus food web and could therefore be expected to affect the processes that regulate populations of plant-parasitic nematodes. The quantity of C and N (the resource base for the detritus food web) is usually lower under conventional tillage than no-tillage, microbial biomass and the ratio of microbial biomass to organic C tends to decline when soil is tilled and bacteria tend to be favoured over fungi. The larger soil organisms (predatory and omnivorous nematodes, springtails and mites) are particularly vulnerable to tillage and all tend to respond positively when tillage is reduced. Given that fungi, predatory nematodes and microarthropods are the main predators of nematodes and tillage is detrimental to all of them, a move from conventional to minimum tillage could be expected to enhance the general suppressiveness of soil to plant-parasitic nematodes. Observations on cereals and sugarcane in Australia (Rovira 1990; Stirling 2008) and results from long-term tillage experiments with soybean in the USA (Westphal et al. 2008; Seyb et al. 2008) indicate that populations of several plant-parasitic nematodes are lower in soils under minimum tillage than in cultivated soils. Although this effect is not necessarily due entirely to enhanced suppressiveness, detailed ecological studies of these and other no-till systems are clearly warranted.

In addition to reducing the frequency and intensity of tillage, practices such as crop rotation, cover cropping, more careful residue management and greater organic inputs from amendments can also be used by farmers to improve levels of soil organic matter and thereby influence the biological status of soil and its general suppressiveness to nematodes. The role of organic matter in enhancing suppressiveness is discussed in the following section, but from a farmer's perspective, the challenge is to integrate these practices into a farming system that is profitable and sustainable. The way this is done will depend on factors such as climate, soil type and the principal crops involved, but results of a recent research program in Australia provide an example of what is achievable.

In the early 1990s, the Australian sugar industry was facing an uncertain future because productivity was declining due to a problem known as yield decline. At that time, sugarcane was grown on beds 1.5 m apart, machinery wheel spacings did not match crop row spacings and the crop residues remaining after harvest were often burnt rather than retained. After a plant and 2–4 ratoon crops, an expensive program of ripping and cultivation was required to remove the old crop, alleviate compaction caused by farm machinery and then replant the field to sugarcane. A multidisciplinary research team was established to develop solutions to the problem and its initial studies showed that soils under long-term sugarcane monoculture were physically and chemically degraded, while large yield responses to soil fumigation and nematicides indicated that biological constraints were also limiting productivity. A 12-year research program (summarised by Garside et al. 2005; Stirling 2008) resulted in the development of a new farming system based on residue retention, minimum tillage, a leguminous rotation crop and controlled traffic using global positioning system guidance. This system is now being adopted by growers because it increases sugar yields, reduces costs, improves soil health and provides additional income from rotation crops such as soybean and peanut. From a nematological perspective, losses from *P. zeae* and *M. javanica* have been reduced because (1) the introduction of a rotation crop has reduced nematode population densities at planting, (2) damage thresholds have increased as soil health has improved and (3) suppressive mechanisms of biological control are now operating more effectively.

Economic pressures and the entrenched attitude of some growers will always make it difficult to make major changes to a farming system. However, the fact that the Australian sugar industry was able to make such a change and in the process overcome obstacles that were initially perceived as insurmountable, indicates that the task is achievable. Reducing losses from nematodes and other soil-borne pathogens may not be the primary reason for embarking on such a process, but is likely to be one of the outcomes.

Globally, the farming system that is perhaps in most need of urgent attention from a farming systems perspective is the plasticulture system commonly used for vegetable production. In many countries, vegetable crops are grown intensively on beds mulched with plastic film; water, nutrients and pesticides are delivered to soil via trickle irrigation tubing; double or multiple cropping is common; soil is bare-fallowed between crops; there is limited crop rotation; organic inputs from cover crops and amendments are rare; and soil is routinely fumigated. This farming system treats the soil as an inert medium to support the plant, and in the absence of any biological buffering, it is not surprising that root-knot nematode and other soil-borne pathogens re-establish following fumigation and quickly build up to high population densities (Desaeger and Csinos 2006). It is therefore disappointing that over the last decade or so, much of the money allocated to finding alternatives to methyl bromide was spent on testing alternative fumigants rather than on developing more sustainable vegetable farming systems. There are production systems that warrant further testing (e.g. Stirling 2008; Stirling and Eden 2008; Bhan et al. 2010), but until the vegetable industry is prepared to take a long-term view, invest in research on alternative farming systems and then persist with those alternatives for 5–10 years, the status quo will remain.

1.6.2 Understanding the Impact of Soil Organic Matter on Suppressiveness

Organic matter has profound effects on many important soil physical and chemical properties (e.g. soil aggregation, soil water availability and nutrient cycling); it promotes biological activity and diversity through affects on the detritus food web; and it plays a key role in developing healthy soils and enhancing their suppressiveness to plant pathogens and pathogenic nematodes (Weil and Magdoff 2004; Magdoff and Weil 2004). Since levels of soil organic matter gradually decline when plant biomass is continually removed as harvested product rather than being returned to the soil, measures which provide additional C inputs and minimise C losses due to microbial respiration and erosion must always be a component of management programs for cropped soils. Retention of crop residues that would otherwise be burnt or taken off-farm, crop rotation, cover cropping, organic amendments and minimum tillage are the main options available, and where practicable, they should be used together to increase the amount of soil organic matter, improve soil health and reduce the impact of soilborne diseases (Stone et al. 2004).

Since Linford's initial work in the 1930s, there have been numerous studies on the role of organic inputs in enhancing suppressiveness to plant-parasitic nematodes (see reviews by Muller and Gooch 1982; Stirling 1991; Akhtar and Malik 2000; Widmer et al. 2002). However, the results of many of these studies cannot be readily extrapolated to the field because they focused on the relatively short-term effects of amendments when applied at rates that are unrealistically high for broadscale agriculture. There is therefore an urgent need to study the medium and long-term biological changes that take place when soil organic matter is conserved and enhanced in ways that are feasible to introduce into a farming system, and understand how they affect the development of suppressiveness. We need to measure parameters such as total and labile C, microbial activity and biological diversity and relate them to suppressiveness; identity the key groups of organisms involved in suppression; understand how they are affected by the quantity and quality of C inputs; and then use the information to find better ways of manipulating organic matter within a farming system to enhance suppressiveness.

Since plant-parasitic nematodes are particularly damaging when populations are high during crop establishment, understanding the temporal effects of crop and soil management practices on the development of suppression is important, as it may then be possible to maximise suppressiveness during the period when crops are being planted. This could perhaps be achieved by altering tillage practices or by selecting rotation crops on the basis of the C/N ratio of their residues or the relative proportion of labile to more recalcitrant compounds in the plant material. In situations where it is possible to include practices known to be beneficial to the soil biology within a cropping system (e.g. an undisturbed pasture ley), the management practices used during the transition back to cropping are likely to have a major impact on whether suppressiveness is maintained or lost.

The main energy channels within the detritus food web are either bacterial or fungal, and soil ecologists suggest that the dominant channel in natural systems is largely determined by litter quality and the environment (Bardgett 2005; Wardle 2005). However, in agroecosystems, soil management practices also determine whether energy flow occurs rapidly through bacterial channels or more slowly through fungal channels. Tillage and nitrogen fertilisation practices have particularly profound effects on the soil food web, stimulating bacterial activity to such an extent that bacterial rather than fungal decomposers predominate in many farming systems. Changes in the proportions of bacteria to fungi and their flow-on effects to other components of the soil food web, together with the detrimental effects of tillage (Wardle 1995) and nitrogen (Tenuta and Ferris 2004) on some predators may explain why soils tend to lose their natural suppressiveness once they are cropped. These issues need to be further explored, but they also raise questions about how agricultural soils should be managed to maintain suppressiveness. Do biological mechanisms of suppression operate in highly-disturbed, nitrogen-enriched and bacterially-dominant soils, and if so, how can their activity be enhanced? What is the impact of N fertilisation practices on various parasites and predators of nematodes, and is it possible to provide a crop with adequate N without detrimental effects on the organisms responsible for suppression? Will minimum tillage and surface mulching increase the activity of fungi and other organisms that parasitise or prey on nematodes? Will the effects of such practices be apparent only in surface layers or will they also occur at depth?

Because of a paucity of research on the biological processes that operate within the root zone of agricultural crops, the list of unanswered questions about interactions between soil and crop management practices, organic matter status and parasitism and predation on plant-parasitic nematodes is almost endless. Unfortunately, the ecological literature provides few answers. Nematode ecologists and soil biologists often refer to the ‘top down’ or predatory processes that regulate nematode populations but usually use the term in a general sense and rarely attempt to identify the organisms responsible. When predation is specifically mentioned, mononchid and Dorylaimid nematodes are often considered to be the main predators of nematodes, and other natural enemies (e.g. nematophagous fungi and arthropods) are usually ignored. Another problem is that predator-prey relationships in soil are poorly understood, particularly in situations where predators have a range of food options available to them (Small 1987). Thus we do not know, for example, whether mononchid predators can be sustained in their natural habitat by ingesting bacteria, protozoans and other soil organisms, or whether they live mainly on certain groups of nematodes. Studies in simple microcosms provide useful information on feeding habits (e.g. Bilgrami and Gaugler 2005; Bilgrami et al. 2005) but we also need to know what predators eat when given a choice in their natural environment. Some dorylaimids are known to consume nematode eggs in agar culture, but are eggs an important food source in the natural environment? Entomologists are using molecular techniques to identify organisms in the gut contents of predators (Symondson 2002; King et al. 2008) and similar approaches could perhaps be used to elucidate the food preferences of nematophagous organisms.

Fungi are perhaps the most important parasites and predators of nematodes, but the impact of organic matter on their predatory activity is poorly understood. Jaffee's recent work with nematode-trapping fungi is therefore an important contribution because it sought to clarify whether these fungi are associated with suppression in organically-amended soils. Briefly, these studies showed that suppression of root-knot nematode was positively correlated to microbial biomass but was not related to management system (organic v. conventional) or to fungal population density (Jaffee et al. 1998). Also, the two fungi tested (*Arthrobotrys oligospora* and *Dactylellina haptotyla*) did not necessarily respond in the same the same way to organic amendments (Jaffee 2004). One of these species (*A. oligospora*) responded to the addition of substrates with relatively low C:N ratios and high N contents but failed to trap nematodes, (Jaffee 2003, 2004; Jaffee et al. 2007; Nguyen Vi et al. 2007), raising questions as to why it invests resources in producing specialised hyphae capable of capturing nematodes.

The role of organic matter in influencing the trapping behaviour of nematode-trapping fungi has perplexed nematologists for many years, and advances in this area would provide vital clues to how organic matter can be better managed to enhance biological control. Currently, there are two models to explain how organic matter stimulates predatory activity (Jaffee et al. 1998). The numerical response model presupposes that nematode-trapping fungi are obligate parasites that are dependent on nematodes for carbon, nitrogen and energy. They therefore respond to the addition of organic matter by consuming the free-living nematodes which multiply on the microorganisms involved in the decomposition process. The supplemental nitrogen model presupposes that the fungi are facultative parasites and obtain nitrogen from nematodes to enable them to compete for energy in carbon-rich/ nitrogen-poor plant litter. Although both nutritional models probably occur within the nematode-trapping fungi, it would be useful to know which model predominates in particular soil types, cropping systems or environments, as this would provide clues to how organic inputs could be managed to maximise trapping activity.

Clearly, there is much more to be learnt about the ecology of the nematode-trapping fungi. However, ecological studies are difficult to undertake because procedures for quantifying these fungi are tedious, their detection efficiency is largely unknown, trap production cannot be quantified and there is not always a consistent relationship between fungal population density and trapping activity (Jaffee 2003). Techniques that could be used to monitor traps would therefore be particularly useful in ecological studies, and could possibly be developed by targeting genes or gene products involved in trap production (Ahrén et al. 2005). When such technologies are combined with the sequencing and genomic techniques being used to study fungal plant pathogens (Xu et al. 2006) and methods likely to become available in the field of transcriptomics, it may eventually be possible to understand the factors which cause nematode-trapping fungi to switch from a saprophytic to parasitic mode of nutrition.

1.6.3 Identifying Nematode-Suppressive Soils

Most agricultural soils are highly disturbed and their organic matter status has declined following many years of cultivation. Since organic matter is the resource that sustains the soil food web, the biodiversity of most soils has been depleted, often to such an extent that the mechanisms regulating populations of plant-parasitic nematodes are not effective enough to prevent them from becoming pests. This lack of biological complexity is manifested in the fact that the nematode community in many agricultural soils is dominated by nematodes with short generation times and relatively high reproductive rates (i.e. plant-parasitic and microbivorous species). Such nematode assemblages are indicative of relatively simple, non-structured food webs, whereas suppressive mechanisms are most likely to operate in soils that have complex food webs with long food chains and many trophic links (Jaffee et al. 1998; Berkelmans et al. 2003; Sánchez-Moreno and Ferris 2007). Suppressiveness is associated with the prevalence of omnivorous and predatory nematodes, but the ratio of predators to prey is also important (Sánchez-Moreno and Ferris 2007). Thus the best way of finding soils likely to be generally suppressive to plant-parasitic nematodes is to identify situations where there is a structured nematode community containing a range of omnivorous and predatory species. Nematode communities of this nature are most likely to be found in farming systems where crops (particularly perennials) are grown continually; there is no disturbance due to tillage; broad-spectrum biocides are not used; and inputs of synthetic fertilisers are not excessive.

Although the presence of omnivorous and predatory nematodes can be used as an indicator of general suppressiveness, this does not necessarily mean that they are the primary suppressive agents. Their presence simply indicates that a relatively complex soil food web is present and that it is likely to contain a range of nematophagous fungi, arthropods and other organisms that will also be contributing to regulatory processes. A challenge of the future is find better ways of quantifying these organisms and monitoring their predatory activities in both suppressive and conducive soils.

Plant nematologists usually focus on areas where nematodes cause problems, but locating suppressive soils requires a different mindset. Field observations must be made with the intention of finding situations where the environment is suitable for a particular nematode but population densities remain low in the presence of a susceptible host. Such situations may be quite localised and difficult to find, but could possibly be identified more easily using techniques in precision agriculture to generate data on biomass or yield variability within fields (Melakeberhan 2002; Srinivasan 2006). Such data could then be linked to high throughput, DNA-based systems for quantifying nematode populations (Ophel-Keller et al. 2008).

A recent study (Robinson et al. 2008) provides and good example of how previously unrecognised suppressiveness can be detected. Comprehensive surveys of cotton fields in the USA had previously demonstrated that reniform nematode (*Rotylenchulus reniformis*) occurred at relatively high population densities in most fields. However, some fields had inexplicably low nematode populations while others had much lower population densities in surface soils that expected. Results of assays in pots then showed that there was a biological reason for these differences in nematode distribution, raising questions about why suppressiveness built up in some soil types or environments, or whether it was enhanced by particular farming practices.

Once candidate soils are identified, a range of techniques can be used to verify suppressiveness and confirm its biological nature (Westphal 2005). One of the most common is to treat the soil with a biocide (often a fumigant or heat), re-inoculate with the nematode and check for differences in nematode multiplication rates in biocide-treated and untreated soil. Another frequently-used method, which is most useful when the suppressive agent(s) have relatively short life cycles and therefore multiply readily, is to transfer small quantities of the test soil to heat-treated or fumigated soil and demonstrate that the transfer reduces nematode multiplication or results in high levels of parasitism or predation on nematodes. However, a weakness of such methods is that plants often do not grow as well in field soil as in partially or fully-sterilized soils and a reduction in the number of feeding sites may confound detection of suppressiveness. An alternative approach is to eliminate plants from the test system. Heated and untreated soil is inoculated with a nematode that is not present naturally in the test soil and nematode mortality is measured following incubation in the laboratory (Jaffee et al. 1998; Pyrowolakis et al. 2002; Sánchez-Moreno and Ferris 2007). Although this assay avoids problems caused by the use of plants, it focuses exclusively on suppressive forces that affect the migratory stages of a nematode's life cycle. Thus the best way of confirming suppressiveness is to demonstrate its occurrence using more than one method.

The organisms associated with suppression have traditionally been determined using cultural, biochemical and microscopic methods, but molecular techniques and other technologies will become increasingly important in future. When used to characterise soil microbial communities, these tools provide new insights into the identity, diversity and functional capacities of microorganisms involved in suppressing soil-borne pathogens (Weller et al. 2002; Mazzola 2004; Garbeva et al. 2004; van Elsas et al. 2008). With regard to nematodes, molecular technologies have contributed to our understanding of specific suppression and will eventually be used to quantify and track both the nematode and its suppressive agents (Borneman and Becker 2007). Ultimately, this will allow us to understand how agronomic practices influence the development of suppressiveness.

1.6.4 Maintenance of Suppressiveness

Once soils suppressive to a particular nematode pest have been identified and characterised, the next challenge is to understand how they are best managed to maintain suppressiveness. Specific suppression is dependent on the presence of the host nematode and usually manifests itself in situations where nematode populations have remained at high levels for many years. Thus the use of nematode-resistant varieties, fallowing and other practices that reduce nematode populations to very low levels may be an impediment to the development and maintenance of specific suppressiveness. Cropping sequences that use tolerant or partially resistant cultivars may be a better option, as they would minimise crop damage while maintaining a food source for the target nematode and its suppressive agents. A comparable strategy for maintaining specific suppressiveness in perennial cropping systems would be to grow nematode-susceptible cover crops in situations where nematode-resistant or tolerant rootstocks are available.

Given the economic importance of the genera *Meloidogyne* and *Heterodera* and the fact that parasitism is relatively easy to study because infective stages of these nematodes are sedentary and their eggs are aggregated, it is not surprising that most of the research on specific suppressiveness has focused on this group of nematodes. Obligate parasites of females (e.g. *Pasteuria penetrans* and *Nematophthora gynophila*) and saprophytic fungi with a relatively specialised capacity to utilise nematode eggs as a food source (e.g. *Pochonia chlamydosporia* and *Brachyphoris oviparasitica*) sometimes parasitise a large proportion of the females or eggs, but future research needs to focus on why these suppressive forces are active in some situations and not others. The factors most likely to be involved include the continuity of supply of host nematodes; particular soil physical, chemical or environmental conditions; soil organic matter status and the genetic makeup of the suppressive agent.

Since root-knot and cyst nematodes have relatively short generation times, high reproductive capacities and relatively low damage thresholds, one shortcoming of host-specific parasites is that populations of the target pest are only reduced when levels of parasitism are high, largely because the nematodes killed by the parasite are often in excess of those required to maintain high population densities. Another potential deficiency is that some host-specific parasites (e.g. *Pasteuria*) do not always prevent the nematode from feeding, while others only act after feeding has occurred (e.g. egg-parasitic fungi). These parasites may therefore have little or no impact on crop damage. In such situations, the challenge is to find ways of maintaining high levels of specific suppressiveness while integrating other management tactics into the farming system.

The key to maintaining general suppressiveness is to sustain a soil food web with enough activity and complexity to prevent plant-parasitic nematodes from becoming predominant. Techniques for analysing nematode assemblages are now readily available (Neher and Darby 2009; Ferris and Bongers 2009) and can be used to indicate whether a soil food web is complex enough to provide the desired suppressive services. Sanchez-Moreno and Ferris (2007) provided an example of how this might be done when they showed that suppressiveness was related to the prevalence of omnivores and predators. Given that the composition of the soil food web is dependent on the quality and quality of C inputs, another way of addressing this issue might be to improve our understanding of the relationship between soil C and suppressiveness. By measuring one or more of the many forms of C in soil, it may be possible to define, in a particular soil type and environment, the soil C status required to achieve adequate suppressiveness.

With the move towards minimum till farming systems in the last 20–30 years, one area that requires more research is the role of organic matter that is retained on the soil surface rather than incorporated, in enhancing suppressiveness. Mulches and surface residues from previous crops not only improve the environment for roots and soil organisms by minimising moisture and temperature fluctuations, but also provide the C inputs required to maintain a suppressive soil food web. Soil mulched with residues from a sugarcane crop was more suppressive to plant-parasitic nematodes than non-mulched soil (Stirling 2008), while C inputs from decomposing residues appeared to be the main reason that sugarcane roots immediately below the trash blanket were healthier and had fewer plant-parasitic nematodes than roots further down the profile (Stirling et al. 2011). The next step is to determine whether the level of suppressiveness is related to the quantity or quality of the organic matter left behind after a crop is harvested.

1.6.5 Monitoring Biocontrol Agents in Soil

Many different groups of organisms are known to parasitise or prey on nematodes, but one of the main problems in working with biological control systems is the difficulty of detecting and quantifying some of these groups in soil. This applies particularly to the predatory and parasitic fungi. Nematode-trapping fungi can be quantified using sprinkle plates and soil dilution plates, but these time-consuming methods tend to detect species that grow well in culture and their efficacy is affected by the bait nematode used, soil type, moisture content and laboratory conditions. Also, estimates of fungal population density do not always correlate with trapping activity (Jaffee 2003; Smith and Jaffee 2009). The situation is even worse with parasitic fungi. Thus with *Hirsutella rhossiliensis*, for example, nematodes must be extracted from soil and examined on agar plates for signs of parasitism (Jaffee et al. 1991) or a suitable assay nematode must be found and checked for adhering conidia (McInnis and Jaffee 1989). This means that nematologists generally report only those predators that can be readily recovered from soil. Although suppressiveness to plant-parasitic nematode is positively related to the prevalence of omnivore and predator species, the lack of a strong relationship between these groups of nematodes suggests that other components of the soil food web are contributing to the regulatory process (Sánchez-Moreno and Ferris 2007).

In recent years the phylogeny and systematics of the Orbiliales (the group of ascomycetes containing most of the nematode-trapping fungi) has been revised using molecular techniques (Ahrén et al. 1998; Hagedorn and Scholler 1999; Scholler et al. 1999; Li et al. 2005; Chen et al. 2007a, b, c). A recent paper by Smith and Jaffee (2009) demonstrates that such techniques are also useful for ecological studies in soil and other substrates. Orbiliales-specific PCR primers for the ITS and 28 rDNA detected many uncultured Orbiliales that were closely related to nematode-trapping fungi and fungal parasites of nematode eggs, suggesting that molecular methods will provide a fuller picture of the nematophagous fungal community than culture-based methods alone. However, there were discrepancies between the results of molecular and culture-based studies that need to be followed up, and this process is likely to improve our understanding of the ecological role of this diverse group of parasitic and predaceous fungi.

In the case of bacterial parasites in the genus *Pasteuria*, the number of spores attached to the host nematode has been used as an indicator of spore concentration in soil (Stirling et al. 1990). However, such bioassays are not entirely satisfactory, as the relationship between spore concentration and the number of attached spores is affected by factors that affect nematode motility. Molecular assays to detect and quantify endospores in soil (Atibalentja et al. 2008) offer the opportunity to directly monitor the parasite in soil and could also be used to improve our understanding of its population dynamics.

One area where it is particularly important to monitor populations of fungal and bacterial parasites and predators is when they are mass-produced and used as biological control agents. The capacity of the introduced organism to come into contact with its target nematode and also survive in the extremely competitive soil environment is vital information from an ecological perspective. In future, data of this nature will largely be obtained using molecular technologies. One recent example is the use of species-specific primers to detect *Paecilomyces lilacinus* in soil and estimate the proportion of eggs infected by the fungus (Atkins et al. 2005). A real-time PCR primer and probe set also provided a method of detecting populations of *P. lilacinus* as low as 10 spores/g soil. These and other similar methodologies provide a new set of tools to assess the impact of various environmental and crop management factors on the spatial and temporal population dynamics of particular biological control agents and it is important that they are now employed in ecological studies.

1.6.6 Developing Biocontrol Products for Targeted Markets

As pointed out by many who have worked on biological control of soilborne pathogens, two major factors limit the potential of inoculants as a control strategy: (1) in most cropping systems, it is uneconomic to mass produce an organism and add it to soil in amounts sufficient to control a pathogen and (2) the buffering effect of the microbial community (which is responsible for the general suppressiveness of soils to pathogens) operates against a biological control agent once it is introduced into soil. These economic and ecological realities must therefore be recognised when deciding whether mass production and release of a biological control agent is a realistic nematode management strategy.

From an economic perspective, it is unreasonable to expect a biological pesticide to be cheaper than a chemical product. Biological control agents cannot be mass produced without a fermentation facility and an appropriate substrate; formulation costs are likely to be relatively high and the specificity of most biocontrol agents limits economies of scale within the production, distribution and marketing process. Furthermore, some organisms require controlled conditions during transport and storage, and this imposes additional costs. Thus applying a biological control agent to soil for nematode control is only likely to be feasible in situations where nematicides are currently the main control tactic. It will never be a realistic option for broad-acre crops (e.g. cereals, grains, oilseeds, cotton and sugarcane), and for most tree and vine crops. Future research should therefore focus on situations where monetary losses from nematodes are high enough to justify the use of a mass-produced biological product.

Root-knot nematode is a major pest of crops grown in glasshouses and other protective structures, and is an obvious target of such research for a number of reasons. First, the nematode causes problems on a global scale; the crops grown in glasshouses are relatively high in value, and the cost of nematode control with fumigants and nematicides is already an accepted component of production costs. Second, the soil environment (particularly moisture and temperature) can be reasonably well controlled; while the highly modified state of glasshouse soils (due to practices such as fumigation and intensive tillage) may mean that they are amenable to maintaining an introduced organism in the root zone throughout the life of the crop. Third, biological products can be applied within protective structures in a number of relatively simple ways (e.g. as a seed inoculants, seedling dips, soil drenches or additives to transplant mixes). I therefore suggest that this cropping system should be used as a test case by nematologists to see whether inundative biological control can be developed to the point where it is a realistic alternative to chemical control. What is needed is a coordinated effort to put our current knowledge of biological control into practice. About 30 years ago, the International Meloidogyne Program made a major contribution to worldwide knowledge of root-knot nematodes (Sasser and Carter 1985; Barker et al. 1985), and a similar program on biological control of these nematodes in glasshouse crops would provide an opportunity to move biological control from the laboratory to the market place. Numerous potentially useful biocontrol agents are available (*Paecilomyces lilacinus*, *Pochonia chlamydosporia*, *Pasteuria penetrans*, various nematode-trapping fungi, a number of readily-cultured diplogastrid predators, a range of plant growth-promoting rhizobacteria and several endophytes), and the aim would be to apply them in an integrated manner to achieve reliable and effective nematode control.

Whether the above research program is initiated or not, one disadvantage of mass production and release as a biological control strategy is that once an organism is applied to roots or soil, it is subject to the rigours of the environment. Efficacy of biological products will therefore be much more subject to environmental influences than the chemical nematicides that they are intended to replace. Thus research teams working with biological control agents should not consider that their job is done when a commercial partner is found and a formulated product is placed on the market. Many years of follow-up research is likely to be required to define the situations where a product will give reliable and effective control. Lists of registered products tend to imply that progress is being made, but the ultimate criterion for success is consistent results and widespread acceptance in the target market.

1.7 Concluding Remarks

Although it is easy to be disheartened by the lack of practical outcomes from biological control research in the last 30 years, it would be wrong to conclude that biological control cannot be developed to the point where it makes a significant contribution to integrated management programs for nematodes. Robust and durable systems of natural suppression are almost certainly operating in some fields, but they need to be sought out and the contributing factors identified, so that farming systems can then be modified to enhance suppressive mechanisms. Nematologists are contributing significantly to our understanding of the soil ecosystem, and since biological control is little more than applied soil biology and microbial ecology, these strengths must now be utilised to better understand the forces that regulate nematode populations and how they can be better deployed against plant-parasitic nematodes.

Research managers and individual scientists also need to recognise that not all impediments to progress are technical. The fragmentation of science into disciplines means that is often difficult for nematologists, plant pathologists, soil ecologists, molecular biologists and agronomists to work together, even though inputs from specialists in all these areas are required to better understand biotic interactions in the root zone, and to apply our collective knowledge to enhancing the suppressive potential of agricultural soils. The recent shift in resources from traditional areas of science into biotechnology continues a long-term trend towards specialisation that must be handled carefully. Intractable problems in biological control need to be tackled with new technologies, but without ecological and agronomic input, the desired outcomes are not likely to be achieved.

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