

NEMATODE INTERACTIONS IN NATURE: MODELS FOR SUSTAINABLE CONTROL OF NEMATODE PESTS OF CROP PLANTS?

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- I. Introduction
- II. Current Practices and Options in Nematode Control in Agriculture
 - A. Cropping Practices: Intercropping and Crop Rotation
 - B. Chemical Control
 - C. Biological Control
 - D. Organic Amendments and Suppressive Soils
 - E. Physical Control: Distance and Treatments
 - F. Genetically Resistant Crops
- III. Nematodes in Natural Systems
 - A. Vegetation Processes: Succession, Diversity, and Invasiveness
 - B. Nematode Diversity, Abundance, and Dynamics in Nature: Food Web Interactions and Controls
 - C. From Resistance Genes to Red Queen Processes
 - D. Origin of Plant-Parasitic Nematodes; Impact of Agriculture and Intensification Processes

- IV. Lessons From Looking Across the Fence
 - A. Theory-Driven Research Approach
 - B. Comparing Natural Systems, Tropical/Original Agriculture, and Intensive Agriculture
 - C. Biodiversity and Crop Protection
- V. Discussions
- VI. Conclusions
 - Acknowledgments
 - References

Plant-parasitic nematodes are major crop pests in agro-ecosystems while in nature their impact may range from substantial to not significant growth reduction. The aim of this review is to determine if nematode population control in natural ecosystems may provide us with a model for enhancing sustainable control of nematodes in crops.

In agricultural systems, monocultures, narrow rotations, alteration of the soil habitat, and fertilization may alter plant-parasitic nematode dynamics and boost nematode numbers while reducing diversity and effectiveness of top-down control organisms and protective mutualisms (endophytes and arbuscular mycorrhizal fungi). Traditional agro-ecosystems (still applied in tropical regions) involve the development of complex practices such as a broad range of plant species of high genetic diversity grown in associations, rotations, and shifting cultivation, which all influence the complexity of plant-parasitic nematode communities and of control organisms.

In nature, plant-parasitic nematodes (and other root feeders and soil pathogens) drive plant community processes, such as succession and plant species diversity. Natural soils contain a wide variety of potential nematode control organisms, but the consequences of this diversity are not known. Wild plant populations also contain more genetic variability than crops, but consequences for coevolution and Red Queen processes for nematode populations have not been studied.

We conclude that integrated crop pest control may benefit from studying plant-parasitic nematode–natural antagonist interactions in natural systems, which have been coevolved for longer than crop–nematode–antagonist systems. Understanding how wild plants control their plant-parasitic nematodes may ultimately result in improving the sustainability of crop protection against plant-parasitic nematodes.

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I. INTRODUCTION

The dependency of current agriculture on pesticides for crop protection is an important obstacle for sustainable crop production and for protection of the environment. Pesticides influence the biological composition and functioning of agricultural soils, while their leaching to surface and

ground water is a threat for the provision of potable water and for the functioning of aquatic systems (Wall, 2004). Reduction of pesticide usage and pesticide impacts on the environment should, therefore, be a major goal of agronomy research. Major progress has been made by biological control research, particularly in the reduction of pesticides used against above-ground insect plagues. Strategies vary from the release of specific parasitoids in greenhouses to designing landscapes that support the survival and spread of biological control organisms (Altieri and Letourneau, 1982; Gurr *et al.*, 2003). In soil, biological control is much more hampered than above ground because of the complex nature of the soil structure and of the interactions in the soil food web (Brussaard *et al.*, 1997; De Ruiter *et al.*, 1995; Whipps, 2001).

Plant-parasitic nematodes are among the major soil-borne crop pests, and their control relies on highly toxic compounds that have an impact on the whole soil community. Plant-parasitic nematodes cause an estimated annual US\$78 billion crop-yield loss worldwide, which makes effective control strategies highly essential (Sasser and Freckman, 1987). Interestingly, non-plant-parasitic nematodes are important components in the soil food web through their involvement in releasing mineral nutrients from the organic nutrient pool (Bardgett *et al.*, 1999; De Ruiter *et al.*, 1995; Wardle *et al.*, 1995) and in controlling numbers of insects in the soil (Strong, 1999). Therefore, controlling plant-parasitic nematodes may introduce a risk of also controlling nematodes that are beneficial for ecosystem processes.

In contrast with the many examples of plant-parasitic nematodes in agricultural ecosystems, relatively few studies in (semi) natural ecosystems have reported on nematode outbreaks. Plant-parasitic nematodes have been studied mainly in seminatural temperate grasslands, where their effects vary from strongly reducing primary productivity (Ingham and Detling, 1990; Stanton *et al.*, 1981) to having only minor effects (Seastedt *et al.*, 1987; Verschoor, 2002; Verschoor *et al.*, 2002). None of these plant-parasitic nematode effects alone resulted in complete die-out of vegetation, which may be partly due to the difficulty of relating the presence of species to their role in ecological interactions, which is a general problem in ecological studies (Harper, 1977).

Could we learn from population ecology of plant-parasitic nematodes and of their control in nature to improve crop protection and to enhance sustainability of agricultural production methods (Fig. 1)? Could we also learn from agronomy research to get a better understanding of the role of plant-parasitic nematodes in nature (Table I)? These are the two main questions for our review of literature on nematode control in crop systems and nematode population dynamics in natural systems. The avenues for improving biological control against plant-parasitic nematodes in crops

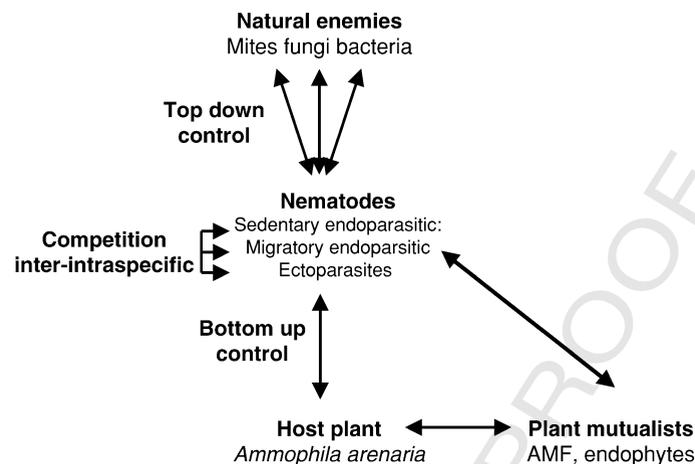


Figure 1 The players in nematode control (natural enemies, host plants, mutualists, and the nematodes themselves), the different sorts of biological control (top-down, bottom-up, and competitive interactions), and the modes of control (indicated as arrows).

and the possibilities for enhancing sustainability of agricultural production processes are discussed.

II. CURRENT PRACTICES AND OPTIONS IN NEMATODE CONTROL IN AGRICULTURE

A. CROPPING PRACTICES: INTERCROPPING AND CROP ROTATION

The presence of high densities of nematodes can be linked to a decrease in crop yield, not only by the direct effect of nematode population density but also by their interactions with other soil-borne pathogens (De Ruijter and Haverkort, 1999; McSorley and Gallaher, 1993; Taylor *et al.*, 1999; Wheeler *et al.*, 1994). A number of cropping practices are used to control nematodes, sometimes unintentionally, for example, when aiming at weed control or “soil sickness” due to accumulation of soil pathogens. Crop rotation can control number of host specific nematodes by growing non-host crops or trap plants (Fig. 2). In agricultural systems, the dynamics and distribution pattern of economically important nematodes (*Meloidogyne* spp., *Heterodera/Globodera* spp., *Pratylenchus* spp.) has been studied under different crop practices and hosts (Been and Schomaker, 2000; La Mondia, 2002; Noel and Wax,

Table I
Major Nematode Control Options Resulting from Agricultural Practices and Translation of these Control Options to Processes and Patterns in Natural Systems

Nematode control	Agriculture	Nature
Time (intra-annual)	Seasonal culture	Life history variation (e.g., winter annual plants)
Time (interannual)	Crop rotation	Vegetation succession
Space (small-scale)	Intercropping (intrafield scale)	Plant community diversity
Space (large-scale)	Farm crop diversity (interfield scale)	Landscape elements: dispersal barriers; soil characteristics Inundation, etc.
Genetic processes	Resistant crops breeding and genetically engineered plants	(Co)evolution, adaptation
Chemicals	Chemical control	Secondary plant compounds
Natural toxins	Green manuring	Organic matter increase (soil ripening?)
Predators and antagonists	Biological control (interactions at the individual plant scale)	Multitrophic interactions (including the linking of above and belowground interactions) around individual plants, plant competition, succession
Predators and antagonists	Suppressive soils (field scale)	Patchyness, heterogeneity within vegetation
Predators and antagonists	Integrated control (farm scale)	Ecosystem and landscape variation

2003; Nombela *et al.*, 1994; Yeates, 1994). Nematode abundance changes during the season and annual cycles differ among species and years depending on the life history of species, food availability and quality, biotic interactions with other organisms, and the physicochemical environment. The usefulness of crop rotation depends on the longevity of survival stages of the nematode.

In developing countries, the intercropping commonly used in low value crops not only controls plant-parasitic nematodes but also a range of other pests and diseases (Fig. 3). The mechanisms of control, besides starvation of the pest and disease causing organisms in the absence of suitable hosts, may be because some of the crops release nematicidal compounds such as tannins, flavonoids, glycosides (Chitwood, 2002). Crops that release nematotoxic compounds either from their roots or during decay of green plants after their incorporation in soil may be used for “biofumigation” (Jourand *et al.*, 2004a,b; Tsay *et al.*, 2004). Intercropping may also simply limit food

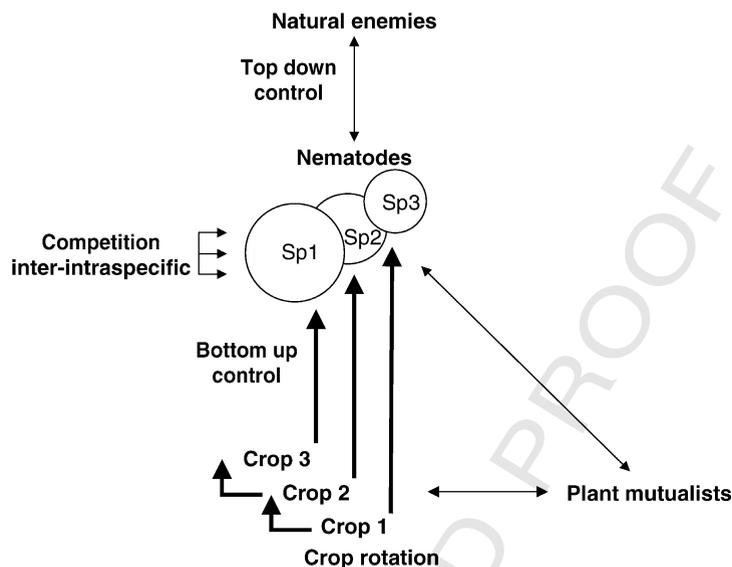


Figure 2 Influences of crop rotation on nematode control in a crop rotation system. The thickness of the arrow indicates the strength of the nematode control (the thicker the arrow, the stronger the nematodes will be controlled by the specified interaction). Crops 1, 2, and 3 are the different crops in the rotation and Sp 1, Sp 2, and Sp 3 are the specific nematode species (this can be one species or a complex of a few nematode species) that are performing well in cultures of crops 1, 2 or 3. In all cases, symbiotic mutualists, top-down control by natural enemies and competitive interactions play a minor role in nematode control; the crop rotation itself is the most important nematode control factor.

resources for host-specific nematodes. A major limitation on the use of both these cropping practices to control nematodes by disrupting the continuity of food resources is that they do not fit some intensive agricultural practices and farmers prefer to grow crops that are more economically rewarding.

B. CHEMICAL CONTROL

The most important nonspecific nematode control measure has been the use of soil fumigants such as methyl bromide, chloropicrin, 1,3 dichloropropene, metham sodium, dazomet and the use of non-fumigant, granular nematicides such as aldicarb, oxamyl, carbofuran, fenamiphos, ethoprophos, and fensulphothion (Whitehead, 1997). These nematicides are reliable

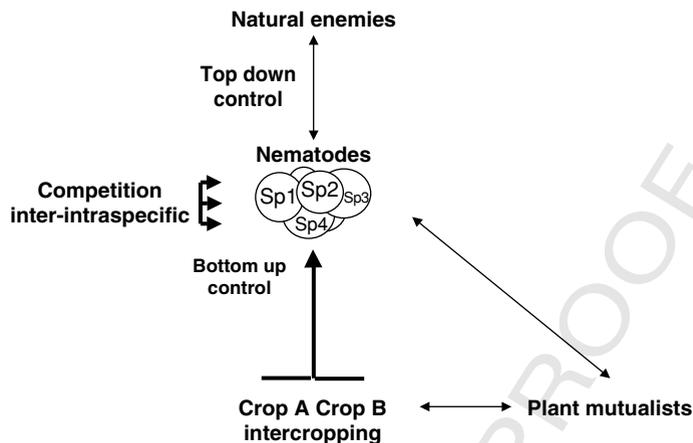


Figure 3 Influences of intercropping on nematode communities. Apart from the isolation of crop species by other crop species interspecific competition is probably the most important nematode control factor in these systems.

and fast working, controlling populations and thereby reducing damage, although not necessarily preventing posttreatment nematode reproduction and population increase. However, the use of these chemicals is increasingly restricted because inappropriate application may have negative environmental impacts and risks to human health. Moreover, side effects of these compounds may have too great an impact on nontarget organisms, including natural enemies of plant pathogens and pests and emblematic species of flora and fauna; others have direct impact as climate change forcing agents. In particular, restrictions on the use of methyl bromide and its impending withdrawal because of its ozone depleting properties have stimulated attention to the development of alternative control strategies (Schneider *et al.*, 2003).

C. BIOLOGICAL CONTROL

Usually, biocontrol strategies favor the introduction of exotic enemies (with the limitation in success due to too narrow a specificity range between the nematode and its parasite), rather than the improvement of the efficiency of indigenous enemies. The conditions of these introductions are often based on laboratory studies that focus on the binary predator–prey interaction without (or only partially) taking into account the impact of the environment on this dynamic. The interactions between soil and plant with plant-parasitic nematode life cycles and those of their enemies are inadequately

understood. In tropical and subtropical countries, the ability to control nematodes with exotic enemies remains unsatisfactory, because of their reduced adaptation to local climatic conditions or soil environments, and because of their inadequate host specificity to local pests. Consequently, studies have been performed on biocenotic mechanisms, which manage the natural development of indigenous enemies (Kerry and Hominick, 2002). The objective is to preserve or to create sustainable nonpathogenic balances, rather than to promote methodologies unable to safeguard soil biodiversity.

Organisms that affect nematodes include mites, collembola, predacious nematodes, fungi, and bacteria. Factors that impose practical limitation on the use of biological control are the difficulties in mass-producing predators and obligate parasites and the varying effectiveness in control due to interactions with soil factors, such as moisture, pH, and antagonism, by other soil organisms. Nevertheless, there are some examples of biological control developing in cropping systems. For example, the cereal cyst nematode *Heterodera avenae*, is controlled in much of Europe by fungi parasitic on females (*Nematophthora gynophila*) and eggs within cysts (*Pochonia chlamydosporia* and others). Similarly, clover cyst nematodes appear to be controlled on white clover in UK grassland by parasitic fungi; and the bacterium *Pasteuria penetrans* (or spp.) reduces numbers of root-knot nematodes (*Meloidogyne* spp.) in some cropping systems (Trudgill *et al.*, 2000). Certainly, *Pasteuria* is commonly encountered on a range of plant-parasitic and free-living nematode species in soils from natural and seminatural vegetation (Chen and Dickson, 1998).

Of the soil environmental impacts on root-knot nematode—bacteria interactions, texture, and structure are key factors (Dabiré *et al.*, 2005a; Mateille *et al.*, 2002). Root-knot nematodes, as well as their infestations by *P. penetrans* are observed more frequently in sandy than in clay soils (Bird and Brisbane, 1988; Mateille *et al.*, 1995; Spaul, 1984). But the amount of clays in sandy soils influences directly the ability of the soil in maintaining a pool of *P. penetrans* spores, which improves nematode infection (Dabiré and Mateille, 2004; Dabiré *et al.*, 2005b). Plant susceptibility to nematodes and its variation with cultural practices influences the proportion of *Meloidogyne* spp. juveniles infested by *P. penetrans*. The production of the bacterial spores and their concentration in soil is directly related to the development of the nematode population as *P. penetrans* is an obligate parasite. Worldwide, there is a close correlation between the vegetable species and the abundance of *Meloidogyne* spp. infested by *P. penetrans* (Giannakou and Gowen, 1996; Hewlett *et al.*, 1994; Ko *et al.*, 1995; Mateille *et al.*, 1995; Tzortzakakis *et al.*, 1995). The continuous culture of vegetables (thus greatly influencing root-knot nematodes) appears unsuitable for the production of *P. penetrans*, because the high multiplication rate of these nematodes does not allow the bacterial population to numerically keep up with

host abundance. Conversely, including non-susceptible crops in the rotations allows the ratio of bacterial spores/nematodes to increase in the soil (Giannakou and Gowen, 1996).

Natural enemy communities tend to build up relatively slowly over 4–5 years and usually under perennial crops or crops grown in monocultures. This slow buildup has been demonstrated by studies on the suppression of *H. avenae* by *N. gynophila* and *P. chlamydosporia*. In such suppressive soils, about 95% of the females and eggs were destroyed by the fungal parasites (Kerry *et al.*, 1982). As well as in the host plant (De Deyn *et al.*, 2004), nematode identity may greatly influence the microbial enemy community in terms of their diversity and population dynamics (Kerry and Hominick, 2002). It is suggested that microbial enemies have a role in the regulation of most nematode populations, but that this only becomes apparent in agricultural conditions where a suppressive soil develops (Stirling, 1991). In intensive cropping systems, a population of microbial enemies is thought to be selected from the natural enemy communities (Kerry and Hominick, 2002), but this seems to be an exception to nematode regulation by microbial enemies.

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Jaffee *et al.* (1992) found that nematode parasitism by fungal antagonists (e.g., *Hirsutella rhossiliensis*) exhibited two intrinsic density-dependent qualities. The first is host threshold density, the upper limit of hosts in a given system required to prevent a pathogen from becoming extinct, and the second is temporal density-dependent parasitism. This refers to changes in nematode and antagonist density, where the latter usually lags behind increases in nematode populations. An initial enrichment of hosts (e.g., nematodes) precedes and subsequently supports the eventual buildup of beneficial organisms that lead to nematode suppression (Jaffee, 1992). This leads to a stable equilibrium between antagonist–pest populations, instead of a complete eradication of the original nematode problem (Kerry, 1977) and is the quintessential definition of biocontrol.

Symbiotic mycorrhizal fungi are widely recognized as key organisms affecting the productivity and diversity of natural plant communities (Van der Heijden *et al.*, 1998). Several mechanisms have been proposed to explain the protective role of the arbuscular mycorrhizal fungi (AMF) symbiosis (Azcón-Aguilar and Barea, 1996; Jeffries *et al.*, 2003; Little and Maun, 1996). The improved plant nutrition may compensate for nematode damage. The AMF may compete directly with the pathogens for photosynthates and infection sites or AMF reduces the suitability of the root for the pathogen through anatomical or morphological changes. AMF-infected plants may change the microbial community in the rhizosphere. There may also be associated with local elicitation of plant defense mechanisms, and/or delayed nematode development within the root tissue. The protective role of AMF against parasitic nematode differs for ectoparasitic and endoparasitic nematodes. It seems that AMF would be more effective in either protecting

the plant or increasing plant resistance against endoparasitic nematodes. However, the effect on ectoparasitic nematodes is variable, and, in some cases a positive effect from AMF in ectoparasitic nematode populations has been found (Hol and Cook, 2005).

The obligate mutualist fungi of the genus *Neotyphodium* (formerly *Acremonium*) infect leaves and stems of grasses and in some conditions are ecologically and economically significant because of the impact of their secondary metabolites on herbivores. There is significant variation in the effectiveness of the interactions depending upon genetic and environmental factors, but some combinations of grass and fungus are fully resistant to several nematodes, including species of *Meloidogyne* and *Pratylenchus* as well as some ectoparasites (Cook and Lewis, 2001).

Studies on biological control of plant-parasitic nematodes that combine two or more microbial enemies can produce better results (Meyer and Roberts, 2002). The importance of the diversity of the natural enemy community is unknown and, in the few studies in which it has been analyzed and compared to rates of regulation of nematode populations, no correlation was found (Jaffee *et al.*, 1996, 1998; Persmark *et al.*, 1995). A wide range of natural enemies occurs in citrus orchards infested with *Tylenchulus semipenetrans* in California (Stirling and Mankau, 1977) and with *Radopholus similis* in Florida (Walter and Kaplan, 1990). The factors that retain a diverse natural enemy community or select specific species are important for our understanding of the biological control of nematodes.

Although it is difficult to generalize, nematode predators do not appear to have significant impacts on plant-parasitic nematode population densities in disturbed soils. Mites and collembola tend to be confined to the surface layers and unable to pursue nematodes into the pore spaces occupied by these prey; in arable agricultural soils, predators, including predatory nematodes are relatively scarce. Difficulties in the development of predators as biological control agents, including their lack of specificity, means that there is little detailed information on the role of predators in the dynamics of plant-parasitic nematodes. Walter *et al.* (1988) suggested that mites may be important in the regulation of nematode populations in short-grass steppe, but food web studies in soil ecosystems (De Ruiter *et al.*, 1995) and under bush lupine (Strong, 1999) suggest that predators may have little influence on plant-parasitic nematodes in natural systems.

D. ORGANIC AMENDMENTS AND SUPPRESSIVE SOILS

Manipulations of the soil environment by processes, such as the application of soil amendments, seek to stimulate the activity of soil biota that produce or improve general pest suppressiveness. The addition of organic

amendments may indirectly influence nematode antagonistic fungal activity in soil (Van den Boogert *et al.*, 1994). Rodriguez-Kabana *et al.* (1987) report that those amendments that are the most efficient at reducing nematode numbers possess low C:N ratios and have a high protein or amine-type content. Hallmann *et al.* (1999) demonstrated the suppressive effect of chitin-amended soil on *M. incognita* infestation levels. This effect was attributed solely to increases in indigenous bacterial and fungal population levels. The incorporation of plant material, such as *Tagetes minuta* synergized the antagonistic activity of the nematophagous fungus, *Paecilomyces lilacinus* toward *M. javanica* (Oduor-Owino, 2003). In general, organic amendments must be applied at high rates (>1 ton ha⁻¹) in order to have a significant effect on nematode populations and so must be cheap and locally produced for exploitation in agriculture.

A special case of biological control is a suppressive soil. In suppressive soils, diseases or nematode outbreaks do not occur (Kerry and Hominick, 2002). While it is encouraging that suppressiveness within soils has been demonstrated to occur in the field, much effort has gone into understanding the physiochemical environments and microbial community structure that underlie this phenomenon (Whipps, 1997). However, the mechanisms involved are still poorly understood (Jaffee, 1992; Oostendorp *et al.*, 1991), despite considerable research effort, this lack of an adequate understanding of the factors that influence parasitism and predation ecology in soil, has hampered the development of effective biocontrol agents (Kerry, 1987).

E. PHYSICAL CONTROL: DISTANCE AND TREATMENTS

Nematode abundance is affected by density-dependent and density-independent factors. Density dependence depends on the capacity of the population development of natural enemies to keep up with population development of the nematodes. The poor response capacity of some obligate parasites to keep up with rapid nematode population development (Kerry *et al.*, 1982) is a limitation to density dependent nematode population control. In a long-term study (Kerry and Crump, 1998), however, nematode and fungal antagonist populations seemed to have a corresponding development over time. There are relatively few of these datasets, which limits the capacity to study consequences of density-dependent nematode control by ecological modeling.

In soil, the most common density-independent factors derive from climate and prevailing meteorological conditions, namely extremes of moisture and temperature, and from physical factors including agricultural practices such as tilling and plant destruction (Stirling, 1991). Using clean planting material, tools, and machinery are important methods of preventing nematode spread

from field to field. At national and international levels, quarantine services regulate plant transport and control, and some nematodes are the subject of these regulations. When plant-parasitic nematodes are present in cropping systems, growers adopt various strategies to limit their impact, using either methods based upon the crop itself or other approaches not specific to the crop. A modern goal is to integrate different control methods in a management scheme that tries to reduce the impact of the nematodes at farm level (rather than in individual fields) and over a consistent period (rather than just the current crop).

Control of plant-parasitic nematodes by physical treatments of soil is widespread, although not always consciously directed at nematodes and often limited by climatic and environmental conditions. Soil heating by solarization generally takes 3 weeks of bright sunshine, and may be enhanced by covering soil with plastic mulches; an advantage may be that solarization is more detrimental to plant-parasitic than to saprophytic nematodes (Ostrec and Grubisic, 2003). Induction of anaerobic conditions in soil by flooding can control root knot and other plant-parasitic nematodes (Sotomayor *et al.*, 1999) and is often done unintentionally. For instance, in China, cyst nematodes damage winter sown wheat grown in rotation with maize, but not the summer crop that is rice grown in flooded paddies. Soil disturbance by tillage can reduce nematode numbers and change the composition of the nematode community in favor of bacterial feeding nematodes (Lenz and Eisenbeis, 2000). Steam treatment of soil is not specific and is expensive, its use being limited to high value crops and for composts. Such physical impacts probably occur in natural systems but at more limited scales.

F. GENETICALLY RESISTANT CROPS

Resistance and tolerance of plants to plant parasitic nematodes is widespread in nature. Naturally occurring resistance is discussed to include multiple genes and pathways (Caicedo and Schaal, 2004). This is in sharp contrast to their cultivated relatives, which exhibit generally a genetically simple, narrow based resistance to pathogens. This narrow resistance is the result of decades of breeding focused on, for example, high yields, fast growth, and more recently on especially vertical, that is, gene-for-gene resistance *sensu lato* (dominant R-genes). The R-genes trigger localized death of pathogen-infested cells; often referred to as a “hypersensitive plant response” (Dangl and Jones, 2001). Plant parasitic nematodes may easily break down narrow resistance, which is supposed to occur especially in local native populations, since introduced species, such as the introduction of the stem nematode *Ditylenchus dipsaci* in Australia, may have too

low genetic variation to overcome selection pressure of plant R-genes (Cook, 2004).

Although experimental work on R-genes is extensive, resistant crops are not widely used in practice (Starr *et al.*, 2002). Among resistant cultivars are those, which are genetically resistant to pathotypes of potato cyst nematodes (*Globodera rostochienis* and *G. pallida*); cereal cyst nematodes (*Heterodera avenae*); beet cyst nematodes (*H. schachtii*); root-knot nematodes (*Meloidogyne incognita*); stem nematodes (*Ditylenchus dipsaci*); and soybean nematodes (*H. glycines*) (Cook, 2004).

Besides the narrow base of resistance of cultivars, the limited use of resistant cultivar genotypes may result from the relatively high costs involved in developing resistance, such as lower yield or other unwanted side effects (Cook, 2004; Rauser, 2001). Present-day research aims at introgression of polygenic resistance (a pyramid of R-genes), instead of single dominant genes, and integrated strategies, such as rotating genotypes containing major R-genes, through time and space, that is, high dose/refuge strategy (Rauser, 2001). There are no examples of application of genetically modified crops with nematode resistance in agriculture.

In addition to genetic modes of resistance, crops may be either treated with chemicals or weak pathogens (Kempster *et al.*, 2001; Oka and Cohen, 2001; Oka *et al.*, 1999) to trigger a genetic resistance response. Both methods, however, have not been exploited in practice. Examples of application of chemicals are DL- β -amino-*n*-butyric acid (BABA) acid that reduce root-galling and egg densities of *M. javanica* (Oka *et al.*, 1999) and salicylic acid (SA) to suppress *M. incognita* (Vasyukova *et al.*, 2003) in tomato. Preventive inoculations of less aggressive or incompatible strains have shown to decrease mortality rates of hosts after attack by virulent nematodes (Kosaka *et al.*, 2001; Ogallo and McClure, 1996).

III. NEMATODES IN NATURAL SYSTEMS

All agricultural crops are derived from wild species by selection and breeding. Major selection criteria have been fast growth and high yield, but selecting genotypes with these traits may have resulted in enhanced sensitivity of the current crop species and races to pests, diseases, and climatic extremes. In the context of this review, a key question is: do nematode populations ever reach damaging population levels, or outbreak densities, in nature? Here we consider some of the ecological characteristics of the two systems in relation to how they affect nematode population dynamics.

A. VEGETATION PROCESSES: SUCCESSION, DIVERSITY, AND INVASIVENESS

Natural vegetation processes, such as succession, plant species diversity, and plant invasiveness, can be considered as natural equivalents of cropping practices. Vegetation processes are the result of the defense strategies of wild plants against their soil-borne enemies (Van der Putten, 2003). Soil pathogens (Van der Putten *et al.*, 1993) and root herbivores (Brown and Gange, 1993; De Deyn *et al.*, 2003) drive succession when early succession plant species are less tolerant to the soil-borne enemies than those plants that appear later in the chronosequence. Plant diversity is maintained mainly by negative feedbacks with the soil community (Bever, 2003). Plants that cannot control their soil-borne enemies are less dominant in natural vegetation than plants that prevent fast development of soil pathogens and root parasites (Klironomos, 2002). These soil-borne enemies control plant abundance (Packer and Clay, 2000), and release from soil-borne enemies may enhance plant invasiveness (Callaway *et al.*, 2004; Knevel *et al.*, 2004; Reinhart *et al.*, 2003).

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The role of plant-parasitic nematodes in vegetation processes has received less attention than the role of soil insects, soil pathogens, or mycorrhizal fungi. In coastal sand dunes, plant-parasitic nematodes are involved in the natural degeneration of three dominant plant species, marram grass (*Ammophila arenaria*), American beach grass (*A. breviligulata*), and sand buckthorn (*Hippophaë rhamnoides*), but their importance is not in a keystone role (De Rooij-van der Goes, 1995; Oremus and Otten, 1981; Seliskar and Huettel, 1993; Van der Stoel *et al.*, 2002; Zoon *et al.*, 1993). Invasiveness of *A. arenaria* outside Europe is correlated with less exposure to feeding-specialist plant-parasitic nematode taxa, such as root-knot and cyst nematodes (Van der Putten *et al.*, 2005), but there can still be considerable biotic resistance from the native soil community in the new habitats (Beckstead and Parker, 2003; Knevel *et al.*, 2004), also suggesting that plant-parasitic nematodes do not play a keystone role in reducing plant growth in dune systems.

In conservation grasslands, plant-parasitic nematodes were heterogeneously distributed and their impact on plant production could only be substantial in small patches with high nematode densities (Verschoor, 2002). This is in contrast with studies in prairie grass ecosystems, where plant-parasitic nematodes were considered to consume substantial amounts of net primary production [reviewed by Stanton (1988)]. This means that the role of plant-parasitic nematodes in vegetation processes is still unclear and reports on vegetation changes due to outbreaks of wild plant-parasitic nematodes are rare.

**B. NEMATODE DIVERSITY, ABUNDANCE, AND DYNAMICS IN NATURE:
FOOD WEB INTERACTIONS AND CONTROLS**

There are a considerable number of studies analyzing the dynamics and/or the composition of plant-parasitic nematode communities of various natural and seminatural temperate ecosystems, including grasslands, coniferous forests, coastal dunes, etc (Armendariz *et al.*, 1996; De Goede, 1993; Imaz *et al.*, 2002; Navas and Talavera, 2002; Porazinska *et al.*, 2003; Van der Stoel *et al.*, 2002; Verschoor *et al.*, 2001; Wall *et al.*, 2002). Factors that may control the diversity and abundance of plant-parasitic nematodes, however, have not been extensively studied. Plant-parasitic nematodes are very responsive to changes in vegetation (Korthals *et al.*, 2001), and plant identity greatly influences their population densities (Wardle *et al.*, 2003; Yeates, 1987). Plant species identity is also a main driver of nematode taxonomic and functional diversity, more than what plant diversity is (De Deyn *et al.*, 2004). Plant removal studies indicated that plant-parasitic nematodes had considerable ability to survive in the absence of host plants (Wardle *et al.*, 1999).

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There seems to be more diversity in nematode communities in relatively undisturbed soil than in agricultural soils (Baujard *et al.*, 1979a,b; Cadet *et al.*, 2003a,b; Hanel, 2003; Pate *et al.*, 2000). However, there are few data on the population structures and dynamics of plant-parasitic nematodes in natural ecosystems at scales appropriate for making comparisons with crop systems. In principal, the aggregated distributions known from agriculture should also occur in natural systems, particularly for host specific nematodes. Data from some northern temperate grassland ecosystems (tabulated in De Goede and Bongers, 1998) confirms that species of *Pratylenchus* (84% incidence) are more frequently encountered than those of cyst (21%) or root-knot (19%) nematodes in plant species rich, not recently cultivated, grassland soils (>700 sample points from 13 grasslands). Population densities in these situations were on average low in comparison to the economic thresholds of comparable crop pests but occasional samples with more individuals are encountered in seminatural grasslands (Verschoor *et al.*, 2001, 2002).

Herbivores may be controlled by resources as well as by predators (Olf *et al.*, 1999). Mycorrhizal fungi (Hol and Cook, 2005) and interspecific competition (see for a review Eisenback, 1993) have been considered as possible nematode control in agriculture. However, there is very little information on the role of mycorrhizal fungi and other microbial antagonists in controlling plant-parasitic nematodes in nature. Most of these studies have concerned the control of bacterial or fungal feeding and entomopathogenic nematodes (Jaffee, 1996; Koppenhofer *et al.*, 1997). In natural dunes, plant-parasitic nematode influences on host plants can be counteracted by arbuscular mycorrhizal fungi

(Little and Maun, 1996). Agricultural intensification disrupts the internal regulation of soil communities (Giller *et al.*, 1997), for example, by reducing the hyphal connections of mycorrhizal fungi (Helgason *et al.*, 1998), which limits mycorrhizal control of nematodes in intensive agriculture. Moreover, mycorrhizal infections are discouraged at high soil (especially phosphorus) fertility, so that in intensive agriculture, both physical and chemical soil conditions do not favor plant protection by mycorrhizal fungi. In sand dunes, the temporal and spatial dynamics of root-knot nematodes is limited by cyst and root-lesion nematodes (Brinkman *et al.*, 2005). In agriculture, nematode communities are dominated by only a few genera of plant-parasitic nematodes and bacterial feeders (Freckman and Ettema, 1993), which may affect the role of competitive interactions in nematode control in agro-ecosystems.

C. FROM RESISTANCE GENES TO RED QUEEN PROCESSES

The host ranges of the root-knot nematodes indicate that crop plants are much more susceptible than wild plant species (Ehwaeti *et al.*, 1999). It is clear that resistance genes to root-knot nematodes are available within species of wild or ancestral relatives of crop plants, and it is likely that gene-for-gene interactions occur (red) between the putative parental nematode species and the crop plant ancestors (Cook, 2004). In both cyst and root-knot nematodes, the evidence suggests that the gene for gene interactions that we seek to exploit have coevolved in situations very different from those in modern agriculture. It is of interest to consider the natural arena and see if there are lessons for enhancing the usefulness, for example, durability in the face of intraspecific variation (virulence) and nematode species selection. If the major pest species of root-knot nematodes are of hybrid origin and have been selected during crop domestication and agricultural simplification, it is not likely that we shall find effective resistance in recent ancestral crop plants. It is more likely that resistance genes will be in related wild progenitors that may have coevolved with the ancestral nematode species. If the ancestral sexual nematodes in natural systems had more restricted host ranges, it is unlikely that plants will have the full range of genes for resistance effectiveness against the polyploid parthenogenetic root-knot nematodes.

Within species, there are no data on the genetic structure of plant-parasitic nematodes in natural systems. There are examples available from animal or entomopathogenic nematodes (Blouin *et al.*, 1995, 1999; Hawdon *et al.*, 2001). For plant-parasitic nematodes, cyst nematodes have been studied at the genetic level in crops (Castagnone-Sereno *et al.*, 1993; Folkertsma *et al.*, 1996, 2001; Hugall *et al.*, 1994; Lasserre *et al.*, 1996; Navas *et al.*, 2001). The cyst nematodes show extensive levels of gene flow (Folkertsma *et al.*, 1996;

Picard *et al.*, 2004; Plantard and Porte, 2004), probably by passive dispersal of cysts via air or (human) vectors. This extensive gene flow would explain the relatively high genetic variability of populations, which might enhance the potential to breakdown local host plant resistance.

The ability of a nematode species to parasitize a host is measured by reproduction. Resistant hosts do not permit female nematodes to develop to reproductive maturity, and host resistance is often expressed as a hypersensitive response. Currently, these relationships appear to conform to the gene-for-gene hypothesis. Nematode populations can be classed by their different degrees of aggressiveness, defined as the relative level of reproduction that occurs on a given host genotype. Therefore, genetic analysis has been applied to understand the bases of parasitism, and unambiguous pathotype classifications have been developed for crop pests (Dong and Opperman, 1997; Semblat *et al.*, 1998, 2000; Wang *et al.*, 2001).

At the intraspecific level, there are very substantial differences between crop plant genotypes in their host status to particular nematodes. Naturally occurring genetic resistance has been used to control nematodes of some crops. The extent of genetic variation in host and nematode populations are very important determinants of durable resistance. Single dominant resistant genes in pure line crops are likely to provide durable control only in unusual situations. Human impacts on plant genetic variation during the relatively recent domestication of crops and their current use in intensive farming have also affected nematode variation. Moreover, the time frame, spatial scales and likely nature of plant-nematode coevolution in the longer period preceding domestication further emphasize the significance and extent of the genetic complexity of the interactions. It is important to take these factors into account during the identification of resistance sources and their exploitation through plant breeding.

In natural populations, genetic variation is probably critical for enabling hosts to persist; the evolutionary arms race between hosts and parasites requires genetic variation and drives the need for sexual reproduction. This is known as the Red Queen hypothesis (Clay and Kover, 1996). Red Queen processes have not yet been tested for plant-parasitic nematodes. However, plant-parasitic nematodes are not only parasites, they are also subject to predation and parasitism by a diverse natural enemy community. The nematophagous and antagonistic bacteria and fungi that have been isolated contain much variability within individual species (Kerry and Hominick, 2002). The importance of this variation in the regulation of nematode populations is unknown and it would be a major challenge to study Red Queen processes in relation to more complex food web processes.

In coevolutionary host-parasite systems, each species constitutes an ever-changing environment to which its opponent has to adapt. Traditionally, plant-pathogen populations have been considered homogenous entities in

which spatial considerations played little role. However, this situation has been proved to be too simplistic and geographic structure is now considered as an important factor in coevolutionary processes (Thompson, 1999). Different populations may show markedly diverse patterns of distribution of genetic variation for resistance and virulence. Consequently, the classical model for gene-for-gene coevolution may be expressed in different ways (Burdon and Thrall, 1999), with short-term interactions in human dominated and homogeneous agricultural systems but natural host-pathogen associations showing dynamic characteristic of metapopulations of a series of populations that show varying degrees of connectedness, with local extinction and colonization events. More knowledge of the spatial pattern of nematode distributions in natural systems may elucidate if outbreaks are significant in these systems, if we are able to define the appropriate spatial, temporal, and genetic scales of investigation (Ettema and Wardle, 2002).

D. ORIGIN OF PLANT-PARASITIC NEMATODES; IMPACT OF AGRICULTURE AND INTENSIFICATION PROCESSES

Some of the major pest species of nematodes are known to occur in natural or seminatural vegetation. This is particularly the case with cyst nematodes; those that are pests of potato (*Globodera* spp.) and soybean (*H. glycines*) are known from wild plants in the centers of diversity of the ancestors of their crop host species. Cereal cyst nematode species also occur in grasslands. The major root-knot nematode pests (*M. arenaria*, *M. incognita*, and *M. javanica*) are not known from natural ecosystems. The several hybrid origins postulated by Trudgill and Blok (2001) for *M. arenaria*, *M. incognita*, and *M. javanica* could have occurred between few ancestral species followed by polyploidy that retained genetic diversity. Hybridization may stimulate invasiveness, particularly where genetic or reproductive mechanisms fix hybridization (Ellstrand and Schierenbeck, 2000). The spread of these root-knot nematodes worldwide may therefore have occurred recently from a geological point of view, certainly in the last 10,000 years of agriculture and more probably in the last few hundred years of mass movement of colonizing people and intensification of agriculture (Cook, 2004).

From published observations, it is impossible to determine the spread of root-knot nematodes as distinct from the spread of knowledge about them. Thus, the first records of root-knot nematodes are from the United Kingdom on cucumber in 1855 and probably the first damage related observations on coffee in Brazil in 1878 and crops in Florida in 1889. Cucumbers have been cultivated for 3000 years since domestication probably in India and were grown under glass in the United Kingdom during the 18th and 19th centuries. Coffee (*Coffea arabica*) having evolved in southwestern Ethiopia

was dispersed via Arabia and India, reaching Indonesia during the late 17th century and then via Europe to the Caribbean and South America in about 1725. Production rapidly increased in Brazil after the railways were developed in the 1860s.

Many other species of both cyst and root-knot nematodes have been encountered in natural vegetation, but are usually not prominent. In the case of the foredune grass *A. arenaria*, which occurs as a natural monoculture on mobile dunes, cyst and root-knot nematodes are an important component of the nematode community (Van der Putten *et al.*, 2005). Root-knot nematodes are potentially harmful to *A. arenaria*, but interspecific competition with cyst and root-lesion nematodes (*Pratylenchus* spp.) reduces their effects on plants (Brinkman *et al.*, 2005). Orion (1979) observed that root knot is also not a problem on primitive farms in Israel, becoming one only where agriculture is improved. It has not yet been resolved whether the “improvement” effect of agriculture may act by reducing nematode diversity, by altering the genetic composition of root-knot nematode populations, or by a combination of factors, also including monocultures, intensification, irrigation, and fertilization. Shifts in composition and structure within plant-parasitic nematode communities have been observed between native and modified grasslands in New Zealand (Bell *et al.*, 2004): in modified grasslands (plowing, soil amendments, introduced species of pastures), *Heterodera* sp. and *Meloidogyne* sp. take over from the criconematids originally present in native lands. It is quite likely that the cyst and root-knot nematodes are also introduced into New Zealand. These effects may all lead to simpler cropping systems allowing maximum nematode population increase due to parasitic adaptations.

The apparently low population densities of host-specific nematodes in natural vegetation probably reflect the relatively low abundance of host plants. There has been increasing research on the role of space in population, community, and ecosystem processes in soil systems (Ettema and Wardle, 2002). The distributions of soil biota as well as the different factors that determine them, influence spatial patterns of decomposition, nutrient supply, and root herbivory, ultimately influencing the spatial structure of plant communities.

IV. LESSONS FROM LOOKING ACROSS THE FENCE

A. THEORY-DRIVEN RESEARCH APPROACH

The prime interest of applied nematological research has been focused on sampling and identification of nematodes, their physiology, molecular ecology, and virulence and interactions with their hosts, rather than on

theory development. While nematode interactions have received considerable attention in nematology (Khan, 1993), theory on multitrophic interactions has been primarily developed by entomologists (Price *et al.*, 1980). Probably a major reason for this is the complexity of the experiments needed when studying belowground multitrophic interactions (Van der Putten *et al.*, 2001). However, nematode control might benefit from a more integrated approach of plant defense, comparing top-down versus bottom-up effects (Walker and Jones, 2001), constitutive versus induced defense (Karban and Baldwin, 1997), and direct versus indirect defense (Price *et al.*, 1980).

Tolerance versus resistance has received considerable attention in nematology (Trudgill *et al.*, 2000) and specialism versus generalism may probably be quite different from what is known of aboveground insects, which have far more options for active dispersal. Still, this type of information may be crucial for designing effective biological control strategies, for example, when determining to rely on specialists or generalists for nematode control (Lehman and Reid, 1993; Snyder and Ives, 2001; Symondson *et al.*, 2002). Other examples may be selective suppression of plant-parasitic nematodes by entomopathogenic nematodes, *Heterorhabditis bacteriophora* and *H. indica*, with no adverse effect on free-living nematodes (Somasekhar *et al.*, 2002). Or evidence that bacterial-feeding nematodes make a greater contribution to the diet of predacious nematodes than do plant-feeding nematodes. Increased numbers of predacious nematodes enhance the cycling of plant nutrients rather than reducing root herbivory (Yeates and Wardle, 1996).

Multitrophic approaches have been advocated for plant-parasitic nematodes (Kerry and Bourne, 1996; Sikora, 1992), but they have already been applied to entomopathogenic nematodes, for example, interactions with trapping fungi and their influence on entomopathogenic nematodes, root-feeding insects, and, finally, survival of bush lupines in coastal systems (Jaffee *et al.*, 1996).

Bacterivorous and fungal feeding nematodes play a major role in soil food webs and these have been included in developing soil food web theory (De Ruiter *et al.*, 1995; Moore *et al.*, 2003; Neutel *et al.*, 2002). However, plant-parasitic nematodes thus far have played a minor role in these detritus-focused food web models. While studies on suppressive soils would provide excellent examples on improving the application and development of ecological theory below ground, very few of these studies have done so. The awareness of linkages between above- and belowground trophic interactions (Masters *et al.*, 1993; Van der Putten *et al.*, 2001; Wardle *et al.*, 2004) is showing that nematodes may stabilize or destabilize aboveground multitrophic interactions (Bezemer *et al.*, 2005). This shows that further development of aboveground multitrophic interaction theory requires that

belowground interactions, including root–nematode interactions, should be considered as well.

B. COMPARING NATURAL SYSTEMS, TROPICAL/ORIGINAL AGRICULTURE, AND INTENSIVE AGRICULTURE

The current large seed crops, such as wheat and rice, are derived from domestication of early succession species that would have been quite ephemeral, having traded off growth against defense (Diamond, 1997; Herms and Mattson, 1992). Probably, the choice of the early farmers, some 10,000 years ago, is influencing current agriculture and crop protection enormously. Breeding for high yield and palatability may have resulted in selection pressures on plant enemies, leading to the current range of pest nematodes; whether or not this may be true should still be investigated. A comparative approach of plant defense strategies against above and belowground natural enemies and higher trophic levels, including early, mid, and late succession plant species, may help us to understand plant defense strategies in natural systems. Comparison of defense in wild plants with intensive, extensive, or biological farming systems in tropical and temperate regions might result in new approaches for crop protection strategies. For example, arbuscular mycorrhizal fungi may be more effective in soils with low phosphorus availability, but application in fertile soils could have neutral or even adverse effects. Similar assessments could be made for bacterial, fungal, or faunal natural enemies of plant-parasitic nematodes and variations therein.

C. BIODIVERSITY AND CROP PROTECTION

Soil faunal diversity is supposed to be greatest in temperate areas, owing to the quite rich C content in soils increasing food resources and also inducing habitat heterogeneity (Wardle, 2002). However, biodiversity of plant-parasitic nematodes in tropical agrosystems is greater than in temperate agro-systems (Fargette and Quénehervé, 1988; Luc *et al.*, 1990; Mateille *et al.*, 1995; Quénehervé and Fargette, 1992). The plant-parasitic nematode diversity in temperate natural areas is supposed to be greater than in temperate agro-ecosystems (Hanel, 2003). Therefore, the relatively low plant-parasitic nematode diversity in temperate agro-ecosystems seems to be due to intensive cropping practices, rather than to climate. Biodiversity may influence the functioning of soil systems, but effects that have thus far been measured show negative, neutral, and positive effects (Wardle, 2002; Wardle *et al.*, 2004). Great nematode diversity could enhance competitive interactions, thereby preventing outbreak events of individual plant-parasitic

nematode species (Brinkman *et al.*, 2005). Considering the soil diversity as a potential resource might help manage the overall pathogenicity of the total plant-parasitic nematode community (Cadet and Floret, 1999; Cadet *et al.*, 2002, 2003a; Rimé *et al.*, 2003).

Patterns in biodiversity of the natural enemies of plant-parasitic nematodes have been less well studied. Soils harbor a variety of microbial and faunal species that all may be involved in nematode control. The question is how these control factors interact and what may be the result for nematode population dynamics. Holling (1973) proposed the “soil resilience concept,” defined as the soil capacity to recover functional and structural integrity after disturbance. In line with more recent biodiversity studies, other aspects, such as niche complementarity, which has been demonstrated for plant mixtures (Van Ruijven and Berendse, 2005) may also be of importance for the control of plant-parasitic nematodes by the community of soil organisms. However, whether or not diversity in these multispecies communities of natural enemies could be considered as redundancy, insurance, or resulting in idiosyncratic nematode control when reducing diversity requires further studies.

V. DISCUSSIONS

Soils that are suppressive to plant-parasitic nematodes and other soil-borne diseases may be called “healthy” from a crop protection point of view, although soil suppressiveness may refer to a variety of different mechanisms, ranging from prevention of pathogen establishment, the presence of pathogens that do not become harmful, or to initial increase and subsequent decrease of pathogen incidence (Baker and Cook, 1974). Soil suppressiveness may or may not relate to soil biodiversity.Suppressions may be general, or specific, for example, due to the presence of biological control organisms (Cook and Baker, 1983). Plant pathologists describe suppressive soils as soils where plant disease is not expressed (Alabouvette, 1986) or considerably decreased as in the well-known Take-All Decline (Cook and Weller, 1987) despite the presence of virulent pathogens. For plant nematologists, a suppression effect results in the decrease of nematode populations by natural enemies exclusively (Kerry and Jaffee, 1997). In the first case, suppression involves complex mechanisms including abiotic as well as biotic factors. In the second one, suppression corresponds to specific biotic interactions.

Resilience (of which suppression is one component), stability, large biodiversity, and active nutrient cycles are all attributes of “soil health” (Elliott and Lynch, 1994). If we assume that too intensively managed agricultural

soils are endangered soils (sick soils), such a concept represents an approach and a new challenge toward soil quality restoration in modern agriculture (Swift, 1994). In highly disturbed environments, such as high input agricultural systems, monitoring soil diversity toward some recovery of more complex top-down, bottom-up, and horizontal (inter- and intraspecific competitive) interactions may lead to more sustainable ways of management. In that respect, it is essential to know the mechanisms of the interactions within or involving nematode communities and their implications for population regulation, since such interactions will contribute to save or partly restore resilience and sustainability.

A widespread dogma is that tropical crops suffer more from nematode damage than those of temperate regions (Luc *et al.*, 1990). This also requires evaluation for the lessons it may have for sustainable control. In developing countries of the tropics and subtropics, crop yields are mostly low due to the erosion of soils and to the low natural fertility of soils. In such conditions, nematode infestations may not be the principal cause of poor crop growth but the damage they cause can be considerable. Moreover, in traditional agro-ecosystems, the requirement for food production to be resilient to multiple stresses has favored the development of a broad range of plant species of high genetic diversity in complex agro-ecosystems involving mixed cropping, rotations, shifting cultivation. Such complexity may have led to the development of complex plant-parasitic nematode communities. Control methods targeting specific nematodes are then not very effective in reducing nematode damage and only nonspecific approaches (chemical nematicides) can be predicted to be generally effective. Such complex agro-ecosystems may be more similar to natural ecosystems than the systems of intensive agriculture.

The lesson from current control practices appears to be that cultivated plants suffer much nematode damage. Nevertheless, many crops, known to be susceptible to one or more nematode species, are grown often without nematodes being recognized as limiting factors. Such crops include fruit, vegetables, cereals, and others, and it seems that when damage does occur it is a consequence of some particular features of an agricultural system rather than a general feature of agriculture.

Likewise, from a consideration of top-down nematode control mechanisms we conclude that large-scale nemato-stasis—the control of particular species by specific or general antagonists—is unlikely to occur. Interactions are more likely to be important at smaller scales. The important lesson is that we have to define these dynamics at smaller scales than has so far been attempted and a major constraint for quantifying nematode population dynamics is the lack of precision of nematode population density estimates and those for their natural enemies (Kimpinski and Sturz, 2003).

VI. CONCLUSIONS

Plant-parasitic nematodes are serious pests in agriculture causing much economic damage, while driving vegetation processes (succession, diversity) in natural plant communities.

Reported nematode effects in natural plant communities are highly variable between studies.

It is not sure whether and, if so, why nematodes are less aggressive in nature: this may be due to invisible effects (e.g., by competition or control by predators), or due to more genetic variability (Red Queen processes), or less aggressive nematodes (resistance breeding effect), and more diversity (diversity-functioning effect).

In natural systems the diversity between and within top-down and horizontal (competition) nematode control effects may lead to insurance or resilience.

Nematology research would benefit from a more conceptual multitrophic interactions approach.

Comparative assessment may reveal the importance of effects of top-down, horizontal, and bottom-up control of plant-parasitic nematodes in nature; the advantage of natural systems is that plants, plant-parasitic nematodes, and their natural enemies may have coevolved considerably longer than multitrophic interactions with crop plants.

Natural systems may be compared with agro-ecosystems with various degrees of intensity of disturbance to analyze the consequences of cultivation for plant-parasitic nematode control; this may result in improved integrated nematode control, which contributes to enhancing sustainability of agriculture.

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