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DEVELOPING SUSTAINABLE SYSTEMS FOR NEMATODE MANAGEMENT

Kenneth R. Barker and Stephen R. Koenning
Plant Pathology Department, North Carolina State University, Raleigh, North Carolina 27695-7616; e-mail: kenneth_barker@ncsu.edu

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ABSTRACT

Early researchers identified key concepts and developed tactics for multiple-option management of nematodes. Although the emphasis on integrated pest management over the past three decades has promoted strategies and tactics for nematode management, comprehensive studies on the related soil biology–ecology are relatively recent. Traditional management tactics include host resistance (where available), cultural tactics such as rotation with nonhosts, sanitation and avoidance, and destruction of residual crop roots, and the judicious use of nematicides. There have been advances in biological control of nematodes, but field-scale exploitation of this tactic remains to be realized. New technologies and resources are currently becoming central to the development of sustainable systems for nematode-pest-crop management: molecular diagnostics for nematode identification, genetic engineering for host resistance, and the elucidation and application of soil biology for general integrated cropping systems. The latter strategy includes the use of nematode-pest antagonistic cover crops, animal wastes, and limited tillage practices that favor growth-promoting rhizobacteria, earthworms, predatory mites, and other beneficial organisms while suppressing parasitic nematodes and other plant pathogens. Certain rhizobacteria may induce systemic host resistance to nematodes and, in some instances, to foliage pathogens. The systems focusing on soil biology hold great promise for sustainable crop-nematode management, but only a few research programs are currently involved in this labor-intensive endeavor.

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INTRODUCTION

There is an extensive literature on the management of plant-parasitic nematodes, their management in sustainable and subsistence agriculture (28), and current options for their management (54, 55). This review, however, focuses on developing strategies and the tactics available for nematode management in intensive agriculture, soil biology–based sustainable and conventional production systems. We plan to follow the operational definitions of sustainable agriculture offered by Benbrook (16); "Sustainable agriculture is the production of food and fiber used in a system that increases the inherent productive capacity of natural and biological resources in step with demand. At the same time, it must allow farmers to earn adequate profits, provide consumers with wholesome, safe food, and minimize adverse impacts on the environment." Sustainable agriculture aims to avoid depletions or losses of the earth's resources, while also rebuilding the reproductive capacity of agricultural soils (41). In contrast, conventional agriculture encompasses the practices, methods, and systems predominant within a given region, although these practices may vary over time and according to soil, climate, and other environmental factors (16). Although the goal of sustaining any production system can be questioned, even conventional practices may be fully sustainable when deployed properly, and they will continue to play important roles in food and fiber production in the future (16). A sustainable agricultural system must meet human needs without incurring long-term damage to the natural resources (125).

Expanding world population and pressure for improved living standards are the impetus to increased agricultural productivity. Intensively managed agroecosystems presently produce more than adequate food and fiber supplies needed in industrial societies with only about 2% of the populace being employed in agricultural production. This high productivity and related inputs for cereals and potato in developed countries contrasts sharply with the subsistence agriculture common in most developing countries (Figure 1) (28, 125), where the greater portion of the world's population lives. The shift from subsistence to intensive agriculture occurred through the application of new technology and exploitation of biotic and abiotic natural resources. Many improvements in productivity are attributable to increased inputs of energy (Figure 2), largely in the form of chemical energy used for mechanization, irrigation, fertilizers, and pesticides. The expenditure of chemical energy is generally viewed as underpinning the stability of intensive agroecosystems (183, 184). Selection of plant populations for agroecosystems has resulted in greater uniformity, and consequently a narrowing in the genetic base of some crop species (30, 75, 184). Recognition of the fact that Earth's resources are finite has raised concern about the stability and sustainability of our agricultural systems (183). Furthermore,

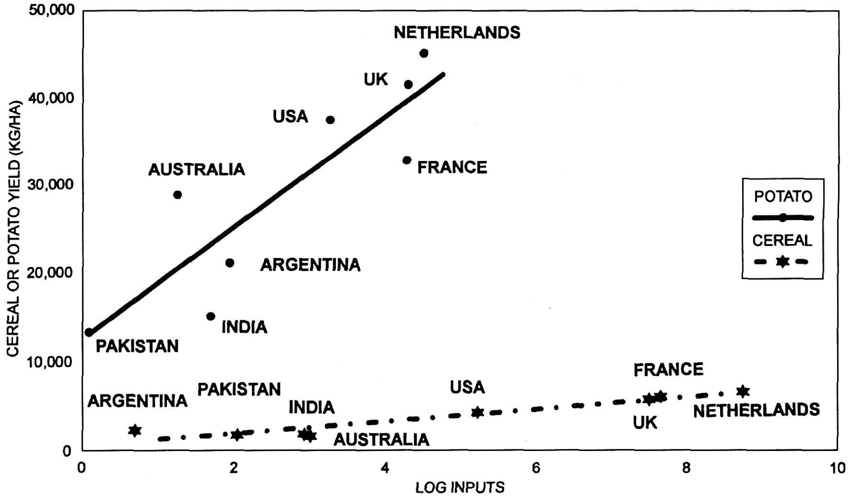

Figure 1 Comparative cereal yields from seven countries and predicted yield from levels of pesticides used in cropping systems (55) and potato yields from the selected countries and predicted yield based on potash consumption/unit land within a country for 1994 [data from *FAO Production Yearbook,* Vol. 48 (1994) and *Fertilizer Yearbook,* Vol. 44 (1994)].

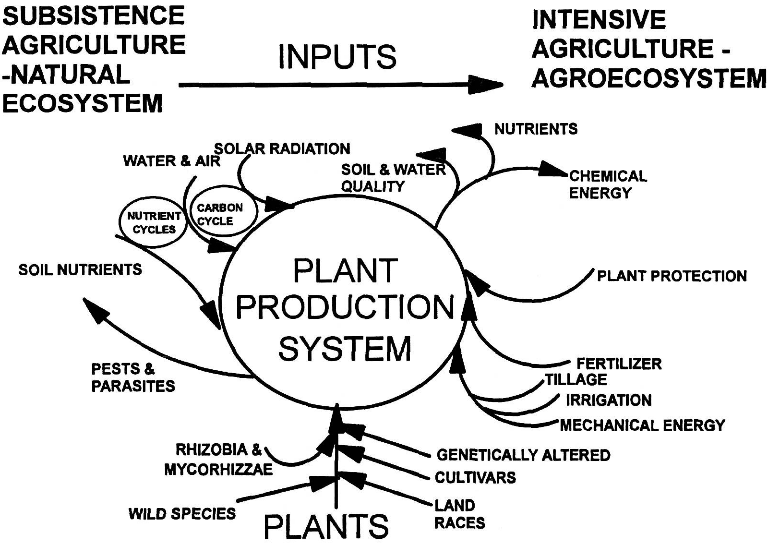

Figure 2 Comparative components of subsistence and intensive agroecosystems.

there is widespread apprehension that many practices utilized in intensive systems contribute to environmental degradation.

The new information and technology forthcoming from research programs involving the genetic engineering of crop plants and microorganisms, ecology, and soil biology–based integrated crop and pest management should contribute to the goals of sustainability of crop-pest management (128). The striking promise for new strategies and tactics for nematode management likely to be deployed during the next decade is in sharp contrast to the lack of change in existing management methods to prevent losses caused by plant-parasitic nematodes (54). However, emerging technologies coupled with concurrent loss of effective and economic nematicides should accelerate change. New strategies and tactics must focus on systems for managing nematodes that minimize the use of energy-intensive technologies, increase the productivity of agroecosystems, and yet enhance the durability of our genetic resources.

The relationships between plant-parasitic nematodes, their hosts, and environment vary greatly with nematode-host combination, geographic region, and given field characteristics. In addition to the direct effects of environment on nematode-host interactions, the expression of host resistance can be influenced by temperature. Root-knot–resistant bean, tomato, tobacco, and other crops may support nematode reproduction at an elevated temperature of 28°C or greater (114). Plant-parasitic nematodes also often limit crop productivity by predisposing plants to attack by fungi and/or bacteria and by serving as vectors of a number of plant viruses (1). In general, the initial numbers of nematodes present when an annual crop is established are inversely related to crop yield for that year, but this relationship is more complex with perennial crops (17, 55). Also, total abundance of nematodes, including beneficial species and the trophic-group structure, may be positively related to the productivity of some pasture/grass ecosystems (177).

Yield losses worldwide to plant-parasitic nematodes have been estimated to range from 5% to 12% annually (143). These losses, however, are influenced greatly by both the production systems and management options utilized. For example, small-scale and subsistence farmers often use traditional management methods that may prevent the build-up of damaging nematode populations; the development of a serious nematode problem is a warning that this farming system has become unsustainable (28). Bridge (28) states that the overriding principle sustaining traditional and subsistence agriculture is that the operational systems were designed to conserve the essential goodness of the land, including beneficial organisms. Long-term monoculture in Poland, in contrast to rotations, resulted in yield losses up to 60–70% or more when population densities of damaging parasitic nematodes were present (185). Yield losses incurred in

Globodera rostochiensis–susceptible potato averaged 38% (12–76%), as compared to 18.3% (12–34%) in resistant potato. Losses were high in fiber flax (43–78%) and field bean (25–61%) under monoculture, whereas winter rape (−31–17%) and maize (0–18%) were more tolerant. In addition to plant-parasitic nematodes, the presence of inhibitory compounds, shifts in weed communities, and the general condition of the crop were related, in part, to these yield losses. The continuous production of susceptible crops in the sandy soils of the southeastern coastal plains of the United States and other similar regions also often result in devastating losses to nematodes, especially *Meloidogyne* and *Heterodera* species.

The rapid growth in world population and expansion of global trade are making sustainable crop and pest management systems and related pest quarantines increasingly important. Although nematode reproduction and survival are dependent upon a suitable soil type, presence of a host plant, temperature, and soil moisture (117, 159), increased shipment of equipment and agricultural products will likely result in new infestations of diverse nematode species in many regions of the world. In the United States, federally mandated quarantines apparently have succeeded in restricting the spread of the potato cyst nematodes, *Globodera* spp., but were unsuccessful in limiting the dispersal of the soybean cyst nematode, *Heterodera glycines*. Currently, European Union members and other countries regulate various agricultural and forest products, including the importation of pine and other coniferous logs, chips, and sawn wood. The regulation on coniferous timber is to protect their forests from the insect-vectored pinewood nematode, *Bursaphelenchus xylophilus* (56).

SYNOPSIS OF STRATEGIES/TACTICS FOR NEMATODE MANAGEMENT

Historical

Early nematologists provided an exceptionally strong conceptual framework for the development of advanced, integrated pest management (IPM) systems for plant-parasitic nematodes. In 1889, Atkinson (6) discussed a range of tactics for nematode management that are surprisingly similar to those available today: sterilization of soil by starvation, including the use of nonhost plants, the potential of trap crops, compost, nematicides, and soil amendments such as hardwood ashes and potash. The early work of Cobb (37) on sampling nematode communities provided a basis for the development of improved tactics and strategies essential for integrated nematode-pest management. Tyler, in 1933, offered recommendations for monitoring root-knot nematodes as well as for their management (162); "A well-planned combination of practices will go much further for controlling nematodes than any of the recommended treatments alone." She further indicated that the presence of nematodes (root-knot) in any soil can be determined by examining the roots of susceptible plants that have been growing for at least 3 weeks in warm, moist conditions. For attempted eradication of root-knot nematodes, she suggested the following: (*a*) burning crop residues two or three times if possible, each preceded by a spading or plowing; (*b*) dry fallowing, frequent plowing; (*c*) one or more well-irrigated trap crops completely destroyed 2 or 3 weeks after sprouting; (*d*) moist fallow during warm weather, without weeds; (*e*) resistant crops in rotation, kept free of weeds; and (*f*) repetition of (*d*) and (*e*). Tyler (162) also emphasized that root-knot nematodes enhanced the susceptibility of crops to such other diseases as cotton wilt, black shank of tobacco, and Rhizoctonia disease of peanuts. These strategies/tactics were based, in part, on much earlier recommendations offered by Atkinson (6) in 1889 and Bessey (18) in 1911.

The specific concepts of integrated pest management (IPM) are a relatively recent development in pest control (19). The principles of IPM have been extensively reviewed (19, 54, 55, 172), and therefore are not discussed in detail here. Three key facets on which IPM is based include (*a*) determining how the biology of a pest must be modified to reduce its density; (*b*) combining current technology with biological knowledge to effect modifications; and (*c*) developing new or improved technologies for control that are compatible with economic circumstances and environmental requirements (54). Over the past two decades, IPM has been incorporated into low-input sustainable agriculture (LISA), alternative agriculture, integrated management or farming, and now sustainable agriculture (19, 21, 41, 57, 90, 186). [For discussion on currently available strategies and tactics for nematode management, related nematode-population and nematode-host response models, interested readers are referred to Duncan & Noling (54, 55).]

Strategies/Tactics

For an operational framework, IPM may be divided into several components: biological monitoring, environmental monitoring, decision-making, the decision-support system, the decision, procedure implementation, and the system (19). In this framework, primary strategies for nematode management include exclusion-avoidance, reduction of initial population numbers, suppression of nematode reproduction, and restriction of current and/or future crop damage (Table 1). Most of these strategies and tactics can be related to Vanderplank's (164) epidemiological parameters r (the reproductive rate of the pathogen or rate of disease increase) and x (the initial amount of disease or, in the case of nematodes, initial inoculum level or Pi).

Table 1 Relative efficacy of nematode- and crop-management strategies and tactics[a]

Strategy[b]	Tactic	Relative efficacy*
1. Exclusion-avoidance	Quarantine	M–H
2. Reduce initial population density	(a) Eliminate established foci	L–M
	(b) Cultural	
	Use of clean planting stock	H
	Crop rotation	L–H
	Inter- and intracropping	L–M
	Cover/trap crops (and antagonistic plants)	L–M
	Soil amendments	L–M
	Fallow or grass fallows (weed-free)	L–H
	Timing of planting/harvesting	L–M
	Farm hygiene and general culture	M–H
	Weed-host control	
	(c) Vertical resistance	H
	(d) Chemical nematicides[c]	
	Fumigants	M–H
	Nonfumigants	L–H
	(e) Biological	
	Natural	L–H
	Introduced, including engineered organisms	L–H
	Organic amendments	L–H
	(f) Physical	
	Tillage, including residual root destruction	L–M
	Heat, including solarization	L–M
	Flooding	L–M
3. Suppress nematode reproduction	(a) Resistance (Horizontal/quantitative)	L–M
	(b) Protection with supplemental chemical nematicides	L–M
	(c) Organic amendments	L–H
	(d) Biology-based crop production systems	M–H
4. Restrict current and/or future crop damage	(a) Tolerant cultivars	L–H
	(b) One or more of tactics under 1–3	M–H
	(c) Biology-based crop production systems (Bridge, 28)	—

[a] In part after Roberts (135); Bridge (28).
[b] Strategies 2 and 3 after Vanderplank (164).
[c] Chemical nematicides often result in high carry-over population densities.
*Abbreviations: L, low; M, moderate; H, high.

Most damage functions and much nematological literature on annual root crops focus on nematode Pi as the primary predictor of nematode damage. Perennial crops and some annual crops such as potato (132) or carrot (134) pose a greater challenge since nonchemical tactics to suppress the rate of reproduction or disease progress are not yet available. Most management tactics listed in Table 1 rely on reduction of initial population density (Pi). Tactics commonly used in intensive agriculture include cultural practices such as crop rotation and destruction of residual crop roots, resistant cultivars, and chemical soil treatments. Bridge (28) outlines and discusses four different strategies for specific nematodes and some other pests in sustainable and subsistence agricultural systems:

1. preventing the introduction and spread of nematodes by the use of nematode-free planting materials;
2. using nonchemical, cultural, and physical control methods, particularly crop rotation and soil cultivation;
3. encouraging naturally occurring biological control agents by understanding of cultivation methods and appropriate use of soil amendments;
4. maintaining or enhancing the biodiversity inherent in traditional farming systems that use multiple cropping and multiple cultivars to increase the available resistance or tolerance to nematodes.

These cultural and low-input techniques for nematode management can be employed by subsistence and small-scale farmers, but adapting some of them to intensive agriculture remains a challenge. As is discussed later, the development of new technologies and improved information on soil biology, including nematode diversity as related to nutrient cycling and soil health, should facilitate ecologically sound and more sustainable nematode–pest management in cropping systems that is applicable to intensive and traditional agriculture.

Integrated Pest-Crop Management

As indicated by Tyler (162), Bridge (28), and Roberts (135), the combination of two or more management tactics can provide highly effective nematode control. The more effective, inexpensive chemical soil treatments have been withdrawn from the market, and frequent usage has resulted in microbial decomposition of other nematicides (153). Furthermore, nematicide contamination of groundwater continues to be a major concern (38). Thus, greater attention is being paid to integrating available tactics and maximizing the potential of cropping systems while limiting nematicide use (120, 135). For example, the application of certain technologies was associated with greatly increased yields of peanut,

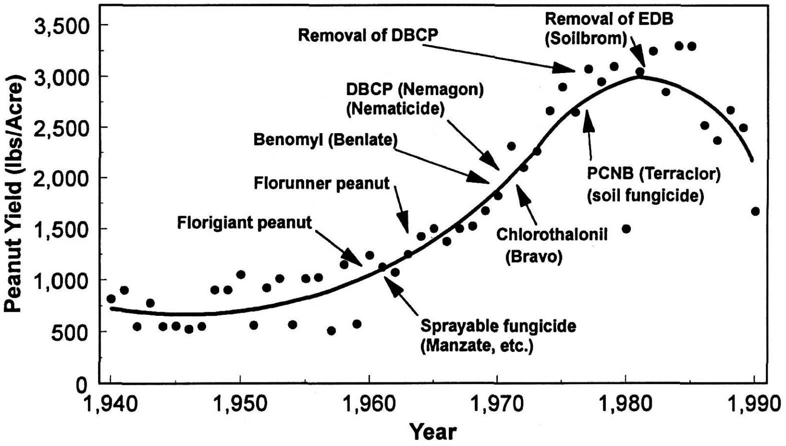

Figure 3 Peanut (*Arachis hypogaea*) yields in Alabama relative to changes in production practices during the past 50 years [after Rodríguez-Kábana & Cannullo (138)].

but the removal of dibromochloropropane (DBCP) and ethylene dibromide (EDB) fumigants is apparently related to recent lower yields in some regions (138) (Figure 3). Until recently, most IPM-nematology research has focused on nematode-population biology, host phenology, modeling, damage functions, and overall pest management decision-making (19, 54, 135). Progress in these areas has clearly facilitated the development of better management programs and has enhanced our understanding of nematode-host interactions. Nevertheless, the integration and assessment of combinations of potentially compatible nematode-management strategies and tactics have received much less attention, in large part because of excessive reliance on the use of nematicides and rotations, when practical, and resistant cultivars, where available (54).

Integrating compatible or complementary tactics, such as host resistance/tolerance and nematicides with biological control, should minimize potential problems associated with the loss of efficacy of specific nematicides or the appearance of nematode biotypes that attack resistant cultivars. Integration of nematode management may be considered at two levels, within nematology, and across pathogen/pest disciplines. Within the context of nematodes, Roberts (135) indicated that multiple management tactics may be applied over time, simultaneously, or both. The temporal approach focuses on season-to-season or year-to-year integration of tactics relevant to cropping cycles. The cycle of integration of tactics might focus on crop rotations within nonhost, resistant cultivars, or both, adding tactics such as nematicides, cultural practices, or biocontrol as they may be available. This approach could involve different control tactics or different crops for given years. The second approach described by Roberts (135) for integrating nematode-control components involves simultaneous use of two or more tactics, which of course requires compatibility among the tactics to be deployed. Finally, the deployment of combinations of tactics must be pragmatically evaluated at the regional and local levels. A tactic effective in one area may be impractical elsewhere or may be unsuitable if deployed regionally. For instance, nematicide usage may be restricted in some locales by soil type, organic amendments may have to be transported over prohibitively long distances, or markets for rotational crops may not be accessible.

Numerous examples of single- and multiple-pest/pathogen management successes can be cited (54, 55, 135). A combination of host resistance and tolerance, nematicides, and rotations involving resistant and susceptible potato crops with nonhost rotation between potatoes provided a successful integrated management program for the potato cyst nematode (135). A very different system focusing on host resistance, crop rotation, residual root destruction immediately after harvest, followed by seeding a cover crop, and an appropriate chemical soil treatment, where warranted, has proven highly effective for *Meloidogyne* species and certain fungi, bacteria, viruses, insects, and weeds on tobacco in North Carolina (111). This approach was successful for a high-value commodity like tobacco, whereas its potential utility and grower acceptance might be questionable for low-value crops such as cereals.

Roberts (135) also offered a theoretical but practical framework for integrating nematode management tactics that are only partially effective. Information would be needed on the damage threshold for target nematodes and the efficacy of specific integrated management tactics to determine how many of these types of treatments would be necessary to achieve satisfactory crop yields. For highly aggressive damaging nematode species such as *Meloidogyne arenaria* on peanut, many of these types of management tactics would likely be required to achieve an acceptable level of control. Clearly, more information on the potential interactions of available management tactics (whether antagonistic, synergistic or simply additive effects) is needed for nematode strategies and tactics to be successfully integrated.

SOIL BIOLOGY IN NEMATODE-CROP MANAGEMENT

Information emerging on soil biology, nematode diversity, the role of nematodes in nutrient cycling, the associated effects of microflora-microfauna on beneficial and plant-parasitic nematodes, and the impact of rhizobacteria in growth promotion and pest/pathogen suppression in various cropping systems has tremendous potential for facilitating development of new strategies and tactics for nematode management and sustainable production systems, as well as for improving the efficacy of currently available options.

Food Webs and Nutrient Cycling

Until recently, the attention of plant nematologists centered almost exclusively on plant-parasitic and entomophilic nematode species. Questions regarding sustainability of crop-production systems and related demands for alternative options for nematode management have impelled researchers into a more holistic approach to fundamental research on plant parasites (21, 27, 57, 62, 87, 108, 186). Research now ranges from characterizing the general diversity of nematode species in given habitats and cropping systems, the role of nematodes in nutrient cycling, to the genetic diversity of different species of plant-parasitic nematodes and other organisms on specific crops. The development of molecular markers for host resistance and nematode virulence (parasitism) genes, DNA probes, and genetically engineered host resistance, including characterizing and cloning genes of resistance, all enter into this picture of exciting research, with promise for new methods of nematode management in the future (32, 34, 39, 43, 52, 81, 122, 173, 174).

Traditionally, the strategies for nematode management in food and fiber crops focused on the exclusion, reduction of initial infestation densities of key plant-parasitic species, and/or suppression of the rate of reproduction. In recent years, however, the ecosystem framework being addressed in soil and plant health is being broadened to encompass all trophic groups of nematodes (plant parasites, bacterivores, fungivores, omnivores, and predators) (21, 63, 65, 176–178). In some instances, more than 100 species of nematodes coexist in specific soils (51, 93). Although measuring of nematode communities is useful in differentiating the effects of tillage, chemical inputs, and general environment (26, 118), difficulties may still be encountered in evaluating the ecological conditions of soils among regions, counties, or fields (116). New molecular techniques such as the arbitrarily-primed polymerase chain reaction (ap-PCR) now greatly facilitate the study of ecological interactions of unique nematode genotypes in soil habitats (93).

To understand, develop, and deploy sustainable nematode management, the scope of related studies must be extended beyond the interaction between plant-parasitic nematodes, their hosts, and the physical environment. For example, a typical soil food web (Figure 4) comprises the plant roots, plant-parasitic nematodes, other trophic groups of nematodes, and fungi, bacteria, mites, insects, amoebas, and earthworms (49). A recent study on the population dynamics in the below-ground food webs in a conventional versus an integrated agricultural system provided a very striking contrast of the biomass of various trophic groups. Nematodes constituted only 0.24% and 0.26% of the total biomass in

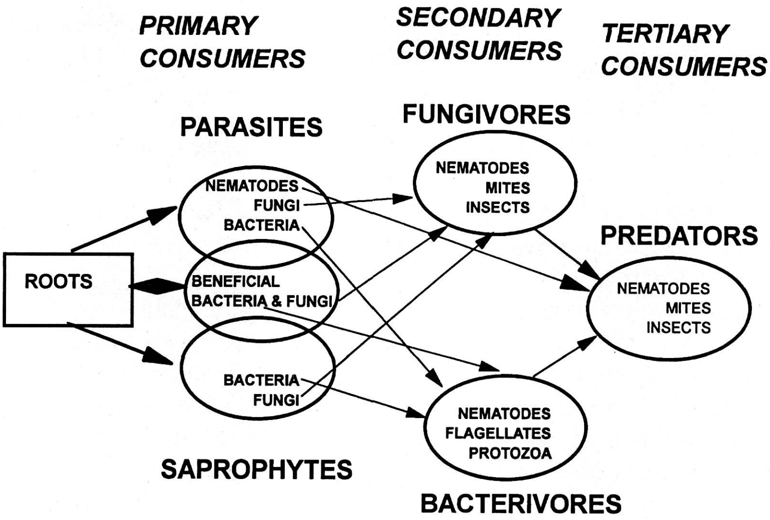

Figure 4 Diagram of various components of a typical soil food web.

the conventional and integrated systems, respectively (186). In contrast, the bacterial biomass constituted 94% and 75% of the total biomass in these systems, respectively. The bacterial biomass varied between 5 and 20 kg ha^{-1} cm^{-1}, whereas the fungal mass was much smaller and ranged from 0.025 to 0.4 kg ha^{-1} cm^{-1}. Protozoans constituted 4.9% and 5.9% of the biomass in the conventional and integrated systems, respectively. Earthworms were completely absent in the conventional system and constituted 17.6% of the total biomass in the integrated system.

Although nematodes constituted a relatively small portion of the soil biomass in that study, their importance in regulating the soil environment must not be underestimated (26, 103, 119, 177). The relative importance of various groups of organisms in the soil in regulating soil processes is a source of considerable debate (49, 69, 83, 186). Some researchers propose that protozoans are crucial in regulating bacterial populations (49), whereas others focus on nematodes (83, 166). The relative importance of a given group of organisms is likely related to soil properties and the plant type present. Bacterivorous nematodes are more capable of promptly migrating to given substrates than are protozoans (69, 73, 139), and thus may be more important bacterial grazers in coarse-textured soils. Nematodes are functional at more trophic levels than these other organisms (Figure 4) since they act as primary consumers (phytophagous), secondary consumers (bacteriophagous and myceliophagous), and tertiary consumers (omnivorous and predaceous). Bacterivorous nematodes made up 48% of the total nematode population in the conventional system versus 40% in the integrated system. Upon soil fumigation, bacterivorous nematodes decreased sharply but regained their initial population density by the following autumn (186). Repeated use of the fumigant methyl bromide, however, may kill most of the soil microflora and fauna (ER Ingham, personal communication).

Nematodes play an important role in the decomposition of organic matter and mineralization of plant nutrients, and they also constitute an important energy pathway from primary production and detritus to higher trophic groups (103). The primary decomposition of organic matter is effected by bacteria and fungi, which, in turn, are grazed upon by microbivorous nematodes and by protozoa and other organisms. Because these nematodes consume bacteria and assimilate more nitrogen than needed, the excess nitrogen is excreted as ammonia (101). It should be emphasized that nutrient cycling is a complex process involving many groups and species of fauna and microflora. Although nematodes are important consumers of bacteria, protozoa are much more efficient consumers (146). The relative importance of these two groups may vary with soil type in that protozoans tend to be more abundant in fine-textured soils, where nematode activities may be limited by pore size (139, 154).

Numerous comparative studies of conventional versus alternative or sustainable cropping systems in regard to pest control, crop productivity, soil structure, and soil processes are currently under way at various locations (57, 62, 186). Microbivorous nematodes, bacteria, and protozoans often reach very high biomasses in the period after harvest in conventional as well as alternative farming systems (186). Since all three groups of organisms are trophically directly related to each other and play a dominant role in nutrient mineralization, their high population densities after harvest may increase the risk of nitrogen leaching during such periods when no crops are present (49). However, increasing the abundance, biomass, and activity of bacterivorous nematodes in the spring in concert with incorporating organic matter (fall-previous season) could reduce nitrogen stress (62). The potentially detrimental effect of microbial nitrogen mineralization can be exploited by establishing appropriate cover crops that may also suppress or reduce the population densities of plant-parasitic nematodes. Compared to conventional farming, sustainable cropping systems (sometimes referred to as alternative management practices or integrated farming) should help resolve the problems of contamination of groundwater by nitrate and pesticides (186). Crop growth theoretically becomes more dependent on biological processes within the soil, including the mineralization and immobilization of nutrients.

Soil amendments such as animal wastes, including cattle slurry (123; R Bulluck et al, personal communication; KR Barker & SR Koenning, unpublished), result in rapid increases in microbivorous nematodes. This augmented nematode activity apparently stimulates N mineralization. In the absence of plants, mineralization increases NO_3^- concentrations in soil (123). Studies of the mineralization of C, N, and P in coniferous forest soils (146) underline the importance of mutual relationships among soil fauna in the decomposition processes. For example, the release of water-soluble N and P was lowest with bacteria-feeding nematodes alone. However, microbivorous nematodes may play a lesser role in the soil ecosystem than other groups, including earthworms, microarthopods, bacteria, and protozoa (57).

In a study of the effects of bacterivorous nematodes and the nematophagous fungi on carbon and nitrogen mineralization, Bouwman et al (27) found that the presence of nematodes enhanced carbon mineralization during the first month, then followed a decline. N mineralization was increased during the first two months and then also diminished. Nematodes affect carbon mineralization indirectly by their effect on bacterial activity, whereas N mineralization is apparently determined by nematodes mineralizing bacterial biomass (27). Because of different temperature optima, certain nematode species within a nematode community may be adapted to predominance at different times and/or soil depths. This overlapping of niches between species within a specific trophic level may determine their relative contribution to N mineralization (61, 165). Similarly, protozoans and nematodes likely occupy different microniches within the soil on temporal, physical, and spatial scales, because moisture availability and type of substrate cause shifts in bacterivore nematode communities (149).

Myceliophagous nematodes also may regulate mineralization in soils and may enhance nutrients available for plants (154). Fungi are efficient mineralizers themselves, and fungivorous nematodes may restrict the rate of fungal growth and hence mineralization (154). The relative ratios of fungivorous to bacterivorous nematodes and the change in this ratio over time may indicate whether a particular system is bacteria-based or fungus-based in decomposition (82). In one study, mycophagous nematodes were more abundant in conventional than in organic plots during periods of organic matter decomposition (62). Soil amendments often enhance rapid build-up of bacterivorous nematodes, and this is followed by a build-up of fungivores.

Emerging Soil-Biology Information as Related to Nematode Management

The relationships of various trophic groups of nematodes with a highly diverse fauna and microflora of soil are a recent object of study, whereas the concept of biological control of nematodes has long attracted the attention of researchers.

A wide range of nematode-trapping fungi, antagonistic bacteria, predaceous nematodes, and other soil fauna have great potential for suppressing the activity of plant-parasitic nematodes (151). Although progress in developing effective biological controls of plant-parasitic nematodes has been slow and, at best, incremental, basic information on the interaction of plant-parasitic nematodes and their antagonists has increased rapidly in recent years. The simplistic food web depicted in Figure 4 indicates only a few possible interactions. Nevertheless, more basic information about soil biology is required to successfully implement biological control of plant-parasitic nematodes (151). For example, predatory nematode species and predatory mites may depress microbivorous nematodes in addition to plant-parasitic nematodes (146). Although predaceous nematodes have received considerable attention, in-depth research on their potential in suppressing plant-parasitic nematodes has been limited. *Allodorylaimus americanus* and *Discolaimus silvicolus* proved to be active predators of *M. incognita* and other endoparasites, but failed to attack ectoparasitic species (88). Recent research has shown that enchytraeids may suppress nematode-parasitic fungi (84).

Certain bacterivorous nematodes may interact with rhizobacteria to enhance plant growth and yield. The bacterivorous nematode tentatively identified as *Diplogaster iheritieri* feeds and reproduces on a number of bacteria associated with the soil around potato roots (89). Three of these bacteria, *Leuconostoc mesenteroids* ss *cremoris*, *Pseudomonas fluorescens* type A, and an unidentified species, enhanced tuber development (dry weight per plant) by as much as two- to more than fourfold over untreated plants under laboratory conditions. *Bacillus cereus* strain S18 circumvented the negative effects of *M. incognita* on the growth of tomato (78). In the field, this bacterium enhanced tomato yields by 18% to 20% over a two-year field test that was free of *M. incognita.*

In a comprehensive study on the interactions of protozoa and the bacterivorous nematode *Pelliodditis pellio* and earthworms, Alphei et al (2) showed that the growth of the grass *Hordelymus europaeus* was increased by about 8% in the presence of the nematode and by some 21% by the presence of the protozoa. The nematodes and protozoa apparently enhanced plant growth by nonnutritional means, possibly as a result of increased bacterial activity in response to grazing pressure, whereas the earthworms increased nutrient availability for the grass. The highly diverse soil invertebrates are important in determining the suitability of given soils for sustainable production of crop plants (154). Nematodes regulate soil microbial populations both directly and indirectly, impacting soil health. While grazing/predation of microorganisms regulates population size, nematodes may also vector these organisms in the soil and thus maintain microbial composition and diversity. Fungivorous nematodes may keep plant-parasitic fungi such as *Rhizoctonia solani* in check (91).

A number of antagonistic plants and/or associated rhizobacteria show promise for suppressing plant-parasitic nematodes while enhancing plant growth (71, 77, 78, 92, 148). One hypothesis to explain how antagonistic plants limit crop damage caused by nematodes is via the direct effect of associated toxic compounds; an alternative explanation focuses on the indirect effects on nematodes via selecting for microorganisms detrimental to nematodes (92, 171). A strain of the fluorescent pseudomonad *Pseudomonas aureofaciens* inhibited *Criconemella* egg hatch and suppressed population densities of this nematode in the greenhouse (171). Kloepper and associates (92) showed that 4 to 6 times as many isolates of bacteria from antagonistic plants (velvet bean, castor bean, Abruzzi rye, or sward bean) restricted disease caused by *M. incognita* and *H. glycines* as compared to those from the test crop, soybean. Furthermore, the bacteria isolated from soybean were largely *Bacillus* spp., whereas those from antagonistic plants included very different taxa such as *Pseudomonas cepacia* and *P. gladioli*. The overall number of bacterial genera also was the lowest for soybean (two) and reached a high of 16 in sward bean. *Pseudomonas chlororaphis* may depress populations of *Pratylenchus penetrans* on strawberries and apple while stimulating the growth of some plants, including strawberries and raspberries (71). The rhizospheres of other legumes (*Crotalaria juncea* and *Vicia villosa*) enhance the population growth of certain bacterivorous nematodes, whereas those of other plants (*Tagetes patula*, *Eragrostis curvula*, *Sesamum indicum*) had no effect on the nematodes tested (166). Other studies on rhizobacteria that suppress plant-parasitic nematodes are summarized by Sikora and Hoffmann-Hergarten (78, 148). Proposed mechanisms of action for this suppression include production of metabolites that interfere with hatch and attraction and/or degradation of specific root exudates that control nematode behavior.

The vascicular-arbuscular mycorrhizal (VAM) fungi increase the capacity of plants to absorb phosphorus, other nutrients, and water. VAM fungi also may limit crop-yield losses to nematodes and other pathogens by improving the availability of phosphorus within the host and/or by antagonistic interactions with the pathogens (147). Inoculations of pigeonpea with *Glomus fasciculatum*, *Bradyrhizobium japonicum*, and/or *Bacillus subtilis* suppressed *Heterodera chajani* and *Fusarium udum* on this plant (147). The presence of the mycorrhizal fungus *Glomus* species may limit the damage caused by *Meloidogyne* species on some plants by increasing host tolerance (80).

One approach to exploit nematode antagonists is to develop highly efficient, mass production systems and application technologies suitable for modern agriculture (152). A second approach is the application of amendments that have inherent nematode-suppressive characteristics and that possibly enhance the activity of nematode antagonists. For example, neem extracts and residue cakes have considerable nematicidal activity (44). Clandosan, a chitin-urea formulation originally produced by Igene Biotechnology, Inc., Columbia, MD, was placed on the market as a biologically based nematicide a decade ago. Interest in soil amendments has been intense; over 220 publications were cited from 1982–1995 (44). While the combinations of soil amendments and improved delivery systems to introduce antagonists have given some encouraging results (112, 152), the goal of readily deployable biological controls of nematodes in a sustainable production system remains elusive. Adapting this technology to intensive systems is restricted by the huge amounts of material needed to effect reductions in nematode numbers. This barrier can be overcome by producing the mass of organic matter through the use of suitable cover crops.

Although attempts to develop axenic cultures of the obligate mesophilic parasite *Pasteuria penetrans* have been only partially successful, our understanding of its pathogenesis on nematodes, life cycle, and ecological requirements is much improved (35). For example, the surface of infective juveniles of *Meloidogyne incognita* apparently contain carbohydrate recognition domains, and these interact within N-acetylglucosamine moieties on the bacterial spore surface (47). Storage of this bacterium for 11 years resulted in decreased levels of infection, but did not affect its ability to attach to juveniles of *M. javanica* (67). *Pasteuria penetrans* also is moderately heat tolerant; preheating spores to 60°C enhances attachment but depresses infection (67). The narrow host-specificity of given strains of this bacterium, the population density–dependent nature of effective control, and often low degrees of parasitism on nematodes such as *Xiphinema diversicadatum* pose challenges (36, 152). Endotoxins from selected strains of *Bacillus thuringiensis* (BT) have been found to be nematicidal (102). The nematicidal effects of these toxins varied with the bacterial isolate examined; most endotoxins have no or little nematicidal activity. Nevertheless, BT-engineered insect-resistant plants could be developed that also suppress the activity of parasitic nematodes.

The challenge is to develop biocontrols as a component of sustainable crop production–nematode management systems that are adaptable for a wide range of crops. Certain nematophagous fungi, including *Verticillium clamydosporium* and *Nematophthora gynophila*, can provide sustainable nematode control in an intensive cropping system (87). In contrast, *Paecilomyces lilacinus* may provide considerable nematode control in soils with limited microflora, but this fungus may have little impact on nematodes in the presence of normal communities of soil microflora (141, 151). In one study involving 20 species of fungi, including *P. lilacinus*, only *Monacrosporium ellipsoporum* failed to provide significant control of *Meloidogyne incognita* on tomato at 60 days after inoculation (141). Many fungi grow slowly in natural soil, and this can be attributed to inherent competition in the highly diverse communities of soil microfauna and microflora. For a fungus to overcome the competition of resident soil microflora, it must produce a resistant resting stage that is rich in food sources (86). Also, a number of organisms, including mites and possibly mycophagous nematodes, may feed on mycelium of these fungi.

Nematodes as Bioindicators of Ecosystem Health

The abundance of soil organisms, particularly key species, has been proposed as a useful biological marker for ecosystem health (119, 154, 177). For a grass agroecosystem, total abundance of nematodes was positively related to productivity, in contrast to the usual inverse relationship of numbers of plant-parasitic nematodes to plant growth (177). In addition to abundance, other measures available for using invertebrates to assess soil quality include biomass, density, species richness, trophic/guild structure, food-web structure, keystone species, and ecosystem engineers (154).

An assay involving the survival and respiration rates of the bacterivorous nematode *Cruznema tipartitum* was useful in assessing the presence and concentration of biologically active toxicants (100). An assay provided a measure of toxicant activity at sublethal concentrations and determined when the toxicant had declined to concentrations no longer deleterious to physiological processes. Assays of soil contaminants based on nematode-community structure of resident-soil nematodes were more useful in undisturbed soils than in agricultural soils that had a relatively narrow range of taxa. A soil-toxicity test utilizing *Caenorhabditis elegans* promises rapid assessments of copper and other metals in soils (53). This nematode, however, is insensitive to toxicants such as pentachlorophenol (85). Also, a study of 12 nematodes showed them to be relatively insensitive to cadmium as compared to other invertebrates (85). Slow colonizers (*k*-strategists) were not more sensitive to cadmium and pentachlorophenol than opportunistic *r*-strategists. In general, carnivorous, omnivorous, and phytophagous nematodes are relatively sensitive to pentachlorophenol, whereas bacterivores and fungivores are tolerant. *Aphelenchus avenae*, a mycophagous nematode that often appears in high numbers after organic soil amendments, was tolerant to both compounds. A *Diplogasteritus* species was most sensitive to cadmium. In a study of pastures contaminated with timber preservatives (Cu, Cr, As), populations of nematodes, earthworms, and enchytraeids were depressed by these materials, but no single measurement was adequate to identify sites that needed remediation (178).

Over the long-term, adverse events such as acid rain may eliminate or reduce the beneficial predatory and omnivorous nematodes with or without significantly affecting the total number of nematodes (51, 140). Some plant parasites (*Paratylenchus* spp.) and fungivores (*Aphelenchoides* spp.) increased with the application of sulfuric acid. Acidification sometimes results in an increase in certain bacterivores [*Acrobeloides buetschlii* and *Wilsonema schuurmansstekhoveni* (140)].

A pilot project was initiated on an agroecosystem component for the US Environmental Monitoring and Assessment Program. Its purpose is to estimate the status of agroecological resources on a regional basis through the use of selected indicators (115). The distribution of nematode-trophic diversity between annual crops and perennial crops was found to be similar in a study by Neher & Campbell (115). These authors found significant differences between annual and perennial systems in maturity indices for phytophagous nematodes and in the ratio of fungivorous- to bacterivorous-feeding nematodes. This work indicated that perennial-crop sites may be the better suited as reference points using nematodes as biological indicators. As information is forthcoming on soil biology, combinations of bacterivorous nematodes and growth-promoting bacterial species could become diagnostic or keystone species to assess soil quality and health in sustainable nematode and crop management (119).

Nematode Interactions with Microorganisms, Insects, and Weeds

Until recent years, studies of interactions of nematodes in regard to crop management have focused largely on how plant-parasitic nematode species predispose plants to attack by associated fungi and bacteria or on their role as vectors of plant viruses and, in a few instances, bacteria. A wide range of weeds associated with agricultural crops often serve as excellent hosts for plant-parasitic nematodes such as the *Meloidogyne* species (15). In addition, the stunting of crop plants by plant-parasitic nematodes often increases associated weed problems and enhances insect activity in some instances. For example, moderate-to-high infestations of the soybean cyst nematode *Heterodera glycines* favor the development of a number of weeds and insects (3). Nematode and weed responses to various "set-aside" management regimes may differ (23). The use of a cover crop of ryegrass or ryegrass-clover may restrict subsequent weed problems but favor nematode build-up. Weeds, including natural weed banks, also may serve as an efficient reservoir for viruses that are often vectored by nematodes (156). Weed management is especially important for *Meloidogyne* species, which have very wide host ranges (15).

Sustainable nematode management must encompass the associated nematode-pathogen-parasite-pest complexes [for discussion of the many complex interactions between nematodes and other parasites/pests and their host plants, interested readers are referred to other articles (1, 29)]. Forthcoming new research and analytical procedures, including more crop cultivars with multiple-pest resistance and the "replacement series" (150), should contribute to this integrated management. Certain plant-parasitic nematodes such as *Heterodera glycines* may interfere with the beneficial relationships between symbionts and their host plants. Much of the damage by some races of *H. glycines* on soybean is directly related to the suppression of nodulation and associated N_2 fixation by the bacterium *Bradyrhizobium japonicum* (94).

Designing Ecology- and Soil Biology–Based Cropping Management Systems for Nematode Management

Traditionally, management of plant-parasitic nematodes has focused largely on these organisms, with related interest in the soil ecosystem limited primarily to associated pathogens and pests with which the nematodes might interact in restricting crop productivity. The concepts of integrated pest management broadened this operational framework to encompass all plant pests and an increased awareness of the need to avoid practices that might be detrimental to nontarget organisms (19, 172). Today's concept of a cropping system for managing nematodes is being expanded to include grass fallows, antagonistic plants and trap plants, cover crops that enhance the activity of beneficial soil fauna and flora, and shifts in the time for planting and/or harvesting of crops to limit nematode damage. Current research and deployment of sustainable and integrated crop/production systems are evolving to address the wide range of beneficial and detrimental soil fauna and flora (49, 57, 186). A number of research programs are now developing integrated cropping systems to enhance the activity of beneficial microflora and microfauna and suppress plant pests (57, 62, 186). For example, an integrated farming system with altered soil tillage, sowing techniques, fertilization, organic manure, and restricted pesticide applications resulted in greatly diminished populations of *Ditylenchus dipsaci* and *Heterodera avenae* (Figure 5) in cereals compared to those in conventional production systems (57).

Sustainable agroecosystems require cropping sequences and systems that incorporate desirable aspects of the subsistence agriculture from which they are partially derived. This statement implies that subsistence agriculture was both sustainable and stable, an issue recently addressed by Bridge (28). The ecological approach taken by many researchers in this context is to consider how pest populations are affected in natural, subsistence, and low-input systems. The philosophical focus on ecology has led to advances in the fields of botanical epidemiology (164, 184), integrated pest management (IPM) (19), and quantitative nematology (31, 60, 145). One key feature that contributes to regulation of populations is the apparent diversity inherent in natural ecosystems. A second feature is the appreciation that food webs rather than the more simplistic food chains are more common in nature, especially in the more complex (and thus more diverse) natural ecosystems (186).

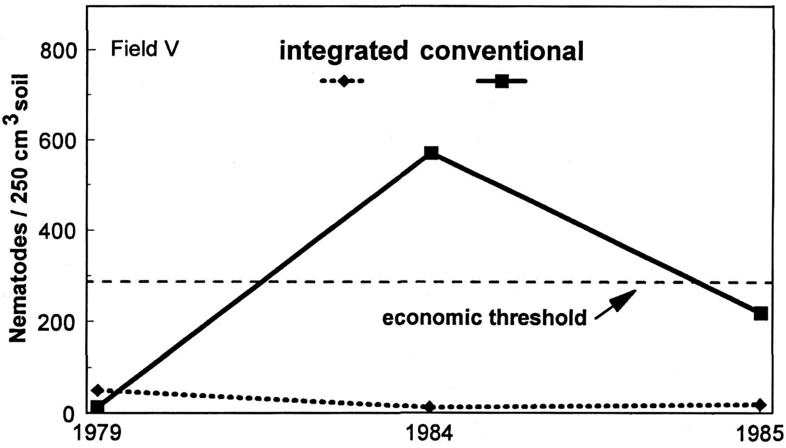

Figure 5 Incidence of infestation by *Heterodera avenae* in integrated and conventional systems expressed as the mean number of eggs + larvae per 250 cm^3 soil. Differences are highly significant, according to Wilcoxon test ($P = 96\%$) from 1984 onwards [after El Titi & Ipach (57)].

Inherent in the philosophy of IPM and the recently proposed Ecologically-Based Pest Management (EBPM) is the realization that some level of predation and/or parasitism is not only allowable but desirable, in that it promotes diversity and thus stability in our agroecosystems. Thus, an important aspect of designing sustainable cropping systems is the incorporation of diversity. Diversity may come in many forms—genetic, integration of plant and animal systems, crop rotation, and other cultural practices (28, 55, 125, 158, 183). Such diversity provides options, and thus opportunities, for managing nematode populations that are not available in simple less diverse systems. Diversity must be promoted and encouraged at every level of integration—from individual fields to local and regional levels and, in some instances, across international borders (184).

Future sustainable crop/nematode/pest management systems must therefore address general soil biology/health as well as specific threats from given pest groups such as plant-parasitic nematodes. Sequential cropping systems that include known nonhosts (Table 2) have been used in subsistence and traditional agriculture for centuries. One of the earliest cropping systems specifically designed for nematode management involved 6–8-year rotations and fallows to avoid low yields in the presence of potato cyst nematodes, *Globodera* spp. (28). The basic principle of crop rotation in nematode management has been the reduction of population densities of target nematode species to allow the subsequent production of an acceptable crop (121).