

Table 2 Partial list of selected nonhost plants useful in crop rotation

Nematode spp.	Nonhosts or hosts*	Nematode spp.	Nonhosts or hosts*	References
<i>Belonolaimus:</i>		<i>Meloidogyne:</i>		
<i>B. longicaudatus</i>	<i>Crotalaria</i> spp., <i>Crotalaria spectabilis</i> hairy indigo, marigold, tobacco	<i>M. chitwoodi</i>	Pea vine (<i>Lathyrus</i> spp.) sudangrass hybrids	68 113
<i>B. gracilis</i>	<i>Crotalaria</i> spp., tobacco, watermelon	<i>M. arenaria</i>	Bahia grass, joint vetch, velvetbean	
<i>Dolichodoros heterocephalus</i>	<i>Crotalaria spectabilis</i>	<i>M. javanica</i>	<i>Andropogon</i> , <i>Crotalaria</i> spp., cotton, peanut, sorghum, velvetbean	
<i>Helicotylenchus dihystrera</i>	Alfalfa, corn, fescue ^a	<i>M. hapla</i>	Corn, cotton, grasses, lettuce, onion, radish, sudangrass, wheat	
<i>Heterodera, Globodera:</i>		<i>M. incognita</i>	Fescue, orchard grass	
<i>H. glycines</i>	Bahia grass, corn, cotton, cowpea, potato, small grains, grains, tobacco, most vegetables	<i>Meloidogyne</i> spp.	<i>Crotalaria spectabilis</i> <i>Indigofera hirsuta</i> , millet, oats, wheat ^a	
<i>H. schachtii</i>	Alfalfa, bean, clover, corn, <i>Hesperis matronalis</i> , onion	<i>Paratrichodoros minor</i>	Corn ^a , <i>Crotalaria spectabilis</i>	
<i>H. zeae</i> ^b	Wide range of crops	<i>Pratylenchus:</i>		
<i>G. rostochiensis</i>	Corn, greenbeans, red clover	<i>P. leiocephalus</i>	Peanut	
<i>Hoplotaimus indicus</i>	Cabbage, chili, eggplant	<i>P. penetrans</i>	Alfalfa ^a , beet, fescue, marigold, oats, sudangrass, rye	
		<i>Pratylenchus</i> spp.	Lettuce, onion, radish	
		<i>Radopholus similis</i>	<i>Crotalaria spectabilis</i> , most grasses	
		<i>Rotylenchulus reniformis</i>	Rhodes grass, Pangolagrass, marigolds	33
		<i>Tylenchorhynchus:</i>		
		<i>T. mirzal</i>	Wheat	
		<i>T. brassicae</i>	Potato, tomato	
		<i>Xiphinema americanum</i>	Alfalfa ^a , corn ^a , fescue ^a , tobacco	

^aPrimarily after Trivedi & Barker (158) (See this article for specific references per nematode/crop combination).

^bHost range needs further study.

*Some populations of respective nematode species will reproduce rapidly on crop plants so identified.

Crop rotation provides for diversity in time and space and is often the preferred means for nematode management. Rotation, however, may be of limited value when several damaging species of nematodes are present or for species with broad host ranges. For growers to accept rotation as a viable tool for nematode management, suitable crops and land must be available. The rotational crop must offer the grower an acceptable return, with similar requirements for labor and equipment. The need to rotate specific crops, however, may vary with location. For example, corn can be grown continuously in some regions with little or no effect on yield (185), whereas the parasitic nematodes predominant in the southeastern United States cause significant yield losses on this crop (124). The highly successful practice of rotating tobacco with fescue (nonhost for *Meloidogyne* spp.) has been in place in the southeastern United States for some five decades (121). Periodic incorporation of the dense grass sod improves the soil structure, increases water-holding capacity, and provides control of associated root diseases including root-knot in the primary crop. Other grass fallows that have proven useful in the management of nematodes, especially *Meloidogyne* spp., include bahiagrass (*Paspalum notatum*), bermudagrass (*Cynodon dactylon*), weeping lovegrass (*Eragrostis curvula*), Rhodes grass (*Chloris gayana*), Pangolagrass (*Digitaria decumbens*), and Guinea grass (*Panicum maximum*) (28, 137, 138). Any significant development of broadleaf weeds in these grass fallows can negate their effects in the control of root-knot nematodes because many are hosts for these pathogens (15, 28). The economic viability of grass or pasture is enhanced when animals are included in the system. An important factor is that many grasses and cereal crops may also support reproduction of many plant-parasitic nematodes, including *Meloidogyne* spp.

Many potential rotations or green manure crops that show promise in nematode management may be antagonistic to some nematode species or even serve as trap crops (92, 95, 138, 158). These plants may be categorized as being either active or passive, depending on whether they produce some antihelminthic compounds or are simply unsuitable hosts for nematodes. Selected *Brassica* species, including rapeseed and mustard, may suppress nematode populations, soilborne pathogens, and weeds in crop rotations (72, 95). These plants produce glucosinolates, and their decomposition products are toxic to nematodes. Nematode-resistant radish is very effective in suppressing *Heterodera schachtii* on sugar beet (95). In contrast, rapeseed is stunted and supports reproduction of *M. arenaria* (KR Barker, unpublished). Some antagonistic (or active) plants, including *Crotalaria* spp., mustard, African marigold, asparagus, castor, and sesame, may be grown as commercial crops, used as cover crops, or established in mixed planting with other crops (28, 138). Caution is needed in selecting from these or other antagonistic plants for cropping

systems in case they contain negative features or hazards in addition to providing nematode control. For example, some of the *Crotalaria* species serve as excellent trap crops for root-knot nematodes, but they also synthesize potent toxins that cause primary tumors or suppress growth of swine, cattle, and poultry. Although the African marigold *Tagetes erecta* and other *Tagetes* spp. may provide effective nematode control under some conditions, the efficacy of the primary nematicidal component (α -terthienyl) is dependent on light activation (9).

The utilization of certain Sudangrass hybrids as a green manure provides excellent control of *Meloidogyne chitwoodi* on potato (113). Sorghum-Sudangrass hybrids also suppress this pathogen, but these plants may contain a higher concentration of dhurrin, a toxin for cattle when these plants are grazed improperly. In addition, the antagonism of these plants may be limited to certain nematode genera or species, e.g. the lesion nematode *Pratylenchus penetrans* is affected little by the use of these plants as green manure crops (106).

Earlier work on a selective nematicidal component in decomposing rye residues indicated that nematodes may have differential sensitivity to these products (144). In that work, *Meloidogyne incognita* proved to be the most sensitive to the associated decomposition products, *P. penetrans* exhibited intermediate sensitivity, whereas microbivorous nematodes were quite tolerant. Thus, lesion nematodes and the bacterivores probably have developed tolerance to decomposition products, whereas sedentary endoparasites would likely be more sensitive. Butyric acid produced by *Clostridium butyricum* was identified as one of the major toxic components in the decomposing rye (144). However, other compounds may be even more important since only limited amounts of butyric acid were detected in leachates from pots with decaying rye (RG McBride, unpublished). Rye as a cover crop has both negative and positive aspects. Although highly effective against *Meloidogyne incognita* on cotton, it is much less efficacious against the Columbia lance nematode, *Hoplolaimus columbus* (KR Barker & SR Koenning, unpublished). The impact of rye on the reniform nematode, *Rotylenchulus reniformis*, was likely related to suppression of dicotyledonous winter weeds (KR Barker & SR Koenning, unpublished). In addition, the timing of its incorporation in soil before the establishment of some crops, particularly cotton, is important in that the decomposition products may prevent the normal germination of cotton seeds.

Other legumes including selected clovers, velvetbean, joint vetch, and Cahaba white vetch provide multifaceted contributions to soil health and crop productivity when used in rotation as green manure cover crops. For example, the use of velvet bean *Mucuna deeringiana* in a soybean rotation enhances the activity of rhizosphere bacteria antagonistic to the soybean cyst nematode, *H. glycines*, and the southern root-knot nematode, *M. incognita* (92).

In addition to suppressing nematodes, certain plant-growth-promoting rhizobacteria may induce systemic resistance to foliage pathogens such as *Pseudomonas syringae* pv. *lacrymans* and *Colletotrichum orbiculare* on cucumber (170). Wei et al (170) suggested that these rhizobacteria may control a spectrum of plant pathogens/pests, including fungi, bacteria, nematodes, and insects. In a split-root system, treatments with *Bacillus sphaericus* B43 or *Agrobacterium radiobacter* G12 also induced a significant degree of resistance in potato to *Globodera pallida* (77). These rhizobacteria suppressed infection of potato roots by the juveniles, but had no effect on egg production.

The use of resistant cultivars, where applicable, is the preferred and most economical means of managing damaging species of nematodes (134, 136, 160, 182). With few exceptions, available nematode-resistant cultivars, as summarized by Young (182), are limited to nematodes (*Meloidogyne*, *Heterodera*, *Globodera*, *Tylenchulus*, *Rotylenchulus* spp.) that induce the development of feeding cells in their hosts. Exceptions include *Ditylenchus dipsaci* on alfalfa and clover, *Xiphinema index* on grape (46), and *Radopholus similis* on banana (107) and citrus (DT Kaplan, personal communication). Although host resistance is an environmentally friendly means of nematode management (46), resistance genes may be considered as a natural resource to be preserved. In fact, resistance has proved to be only a temporary solution, particularly in the case of *r* genes used to manage the amphimictic cyst nematodes (182). Thus, cropping systems must be designed to protect the durability of resistant cultivars (4, 5, 133, 181). These *r* genes should be introduced into agroecosystems in concert with other management measures to prevent or delay the emergence of biotypes that circumvent the resistance mechanisms. Temporal and spatial deployment of resistance genes to *H. glycines* and *H. avenae* has been evaluated (4, 5, 133, 181). For example, continuous use of *H. avenae*-resistant cereal cultivars may negatively affect their resistance while allowing the lesion nematode *Pratylenchus neglectus* to increase to damaging densities (133). Although the durability of host resistance to parthenogenetically reproducing nematodes may be affected less than with amphimictic species, monoculture of *M. incognita*-resistant cultivars may still result in the appearance of resistance-breaking host races or other species of root-knot nematodes (11, 46, 163, 174). The origin and type of host resistance as well as the reproductive biology of the target nematodes should be considered in addressing the durability of resistance genes (20).

Combinations of management tactics for nematodes such as the potato cyst nematodes (*Globodera* spp.) often rely on rotation, nematicides with or without tolerant cultivars, and/or resistant cultivars (40, 87). Although sources of tolerance to a few other nematodes such as the soybean cyst and Columbia lance nematodes have been identified (25, 70), attempts to incorporate tolerance to nematodes in other crops have encountered only limited success. Dalmasso

et al (46) concluded that tolerance to nematodes is an advantageous character only when linked to active resistance. If used without resistance, it leads to increased nematode population densities and thereby could be a disadvantage. Nevertheless, in perennials such as ornamentals, the only practical management option is to replace highly susceptible plants with tolerant plants (17).

Another potential nematode-management strategy involves adjusting the schedules for susceptible crop production to limit nematode reproduction. For example, delayed planting of soybean, which occurs in wheat-soybean double-cropping systems, allows for greater nematode attrition in the absence of a host and results in lower at-planting population densities of *Pratylenchus brachyurus* and *H. glycines* (96, 99). The wheat-soybean double-cropping system was shown to be economically superior to a rotation with grain sorghum in Arkansas (50). This practice may give variable results over time and region (74) and is not well adapted to northerly latitudes where the length of the soybean growing season is limited. This approach also has been tried for root-knot nematode in carrot. Shifts in the planting and harvest dates of carrot to minimize root-knot development caused by *M. incognita* have produced striking results (135). Delaying planting to late autumn or early winter clearly restricts root-gall development on carrot. Although the efficacy of this management strategy increases with lateness of planting, some root galling and crop loss occurred even with the best treatments. Thus, this management strategy should be used in concert with available, compatible tactics (134). In some regions, early harvest of peanut is critical to limiting damage to seeds by *Ditylenchus africanus* (167). Although approaches that limit infection by either promoting greater nematode attrition or limiting infection due to physical constraints such as temperature/planting time are useful in some nematode-host interactions, they have not been effective in limiting damage of *Hoplolaimus columbus* to cotton or soybean (SR Koenning, unpublished; 127).

Many crops vary phenotypically for physiological maturity, a factor that can be exploited to suppress final nematode population densities. Soybean cultivars, for example, are classified by maturity groups that range from 000 to IX; each group is separated by 1 to 2 weeks. Late-maturing cultivars support greater reproduction of *H. glycines* in North Carolina (76). The use of early-maturing cultivars suppresses nematode-population increase and benefits succeeding crops (98). Many other cultivated plants including cotton, corn and small grains differ in maturity, and this technique may have wider applicability.

Various types of soil tillage may have different effects on nematodes. The "plowing out" of the residual roots of *Meloidogyne* hosts after the final harvest of tomato, tobacco, or other perennial-type crops is a long-established practice dating back for 100 years (6, 18). This single practice can reduce surviving *Meloidogyne* populations by 90% or more compared to allowing residual roots to grow (13). For total nematode and soil fauna-flora abundance, the issue of

tillage is more complex. Soil tillage also affects beneficial soil organisms, as well as suppressing undesirable plant (weed) species and improving plant-root growth, the primary reasons for this practice. Improved chemical control of weeds and the development of implements capable of ensuring good seed-to-soil contact have resulted in a wide variety of types of plant culture defined as no-till or minimum-till systems. These systems, often referred to collectively as conservation tillage, that eliminate or reduce tillage have become common in many regions because of government mandate, and also result in economy of time and equipment (129).

Although tillage has long been an important tool in suppressing certain diseases and problems associated with plant-parasitic nematodes, numerous benefits may accrue from conservation tillage systems. Typically, conservation tillage results in increased soil organic matter, with more residue on the soil surface, improved soil structure, and infiltration of water (48). Potentially negative effects of reduced tillage include less mixing of soil nutrients, increased soil strength with associated higher soil bulk density, lower yields for some crops, and greater reliance on herbicides. Secondary effects of changing tillage practices may include changes in the weed spectrum, the use of cover crops, and alterations in other cultural practices. Depending on the type of implements used, nematicide applications may be limited in these systems. Changes in soil biota, including nematodes, effected in agroecosystems by different tillage practices have been documented (79, 126). Earthworms, in particular, tend to increase in numbers when tillage is limited (57, 79), and they are considered a major factor related to improved soil structure. Increases in soil organic matter where tillage is reduced generally are reflected in higher numbers of bacterivorous and fungivorous nematodes (65). Although the available data are diverse and sometimes contradictory, the impact of tillage, or the lack thereof, is likely related to different soil type/genesis, texture, the organisms studied, and climate.

Research in the United States' eastern coastal plain has shown minimal effects of short-term tillage practices on plant-parasitic nematodes (66, 109). Thomas (157) found higher population densities of plant-parasitic nematodes associated with corn in no-till versus conventional till in Iowa. In contrast, population densities of *H. glycines* were suppressed by conservation tillage (97, 161). Several years of continuous no-till were required before suppression of *H. glycines* was measurable, however. Apparent discrepancies about the impact of tillage on nematode communities may be related to the length of time a portion of crop land has been subjected to minimum tillage (126). Several reasons for suppression of *H. glycines* in conservation tillage have been postulated, including the impact of the cover crop (8, 74), or increases in bulk density of the soil that may have restricted aeration (97, 180).

Wardle and associates (169) found that cultivation for weed control was an important factor influencing the species diversity of the nematode community.

Increased numbers of fungivorous nematodes were found in one study in Georgia in reduced tillage plots compared to conventional tillage (126) during the summer, but the reverse was true at other times of year. Similarly, higher numbers of the plant parasite *Helicotylenchus dihystrera*, *Tylenchus*, and *Aphelenchoides* spp. and dorylamids and mononchidae were associated with conventional till systems in North Carolina (105). Numbers of bacterial feeding and total nematode numbers were greatest in a no-till system in Spain (104). However, Freckman & Ettema (65) found only small differences in total nematode abundance related to tillage; the trophic diversity was increased, and the ratio of fungivores to bacterivores was decreased in no-till compared to conventional tillage practices. The ratio of fungivores to bacterivores can be regarded as an indicator of the decomposition pathway in detrital food webs (65). The decrease in this ratio associated with no-till may indicate a shift from a bacteria-based food web to a fungus-based food web.

More comprehensive integrated management farming systems that include more restricted tillage, fertilization, pesticide use, the addition of organic manure, and undersowing with clover greatly alter the soil fauna and microflora (57). For example, the numbers and biomass of earthworms were six times greater in the integrated plot with limited tillage than in the conventionally managed plot. Predatory mites and microbivorous nematodes (bacterivores and fungivores) also are often greatly increased through this type of integrated management (57). Population densities of *Heterodera avenae* and *Ditylenchus dipsaci* were lower in integrated systems with minimal tillage than in conventional systems with standard tillage practices (57).

Unfortunately, many new technologies used in intensive production systems may result in loss of stability in agriculture (183). Zadoks (183) identified several developments contributing to this loss of stability; these include increase in field aggregation, larger field size, increase in plant density, increase in genetic uniformity-crop level, greater farmer specialization (loss of rotation), increased mechanization, increase in international exchange of seed and planting stock, and plant breeding. Thus, it is critical to assess the sustainability of nematode-crop production systems as more complex and larger production systems emerge.

To assess the sustainability of crop-pest production systems, key biophysical and socioeconomic factors must be monitored in measurable terms (110). Proposed characteristics for monitoring the agroecological sustainability of production systems and the respective level and time frame of processes encompass the following:

1. nutrient balance sheet (farm and regional level: 5–10 years);
2. vegetation cover and species composition (farm and regional level: >5 years);

3. water infiltration run-off (farm and regional level: >3 years);
4. replenishment and use of fossil water (regional level: 5–10 years);
5. characteristic in relation to biotic environment economic threshold (farm level: <1 year);
6. pest complex and type of outbreak (farm and regional level: >5 years);
7. host-plant resistance (regional level: >3 years);
8. pest resistance against pesticides (regional level: >5 years);
9. biological control agents (crop, farm, and regional levels: <1 year); and
10. pesticide use (crop, farm, and regional level: >1 year).

Economic viability and soil-fauna-flora diversity could also be added to this list. Although these factors and processes are beyond the scope of this review, their magnitude reflects the huge requirements in developing sustainable crop-pest-nematode production systems.

NEW TECHNOLOGIES AND NEMATODE MANAGEMENT

As sustainable nematode management becomes increasingly based on soil biology–health, new complementary technologies are developing. These new tools undoubtedly will improve the accuracy of nematode diagnoses and assessments of potential problems, and will result in more effective management, reduced pesticides, pesticide usage, and less contamination of groundwater with agricultural chemicals such as nematicides, nitrogen, and fertilizers.

Precision Agriculture

Modern computerized harvest-management and data systems offer new opportunities for more precise management of nematodes and general crop production. This technology has the potential to improve water use and limit fertilizer and pesticide application on a spatial and temporal basis as dictated by soil fertility and, more important, differential spatial crop yields (45, 59). Based on early results, this management tool should allow specially prescribed nematode control in high-intensive crop production such as *Radopholus similis* on banana (DH Marin-Vargas, personal communication) and root-knot nematodes on potato in the northwestern United States (59). Approaches that focus on a harvest index to locate environmental stress (42) should be able to relate nematode kinds and numbers to poor yield and other stress factors. This

approach is now being used in some banana operations in which fruit is harvested in small subunits and yield data are recorded and analyzed by computer (DH Marin-Vargas, personal communication). Poor-yielding sections can be examined for nematode densities and other potential problems.

Nematode Identifications and Population Assessments

The tools of rDNA technology, especially when allied with traditional taxonomic characters and host differentials, have greatly facilitated identification of nematode species and often host race (12, 34, 58, 64, 81). Isolated specimens of a range of nematode species have been identified by differential isozyme pattern and/or specific DNA probes, and there has been some progress in identifying and quantifying nematodes from processed soil samples (43).

Continuing restrictions in the size of samples and numbers of nematodes that can be examined make it very difficult to fully diagnose the nematode species present in large fields. However, this new technology should facilitate a more complete characterization of the diverse nematode trophic groups and species that are affected by disturbance and management practices in various ecosystems (93). The availability of mobile soil-samplers, especially when used in precision production systems (175), could facilitate more directed, selective sampling for general nematode assays and identifications (10). Geostatistical analyses could be interfaced with these improved sampling apparatus for more precise measurement of data on nematode population (168). Image analysis has been adapted to count specific nematodes, but differentiating species with computers currently available would be too time-consuming (14).

Genetically Engineered and Traditional Host Resistance

Although almost 100 years elapsed between the appearance of Mendel's rules and the initial discoveries in molecular biology, dramatic progress in the latter area has occurred during the last 30 years (128). The increasing complexity and costs of genetic engineering of plants for pest resistance or altering biocontrol agents make it unlikely that significant economic repercussions of molecular biology will be felt on agricultural production in the near future (128). There has been considerable progress made in engineering host resistance to nematodes, genetic mapping, and diagnostics (32, 34, 122, 174). However, genetically engineered resistance to nematodes is still at the developmental stage in contrast to the recently deployed herbicide- and insect-resistant cultivars of cotton, soybean, and other crops. One strategy involves transformation of plants with a transgene(s) encoding a product detrimental to the target nematode or that suppresses the expression of key plant genes involved in the nematode-host interaction (122, 174). Candidate genes for this strategy include collagenase, genes expressed in the development of specialized feeding cells induced by

species of *Globodera* or *Heterodera* (syncytia) and *Meloidogyne* (giant cells). Constructs of the root-specific *TobRB7* gene in tobacco have been used to develop promising root-knot nematode-resistant genotypes (122). Linking this gene with a BARNASE gene resulted in root knot-resistant plants, but difficulties were encountered in recovering resistant lines from progeny of the transformants. Transformed plants with an antisense *TobRB7* construct also exhibited root-knot resistance; root-gall development was about 70% less in than susceptible plants (122).

A second approach for engineering nematode-resistant plants involves identifying, cloning, and introducing natural plant-resistance genes into susceptible crop plants. Exciting results with this strategy were recently reported with *Heterodera schachtii* on sugar beet (32). In one major development, Cai et al (32) cloned the cyst-resistant gene in wild *Beta* species. A transformed, normally susceptible sugar beet line exhibited the typical incompatible resistant reaction. Similar progress is being made with the *Mi* gene, which confers resistance to the common *Meloidogyne* species and populations attacking tomato (VM Williamson, personal communication; see pp. 277–293). With the wide host range of these nematodes, the transfer of the *Mi* gene to numerous crop species, for which root-knot nematodes affect major crop yields, has great economic promise. Because populations of *M. incognita* may overcome this resistance, much care is needed in developing cropping systems to prolong the durability of this resource in a wider range of genetically engineered resistant crops.

New molecular techniques and markers also have positively affected traditional plant-breeding programs related to the development of host-resistance to nematodes. Recently, two markers for parasitism in *H. glycines* were identified (52) and molecular markers for crop resistance for various cyst nematodes are being investigated. These resistance markers included soybean (*H. glycines*) (41), potato (*G. rostochiensis*) (131), and wheat (*H. avenae*) (173). Markers for *M. incognita* races 1 and 3 resistance in tobacco also have been described (179). Undoubtedly, combining markers for parasitism (virulence) within different nematode populations and host-resistance genes should spur advances through traditional plant breeding.

Advisory Programs

Despite the development of nematode advisory programs in some states in the United States in the 1960s and earlier elsewhere (13), low-cost, highly effective nematicides remained in use as a form of insurance until recently. The unreliability of nematode assays, due to difficulties in sampling the contagious infestations, identification of related species, and lack of information on economic thresholds helped to prolong nematicide use. Nevertheless, advisory

programs have successfully contributed to lower pesticide usage and greater farm profits. For peanut alone, growers in Virginia were able to reduce their nematicide use by 35% after a predictive nematode assay program was established (130). Savings in production costs for 1989 were estimated at \$800,000, primarily through fewer nematicide applications. Currently, about one half of the states in the United States offer their farmers some type of nematode advisory program, usually through the Extension Service, State Departments of Agriculture, or private consultants. Many growers monitor the relative magnitude of nematode problems in given fields by observing root symptoms and signs of nematodes and through field histories.

The use of hazard indices in lieu of damage or economic thresholds has promoted better communication to growers on the relative nematode-damage potential for annual crops in given fields (13). These hazard indices are based on the relative damage potential of the nematode species/races present, their population densities, the cropping history, and soil type.

Where detailed data on production and nematode populations are maintained, more precise approaches in decision-making are becoming available. Burt & Ferris (31) developed a sequential decision rule to aid in choosing a rotation crop versus host crop where this practice is the management tactic rather than using a nematicide. The static model used by Ferris (60) is unsuitable for quantifying the optimal dynamic threshold that would be characterized by population densities lower than where returns from the nematode host and nonhost are equal. A dynamic model for this type of crop-nematode management system was recently developed (31). Application of this model should allow better economic management of nematodes, but data will still be needed on annual nematode population change under host and nonhost crops and the relationships between nematode numbers and crop yields. More comprehensive pest-host simulators and expert systems (142) have bolstered research in recent years (108).

Management of nematodes, including advisory programs, poses greater challenges for perennial crops than for annual crops. Control options are limited, and very low population densities often build up to cause severe damage over time. Integrated management, including assays to determine numbers and kinds of nematodes present, and appropriate control tactics such as preplant fumigation where necessary, use of nematode-free stock, tolerant cultivars where available, and organic mulches are useful for woody ornamentals (17).

CONCLUSIONS

New approaches to nematode control hold great promise for sustainable, integrated crop-pest-management systems. Rapidly evolving knowledge and understanding of soil biology and crop molecular biology can be exploited in

highly productive, intensive cropping systems. The challenge is to develop primary cover-crop, animal-waste, tillage systems that result in the build-up of favorable rhizobacteria, fungi, nematodes, protozoa, earthworms, and other fauna while also suppressing plant-parasitic nematodes and other crop pathogens. Combining this new, integrated soil biology-based nematode-pest-crop management with traditional and/or genetically engineered host resistance and cultural practices such as rotation should reduce the need for pesticides. However, Kiraly (90) concluded that worldwide the area dedicated to crop production is unlikely to expand during the next two decades; on the contrary, there is a continuous and substantial decline in grain-producing area per person. Thus, food production per hectare must be increased. The data in Figure 1 may indicate that considerable opportunities for this exist in many countries.

Avery (7) claimed that widespread use of pesticides and plastics must be employed in intensive agriculture to “save the planet.” Although this is an obvious overstatement, the use of pesticides in agriculture has indeed been critical to large-scale production of inexpensive, high-quality fruits and vegetables for human consumption (90). However, we need to weigh the negative effects of use of pesticides and excessive tillage on soil organisms (110). Concepts for measuring the impact of given practices on sustainability versus instability are emerging (110, 183), but they remain to be widely adopted.

Exciting new technologies for crop-pest management are on the horizon at the same time as new challenges are emerging. In today’s global marketplace, any incident involving international shipment of produce contaminated with a nematocidal or other pesticide generally elicits a reaction that often has no bearing on or recognition of the importance of these products in food production (90). This problem is even greater if pests “accompany” the produce. Introduction of new crops or even transplants of current crops into an area could well lead to the establishment of new nematode species (117). The risks of introducing key nematodes such as *Bursaphelenchus xylophilus* greatly restricts international shipment of some products (56). Based on analyses by the CLIMEX computer program (22), the European virus-vectoring nematode, *Xiphinema diversicaudatum*, could become established in North America, Australia, New Zealand, and parts of Asia. Hence, quarantine restrictions on movement of plants and soil will likely become more stringent in the face of expanding international trade and global climate warming. Molecular diagnostics should increase the reliability of such nematode-regulatory programs (155).

The predicted global climate warming is being debated as sustainable nematode and crop management strategies and tactics are under development. For example, an increase of only 1°C could enable the ectoparasite *Longidorus caespiticola* to become established in all of England and most of Scotland (24). Currently, the most damaging of nematodes, *Meloidogyne* spp., generally are

favored by warm to tropical conditions (160). Will warming in many countries, including the United States, be sufficient to effect the spread of the highly aggressive root-knot species *Meloidogyne javanica* and *M. arenaria* into regions presently unsuitable for these pathogens? Such a development would require new initiatives in the development of durable heat-tolerant nematode resistance in most crop plants and shifts in crop cultivars.

In conclusion, the development of sustainable nematode-management systems is not an option. It is imperative that scientists devise the requisite sustainable tactics as one component of the world's complex food-fiber production system to meet the pressure of the rapid population increase. Management of plant-parasitic nematodes is essential to sustainability, since impaired efficiency of plants' water and nutrient utilization caused by these pathogens limits production and degrades the environment. The proposed strategy of increased use of pesticides and plastics to meet this challenge (7) would likely provide only short-term benefits. For example, the repeated heavy use of chemicals such as methyl bromide essentially sterilizes the soil and eliminates beneficial soil microflora and fauna as well. Many other current crop- and pest-management practices also contribute to the instability of our food production (83). Fortunately, the new technologies forthcoming from molecular and soil biology and truly integrated cropping-nematode-pest management systems are providing new strategies and tactics that can be linked to traditional nematode management for more general integrated and sustainable food and fiber production. In fact, the wide gaps between and within developing and developed countries (Figure 1) indicate that global food production still can be increased.

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