The role of weeds in nematode management

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Symposium

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Weeds are alternative hosts for plant-parasitic nematodes and have long been recognized for their ability to maintain nematode populations targeted for suppression by various management strategies. The impact of weeds as alternative hosts depends largely on nematode feeding behavior, which is determined by the level of host specialization required for the parasite to feed successfully. In general, the more specialized feeding adaptations are associated with greater crop damage, more diverse nematode management options, and greater negative impact from weeds. Besides serving as alternative hosts, certain weeds can protect nematodes from pesticides and the environment, provide nematode suppression through antagonism, contribute to changes in future nematode biotic potential, or exert indirect effects through competition with crops or by the effects of weed control strategies on nematode populations. Shrinking nematicide options and increasing environmental concerns are making integrated pest management (IPM) a necessity for nematode management in many crops. A prominent similarity between most major weeds and plant-parasitic nematodes is that both are place-bound organisms that are passively dispersed. Weed–nematode interactions in agricultural production systems may be more intricate and complex than the simple function of weeds as alternative hosts. Their relationship may represent a normal adaptation resulting from the limited mobility of both groups of organisms and the obligate parasitism of phytophagous nematodes. The challenge that faces weed scientists and nematologists is to identify effective, compatible IPM strategies that address weed and nematode management collectively.

Key words: Alternative hosts, host–parasite interactions, integrated pest management, plant-parasitic nematodes.

Weeds nearly always interfere with management practices for plant-parasitic nematodes. Over the past two decades as the number of nematicides has decreased, crop losses from plant-parasitic nematodes have increased (Koenning et al. 1999; Roberts 1993). The limited number or total lack of economically viable pesticide options for nematode management, combined with environmental considerations, increasingly necessitates the use of integrated pest management (IPM) strategies in many crops (Duncan and Noling 1998; Roberts 1993). Fundamental IPM recommendations for nematode management, such as crop rotation, planting of nematode-resistant varieties, and clean fallowing (a phrase typically used by nematologists to refer to weed-free conditions), are rarely as effective individually as nematicides and will likely need to be pyramided to provide acceptable nematode control (Duncan and Noling 1998; Roberts 1993).

Weeds are recognized for their ability to serve as alternative hosts for plant-parasitic nematodes, thereby reducing the success of certain nematode management strategies (Duncan and Noling 1998; Norton 1978). As a result, many publications have catalogued and annotated the numerous reports that address the host status of various weeds to different plant-parasitic nematodes (Bendixen 1988a, 1988b, 1988c; Caswell-Chen et al. 1995; Goodey et al. 1965; O'Bannon et al. 1982; Riggs 1992; Robinson et al. 1997; Townshend and Davidson 1962). Examination of such reports shows that most focus on a relatively small group of highly pathogenic nematode genera that affect major crops, due partly to economic considerations and partly to differences in nematode biology that will be elaborated on later. Most articles also provide only limited quantitative information for use in comparing host suitability among weeds and crops. One exception is NEMABASE (Caswell-Chen et al. 1995), which encompasses all plant-parasitic nematode genera and provides a numerical measure of host suitability for comparative use, if such information is discernable from the original reports. Despite the numerous references to host status, the actual impact of weeds on management of plant-parasitic nematode populations in crops is a subject that has received surprisingly little primary investigation (Griffin 1982; Hogger and Bird 1976; Jordaan and De Waele 1988; Schroeder et al. 1993, 1994, 1999; Thomas et al. 1997; Yeates et al. 1993).

Despite the vast phylogenetic differences that separate weeds and plant-parasitic nematodes at the kingdom level, both share certain characteristics that contribute to their respective pest status in agricultural systems. Most major pests in both groups lack significant means of active dispersal and are largely restricted to similar methods of passive dispersal, such as through the movements of soil, water, plant material, or animals. Both are influenced by soil properties. Soil factors affect the establishment and growth of weeds and crops as primary producers of plant biomass, the active movement of nematodes, and the quantity and quality of roots available for use by plant-parasitic nematodes as place-bound primary consumers. As previously mentioned, weeds have most often been viewed by nematologists as potential

alternative hosts that may support nematode reproduction under field conditions. Another consideration is that weed–nematode associations may represent a normal adaptation resulting from the limited mobility of both groups of organisms and the obligate parasitic behavior of plant-feeding nematodes. This paper addresses the ways in which plant-parasitic nematode biology and the presence of weeds can impact nematode management.

Plant-Parasitic Nematode Characteristics Affect Management

Nematodes are the most numerous multicellular organisms on earth and are adapted to live in any habitat that supports multicellular life (Norton 1978). All nematodes are obligate biotrophs that must obtain energy through the consumption of living matter. Plant-parasitic nematodes, which are the focus of this paper, make up only part of the nematode community that populates the moisture film present in soil macropores. This community also comprises nematodes that are microbivores, fungivores, and predators (Baird and Bernard 1984; Niles and Freckman 1998). Even when root substrate is greatest and conditions are most favorable for plant-parasitic nematode populations, the majority of the soil nematode community is composed of other trophic groups (Baird and Bernard 1984; Parmelee and Alston 1986; Thomas 1976). The inherent benefit to soil nutrient-cycling processes provided by these other groups, particularly the microbivores and fungivores (Ingham et al. 1985; Niles and Freckman 1998), makes general biological suppression of soil-inhabiting nematode communities undesirable. Most biological suppression of plant-parasitic nematodes has been accomplished through augmentation that enhances naturally occurring populations of predators and parasites (Duncan and Noling 1998; Stirling 1991), most of which opportunistically attack any member of the nematode community. While natural enemies undoubtedly contribute to the suppression of phytophagous nematodes (Stirling 1991), they have rarely been successfully manipulated as part of an IPM strategy to help manage plant-parasitic nematodes and therefore are not discussed in this paper.

Development and implementation of effective plant-parasitic nematode management strategies requires a fundamental understanding of the targeted nematode, as is the case when managing weeds, insects, or other pathogens. As obligate plant parasites, all nematodes must maintain a relatively lengthy feeding association with one or more hosts throughout their lives. Under favorable conditions, the generation time for most species is 25 d or longer, but may be extended considerably by environmental conditions and the poikilothermic nature of nematodes. With the exception of the cyst nematodes (*Heterodera* spp. and *Globodera* spp.), nearly all genera lack adaptations for long-term survival in the absence of suitable hosts and, as previously discussed, lack mechanisms for active dispersal to locate distant hosts. Considering these constraints, one may deduce that plant-parasitic nematodes have experienced adaptive pressure to maintain a diverse host range and to avoid inducing host mortality. Exceptions to such adaptation may develop under situations of intensive agricultural production in which nematodes are actively provided with large numbers of genetically uniform, nutritionally supplemented hosts, en-

abling populations to reach levels pathogenic to the crop (Gallaher and McSorley 1993). Nematode management options are designed to exploit the vulnerabilities of predominant parasites that have increased to pathogenic levels. If the targeted nematodes are endemic, it is likely that many of the endemic weeds will serve as alternative hosts for the obligate parasites.

Plant-parasitic nematode management decisions are triggered by expectations that after a crop is established, one or more species within the nematode population will develop to a level where economic injury exceeds the cost of management. Many biotic and abiotic factors affect the rate of population increase, such as initial nematode population levels, species diversity and biotic potentials, feeding behavior, specialized adaptations for survival, soil type and environmental conditions, and host status of the crop and associated weeds. Management procedures must generally be implemented at or before crop establishment. Unlike many weed and insect pests, few rescue treatments are available to aid in the management of nematode problems that arise during the growing season, heightening the consequences of initial management decisions and encouraging the prophylactic use of nematicides.

As with most pests, it is rarely feasible to eliminate problematic plant-parasitic nematodes from agricultural production systems, so the management goal is to reduce populations to subeconomic levels (Roberts 1993). Some of the methods used to achieve such reductions include nematicides; cultural control through crop rotation, fallow, cover crops, asynchrony (or temporal avoidance), or soil organic matter supplementation (Duncan and Noling 1998; Noe 1998; Widmer et al. 2002); host-plant resistance (Starr et al. 2002); and physical control through cultivation-induced desiccation of nematodes in soil or within roots of alternative hosts. Many of these techniques are discussed in greater detail in the following sections that address how nematode feeding behavior and the presence of weeds affects parasite populations and the efficacy of management strategies.

Direct Effects of Weeds on Plant-Parasitic Nematodes

Weeds affect nematode populations in many ways, of which the most widely recognized is by providing plant-parasitic nematodes with additional substrate as alternative hosts (Belair and Benoit 1996; Bendixen 1988a, 1988b; Riggs 1992; Townshend and Davidson 1962). The presence of alternative hosts reduces the efficacy of management techniques designed to lower plant-parasitic nematode populations and thereby enhances crop injury that is proportional to the size of the nematode population. Other direct effects of weeds include protection of certain nematodes from pesticides or the environment (Bird and Hogger 1973; Schroeder et al. 1993, 1994; Thomas et al. 2004), nematode suppression by antagonistic weeds or by the incorporation of weed biomass into soil (Huang 1985; Omidvar 1962), and perhaps through host-induced changes in future nematode biotic potential (Thomas et al. 1997). Although a few of these effects aid nematode management efforts, most have a deleterious effect by enhancing populations or the adaptability of plant-parasitic nematodes.

The extent to which weeds that are alternative hosts im-

pact nematode management depends largely on feeding behavior. Plant-parasitic nematode taxa can be grouped into three broad feeding categories: sedentary endoparasites, migratory endoparasites, and ectoparasites (Ferris and Ferris 1998; Sijmons et al. 1994). The categories differ most noticeably with regard to the level of host specialization that is required in order for the parasite to feed successfully. Each feeding method imparts certain adaptive advantages and limitations on the nematodes that exhibit such behavior. With the exception of nematicides, management strategies have most often been designed to exploit nematode vulnerabilities related to feeding behavior. The following discussion explains how each feeding behavior affects nematode pathogenicity and management, and how alternative weed hosts impact such strategies.

Sedentary endoparasites require the highest level of host specialization when feeding. Instead of remaining in the soil, juveniles or prereproductive females enter roots and induce host transformations that result in special feeding sites. These sites are induced primarily within the vascular cylinder and function as permanent sources of nutrients for growth and reproduction, enabling the nematode parasite to feed in one location for the duration of its life. Specialized feeding sites vary in name (giant cells, syncytia, nurse cells) and developmental specificity among different genera of sedentary endoparasites, but share similarities in function (Hussey and Williamson 1998; Sijmons et al. 1994). All are induced by nematode secretions delivered to plant cells through the hollow stylet that nematodes use during feeding. These secretions cause modifications of plant cell morphology and function, resulting in increased metabolic rates that cause feeding sites to function as photosynthetic sinks in roots (Bockenhoff et al. 1996; Hussey and Williamson 1998; McClure 1977; Melakeberhan and Ferris 1988; Sijmons et al. 1994) and diverting energy from other plant processes. As a group, sedentary endoparasites, such as root-knot nematodes (*Meloidogyne* spp.), cyst nematodes, the reniform nematode (*Rotylenchulus reniformis* Linford and Oliveira), false root-knot nematodes (*Nacobbus* spp.), and the citrus nematode (*Tylenchulus semipenetrans* Cobb), are the most economically important of the plant-parasitic nematodes (Sasser and Freckman 1987; Koenning et al. 1999).

The diversity in nematode management options available for sedentary endoparasites is greater than for other feeding behaviors, mainly because of the amount of special host modification that must occur in order for these nematodes to feed and reproduce. Host ranges for sedentary endoparasites are typically more restricted than for other feeding behaviors because the nematode secretions needed to induce feeding sites are more likely to affect plants that are phylogenetically similar (Hussey and Williamson 1998; Sijmons et al. 1994). Even though a few sedentary endoparasites have relatively broad host ranges, such as the more common species of root-knot nematodes, many non-host plant species have been identified for all sedentary endoparasites. Crops that are not affected by nematode secretions offer effective rotations that provide nematode population suppression. The highly specialized nature of the host–parasite relationship involving sedentary endoparasites also means host-plant resistance is more likely to involve traits that are controlled by single genes (Starr et al. 2002). Such traits are more amenable to manipulation by plant breeders and typically

involve a host hypersensitive response to the invading nematode (Hussey and Williamson 1998; Sijmons et al. 1994). Resistant varieties are most often a part of IPM strategies for management of sedentary endoparasites compared to nematodes with other feeding behaviors (Duncan and Noling 1998). The presence of weeds that are alternative hosts for targeted nematodes in rotation crops, fields planted to resistant varieties, or during fallow periods designed to suppress nematodes can greatly reduce the efficacy of such management techniques (Belair and Parent 1996; Inserra et al. 1985; Riggs 1992; Roberts 1993). Weeds can also serve as reservoirs for sedentary endoparasites in susceptible crops, leading to increased early-season crop infection and contributing to the overall residual nematode population that will affect subsequent crops (Schroeder et al. 1993, 1994; Bird and Hogger 1973). Weeds along irrigation ditches have also been implicated in the maintenance and dissemination of the false root-knot nematode, *Nacobbus aberrans* Thorne, into noninfested fields through irrigation water (Inserra et al. 1985).

Migratory endoparasitic nematodes invade the roots of host plants, but normally do not induce specialized feeding sites. These nematodes typically use their stylets to pierce and feed upon cortical cells, which often subsequently die and collapse as the nematodes migrate through root tissue, causing extensive damage in the process. The wounded roots may also predispose crops to infection by fungal pathogens, resulting in damaging disease complexes (Abawi and Chen 1998; Rowe et al. 1985). Host pathogenicity associated with feeding by migratory endoparasites, such as lesion nematodes (*Pratylenchus* spp.), stem nematodes (*Ditylenchus* spp.), burrowing nematodes (*Radopholus* spp.), and the rice-root nematode (*Hirschmanniella oryzae* van Breda de Haan), tends to be less severe than for sedentary endoparasites, but greater than the damage resulting from most ectoparasites. Most of the management techniques for sedentary endoparasites can also be applied to migratory endoparasites. However, crop rotation and host-plant resistance, in particular, are less effective against some migratory endoparasites that are less dependent on host specialization for feeding and reproduction. Since fewer crops are nonhosts for certain migratory endoparasites such as lesion nematodes, rotations must make use of poorer hosts that may support some nematode reproduction. As a result, few rotation schemes are recognized as having significant potential for suppression of migratory endoparasites (Noe 1998). In similar fashion, reduced host specialization has led to greater difficulty identifying and successfully incorporating acceptable levels of resistance to migratory endoparasites into some crops (De Waele and Elsen 2002). Therefore, while weeds as alternative hosts may contribute substantially to the maintenance and increase of migratory endoparasite populations under fallow conditions, their deleterious effects on rotations and resistant crops is likely to be less than with sedentary endoparasites.

Ectoparasitic nematodes normally remain in the soil near the host, only penetrating plant roots with their stylets during feeding. Ectoparasites typically have broad host ranges and require little or no host specialization to feed. Although some genera, such as ring nematodes (*Criconemella* spp.), may feed at the same location on a root for extended periods of time (Hussey and Williamson 1998; Westcott and Hussey

1992), most ectoparasites browse on epidermal and cortical tissue at different locations along roots. Common examples of other ectoparasites include spiral nematodes (*Helicotylenchus* spp.), stunt nematodes (*Tylenchorhynchus* spp.), stubbyroot nematodes (*Trichodorus* spp.), sting nematodes (*Belonolaimus* spp.), and lance nematodes (*Hoplolaimus* spp.). Crop damage results from direct injury to cells during feeding and is usually a function of the number of nematodes present, their size, rate of population increase, and specific host sensitivity. Management of ectoparasites is limited to nonspecific strategies such as fallow or the use of nematicides. Because most ectoparasites can feed on a wide range of plants, weeds that are present during fallow periods can negate any benefit for nematode suppression (McSorley et al. 1994).

Though much less widely studied, there are indications that weeds can directly affect plant-parasitic nematodes in ways other than as alternative hosts. Below-ground weed biomass may help protect endoparasites from pesticides and the environment. For example, tubers of yellow nutsedge (*Cyperus esculentus* L.) and purple nutsedge (*C. rotundus* L.) can protect the southern root-knot nematode [*Meloidogyne incognita* (Kofoid and White) Chitwood] from the widely used fumigant nematicide 1,3-dichloropropene, resulting in infection of chile pepper (*Capsicum annuum* L.) by nematodes harbored in the fumigated tubers (Thomas et al. 2004). Alternatively, some weeds may help suppress nematodes by producing antagonistic phytochemicals that are released into the soil in root exudates or by the decomposition of plant tissues (Chitwood 2002). Weeds in the Asteraceae, such as *Cirsium japonicum* Fisch. ex DC., Philadelphia fleabane (*Erigeron philadelphicus* L.), and Canada goldenrod (*Solidago canadensis* L.), along with well-known ornamentals such as certain marigolds (*Tagetes* spp.), are widely recognized for their production of such compounds, although chemical antagonists of nematodes are also produced by certain species within many other plant families (Chitwood 2002; Huang 1985; Omidvar 1962). Other weeds such as showy crotalaria (*Crotalaria spectabilis* Roth.), hairy indigo (*Indigofera hirsuta* Harvey), and partridgepea (*Cassia fasciculata* Michx.) are nonhosts that can also help suppress certain nematodes (McSorley 1998). Finally, some weeds may directly affect the pathogenicity and biotic potential of nematodes on future hosts. Southern root-knot nematode inoculum recovered from yellow nutsedge or tomato proved more pathogenic to chile pepper than did inoculum recovered from other chile peppers (Thomas et al. 1997). Root-knot nematode reproduction rates on chile also differed among inoculum sources in this study, suggesting that the previous host may influence future host suitability for some sedentary endoparasites.

Indirect Effects of Weeds on Plant-Parasitic Nematodes

In addition to the direct effects just discussed, weeds in agricultural systems also exert indirect effects on plant-parasitic nematode populations. Weed competition can lead to crop stress and stunting, resulting in fewer available photosynthates for allocation to sedentary endoparasites through specialized feeding sites and less root mass for parasitization by nematodes in general. Alston et al. (1993) reported fewer

soybean cyst nematodes (*H. glycines* Ichinoe) on soybeans that were stressed by nonhost weeds than on soybeans growing without weed competition.

The implementation of weed control measures is another way in which weeds can indirectly affect plant-parasitic nematode management and survival. Cultivation interferes with nematode feeding by disrupting the location of parasites in soil, exposes them to desiccation, and helps break up plant debris that harbors nematodes (Norton 1978). Cultivation also damages or destroys young weeds that may be alternative hosts for sedentary endoparasites. Once feeding sites have been established, death of such hosts results in death of the now-sedentary nematodes that are trapped in the plant. Herbicide use may also affect certain nematodes, particularly the cyst nematodes. Both alachlor and trifluralin have been reported to enhance soybean cyst nematode egg hatch (Bostian et al. 1984; Riggs and Oliver 1982), while acifluorfen and bentazon reduced soil densities of soybean cyst nematode eggs and juveniles (Browde et al. 1994). Several thiocarbamate herbicides have been reported to suppress sugarbeet cyst nematode (*H. schachtii* A. Schmidt) and potato cyst nematode (*Globodera rostochiensis* Wollenweber) egg hatch (Perry and Beane 1989). Herbicides have also been found to interact with, and influence the efficacy of, nematicides used against soybean cyst nematodes. Sipes and Schmitt (1989) found alachlor to be antagonistic to the nematicide fenamiphos, possibly helping to explain late-season cyst nematode resurgence in soybeans treated with both pesticides (Schmitt et al. 1983). The mechanisms by which herbicides affect cyst nematode egg hatch are unknown at this time. Evidence also indicates that soil-applied pre-emergence herbicides may affect nematodes directly, while postemergence herbicide applications to crops may affect nematodes indirectly through alterations in host physiology (Browde et al. 1994; Levene et al. 1998). The influence of pesticide–pesticide and herbicide–crop interactions on plant-parasitic nematode population dynamics is a complex area with enormous potential implications for future nematode IPM decisions.

Consequences for IPM

Historically, the complexity of any plant-parasitic nematode management strategy has been inversely proportional to the value of the crop involved (Duncan and Noling 1998), limiting emphasis on IPM. Cereals or forages, for example, have never been candidates for an expensive chemical control option like methyl bromide, which has been widely used for general pest suppression in strawberry and certain vegetables. Instead, nematode management in cereals or forages will likely involve a combination of crop rotation and the planting of resistant varieties to help reduce problematic sedentary endoparasite populations. Shrinking nematicide options and increasing concerns about environmental quality, however, are making IPM more of a necessity for nematode management in high-value crops as well. Roberts (1993) described two goals that can be applied to any nematode IPM effort: (1) short-term suppression of plant-parasitic nematode populations below the economic threshold for the crop of interest, and (2) ultimately a reduction in the carry-over nematode population to a level below that which was initially present at the time of crop establishment. Accomplishment of these goals will almost certainly require

the combined application of a number of different management techniques, none of which is likely to approach the level of overall nematode suppression achieved with nematicides, and most of which will be negatively impacted in some way by the presence of weeds (Duncan 1991; Duncan and Noling 1998; Roberts 1993).

To be effective, IPM strategies should address nematode and weed management collectively. As alternative hosts, weeds do more to enhance plant-parasitic nematode populations than any factor other than the crop, and are the most important factor for maintaining nematode diversity. Unlike crops, some weed hosts are not injured by extremely high nematode populations (Schroeder et al. 1999), and may even benefit from nematode parasitism (Schroeder et al. 2004, 2005). Weeds and plant-parasitic nematodes most likely share a common host–parasite relationship that predates human agricultural endeavors. This is evident from the similarities in how both groups of organisms interact with each other, the environment, and other groups of organisms in the agroecosystem (Norris et al. 2003). To be successful over time, both nematodes and weeds have been obliged to adapt and coexist with each other. As successful parasites, phytophagous nematodes have evolved in close association with and dependence on the plants that coexist in their environment. Nematode pathogenicity toward crops, especially by sedentary endoparasites, would be a detrimental trait for survival of these obligate parasites, were it not for human intervention that repeatedly supplies a highly susceptible food source in crop plants.

IPM and agricultural sustainability are two concepts that are inextricably linked. When it comes to management of plant-parasitic nematodes, natural resources are used most efficiently by practices that provide maximum profitability to growers (Duncan and Noling 1998; Noe et al. 1991). It appears that weed–nematode interactions in agricultural production systems may be more intricate and complex than simply the role of weeds as alternative hosts, especially where sedentary endoparasites are involved. Weed–crop competition impacts nematode populations and nematode parasitism reduces crop competition with weeds, yet plant-parasitic nematodes and weeds seem well adapted to benign coexistence with each other. The challenge that faces weed scientists and nematologists is to identify compatible strategies for crop production.

Acknowledgments

Literature Cited

Abawi, G. S. and J. Chen. 1998. Concomitant pathogen and pest interactions. Pages 135–158 in K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Alston, D. G., D. P. Schmitt, J. R. Bradley, Jr., and H. D. Coble. 1993. Multiple pest interactions in soybean: effects on Heterodera glycines egg populations and crop yield. J. Nematol. 25:42–49.

Baird, S. M. and E. C. Bernard. 1984. Nematode population and community dynamics in soybean–wheat cropping and tillage regimes. J. Nematol. 16:379–386.

Belair, G. and D. L. Benoit. 1996. Host suitability of 32 common weeds to Meloidogyne hapla in organic soils in southwestern Quebec. Suppl. J. Nematol. 28:643–647.

Belair, G. and L. E. Parent. 1996. Using crop rotation to control Meloidogyne hapla Chitwood and improve marketable carrot yield. Hortscience 31:106–108.

Bendixen, L. E. 1988a. A comparative summary of the weed hosts of Heterodera, Meloidogyne, and Pratylenchus nematodes. Special Circular 118. Wooster, OH: Ohio State University Ohio Agricultural Research and Development Center. 33 p.

Bendixen, L. E. 1988b. Major weed hosts of nematodes in crop production. Special Circular 119. Wooster, OH: Ohio State University Ohio Agricultural Research and Development Center. 22 p.

Bendixen, L. E. 1988c. Weed hosts of Heterodera, the cyst, and Pratylenchus, the root-lesion, nematodes. Special Circular 117. Wooster, OH: Ohio State University Ohio Agricultural Research and Development Center. 52 p.

Bird, G. W. and C. H. Hogger. 1973. Nutsedges as hosts of plant-parasitic nematodes in Georgia cotton fields. Plant Dis. Rep. 57:402.

Bockenhoff, A., D.A.M. Prior, F.M.W. Grundler, and K. J. Oparka. 1996. Induction of phloem unloading in Arabidopsis thaliana roots by the parasitic nematode Heterodera schachtii. Plant Physiol. 112:1421–1427.

Bostian, A. L., D. P. Schmitt, and K. R. Barker. 1984. In vitro hatch and survival of Heterodera glycines as affected by alachlor and phenamiphos. J. Nematol. 16:22–26.

Browde, J. A., G. L. Tylka, L. P. Pedigo, and M.D.K. Owen. 1994. Responses of Heterodera glycines populations to a postemergence herbicide mixture and simulated insect defoliation. J. Nematol. 26:498–504.

Caswell-Chen, E. P., H. Ferris, B. B. Westerdahl, and R. L. Sloan. 1995. A PC/MAC-platform database on the host status of crop and weed species to plant-parasitic nematodes. Nematol. Newsl. 41:7–8. Also available at http://ucdnema.ucdavis.edu/Tango/Tango.acgi$/Tutorial/INTERACT.QRY?function=form. Accessed October 23, 2003.

Chitwood, D. J. 2002. Phytochemical based strategies for nematode control. Annu. Rev. Phytopathol. 40:221–249.

De Waele, D. and A. Elsen. 2002. Migratory endoparasites: Pratylenchus and Radopholus species. Pages 175–206 in J. L. Starr, R. Cook, and J. Bridge, eds. Plant Resistance to Parasitic Nematodes. Wallingford, U.K.: CABI International.

Duncan, L. W. 1991. Current options for nematode management. Annu. Rev. Phytopathol. 29:469–490.

Duncan, L. W. and J. W. Noling. 1998. Agricultural sustainability and nematode integrated pest management. Pages 251–287 in K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Ferris, J. M. and V. R. Ferris. 1998. Biology of plant-parasitic nematodes. Pages 21–35 in K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Gallaher, R. N. and R. McSorley. 1993. Population densities of Meloidogyne incognita and other nematodes following seven cultivars of cowpea. Nematropica 23:21–26.

Goodey, J. B., M. T. Franklin, and D. J. Hooper. 1965. The Nematode Parasites of Plants Catalogued under their Hosts. Farnham Royal, U.K.: Commonwealth Agricultural Bureaux. 214 p.

Griffin, G. D. 1982. Differences in the response of certain weed host populations to Heterodera schachtii. J. Nematol. 14:174–182.

Hogger, C. H. and G. W. Bird. 1976. Weed and indicator hosts of plant-parasitic nematodes in Georgia cotton and soybean fields. Plant Dis. Rep. 60:223–226.

Huang, J. 1985. Mechanisms of resistance to root-knot nematodes. Pages 165–174 in J. N. Sasser and C. C. Carter, eds. An Advanced Treatise on Meloidogyne. Volume I. Raleigh, NC: North Carolina State University Graphics.

Hussey, R. S. and V. M. Williamson. 1998. Physiological and molecular aspects of nematode parasitism. Pages 87–108 in K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Ingham, R. E., J. A. Trofymow, E. R. Ingham, and D. C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. 55:119–140.

Inserra, R. N., G. D. Griffin, and J. L. Anderson. 1985. The false root-knot nematode *Nacobbus aberrans*. Bulletin 510. Logan, UT: Utah Agricultural Experiment Station. 14 p.

Jordaan, E. M. and D. De Waele. 1988. Host status of five weed species and their effects on *Pratylenchus zeae* infestation of maize. J. Nematol. 20:620–624.

Koenning, S. R., C. Overstreet, J. W. Noling, P. A. Donald, J. O. Becker, and B. A. Fortnum. 1999. Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. Suppl. J. Nematol. 31:587–618.

Levene, B. C., M.D.K. Owen, G. L. Tylka. 1998. Response of soybean cyst nematodes and soybeans (*Glycine max*) to herbicides. Weed Sci. 46:264–270.

McClure, M. A. 1977. *Meloidogyne incognita*: a metabolic sink. J. Nematol. 9:88–90.

McSorley, R. 1998. Alternative practices for managing plant-parasitic nematodes. Am. J. Altern. Agric. 13:98–104.

McSorley, R., D. W. Dickson, J. A. de Brito, and R. C. Hochmuth. 1994. Tropical rotation crops influence nematode densities and vegetable yields. J. Nematol. 26:308–314.

Melakeberhan, H. and H. Ferris. 1988. Growth and energy demand *of Meloidgyne incognita* on susceptible and resistant *Vitis vinifera* cultivars. J. Nematol. 20:545–554.

Niles, R. K. and D. W. Freckman. 1998. From the ground up: nematode ecology in bioassessment and ecosystem health. Pages 65–85 *in* K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Noe, J. P. 1998. Crop- and nematode-management systems. Pages 159–171 *in* K. R. Barker, G. A. Pederson, and G. L. Windham, eds. Plant and Nematode Interactions. Agronomy Monograph 36. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

Noe, J. P., J. N. Sasser, and J. L. Imbriani. 1991. Maximizing the potential of cropping systems for nematode management. J. Nematol. 23:353–361.

Norris, R. F., E. P. Caswell-Chen, and M. Kogan. 2003. Concepts in Integrated Pest Management. Upper Saddle River, NJ: Prentice Hall. 586 p.

Norton, D. C. 1978. Ecology of Plant-Parasitic Nematodes. New York: Wiley Interscience. 268 p.

O'Bannon, J. H., G. S. Santo, and A. P. Nyczepir. 1982. Host range of the Columbia root-knot nematode. Plant Dis. 66:1045–1048.

Omidvar, A. M. 1962. The nematicidal effects of *Tagetes* spp. on the final population of *Heterodera rostochiensis* Woll. Nematologica 7:62–64.

Parmelee, R. W. and D. G. Alston. 1986. Nematode trophic structure in conventional and no-tillage agroecosystems. J. Nematol. 18:403–407.

Perry, R. N. and J. Beane. 1989. Effects of certain herbicides on the *in vitro* hatch of *Globodera rostochiensis* and *Heterodera schachtii*. Rev. Nematol. 12:191–196.

Riggs, R. D. 1992. Host range. Pages 107–114 *in* R. D. Riggs and J. A. Wrather, eds. Biology and Management of the Soybean Cyst Nematode. St. Paul, MN: APS.

Riggs, R. D. and L. R. Oliver. 1982. Effect of trifluralin (Treflan) on soybean cyst nematode. J. Nematol. 14:466.

Roberts, P. A. 1993. The future of nematology: integration of new and improved management strategies. J. Nematol. 25:383–394.

Robinson, A. F., R. N. Inserra, E. P. Caswell-Chen, N. Volvas, and A.

Troccoli. 1997. *Rotylenchulus* species: Identification, distribution, host ranges, and crop plant resistance. Nematropica 27:127–180.

Rowe, R. C., R. M. Riedel, and M. J. Martin. 1985. Synergistic interactions between *Verticillium dahliae* and *Pratylenchus penetrans* in potato early dying disease. Phytopathology 75:412–418.

Sasser, J. N. and D. W. Freckman. 1987. A world perspective on nematology: the role of the society. Pages 7–14 *in* J. A. Veech and D. W. Dickson, eds. Vistas on Nematology. Hyattsville, MD: Society of Nematologists.

Schmitt, D. P., F. T. Corbin, and L. A. Nelson. 1983. Population dynamics of *Heterodera glycines* and soybean response in soils treated with selected nematicides and herbicides. J. Nematol. 15:432–437.

Schroeder, J., M. J. Kenney, S. H. Thomas, and L. Murray. 1994. Yellow nutsedge response to southern root-knot nematodes, chile peppers, and metolachlor. Weed Sci. 42:534–540.

Schroeder, J., S. H. Thomas, and L. Murray. 1993. Yellow and purple nutsedge and chile peppers host southern root-knot nematode. Weed Sci. 41:150–156.

Schroeder, J., S. H. Thomas, and L. W. Murray. 1999. Yellow (*Cyperus esculentus*) and purple nutsedge (*Cyperus rotundus*) are not injured by increasing root-knot nematode (*Meloidogyne incognita*) population density. Weed Sci. 47:201–207.

Schroeder, J., S. H. Thomas, and L. W. Murray. 2004. Root-knot nematodes affect annual and perennial weed interactions with chile pepper. Weed Sci. 52:28–46.

Schroeder, J., S. H. Thomas, and L. W. Murray. 2005. Impacts of crop pests on weeds. Weed Sci. 53:918–922.

Sijmons, P. C., H. J. Atkinson, and U. Wyss. 1994. Parasitic strategies of root nematodes and associated host cell responses. Annu. Rev. Phytopathol. 32:235–259.

Sipes, B. S. and D. P. Schmitt. 1989. Development of *Heterodera glycines* as affected by alachlor and fenamiphos. J. Nematol. 21:24–32.

Starr, J. L., J. Bridge, and R. Cook. 2002. Resistance to plant-parasitic nematodes: history, current use and future potential. Pages 1–22 *in* J. L. Starr, R. Cook, and J. Bridge, eds. Plant Resistance to Parasitic Nematodes. Wallingford, England: CAB International.

Stirling, G. R. 1991. Biological Control of Plant Parasitic Nematodes. Wallingford, England: CAB International. 282 p.

Thomas, S. H. 1976. Population fluctuations of plant parasitic nematodes under different tillage systems in corn. M.S. thesis. Iowa State University, Ames, IA. 90 p.

Thomas, S. H., J. Schroeder, M. J. Kenney, and L. W. Murray. 1997. *Meloidogyne incognita* inoculum source affects host suitability and growth of yellow nutsedge and chile pepper. J. Nematol. 29:404–410.

Thomas, S. H., J. Schroeder, and L. W. Murray. 2004. *Cyperus* tubers protect *Meloidogyne incognita* from 1,3-dichloropropene. J. Nematol. 36:131–136.

Townshend, J. L. and T. R. Davidson. 1962. Some weed hosts of the northern root-knot nematode *Meloidogyne hapla* Chitwoodi, 1949, in Ontario. Can. J. Bot. 40:543–547.

Westcott, III, S. W. and R. S. Hussey. 1992. Feeding behavior of *Criconemella xenoplax* in monoxenic culture. Phytopathology 82:936–940.

Widmer, T. L., N. A. Mitkowski, and G. S. Abawi. 2002. Soil organic matter and management of plant-parasitic nematodes. J. Nematol. 34:289–295.

Yeates, G. W., D. A. Wardle, and R. N. Watson. 1993. Relationships between nematodes, soil microbial biomass and weed-management strategies in maize and asparagus cropping systems. Soil Biol. Biochem. 25:869–876.