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PERSPECTIVES ON PLANT AND SOIL NEMATOLOGY

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■ **Abstract** During my career in Plant Pathology/Nematology, many major advancements have occurred in the study of nematodes—even with their being largely soilborne and thus often overlooked. These biotrophic organisms include the most widespread and important group of plant pathogens—the root-knot nematodes *Meloidogyne* species—which attack most major crops, as well as thousands of non-crop plant species. Landmark achievements that catalyzed research on these organisms included the discovery of effective nematicides, ectoparasitic forms, elucidation of disease complexes, nematodes as virus vectors, development of host resistance, and new technologies for research. Evolving research thrusts involve interfacing traditional and molecular systematics/diagnostics, adoption of the *Caenorhabditis elegans*-molecular genetics resource for general nematological research, focus on genetics of parasitism, use of molecular tools in developing host resistance, ecological and quantitative facets, and soil-biology-ecology based integrated management. Educational and international programs are encountering many changes and challenges, as is support for nematology in general.

INTRODUCTION

An invitation to develop the Prefatory Chapter for this volume of the Annual Review of Phytopathology was an unexpected and intimidating honor. A review of many of previous prefatory chapters, including the first on the "Future of Plant Pathology" in 1963, by J.C. Walker (102) and the 1995 chapter by another key mentor, Arthur Kelman (55), was a humbling but enlightening experience. Earlier treatments by Walker (102), Stakman (91), Baker (5), and other authors still offer much insight, wisdom, and philosophy to consider in today's rapidly evolving plant pathology. Recent prefatory chapters document incredible advances and changes in the discipline over the past century as well as the current challenges. Being a plant pathologist-nematologist, this chapter reflects primarily my views on the development and advances in plant nematology and some of its interfacing with related disciplines.

EVENTS LEADING THE AUTHOR TO PLANT PATHOLOGY-NEMATOLOGY

While completing my senior year in high school in western North Carolina, my first introduction to nematodes and other plant pathogens was at a community Plant Disease Clinic conducted by Howard Garris, Extension Specialist at N.C. State College. His uniquely enthusiastic descriptions of root knot and other diseases have remained with me for more than 50 years. Upon enrollment in Agricultural Education at N.C. State in 1952, other undergraduate students were soon recommending an exciting course, Introductory Plant Pathology, as an elective. Thus, I soon was privileged to find myself in Dr. Arthur Kelman's widely known course in which he taught the lectures as well as the laboratories in a superbly masterful fashion. The quality and magnetism of Dr. Kelman's teaching were reflected by some 45 former students in his classes enrolling in graduate programs in plant pathology. My M.S. thesis, under the direction of Joseph N. Sasser, at N.C. State, focused on the nature of resistance in alfalfa to the stem nematode, *Ditylenchus dipsaci*. In addition to benefiting immensely via research under Dr. Sasser, my initial adviser, Louis Allison (USDA Plant Pathologist), and other faculty and students greatly augmented my insight and knowledge of nematology and plant pathology. Another very beneficial feature of the rapidly expanding nematology program at that time (1956–1958) was the frequent presentations/demonstrations by visiting nationally and internationally renowned nematologists, including Maurice Linford, M. Oostenbrink, J.W. Seinhorst, among others.

The philosophy of the Plant Pathology Department at N.C. State, and especially that of its head Don Ellis, during that era essentially precluded an individual from seeking a third degree from the same institution. After considering a number of possibilities for a doctorate program in nematology, I chose to broaden my research experience and accepted an assistantship with Dr. J.C. Walker in Plant Pathology at the University of Wisconsin (with an annual stipend of $1800). Although living costs were low at that time, the limited stipends apparently were designed to ensure that each graduate student focused almost exclusively on his/her coursework and research. Rather than pursing a primary research project on nematodes, however, my PhD thesis project with Walker involved a range of factors affecting the pathogenicity and virulence of selected isolates of *Pellicularia filamentosa* (*Thanatephorus cucumeris*) on bean and potato. However, my study of nematodes also continued via special projects with the highly energetic and enthusiastic Professor Gerald Thorne. Pursuing graduate research in Madison during the late 1950s and early 1960s was a challenge for the 70 plant pathology graduate students that required maximum efficiency and innovative use of very restricted space and facilities—including a temporary World War II building where my desk/lab was located. Getting to know and interacting with that exceptionally able and diverse group of aspiring scientists proved to be a most rewarding highlight of my career. Also, accompanying Dr. Walker on his frequent vegetable-disease-assessment trips brought a deep appreciation of his philosophy of "keeping one foot in the furrow" [see Mathre (66)] as well as acquiring much information on plant diseases and the climatic-topographical history of Wisconsin.

After completing the PhD requirements in the spring of 1961, Dr. Glenn Pound (Department Chair), in a surprising Saturday morning call, asked me to come to his office to discuss my future with him and Dr. Walker. Following that discussion and a brief visit to the Dean's office, I discontinued all job-seeking activities and joined the Department as an assistant professor with research-teaching assignments in nematology—without any application or employment forms, nor even a seminar. With considerable research and teaching responsibilities, including directing graduate research, I developed a keen interest in graduate education that continued over four decades. Pursuing extensive field research in Wisconsin with the often severe and prolonged winters was an eye-opening and invigorating experience. For example, sampling for nematodes in alfalfa or cranberry bogs in the spring required an ax for chopping through a thick layer of snow/ice and frozen soil. My most memorable collection trip, involving a study on jack and red pine in Northern Wisconsin, was on November 22, 1963; at a service station stop, the attendant advised us that President John F. Kennedy had been assassinated—a day that was as shocking as 9-11.

After a most difficult decision in 1965–1966, I found myself challenging Thomas Wolfe's 1940 book, *You Can't Go Home Again*. This involved a March 15, 1966, return to the Plant Pathology Department at N.C. State University with a primary assignment involving the development of a pilot nematode advisory program. My initial research projects focused on nematode ecology—population dynamics, host responses/damage thresholds and related effects of environmental factors, and improvement of methodology for assessing nematode infestations. The earlier research by C.J. Nusbaum and associates on the feasibility of this type of program, combined with well-known crop losses to nematodes in the state, and the University securing considerable state funding, enhanced the attractiveness of this new endeavor. An additional project involved the nature of nematode-suppression of nodulation in soybean. After eight years of research and evaluations, the nematode advisory program for growers and homeowners was transferred to the North Carolina Department of Agriculture where it serves a vital function by processing some 30,000 samples per year for growers and homeowners.

The above research projects meshed well with graduate research, and my commitment to teaching and the graduate program increased sharply. The experience in directing/codirecting the research of a significant number of superb graduate students and postdoctorates proved to be the most rewarding component of my very long career in plant pathology. Those interactions combined with extensive classroom teaching and observing our research findings contribute to resolving production agriculture and homeowner problems gave me a deep appreciation of our 150-year Land-Grant-College/University system. As discussed later, I trust that we are not evolving away from that concept of interfacing research, education, and information transfer.

Two dramatic and attention-riveting developments during my career are the new high-technology equipment and molecular biotechnology systems that are now commonly utilized in research. Reflecting on the changes in nematology during the past 50 years—from using mechanical calculators and typewriters to high-capacity computers for data management, development of nematode-host-environment simulation systems (38, 63); basic physiological work to molecular biology and related analytical equipment, including development of DNA probes (80), cloning of genes, engineering host resistance, and genomics (4, 20, 33, 41, 50, 90, 101); ecology-based nematode-IPM-crop management (12, 78); to using the Internet to instantly share information worldwide—is sometimes mind boggling (7).

NEMATODES AND NEMATOLOGY

The small autonomous discipline of nematology that developed during the past four decades is limited largely to plant, insect, and soil taxa. Until recently, agricultural nematologists focused only on plant- and insect-parasitic species and generally ignored the mycophagous- and bacterivorous-feeding nematodes. In addition to the highly characterized *Caenorhabditis elegans*–-a bacterial-feeding soil nematode, both of the latter trophic groups are proving to be important in carbon and nitrogen mineralization and nutrient cycling in soils. Omnivores and predaceous nematode taxa also may play important roles in soil health. Bacterial-feeding nematodes also may enhance the activities of the plant growth–promoting rhizobacteria. Being largely microscopic and hidden in soil and or in their hosts/niches, nematodes were and I am confident are still often overlooked—as reflected by the limited federal funding for nematology. Of interest, investments for controlling animal-parasitic nematode species, especially those such as human parasites in developing countries, and heart worms in dogs dwarfs the funds directed toward research and management of plant-attacking species.

Like other pathogens, nematodes are studied in numerous disciplines, including plant pathology, entomology, biology, zoology, ecology, medicine, veterinary science, and nematology. Plant and animal parasitic nematodes apparently evolved from microbivorous species. A recent phylogenetic analysis that involved ribosomal DNA sequences from diverse nematode taxa suggested that plant parasitism arose independently three times and animal parasitism at least four times (21). For plant parasites, Blaxter et al. (21) concluded that parasitism evolved once for the largest group—the Tylenchida (cyst, root-knot, etc., class Secernentea) and twice for the minority groups of plant parasites in the Dorylaimida (dagger, needle) and Triplonchida (stubby-root) (class Adenophorea).

NEMATODES AND PLANT DISEASE

Acceptable Means of Proving Pathogenicity

Because plant nematodes are obligate, usually soil-inhabiting parasites, documenting their pathogenic capabilities experimentally involved long-term challenges.

Although Byars reported his 1914 attempts of pure culture of root-knot nematodes, acceptable monoxenic culture techniques were delayed until the 1950s work by Mountain (68, 69) with the lesion nematode, *Pratylenchus penetrans*, on peach and tobacco. By introducing these nematodes onto tobacco roots in an otherwise microorganism-free system, he proved definitively that they caused brown-root rot of that crop. In similar monoxenic cultures of *P. penetrans* on peach, he and associates in their landmark research elucidated the mechanism of pathogenesis as well as documenting the disease-inducing capacity of this nematode. For example, the movement of the nematodes in peach roots and interactions between plant glycosides and enzymes released by *P. penetrans* result in hydrolysis of the glycosides and release of phytotoxic products—giving rise to root necrosis (69). The terms and concepts for various types of cultures of nematodes were first delineated by another distinguished pioneer, E.C. Doughtery (34), who was one of the early scientists using *C. elegans* as a model for biological research.

Types of Parasitism/Pathogenesis

Although plant-oriented nematologists until recently have focused primarily on the obligate parasitic/damaging nematode taxa, other forms—microbivorous groups and entomophilic species—are increasingly studied. Like other soil microflora and certain microfauna, the levels of direct and indirect interactions of nematodes with plants vary enormously.

The sedentary, sexually dimorphic root-knot nematodes (*Meloidogyne* spp.) are considered to be the most advanced group in regards to parasitism. They infect roots by moving intercellularly, thereby altering host physiology, root anatomy, and gene expression in a very compatible manner without necrosis or eliciting defense reactions (51). The three common species—*M. arenaria*, *M. incognita*, and *M. javanica*—are apomictic or mitotic parthenogenetic, and have a potential host range that encompasses a majority of flowering plants (99). *Meloidogyne* spp. exhibit great cytogenetic diversity that likely is unparalleled in any other group (97–99). The uniquely effective utilization of parthenogenesis by these organisms enables them to thrive under diverse habitats, including a wide range of soil types and textures. Their polyploidy (diploid to tetraploid, but typically triploid) apparently resulted in conserved genetic diversity, yet in some manner enables them to adapt to very different environments and hosts. For example, repeated exposure to the resistant *Mi* gene in tomato under greenhouse conditions gives rise to virulent populations of *Meloidogyne*, but this occurs infrequently in the field (105). Continuous deployment of the *Rk* resistant gene in tobacco in given fields results in the development of resistance-circumventing populations or host races of *M. arenaria* or *M. incognita* (6). The North Carolina differential hosts (six plant species including resistant tobacco) (44) are helpful in agronomically delineating interspecific variants of some root-knot nematode species. However, Roberts and associates (81, 82) found that those differentials do not account for the large avirulence diversity within this genus. He proposed a more comprehensive scheme for characterizing *Meloidogyne* spp. (a)virulence factors that could be differentiated on R genes in any host.

In any case, root-knot nematodes are unique in nematology because they benefit from an often "dead-end" type of reproduction—parthenogenesis. Only one other nematode (*Rotylenchulus reniformis*) and some arbuscular fungi have such wide host ranges. Of interest, some 5500 (60%) of the records of plant-parasitic nematodes worldwide listed in a comprehensive host index were *Meloidogyne* spp. versus 3900 records for all others (42, 99). Those records, however, could be biased due to the readily visible symptoms (root galls) induced by *Meloidogyne*. The means by which root-knot nematodes gained worldwide distribution can be debated. However, these heterozygous organisms thrive over a wide range of soils and environments—whether in natural ecosystems in western Brazil or on vegetables in California. Undoubtedly, keys to their success include their capacity for a maintenance-level reproduction on weeds versus their explosive increase on highly suitable annual crop hosts and their ability to recover promptly form extremely low levels. Thus, the survival strategy for these mostly parthenogenetic parasites interfaces their capacity for rapid reproduction on highly suitable hosts (*r* strategy) and an exceptionally wide host range. In contrast to the parthenogenetic *Meloidogyne* species, all amphimictic root-knot nematode species have narrow host ranges—often on woody plants. Examples of the isolated and rarely mentioned root-knot nematode species on woody plants include *M. ovalis* on maple in northern Wisconsin and *M. carolinesis* on blueberry in North Carolina.

The sedentary, sexually dimorphic cyst nematodes *Heterodera* spp. and *Globodora* spp. also alter host physiology and gene expression and induce feeding cells in roots, (but not root galls) with some root necrosis—due in part to their intracellular movement during the infection process (50, 51). While these amphimictic nematodes have a much lower reproductive capacity (most have a *k* strategy) and a very restricted host range, they can survive in soil for years in a dormant state (diapause). Generally, root diffusates from a favorable host are required to induce egg hatch. This long-term dormancy trait is usually limited to nematode species that attack aboveground plant parts. The cyst nematodes, including *H. glycines* on soybean, *H. schachtii* on sugarbeet and *Brassica* spp., and *Globodera* spp., have much genetic variability, resulting in ongoing challenges in extending the durability of resistant cultivars. Nevertheless, because of the associated crop losses and the intimate host-parasite relationships for root-knot and cyst nematode taxa, research directed toward developing host resistance has been very successful for a number of crops.

The migratory endoparasitic lesion nematodes (*Pratylenchus* spp.) and the burrowing nematode (*Radopholus similus*), although obligate parasites, have "hit and run" host-parasite relationships that depict a less specialized level of parasitism. As they feed, both females and males (if present) of these nematodes move through root tissues, causing cell damage and root necrosis. Thus, the symptoms associated with these pathogens are similar to those induced by root-attacking fungi such as *Rhizoctonia solani* and *Pythium* spp. Because of difficulties in producing suitable inocula, the lack of distinctive symptoms or signs, and limited sources of resistance (if any), efforts toward developing host resistance have been rather limited with both of these nematode groups (82, 110).

The ectoparasitic nematodes were overlooked as potentially important to agriculture for almost 100 years after the discovery of the root-knot nematode. While some ectoparasites are sedentary in their parasitism (*Mesocriconema*), others are migratory (*Belonolaimus* spp., *Xiphinema* spp., *Paratrichodorus* spp.), all of which were ignored until the classic work of Christie and Perry (30). Some nematologists have suggested that these ectoparasites be considered as browsers rather than true parasites. However, a number of these nematodes, including *Mesocriconema xenoplax* and some *Xiphinema* species induce the formation of feeding cells in host roots (50).

DISCOVERIES THAT CATALYZED THE SCIENCE OF PLANT NEMATOLOGY

In addition to the development of methodology for clearly establishing nematodes as plant pathogens and the discovery of ectoparasitic forms of nematodes, I believe that four other breakthroughs were crucial to these parasites receiving worldwide study as plant pathogens. The first of these discoveries was effective nematicides, starting with the soil fumigant D-D (1,3-dichloropropene-1.2-dichloropropane) in 1943. This finding by Carter in Hawaii provided an efficient tool for preventing crop loss due to nematodes and for demonstrating nematode damage to crops in fields. The development of agronomically acceptable nematode-resistant crop cultivars also was an invaluable tool for assessing losses to nematodes as well as proving their damage potential (25). The discovery that an ectoparasitic nematode (*Xiphinema index*) vectors the grape fan-leaf virus (45) opened another new area of nematological research. Subsequent work showed that a number of ectoparasitic nematodes in the Dorylaimida (*X. american*, *X. diversicaudatum*, *Trichodorus* spp., *Paratrichodorus* spp., *Longidorus* spp., *Paralongidorus* spp.) also vector certain viruses (93), whereas no endoparasite has been shown to serve as a virus vector.

A definitive explanation as to why nematode taxa that vector plant viruses are limited to the migratory ectoparasites (longidorids and trichodorids) remains to be elucidated. Taylor & Brown (93) concluded that the relative large diameter of the food canals (lumen) in the esophagi of the members of these groups provides ample sites for virus retention. They also noted that the longidorids differ from other major nematode groups by having the duct of their dorsal esophageal gland join the lumen in the posterior rather than the anterior portion of the esophagus. Specificity of virus transmission by nematodes may involve the interaction of complementary molecules at their point of contact as well as the mechanism of dissociation (93). Of interest, the virus vectors have feeding spears (odontostylets) that apparently evolved from a "tooth," but most other plant-parasitic species (and non-virus vectors) have a stomatostyle that evolved from a closing of the buccal capsule (stoma) walls.

Lastly, the frequent nematode (especially *Meloidogyne* spp.) predisposition of plants, including related effects on host physiology and root architecture, to attack by fungi and bacteria is well documented. These effects included negating host resistance to certain fungal and bacterial pathogens (1, 79). This type of disease complex has necessitated the development of multiple-pathogen resistance in crops such as tomato and tobacco. Certain nematodes such as the soybean cyst (*Heterodera glycines*) cause much of their damage by suppressing nodulation and nitrogen fixation by *Bradyrhizobium japonicum* (14, 48).

I believe that some of these landmark discoveries had negative as well as positive impacts on the development of nematology. The focus only on plant-parasitic species restricted research on the possible beneficial or detrimental effects of microbivorous nematodes and many soil rhizobacteria in the soil environment until recently. Nematicides, while providing economic benefits, inadvertently slowed the development of nematology as a science. Too many person-hours were directed toward assessing the efficacy of these pesticides on plant parasites. Also, related to Rachael Carson's 1962 explosive book (26) on the negative impact of pesticides on health and the environment and subsequent EPA programs, a number of the key nematicides were eventually removed from the market. This greatly reduced the funds for applied nematological research as well as restricting the management options for the grower. Thus, this situation has resulted in a near void in options for nematode management. Also, because funds and research efforts were allocated for nematicides at the expense of basic biology, nematology lags behind other areas of plant pathology in developing alternatives for nematode management. Furthermore, with limited developmental research on new chemistries and potentially safer compounds, almost no new nematicides have been released during the past three decades. A positive recent outcome of nematicide restrictions has been the deployment of IPM approaches that have contributed to the ongoing development of a more comprehensive, holistic and environmentally sound strategies and systems for managing nematodes (12, 78).

EVOLVING RESEARCH THRUSTS

Like most agricultural disciplines, nematological research is undergoing a revolution. The evolution of the nematology group in plant pathology at N.C. State University during the past four decades is discussed briefly as representative of the related changes in the discipline across much of the United States and other countries. Significant progress was made toward enhancing our understanding and clarification of the taxonomic and phyletic relationships of root-knot and cyst nematodes as well as characterizing nematode fine structure. This work by H. Hirschmann, A.C. Triantaphyllou and associates included the integration of classical taxonomy with genetics and biochemistry (35, 46, 97, 98). Related contributions included characterizations of the cytogenetics of these nematodes, including karyotypes, degree of ploidy, DNA content, and chromosome behavior as well as gametogenesis, oogenesis, and mode of reproduction. Other contributions by A.C. Triantaphyllou encompassed the elucidation of sex differentiation in nematodes as related to the environment and genetic factors, the genetics of parasitism of the soybean cyst nematode, and the utility of biochemical characteristics of nematodes in taxonomy. Much of this research was interfaced with the "International *Meloidogyne* Project," led by J.N. Sasser (84). He and associates characterized the morphological, cytogenetic, and differential host variation per population of a world collection of root-knot nematodes (8, 83, 84). Cropping systems for managing nematodes also were developed (12, 59, 83). The focus of a related program concerned the impact (damage thresholds and functions) of major nematodes on crop growth and yield, including effects of infestation levels, soil parameters, and general environment (11, 58). In concert, the nematodes' spatial and temporal population dynamics were characterized as well as the development of improved population-assessment methodologies (8, 9). A similar project involved the development of damage thresholds and functions for nematodes on ornamentals as well as determining relative tolerance of given ornamentals to key nematode species (16). This information now serves as the database for the North Carolina Nematode Advisory Service. Neher and associates (70, 71) in another ecology-oriented program characterized the effects of cropping systems, geographic location, and edaphic factors on plant and other trophic groups of nematodes.

Additional projects at N.C. State involved the development of nematode-resistant cultivars; the elucidation of how nematodes predisposed plants to attack by associated fungi, bacteria, and other pests (2, 79); the integration of nematode control in IPM (2, 11, 12, 59, 96); and interactions of nematicides with other pesticides (89). The first soybean cultivar resistant to *H. glycines* 'Pickett' was developed by USDA scientists at N.C. State (23) as well as numerous nematode-resistant tobacco cultivars (31). The differential effects of *H. glycines* host races on soybean yield are often directly related to the nematode population's capacity to inhibit nodulation and nitrogen fixation (13, 58). Related physiological mechanisms involved in this systemic nematode-bacterial-host interaction include suppression of binding of bacteria to root hairs (48) and the accumulation of phytoferrin and starch granules in the limited number of nodules on nematode-infected roots (60). An associated effect of the resulting nitrogen deficiency is depressed photosynthesis (58). In contrast to the above mutually antagonistic interaction, *Meloidogyne* spp. and *B. japonicum* interact neutrally on soybean with nodules developing on root-knot galls and the nematodes developing in nodules. The extension specialists at N.C. State University continue to integrate diverse research findings (96), but now must manage applied research in order to formulate disease/pest management programs.

Graduate education was central to all of the above programs, with 10 to 15 graduate students usually pursuing degrees with nematological thesis projects annually. Many of these students were from allied departments at N.C. State.

The contributions coming from the above biology-ecology-genetics-morphology-taxonomy- and nematode-management projects set the stage for the era of modern molecular nematology at N.C. State University. Presently, three faculty members in the department have fundamental nematode research projects that focus on various facets of the genetics of parasitism/host-parasite relationships, transgenic host resistance, and biological control. In addition, research on developing nematode resistance and related genetics in selected vegetable and field crops is continuing in allied departments. Unfortunately, applied nematology at N.C. State has been greatly downsized and is now largely managed by two extension specialists. Undoubtedly, there were numerous reasons why applied research was diminished, including a decline in grower groups and their support, a shift from general plant pathology to very specialized research, and the opportunities offered by molecular biology. Graduate education, although still a critical program, also has been downsized with more of the research being conducted by technicians and postdoctorates. The ongoing changes in nematology at N.C. State are a microcosm of the discipline worldwide. Although these striking changes in nematology are resulting in exciting new information, questions about the loss of positions/projects and the future of the discipline are surfacing. For example, dynamic and stable graduate programs in plant pathology/nematology are essential for the future of the disciplines. I believe that each project leader, even with the increasing pressures to secure extramural funding, should have a balance between numbers of graduate students and research associates. During this transition period with much of agriculture entering the so-called golden age of biology (54), research scientists within Land-Grant and other universities must be innovatively productive, encompassing the rapidly changing research environment—without circumventing the concepts and mission of their institutions. This presence in cutting-edge research is essential to attract aspiring student scientists as well as retaining established faculty members (88). Although a significant number of nematologists are at the forefront of plant nematological molecular biology, I suggest that many nematologists in the United States still face the challenge of exploiting the opportunities offered by modern technologies.

As in the past, maintaining a critical base of research positions devoted to nematology and plant pathology for many governments and universities continues to be increasingly difficult (10, 88). Unfortunately, after reaching record numbers of professional positions as well as graduate student enrollments in the early 1980s, nematology across the United States and in several other countries has been severely impacted by downsizing. These losses were compensated for, in part, by major changes in focus in many instances, and greater collaborations within nematology and with other disciplines, including genetics/molecular biology, biochemistry, ecology, and the pest management areas. These research projects, often international in scope (33, 90), also are producing many exciting and promising advances.

Traditional Taxonomy/Systematics Interfaces with Molecular Biology

The first century of nematological research (1850s to 1950s) focused heavily on taxonomy/systematics and discovery of major nematode species in given geographic regions. For example in the United States, the burrowing nematode *Radopholus similis*, a major pathogen of citrus and banana, was shown to cause the spreading decline of citrus in Florida in 1953 (29); the citrus nematode *Tylenchulus semipenetrans* was found on citrus in California in 1912 (29); and the soybean cyst nematode *Heterodera glycines* in North Carolina in 1954. The latter nematode was detected in Brazil in 1992. Known and new species of plant-parasitic nematodes continue to be discovered in many developing countries (64). Such discoveries, combined with the characterization of hundreds of new species (including those of *Anguina*, *Belonolaimus longicaudatus*, *Bursaphelenchus*, *Criconemella*, *Longidorus*, *Meloidogyne*, *Paratrichodorus*, *Pratylenchus*, *Xiphinema*), provided crucial thrusts to the development and support of nematology.

Today, molecular genetics, in addition to validating most classically delineated nematode species, provides new insight for systematists and general nematologists (80). As the genomes of nematodes in diverse taxonomic and biological groups are elucidated, understanding of their evolutionary and biological relationships will be forthcoming. Although molecular identification kits for multitaxa (including subspecies or host races/pathotypes) remain to be utilized for nematodes, DNA probes are being developed for the major plant-parasitic species (80). An example of ongoing use of DNA probes is found with the cereal cyst nematode *Heterodera avenae* and associated pests where in Australia they are deployed for diagnostic/advisory purposes (J. Currans, personal communication). These advancements are especially important for supplementing the rapidly declining classical taxonomic component of nematology.

C. elegans, the Model Nematode

As indicated previously, the early and ongoing research achievements on the model nematode *C. elegans* have provided an invaluable resource for plant and soil nematology as well as for biology and genetics in general. The early work of Doughtery and associates (34) provided the concepts and methods of axenic and monoxenic cultures. The initiation of the research using *C. elegans* by Sidney Brenner in the 1960s resulted in a large number of worldwide research projects on this nematode. The openly shared research advancements on the developmental biology—life cycle, cell lineage, embryology, survival mechanisms including dauer larvae, biochemistry, and genetics—has offered a rapidly growing information resource for the scientific community at large. The project initiated by Sulston and associates to construct a physical map of the entire genome of *C. elegans* in the mid-1980s and the publication of the complete genome of *C. elegans* in 1998 contributed much to opening genomics as a discipline (19, 21).

The resulting genome sequence of *C. elegans* is an invaluable resource for the study of plant- and animal-parasitic nematodes. The related genetics in developmental biology and pathways/processes, including vulva formation, the dauer larvae pathway, programmed cell death, and underlying biochemistry apply to insects, mammals (including man), as well as nematodes and likely other organisms

(19). For example, Sulston's delineating cell lineage and the role of cell death in *C. elegans* and Horvitz's identifying a number of genes that control this programmed suicide brought new insight on the developmental biology of that animal and all of its cells. While the *C. elegans* model now serves as an immense resource for investigating systems and genes in parasitic nematodes, the open collaboration/cooperation by the involved scientists in many laboratories around the world also is serving as a fruitful model for plant nematology. Of interest, the 2002 Nobel Prize in Medicine was awarded to Sidney Brenner, H. Robert Horvitz, and John Sulston for their pioneering research on the developmental biology (organ development and programmed cell death) and related molecular genetics of *C. elegans*. Although this milestone does not encompass plant and soil nematology, it brings much attention to nematodes.

Physiology, Molecular Biology, and Genetics of Host-Parasite Relationships: Parasitism

Although much information on the physiology of plant-parasitic nematodes is now available (33, 37, 50, 51, 77), research in this area until recently has lagged behind that of animal-parasitic forms and *C. elegans*. This situation is due to the challenge of securing sufficient axenic material of these obligate parasites. Biochemical pathways and developmental biology/cytogenetics in the nematodes themselves, survival mechanisms (often diapause with host reactivation), attraction to hosts, parasitism genes, induction of feeding cells in hosts, role of sex hormones in reproduction, host-resistance mechanisms, and predisposition of host to attach by fungi or bacteria have been partially elucidated.

The specialized equipment of plant nematodes for attacking their hosts includes extensive nervous and behavioral systems, feeding spears (stylets), and esophagi with specialized secretory glands (33, 41, 50, 51, 77). As indicated earlier, a principal emphasis of the recent nematological research concerns the molecular genetics of the host-parasite relationships of root-knot and cyst nematodes, which involves a cascade of physical/anatomical and biochemical interactions. These events are most striking in the elaborate feeding cells that are induced by the nematode infective juveniles and are their sole food source. A number of molecular approaches are being utilized to address genes and gene expression in the nematode feeding sites (17, 18, 33, 41, 47, 49). This encompasses ongoing investigations on nematode parasitism genes as well as modified host-gene functions. As extensive treatments of this ongoing research are available (33, 37, 47, 49, 90), only a few examples of recent developments follow.

An esophageal subventral gland cell-specific monoclonal antibody was employed to isolate and clone the first cellulase gene (β-1,4-glucanase) from an animal—*Globodera rostochiensis* and *H. glycines* (33, 90). Subsequent contributions showed that other endoparasitic and ectoparasitic as well as mycophagous nematodes possess one or more cellulase genes (33, 41). A pectate lyase gene expressed in the esophageal glands of *M. javanica*, *H. glycines*, and *Globodera* *rostochiensis* has been cloned (33). Based on detailed characterizations of the nematode cellulases and comparisons with those from various organisms, cellulases from cyst and other plant nematodes were found to have their greatest similarity to bacterial endoglucanases. Thus, these and related findings indicate that some parasitism genes (cellulases) in plant nematodes may have been acquired from bacteria via horizontal gene transfer, and this surprisingly includes ectoparasites as well as endoparasites (18, 33, 90). While the origin (where and when) of cell-wall degrading enzymes and nature of plant response to their attack remain to be definitively resolved, plant pathogens apparently are copy cats (54). Thus, an ancient relative of the bacterial-feeding *C. elegans*, lacking the genes required for parasitizing plants, may have acquired cellulases, pectinases, and possibly other genes for parasitism from bacteria—eventually giving rise to root-knot, cyst, and other plant parasites. Still, recent findings suggest that nematodes have evolved their own set of tools to enable them to parasitize plants (41, 47, 49). A fascinating recent discovery related to nematode parasitism genes is the large number of candidate parasitism genes that encode novel proteins. Remarkably, over 70% of the parasitism genes identified have no homology with functionally annotated genes in the databases. These pioneer parasitism genes could represent genes specific for nematode parasitism of plants, a hypothesis supported by the unique and complex interactions that many sedentary endoparasitic nematodes have with their host plants. As Keen & Roberts (54) indicated, the golden age of biology with its revolutionary techniques is now extending into areas such as plant nematology that earlier had been impenetrable.

Gheysen & Fenoll (41) have provided a comprehensive synopsis of parasite and host genes that are or could be involved in nematode parasitism of plants. Of interest, genes at feeding sites for cyst or root-knot nematodes may be upregulated, whereas others are down-regulated (17, 18, 41). This research work is bringing new understanding to the nature of nematode parasitism of plants.

Host Resistance, Including Genetic Engineering

Classical research directed toward the development of agronomically acceptable host resistance to nematodes has been under way for almost a century (25, 110). Successful projects have focused largely on endoparasitic species, especially sedentary species that are easily cultured and produce large numbers of eggs that can be used in related tests. Exceptions include *D. dipsaci*, which has a highly persistent dauer juvenile stage, and *R. similis*. Very limited progress has been achieved with less specialized ectoparasites and most migratory endoparasites. Related problems for these pathogens include the ready availability of adequate inoculum, efficient assessment procedures, and the fundamental issue of their having less specialized host-parasite feeding relationships, including a lack of selection pressure for the evolution of host resistance. As with other plant pathogens, genetic diversity and adaptability of most nematode species pose challenges for maximizing the durability of host resistance. A major example of this problem is the genetically diverse soybean cyst nematode *H. glycines* (82, 110).

The very limited available options for managing nematodes on most crops call urgently for new tactics. Endeavors to genetically engineer crop resistance to these pathogens show much promise for root-knot and cyst nematodes, but transgenic crops with resistance to these pathogens remain to be deployed. Major strategies employed to bioengineer host resistance to plant nematodes include: (*a*) the transfer of natural resistance genes to susceptible crops; (*b*) disruption of biochemical signals between nematodes and plants during the parasitism processes; and (*c*) expression of nematode toxic proteins in plant cells (101). Progress in developing conventional host resistance (81, 82, 110) and genetically engineered resistance (4, 76, 101) has been well documented. Williamson (105) and associates cloned the *Mi* gene in root-knot resistant tomato, but attempts to utilize that gene in tobacco failed. Cai et al. (24) cloned a resistance gene from wild sugar beet and developed a line of sugar beet resistant to *H. schachtii*. Transgenic lines of tobacco with the nematode-responsive element of the promoter *TobRB7* gene to give an antisense-*TobRB7* construct provided a moderate level of root-knot resistance (76). Transgenic plants with introduced proteinase inhibitors also provide significant control of cyst and root-knot nematodes (4). [Current information on this topic is presented in H.J. Atkinson et al., this volume.]

Progress in Ecological and Quantitative Nematology

Ecology has been central to the study of plant-parasitic nematode species for the past five decades, with the focus largely on given pathogens, their hosts, the physical environment, and associated fungal, bacterial, and viral parasites of crops (72). Potential interactions with other soil fauna-microflora have been considered only recently. While most plant nematologists worked only with plant-growth suppressing nematode species (11, 15, 16, 64), Yeates (108) showed that total numbers of nematodes, including large numbers of microbivorous forms, were positively related to the growth of sod grasses. Similarly, in a rotation study, numbers of microbivorous nematodes were positively related to increased yield of cotton and peanut versus the suppressed yields by plant parasites (94). Sod crops such as tall fescue greatly reduce population levels of root-knot nematodes and other pathogens of tobacco while enhancing soil structure and water-holding capacity (73). Other cover crops also suppress plant-parasitic nematodes and other soilborne pathogens (65). Among soil treatments that included selected bacteria and/or nematodes, Ingham et al. (52) found that a combination of soil bacteria and bacterial-feeding nematodes resulted in the greatest rate of plant growth. Nematodes play a significant role in soil food webs (12, 39, 40, 109). In addition to interactions at different levels, various trophic groups of nematodes are involved in nutrient cycling, including enhanced carbon and nitrogen mineralization. Plant growth–promoting bacteria are now known to induce a significant level of systemic host resistance to certain nematodes including some root-knot and cyst species (12).

Research on the quantification of nematode inoculum potential, population dynamics, and modeling host responses has provided invaluable databases for integrated pest and crop management. Of the many scientists who contributed to these areas, the key pioneers included Jones (62), Oostenbrink (75), and Seinhorst (87). The related construction of comprehensive computer simulation models for the above systems (38, 63, 67) proved to be useful teaching-research tools. However, like many other pest simulators, their promise of delivering comprehensive pest-problem-management systems failed to materialize. Unfortunately, the complexity of cropping-pest-environmental systems is too great and variable over space and time to be described and programmed via current technology (R. Stinner, personal communication).

NEMATODE CONTROL: SOIL BIOLOGY-BASED INTEGRATED MANAGEMENT

As indicated earlier, the 1940s discoveries of effective soil-fumigant nematicides resulted in much of the research on nematode management being shunted to control via pesticides. Fortunately, a number of comprehensive IPM grant programs (during the 1970s to 1980s) included nematodes, giving renewed emphasis to a more comprehensive approach. The traditional strategies for nematode management were limited largely to exclusion, reduction of initial infestations, and suppression of the rate of reproduction. Unfortunately, the overriding need for information on the ecological interactions of plant nematodes with various soil microflora and fauna has limited success in their biological control. This deficiency includes our fragmented understanding of the diverse factors affecting potential biological control agents.

Biological Control

The notion of using another organism to control plant nematodes dates back to 1881 when Kühn was testing trap crops as a means of managing the sugar beet cyst nematode *H. schachtii* (61). Instances of suppressive soils to plant-parasitic nematodes, due to fungi, bacteria, or other antagonistic organisms, have been documented (27, 56, 92). *Pasteuria penetrans*, an obligate bacterial parasite of nematodes, is responsible for the suppressiveness found in a number of soils (27). However, only a few commercial biocontrols (mostly fungi) for plant-parasitic nematodes have been deployed, with only limited success. A very promising strategy for biocontrol of soilborne plant pathogens is the exploitation of plant-growth promoting rhizobacteria. For example, the use of velvetbean in rotation with soybean enhances the activity of rhizoshere bacteria, which proved to be antagonistic to cyst (*H. glycines*) and root-knot (*M. incognita*) nematodes (57). A number of rhizosphere bacteria may suppress a range of plant pathogens/pests, including fungi, bacteria, nematodes, and insects (12, 57, 104).

To date, the greatest success for biocontrols involving nematodes has been the utilization of entomopathogenic nematode species for controlling certain insects (106). *Steinernema* and *Heterorhabditis* species are parasitic on a wide range of insects and transmit bacteria that are lethal to their insect hosts. Thus, they are highly suitable for biological control of a range of insects including a number of species of beetles, weevils, wood-tunneling insects, *Lepidoptera* larvae, bark beetles, and flies (106). Enhanced understanding of soil biology/ecology should open new and potentially rewarding horizons for these endeavors with plant-parasitic nematodes (12, 56).

Ecology-Based Management/Cropping Systems Including Durable Host Resistance

The idea of expanding ecological research on nematodes beyond that of soil environment and other soilborne plant pathogens has been pursued only during the past two decades (12, 39, 52, 70, 71). For example, Ingham et al. (52) conducted one of the first studies to document the positive effects of a combination of microbivorous nematodes, fungi, and bacteria on soil nutrient cycling and plant growth. Today, promising advances related to plant and soil health include the impact of plant growth–promoting rhizobacteria on nematode/pathogen suppression in various cropping systems, importance of nematode diversity and role of these organisms in nutrient cycling, associated effects of other microflora-microfauna on beneficial and plant-parasitic nematodes, and other factors affecting the activities of these soil communities (12, 40, 57, 78). Molecular and other analytical technologies as well as augmented computer systems programs now increase research options for these complex soil environments.

Combining Nematode Control with Sustainable and Organic Agriculture

The more than twofold increase in agricultural production in the United States since 1945 resulted largely via improvements in conventional farming systems (3). Today's goal of sustaining agricultural productivity while protecting the environment and improved food quality and human health presents nematology and other pest-protection disciplines with an enormous challenge. Compounding the challenge are the rapid increases in organic production, 10% to 20% per year, (with its great restrictions on the use of pesticides and exclusion of genetically modified organisms) and the loss of the most effective nematicides. For example, the phase-out of methyl bromide will require the development of highly effective alternatives for managing nematodes and other soilborne pathogens/pests of high-value vegetable and fruit crops. Undoubtedly, sustainable systems will require multiple strategies and tactics, and related organic production will demand even greater research, especially for sandy soils that favor plant-parasitic nematodes and disease complexes.

Precision agriculture technologies have some potential in nematode management, but strategies to overcome the high cost and other problems inherent in nematode population assessments are needed. Still, site-specific management technologies e.g., global positioning systems (GPS) and geographical information systems (GIS), may facilitate a reduction of nematode management costs in some intensive cropping systems (74, 107). For a few nematodes such *H. glycines* on soybean that affect foliage color and density, a combination of remote sensing and GIS technologies could become effective tools for nematode population assessments and their effects on crop yield (74). For specific-site nematode management, however, Evans et al. (36) showed that large-scale sampling for potato cyst nematodes can involve serious problems regarding sampling and nematode inoculum potential that would likely result in misleading field maps. In contrast, Shomaker & Been (86) developed the very precise Flevoland simulation model, based on intensive sampling (a large soil sample for each meter) in selected portions of potato-cyst infested fields, that facilitated the identification of scattered infestation foci. Application of the above model and sampling in the Netherlands could decrease nematicide usage by 86% in fields with highly contagious dispersal patterns of cyst nematodes.

With much increased knowledge and understanding of ecology-based crop-disease management, nematode control still will be crucial for achieving sustainable food and fiber production. Cover crops and carefully developed rotations that include nonhosts and durable host resistance result in increased soil organic matter; this, in turn, contributes very significantly to the increase of antagonists of plant pathogens (65). However, the build-up of soil organic matter is a long-term process and is heavily influenced by soil temperature and moisture. In California, Poudel et al. (78) found that after 8 years, there was a 10% increase in low-input plots and 20% increase in organic plots versus conventional plots. Benefits of the greater organic matter on soil quality included a reduction of soilborne diseases, greater pools of P and K, elevated microbial biomass and activity, and increased soil water-holding capacity. Thus, a central goal for sustainable crop production should be the development of sufficient information and understanding that cropping systems can be synchronized to effect a biological symphony—with all biocontrol and antagonistic agents in syncrony within a balanced agroecosystem. This would include increased numbers of plant-growth promoting bacteria, microbivorous nematodes and organic matter, but greatly depressed numbers of plant pathogens.

EDUCATION PROGRAMS

The first (1880–1920) generation (led by Atkinson, Bastian, Bütschli, Cobb, De Man, Goldei, T. Goodey, Filipjev, Kühn, Ritzema Bos, among others) combined with the larger second (1920–1960) generation (led by Allen, Chitwood, Christie, De Coninck, J.B. Goodey, Linford, Schuurmans Stekhoven, Steiner, Taylor, and Thorne) of nematologists developed an extensive information resource on the biology, anatomy, taxonomy, and control of the major endoparasitic plant nematodes (85, 95). In the United States, many early nematologists were USDA employees, but they made major contributions toward the education of young nematologists in the country. The Beltsville, Md, group, initially led by Cobb and later by Steiner, subsequently followed by Taylor, Good, and others, was long the only center of nematology in the country. Competition between those located in the eastern region and the western states led Thorne (one of the few early western nematologists) to suggest that eastern second-generation nematologists tended to ignore some of the basic facets of the science, especially permanent slide collections for taxonomic research. Thorne's training of Merlin Allen in nematode taxonomy/systematics and Allen's subsequent development of a graduate program eventually resulted in the organization of the only two academic departments of nematology in the United States (at the University of California at Davis and Riverside). Allen taught the first nematology graduate-level course in the country at U.C. Berkeley in 1948, and moved to Davis in 1958. Through a collaborative program between the University of Maryland and the USDA at Beltsville, Steiner directed the graduate training of a number of third-generation U.S. nematologists, including Sasser, Jenkins, Tarjan, and Cairns. Other early centers for education in nematology were soon established across the United States.

An extensive demand for nematological courses and programs developed only after World War II. During the early 1950s, however, many plant pathologists, entomologists, and other agricultural scientists, due to the lack of PhD graduates with expertise on nematodes, trained themselves to work in the field of nematology. These endeavors were enhanced through the establishment of intensive short courses offered at certain universities. Some courses were sponsored by interested chemical companies, and others through Regional Nematology Research Projects. The 1959 "Southern Regional Graduate Summer Session in Nematology" at N.C. State involved a mammoth collaborative program with invited lecturers from across the United States and several other countries. The resulting 1960 textbook, *Nematology,* edited by J.N. Sasser and W.R. Jenkins (85), was used widely. A similar course (developed by W.F. Mai) was also offered shortly thereafter at Cornell University.

By the early 1980s, highly active educational centers for nematology were ongoing at many universities across the country. Large numbers of prospective graduate students were interested in the various facets of agricultural sciences, including nematology and plant pathology. For example, many more highly qualified applications came to the department of plant pathology at N.C. State than could be accommodated. As discussed by Keen (53), that situation has changed, as most U.S. students are no longer interested in these disciplines. With fewer graduate students and with the greater needs for specialization in related disciplines, the number and structure of nematology courses have changed dramatically. The challenges related to recruitment, curricula, support, and placement of aspiring nematologists (10) and plant pathologists (53) will continue to receive much attention.

INTERNATIONAL PROGRAMS: A TRADITION IN NEMATOLOGY

The developmental phases of nematology benefited much through collaboration and educational programs in Europe. As indicated earlier, Cobb earned his doctorate in Germany and his mastery of the field was instrumental in forming the nematology division in the USDA. The publication in 1941 of *A Manual of Agricultural Helminthology* was the result of collaboration between Filipjev in

USSR and Schuurmans Stekhoven in The Netherlands (32, 95). That manual together with *Plant-parasitic Nematodes and the Diseases They Cause* (43) and *An Introduction to Nematology* (28) were indispensable to early nematologists worldwide. European nematologists developed numerous international programs and meetings, and in the mid-1950s organized the European Society of Nematologists and facilitated publication of the first nematology journal *Nematologica*, now named *Nematology* (32, 103).

As a graduate student in the discipline during the mid-1950s, I benefited greatly from the continuing international exchange of information. For example, Seinhorst and Oostenbrink (The Netherlands), Jones (UK) and others provided the latest information on ecology, population assessments, crop responses, and management through their invited seminars and demonstrations. As a key component of the International *Meloidogyne* Project (IMP), Sasser and associates (84) and invited lecturers from around the world developed an even more extensive international course in nematology in 1984. The resulting two volumes, *An Advanced Treatise on Meloidogyne* (8, 83), along with many other publications of the IMP augmented the study of nematodes by more than 100 collaborators in 70 countries. Central facets of the IMP included worldwide training in nematological research/information transfer, educational support and materials, and extensive collaborative research on the ecology/habitat, physiology, biochemistry, and genetics of more than 1000 *Meloidogyne* populations (collected from cooperating countries). Getting to know many IMP collaborators and having them and other international graduate students work in my lab catalyzed my deep interest in world nematology. While the above developmental, educational, and informational exchange programs were at N.C. State University, others still are ongoing in other U.S. universities and other countries. However, support for international agricultural research has diminished greatly in recent years (88).

Despite the longstanding record of important collaborative international research on nematodes, recent changes in the types of research and personnel have brought this collaborative activity to the forefront. As with the *C. elegans* genome project, research on the molecular genetics of parasitism and host resistance requires enormous inputs. Recent progress in these areas (4, 24, 33, 37, 41, 90, 105) often involved international collaboration. This shift is due, in part, to the limited number of nematologists, the need for multidisciplinary inputs to address very complex issues, and downsized programs (including graduate research).

ROLE OF PROFESSIONAL SOCIETIES, THE INDIVIDUAL, AND THE FUTURE OF NEMATOLOGY

Professional societies provide unquestioned roles for all major disciplines. Members of small subdisciplines such as nematology, however, often feel lost in larger umbrella societies or institutional departments. To provide effective means of communication and exchange of information, more than 30 nematology societies have been organized. As a means of broadening worldwide interactions, there is now an International Federation of Nematology Societies, involving 14 nematology societies. These societies publish 12 journals that focus on nematology and are involved in the development of international congresses of nematology every 6 years (22). Although effective in these functions, the narrowly based societies may limit the horizons of many nematologists (22, 100). The expanding fundamental research on plant and soil nematodes is helping rectify this problem for many individuals. Nematology Societies, including The Society of Nematologists (SON), however, have been (100) and continue (22) to be challenged to take the lead in interfacing with closely related disciplines as well as fostering greater fundamental research. Bolla (22) concluded that SON is on the edge of continued success or on the abyss of failure. He further concluded that the outcome—success versus failure—"depends on the administration of the Society, on the involvement of the membership, and on the willingness to be open to new ideas, collaborations, and advantages of the decade of biology."

Because of the broad responsibilities and often-limited cutting-edge fundamental research of many nematologists in the USA, securing adequate funding is a continuing challenge. Still, support for basic studies is crucial for nematology and the future of its societies. Walker's (66) concept of a balance between applied and basic research with "one foot in the furrow" should well serve nematology and plant pathology today and into the future. Although this notion should not necessarily be at the forefront for fundamental research scientists, eventual practical applications of their research, including collaboration with applied nematologists/plant pathologists, is essential to ensure a sustainable food supply.

A number of SON symposia/colloquia on the future of nematology and a special study on the national needs and priorities in nematology research, education, and extension (10) have focused on this discipline. The report of the '94 group, sponsored in part by SON and the Cooperative State Research, Education and Extension Service (CSREES), was envisioned as a tool to offer guidance to administrators, granting agencies, and state and national groups concerned with research and funding. In contrast to the role of the American Phytopathological Society, we soon realized that a small society with no permanent staff could have only a very limited impact, if any, at the national level. Thus, the major benefactors of these endeavors have been the individual nematologists. Although the goals of the '94 study, including a renewal of graduate education in nematology and greater support for research/education, have not been fulfilled, several milestones related to the research priorities have been attained. The exciting research breakthroughs briefly mentioned earlier reflect these advancements.

CONCLUSIONS

In summary, I have had the privilege of participating in an awesome activity, including the log phase in the development of plant and soil nematology, and of meeting many of the pioneer researchers and educators. This involved working with a large number of graduate and postgraduate students—the highlight of my career. Plant nematology has reached a downsized level that, it is hoped, will be only temporary, rather than becoming a lost “specialty” group, as Walker warned in 1963 (102). The challenges of renewed emphasis on graduate education and funding constraints may continue for some time. However, extending recent milestone advancements to effect solutions to sustainable nematode-pest-crop management—including durable host resistance for root-knot and cyst nematodes, and other taxa—will provide a foundation for the future. Renewed interest and opportunities in graduate education are essential to ensure future scientists for this discipline. That success will be dependent upon increased highly productive and innovation research programs that answer fundamental questions and resolve pressing applied problems (22, 100). With the new research areas and tools of today—even with the many challenges, I envy the incoming graduate students.

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