

BIOLOGY AND MANAGEMENT OF  
SOYBEAN CYST NEMATODE

SECOND EDITION

EDITED BY

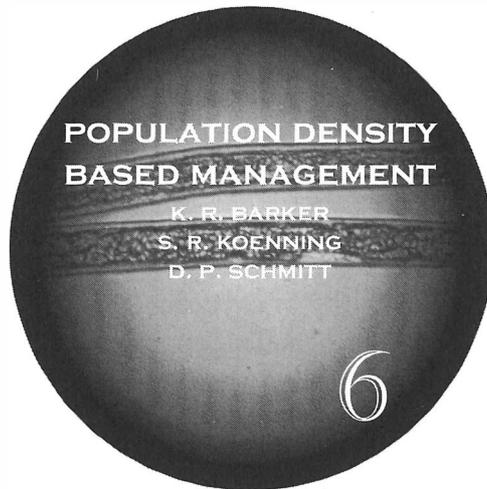
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Development of a program for the management of soybean cyst nematode can be most logically developed when it is based on data from assays. These assays provide numbers of nematodes per unit of soil or population density. In the simplest form, the detection of the nematode is the basis for implementing a management program. In an effort to add more precision, an economic or damage threshold based on a relationship of number of cysts, eggs and/or juveniles to expected crop yield is employed to predict loss. Sampling for predictive purposes is typically done several weeks to several months before planting. Consequently, a management decision needs to be made on a projection of the number of infective juveniles that will survive from sampling to planting (Ferris, 1987). These methods used for prediction are static and do not account for the dynamics of the agroecosystem.

After the discovery of soybean cyst nematode in the USA in 1954, the focus was on management, giving little attention to host-parasite interactions. The ease of control with nematicides, espe-

cially DBCP (Sasser and Uzzell, 1991), crop rotation (Sasser and Uzzell, 1991) and resistance (Brim and Ross, 1966), diminished the priority to understand the biology and population dynamics of the nematode. With the withdrawal of DBCP and EDB from the market and with the realization that the nematode had considerable genetic variability, some research efforts were shifted to understanding population behavior and survival in relation to crop response. The need for basic soybean cyst nematode population information in relation to crop damage was further stimulated by the recognition of the ability of soybean cyst nematode to survive for long periods, the related challenges posed by grower utilization of short-term rotations and the development of Integrated Pest Management programs.

Most diagnostic programs conducted by the Cooperative Extension Service, state agriculture departments, private consultants or research nematologists use the egg stage for diagnosis and prediction of crop loss (Tyłka and Flynn, 1999). Management based on egg count data is adequately reliable. Unfortunately, soybean yield losses from damage caused by soybean cyst nematode are still high because of the limited adoption of nematode-management programs. Even with a number of highly visible programs directed at managing this pathogen, sampling of fields to determine its presence is well below the level needed to optimize management. The laborious and time-consuming nature of sampling is the likely reason for the lack of adoption by growers.

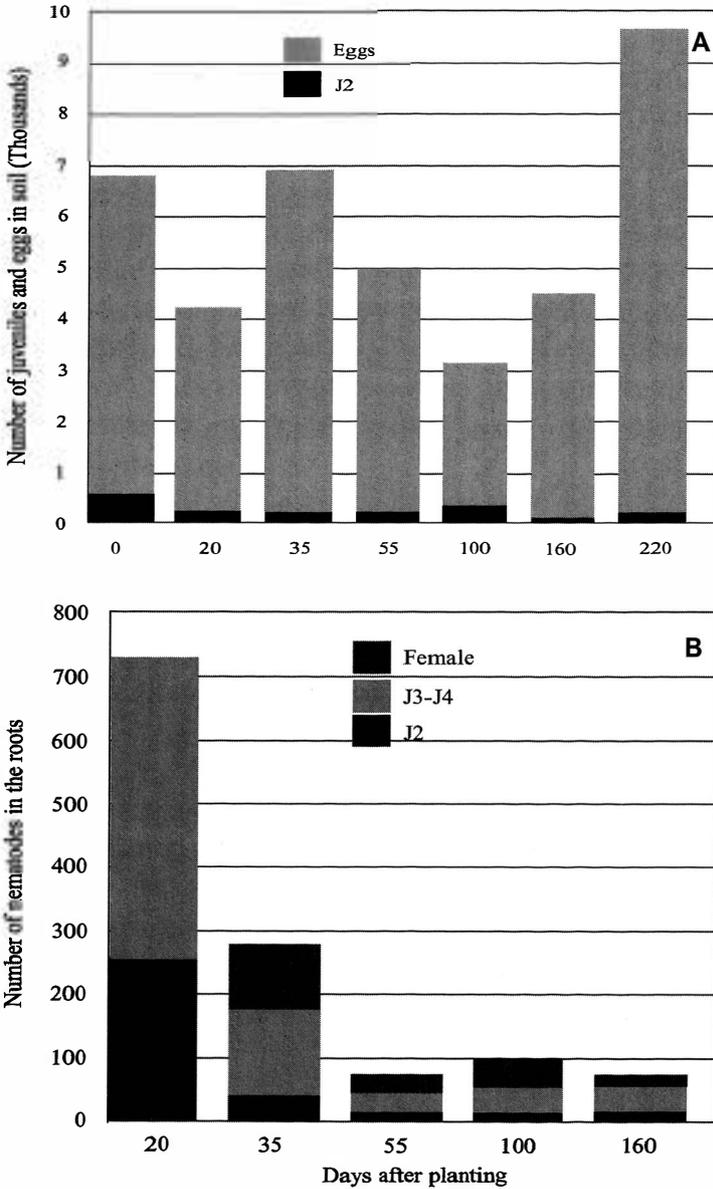
In order to understand the rationale for timing and methods of sampling, aspects of population dynamics will be presented that will show how populations of soybean cyst nematode fluctuate through time and how some factors influence these fluctuations. The reasons for sampling are concisely explained in the second section entitled "Predictive Sampling". This brief section is followed by a relatively in-depth discussion of practical damage and economic thresholds. The chapter concludes with an assessment of the need for new developments that could, if adopted, enable more effective management of soybean cyst nematode.

## POPULATION DYNAMICS

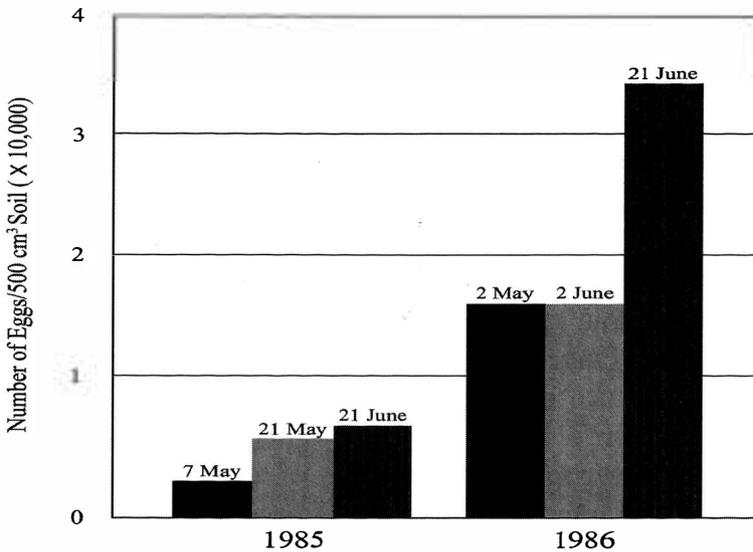
Interest in understanding population dynamics of soybean cyst nematode is based on the economic need to prevent this pathogen from increasing to damaging levels. In general, understanding nematode life cycles and the factors governing changes in their population densities is basic to understanding nematode distribution and related plant disease (Norton, 1978). The dynamics of populations are determined by two intrinsic factors: birth rate and death rate. Both egg production rates and life expectancy are genetically determined. These factors are modified by extrinsic factors including: host status, host vigor, environmental and edaphic factors.

A reliable population census requires knowledge of the location of the nematode in the soil profile and population fluctuations of the nematode life stages through time. With the widespread occurrence of soybean cyst nematode in the primary soybean producing regions, the assumption can be made that this nematode is present in most fields in measurable quantities, especially where symptoms of the associated host disease are evident. Thus, sampling should be done at times of the year that provides the best estimate of the population density that is likely to be present at soybean planting time. The sampling protocol needs to consider the spatial distribution of the nematode.

Host-parasite biology and the environment impact population fluctuations of soybean cyst nematode. In the spring when diapause is broken, eggs begin to hatch (Bonner and Schmitt, 1985; Koenning and Anand, 1991; Koenning *et al.*, 1996), a process increased by host plant root exudates (Schmitt and Riggs, 1991). During this period of hatching and penetration, the soil population of eggs and juveniles decline until the first generation is mature and begins producing eggs (Fig. 1A) (Bonner and Schmitt, 1985). Concurrent with the decrease in egg and juvenile numbers per unit of soil, large numbers of second-stage, third-stage and fourth-stage juveniles accumulate in the soybean root system (Fig. 1B). Then,



**Figure 1.** Temporal population changes of soybean cyst nematode life stages during a soybean growing season. A) Soil. B) Roots. (Sources: Bonner and Schmitt, 1985; Schmitt and Ferris, 1998).



**Figure 2.** End of growing season population density of soybean cyst nematode eggs in southeast Missouri from plots planted in early May, late May to Early June and late June. (Source: Koenning and Anand, 1991).

as females mature, there is a decrease in the number of third-stage and fourth-stage juveniles in the root system (Fig. 1B). From 28% to 56% of the juveniles that penetrate the roots of a susceptible soybean plant develop into adults (Acedo *et al.*, 1984; Schmitt and Riggs, 1989). After the first generation, number of the life stages will vary in their fluctuation pattern. As soil temperatures cool late in the growing season and plants mature, the number of juveniles and adult females decrease and the number of eggs increase with the onset of diapause (Bonner and Schmitt, 1985; Koenning and Anand, 1991; Schmitt *et al.*, 1983) (Fig. 1-2).

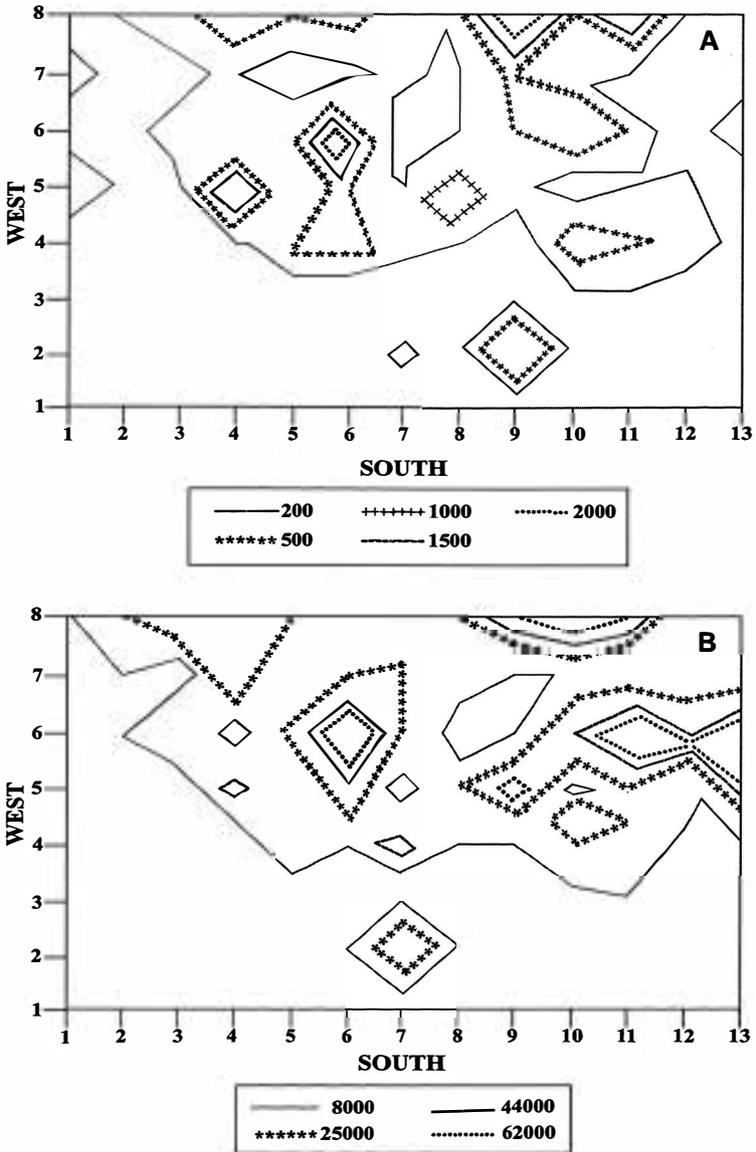
Under favorable conditions during the growing season, generations of soybean cyst nematodes likely overlap because infection of the root by juveniles is continuous over time (Alston and Schmitt, 1988; Bonner and Schmitt, 1985). In addition, there is variability in the rate of completion of life stages. Unfavorable

environmental conditions, such as drought, may prevent or slow hatching, penetration and development.

Over-winter or over-season survival of eggs varies by environment and time (Schmitt and Riggs, 1989) (See Chapter 5). Up to 100% of soybean cyst nematode eggs survive from fall to spring in several northern states in the USA (Riggs *et al.*, 2001). In North Carolina, winter survival varies from year to year, but at least 40% to 60% of the eggs survive over winter, whereas the survival rate in Florida is low. Soil factors (including texture, moisture and temperature), fungal parasites and production systems probably account for much of this variability (Chen and Dickson, 2004; Schmitt and Ferris, 1998). Some adaptations in diapause and other features of the population dynamics of soybean cyst nematode have likely occurred and are probably occurring as this nematode spreads to new habitats.

During the growing season, the use of nonhost crops results in population declines of soybean cyst nematode and is central to successful soybean cyst nematode management programs. In some environments, growing a nonhost for one to two years may be adequate to reduce the population density sufficiently to produce a profitable crop. However, growing a nonhost for several seasons may be necessary in other environments to reduce soybean cyst nematode populations to levels that will not damage a susceptible crop. This situation can be attributed to the capacity of the nematode to survive for many years in significant numbers in the absence of a host (Schmitt and Riggs, 1989).

The horizontal spatial distribution pattern of most plant-parasitic nematodes, including soybean cyst nematode, are usually aggregated (Fig. 3) and can be represented statistically by a negative binomial (Francl, 1986a; Shomaker and Been, 1999). Factors impacting relative horizontal distribution include: in-field variation of soil factors, distribution of weed hosts, cropping history, antagonists, parasites, soil erosion direction (wind and water) and direction of cultivation. For example, the orientation of nematode population densities usually parallels the direction of rows for row



**Figure 3.** Horizontal distribution patterns of soybean cyst nematode in a Greene County, North Carolina soybean field. A) juveniles and B) eggs. Note that the infestation patterns for eggs and juveniles are similar even though numbers of eggs are much greater. (Courtesy of K. R. Barker).

crops (Alston and Schmitt, 1987; Francl, 1986b). The horizontal distribution of second-stage juveniles (Fig. 3A) is similar to that of eggs (Fig. 3B). However, the number of eggs are typically much greater than that of the juveniles, a factor that can be very important in sampling. Regardless of the life stage assessed, the aggregated distribution pattern of soybean cyst nematode must be considered in assaying populations. The numbers generated from sampling could be incorporated into databases usable in "precision agriculture" application technology (Nutter *et al.*, 2002; Tylka *et al.*, 1998).

Just as horizontal patterns of spatial distribution vary from field-to-field and over time, the vertical spatial pattern of soybean cyst nematode varies by field and over time. Soil type and host-root growth patterns greatly impact the vertical distribution pattern of this nematode. Its greatest numbers typically occur in the upper 20- to 30-centimeters of the soil profile. However, considerable numbers of cysts may be found at much lower depths in some soils (Alston and Schmitt, 1987), especially in deep sandy soils.

## **PREDICTIVE SAMPLING**

Populations of soybean cyst nematode are assayed for a variety of reasons. These reasons include: detection, measuring abundance, determining changes in population density, especially as related to management practices, and determining genotype variability. The intensity of sampling depends on the purpose of the assay. Abundance and genotype variability are the most useful aspects of assays in predicting losses from damage caused by this pathogen.

Estimating the number of soybean cyst nematode with reasonable accuracy from infested fields in which the nematode population is usually highly clustered requires careful sampling of the field and maximum efficiency in extraction. Accuracy in determining the mean population density is associated with the number of cores per sample (Francl, 1986b). Collecting paired samples in

each field increases the precision of the population estimate (Schmitt *et al.*, 1990). In addition to these quantitative assays, assessment of HG Type (race) is needed for the selection of the most suitable resistant cultivar or cultivars (Koenning, 2000; Niblack *et al.*, 2003) (See Chapters 4 and 9). Extraction methods vary in their efficiency and thus influence the number of specimens isolated. The number of eggs gives a reliable estimate of the population density of soybean cyst nematode.

## DAMAGE AND ECONOMIC THRESHOLDS

Nematode damage functions are essential components in the formulation of thresholds for sustainable management practices (Noe *et al.*, 1991). They can be used to predict yield suppression and to calculate economic thresholds. Even though this approach employs a static concept, it is useful in understanding the system and also has utility for optimizing decisions for soybean cyst nematode management.

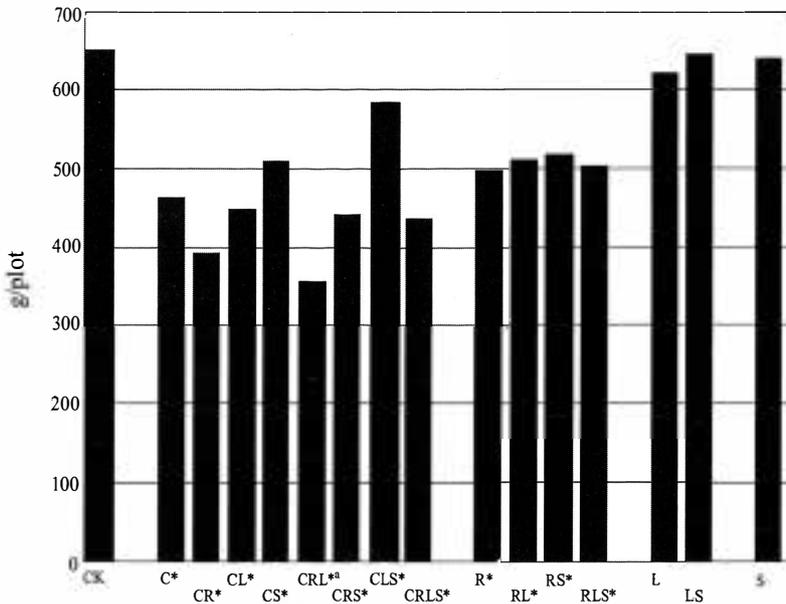
Thresholds for action in the management of soybean cyst nematode are based on the inverse relationships between the initial number of nematodes and crop yield. These inverse relationships were first described by Jones (1956), Seinhorst (1965) and Oostenbrink (1966) for potato cyst nematodes. They provided a logical basis for facilitating management decisions. Damage function models have been developed for several species of nematodes, including soybean cyst nematode (Schmitt and Ferris, 1998). The principle component of the damage relationship is based on the initial number of nematodes (i.e., the population density at planting). The initial population of soybean cyst nematode must be deduced because sampling is generally done several weeks prior to planting. Sampling of egg populations can be performed at any time prior to soybean planting but adjustments may be needed for mortality from the time of sampling to the time of planting. For fields with low levels of infestation, the probability of detection

can be increased using bioassays.

Some factors that affect damage to the soybean crop by soybean cyst nematodes include: host status, genetic variability of the pathogen, biological antagonists and environment (Schmitt and Ferris, 1998). Tolerance of soybean to soybean cyst nematode is impacted by the level of resistance in the host and the particular population of soybean cyst nematode (Koenning, 2000). The health of the juveniles and eggs affects the amount of damage caused by the nematode (Porter *et al.*, 2001). Site-specific factors (sometimes referred to as the 'law of limiting factors'), such as soil and weather, impact the soybean cyst nematode-soybean interaction (Schmitt *et al.*, 1987).

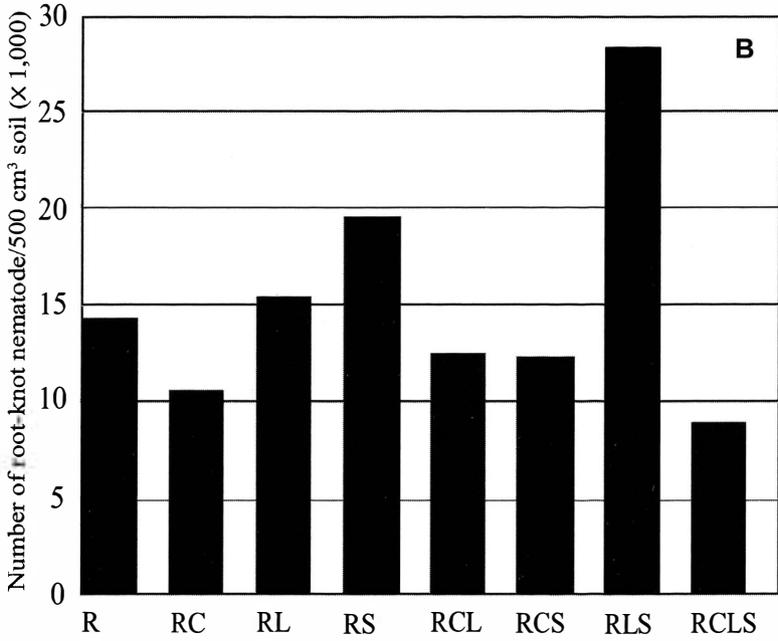
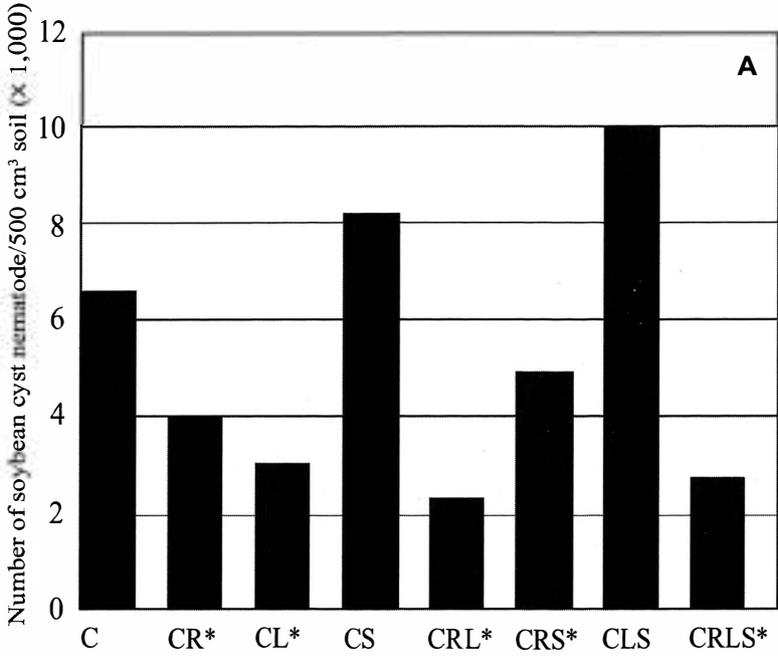
Host status and genetic variability of soybean cyst nematode involve complex interactions. The levels of soybean resistance to any given population of the nematode may vary depending on the source of resistance and the amount of resistance captured from the parents (See Chapters 4 and 9). Likewise, the expression of resistance by any given cultivar varies with population of the nematode. Most populations of soybean cyst nematode are mixtures of several genotypes. Even when a population is classified as a specific HG Type, there is usually a range of responses of a specific cultivar to the multitude of populations of that HG Type. The HG Types also vary in their mechanism of plant damage. For example, HG Type 2- (race 1) suppresses nodulation and nitrogen fixation much more than HG Type 0- (race 3) (Lehman *et al.*, 1971). The consequence is more plant damage by HG Type 2- (race 1) than by HG Type 0- (race 3) due to nitrogen deprivation.

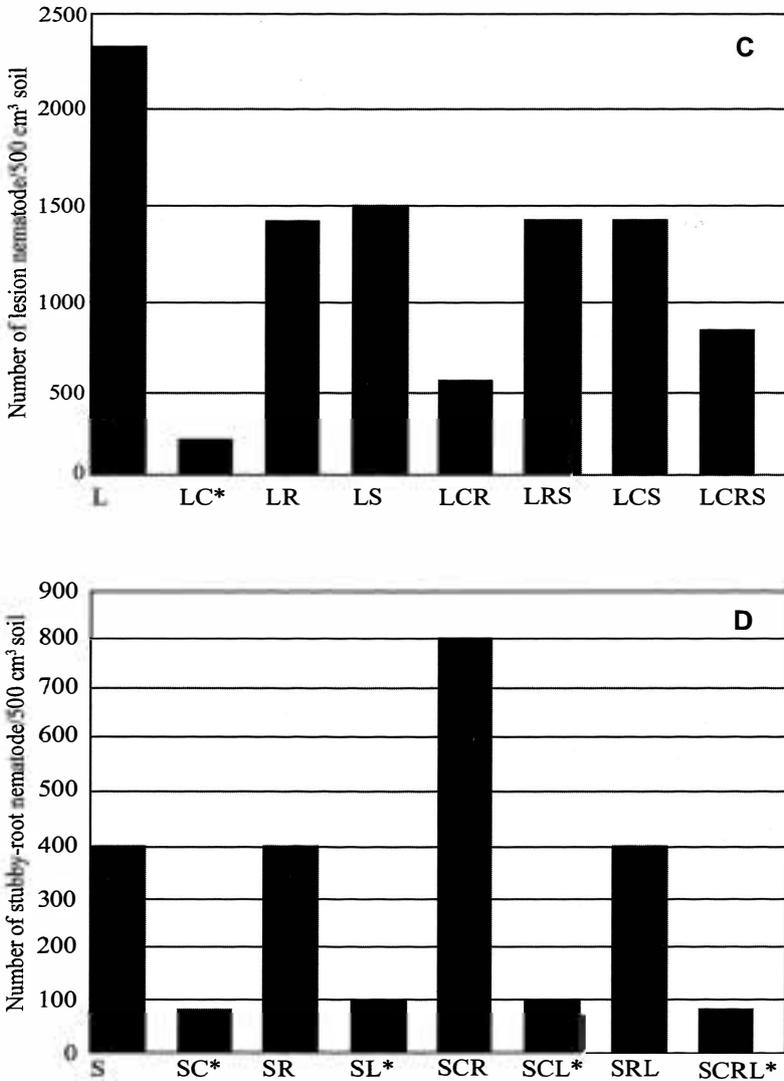
Many biological factors can alter nematode damage by affecting the vigor of the infective juveniles before and after hatching (See Chapter 11). For example, egg parasites can affect hatching and therefore alter expected crop yield (Chen and Dickson, 2004). Project leaders of some soybean breeding programs have been forced to relocate their nurseries because of severe decline of soybean cyst nematode populations (Hartwig, 1981). Similarly, continuous soybean in no-till plots in North Carolina resulted in near



**Figure 4.** Yield of soybean in microplots infested with soybean cyst nematode (C), southern root-knot nematode (*Meloidogyne incognita*) (R), lesion nematode (*Pratylenchus penetrans*) (L) and/or stubby-root nematode (*Paratrichodorus minor*) (S). CK = not infested (control). \* = significantly different from control ( $P < 0.05$ ); <sup>a</sup> = significantly different from soybean cyst nematode alone treatment ( $P < 0.05$ ).

zero population levels of soybean cyst nematode (Koenning *et al.*, 1995), probably resulting from biological control. In addition to predators and pathogens, polyspecific nematode communities develop on soybean and other crops that may modify the impact of each nematode in the community. In North Carolina, for example, nematode taxa associated with soybean cyst nematode include several species of root-knot nematode (*Meloidogyne* spp.), at least two species of lesion nematode (*Pratylenchus* spp.), stubby-root nematode (*Paratrichodorus minor*), dagger nematode (*Xiphinema americanum*), stunt nematode (*Tylenchorhynchus claytoni*), two or more species of lance nematodes (*Hoplolaimus* spp.), spiral nematodes (*Helicotylenchus* spp., *Scutellonema* spp.) and other nema-





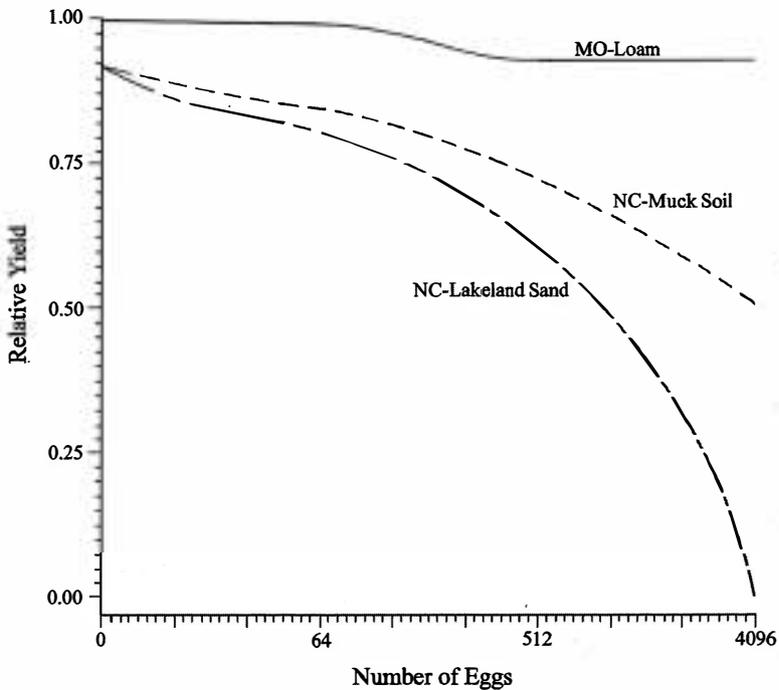
**Figure 5.** End-of-season population densities of soybean cyst nematode, southern root-knot nematode, lesion nematode and stubby-root nematode in single and polyspecific communities. A) Soybean cyst nematode (C), B) Southern root-knot nematode (R), C) Lesion nematode (L) and D) Stubby-root nematode (S). \* = numbers of nematodes are different ( $P < 0.05$ ) in the polyspecific community than in the nematode alone treatment.

todes. For example, a microplot experiment in North Carolina illustrates the interactive affects of soybean cyst nematode and some of the associated nematode species (Fig. 4-5). HG Type 2- (race 1) is so aggressive on soybean and damage is so severe that the presence of one or more of these other parasitic nematode taxa have only slight affects of the interactions between soybean cyst nematode and soybean yield (Fig. 4). The presence of southern root-knot nematode and lesion nematode had a negative impact on the reproduction of soybean cyst nematode (Fig. 5A). In turn, soybean cyst nematode suppressed reproduction of lesion nematode and stubby-root nematode (Fig. 5C-D).

Microbivorous nematode activity within nematode and plant communities, including soybean cyst nematode, is probably beneficial to the plant. This aspect has been largely neglected in nematode community research. Rhizobacteria, often associated with bacterial-feeding nematodes, can suppress the population development of a number of plant pathogens, including nematodes, and enhance plant growth (Barker and Koenning, 1998; Kloepper *et al.*, 1992). Population densities of bacterial-feeding nematodes can increase through certain cropping systems. Their numbers are directly correlated with yield of cotton and peanut (Taylor and Rodriguez-Kàbana, 1999). Cropping systems probably could be designed for soybean cyst nematode infested-farms that would favor the development of microbivorous nematode populations. This biotic community should be beneficial to the soybean crop.

Physical properties of soil are important determinates for the dynamics of soybean cyst nematode populations and the damage incurred. This nematode reproduces over a wide range of soil types (Koenning and Barker, 1995; Schmitt *et al.*, 1987). It often produces the greatest number of progeny in the finer textured soils but usually causes less damage in fine-textured soils than in course-textured soils (Fig. 6).

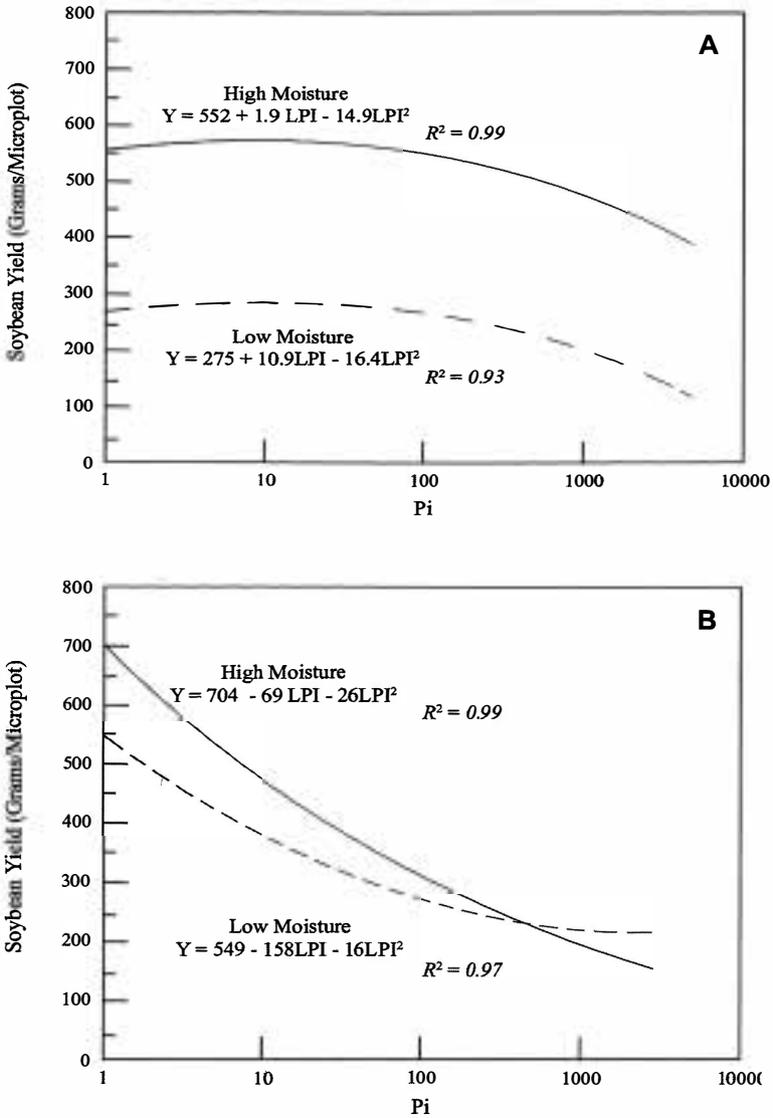
Soil oxygen and moisture content influence the nematode population. Considering only soil moisture, it is not easy to discern its effect on soybean cyst nematode population change and soybean



**Figure 6.** Effect of soil and soybean cyst nematode on soybean yield (MO = Missouri; NC = North Carolina) (Source: Barker and Noe, 1987).

studies and for management decisions. For identification, the nematode population must be sampled first and then the nematode extracted from the soil. Efficiency (time and cost) of sampling and assay needs to be improved for assessing population densities of soybean cyst nematode since the host crop has a relatively low value.

Even though precision agriculture technologies are not used today for soybean cyst nematode management, they do offer opportunities for more precise management (Nutter *et al.*, 2002). Global Positioning Systems coupled with Global Information Systems can provide growers and their consultants with cost-effective and timely means of diagnosing the cause of plant stress in soybean fields (Nutter *et al.*, 2002). Remotely sensed images



**Figure 7.** Impact of soybean cyst nematode on 'Ransom' soybean yield in microplots as affected by soil texture and moisture. A) Cecil Sandy Clay Loam. B) Norfolk Loamy Sand. Y = seed yield. LPI =  $\log_{10}$  of the initial population density (Pi) of soybean cyst nematode. (Source: Modified from Koenning and Barker, 1995).

indicating plant stress could be used to alert soybean growers when and where to check fields for the presence of soybean cyst nematodes (Tylka *et al.*, 1998).

Until the site-specific and precision agriculture technologies are widely adapted to soybean cyst nematode management, decisions for managing the nematode could be based on harvest indices obtained from yield monitor data (Copeland *et al.*, 1996). These data can be used to locate areas of fields with stressed plants (Schneider *et al.*, 1996; Tylka *et al.*, 1998) as a means of evaluating the cause of the lower yields. If soybean cyst nematode is present, then its numbers can be related to yield.

Besides the field diagnosis, the laboratory component is still essential since most identification and quantification of nematode populations are done with the aid of a microscope. Automated identification and counting has been proposed. Differentiating various nematode species in most cases can still be accomplished more rapidly with manual methods, even though an automated system reduces the time requirement for counting by 80% (Been *et al.*, 1996). In North Carolina, nematode identification and counting are determined manually, but the numbers are entered directly into the computer (Imbriani *et al.*, 1997). The numbers are converted into a flexible hazard-index system and written to a database. These databases can be used for Web-based decision thresholds, which integrate the numbers with information about host (cultivar) status and environmental effects.

In the future, computer recognition and counting systems coupled with molecular diagnostic tools could be vital aids for identification. Technologies that could be included for molecular diagnosis include: protein profiles (Ferris *et al.*, 1986), isozyme analysis (Esbenshade and Triantaphyllou, 1988), serology and DNA Protocols (Barker and Davis, 1996; Fleming and Powers, 1998). Fleming and Powers (1998) suggested that PCR-RFLP might become the method of choice for cyst nematode diagnostics because of the sensitivity and robust nature of this technique. In Australia, DNA-based probes for the identification of cereal cyst

nematode (*Heterodera avenae*) and other associated pathogens in soil samples are now employed commercially for advisory purposes (J. Curran, personal communication). Highly efficient and reliable DNA means of identifying all soybean cyst nematode biotypes remain to be developed. The goal is a system that is accurate, rapid, simple, sensitive and quantitative at both the species and subspecies levels.

Regardless of the technological sophistication for diagnosing soybean cyst nematode, educational programs for growers should enhance the level of adoption. However, adoption on a large scale may require incentives in addition to education. This will almost certainly require the involvement of social scientists.

## LITERATURE CITED

- ACEDO, J. R., V. H. DROPKIN, and V. D. LUEDDERS. 1984. Nematode population attrition and histopathology of *Heterodera glycines*-soybean associations. *Journal of Nematology* 16:48-57.
- ALSTON, D. G., and D. P. SCHMITT. 1987. Population density and spatial pattern of *Heterodera glycines* in relation to soybean phenology. *Journal of Nematology* 19:336-345.
- ALSTON, D. G., and D. P. SCHMITT. 1988. Development of *Heterodera glycines* life stages as influenced by temperature. *Journal of Nematology* 20:366-372.
- BARKER, K. R., and E. L. DAVIS. 1996. Assessing plant nematode infestations and infections. *Advances in Botanical Research* 23:103-136.
- BARKER, K. R., and S. R. KOENNING. 1998. Developing sustainable systems for nematode management. *Annual Review of Phytopathology* 36:165-205.
- BARKER, K. R., and J. P. NOE. 1987. Establishing and using threshold population levels. Pp. 75-81 in J. A. Veech and D. W. Dickson, editors. *Vistas on Nematology*. Hyattsville, MD: Society of Nematologists.
- BEEN, T. H., M. J. MEIJER, A. E. BENIERS, and J. W. KNOL. 1996. Using image analysis for counting larvae of potato-cyst nematodes (*Globodera* spp.). *Fundamental and Applied Nematology* 19:297-304.
- BONNER, M. J., and D. P. SCHMITT. 1985. Population dynamics of *Heterodera glycines* life stages on soybean. *Journal of Nematology* 17:153-158.
- BRIM, C. A., and J. P. ROSS. 1966. Registration of Pickett soybeans. *Crop Science* 6:305.

- BROWN, R. H. 1987. Control strategies of low value crops. Pp. 351-387 in R. H. Brown and B. R. Kerry, editors. Principles and Practices of Nematode Control in Crops. New York: Academic Press.
- CHEN, S. Y., and D. W. DICKSON. 2004. Biological control of nematodes by fungal antagonists. Pp. xxx in Z. X. Chen, S. Y. Chen and D. W. Dickson, editors. Nematology, Advances and Perspectives. Vol II. Nematode Management and Utilization. China: Tsinghua University Press. (in press).
- COPELAND, P. J., G. L. MALZER, J. G. DAVIS, J. A. LAMB, P. C. ROBERT, and T. W. BRUULSEMA. 1996. Using harvest index to locate environmental stress. Pp. 531-540 in P. C. Robert, R. H. Rust and W. E. Larson, editors. Proceedings of the Third International Conference on Precision Agriculture. Madison, WI: ASA, CSSA, SSSA.
- ESBENSHADE, P. R., and A. C. TRIANTAPHYLLOU. 1988. Genetic analysis of esterase polymorphism in the soybean cyst nematode, *Heterodera glycines*. Journal of Nematology 20:486-492.
- FERRIS, H. 1987. Components and techniques for integrated pest management threshold determinations for soilborne pathogens. Plant Disease 71:452-455.
- FERRIS, V. R., J. M. FERRIS, L. L. MURDOCK, and J. FAGHIHI. 1986. *Heterodera glycines* in Indiana: III. 2-D protein patterns of geographical isolates. Journal of Nematology 18:177-182.
- FLEMING, C. C., and T. O. POWERS. 1998. Potato cyst nematode diagnostics: morphology, differential hosts, and biochemical techniques. Pp. 91-113 in R. J. Marks and B. B. Brodie, editors. Potato Cyst Nematodes. Wallingford, UK: C.A.B. International.
- FRANCL, L. J. 1986a. Spatial analysis of *Heterodera glycines* populations in field plots. Journal of Nematology 18:183-189.
- FRANCL, L. J. 1986b. Improving the accuracy of sampling field plots for plant-parasitic nematodes. Journal of Nematology 18:190-195.
- HARTWIG, E. E. 1981. Breeding productive soybean cultivars resistant to the soybean cyst nematode for the Southern United States. Plant Disease 65:303-307.
- HEATHERLY, L. G., H. C. PRINGLE, G. L. SCIUMBATO, L. D. YOUNG, M. W. EBELHAR, R. A. WESLEY, and G. R. TUPPER. 1992. Irrigation of soybean cultivars susceptible and resistant to soybean cyst nematode. Crop Science 32:802-806.
- IMBRIANI, J., S. SAXENA, and D. BURNS. 1997. NEMAREC: a computerized predictive nematode-management recommendation system. Journal of Nematology 29:585 (Abstract).
- JOHNSON, A. B., K. S. KIM, R. D. RIGGS, and H. D. SCOTT. 1993. Location of *Heterodera glycines*-induced syncytia in soybean as affected by soil water regimes. Journal of Nematology 25:422-426.
- JONES, F. G. W. 1956. Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. II. Microplot and field plot results.

Annals of Applied Biology 44:25-56.

- KLOEPPER, J. W., R. RODRÍGUEZ-KÁBANA, J. A. MCINROY, and R. W. YOUNG. 1992. Rhizosphere bacteria antagonistic to soybean cyst (*Heterodera glycines*) and root-knot (*Meloidogyne incognita*) nematodes: identification by fatty acid analysis and frequency of biological control activity. *Plant Soil* 139:1141-1184.
- KOENNING, S. R. 2000. Density-dependent yield of *Heterodera glycines*-resistant and -susceptible cultivars. Supplement to the *Journal of Nematology* 32:502-507.
- KOENNING, S. R., and S. C. ANAND. 1991. Effects of wheat and soybean planting date on *Heterodera glycines* population dynamics and soybean yield with conventional tillage. *Plant Disease* 75:301-304.
- KOENNING, S. R., and K. R. BARKER. 1995. Soybean photosynthesis and yield as influenced by *Heterodera glycines*, soil type and irrigation. *Journal of Nematology* 27:51-62.
- KOENNING, S. R., D. P. SCHMITT, and K. R. BARKER. 1995. Impact of crop rotation and tillage system on *Heterodera glycines* population density and soybean yield. *Plant Disease* 79:282-286.
- KOENNING, S. R., D. P. SCHMITT, and K. R. BARKER. 1996. Soybean maturity group and planting date effects on seed yield and population densities of *Heterodera glycines*. *Fundamental and Applied Nematology* 19:135-142.
- LEHMAN, P. S., D. HUISINGH, and K. R. BARKER. 1971. The influence of races of *Heterodera glycines* on nodulation and nitrogen-fixing capacity of soybean. *Phytopathology* 61:1239-1244.
- NIBLACK, T. L., P. R. ARELLI, G. R. NOEL, C. H. OPPERMAN, J. H. ORF, D. P. SCHMITT, J. G. SHANNON, and G. L. TYLKA. 2003. A revised classification scheme for genetically diverse populations of *Heterodera glycines*. *Journal of Nematology* 34:279-288.
- NOE, J. P., J. N. SASSER, and J. L. IMBRIANI. 1991. Maximizing the potential of cropping systems for nematode management. *Journal of Nematology* 23:353-361.
- NORTON, D. C. 1978. *Ecology of Plant-Parasitic Nematodes*. New York: John Wiley and Sons.
- NUTTER, R. W., JR., G. L. TYLKA, J. GUAN, A. J. D. MOREIRA, C. C. MARETT, T. R. ROSBURG, J. P. BASART, and C. S. CHONG. 2002. Use of remote sensing to detect soybean cyst nematode-induced plant stress. *Journal of Nematology* 34:222-231.
- OOSTENBRINK, M. 1966. Major characteristics of the relation between nematodes and plants. *Mededelingen Landbouwhogeschool Wageningen* 66: 1-46.
- PORTER, P. M., S. Y. CHEN, C. D. REESE, and I. D. KLOSSNER. 2001. Population response of soybean cyst nematode to long term corn-soybean cropping sequences in Minnesota. *Agronomy Journal* 93:619-626.

- RIGGS, R. D., T. L. NIBLACK, R. A. KINLOCH, A. E. MACGUIDWIN, A. MAUROMOUSTAKOS, and L. RAKES. 2001. Overwinter population dynamics of *Heterodera glycines*. *Journal of Nematology* 33:219-226.
- SASSER, J. N., and G. UZZELL, JR. 1991. Control of the soybean cyst nematode by crop rotation in combination with a nematicide. *Journal of Nematology* 23:344-347.
- SCHMITT, D. P., and H. FERRIS. 1998. Pathogenicity and damage levels. Pp. 239-265 in S. B. Sharma, editor. *The Cyst Nematodes*. London: Kluwer Academic Publishers.
- SCHMITT, D. P., and R. D. RIGGS. 1989. Population dynamics and management of *Heterodera glycines*. *Agricultural Zoology Review* 3:253-269.
- SCHMITT, D. P., and R. D. RIGGS. 1991. Influence of selected plant species on hatching of eggs and development of juveniles of *Heterodera glycines*. *Journal of Nematology* 23:1-6.
- SCHMITT, D. P., K. R. BARKER, J. P. NOE, and S. R. KOENNING. 1990. Repeated sampling to determine precision of estimating nematode population densities. *Journal of Nematology* 22:552-559.
- 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. *Journal of Nematology* 15:432-437.
- SCHMITT, D. P., H. FERRIS, and K. R. BARKER. 1987. Response of soybean to *Heterodera glycines* races 1 and 2 in different soil types. *Journal of Nematology* 19:240-250.
- SCHNEIDER, S. M., S. L. RAWLINS, S. HAN, R. G. EVENS, and R. H. CAMPBELL. 1996. Precision agriculture for potatoes in the Pacific Northwest. Pp. 443-452 in P. C. Robert, R. H. Rust and W. E. Larson, editors. *Proceedings of the Third International Conference on Precision Agriculture*. Madison, WI: ASA, CSSA, SSSA.
- SEINHORST, J. W. 1965. The relation between nematode density and damage to plants. *Nematologica* 11:137-154.
- SHOMAKER, C. T., and T. H. BEEN. 1999. A model for infestation foci of potato cyst nematodes, *Globerodera rostochiensis* and *G. pallida*. *Phytopathology* 89:583-590.
- TAYLOR, C. R., and R. RODRÌGUEZ-KÀBANA. 1999. Population dynamics and crop yield effects of nematodes and white mold in peanuts, cotton and velvet beans. *Agricultural Systems* 59:177-191.
- TYLKA, G. L., and P. FLYNN. 1999. Interpreting SCN soil sample results. Iowa State University Publication No. IPM 61.
- TYLKA, G. L., C. SANOGO, and S. K. SOUHRADA. 1998. Relationships among *Heterodera glycines* population densities, soybean yields, and soil pH. *Journal of Nematology* 30:519-520 (Abstract).