V. H. Dropkin

University of Missouri, Columbia

Soybean Cyst Nematode Control

Among the nematode parasites of plants, the cyst nematodes represent a most successful adaptation to parasitism with characteristics that make them difficult to control. Cyst nematodes cause problems in beet, potato, small grain, rice, and soybean production in many parts of the world. Their capacity to survive in soil for long periods without hosts and their high reproductive potential in the presence of hosts make them potent competitors of man for a share of the crop. As the pressures for high production per unit of arable land increase, the importance of cyst nematodes and other phytonematodes becomes more evident and the need for effective controls greater.

The soybean cyst nematode (SCN), the most prominent cyst nematode in the United States, is a serious pest of soybeans in the central and southeast areas of the country and is increasing in significance in the north-central area. Soybean yield losses caused by SCN are very large but seem to be declining in some southern states. The Southern Sovbean Disease Workers estimated that losses due to SCN in 15 southern states were 3.7% (39.4 million bu) in 1979, 3.38% (23.8 million bu) in 1980, 2.8% (21.5 million bu) in 1981, and 2.29% (18.8 million bu) in 1982. Increased awareness of this problem by farmers and their utilization of SCN controls are largely responsible for these reductions in losses. Further reductions depend on educating the farmer, improving the efficacy of control techniques, and developing new controls.

The Pathogen

The soybean cyst nematode (Heterodera glycines Ichinohe) is a member of the order Tylenchida and the family Heteroderidae. All of the more than 45 species in the genus Heterodera are characterized by cyst-forming females, with "cyst" referring to the thick-walled body of the female that encapsulates her eggs.

SCN was discovered in the United States in 1954 in New Hanover County,

Contribution from the Missouri Agriculture Experiment Station, Journal Series No. 9607.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

9 1984 The American Phytopathological Society

North Carolina. The nematode is now distributed over portions of 22 central and southeastern states, but distribution within these states is not uniform. Although its importance is greatest in the United States, SCN is not restricted to this country. In 1915, Hori discovered SCN-damaged soybeans in Japan, and since then, scientists have observed damage in China, Korea, and Columbia.

The life cycle begins with the fertilization of an egg in the mature female. After embryonation, the firststage larva molts inside the egg. The second-stage larva hatches from the egg and moves through the soil in search of a host. Upon contact with a susceptible host root, the parasite initiates the infection process. It moves into the root near the root cap, finds a suitable feeding site, and stimulates the plant to produce a syncytium (Fig. 1), from which it draws nourishment. The nematode molts three more times, becoming an adult at the final molt. Developing males and females become sausage-shaped and sessile. The adult female continues to swell and eventually breaks through the root surface. Her body at this stage is white and pear-shaped. The adult male reverts to a vermiform shape and leaves the root to move about in the soil. The male and female then mate, and 200-500 eggs develop inside the female. She lays some of the mature eggs in a gelatinous secretion and retains the remainder. After death, her body becomes light yellow, then brown and is transformed into a tough protective covering for the unlaid eggs. The egg is about $100 \times 47~\mu m$, the second-stage larva $450 \times 18~\mu m$, the mature male $1.3~mm \times 30~\mu m$, and the cyst $470-790 \times 210-580~\mu m$. Variations in size may be due to the host cultivar, the environment, and the qualitative or quantitative structure of the nematode nonulation

Soil temperature affects the length of the life cycle. A generation lasts about 24 days at 23 C and 40 days at 18 C. Thus, under field conditions, several generations can develop in one growing season. Eggs within the cyst may be viable for several years, depending primarily on soil temperature and moisture. Hatching ceases in the central states during the fall, as soil temperature drops, but continues throughout the winter in the southernmost areas of the United States. To hatch, eggs of many species of cyst nematode require stimulation from root leachates. Although SCN does not depend completely on root leachates, larval emergence is enhanced in the presence of soybean plants.

SCN can move through the soil a few centimeters a year by its own efforts, but

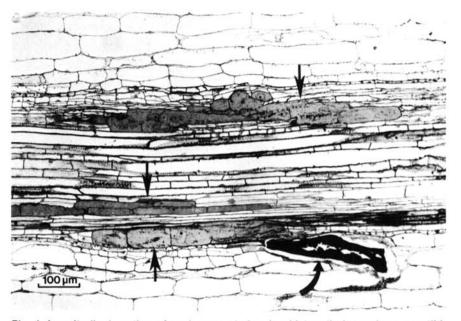


Fig. 1. Longitudinal section of soybean root showing histopathology of a compatible Heterodera glyclnes/plant association. Three syncytia (straight arrows), each induced by a separate nematode, and one adult female nematode (curved arrow) are evident.

it is easily spread long distances in soil attached to farm equipment and to roots of transplants. The nematode also may be transported in drainage and flood water, by wind and birds, and in infested balls of soil (peds) in bagged soybean seed.

Symptoms

Soybean cyst nematode feeding disrupts the function of the soybean root and reduces its ability to translocate water and nutrients to the top of the plant. Severely affected plants are stunted and usually have yellow-green leaves (Fig. 2). Japanese scientists in the early 1900s named the disease Daizu-iwo-byo ("soybean yellow dwarf disease") after the characteristic symptoms of stunting and discoloration. In the midday summer sun, the leaves of infected plants wilt more readily than those of healthy plants, and premature defoliation may occur. Yields of infected plants are reduced, the degree depending on the amount of damage. These symptoms can be mistaken for those induced by such other factors as root rot, nutrient deficiency, misapplied herbicides, and drought.

Infected roots are stunted and necrotic and usually have fewer rhizobium nodules than healthy roots. Reduced nodulation enhances foliar yellowing because the plant is starved for nitrogen. White females and young light yellow cysts may be visible on the roots (Fig. 3), but brown cysts usually are detached during extraction of the roots from the soil. The pattern of damage in a field ranges from small circular to oval spots a few feet in diameter (Fig. 4) to large areas encompassing the whole field.



Fig. 2. (Left) Susceptible soybean cultivar showing typical symptoms of soybean cyst nematode damage. (Right) Resistant cultivar.



Fig. 3. White cysts of *Heterodera glycines* and brown rhizobium nodules attached to soybean roots.

Physiological Races

Four physiological races of SCN have been recognized (5), based on their differential reproduction on four soybean lines. The cultivar Lee is susceptible to all races, Peking is resistant to races 1 and 3, PI 88788 is resistant only to race 3, and PI 90763 is resistant to races 1, 2, and 3. This race nomenclature has been questioned by several researchers, since PI 88788, supposedly susceptible to race 4, has been widely used as a source of race 4 resistance in cultivar development. This classification of races is based on separating soybean cultivars into susceptible and resistant categories. A race-host combination is classed as resistant when the number of adult female nematodes is 10% or less of the number produced on Lee. Thus, race determination is not in finite terms but, rather, in quantitative terms. Triantaphyllou (13) suggested using the term "gene frequencies" rather than "races," since quantitative differences exist within populations of the same race.

Field populations of SCN are usually a mixture of several races, depending on the resistance of the host cultivars on which they reproduced during previous growing seasons. From a sample of one such population, Anand and Brar (1) developed seven distinct SCN populations by continuous selection on different resistant soybean lines. This demonstrated the genetic heterogeneity of field populations and indicated that the cysts from the original field sample had genes for virulence on all of the resistant lines.

The continuous cultivation of resistant cultivars places selection pressure on the nematode, resulting in new races in the



Fig. 4. Soybean field area infested with the soybean cyst nematode.

Table 1. Effect of continuous planting of the soybean cultivar Bedford on soil populations of *Heterodera glycines* at Portageville, MO

| Numbers of years Bedford | Ratio of cyst numbers on Bedford and PI 88788 to numbers on Essex | | |
|--------------------------------|--|----------|--|
| planted | Bedford | PI 88788 | |
| 0 | 0.10 | 0.07 | |
| 1 | 0.19 | 0.07 | |
| 2 | 0.44 | 0.37 | |
| 5 | 0.94 | 0.38 | |

field. This has been observed in Missouri and Tennessee where race 3 originally predominated. With the widespread use of cultivars resistant to race 3, race 4 has become more prevalent. The continuous use of Bedford and other cultivars with race 4 resistance derived from PI 88788 has created a new race of SCN. We have isolated this race (similar to race 5 reported from Japan) from some fields in southeast Missouri in which Bedford was planted for a number of years. This race reproduces readily on Forrest and Bedford, and its frequency increases with continuous planting of Bedford. Soils collected from fields planted to Bedford for one or more years were assayed for SCN race structure (Table 1). The number of white females on Bedford expressed as a proportion of the number on the susceptible Essex increased from 0.10 in the first year to 0.94 after 5 years of continuous Bedford cultivation.

Changes in the ability of SCN populations to reproduce on resistant soybean cultivars are due to changes in frequencies of the genes for parasitism. Luedders and Dropkin (8) subjected two SCN populations, each initially selected for its ability to reproduce on a different host cultivar, to secondary selection on another cultivar and observed a rapid change in the reproductive ability of both populations. The secondary selection resulted in lowering the reproductive ability on primary hosts, indicating that the SCN genes for parasitism were not independent or fixed by primary selection.

Control

SCN is controlled by reducing and maintaining populations below the level at which the crop is damaged. Possible measures are resistant varieties, crop rotation, nematicides, and biological control. The grower must take many factors into account when deciding which single measure or combination to use, but the final decision is based on economics, primarily crop prices and available finances.

Resistant varieties. Soon after the discovery of SCN in the United States, plant breeders initiated a major research effort to develop resistant cultivars. In the initial screening, Peking, PI 90763, PI 84751-1, and Ilsov were found to be resistant to a field population of SCN (10). Because of its agronomic superiority, Peking was extensively used in the breeding program. Three cultivars-Custer, Dyer, and Pickett in maturity groups IV, V, and VI, respectively-were developed and released in the late 1960s. These cultivars, bred and selected in the first cycle of selection, were somewhat less productive than the best adapted cultivars in the absence of disease, but they served as breeding material for further improvement.

The second cycle of cultivar develop-

Table 2. Publicly released soybean cultivars resistant to soybean cyst nematode (SCN)

| Cultivar | Year of release | Maturity group | SCN races resistant to | Other characteristics |
|----------------------|-----------------|----------------|---------------------------|---|
| Pickett ^a | 1967 | VI | 1 and 3 | Susceptible to Phytophthora |
| Dyer" | 1968 | V | 1 and 3 | Susceptible to Phytophthora, resistant to Meloidogyne incognita |
| Custer* | 1968 | IV | 1 and 3 | Resistant to Phytophthora, susceptible to M. incognita |
| Pickett 71 | 1971 | VI | 1 and 3 | Resistant to Phytophthora |
| Forrest | 1972 | V | I and 3 | Resistant to Phytophthora and M. incognita |
| Mack | 1972 | V | 1 and 3 | Resistant to Phytophthora, susceptible to M. incognita |
| Centennial | 1976 | VI | 1 and 3 | Resistant to Phytophthora and M. incognita |
| Franklin | 1977 | IV | 1 and 3 | Resistant to Phytophthora |
| Bedford | 1977 | V | 3 and 4 | Resistant to Phytophthora and M. incognita |
| Nathan | 1981 | V | 3 and 4 | Earlier (7 days) than Bedford |
| Fayette | 1981 | III | 3 and 4 | Similar to Williams |
| Foster | 1981 | VIII | 3 | Resistant to M. incognita |
| Jeff | 1982 | VI | 3 and 4 | Similar to Centennial |
| Kirby | 1982 | VIII | 3 | Resistant to M. incognita and M. arenaria |
| Bradley | 1983 | VI | 3 and 4 | Similar to Centennial but 6 days earlier |
| Epps | 1983 | V | 3 and 4 | Resistant to Phytophthora, M. incognita, and soybean mosaic virus |
| CN 210 | 1983 | II | 3 | Resistant to Phytophthora |
| CN 290 | 1983 | 11 | 3 | Later (10 days) than CN 210 |

Mostly replaced by newer and better cultivars.

ment resulted in the release of Forrest. Mack, Franklin, and Centennial, which combine high yielding abilities and resistance to race 3 of SCN. Within a few years, a new race, later designated race 4, was found to be attacking these cultivars in Missouri, Tennessee, and Arkansas. Research on race 4 resistance led to the use of PI 88788 in developing Bedford and Nathan in maturity group V and Jeff and Bradley in group VI. Fayette, with resistance to races 3 and 4, was the first resistant group III cultivar released for areas farther north. Two new group II cultivars, CN 210 and CN 290, which are resistant to race 3, are being released as the result of the recent discovery of SCN in the north-central states. Publicly released SCN-resistant cultivars are listed in Table 2

At present, all our resistance cultivars carry race 3 resistance from Peking and race 4 resistance from PI 88788. Thus, our varieties have a narrow germ plasm and probably do not provide a broad spectrum of resistance to all the biotypes of SCN.

The original screening for SCN resistance was done against a field population of the nematode. Because most field populations are mixtures of races, some of the differences between sources of resistance were probably undetected. We tested several resistant lines against the SCN populations that developed by continuous reproduction on the same soybean line. The reactions Anand and Brar (1) observed in three of the lines against three SCN populations are shown in Table 3. In our studies, PI 90763 showed a high level of resistance to the SCN population developed on PI 88788, indicating that PI 88788 and PI 90763 have different genes (or alleles) for resistance to one or more biotypes. McCann et al (9) concluded that PI 88788, PI 87631-1, PI 90763R, PI 209332,

Table 3. Number of white females per plant inoculated with soybean cyst nematode (SCN) populations developed by continuous reproduction on selected soybean cultivars'

| Inoculated soybean line ^y | SCN populations developed on | | | |
|--|------------------------------|----------|----------|--|
| | Essex | PI 88788 | PI 90763 | |
| Essex | 104 a' | 315 a | 221 a | |
| PI 88788 | 5 b | 97 b | 9 c | |
| PI 90763 | 16 b | 4 c | 78 b | |

^{&#}x27;From Anand and Brar (1).

and Cloud had at least some genes in common but different from some genes in Pickett 71 and PI 89772. A number of plant breeders are now using PI 90763 and PI 89772 in their breeding programs to develop cultivars resistant to the races and biotypes of the SCN attacking the cultivars with resistance derived from PI 88788.

The inheritance of resistance is complex. Besides three recessive genes and one dominant gene controlling resistance in Peking, additional genes have been found in PI 90763 and PI 88788 (12). The procedures for postulating the number of genes have been based on arbitrary separations into susceptible and resistant categories, although in practice there is a wide range of variation between susceptibility and resistance. Some resistance genes may be closely linked or may be multiple alleles, making certain combinations difficult or impossible to achieve. Linkage of resistance with certain undesirable characters may impose further constraints. For example, resistance in Peking is closely linked with the black seed coat.

Because the area of SCN infestation stretches from Minnesota to Florida, there is a need for resistant cultivars in each maturity group from I through VIII. There is no resistant cultivar in group I, and those in groups II, III, and IV are not as productive as the best susceptible commercial cultivars on uninfested land. The programs for development of SCN-resistant cultivars in the northern states are relatively new and poorly funded. Several private companies are now working on SCN resistance, however, so the situation is likely to improve.

Crop rotation. Alternate planting of susceptible and nonhost crops is an effective measure for controlling *H. glycines*. Planting a nonhost crop for 1 or 2 years results in a decrease in SCN populations and an increase in yields of subsequent soybean crops (11). Nematode populations have been reduced up to 75% by 1-year rotations and up to 92% by 2-year rotations, but additional years result in very small further reductions. A resistant soybean cultivar has virtually the same effect on a SCN population as a nonhost crop (2), except reproduction is somewhat limited on resistant cultivars.

Populations of SCN resurge rapidly when susceptible cultivars are planted in a rotation program (3). Yields may not be affected the first year but losses may occur if the susceptible cultivar is planted the next year. Therefore, crop rotation programs must be continued to manage

Inoculum concentration = 1,000 eggs/100 ml soil.

Counts not having the same letters are significantly (P = 0.05) different.

the nematode population and prevent excessive reduction in yield. Many growers rotate soybeans with nonhost crops every other year, but longer intervals are not feasible for most.

Rotation program decisions (crops to plant and rotation length) are complicated by the presence of more than one phytopathogenic nematode species in the soil. Crops resistant to SCN may be susceptible to other nematode species in the soil. C. H. Baldwin and J. A. Wrather (unpublished) found a decline in SCN populations in rotation plots when corn was grown, but the population of lesion nematodes (Pratylenchus sp.) increased and damaged the corn.

Soybean is the major economic crop attacked by SCN. The presence of other host plants—some field crops, vegetables, and weeds—in and around soybean fields can interfere with control strategies by providing the nematode with a food source. Thus, effective weed control should be part of a SCN control program.

Nematicides. Two types of nematicides are used for SCN control: fumigants (halogenated aliphatic hydrocarbons, eg, ethylene dibromide) and nonfumigants (oxime carbamates, eg, Temik, and carbamates, eg, Furadan). Fumigants are liquid formulations that vaporize when injected into the soil; when the gas

concentration exceeds a lethal threshold for a sufficient time, nematode larvae are killed. The use of ethylene dibromide as a soil fumigant was recently suspended by the EPA. At present, no fumigant nematicides are as effective and economical as EDB. Nonfumigants are watersoluble and move with water through the soil; these chemicals kill nematode larvae on contact or disrupt their behavior (movement, root penetration, etc.). The efficacy of nematicides varies according to the chemical, method of application, soil type, rainfall, temperature, and edaphic factors. No one chemical is best suited to all conditions.

The nematicides commonly used for SCN control remain effective for 2-4 weeks, then effectiveness declines rapidly because of evaporation, decomposition, and/or leaching out of the target area by water. Removal of root protection usually results in a resurgence in SCN populations by harvest. Nematicide-protected roots develop more profusely than unprotected roots, thus supplying more feeding sites for the nematodes later in the crop season. Newly hatched larvae then attack unprotected roots, resulting in a greater SCN population.

Nematicides are apparently more beneficial when soybeans are planted late. Hussey and Boerma (7) observed greater yield increases in Georgia when a nematicide was used with soybeans planted 15 June through 15 July than with beans planted in May. Nematode activity in the soil is likely to be greater with later planted soybeans because of higher temperatures.

Nematicides are useful when resistant cultivars are unavailable and will provide short-term protection to susceptible cultivars, usually resulting in a yield increase. Nematicides have not, however, provided the desired SCN control in the United States. Results from nematicide use often are erratic, and susceptible cultivars protected with the best nematicides usually yield significantly less than resistant cultivars (4).

Biological control. Natural enemies of SCN offer considerable promise in managing nematode populations. Hartwig (6) observed a decline in SCN populations after 5 years of continuous cropping with a susceptible cultivar and speculated that the decline was due to a parasite. There is substantial evidence that parasitism of H. glycines is common where the nematode has been long established in fields. Fungi such as Fusarium oxysporum, F. solani, and Exophiala pisciphila have been found infecting eggs and cysts in Alabama, and cysts and eggs infected with Nematophthora gynophila and



J. A. Wrather

Dr. Wrather is a plant pathologist at the University of Missouri Delta Center in Portageville. He received his B.A. from Central Methodist College, his M.S. from Purdue University, and his Ph.D. from the University of Missouri. He has been involved in research on soybean cyst nematode control since 1972 and in extension plant pathology since 1980.



S. C. Anand

Dr. Anand is a soybean breeder at the University of Missouri Delta Center in Portageville. He was with the McNair Seed Company for 6 years before joining the university in 1979. He obtained his B.S. from Delhi University, his M.S. from North Carolina State University, and his Ph.D. from the University of Wisconsin. His research emphasis is on the development of soybean cultivars resistant to the cyst nematode.



V. H. Dropkin

Dr. Dropkin is professor and past chairman of the Department of Plant Pathology at the University of Missouri, Columbia. He received his Ph.D. in zoology from the University of Chicago and has studied plant-parasitic nematodes since 1952. Before joining the faculty at the University of Missouri in 1969, he taught at Roosevelt University in Chicago and was a research scientist with the U.S. Department of Agriculture.

Catenona auxiliaris have been found in Tennessee.

Control of SCN by nematophagous fungi has not been demonstrated. N. gynophila and C. auxiliaris could play a significant role, however, because they have been associated with the decline of H. avenae populations in England. Further research into fungus-nematode relations could determine the conditions favoring parasitism of SCN by these fungi and their potential as biological control agents.

Outlook

The impact of SCN as a major soybean disease in the United States appears to be declining somewhat. At present, crop rotation and resistant cultivars are responsible for the majority of this decline, and nematicides have helped somewhat. Current research efforts are directed toward improving these controls and developing new ones.

All our current resistant cultivars get their resistance to race 3 from Peking and to race 4 from PI 88788. Our cultivars therefore have a narrow germ plasm, a situation that could result in a resurgence of SCN impact on soybean production. A massive effort is under way to screen the entire U.S. soybean collection against purified populations of races 3, 4, and 5. Resistant lines found in this research

would provide an expanded source of germ plasm for future breeding programs.

The search for more effective nematicides in conjunction with methods and timing of application is being continued, and improved rotation and cultural programs designed to limit nematode numbers and reduce disease severity are being developed.

Acknowledgment

We thank the Missouri Soybean Merchandising Council for their support of soybean cyst nematode research at the University of Missouri.

Literature Cited

- Anand, S. C., and Brar, G. S. 1983. Response of soybean lines to differentially selected cultures of soybean cyst nematode Heterodera glycines Ichinohe. J. Nematol. 15:120-123.
- Epps, J. M., and Chambers, A. Y. 1965. Population dynamics of Heterodera glycines under various cropping sequences in field bins. Phytopathology 55:100-103.
- Epps, J. M., Sasser, J. N., and Uzzell, G., Jr. 1964. Lethal dosage concentrations of nematicides for the soybean cyst nematode and the effect of a nonhost crop in reducing the population. Phytopathology 54:1265-1268.
- Epps, J. M., Young, L. D., and Hartwig, E. E. 1981. Evaluation of nematicides and resistant cultivar for control of soybean cyst nematode race 4. Plant Dis. 65:665-666.
- 5. Golden, A. M., Epps, J. M., Riggs, R. D.,

- Duclos, L. A., Fox, J. A., and Bernard, R. L. 1970. Terminology and identity of infraspecific forms of the soybean cyst nematode *Heterodera glycines*. Plant Dis. Rep. 54:544-546.
- Hartwig, E. E. 1981. Breeding productive soybean cultivars resistant to the soybean cyst nematode for the southern United States. Plant Dis. 65:303-307.
- Hussey, R. S., and Boerma, H. R. 1983. Influence of planting date on damage to soybean caused by *Heterodera glycines*. J. Nematol. 15:253-258.
- Luedders, V. D., and Dropkin, V. H. 1983.
 Effect of secondary selection on cyst nematode reproduction on soybeans.
 Crop Sci. 23:263-264.
- McCann, J., Luedders, V. D., and Dropkin, V. H. 1982. Selection and reproduction of soybean cyst nematodes on resistant soybeans. Crop Sci. 22:78-80.
- Ross, J. P., and Brim, C. A. 1957. Resistance of soybeans to the soybean cyst nematode as determined by a double-row method. Plant Dis. Rep. 41:923-924.
- Slack, D. A., Riggs, R. D., and Hamblen, M. L. 1981. Nematode control in soybeans: Rotation and population dynamics of soybean cyst and other nematodes. Arkansas Agric. Exp. Stn. Rep. Ser. 263. 36 pp.
- Thomas, J. D., Caviness, C. E., Riggs, R. D., and Hartwig, E. E. 1975. Inheritance of reaction to race 4 of soybean cyst nematode. Crop Sci. 15:208-210.
- Triantaphyllou, A. C. 1975. Genetic structure of races of *Heterodera glycines* and inheritance of ability to reproduce on resistant soybeans. J. Nematol. 7:356-364.