Soybean Cyst Nematode Management Reconsidered

A well-known nematologist once said (in public) that soybean cyst nematode (SCN, *Heterodera glycines* Ichinohe) was easy to control: "Don't grow soybeans." Shortly thereafter, following a barrage of good-natured criticism for this bit of unhelpful advice, he amended the statement to: "Don't grow soybeans more than once every 5 years or so." (He made a similar statement in print [22]). From a nematological standpoint, he was quite right in that rotation to a nonhost is the most effective way to reduce SCN population densities and thereby avoid the soybean yield losses associated with moderate to heavy infestations. However, reality often trumps theory, and the reality is that most soybean producers in the U.S. Soybean Belt states (Illinois, Indiana, Iowa, Minnesota, Ohio, Missouri, Wisconsin, and adjacent states) have been unwilling to intersperse their soybean crops with more than a year or two of a nonhost, usually corn. In the South, soybean production has declined dramatically (9). For this reason, most of what follows will emphasize SCN in the Midwestern and North Central states, identified in the preceding sentence as the Soybean Belt. Information on a wide range of issues related to SCN management may be found in the recently published *Biology and Management of the Soybean Cyst Nematode, Second Edition* (29).

As the bulk of soybean production in the United States has shifted northward and westward, so has the known distribution of SCN (Figs. 1 and 2). The most recent discovery of SCN was in North Dakota in 2004 (3). For about the past decade, SCN has been considered the most economically important pathogen of soybean in the

United States (7,37,38). Since the last time a feature article appeared in *Plant Disease* about SCN (36), some changes have occurred in our thinking about this pathogen and in approaches to managing soybean in infested fields. These changes include recommendations for scouting, the meaning and use of damage thresholds, and the means of classifying field populations according to virulence phenotypes ("races"). Some of what is included in this article is still very much a matter of debate, and readers are invited to check with their favorite nematologists regarding varying opinions, or with recent reviews (21,29).

Soybean Cyst Nematode Life Cycle

For readers unfamiliar with this obligately parasitic animal, we begin with a brief summary of the life cycle so that references to various stages will be clear. Durations given for each life stage are those that occur under optimum conditions: a suitable host, sufficient moisture, and a constant temperature of about 25°C (13). The nematode's life as a pathogen begins with its hatching from an egg (Fig. 3) as a second-stage juvenile, or J2 (Fig. 4), formerly referred to as a second-stage larva. It is called a J2 because the first molt, punctuating the transformation from first to second stage (i.e., J1 to J2), occurs while the juvenile is still within the eggshell. Hatching may be temperature-mediated, host-mediated, or time-mediated, meaning that some eggs from the same clutch hatch when the temperature rises to a certain point, others hatch only when influenced by exudates from a host plant, and still others hatch only when a certain (unknown) amount of time has passed (39). The mechanisms of hatching are not well understood, but may involve a combination of enzymatic activity and physical force. Following hatching, the J2 locates a root, presumably by chemolocation, and produces cellulases and other enzymes in order to enter the root and migrate intracel-

lularly to the vascular tissue (5). Once the J2 identifies a suitable location in or near the vascular tissue, the location depending at least partially on the water status of the plant (11), the J2 pierces the cell wall through enzymatic degradation and physical force exerted by its stylet and invaginates the plasma membrane without piercing it (Fig. 5). Through various secretions from its gland cells, the J2 induces the cell to initiate morphological changes reminiscent of transfer cells (24). This initial cell and surrounding cells are recruited into a feeding site known as a syncytium, which acts as a metabolic sink and is maintained as long as the nematode is present and actively feeding. Meanwhile, the J2 itself undergoes a transformation, swelling into a "sausage-stage" (Fig. 6) and molting, 3 to 4 days after infection, to the third juvenile stage, and at 6 to 7 days to the fourth juvenile stage. The final molt occurs at 8 to 9 days for males and 9 to 10 days for females. Males regain a vermiform shape, whereas females continue to swell and eventually are too large to be contained within the root (Fig. 7), although the head and neck remain embedded. Males exit the root and probably do not feed or directly contribute further to disease. Reproduction in SCN is obligately sexual. Sex is apparently determined genetically in SCN, but observed sex ratios may be skewed from 1:1 by various conditions, such as host resistance or environmental conditions (4). Mating takes place in the soil between the motile males and sedentary females still attached to their feeding sites. Egg production per female can range from only 40 to more than 600 (30). The average is generally given as 200 per female. Some of the eggs are deposited outside the female's body in a gelatinous matrix, and the remaining eggs are retained within the female's body, which darkens from yellow to dark brown as the females age and die (Fig. 8). The eponymous "cyst" is the remains of a dead female. The entire process, from infective J2 to viable egg, takes 21 to 22 days under optimum conditions.

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Fig. 1. Distribution of the soybean cyst nematode, *Heterodera glycines*, in the United States, 1962. Gray areas indicate counties in which the nematode was found in at least one field. (Image courtesy R. D. Riggs)

Fig. 2. Distribution of the soybean cyst nematode, *Heterodera glycines*, in the United States, 2005. Red indicates counties in which the nematode was found in at least one field. (Image courtesy R. D. Riggs)

Fig. 3. Fully developed soybean cyst nematode second-stage juvenile within eggshell. (Image courtesy M. Mota)

Fig. 4. Second-stage juvenile, the infective stage of soybean cyst nematode, *Heterodera glycines*.

Fig 5. Feeding tubes (FT) in the initial syncytial cell (SC) of a syncytium, a feeding cell induced by soybean cyst nematode, *Heterodera glycines*, in a root of susceptible soybean cultivar Lee, 2 days after infection. The stylet tip (St) protrudes through the feeding plug (FP) and is surrounded by plasmalemma (unlabeled arrows surrounding the stylet, St). Plastid (Pd); cell wall opening (CWO); mitochondria (Mc); vacuole (Va). Bar = 1.0 μ m. (Photo courtesy B. Y. Endo)

Disease and Scouting

In the early days of dealing with SCN as a pathogen of soybean, a great deal of emphasis was placed on the identification of damage thresholds, the SCN population density at which soybean yield loss could be expected to occur. The numbers turned out to be quite similar in the midwestern United States; for example, 600 eggs and J2/250 cm^3 soil for Illinois (22), 200 eggs/250 cm^3 soil for Ohio (26), and 500 eggs/250 cm^3 for Missouri (6). Lower threshold values were measured in artificially infested field microplots (17). Soybean producers (obviously having been trained well by entomologists) had faith in these threshold values, a faith that was reinforced by the use of these numbers by public and private nematode-testing laboratories. There are several problems with using damage thresholds to make management recommendations. The primary problem is that damage functions, or the relationship between SCN population densities at planting and soybean yield, vary with soils and other conditions (1) and cannot be applied with confidence to any individual field. The two biggest secondary problems are whether the life stage used to establish the damage threshold is a good indicator of risk, and whether a damage

threshold is a useful concept in managing a pathogen for which there are no recommended therapeutic treatments once the growing season has started.

The damage threshold of 3 cysts/100 cm^3 soil, used by many commercial laboratories in Illinois and other states, gives a good illustration of the life-stage problem. First, cyst densities are relatively poor predictors of yield loss (12,14) because cysts are not the infective units. J2 infect roots, and the level of infection with J2 is a good predictor of yield loss, at least for susceptible cultivars (19,35). Root infection is exceptionally difficult to assess, however, especially in field situations, and

interpretation of numbers of J2 in the soil may be confounded by time of year, presence of a host, and extraction efficiency, among other factors. In contrast, cyst population densities are relatively easy to determine and require little in the way of specialized equipment. For this reason, cysts became the preferred life stage for SCN assessment by commercial laboratories. The compromise position is to recommend risk assessment based on SCN egg densities. Borrowing the concept of "inoculum potential" from research on soilborne fungal pathogens (2), we can say that the number of SCN eggs represents the inoculum potential of a field. Egg

Fig. 6. Second- and third-stage juveniles of soybean cyst nematode stained with acid fuchsin in a soybean root cleared with sodium hypochlorite.

Fig. 7. Female soybean cyst nematode with head embedded in soybean root. (Photo courtesy T. A. Jackson)

Fig. 8. Females (white to yellow) and cysts (brown) of soybean cyst nematode.

Fig. 9. Average yields of soybean cyst nematode-resistant and -susceptible cultivars grown in fields with an average of 3 cysts/100 cm³ soil in Illinois, 2002.

numbers are reasonable predictors of yield loss (12,14), and for this reason, quantification of eggs is standard for SCN research published in journals like *Plant Disease* and *Journal of Nematology*.

When a diagnostic lab has no other information, such as soil pH, organic matter content, P and K levels, soybean cultivar, and so forth, then threshold value may be the only indicator of whether a yield problem in a field is due to SCN infestation. It suffers, however, from the same failing as many other average values: it may not apply to a particular situation. An average population density of 3 cysts/100 cm³ may be insufficient to cause any detectable yield loss in one environment, whereas it may exceed the true damage threshold in another environment (Fig. 9). Considering that some females may contain 10-fold or more eggs than others, one need not look very far for an explanation of the inconsistency in predicting damage or yield loss based on threshold values.

Because management of soybean in SCN-infested fields has two purposes—maximizing yield and at the same time minimizing SCN population densities—a more useful concept than the damage threshold is the action threshold, or the population density at which action is taken to manage the pathogen (8). Because of the potential for exponential increases in the SCN population on susceptible soybean, a reasonable action threshold is *one cyst*. The ability to detect cysts through soil sampling lags well behind their spread throughout a field (25). Collaborators on a 10-state project to study SCN in the north central United States agreed that one cyst was a reasonable action threshold (33) because keeping SCN population densities low is much simpler than reducing high ones.

Current consensus among nematologists in the U.S. Soybean Belt is that SCN egg population densities should be assessed when the purpose of sampling is for research or monitoring the effects of management tactics in actual practice. Growers are encouraged to sample infested fields every few years (the actual number depending on the starting population density). Extraction and enumeration of cysts alone can reasonably be used for initial detection purposes, and the presence of one cyst should precipitate implementation of an SCN management strategy. *Caveat emptor*: other species of cyst nematodes may be found in soybean fields, and it is best if one makes sure that the laboratory is qualified to do SCN analysis.

Don't Look for Visual Symptoms of SCN Damage

One observation cannot be emphasized enough: SCN does not necessarily cause symptoms that can be detected visually (Fig. 10). Soybean fields should not be scouted for the "typical" symptoms of

stunting and chlorosis, or given a clean bill of health because symptoms are absent. The nematode's ability to reduce soybean yields up to 30% without causing any visually detectable symptoms has been reported in the literature at least since 1992 (23), and has been verified in several reports (25,33,40). Anecdotally, I can report that every single soybean field I visited in 2003—scores of symptomless and symptomatic fields in Illinois between Interstate 70 and 80—was infested with SCN.

Workneh et al. (34) showed that the frequency of occurrence of SCN in six midwestern states ranged up to 83% of the soybean fields sampled. They employed an area-frame sampling strategy that is considered to be robust, and any given soybean field in the areas sampled has a greater than 50% probability of SCN infestation. The percentage of fields infested with SCN far exceeds the percentage of fields in which symptoms of SCN infection can be detected. The emphasis on describing symptoms in the early years of SCN detection in the midwestern United States has led to some difficulty in convincing growers with symptomless fields that they would profit from sampling for SCN regularly. It also probably limits estimates of the total amount of yield loss caused by SCN, because these are often "guesstimates" based on visual observations. Unfortunately, funding agencies are loathe to fund "survey work." Surely having better estimates of the actual damage caused by SCN would be to everyone's advantage, and if higher than now apparent, would spur "the industry" to improve and diversify the products they offer for SCN management.

Improving Cultivar Choices

In the standard corn-soybean rotation, SCN management can be improved through improving cultivar choices. To optimize cultivar choice for SCN-infested fields, at least four items of information are needed, two about the cultivar and two about the SCN population in the field: (i) yield potential of the cultivar; (ii) level of resistance of the cultivar; (iii) level of SCN in the field; and (iv) virulence profile of the SCN population in the field.

Cultivar information. In most soybean production states, unbiased information about the yield potential of cultivars can be obtained from soybean variety trials (e.g., those published in the online journal *Crop Management* under "Public Access" or "Soybean"). However, getting information about the level of resistance is more difficult. SCN-resistant cultivars are typically labeled, "resistant to race 3" or "moderately resistant to race 14," for example. The meaning of these labels is not clear and can be highly misleading (Fig. 11), although probably not intentionally so on the part of the labelers. Two examples of screening programs for the levels of SCN

resistance are in Iowa (31,32) and Illinois (18). The Iowa tests are field-based and include both yields and SCN reproduction levels, whereas the Illinois tests are greenhouse-based (described in the following section entitled "SCN information") and must be combined with data from yield trials to be useful at this point.

The Illinois screening program focuses on the level of resistance, which is defined by a Female Index (FI) calculated as follows: $(N_x/N_s) \times 100$, where N_x = average number of females on the test cultivar, and N_s = average number of females on the standard susceptible cultivar, Lee 74. The typical resistance scale is that of Schmitt and Shannon (28), which categorizes soy-

bean cultivar reactions to SCN as follows: FI < 10, resistant (R); FI = 10 to 30, moderately resistant (MR); FI = 31 to 60, moderately susceptible (MS); and FI > 60, susceptible (S). The Illinois resistance scale, in contrast, does not include a susceptible category because the cultivars tested are only those labeled resistant by the companies that market them. The Illinois resistance scale categorizes resistance levels as follows: FI < 10, highly resistant (HR); FI = 10 to 24, resistant (R); FI = 25 to 39, moderately resistant (MR); FI = 40 to 59, low resistance (LR); and FI ≥ 60, no effective resistance (N or NR). Results from the Illinois screening program (Fig. 11) show that approximately two-thirds of

Fig. 10. Soybean cyst nematode can reduce the yields of susceptible cultivars by 30% without causing obvious symptoms, as illustrated in this photograph.

Fig. 11. Female indices of 245 soybean cultivars labeled "resistant to race 3" in a greenhouse test with a race 3 population of soybean cyst nematode, *Heterodera glycines*, in 2003. Resistance is conventionally defined by a Female Index (FI) of less than 10, calculated as follows: $(N_x/N_s) \times 100$, where N_x = average number of females on cultivar "x", and N_s = average number of females on the standard susceptible cultivar, Lee 74.

the cultivars labeled as “resistant to race 3” express a high level of resistance to a standard HG Type 0 (~race 3; see the following section). The importance of information of this kind is twofold: (i) confirming label claims of resistance independently and under identical conditions; and (ii) providing producers with the information necessary to choose cultivars that will address *both* aims of SCN management, to wit, increasing yields and suppressing SCN population densities.

SCN information. In a preceding section of this paper, issues surrounding determination of the level of SCN in a field were covered. Numbers of eggs or cysts

are not the only issue, however. SCN is also capable of adapting to and reducing the yields of resistant cultivars. This ability, formerly referred to as “race shift,” creates another problem for management of soybean in SCN-infested fields: how to ascertain whether such a shift has occurred.

Race shift can be assessed by means of bioassays on SCN-resistant soybean lines. Beginning in 1970, the standard bioassay was a race test described by Golden et al. (10) and further characterized by Riggs and Schmitt (27). For various reasons, explained in Niblack et al. (16), a more informative modified bioassay has been

proposed for use in characterizing field populations of SCN. This HG (for *Heterodera glycines*) Type test is simple and predictive of the nematode’s ability to reproduce on resistant cultivars. To conduct the test, a field population is sampled for determination of average population densities. SCN eggs are extracted from the samples, and the test is set up according to published guidelines (16). Briefly, replicated sets of each of seven soybean indicator lines (Table 1) are germinated in sterilized germination paper, selected for uniformity, and transplanted into soil, which is then infested with a standard number of eggs of the SCN population. The infected plants are maintained for 30 days at 25°C, at which time the females are removed from the roots and counted. A Female Index (FI) is calculated for each indicator line as described above: $(N_i/N_s) \times 100$, where N_i = average number of females on the indicator line, and N_s = average number of females on the standard susceptible cultivar, Lee 74. The HG Type of an SCN population is indicated by the FI values on each indicator line. If the FI is 10 or more, the SCN population is given the number of that indicator (Table 2). A population with no FI values greater than 10 is called an HG Type 0.

Replacing races. Two characteristics of the race test were maintained in the HG

Table 1. Soybean indicator lines used for determination of *Heterodera glycines* (HG) Type

Indicator number	Line ^a	Comment
1	PI 548402	Along with several other PIs, also known as ‘Peking’; included in original SCN ^b race test
2	PI 88788	Source of resistance in most SCN-resistant cultivars; included in original SCN race test
3	PI 90763	Included in original SCN race test
4	PI 437654	Source of resistance in ‘Hartwig’ and CystX TM
5	PI 209332	Resistance is similar to PI 88788 and PI 548316
6	PI 89772	Resistance is similar to PI 548402
7	PI 548316	Also known as ‘Cloud’

^a Plant Introduction.

^b Soybean cyst nematode.

Table 2. Examples of HG Type designations for soybean cyst nematode (SCN), *Heterodera glycines*, isolates

Isolate	Females on Lee 74	Female Index ^a							HG Type ^b
		PI 548402	PI 88788	PI 90763	PI 437654	PI 209332	PI 89772	PI 548316	
PA3	130	0	1	0	0	1	0	1	0
TN1	196	12	22	0	0	23	9	25	2.5.7
TN2	164	27	2	9	0	1	21	8	1.6
TN8	177	61	5	21	0	7	45	30	1.3.6.7
TN9	131	16	1	1	0	1	8	4	1
TN10	149	28	12	8	0	7	16	12	1.2.6.7
TN17	141	7	12	0	0	12	3	15	2.5.7
TN18	155	7	12	0	0	9	4	13	2.7
TN21	288	38	31	32	21	40	30	41	1-7
TN22	167	50	89	1	0	53	2	69	1.2.5.7

^a Female Index is calculated as follows: $(N_i/N_s) \times 100$, where N_i = average number of females produced by the SCN population on the indicator plant introduction (PI), and N_s = average number of females on the standard susceptible cultivar, Lee 74.

^b HG Type is assigned according to the indicator number (Table 1) corresponding to the plant introductions (PI) on which the Female Index is 10 or higher.

Table 3. Soybean cyst nematode (SCN) profiles for four fields in Illinois^a

Field	Previous crop	Eggs/250 cm ³ soil	No. of females on Lee 74	Female Index ^b			SCN Type
				PI 548402	PI 88788	PI 437654	
A	Susceptible soybean	23,960	354	6	4	0	0-
B	Resistant soybean	6,440	128	25	82	1	1.2-
C	Corn	4,200	230	3	23	0	2-
D	Corn	10,340	160	18	54	4	1.2-

^a The columns “previous crop” and “eggs/250 cm³ soil” describe the condition of the field at planting in spring based on samples taken the previous fall (assuming overwinter survival is 100%). The remaining five columns show results of an Illinois SCN Type test. Optimum recommendations for management of each field can be based on previous crop, SCN population density, and SCN Type.

^b Female Index is calculated as follows: $(N_i/N_s) \times 100$, where N_i = average number of females produced by SCN population on the indicator plant introduction (PI), and N_s = average number of females on the standard susceptible cultivar, Lee 74.

Type test in order to make the HG Type test backwardly compatible with the race test: first, Lee 74 was retained as the standard susceptible; and second, the first three indicator lines (Table 1) are identical to, and in the same order as, the three sources of resistance included in the race test. Provision is made in the description of the HG Type test for incomplete tests (16), such as race tests, which are indicated by a “–” following the HG Type number. Incomplete tests can be used for at least two purposes: (i) to express race test results in terms of HG Types, for those who prefer to maintain the classic race test; and (ii) to modify the test for local applications. The first purpose can be misleading, but the second can be quite useful for making cultivar recommendations to soybean producers. The Illinois SCN Type test described in the following paragraph is an example of such a test.

The Illinois SCN Type test is an incomplete HG Type test in that it includes only three indicator lines. These three lines, Plant Introduction (PI) 548402, PI 88788, and PI 437654, represent the entire range of sources of resistance in cultivars available currently to soybean producers in Illinois. The Illinois SCN Type test is intended to be used in conjunction with estimates of population densities and screening programs in order to optimize cultivar choices for producers with SCN-infested fields. For example, profiles of SCN populations from four fields in Illinois (Table 3) suggest specific initial recommendations. (All fields were in corn-soybean rotations.) For field A, which has a high SCN population density, rotation to corn, followed in year 2 by any highly resistant soybean cultivar and in year 3 by corn, should reduce SCN populations considerably. Field B, which has a moderate SCN population partially adapted to PI 548402 and well-adapted to PI 88788, should be rotated to corn in year 1, and a PI 437654-derived soybean cultivar in year 2, and corn again in year 3. Fields A and B should be checked again following year 3 to determine the effects of the rotations on their SCN populations and to formulate plans for year 3 and beyond. Cultivars with resistance from PI 548402 or PI 437654 should be recommended for year 1 in fields C and D, followed by corn in year 2. These two fields should be checked after the corn in year 2 to determine the effects of their rotations. One caveat should be mentioned here: data from race and HG Type tests for the past 10 years show that increasing FI values on PI 437654 are always accompanied by higher FI values on every other soybean indicator line (unpublished data). The reason for this is not known, but the management implication is that cultivars carrying resistance from PI 437654 should not be used consecutively in a rotation strategy, in order to avoid rendering other sources of resistance less effective in those

fields. Further research that sheds light on SCN adaptation to PI 437654 is needed.

SCN Management: Rotate – Rotate – Rotate

Recommendation of a cultural management strategy would be a simple matter if all the studies conducted pointed to one or more specific tactics that would always aid in reducing yield losses due to SCN. Unfortunately, that has not been the case for any particular tactic other than rotation. Other practices, including chemical control, may be valuable in certain situations.

In two extension publications supported and distributed widely by soybean check-off boards, W. J. Wiebold (a contributor to 15,20) distilled the SCN management message into the short phrase, “Rotate – Rotate – Rotate.” Rotate 1 refers to crop rotation, using nonhost crops (corn) to reduce SCN population densities. Rotate 2 refers to the use of SCN-resistant cultivars in the rotation, to maximize yields in SCN-infested fields. Rotate 3 refers to the admonishment to rotate the resistant cultivars, in other words, to avoid using the same resistant cultivar in the same field more than once in the rotation. Some interpret this last “rotate” to mean that growers need to choose cultivars with different sources of resistance, but since that is often not possible, they should at least use different cultivars in order to avoid the rapid adaptation of which SCN is capable.

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