

Research

Increase in Soybean Cyst Nematode Virulence and Reproduction on Resistant Soybean Varieties in Iowa From 2001 to 2015 and the Effects on Soybean Yields

Michael T. McCarville, Department of Entomology, Iowa State University, Ames 50011 (current address, Bayer Crop Science Division, Field Operations North, Omaha, NE 68154); and **Christopher C. Marett**, **Mark P. Mullaney**, **Gregory D. Gebhart**, and **Gregory L. Tylka**,[†] Department of Plant Pathology and Microbiology, Iowa State University, Ames 50011

Accepted for publication 23 May 2017.

Abstract

Management of the soybean cyst nematode (SCN) relies heavily on use of SCN-resistant soybean varieties to limit nematode reproduction and minimize yield loss. For Iowa, almost all SCN-resistant soybean varieties contain SCN resistance genes from a breeding line named Plant Introduction (PI) 88788. Iowa State University conducts experiments to evaluate numerous SCN-resistant and three to four SCN-susceptible soybean varieties in up to nine field experiments across Iowa each year. Data on SCN population density, virulence (SCN race and HG type), soybean yield, precipitation, and growing degree days from more than 25,000 four-row plots in field experiments conducted from 2001 to 2015 were analyzed to determine how these factors affected SCN reproduction

and yield. SCN population densities were positively correlated with temperatures and negatively associated with precipitation during the growing seasons, indicating that SCN reproduction was greatest in hot, dry years. Over the years, virulence of SCN populations on PI 88788 increased in the fields in which the experiments were conducted, resulting in increased end-of-season SCN population densities and reduced yields of SCN-resistant soybean varieties with the PI 88788 source of resistance. These results indicate that soybean yield loss caused by SCN on resistant varieties with the common PI 88788 source of resistance likely will increase as virulence of SCN populations increases unless new sources of resistance become widely available and used in the future.

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is the leading yield-reducing pathogen of soybean in the United States and Canada (Allen et al. 2017). The nematode is widely distributed throughout the Midwestern United States (Tylka and Marett 2014; Workneh et al. 1999). A primary recommendation for managing SCN is to grow SCN-resistant soybean varieties (Niblack and Tylka 2009; Tylka 2012). In general, SCN-resistant soybean varieties produce greater yields and allow less reproduction of the nematode than varieties that are susceptible (Tylka et al. 2016; Tylka 2016). The number of SCN-resistant soybean varieties available to Iowa soybean farmers has increased from 29 in 1991 to 956 in 2016 (Fig. 1) (Tylka and Mullaney 2016).

There are more than 100 soybean breeding lines reported to be resistant to SCN (Arelli et al. 2000), and seven breeding lines have been used as sources of resistance in soybean varieties registered in the journal *Crop Science* (Niblack et al. 2002). Despite the availability of multiple breeding lines with resistance to SCN, most SCN-resistant soybean varieties for Iowa possess resistance genes from one breeding line, named Plant Introduction (PI) 88788 (Tylka and Mullaney 2016), as illustrated in Figure 1. The analyses reported herein assessed changes in virulence of SCN populations and the effects of such changes on SCN population densities and soybean yields in Iowa fields in which experiments were conducted to evaluate SCN-resistant varieties from 2001 through 2015.

Field Evaluation of Resistant Varieties

Soybean varieties with resistance to SCN vary in their agronomic performance. The varieties also can vary in control of the nematode (Tylka et al. 2016). Resistance is conferred by several soybean genes (Concibido et al. 2004) and by the number of copies of a set of resistance genes (Cook et al. 2012). Consequently, not all SCN-resistant soybean varieties contain the same number or combination of resistance genes and not all varieties provide the same level of suppression of SCN reproduction.

Since the early 1990s, Iowa State University has conducted field experiments throughout Iowa to assess the agronomic performance and nematode control provided by hundreds of SCN-resistant soybean varieties. It is necessary to assess the effectiveness of the nematode control provided by resistant varieties in experiments conducted in SCN-infested fields rather than in 30-day-long greenhouse evaluations because results of greenhouse studies measuring SCN reproduction on the roots of resistant soybean varieties do not correlate well with changes in SCN population densities when the same varieties are grown in the field (Tylka et al. 2013).

The locations of the variety evaluation experiments conducted in 2015 are shown in Figure 2 as an example of the geographic distribution of the experimental sites throughout the state. In any given year, the same set of varieties was grown in experiments conducted across three northern, central, or southern experimental locations in the state, but the varieties among the northern, central, and southern regions of Iowa varied within a year and from year to year. Most of the varieties (up to 51 per experiment) were resistant to the broad-spectrum herbicide glyphosate (i.e., were Roundup

[†]Corresponding author. E-mail: gtylka@iastate.edu

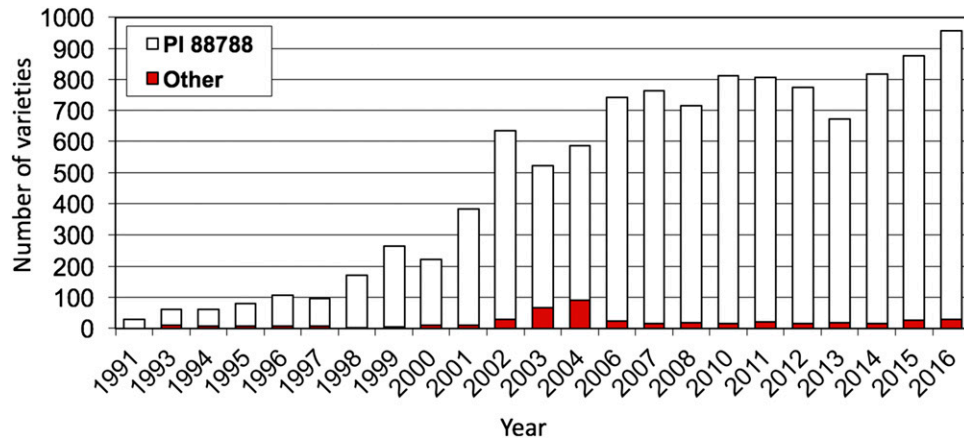


FIGURE 1

Number of SCN-resistant soybean varieties available to Iowa farmers from 1991 to 2016 and the proportion of varieties with resistance from PI 88788 versus all other sources of resistance (Tylka and Mullaney 2016). Information was not collected in 1992, 2005, and 2009.

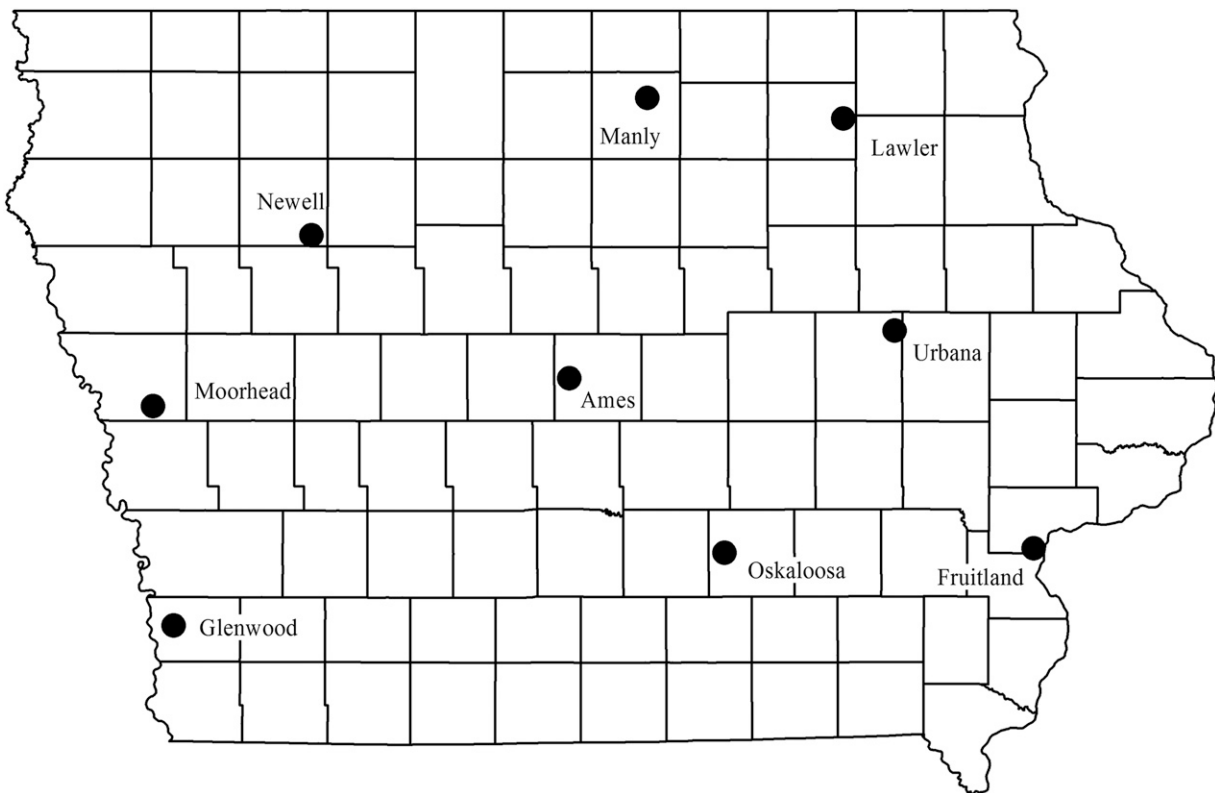


FIGURE 2

Location of variety evaluation experiments conducted in Iowa in 2015.

Ready), but some (up to 10 per experiment) were not. Glyphosate was used for weed control in the plots containing varieties that were resistant to glyphosate; conventional pre- and postemergence herbicides were used for weed control in plots containing varieties that were not glyphosate resistant.

From the early 1990s through 2009, seed companies paid fees to have their SCN-resistant soybean varieties included in the experiments. But beginning in 2010, the research became supported in large part by soybean checkoff funds from the Iowa Soybean Association. Having checkoff funding for the work allowed specific

varieties to be selected for the experiments, and as a result, more Peking-derived SCN-resistant soybean varieties were included in more of the experiments starting in 2010.

In each experiment, three or four widely grown, SCN-susceptible varieties were included, along with the resistant varieties, as control treatments. All plots consisted of four 17-foot-long (5.2-m-long) rows, spaced 30 inches (76 cm) apart and were planted at 10 seeds per ft (33 seeds per m). Each variety was randomly assigned to four replicated plots in each experiment, and replications were geographically situated in the field (i.e., were blocked) to account for agronomic features

of the field in which the experiment was located. The plots with varieties that were not resistant to glyphosate were blocked together and kept separate from the glyphosate-resistant varieties to avoid application of glyphosate onto the non-glyphosate-resistant varieties. Fields were managed according to predominant local practices with regard to all other cultural practices and pesticide usage.

At the beginning of the growing season, a soil sample was collected from each 4-row plot to determine the initial SCN population density. Soil samples consisted of ten 1-inch-diameter, 6- to 8-inch-deep (2.5-cm-diameter, 15- to 20-cm-deep) soil cores that were combined and mixed. The cores were collected from the center 14 feet (4.3 m) of the center two rows of each plot immediately after planting. SCN cysts were extracted from each soil sample using a semiautomatic elutriator (Byrd et al. 1976) or a modified wet-sieving decanting method (Gerdemann 1955), and SCN eggs were extracted from the cysts with a motorized rubber stopper (Faghihi and Ferris 2000) and counted. The same procedure was used to determine SCN egg population densities in each plot at the end of the growing season.

Virulence of the SCN populations present in each experimental field was determined by conducting a race test prior to 2002 and an HG type test from 2002 to 2015 on the SCN population obtained from the spring soil samples from each location. The race test (Golden et al. 1970) and HG type test (Niblack et al. 2002) are greenhouse assays that measure the virulence of an SCN population. Virulence is the ability of an SCN population to reproduce on the different sources of resistance used in breeding SCN-resistant soybean varieties (Niblack et al. 2002).

In September each year, the experimental plots were trimmed to 14 feet (4.3 m), and the center two rows of each plot were harvested with a plot combine. Total seed weight per plot and seed moisture content were measured, and total plot seed weights were converted to yields expressed as bu/acre.

All of the agronomic and SCN data were compiled and averaged for each location and then put into a report that was published as an Iowa State University Extension publication and posted on the Internet. Reports dating back to 1997 are available for download online at www.isuscntrials.info.

The yield and nematode control benefits of SCN-resistant soybean varieties compared with susceptible varieties are apparent when comparing overall means of the two types of varieties in the various experiments. The magnitude of differences varied among locations and among years, but overall mean yields of SCN-resistant soybean varieties almost always were greater than mean yields of the susceptible varieties in the experiments (Tylka 2016). Also, the mean end-of-season SCN egg population densities of SCN-resistant soybean varieties almost always were lower than those for the susceptible soybean varieties (Tylka 2016).

Increased Virulence and Reproduction of SCN Populations on PI 88788 Resistance

Many surveys have been conducted in the Midwestern United States and in Ontario, Canada, to assess the virulence of SCN populations on the different sources of resistance used in the SCN race test and HG type test (Acharya et al. 2016; Chen et al. 2010; Faghihi et al. 2010; Hershman et al. 2008; Kim et al. 1994; Mitchum et al. 2007; Niblack et al. 2003; Niblack et al. 2008; Sikora and Noel 1991; Willson et al. 1996; Zheng et al. 2006). Almost all of the surveys conducted and published since 2000 report that SCN populations with increased virulence on the PI 88788 source of resistance are common in the areas that were sampled.

The variety evaluation experiments conducted by Iowa State University and described herein were not established to survey the

state for SCN virulence. The experiments were not conducted in randomly selected fields or fields located systematically throughout all parts of the state. Instead, fields were picked based on general geographic locale in the state and also based on soil and topologic uniformity of the fields. Still, the results of the race test (prior to 2002) and HG type tests (beginning in 2002) on the SCN populations in the fields in which the experiments were conducted likely reflect the virulence of SCN populations in other fields in Iowa because almost all of the experiments were conducted in commercial farm fields, not on research farms owned and managed by the university, and the fields were managed by the farmers using practices that were common and prevalent among Iowa farmers at that time the experiments were conducted. This common, uniform management included the almost exclusive availability of PI 88788-derived SCN-resistant soybean varieties and a simple corn-soybean crop rotation. While the variety evaluation experiments are not a formal survey for SCN virulence in Iowa, the data from the experiments provide a way to evaluate how changes in SCN virulence across the state affected SCN management and soybean yield.

Prior to 2001, the SCN populations in almost all of the fields in which the variety evaluation experiments were conducted had less than 10% reproduction (i.e., had female indices less than 10) on all of the SCN race differentials, namely Peking, Pickett, PI 88788, and PI 90763. That is, the SCN population in almost every field in which experiments were conducted was race 3 (e.g., Tylka and Souhrada 1997). But an increase in virulence of SCN populations on PI 88788 in Iowa fields began to be observed in 2001, and the increased virulence continued through 2015 (Fig. 3). A similar increase in SCN virulence on Peking was not observed in the nematode populations tested during that same 15-year period.

SCN reproduction in each plot was assessed by calculating a reproductive factor, which was the final egg population density divided by initial egg population density in a plot. For the analyses reported herein, reproductive factor values were averaged among replications for each variety and then averaged for all varieties in three variety types—SCN susceptible, PI 88788-derived SCN resistant, and Peking-derived SCN resistant varieties—for each experiment and then compared among years. The reproductive factor values for PI 88788-derived resistant varieties in the experiments remained low (6.0 or below) from 2001 through 2006, but then began increasing in 2007 (Fig. 4). The increase in reproductive factor on PI 88788-derived resistant varieties occurred in years that coincided with increased virulence of the SCN populations on PI 88788 (Fig. 3). An increase in reproductive factor values on Peking-derived SCN-resistant soybean varieties was limited to just a few experiments in a few years between 2010 and 2015 (Fig. 4).

Decreased Yields of SCN-resistant Soybean Varieties as Virulence and Reproduction of SCN Populations on PI 88788 Increased

The overall average yields of the SCN-resistant varieties were calculated for each experiment in each year and plotted versus the SCN reproductive factor for each experiment. There was a significant negative linear relationship between yield and reproductive factor for the years 2006 through 2015 (Fig. 5). Yield data prior to 2006 were not included in the linear regression analyses because it obscured the relationship between SCN reproduction and harvested yield across years, most likely due to the lower yield potential of varieties in early years of the experiments. Multiple regression analyses were conducted on yield data from all experiments conducted from 2001 through 2015, and the results are described in the next section.

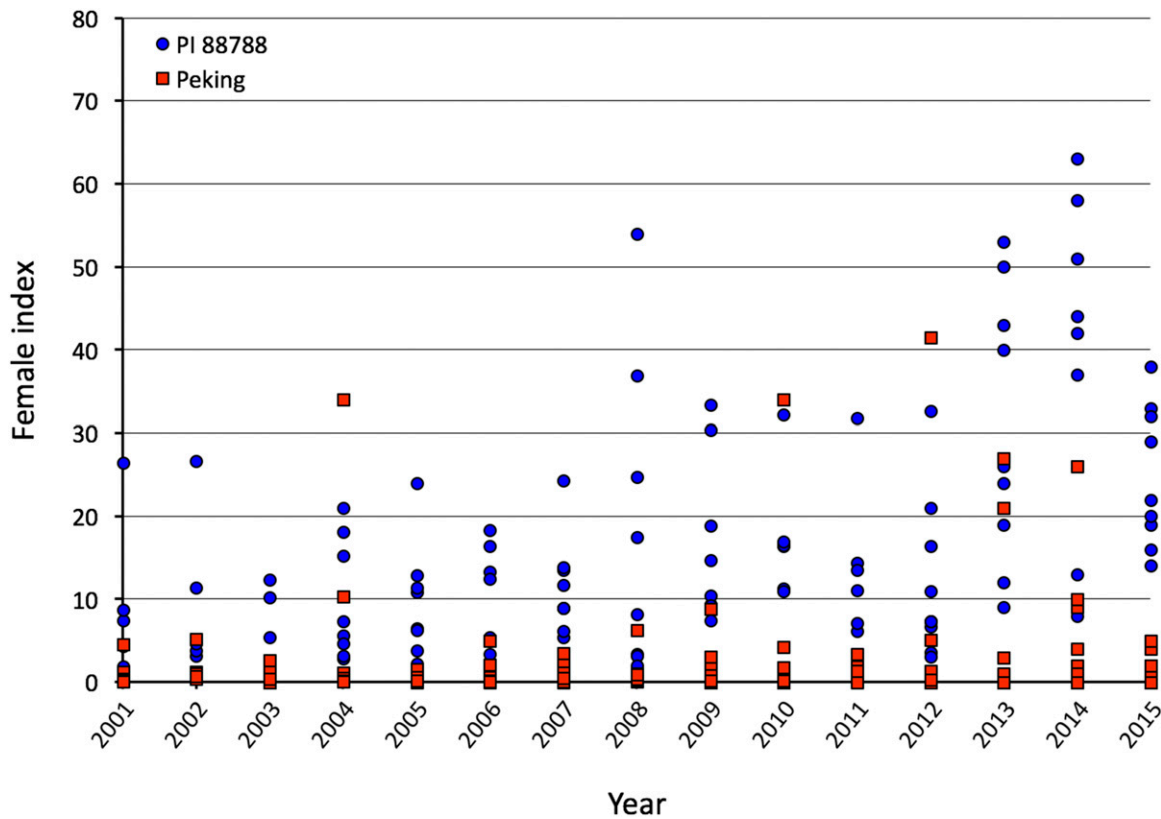


FIGURE 3

Virulence of SCN populations in field experiments from 2001 through 2015 on PI 88788 and Peking. Each data point on the graph represents the female index on PI 88788 (blue circles) and Peking (red squares) for the SCN population in a single field in which a variety evaluation experiment was conducted. The female index of the SCN populations was calculated relative to reproduction of the SCN population on susceptible Williams 82 or Lee 74 soybean varieties in an SCN race test (Golden et al. 1970) for 2001 and an HG type test (Niblack et al. 2002) for 2002 to 2015.

For varieties with PI 88788 resistance, linear regression analysis revealed the average soybean yield potential to be 58.4 bu/acre (3,927 kg/ha) and that yield decreased by approximately 1.7 bu/acre (114 kg/ha) for every 1.0 change in the natural log of the SCN reproductive factor. For example, if the SCN population doubled during the season (reproductive factor = 2.0), the average yield loss from SCN would be approximately 1.2 bu/acre (81 kg/ha) compared with yield if the SCN population densities remained unchanged during the growing season (i.e., reproductive factor = 1.0).

Factors Affecting SCN Virulence, SCN Population Densities, and Yields

Multiple regression analyses were conducted using PROC REG in SAS 9.3 (SAS Institute Inc., Cary, NC) on the 122 site-years of data that were compiled to determine the significance and relative importance of factors that possibly affected SCN virulence (race and HG type test female indices), SCN reproduction, and soybean yield in the experiments from 2001 to 2015. More specifically, we assessed whether changes in virulence of the SCN populations and other factors affected SCN reproduction in the field experiments and how these changes and variables affected soybean yield. We summarized data for each experimental location across the three variety types (SCN-susceptible, PI 88788-derived SCN-resistant, and Peking-derived SCN-resistant varieties), and then conducted the analyses on the data for each variety type. Varieties with SCN resistance from other resistance sources (e.g., PI 437654) were not used in the analysis because there were too few varieties included in

the experiments, a reflection of their limited commercial availability. Variables were selected for inclusion in the model via a stepwise selection criteria using the default cutoff of $P = 0.15$ (PROC REG, SAS 9.3).

We summarized data for each experimental location including year, precipitation, growing degree days, female index on PI 88788, female index on Peking, initial SCN egg population density, SCN reproduction, and yield of each of the three variety types. The variable “year” referred to the relative year of the experiment in the data set, with 2001 designated year “1” and 2015 designated year “15”. Year, therefore, provided a measure of change over time. Female index data for PI 88788 and Peking were obtained from the race and HG type tests that were conducted on the SCN populations in each field. Female index (number of females on resistant line divided by number of females on susceptible line $\times 100$) provides a measure of the virulence of an SCN population to a resistance source, with higher numbers indicating increased virulence (Niblack et al. 2002). Initial SCN egg population density was calculated as the average spring egg count (eggs/100 cc soil) for all the plots at a given location. SCN reproduction in each plot was included in the analyses as the natural log of the calculated reproductive factor (final egg population density divided by initial egg population density in a plot). Weather data were obtained for each experimental location from the Iowa Environmental Mesonet (IEM 2014). The weather data are reported on a daily basis, so we selected the planting date and harvest date for each experiment as the beginning and end points of the ranges for our data queries.

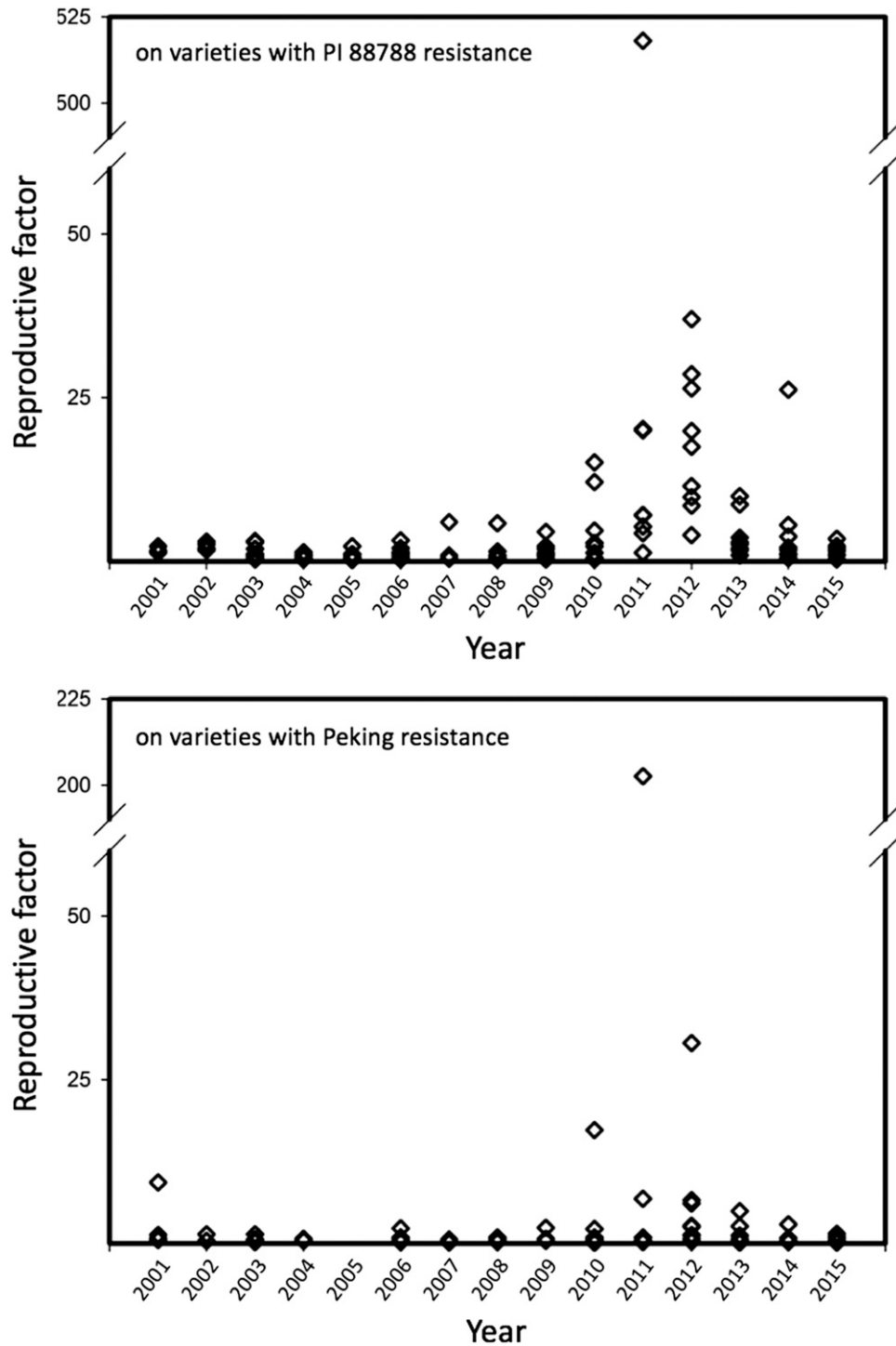


FIGURE 4

The overall mean reproductive factor for PI 88788-derived (top graph) and for Peking-derived (bottom graph) SCN-resistant soybean varieties in field experiments in Iowa from 2001 through 2015. Reproductive factor was calculated by dividing the final egg population density by the initial egg population density in a plot then averaging among replications and all varieties within a specific variety type (PI 88788-derived SCN-resistant or Peking-derived SCN-resistant varieties) for each experiment in each year. A value of “2.0” would indicate the SCN population densities (numbers) doubled during the growing season. Each data point on the graph represents the mean reproduction factor for all varieties of a specific variety type at a single location within a year. There were no varieties with the Peking source of resistance in the experiments conducted in 2005.

Growing degree days, a commonly used measure of heat accumulation, were calculated using a development threshold of 10°C.

Different variables were included in each regression analysis to investigate which factors influenced SCN virulence, SCN reproduction

in the field, and soybean yield of the three variety types. The variables year and female index of the other resistant variety type (i.e., female index on PI 88788 for Peking-derived resistant varieties and vice versa) were included in the analyses for SCN virulence. The same variables plus the

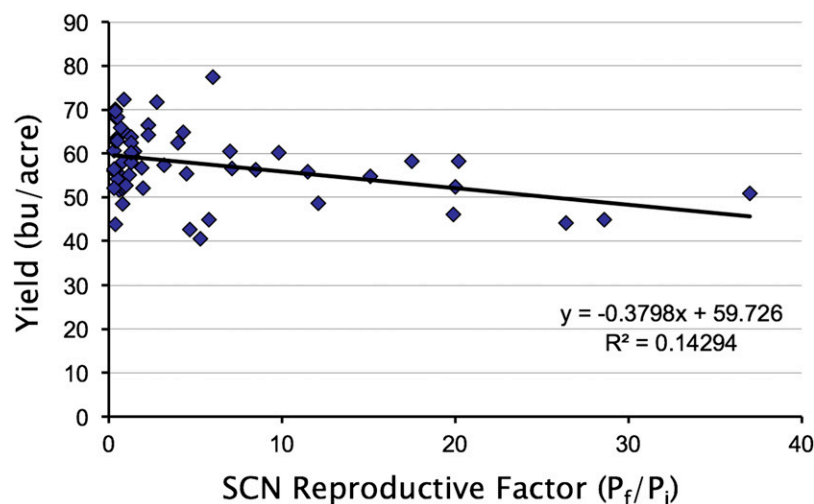


FIGURE 5

Overall average yield of SCN-resistant soybean varieties versus the natural log of SCN reproductive factor in variety trial experiments from 2006 through 2015. Inclusion of yield data prior to 2006 in the analyses obscured the relationship between SCN reproduction and harvested yield across years due to the low yield potential of varieties in those early years of the experiments. Reproductive factor was calculated by dividing the final egg population density (P_f) by the initial egg population density (P_i) in a plot then averaging among all replications and all varieties with PI 88788-derived SCN resistance for each experiment. A value of “2.0” would indicate the SCN population densities (numbers) doubled during the growing season.

TABLE 1
Factors affecting virulence of soybean cyst nematode populations in variety evaluation experiments from 2001 through 2015^a

Dependent variable	Estimate	Standard error	F-statistic	P-value	R ² value
Virulence on PI 88788			40.73	<0.0001	0.4064
Intercept	-0.942	2.136	0.19	0.6600	
Year ^b	1.594	0.231	47.57	<0.0001	0.2956 ^c
Peking female index ^d	0.678	0.144	22.20	<0.0001	0.1108
Virulence on Peking			24.42	<0.0001	0.1691
Intercept	-0.158	0.875	0.04	0.8465	
PI 88788 female index ^e	0.204	0.041	24.42	<0.0001	0.1691

^a Only factors that had a significant effect on virulence of SCN populations in the stepwise regression are listed in the table ($P \leq 0.15$), and they are listed in decreasing order of magnitude of effect (partial R² value).

^b Chronological year, with 2001 as year 1, 2015 as year 15.

^c Partial R² indicating each factor’s contribution to the model.

^d SCN population virulence (female index) on Peking, as measured in a race test or HG type test.

^e SCN population virulence (female index) on PI 88788, as measured in a race test or HG type test.

addition of growing degree days, precipitation, and female index on the same variety type were included in the analyses of SCN reproduction. Finally, the variable of SCN reproduction on a variety type was added to the analysis of yield for the same variety type (i.e., SCN reproduction on Peking-derived varieties was added to the yield analysis of Peking-derived varieties). The same multiple regression procedure described above was utilized for all analyses.

Our analyses of SCN virulence revealed that chronological year was positively correlated with virulence on PI 88788, but was not correlated to virulence on Peking (Table 1). In 2001, virulence of the SCN populations in our experiments on PI 88788 and Peking did not differ significantly from 0% (i.e., the y-intercept values were not significantly different from 0). But after 2001, virulence on PI 88788 increased 1.6% per year, while virulence to Peking did not increase significantly. These results suggest that SCN virulence to PI 88788 might have increased in SCN populations across the state of Iowa during that time period, while virulence to Peking remained limited. In our data, we also observed evidence of an increase in virulence on one source of resistance being associated with

increased virulence on the other source of resistance. For example, a 1% increase in virulence of an SCN population on PI 88788 corresponded with a 0.2% increase in virulence to Peking (Table 1). The analyses indicated that the cross-virulence was incomplete and limited, and the biological basis and practical implications of this finding are unclear.

Regression analyses of SCN reproduction revealed the importance of temperature and rainfall in affecting SCN reproduction in the field (Table 2). Growing degree days were positively correlated with SCN reproduction and precipitation was negatively correlated with SCN reproduction across all three variety types, indicating that SCN reproduction in the experiments was greatest in hot, dry years. The magnitude of the effect of these variables and their explanatory power were greater for SCN-susceptible and PI 88788-derived SCN-resistant varieties than for Peking-derived resistant varieties. One possible explanation for this difference in magnitude of effect is that abiotic factors may be less important drivers of nematode reproduction when varieties display a high level of effective resistance to the nematode, such as those varieties with Peking-derived SCN resistance.

TABLE 2
Factors affecting reproduction of soybean cyst nematode populations in variety evaluation experiments from 2001 through 2015^a

Dependent variable	Estimate	Standard error	F-statistic	P-value	R ² value
Susceptible varieties			8.00	<0.0001	0.1678
Intercept	-0.831	0.875	0.90	0.3445	
Growing degree days ^b	0.118	0.035	11.13	0.0011	0.0705 ^c
Precipitation ^d	-0.002	0.001	9.78	0.0022	0.0595
Year ^e	0.062	0.029	4.76	0.0310	0.0333
PI 88788-derived resistant varieties			14.38	<0.0001	0.3276
Intercept	-2.252	0.727	9.59	0.0024	
Year	0.073	0.028	6.73	0.0107	0.1211
Precipitation	-0.003	0.001	24.59	<0.0001	0.0925
Growing degree days	0.128	0.029	18.86	<0.0001	0.0980
PI 88788 female index ^f	0.014	0.008	2.82	0.0955	0.0161
Peking-derived resistant varieties			11.91	<0.0001	0.2960
Intercept	-1.152	0.875	1.73	0.1918	
Peking female index ^g	0.789	0.016	24.15	<0.0001	0.2338
Precipitation	-0.001	0.001	6.37	0.0135	0.0423
Growing degree days	0.053	0.034	2.40	0.1253	0.0198

^a Only factors that had a significant effect on SCN reproduction in the stepwise regression are listed in the table ($P \leq 0.15$), and they are listed in decreasing order of magnitude of effect (partial R² value).

^b Incorporated as 100 growing degree days.

^c Partial R² indicating each factor's contribution to the model.

^d Incorporated as millimeters of precipitation.

^e Chronological year, with 2001 as year 1, 2015 as year 15.

^f SCN population virulence (female index) on PI 88788, as measured in a race test or HG type test.

^g SCN population virulence (female index) on Peking, as measured in a race test or HG type test.

TABLE 3
Factors affecting soybean yields in variety evaluation experiments from 2001 through 2015^a

Dependent variable	Estimate	Standard error	F-statistic	P-value	R ² value
Susceptible varieties			7.41	0.0001	0.1563
Intercept	52.277	2.616	399.21	<0.0001	
Year ^b	0.556	0.202	6.24	0.0139	0.0486 ^c
Reproductive factor ^d	-2.415	0.703	4.11	0.0448	0.0313
Initial population density ^e	-1.010	0.305	10.87	0.0013	0.0764
PI 88788-derived resistant varieties			7.16	0.0002	0.2036
Intercept	49.078	1.897	669.36	<0.0001	
Year	0.970	0.221	19.37	<0.0001	0.0964
PI 88788 female index ^f	-0.156	0.069	5.08	0.0268	0.0661
Reproductive factor	-1.386	0.666	4.34	0.0403	0.0411
Peking-derived resistant varieties			11.13	<0.0001	0.2076
Intercept	46.147	2.115	475.85	<0.0001	
Year	0.794	0.208	14.57	0.0003	0.1219
Reproductive factor	-2.230	-0.736	9.19	0.0032	0.0857

^a Only factors that had a significant effect on yield in the stepwise regression are listed in the table ($P \leq 0.15$), and they are listed in decreasing order of magnitude of effect (partial R² value).

^b Partial R² indicating each factor's contribution to the model.

^c Chronological year, with 2001 as year 1, 2015 as year 15.

^d Reproductive factor on specific type of variety (susceptible, PI 88788 resistant, or Peking resistant).

^e Incorporated as 1,000 soybean cyst nematode eggs per 100 cc soil at planting.

^f SCN population's virulence (female index) on PI 88788, as measured in a race test or HG type test.

The variable year was positively correlated with SCN reproduction on SCN-susceptible and PI 88788-derived resistant varieties, but not on Peking-derived resistant varieties. The variable year explained over three times more variation in SCN reproduction on PI 88788-derived resistant varieties than on SCN-susceptible

varieties (Table 2). The changes in SCN reproductive factor on PI 88788-derived and Peking-derived resistant soybean varieties from 2001 through 2015 are illustrated in Figure 4. SCN virulence was significantly correlated to SCN reproduction on both PI 88788-derived and Peking-derived resistant varieties. SCN virulence to

Peking explained 23.4% of the variability in SCN reproduction on Peking-derived varieties. SCN virulence to PI 88788 only explained 1.6% of the variability in SCN reproduction on PI 88788-derived varieties. However, it should be noted this result is likely partially due to the correlation between virulence to PI 88788 and chronological year reported above (Table 1).

Initial multiple regression analyses of yield data revealed that growing degree days were only significantly correlated to yield for SCN-susceptible varieties. Growing degree days were only marginally significant ($P = 0.11$) and provided little explanatory power while adding greatly to the overall error of the model. Therefore, we excluded the variable from all further yield analyses. Subsequent yield analyses revealed evidence for differences in initial yield potential among the variety types, as defined by the y-intercept in the regression analyses (Table 3). The greatest initial yield potential was found in the SCN-susceptible variety type (52.3 bu/acre or 3,517 kg/ha), followed by PI 88788-derived resistant varieties (49.1 bu/acre or 3,302 kg/ha) and Peking-derived resistant varieties (46.1 bu/acre or 3,100 kg/ha). Analyses also revealed that in general, soybean yield was positively correlated to chronological year, indicating that soybean yields increased over the 15 years of data we evaluated. And more specifically, yield potential was estimated to have increased by 0.6 to 1.0 bu/acre (40 to 67 kg/ha) per year. The yield of PI 88788-derived SCN-resistant varieties increased at the greatest rate (1.0 bu/acre or 67 kg/ha per year), followed by

Peking-derived resistant varieties (increasing at 0.8 bu/acre or 54 kg/ha per year), and then SCN-susceptible varieties (increasing at 0.6 bu/acre or 40 kg/ha per year). These results are consistent with reports of lower yield potential or so-called “yield drag” associated with SCN-resistant varieties upon their initial commercial release and with “yield drag” subsequently being overcome through breeding efforts in the decades following initial releases.

Analyses of the data also indicated that SCN population dynamics were important in determining soybean yield (Table 3). Initial population density of the nematode was significantly negatively correlated only with the yield of SCN-susceptible varieties. Susceptible soybean yields decreased on average by 1.0 bu/acre or 67 kg/ha for every 1,000 SCN eggs per 100 cc of soil present at planting. Reproduction of SCN was significantly negatively correlated with the yield for all three variety types. And SCN virulence was negatively correlated with the yield of PI 88788-derived varieties, but not Peking-derived varieties.

These results as a whole indicate that higher initial SCN population densities led to greater yield loss on susceptible varieties. However, for resistant varieties, the initial SCN population density was less important for yield loss than the degree to which the SCN population reproduced on the variety. This trend likely is due to effective resistance displayed of SCN-resistant soybean varieties that prevents a large percentage of the population from successfully reproducing on the soybean plant throughout the growing season.

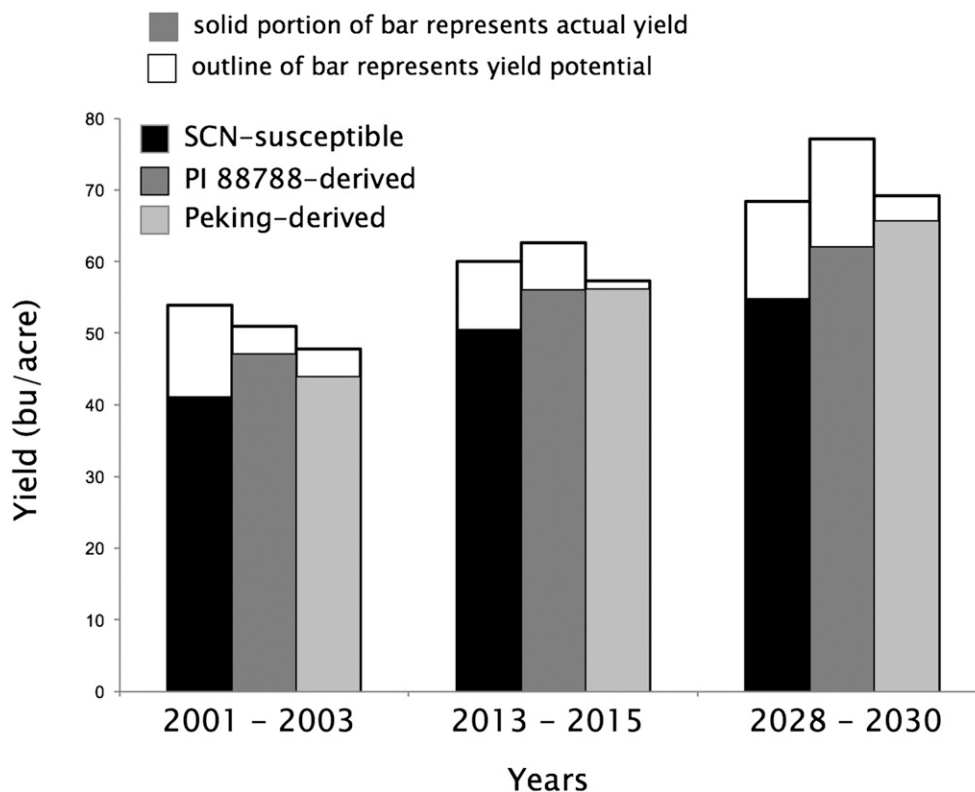


FIGURE 6

Potential yield and observed yield values for SCN-susceptible, PI 88788-derived SCN-resistant, and Peking-derived SCN-resistant soybean varieties across three time periods. Each time period is the average of three years. Potential yields are depicted by the overall outline of the bars and were calculated from regression models (y-intercept and slope of effect of year) from the data for the three variety types that were analyzed. Observed yields are the solid portion of each bar and are the actual mean yields calculated from the data for the three variety types that were analyzed for the first two time periods. Observed yields are lower than yield potential due to abiotic stress and SCN damage. Observed yields for the time period 2028 to 2030 were calculated by reducing the projected potential yield for that time period by a proportion equivalent to the yield reduction from SCN alone (no abiotic stress) calculated in regression models for the three variety types that were analyzed for the first two time periods.

Finally, SCN virulence was an important indication of overall yield for PI 88788-derived varieties, but not for Peking-derived varieties, which may have been due to the limited variation in SCN virulence on Peking among the experiments over time.

Practical Implications

Similar to previously published studies (Alston and Schmitt 1988; Koenning and Barker 1995), we observed SCN reproduction was positively correlated with increased temperatures and decreased soil moisture in our experiments. However, none of our regression analyses investigating SCN reproduction were able to explain more than 50% of the variability in SCN reproduction among location-years. We believe there are several important factors that limited our ability to explain the variability among location-years. First, we considered only precipitation and growing degree days, not other abiotic factors that can influence SCN reproduction such as soil type (Francl 1993), soil pH (Anand et al. 1995; Francl 1993; Pedersen et al. 2010), and soil nutrient content (Duan et al. 2009). Data on those factors were not readily available for all of the experimental location-years included in our analyses. Second, female index data were used as a measurement of SCN virulence on PI 88788 and Peking, and these data are an imperfect measurement of an SCN population's virulence on the commercial varieties derived from these sources. Resistance to SCN in PI 88788 and Peking has been reported to be oligogenic, involving multiple genes (Anand 1994). Not all commercial SCN-resistant varieties derived from the sources of resistance (i.e., PI 88788 or Peking) possess the full complement of resistance genes that were present in the parent source of resistance. There likely would have been more significant and impactful relationships detected between the virulence of the SCN populations and the factors that affected virulence in our experiments if the SCN-resistant soybean varieties in our experiments all contained the full complement of resistance genes.

Our results illustrate a growing challenge for soybean production in the Midwestern United States, namely increased reproduction of SCN populations on SCN-resistant soybean varieties. Management of SCN relies extensively on growing nonhost crops to reduce nematode population densities in rotation with resistant soybean varieties to limit reproduction of the nematode while producing profitable yields. Unfortunately, farmers are almost completely reliant on a single source of soybean resistance to SCN, PI 88788. There are very few resistant varieties with any other source of resistance. We found that virulence to the PI 88788 source of resistance is increasing in the farm fields across Iowa in which we conducted our experiments. Furthermore, our results revealed that increases in virulence to PI 88788 correlated with increased reproduction on PI 88788-derived commercial varieties in the field leading to measurable yield losses on these resistant varieties.

Looking Forward

The lower yield potential, or “yield drag,” associated with SCN-resistant soybean varieties upon initial and early commercialization of the varieties was evident in our results. The y-intercept values for both PI 88788-derived and Peking-derived SCN-resistant varieties were lower than the y-intercept for susceptible varieties in the data we analyzed. But yield of the PI 88788-derived SCN-resistant soybean varieties increased at a rate double that of the increase of yield of susceptible varieties from 2001 through 2015, and the rate of yield increase of Peking-derived SCN-resistant soybean varieties in our experiments from 2001 to 2015 was roughly 60% greater than for susceptible varieties.

Increased virulence of SCN populations on PI 88788 threatens the long-term effectiveness of soybean resistance to the nematode

and the sustained profitability of soybean production in the future. Until now, yield losses due to increased virulence of SCN populations on SCN-resistant soybean varieties with PI 88788 resistance have been mostly offset by concurrent increases in the yield potential of the commercially available soybean varieties, as mentioned immediately above. However, it is uncertain (and perhaps unlikely) that the inherent yield potential of new SCN-resistant soybean varieties with PI 88788 SCN resistance can continue to increase at a rate that keeps pace with or exceeds the rate of increasing virulence and associated yield loss caused by SCN populations with greater reproduction on PI 88788.

Increased virulence on PI 88788 is likely widespread in the SCN populations of Iowa and has been documented throughout many of the Midwestern United States. The genetic base of SCN resistance in commercially available soybean varieties is currently too narrow to provide sustainable, long-term management of this pest for the future. The trends in our data indicate that in the future, the gap between potential yields and actual, attained yields for PI 88788-derived SCN-resistant soybean varieties will be similar to that of susceptible soybean varieties (Fig. 6). And the attained yields of PI 88788-derived SCN-resistant soybean varieties also will begin to lag behind yields of Peking-derived SCN-resistant soybean varieties as virulence on PI 88788 continues to increase among SCN populations throughout the soybean-producing regions of North America (Fig. 6).

Conclusions

The data set used for the analyses described herein contained information from more than 25,000 experimental plots at 122 location-years spanning 15 years. These data are unique in their depth, geographic breadth, and temporal range. The results show an increase in virulence of SCN populations on PI 88788 across a wide geographic range (the state of Iowa) from 2001 to 2015 and the associated consequences in the form of increased SCN reproduction and decreased yields of PI 88788-derived SCN-resistant soybean varieties. The crop management practices and crop rotations used in the soybean-producing areas of the Midwestern United States and Canada were similar to those used in Iowa during the years that the experiments were conducted. So the results reported herein likely are applicable to all of the soybean-producing areas in which increased virulence of SCN populations on PI 88788 have been documented (Acharya et al. 2016; Chen et al. 2010; Faghihi et al. 2010; Hershman et al. 2008; Mitchum et al. 2007; Niblack et al. 2008).

It is clear that major changes in SCN management are critically needed. The effectiveness of PI 88788 SCN resistance as a management practice very likely will continue to diminish if new sources of resistance do not become widely available quickly. Long-term, sustainable SCN management will require a multifaceted, integrated pest management approach that includes use of nonhost crops, nematode-protectant seed treatments, conventionally bred soybean varieties with resistance from multiple, different breeding sources, and varieties with transgenic SCN resistance, if they become available.

Acknowledgments

This research was funded, in part, by the soybean checkoff through the Iowa Soybean Association. We thank the many farmers who rented us land and allowed us to conduct these experiments on their farms throughout Iowa. Gratitude also is expressed to the staff of the Iowa State University Research and Demonstration Farms for their assistance with experiments in central and southeast Iowa. Thanks also are extended to the many Iowa State University undergraduate research assistants who processed and

counted SCN eggs from many, many thousands of soil samples. Finally, appreciation is expressed to the University of Missouri Plant Nematology Laboratory for conducting many of the SCN HG type tests.

Literature Cited

- Acharya, K., Tande, C., and Byamukama, E. 2016. Determination of *Heterodera glycines* virulence phenotypes occurring in South Dakota. *Plant Dis.* 100: 2281-2286. 10.1094/PDIS-04-16-0572-RE
- Allen, T. W., Bradley, C. A., Sisson, A. J., Byamukama, E., Chilvers, M. I., Coker, C. M., Collins, A. A., Damicone, J. P., Dorrance, A. E., Dufault, N. S., Esker, P. E., Faske, T. R., Giesler, L. J., Grybauskas, A. P., Hershman, D. E., Hollier, C. A., Isakeit, T., Jardine, D. J., Kelley, H. M., Kemerait, R. C., Kleczewski, N. M., Koenning, S. R., Kurl, J. E., Malvick, D. K., Markell, S. G., Mehl, H. L., Mueller, D. S., Mueller, J. D., Mulrooney, R. P., Nelson, B. D., Newman, M. A., Osborne, L., Overstreet, C., Padgett, G. B., Phipps, P. M., Price, P. P., Sikora, E. J., Smith, D. L., Spurlock, T. N., Tande, C. A., Tenuta, A. U., Wise, K. A., and Wrather, J. A. 2017. Soybean yield loss estimates due to diseases in the United States and Ontario, Canada, from 2010 to 2014. *Plant Health Prog.* 18:19-27.
- Alston, D. G., and Schmitt, D. P. 1988. Development of *Heterodera glycines* life stages as influenced by temperature. *J. Nematol.* 20:366-372.
- Anand, S. C. 1994. Genetic diversity for resistance to *Heterodera glycines* race 5 in soybean. *J. Nematol.* 26:76-79.
- Anand, S. C., Matson, K. W., and Sharma, S. B. 1995. Effect of soil temperature and pH on resistance of soybean to *Heterodera glycines*. *J. Nematol.* 27:478-482.
- Arelli, A. P., Slepner, D. A., Yue, P., and Wilcox, J. A. 2000. Soybean reaction to races 1 and 2 of *Heterodera glycines*. *Crop Sci.* 40:824-826.
- Byrd, D. W., Jr., Barker, K. R., Ferris, H., Nusbaum, C. J., Griffin, W. E., Small, R. H., and Stone, C. A. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *J. Nematol.* 8:206-212.
- Chen, S., Potter, B., and Orf, J. 2010. Virulence of the soybean cyst nematode has increased over years in Minnesota. *J. Nematol.* 42:238.
- Concibido, V. C., Diers, B. W., and Arelli, P. R. 2004. A decade of QTL mapping for cyst nematode resistance in soybean. *Crop Sci.* 44:1121-1131.
- Cook, D. E., Lee, T. G., Guo, X., Melito, S., Wang, K., Bayless, A., Wang, J., Hughes, T. J., Willis, D. K., Clemente, T. E., Diers, B. W., Jiang, J., Hudson, M. E., and Bent, A. F. 2012. Copy number variation of multiple genes at *Rhgl* mediates nematode resistance in soybean. *Science* 338:1206-1209.
- Duan, Y.-X., Zheng, Y.-N., Chen, L.-J., Zhou, X.-M., Wang, Y.-Y., and Sun, J.-S. 2009. Effects of abiotic environmental factors on soybean cyst nematode. *Agric. Sci. China* 8:317-325.
- Faghihi, J., Donald, P. A., Noel, G., Welacky, T. W., and Ferris, V. R. 2010. Soybean resistance to field populations of *Heterodera glycines* in selected geographic areas. *Plant Health Prog.* doi:10.1094/PHP-2010-0426-01-RS
- Faghihi, J., and Ferris, J. M. 2000. An efficient new device to release eggs from *Heterodera glycines*. *J. Nematol.* 32:411-413.
- Francl, L. J. 1993. Multivariate analysis of selected edaphic factors and their relationship to *Heterodera glycines* population density. *J. Nematol.* 25: 270-276.
- Gerdemann, J. W. 1955. Relation of a large soil-borne spore to phycomycetous mycorrhizal infections. *Mycologia* 47:619-632.
- 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. Report.* 54:544-546.
- Hershman, D. E., Heinz, R. D., and Kennedy, B. S. 2008. Soybean cyst nematode, *Heterodera glycines*, populations adapting to resistant soybean varieties in Kentucky. *Plant Dis.* 92:1475.
- IEM. 2014. Download QC and estimated data. Nat. Weather Servi., Coop. Observer Prog. (NWS-COOP), and Iowa Environ. Mesonet (IEM), Iowa State Univ., Ames. www.mesonet.agron.iastate.edu/request/coop/fe.phtml
- Kim, D. G., Riggs, R. D., Robbins, R. T., and Rakes, L. 1994. Distribution of races of *Heterodera glycines* in the United States. *J. Nematol.* 29:173-179.
- Koenning, S. R., and Barker, K. R. 1995. Soybean photosynthesis and yield as influenced by *Heterodera glycines*, soil type and irrigation. *J. Nematol.* 27:51-62.
- Mitchum, M. G., Wrather, J. A., Heinz, R. D., Shannon, J. G., and Danekas, G. 2007. Variability in distribution and virulence phenotypes of *Heterodera glycines* in Missouri during 2005. *Plant Dis.* 91:1473-1476.
- Niblack, T. L., Arelli, P. R., Noel, G. R., Opperman, C. H., Orf, J. H., Schmitt, D. G., Shannon, J. G., and Tylka, G. L. 2002. A new classification scheme for genetically diverse populations of *Heterodera glycines*. *J. Nematol.* 34:279-288.
- Niblack, T. L., Colgrove, A. L., Colgrove, K., and Bond, J. P. 2008. Shift in virulence of soybean cyst nematode is associated with use of resistance from PI 88788. *Plant Health Prog.* doi:10.1094/PHP-2008-0118-01-RS
- Niblack, T. L., and Tylka, G. L., eds. 2009. The Soybean Cyst Nematode Management Guide, 5th Ed. North Central Soybean Res., Univ. of Missouri, Columbia.
- Niblack, T. L., Wrather, J. A., Heinz, R. D., and Donald, P. A. 2003. Distribution and virulence phenotypes of *Heterodera glycines* in Missouri. *Plant Dis.* 87: 929-932.
- Pedersen, P., Tylka, G. L., Mallarino, A. P., MacGuidwin, A. E., Koval, N. C., and Grau, C. R. 2010. Correlation between soil pH, *Heterodera glycines* population densities, and soybean yield. *Crop Sci.* 50:1458-1464.
- Sikora, E. J., and Noel, G. R. 1991. Distribution of *Heterodera glycines* races in Illinois. *J. Nematol.* 23:624-628.
- Tylka, G. L. 2012. Soybean Cyst Nematode Field Guide, 2nd Ed. Ext. Publ. CSI 0012. Iowa State Univ., Ames.
- Tylka, G. L. 2016. SCN resistance continues to pay twice in 2015. Integrated Crop Management News. Paper 2325. Iowa State Univ., Ames. <http://lib.dr.iastate.edu/cropnews/2325>
- Tylka, G. L., Gebhart, G. D., Marett, C. C., and Mullaney, M. P. 2016. Evaluation of soybean varieties resistant to soybean cyst nematode in Iowa – 2016. Ext. Publ. 99. Iowa State Univ., Ames. http://lib.dr.iastate.edu/extension_pubs/99.
- Tylka, G. L., and Marett, C. C. 2014. Distribution of the soybean cyst nematode (*Heterodera glycines*) in the United States and Canada: 1954 to 2014. *Plant Health Prog.* 15:85-87.
- Tylka, G. L., McCarville, M. T., Marett, C. C., Gebhart, G. D., Soh, D. H., Mullaney, M. P., and O'Neal, M. E. 2013. Direct comparison of soybean cyst nematode reproduction on resistant soybean varieties in greenhouse and field experiments. *J. Nematol.* 45:322-323.
- Tylka, G. L., and Mullaney, M. P. 2016. Soybean cyst nematode-resistant soybeans for Iowa. Ext. Publ. PM 1649, Iowa State Univ., Ames. http://lib.dr.iastate.edu/extension_pubs/100.
- Tylka, G. L., and Souhrada, S. K. 1997. Evaluation of soybean varieties resistant to soybean cyst nematode in Iowa - 1997. Ext. Publ. IPM 52, Iowa State Univ., Ames. <https://www.plantpath.iastate.edu/tylkalab/files/page/files/ISU%20SCN-resistant%20Soybean%20Variety%20Trial%20Report%20-%201997.pdf>
- Willson, H. R., Kauffman, P. H., Wheeler, T. A., Stuart, M. C., Pierson, P. E., Easley, J. B., Riedel, R. M., Jasinski, J. R., and Young, C. E. 1996. Distribution of *Heterodera glycines* in Ohio. *J. Nematol.* 28:599-603.
- Workneh, F., Tylka, G. L., Yang, X. B., Faghihi, J., and Ferris, J. M. 1999. Regional assessment of soybean brown stem rot, *Phytophthora sojae*, and *Heterodera glycines* using area-frame sampling: Prevalence and effects of tillage. *Phytopathology* 89:204-211.
- Zheng, J., Li, Y., and Chen, S. 2006. Characterization of the virulence phenotypes of *Heterodera glycines* in Minnesota. *J. Nematol.* 38:383-390.