International Journal of Nematology and Entomology Vol. 1 (6), pp. 111-116, November, 2013. Available online at www.internationalscholarsjournals.org © International Scholars Journals

Full Length Research Paper

Estimation of virulence type and level of soybean cyst nematode field populations in response to resistant cultivars

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Accepted 16 March, 2013

The use of resistant cultivars is the most common practice in managing the soybean cyst nematode (SCN), *Heterodera glycines.* Currently, most commercial SCN-resistant soybean cultivars were developed from a single source of resistance, plant introduction (PI) 88788. The effect of crop sequences including rotations of SCN-susceptible soybean 'sturdy' with SCN-resistant soybean 'freeborn' carrying resistance derived from PI 88788, soybean 'Pioneer 9234' carrying resistance derived from PI 548402 (peking), and nonhost corn was studied at two field sites in southern Minnesota, the United States. Parasitic ability of SCN measured as a female index (FI) on PI 88788 and freeborn increased with the number of years freeborn was planted. After more than 5 years of freeborn, either in monoculture or rotation with other soybean cultivars and corn, the SCN population changed from the original race 3 (HG type 0 or 7) to race 1 (HG type 2.7 or 2.5.7). After 10 years of freeborn, the changed nematode population reproduced freely on the once resistant cultivar (FI > 60). There was no selection pressure from the use of PI 88788-resistance on SCN populations that can overcome peking resistance. Planting 3 or fewer years of Pioneer 9234 had no noticeable effect on the virulence phenotype of the SCN population. This study suggests that more cultivars from resistance sources other than PI 88788 are urgently needed for effective management of the nematode in Minnesota and other regions in the world.

Key words: *Heterodera glycines, HG* type, host-parasite relationship, race, soybean cyst nematode, virulence phenotype.

INTRODUCTION

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is a major soybean yield-limiting factor (Wrather and Koenning, 2006). Use of resistant cultivars and crop rotation are the most effective means to manage the nematode (Niblack, 2005; Niblack and Chen, 2004). However, the effectiveness of using resistant cultivars may depend on the interaction between the cultivars and nematode populations. Breeding and deployment of resistant cultivars is challenging due to the genetic variability of SCN (Niblack and Riggs, 2004), the selection pressure on SCN when resistance is used (Anand and Shumway, 1985; Luedders and Dropkin, 1983; McCann et al., 1982; Riggs et al., 1977; Triantaphyllou, 1975; Young, 1994; Young and Hartwig, 1992; Young et al., 1986) and the linkage of yield-suppressive factors with SCN-resistance genes (Kopisch-Obuch et al., 2005; Mudge et al., 1996). A number of soybean lines have resistance to SCN, but only a few of them have been used in breeding commercial soybean

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cultivars (Shannon et al., 2004). Most (> 90%) commercial SCN-resistant cultivars in the North Central United States were derived from crosses with PI 88788 and only a few cultivars were from PI 548402 (peking) and PI 437654 ('cystx' or 'hartwig' resistance) (Shier, 2011). Changes in virulence phenotypes, measured as races (Riggs and Schmitt, 1988) or HG types (Niblack et al., 2002) of SCN populations following the use of resistant soybean cultivars have been reported from a number of surveys.

Nationwide surveys in the late 1980s and early 1990s suggested that the frequency of SCN populations that could develop (FI ≥ 10) on resistant cultivars was higher in the southern than in the northern USA, probably due to longer use of resistant soybean cultivars in the southern states (Anand et al., 1994; Kim et al., 1997). In Tennessee, most SCN populations could not develop well on PI 88788 in the 1970s, but after cultivars derived from PI 88788 for two decades, the prevalent virulence phenotypes in the state became HG type 1.2 and 2, which can develop on the resistance source PI 88788 (Young, 1990, 1998b). In North Carolina, the frequency of races 2 and 4, which can develop on both peking and PI 88788, increased from 28 to 62% over a span of approximately 10 years from the 1980s to 1990s (Koenning and Barker, 1998). The increase of the frequency of virulent populations has also been reported recently from central states in the USA (Hershman et al., 2008; Mitchum et al., 2007; Niblack et al., 2006). In Illinois, 70% of populations were virulent on PI 88788 (HG type 2) in 2004 to 2005, whereas 64% of populations collected in 1989 to 1990 were HG type 0, which does not develop on PI 88788 (Niblack et al., 2006; Sikora and Noel, 1991).

In Missouri, the percentage of populations that develop well on PI 88788 increased from 58% in 1998 (Niblack et al., 2003) to 78% in 2005 (Mitchum et al., 2007). In Kentucky, 60% of the 20 populations collected in 2006 to 2007 were able to develop on PI 88788, contrasting to that most common HG type in late 1980s was HG type 0 (race 3) (Hershman et al., 2008). The increase of virulent populations of SCN in Illinois, Missouri and Kentucky presumably resulted from the extensive use of soybean cultivars derived from PI 88788 in the past two decades. Use of SCN-resistant cultivars in managing the nematode has a relatively short history in Minnesota compared with the southern states. The frequency of virulence phenotypes in Minnesota did not change significantly from 1997 to 2002 and most populations (more than 80%) did not develop well on PI 88788 and peking (Zheng et al., 2006).

A recent survey conducted in 2007 to 2008 showed that virulence level of the SCN populations has increased over years in Minnesota, with 72.6% of the SCN populations in the state were virulent to PI 88788 soybean, and 12.1% virulent to Peking (Chen et al., 2010). It is expected that the frequency of populations that can develop on PI 88788 and Peking will further increase in the future with longer and more extensive use of SCN-resistant cultivars in Minnesota. Knowing the virulence phenotypes of SCN in fields and speed of change following the use of resistant cultivars is important for strategically deploying and breeding resistant cultivars and making management recommendations to farmers. The objective of this study was to estimate virulence types and levels of SCN field populations in response to crop sequences including non-host crop and SCN-resistant soybean cultivars in the northern climate.

MATERIALS AND METHODS

Field sites and soil sample collection

Soil samples were collected from the plots at two field sites in Waseca County, Minnesota. Site A was initiated in 1993 in a field in New Richland for study of the effect of tillage and row spacing on SCN populations (Chen, 2007; Chen et al., 2001b). The soil at Site A was a Webster clay loam (fine-loamy, mixed, mesic, Typic Endoaquoll) with 37.4% sand, 32.4% silt, 30.2% clay, 7.3% organic matter and pH 7.8 measured in 1998. The initial SCN population was HG type 0 (race 3). SCN-resistant soybean cultivar had not been used in the field before the experiment. At this site, nine combinations of the SCN-susceptible 'sturdy', resistant 'freeborn' carrying resistance from PI 88788 (R1) and 'Pioneer 9234' carrying resistance from peking (R2) soybean were rotated annually with the nonhost corn (Table 1). In the fall of 2002 when the tillage study was terminated, soil samples were collected from the no-till plots of each crop sequence and composited. The nematode population density was increased on the susceptible soybean sturdy and maintained in the greenhouse until they were used for HG type analysis. Site B was established in 1996 in a field near Waseca to study the effect of crop sequences including corn and soybean rotations on the SCN population density and soybean yield (Chen et al., 2001a).

The soil at Site B was a Webster clay loam (fine-loamy, mixed, mesic Typic Endoaquoll) with 22% sand, 46% silt, 32% clay, 9.9% organic matter and pH 7.8. The initial SCN population was HG type 0 or 7 (Race 3). SCN-resistant soybean cultivar had not been used in the field before the experiment. At this site, the SCN-resistant soybean freeborn was included in rotations. In spring 2004, soil samples were collected from the four replicated plots each of the five selected crop sequence treatments (Table 1) and composited by treatment. The nematode population density was increased on sturdy in the greenhouse for analysis of HG types. In addition, soil samples were collected in the spring of 2007 from five crop sequences containing various numbers of years of freeborn (Table 2). The nematode population density was increased on sturdy and parasitic ability of the populations was analyzed on peking, PI 88788 and freeborn with Lee 74 as the control.

Bioassay

Newly formed females on the roots were collected and eggs were released from the cysts. The eggs were used as inoculums for tests of HG types and races of SCN following the procedures used in previous studies (Niblack et al., 2002; Riggs and Schmitt, 1988) with some modification (Zheng et al., 2006). The HG type soybean

Table 1. HG types and races of *Heterodera glycines* from different crop sequences in Minnesota fields.

			Female index on HG type indicators[a]										
Field site	Population	Crop sequence [b]	1 (peking)	2 (PI 88788)	3 (PI 90763)	4 (PI 437654)	5 (PI 209332)	6 (PI 89722)	7 (PI 548316)	FI on picket	Females/plant on Lee 74	HG type	Race
A	N1	C-R_1-C-R_1-C-R_1-C-R_1-C-R_1	0	12.1	0	0	6.2	0	13.4	0	114	2.7	1
	N2	C- R_1-C-R_1-C-R_2-C-R_2-C-R_1	0	2.1	0	0	4.9	0	1.5	0	98	0	3
	N3	C-S-C-S-C-S-C-S-C-S	0	3	0	0	0.4	0	3.4	0	65	0	3
	N4	C-S-C-S-C-R_2-C-R_2-C-R_2	0	0.4	0	0	1.7	0	7.5	0	60	0	3
	N5	C-R_1-C-S-C-R_2-C-R_1-C-R_2	0	2.2	0	0	0.9	0	3.8	3.9	77	0	3
	N6	C-R_1-C-S-C-R_2-C-S-C-R_1	0	2.5	0	0	1.8	0	7.1	2.4	81	0	3
	N7	C-R_1-C-S-C-R_1-C-S-C-R_2	0	0.7	0	0	3.4	0	18.6	0	109	7	3
	N8	C-R_1-C-S-C-R_1-C- R_1-C-R_2	0	5.3	0	0	10.1	0	17.2	4.9	103	5.7	3
	N9	C-R_1-C-S-C-R_1-C- R_2-C-R_1	0	2.8	0	0	3.7	0	14.7	1.4	71	7	3
B	W1	S-S-S-S-S-S-S-S	0	1	0	0	1.9	0	5.2	0	102	0	3
	W2	S-C-S-C-S-C-S-C	0	4.1	0	0	3.4	0	14.5	0	127	7	3
	W3	R_1-C-S-C-R_1-C-S-C	0	1.2	0	0	3.1	0	3.5	0	122	0	3
	W4	R_1-C- R_1-C-R_1-C-R_1-C	0	4.2	0	0	5.3	0	16.1	0	137	7	3
	W5	R_1-R_1-R_1-R_1-R_1-R_1-R_1-R_1	0	22.3	0	0	27.8	0	19.9	1.7	116	2.5.7	1

[a] Female index (FI) = 100 × number of females on indicator/number of females on Lee 74. [b] The letters represent the sequence of crops from 1993 to 2002 at Site A and 1996 to 2003 at Site B: C = corn; S = susceptible soybean 'sturdy'; R_1 = SCN-resistant soybean 'freeborn' (PI 88788 source of resistance – SR); and R_2 = SCN-resistant soybean 'Pioneer brand 9234' (peking SR).

Table 2. Parasitic ability of *Heterodera glycines* populations after planting the SCN-resistant soybean 'freeborn' for various years during 1996 to 2006 in a Minnesota field (Site B) infested with an original population of HG type 0 (Race 3).

		Female index[a]			Females/plant on Lee 74
Population	Crop sequence[b]	Peking	PI 88788	Freeborn	
W1-07	SSSSSSSSSCS	0.3	2.5	15.9	174
W3-07	RCSCRCSCRCS	0.2	8.2	15.6	239
W4-07	RCRCRCRCRCR	1.2	13.5	34.3	145
W5-07B	RRRRRRRRSCS	0.7	25.5	39.7	207
W5-07A	RRRRRRRRRCR	1.6	48.7	70.9	158

[a]Female index (FI) = 100 × number of females on indicator/number of females on Lee 74. [b] The letters represent the sequence of crops from 1996 to 2006: C = corn; S = susceptible soybean 'sturdy'; R = SCN-resistant soybean 'freeborn'.

indicator lines PI 548402 (peking), PI 88788, PI 90763, PI 437654, PI 209332, PI 89772, and PI 548316 (cloud) and the susceptible cultivar Lee 74 were obtained from USDA soybean Germplasm Collection (Urbana, Illinois, USA) for the study. In addition, "Pickett" was included for SCN race determination. The soybean seeds were germinated in moist, sterilized germination paper in Petri dishes at 29°C in an incubator. After 48 h, the seedlings with root radicles 2 to 3 cm long were selected for the tests. A cone-tainer (4 cm diameter and 13.5 cm high) was filled with autoclaved sandy loam soil to half and 2,000 eggs in 2.5 ml water were added. Additional soil was placed in the cone-tainer to approximately 1 cm from the top. A hole was made at the center to a depth of 3 cm with a glass stick (0.5 cm diameter). A soybean seedling was placed in the hole. Another suspension of 2,000 eggs in 2.5 ml water was added near the seedling and the seedling was covered with additional soil to about 1 cm depth. Each soybean line was replicated five times (five cone-tainers). All of the cone-tainers for each SCN population were inserted into autoclaved sand in a container (35 · 31 · 15 cm). The cone-tainers were maintained in the greenhouse at 25 to 28°C and watered daily.

After 30 days, the seedlings with soil were separately removed from the cone-tainers and soaked in water in 1 L beakers for at least 30 min. The soybean plants were gently removed from the beakers and the soil on the roots was gently washed off. The females on the roots were counted directly with the aid of a magnifier in the 2005 assay. In the 2007 assay, the females were extracted from the roots and then counted. The Female index (FI) was determined for each soybean line by dividing the mean female count on the indicator line (or other assay soybean) by the mean female count on the susceptible check 'Lee 74', and expressed as percentage. The populations were classified to HG type and races (Niblack et al., 2002; Riggs and Schmitt, 1988).

RESULTS

At Site A, two resistance sources (PI 88788 and peking) were used during 1993 to 2002. The ten years of corn/freeborn annual rotation (5 years of freeborn; SCN population N1) resulted in higher FI (12.1) on PI 88788, the source of resistance for freeborn, compared with the susceptible soybean annually rotated with corn (N3) and all other sequences involving two resistant sources (all other SCN populations) (Table 1). The virulence phenotype of N1 was changed from HG type 0 (race 3) to HG type 2.7 (Race 1) with the ten years of corn/freeborn annual rotation. In the rest of the crop sequences, whether corn was rotated with the susceptible cultivar or with two different sources of resistance, there was no significant change of virulence phenotypes except that the FI was more than 10 on PI 209332 for N8, and PI 548316 for N7, N8, and N9 SCN populations (Table 1). At Site B, 8 years of SCN-resistant freeborn monoculture from 1996 to 2003 increased parasitic ability of the SCN population (W5) on PI 88788; the FI on PI 88788 following the freeborn monoculture was 22.3, contrasting to 1 of the population from plots following susceptible soybean monoculture (W1) (Table 1). The virulence phenotype of the W5 population was changed from HG type 0 (race 3) to HG type 2.5.7 (Race 1), which is virulent to freeborn and probably other commercial soybean cultivars with the PI 88788 source of resistance. The parasitic ability of the W5 population also increased on the soybean lines PI 209332 and PI 548316 compared with the population from the monoculture of susceptible soybean (W1) (Table 1). However, there was no noticeable change of parasitic ability in the plots of corn/resistant soybean annual rotation (W4) or resistant soybean/corn/susceptible soybean rotation (W3) within the 8 years (Table 1).

In 2007, soil samples were taken from plots with different number of years of the resistant cultivar freeborn at Site B, and the FI was analyzed on freeborn, peking and PI88788. The FI of the SCN population from the plots with monoculture of susceptible soybean (W1-07) was only 0.3 and 2.5 on peking and PI 88788, respectively, confirming that the initial population was HG type 0 and the FI of this population on freeborn was 15.9, indicating freeborn was moderately resistant to HG type 0 (Race 3) (Table 2). In the sequences with freeborn more than 5 years, the FI was more than 10 on PI 88788 and it increased with increasing number of years of freeborn (Figure 1). After 10 years of freeborn, the FI increased to 48.7 on PI 88788 and 70.9 on freeborn, respectively and the resistant cultivar freeborn became susceptible to the changed nematode population. There was no noticeable change of FI on peking after the ten years of use of PI 88788 source of resistance (Table 2).

DISCUSSION

A number of previous studies with field plot experiments in southern and central USA have demonstrated that planting an SCN-resistant cultivar selected SCN populations with increased parasitic ability of the nematode population on the selecting cultivar and other cultivars with similar resistance. In Tennessee, Young and coworkers conduced extensive long-term experiments in two fields initially infested with populations virulent to cultivars carrying peking resistance (Race 14 or HG type 1) and found that planting soybean cultivars with PI 88788 source of resistance increased parasitic ability of the SCN populations on the selecting soybean cultivars and PI 88788, while planting cultivars with peking source of resistance did not significantly change the level of virulence (Young, 1994, 1998a; Young and Hartwig, 1992; Young et al., 1986). Similar results were obtained in Missouri and Arkansas in fields infested with HG type 1 (Race 14) (Anand et al., 1995; Young et al., 1986). In another study in a Mississippi field initially infested with HG type 0 (race 3), which is avirulent to the current common sources of resistance, after 10 years of various crop sequences, parasitic ability of the nematode populations on peking increased in the sequences with 6 or more years of planting a cultivar with peking source of resistance (Young and Hartwig, 1988). The present study

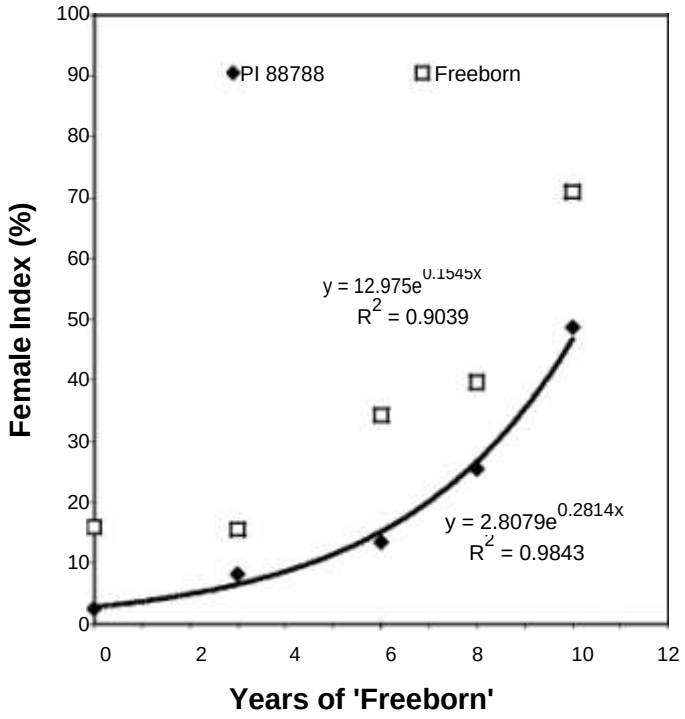

Figure 1. Relationship between parasitic ability (female index) of *Heterodera glycines* on PI 88788, and 'freeborn' after the use of the SCN-resistant soybean freeborn for various years during 1996 to 2007 in a Minnesota field (Site B) infested with an original population of race 3 (HG type 0 or 7).

demonstrated that use of freeborn carrying PI 88788 resistance had a significant effect on virulence phenotype of SCN populations in the northern climate in Minnesota fields initially infested with HG type 0 (race 3) populations.

The parasitic ability of SCN on PI 88788 increased with increasing number of years of planting the resistant cultivar. After 5 years, the original population of HG type 0 (Race 3) became a population that was able to overcome the resistance of PI 88788 (FI > 10). After 10 years, freeborn that was moderately resistant (FI ≈ 15) to the original population became susceptible (FI > 60) to the resulting population. Selection pressure may depend on a number of factors including resistance level of hosts, virulence types and level of initial nematode population, and climate and soil conditions that may affect nematode parasitism and survival. For developing a comprehensive model to predict the virulence types and level of SCN populations in response to the use of resistant cultivars, additional data from long-term field experiments are needed. Nevertheless, the present study provided approximate estimation of virulence level of SCN populations following the use of the resistant cultivars. Our results may be useful for estimating the change of virulence of SCN populations following the use of a cultivar with similar resistance in fields infested with HG type 0 (Race 3) in the similar climatic conditions such as in the Northern USA and Northeastern China.

In some fields in Minnesota, SCN populations are still HG types with low parasitic ability on PI 88788. Similarly, most populations in Northeastern China are probably still HG type 0 (Race 3) (Liu et al., 1997) because there has been limited use of SCN-resistant cultivars. The results may also be useful for estimating change of virulence of SCN populations in other recently infested regions such as Iran where most of populations are HG type 0 or 7 (Race 3) (Maafi et al., 2008). Based on our study, if a cultivar carrying PI 88788 resistance and having similar level of resistance as in freeborn is used in the fields infested with HG type 0 (Race 3) populations in the northern climates, it may take approximately 20 years for the cultivar to become susceptible to the resulting populations if the cultivar is annually rotated with a nonhost, a common practice in the Northern USA and Northeastern China, and there is no other source of resistance in the rotation. The results of this field plot study agree with the statewide surveys (Chen et al., 2010; Zheng et al., 2006). The frequency of virulence phenotypes on PI 88788 in Minnesota did not differ significantly from 1997 to 2002 (Zheng et al., 2006), but significant increase occurred after 2007 (Chen et al., 2010) because use of SCN-resistant cultivars in many fields by 2007 in the state was approximately for 5 years of soybean or 10 years of soybean-corn annual rotation, and most of the cultivars carried PI 88788 resistance. We could not detect any significant change of virulence phenotype of SCN following the use of a cultivar (Pioneer 9234) carrying resistance derived from peking for 3 or fewer years. However, change of virulence phenotypes on peking cultivars is also expected because it will pose a selection pressure on the nematode populations (Riggs et al., 1977; Triantaphyllou, 1975; Young, 1994; Young and Hartwig, 1988, 1992; Young et al., 1986).

Soybean is a major crop and in most cases it is annually rotated with corn in Minnesota. One year of nonhost corn or other crops is insufficient in lowering SCN population density to a level where there is limited damage to soybean (Chen et al., 2001a). Other practices have yet limited success. Consequently, the SCN management largely relies on the use of resistant cultivars. However, with the current resistant cultivars, most from the single source PI 88788, the use of resistant cultivars will become ineffective in the foreseeable future. Efforts are needed to develop commercial cultivars with other sources of resistance for long-term effective management of the nematode (Young, 1998b). Our results indicate that planting PI 88788-resistance freeborn had little or no selection pressure towards SCN populations that can overcome peking resistance because the resistances of the two sources did not correlate (Colgrove and Niblack, 2008;

Niblack et al., 1993; Young, 1994; Zheng et al., 2006). Consequently, rotation of cultivars from PI 88788 with the cultivars from peking is a good practice to slow down the change of virulence. However, additional sources of resistance may be needed for long-term effective management with the use of resistant cultivars.

Conclusion

In this study, field experiments were conducted in Minnesota to determine the virulence types and levels of SCN in response to the use of SCN-resistant cultivars. Planting 3 or fewer years of Pioneer 9234 carrying peking resistance had no noticeable effect on the virulence phenotype of the SCN population. There was no selection pressure from the use of PI 88788-resistance on SCN populations that can overcome peking resistance. Parasitic ability of SCN on PI 88788 and freeborn increased with the number of years freeborn was planted. After more than 5 years of freeborn, either in monoculture or rotation with other soybean cultivars and corn, the SCN population changed from the original HG type 0 or 7 (Race 3) to HG type 2.7 or 2.5.7 (Race 1). After 10 years of freeborn, the resistant cultivar was susceptible (FI > 60) to the changed nematode popula-tion. It may take approximately 20 years of corn-soybean annual rotation for a cultivar carrying similar resistance as in freeborn to become susceptible to the resulting SCN populations if nonhost corn does not affect SCN virulence, and there is no other source of resistance in the rotation.

This study suggests that more cultivars from resistance sources other than PI 88788 are urgently needed for effective management of the nematode in Minnesota and other regions in the world.

ACKNOWLEDGEMENTS

This research was supported by Minnesota Soybean Producers check-off funding through the Minnesota Soybean Research and Promotion Council and the Minnesota Agricultural Experiment Station. The authors thank D. Miller for reviewing the manuscript prior to the submission, and C. Johnson, W. Gottschalk and J. Ballman for technical assistance.

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