Response of Old and New Soybean Cultivars to *Heterodera glycines* Ichinohe

Jason L. De Bruin* and Palle Pedersen

Soybean

ABSTRACT

Soybean [*Glycine max* (L.) Merr.] cyst nematode (*Heterodera glycines* Ichinohe; SCN) causes significant yield loss each year. New cultivars (released since 1997) have superior yield compared with older cultivars (released between 1938 and 1983), but responses to SCN have not been evaluated. Studies were established at three locations in Iowa for 2 yr to measure yield loss of 23 cultivars that differed in year of release and SCN resistance in locations with varying SCN population density and *Heterodera glycines* Type (HG Type). Initial SCN population densities (Pi) were <1000 eggs 100 cm^{-3} (HG Type 2.7) at Whiting, between 1000 and 4000 eggs 100 cm^{-3} (HG Type 1.2.5.7 and 2.5.7) at Nevada, and between 4000 and 12,500 eggs 100 cm^{-3} (HG Type 0 and 7) at De Witt in 2005 and 2006. Analysis of simple effects from year × location interactions consistently showed that new SCN-resistant cultivars had lower final SCN population densities (Pf) and reproduction factors (Rf) compared with old and new SCN-susceptible cultivars. Among all locations, seed yield of new SCN-resistant cultivars was 14% greater than new SCN-susceptible cultivars and 32% greater than old SCN-susceptible cultivars. Yield increase was a result of increased seed production (seeds m^{-2}) and not from a change in seed mass. Yield of new SCN-susceptible cultivars was 18% greater than old SCN-susceptible cultivars but did not provide greater control of SCN. These data indicate that yield increases with new SCN-susceptible cultivars are not the result of improved SCN management. Data support the selection of SCN-resistant cultivars for fields in which SCN has been identified, regardless of Pi or HG Type to increase yield and reduce SCN population densities.

Soybean yield of 8000 kg ha^{-1} has been suggested as a reasonable yield limit for soybean productivity (Specht et al., 1999). Average yields in Iowa are approximately 50% of this (National Agriculture Statistics Service, 2007). In rare instances yields have approached or surpassed this suggested maximum but only occur when all environmental conditions are favorable (Cooper, 2003). Each cultivar has a genetic yield potential (Evans and Fischer, 1999) that can only be attained in a "stress-free" environment. Abiotic and biotic stresses within the environment influence plant growth and reduce yield (Cook, 2000). As noted by Sinclair (1993), there are physiological limitations to crop yield potential and "alleviation of stress barriers to achieving full yield potential offers many opportunities…to sustaining and increasing crop yields in the future."

Soybean cyst nematode is an important biotic stress, was first identified in Iowa in 1978 (Edwards, 1988), and causes estimated yield losses greater than 1.2 million tonnes in 2004 (Wrather and Koenning, 2006). Population densities as low as 10 to 50 eggs 100 cm^{-3} can reduce yield (Niblack et al., 1992), and greater population densities can reduce water uptake (Fallick et al., 2002), and plant biomass and canopy development (Alston and Schmitt, 1987; Fallick et al., 2002). Distribution of SCN throughout Iowa is widespread and has been identified in all but three of the 99 counties and >65% of randomly selected fields (Tylka, 2007). Field history and cultivar selection have generated a range of population densities from 100 to <5000 eggs 100-cm^{-3} soil among sampled fields (Tylka et al., 2008).

Already in the 1960s and 1970s it was realized that SCN populations were genetically unique and differed in their ability to reproduce on resistant cultivars. Initially a scheme was outlined with four races (Golden et al., 1970) and expanded to 16 races by Riggs and Schmitt (1988). In 2002, the notation was changed to *H. glycines* (HG) Type (Niblack et al., 2002). The HG Type tests evaluate the potential for a SCN population from a specific field to reproduce on various sources of SCN resistance. As an example, fields with HG Type 2 SCN populations show the ability to overcome the PI 88788 source of resistance at a reproduction level >10% of the susceptible check cultivar Lee 74 (Niblack et al., 2002).

Marker assisted selection methods have improved the rate and accuracy at which resistance genes are integrated into new cultivars (Concibido et al., 2004). However, there are still wide ranges of SCN control from these cultivars (Niblack et al., 2006). There is extensive knowledge for PI 88788 and Peking sources and these have been successfully integrated into numerous new cultivars (Concibido et al., 2004; Glover et al., 2004; Kopisch-Obuch et al., 2005). Although these two sources of resistance are widely available and can be readily deployed they may not be adequate for fields with HG Type 1 or 2 SCN populations, allowing population densities to increase and/or not providing a yield benefit.

Dep. of Agronomy, Iowa State Univ., 2104 Agronomy Hall, Ames, Iowa 50011-1010. Received 9 July 2008. *Corresponding author (jsndbrn@iastate.edu).

Published in Agron. J. 100:1347–1353 (2008).
doi:10.2134/agronj2008.0028

AJ AGRONOMY JOURNAL 1908–2008

Abbreviations: SCN, soybean cyst nematode; HG, *Heterodera glycines*; Pi, initial SCN population density; Pf, final soybean cyst nematode population density; Rf, reproduction factor

Use of resistant cultivars can reduce population densities and increase yield (Chen et al., 2001a, 2001b; Niblack et al., 1992; Tylka et al., 2008). Crop rotation and use of nonhost crops has also proven effective at reducing initial SCN population densities and increasing yield (Chen, 2007; Koenning et al., 1995; Miller et al., 2006). However, simply reducing the density or starting with a small population density may still cause a high level of yield damage if the wrong source of SCN resistance or a resistant cultivar with ineffective resistance is selected.

Questions that arise with SCN management are (i) how predictive is the initial SCN population for potential yield reduction (i.e., egg counts) (ii) how important is knowledge of the genetic profile of the population (i.e., HG Type). Attempts have been made to use the Pi values estimated before planting as a predictive measure for crop injury. Damage threshold is as low as 10 to 50 eggs 100 cm^{-3} of soil (Niblack et al., 1992) and 470 eggs kg^{-1} soil (Francl and Dropkin, 1986). Declining exponential (Appel and Lewis, 1984; Chen et al., 2001a), quadratic (Alston and Schmitt, 1987) and linear (Chen et al., 2001b; Niblack et al., 1992; Sasser and Uzzell, 1991) models have all been used to describe the yield loss to increasing SCN Pi. These models have all shown to be year, location, and cultivar dependent and often provide inconsistent predictive ability to determine yield loss. This has led to an action threshold of one cyst 100 cm^{-3} of soil to initiate management compared with a damage threshold (Niblack et al., 2006).

The most common source of resistance to SCN is from PI 88788 and is in more than 90% of SCN resistant cultivars (Tylka, 2006). Soybean cyst nematode populations classified as HG Type 2 have the ability to reproduce at a level >10% on cultivars with PI 88788 source of SCN resistance. For a producer, this means that selection of cultivars with PI 88788 source of resistance may not be sufficient to manage the population and/or maintain yield compared with other sources of resistance. An ongoing investigation in Iowa has determined that many HG Types are present within the state, including HG Type 0, 7, 2.7, 2.5.7, and 5.7 (Tylka, 2007). Tylka (2007) sampled 23 locations where 11 of the locations included a 2 as part of their HG Type description potentially limiting the effectiveness of this source of resistance as a high-yielding SCN-resistant cultivar. Yield trials conducted in Iowa indicated that even in the presence of HG Type 2 SCN populations, cultivars with PI 88788 still produce greater yields and reduce SCN reproduction (Tylka et al., 2008).

Yield is the cumulative result of the interaction between a cultivar and environment factors. Our hypothesis is that a combination of density and HG Type of the SCN population will determine the effectiveness of resistant cultivars to increase yield and manage SCN population densities relative to susceptible cultivars. It is speculated that older cultivars that do not contain SCN-resistance genes, and were selected and introduced in areas where SCN was absent, may have a different response to SCN compared with new SCN-susceptible cultivars that were likely selected and evaluated in the presence of SCN. In addition, cultivars with PI 88788 source of SCN resistance may not be effective cultivars for fields with HG Type 2 SCN populations. The objective was to measure the yield, yield components, and SCN population density responses of a wide range of cultivars, that differ in resistance to SCN and the year that they were released for commercial production, to SCN populations of different density and HG Type in Iowa.

MATERIALS AND METHODS

Field research plots were established at three locations during the 2005 and 2006 growing seasons. In this study, high-yielding and low-yielding environments were selected based on those that typically yield above or below the 5-yr state average yield of 3118 kg ha^{-1}, respectively (National Agriculture Statistics Service, 2007). Fields were selected in eastern Iowa at a high-yielding environment near De Witt. Soils were classified as a Tama silt loam (fine-silty, mixed, superactive, mesic Typic Argiudolls) with a pH of 6.7, 39 mg kg^{-1} P, 217 mg kg^{-1} K, 3.4 g kg^{-1} organic matter, and 13 mg kg^{-1} of NO_3^--N. In central Iowa at a low-yielding environment near Nevada with predominately Webster clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquolls) with a pH of 7.6, 21 mg kg^{-1} P, 234 mg kg^{-1} K, 5.4 mg kg^{-1} organic matter, and 5.2 mg kg^{-1} of NO_3^--N. In western Iowa at a high-yielding environment with access to irrigation near Whiting with Salix silty clay loam (fine-silty, mixed, superactive, mesic Typic Hapludolls) with a pH 6.1, 56 mg kg^{-1} P, 489 mg kg^{-1} K, 3.9 g kg^{-1} organic matter, and 19.2 mg kg^{-1} NO_3^--N. Irrigation at Whiting in 2005 was 24 mm on 18 July and 34 mm on 7 August; in 2006 was 13 mm on 20 May, 26 mm on 16 June, 25 mm on 10 July, 13 mm on 17 August, and 13 mm on 19 August. These research sites were all located at approximately 42°N latitude, across the central part of the state, and were chosen to represent the variation in soil type, moisture regimes, and soil pathogens characteristic to Iowa.

The experimental design was a randomized complete block with four replications. The 23 cultivars that varied in year of release from the private and public sectors and SCN resistance were tested each year (Table 1). For this study, resistance indicated that the cultivar contained genes known to provide a resistant reaction to SCN (Peking, PI 88788, and PI 437654). No attempt was made to evaluate each cultivar for its level of resistance based on greenhouse tests and calculated female index as is often done to evaluate resistance (Niblack, 2005).

Before planting, the pre-emergent herbicides s-metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl) acetamide] and metribuzin [4-amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one] were applied at 180 g a.i. ha^{-1} and 40 g a.i. ha^{-1}, respectively, to the study at Whiting (2005 and 2006), Nevada (2006), and De Witt (2005 and 2006). No pre-emergent herbicide was used at Nevada in 2005. Following herbicide application, the field was cultivated to a depth of 10 cm to incorporate the herbicide and provide a level seed bed.

Seeds were inoculated with *Bradyrhizobium japonicum* (EMD Crop BioScience, Brookfield, WI) and planted with an Almaco grain drill (Almaco, Nevada, IA) at a seeding rate of 432,000 seeds ha^{-1} and row spacing of 38 cm. Planting occurred between 24 April and 9 May. Plot size was 2.7 by 6.7 m. Glyphosate [*N*-(phosphonomethyl)glycine] was applied twice during the season at a rate of 865 g a.e. ha^{-1} to the glyphosate-tolerant cultivars (Table 1). The combination of acifluorfen [5-[2-chloro-4-(trifluoromethyl)phenoxy]-2-nitrobenzoic acid] at a rate of 300 g a.i. ha^{-1} and sethoxydim [2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one] at a rate of 400 g a.i. ha^{-1} was applied once to nonglyphosate-tolerant cultivars (Table 1), and plots were kept weed free by hand weeding during the growing season. The insecticide Lorsban [chlorpyrifos 0,0-diethyl-0-(3,5,6-

trichloro-2-pyridinyl) phosphorothioate] was applied at a rate of 840 g a.i. ha^{-1} to the experiment at De Witt twice in 2005 for the control of spider mites (*Tetranychus urticae*) and soybean aphids (*Aphis glycines*) and to Nevada in 2006 for the control of bean leaf beetles (*Ceratoma trifurcata*). To control bean leaf beetles at Whiting in 2005, the insecticide Baythroid, [cyfluthrin,cyano (4-fluoro-3-phenoxyphenyl) methyl-3-(2,2-dichloroethenyl)-2,2-dimethyl-syclopropane-carboxylate] was applied at 490 g a.i. ha^{-1}.

Before planting and following harvest, each plot was sampled for SCN by taking 20 soil cores to approximately 15 to 20 cm depth. Egg number 100-cm^{-3} soil was determined by extracting the cysts (egg-filled dead females) and crushing the cysts to remove the eggs, followed by counting the eggs under a microscope at a 1:100 dilution as outlined by Tabor et al. (2003). Tests to determine HG Type were conducted following the procedures outlined by Niblack et al. (2002). HG Type is determined based on the percent female reproduction on seven indicator lines and compared with female reproduction on the susceptible cultivar Lee 74. Indicator lines with reproduction values >10% of the standard susceptible cultivar indicate that the nematode population present in the field was virulent to the indicator line.

Data collected at harvest included final plant density, seed mass based on a 300-seed sample and seed number m^{-2} based on seed mass and plot yield (Board and Modali, 2005). The center four rows were harvested with an Almaco small plot combine (Almaco, Nevada, IA) and harvest weights were adjusted to 130 g kg^{-1} moisture for final yield.

Statistical analysis was conducted with Proc Mixed in SAS (SAS Institute, 2003). Due to strong location × cultivar and year × location interactions, data are presented by location. Years were considered a fixed effect in the analysis of all variables due to the varying Pi and HG Types. Cultivar was nested within SCN-group (new SCN-resistant and susceptible and old SCN-susceptible cultivars) indicating that cultivar was considered a random effect along with replication. Single-degree-of-freedom contrasts were used to determine simple effects of the interaction between year and cultivar and to make comparisons between new SCN-resistant cultivars and new SCN-susceptible cultivars and new SCN-susceptible cultivars and old SCN-susceptible cultivars. Relative yields were calculated by dividing the yield of the individual plot yield for each cultivar within year × location combinations by the average yield of the new SCN-resistant cultivars. A combined location and year analysis was used to analyze relative yields, treating replications and years as random factors following the method outlined by McIntosh (1983). Initial SCN population densities (Pi) and final SCN population densities (Pf) were variable and ranged from 0 to greater than 12,000 eggs 100 cm^{-3} of soil depending on the environment. Data were transformed with $\log_{10}(x + 1)$ to improve homogeneity of variance of count data; an acceptable transformation of SCN population densities (Chen et al., 2001a; Koenning et al., 1995; Niblack et al., 1992). Reproduction factor (Rf = Pf/Pi) values were calculated with transformed Pf and Pi values. Correlations among yield, seed mass, seeds m^{-2}, Pi, Pf, and Rf for each cultivar class were conducted with Proc Corr in SAS.

Table 1. Traits for 23 cultivars used at three locations in Iowa during 2005 and 2006.

Cultivar	Company name	Year of release†	Source of resistance	Glyphosate tolerance‡
Old SCN-susceptible				
Hardin	Iowa State University	1983	susceptible	NT
Harosoy	Dominion Experimental Farm, Harrow, Ontario	1951	susceptible	NT
Hawkeye	Iowa Agriculture Expt. Station and U.S. Regional Soybean Laboratory	1948	susceptible	NT
Lincoln	Illinois Experimental Station	1944	susceptible	NT
Richland	Purdue University	1938	susceptible	NT
Williams 82	USDA-ARS and Illinois Agricultural Experiment Station	1981	susceptible	NT
New SCN-susceptible				
AG2403	Monsanto Company	2004	susceptible	T
NE3001	University of Nebraska-Lincoln	2001	susceptible	NT
NK-S32-G5	Syngenta	2003	susceptible	T
P92M91	Pioneer	2004	susceptible	T
S25J5	Syngenta	2003	susceptible	NT
S-2743-4	Stine Seeds	2004	susceptible	T
New SCN-resistant				
2509CN	Croplan	2003	(PI 88788)	NT
AG2801	Monsanto Company	2003	(PI 88788)	T
Dwight	University of Illinois	1997	(PI 88788)	NT
E2620RX	Latham Seeds	2003	(PI 437654)	T
IA2068	Iowa State University	2003	(PI 88788)	NT
L2811RX	Latham Seeds	2004	(PI 437654)	T
S-3012-4	Stine Seeds	2004	(PI 88788)	T
PB291N	Prairie Brand Seeds	2003	(PI 88788)	NT
SOI2642NRR	Sands of Iowa	2003	(PI 88788)	T
SOI2858NRR	Sands of Iowa	2003	(PI 88788)	T
P91M90	Pioneer	2003	(Peking)	T

† Year of release estimated by published articles or when cultivar first appeared on the market.

‡ NT = not tolerant, T = tolerant to glyphosate.

RESULTS

Heterodera glycines Type

Greenhouse HG Type assessments are presented in Table 2. Populations at De Witt were HG Type 0 and 7 in 2005 and

Table 2. HG Type test values on seven indicator cultivars and one susceptible cultivar, Hg-Type, and initial (Pi) SCN egg densities at three locations in Iowa, 2005 and 2006.

Year	Location	Indicator line 1	2	3	4	5	6	7	Susceptible	HG-type	Pi†
		females $plant^{-1}$									eggs 100 cm^{-3}
2005	De Witt	0	4	0	0	2	0	11	156	0	3.6b‡
2006	De Witt	0	3	1	1	4	0	26	161	7	4.1a
2005	Nevada	17	40	2	0	37	5	72	129	1.2.5.7	3.6a
2006	Nevada	1	3	0	0	3	0	6	26§	2.5.7	2.8b
2005	Whiting¶	1	47	0	0	24	0	53	356	2.7	2.0b
2006	Whiting	1	47	0	0	24	0	53	356	2.7	3.0a

† $\log_{10}(x + 1)$.

‡ Letters following the mean are for comparison of years within a location. Values followed by the same letter are not significantly different at $P \leq 0.05$.

§ Susceptible cultivar Kenwood 94 was substituted for Lee 74 in this test due to poor emergence of Lee 74.

¶ Experiments were located on different parts of land within the same field at Whiting in 2005 and 2006. Only one HG Type test was conducted to determine the HG Type of the field.

2006, respectively, indicating that these populations were not expected to have the ability to reproduce on the resistant cultivars with Peking source of resistance (HG Type 1), PI 88788 source of resistance (HG Type 2), or PI 437654 (HG Type 4). At Whiting, HG Type was 2.7 indicating >10% reproduction on PI 88788. HG Type at Nevada was HG Type 1.2.5.7 and 2.5.7 in 2005 and 2006, respectively and was similar to Whiting as SCN populations reproduced at levels >10% nematode reproduction on PI 88788. In addition, >10% reproduction on Peking (HG Type 1) was observed in Nevada in 2005.

Table 3. Significance of *F* values from analysis of variance of yield, seed number, seed mass, initial (Pi) and final (Pf) SCN population densities, and SCN reproduction factor (Rf) at three locations in Iowa during 2005 and 2006.

Source	Yield	Seed number	Seed mass	Pi	Pf	Rf
			P > *F*			
De Witt						
Year (Y)	<0.01	0.01	0.28	<0.01	0.02	<0.01
Variety (V)	<0.01	<0.01	0.45	0.34	<0.01	<0.01
Y × V	0.28	0.13	0.12	0.92	0.03	<0.01
Nevada						
Year (Y)	<0.01	<0.01	0.46	<0.01	0.23	<0.01
Variety (V)	<0.01	<0.01	0.77	0.74	<0.01	<0.01
Y × V	<0.01	<0.01	<0.01	0.50	0.42	0.67
Whiting						
Year (Y)	<0.01	0.30	<0.01	<0.01	<0.01	0.09
Variety (V)	<0.01	<0.01	0.22	0.81	<0.01	0.02
Y × V	<0.01	0.48	<0.01	0.36	0.09	0.08

Table 4. Year × cultivar interactions for final SCN population density (Pf) and reproduction factor (Rf) at three locations in Iowa, 2005 and 2006.

	De Witt		Nevada		Whiting	
	2005	2006	2005	2006	2005	2006
Cultivar type			Pf (eggs 100 cm^{-3})†			
New SCN-resistant (NSCNR)	3.08a‡	3.15a	3.56a	3.25a	2.60a	2.11b
New SCN-susceptible (NSCNS)	4.01a	3.80a	4.03a	3.80a	4.14a	3.23b
Old SCN-susceptible(OSCNS)	3.92a	3.64b	3.84a	3.76a	4.20a	3.39b
Contrast			*P* > *F*			
NSCNR vs. NSCNS	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
NSCNS vs. OSCNS	0.64	0.36	0.28	0.80	0.83	0.56
Cultivar type			Rf			
New SCN-resistant (NSCNR)	0.87a	0.77b	0.98b	1.33a	1.16a	0.74a
New SCN-susceptible (NSCNS)	1.17a	0.95b	1.15b	1.53a	4.10a	1.17a
Old SCN-susceptible (OSCNS)	1.14a	0.91b	1.11b	1.52a	5.00a	1.21b
Contrast			*P* > *F*			
NSCNR vs. NSCNS	<0.01	<0.01	<0.01	<0.01	0.02	0.58
NSCNS vs. OSCNS	0.52	0.30	0.55	0.86	0.33	0.97

† $\log_{10}(x + 1)$.

‡ Means in rows within each location with the same letter are not significantly different at $P \leq 0.05$, comparison using single-degree-of-freedom contrasts.

Reproduction on PI 88788 averaged 13% of the control for the Whiting test, and 31% and 12% at Nevada in 2005 and 2006, respectively (Table 2)

Analysis of variance indicated that initial population densities (Pi) varied among years at each location (Table 3). Soybean cyst nematode Pi averaged 100 and 1000 eggs 100-cm^{-3} soil in 2005 and 2006 at Whiting, respectively. Initial population densities were 3700 eggs 100 cm^{-3} less at Nevada in 2006 compared with 2005. The greatest difference between years occurred at De Witt as Pi were 4000 eggs 100 cm^{-3} in 2005 and 12 600 eggs 100 cm^{-3} in 2006 (Table 2).

Year × cultivar interactions were present for both Pf and Rf at De Witt (Table 3). Reproduction factors were greater in 2005 compared with 2006, when values were <1 for all cultivar types (Table 4). Consistent among years was the fact that Pf and Rf were similar for old and new SCN-susceptible cultivars. New SCN-resistant cultivars were always superior to susceptible cultivars for managing SCN (Table 4). No interaction was detected at Whiting or Nevada. Final SCN population densities were twice as great in 2005 at Nevada compared with 2006, but Rf was 27% greater in 2006 and were >1 for all cultivar types. At Whiting, population densities increased more in 2005 compared with 2006 as Rf values averaged 4.6 for susceptible cultivars but only 1.2 for resistant cultivars (Table 4). Consistent among both locations and years, and similar to De Witt, new SCN-resistant cultivars had significantly lower Pf and Rf values compared with old and new SCN-susceptible cultivars (Table 4). Reproduction factors were <1 at De Witt for SCN-susceptible cultivars.

Yield

Substantial yield variability existed among years at both De Witt and Nevada (Table 3). Yields in 2005 at De Witt were less in 2006 as a result of the dry conditions that began in May and continued through July, with rainfall totals more than 40 mm below the 30-yr averages each month (Table 5). A similar situation occurred at Nevada in 2006 as dry conditions occurred from May through July. Yield was similar among years for each type of cultivar at Whiting.

Under severe drought at De Witt in 2005, new and old SCN-susceptible cultivars produced yields that were 42% less than the new SCN-resistant cultivars (Table 6). At Nevada in 2005 yields were similar between new SCN-resistant and susceptible cultivars ($P = 0.06$), but greater than old SCN-susceptible cultivars. At Whiting both

Table 5. Precipitation and air temperature data recorded at the three locations in Iowa during 2005 and 2006 using field weather stations. Deviations from the 30-yr average reported in parentheses.†

		May		June		July		August		Average	
Year	Location	Air temp.	Precipitation	Air temp.	Precipitation	Air temp.	Precipitation	Air temp.	Precipitation	Air temp.	Precipitation
		°C	mm	°C	mm	°C	mm	°C	mm	°C	mm
2005	De Witt	14.7 (–2.1)	56 (–43)	24.0 (2.3)	31 (–75)	23.7 (–0.2)	47 (–40)	22.4 (–0.3)	54 (–62)	21.2 (–0.1)	188 (–221)
	Nevada	15.8 (–0.6)	85 (–27)	23.1 (1.8)	136 (12)	24.0 (0.6)	78 (34)	21.7 (–0.3)	147 (31)	21.2 (0.4)	446 (–18
	Whiting	16.6 (–0.2)	102 (–6)	23.5 (1.6)	101 (6)	24.6 (0.4)	72 (23)	22.1 (–1.0)	96 (15)	21.7 (0.2)	371 (–20)
2006	De Witt	16.1 (–0.7)	165 (65)	22.8 (1.1)	69 (–36)	24.6 (0.7)	107 (17)	22.6 (–0.1)	132 (15)	21.5 (0.3)	473 (62)
	Nevada	17.3 (0.9)	53 (–58)	24.1 (2.7)	22 (–97)	24.5 (1.1)	85 (–31)	22.1 (0.1)	158 (40)	22.0 (1.2)	318 (–145)
	Whiting	16.8 (0.1)	60 (–47)	24.1 (2.1)	51 (–51)	25.0 (0.8)	68 (–27)	22.3 (–0.7)	212 (127)	22.1 (0.6)	391 (2)

† 30-yr averages determined based on weather station data from Clinton, Ames, and Onawa, IA, for De Witt, Nevada, and Whiting, respectively.

years, and at Nevada and De Witt in 2006, cultivar yields were always new SCN-resistant > new SCN-susceptible > old SCN-susceptible.

Based on the multilocation analysis the relative yield of new SCN-susceptible cultivars was 14% less than new SCN-resistant cultivars (Table 6). This difference increased to 32% compared with old SCN-susceptible cultivars. This response was not influenced by location ($P = 0.74$) and there was no evidence of an interaction ($P = 0.15$).

Table 6. Yield response for three cultivar types at three locations in Iowa, 2005 and 2006.

	De Witt		Nevada		Whiting		Relative yield
	2005	2006	2005	2006	2005	2006	
Cultivar type	kg ha^{-1}						% of New SCN-resistant cultivars
New SCN-resistant (NSCNR)	3100b†	4440a	3760a	3480a	5160a	5030a	100a‡
New SCN-susceptible (NSCNS)	1960b	3740a	3430a	2230b	4440a	4300a	86b
Old SCN-susceptible (OSCNS)	1650b	2900a	2630a	1650b	3630a	3010a	68c
Contrast type	$P > F$						
NSCNR vs. NSCNS	<0.01	<0.01	0.06	<0.01	<0.01	<0.01	
NSCNS vs. OSCNS	0.29	<0.01	<0.01	0.01	<0.01	<0.01	

† Means in rows within each location with the same letter are not significantly different at $P \leq 0.05$, comparison using single-degree-of-freedom contrasts.

‡ Values are the result of a combined analysis among all locations treating years and replications as random effects. Location and location × cultivar effects were not significant at $P \leq 0.05$. Cultivar values followed by the same letter are not significantly different at $P \leq 0.05$.

Primary Yield Components

Cultivar responses were similar among years at De Witt and Whiting, but year dependent at Nevada (Table 3). Resistant cultivars produced 12% more seeds m^{-2} at Nevada in 2005 compared with new SCN-susceptible cultivars, however, under dry conditions, seeds m^{-2} production increased by 53% for SCN-resistant cultivars (Table 7). This response was similar to De Witt in 2005 as new and old SCN-susceptible cultivars produced the same number of seeds m^{-2} but 47% increase with new SCN-resistant cultivars. Soybean cyst nematode resistant cultivars always produced a greater number of seeds m^{-2} compared with new SCN-susceptible cultivars and old SCN-susceptible cultivars at Whiting (Table 7). Seed mass was similar among years at both De Witt and Nevada, but greater in 2006 at Whiting. Cultivars produced seed of similar mass at all locations, although there was some evidence that new SCN-resistant produced 6% larger seeds at Nevada in 2006 ($P = 0.06$) (Table 7).

Table 7. Year × cultivar interactions for primary yield components at three locations in Iowa, 2005 and 2006.

	De Witt		Nevada		Whiting	
	2005	2006	2005	2006	2005	2006
Cultivar type	Seed number (seeds m^{-2})					
New SCN-resistant (NSCNR)	2200b†	2790a	2650a	2340a	3080a	3280a
New SCN-susceptible (NSCNS)	1500b	2350a	2370a	1530b	2500a	2700a
Old SCN-susceptible (OSCNS)	1490a	1910a	1890a	1150b	2010a	2050a
Contrast	$P > F$					
NSCNR vs. NSCNS	<0.01	0.02	0.03	<0.01	<0.01	<0.01
NSCNS vs. OSCNS	0.96	0.03	<0.01	0.02	0.02	<0.01
Cultivar type	Seed mass (mg seed^{-1})					
New SCN-resistant (NSCNR)	147a	146a	130a	135a	148a	136b
New SCN-susceptible (NSCNS)	147a	143a	133a	127a	156a	145b
Old SCN-susceptible (OSCNS)	144a	136a	134a	128a	158a	135b
Contrast	$P > F$					
NSCNR vs. NSCNS	0.98	0.59	0.41	0.06	0.10	0.09
NSCNS vs. OSCNS	0.57	0.29	0.98	0.97	0.71	0.09

† Means in rows within each location with the same letter are not significantly different at $P \leq 0.05$, comparison using single-degree-of-freedom contrasts.

Correlations

Positive correlation among yield and seeds m^{-2} existed ($r > 0.80$) for all cultivar types, regardless of location (data not shown). Relationships among yield and seed mass were location and cultivar specific (Table 8). Seed mass was strongly associated with yield at Nevada for all classes ($r > 0.52$, $P < 0.01$) and for old SCN-susceptible cultivars at De Witt. No association was detected at Whiting for any of the cultivar types.

At the two high yielding locations (De Witt and Whiting), yield and primary yield components showed both positive and negative responses with increasing Pf and Rf. A significant negative correlation occurred between yield and Pf only for the old SCN-susceptible cultivars (Table 9). A negative relationship was detected between seeds m^{-2} and Pf for both classes of new cultivars and Rf for SCN-resistant cultivars. Positive relationships existed between yield and Rf and seed mass and Rf at Whiting for both old and new SCN-susceptible cultivars. Similarly, at De Witt, seed mass was positively associated with both Pf and Rf for new SCN-resistant cultivars and for Rf for new SCN-susceptible cultivars. Nevada was the most consistent location as yield was negatively influenced by increasing Pf and Rf values for all cultivar classes. Primary yield components showed a similar response in all but one of the relationships (Table 9).

Table 8. Correlation coefficients between seed mass and yield at three locations in Iowa averaged across 2005 and 2006.

	New SCN-resistant	New SCN-susceptible	Old SCN-susceptible
De Witt	–0.05	0.28	0.48***
Nevada	0.52***	0.86***	0.61***
Whiting	0.15	–0.13	0.25

*** Significant at $P \leq 0.001$.

Table 9. Correlation coefficients among yield and the primary yield components seeds m^{-2} and seed mass with final SCN population density (Pf) and reproduction factor (Rf) at three locations in Iowa averaged across 2005 and 2006.

		New SCN-resistant		New SCN-susceptible		Old SCN-susceptible	
Location	Variable	Pf	Rf	Pf	Rf	Pf	Rf
De Witt	Yield	–0.10	–0.05	–0.21	–0.08	–0.29*	–0.16
	Seed mass	0.42***	0.47***	0.11	0.36*	0.01	0.27
	Seeds m^{-2}	–0.22*	–0.21*	–0.34*	–0.21	–0.08	–0.17
Nevada	Yield	–0.29**	–0.38***	–0.44**	–0.41**	–0.74***	–0.58***
	Seed mass	–0.37***	–0.37***	–0.34*	–0.32*	–0.27	–0.44**
	Seeds m^{-2}	–0.12	–0.24*	–0.39**	–0.37**	–0.77***	–0.53***
Whiting	Yield	0.01	0.14	–0.14	0.40**	–0.09	0.47***
	Seed mass	0.26*	–0.00	0.22	0.18	0.35*	0.29*
	Seeds m^{-2}	–0.14	0.12	–0.20	0.29*	–0.18	0.38**

* Significant at the $P \leq 0.05$.

** Significant at the $P \leq 0.01$.

*** Significant at the $P \leq 0.001$.

Discussion

New SCN-resistant cultivars had lower Pf and Rf than new SCN-susceptible and old cultivars and this was clearly reflected in the consistent yield improvement for SCN-resistant cultivars. Rapid population increase from a low Pi at Whiting in both 2005 and 2006 documented the tremendous reproduction potential of SCN. Rapid population increase from low Pi has been documented by Alston and Schmitt (1987) and Chen et al. (2001a, 2001b). Our data reemphasize the important management criteria to begin SCN management early and keep Pi low, rather than attempting to reduce a large Pi later with resistant cultivars and rotation with nonhost crops (Niblack, 2005).

New SCN-susceptible cultivars showed a similar inability to control SCN as did old SCN-susceptible cultivars based on equal Rf. This response indicated that although new cultivars have increased yield potential, it is not a direct result of improved SCN control.

Using identical production methods, new cultivars, regardless of SCN resistance, performed consistently better than old cultivars, pointing to improved genetic yield potential. The ability of new cultivars to set more seeds m^{-2} was the primary factor that contributed to yield improvement. This response was similar to the results of Wang et al. (2003) as the presence of SCN suppressed biomass accumulation of susceptible cultivars. This study differs from Wang et al. (2003) and Niblack et al. (1992) in that no consistent difference in seed mass was detected between resistant and susceptible cultivars.

At the low yielding Nevada location, yield benefit from SCN-resistant cultivars in 2006 was 16% compared with new SCN-susceptible cultivars, even though the Pi was 630 eggs 100 cm^{-3}. At Whiting, the benefit was 17% regardless of when Pi was 100 or 1000 eggs 100 cm^{-3} of soil in 2005 and 2006, respectively. Based on this study the potential loss from selecting a new SCN-susceptible cultivar caused a 14% yield reduction regardless of Pi or HG Type in the field. This yield benefit from resistant cultivars is in agreement with yield trials conducted each year to compare SCN-resistant and SCN-susceptible cultivars in SCN infested environments (Tylka et al., 2008).

Two of the locations included a 2 in their HG Type description. The highest level of reproduction was between 11 and 30% in greenhouse trials. Eight of the 11 SCN-resistant cultivars in this study contained resistance from PI 88788. Upon individual cultivar analysis these cultivars were often the highest yielding cultivars even in the presence of HG Type 2. Consistently, they provided a yield advantage of nearly 15% over SCN-susceptible cultivars and with Rf less than one. This response was encouraging because the majority of SCN resistant cultivars available today have the source PI 88788. Data from this study supports the continued use of PI 88788 as a source of SCN-resistance, even in fields with SCN populations identified as HG Type 2. Recently, cultivars with Peking source of resistance have been released and are highly resistant to HG Type 2 populations in greenhouse screening (Kull et al., 2007), have strong yield performance, and reduce SCN population densities during the season (Tylka et al., 2008).

Comparison of new and old SCN-susceptible cultivars, new SCN-susceptible cultivars did not provide greater control of SCN as Pf and Rf were similar for all years and locations regardless of the Pi or the HG Type. However, averaged across locations there was an 18% yield advantage for new cultivars compared with old SCN-susceptible cultivars. Our data provides evidence that increased yields of new SCN-susceptible cultivars are not due to improved SCN tolerance. However, there is evidence that in high-stress environments, such as drought in combination with SCN, yields of new SCN-susceptible cultivars can be brought down to the same level as old SCN-susceptible cultivars.

At Pi greater than 10,000 eggs 100-cm^{-3} soil, Pf decreased and Rf was less than one for all cultivar types. This was an unexpected response. This reduction from large population densities may reflect a population whose reproduction cannot be supported by susceptible cultivars. This response was previously documented by MacGuidwin et al. (1995) in Wisconsin and Chen et al. (2001a) in Minnesota.

At other locations, new and old SCN-susceptible cultivars allowed populations to increase from 100 to 15,000 eggs 100 cm^{-3} of soil or a 150-fold increase when SCN population densities were low and yield potential was high as was the case at Whiting in 2005 (Table 4). Other estimations were a 67-fold and sixfold increase at Nevada, 2005 and Whiting 2006 on susceptible cultivars, respectively. A unique response occurred at Nevada in 2006. At this environment new SCN-resistant cultivars allowed populations to triple from the initial density. This level of control was still significantly better than old and new SCN-susceptible cultivars but clearly, in the presence of HG Type 2 SCN populations and stressful drought conditions resistant cultivars could not suppress SCN population densities. Reproduction factors greater than one for SCN-resistant cultivars have been observed at one location in Minnesota with a female index of 15% on PI 88788 (Chen et al., 2001a, 2001b).

CONCLUSION

Yield is the result of the interaction between a cultivar and the environment through the growing season. Soybean cyst nematode negatively influences this interaction and reduces yield. In addition to crop rotation, cultivar selection is a critical management component that must be implemented to achieve greater soybean yields in all production environments in Iowa where SCN has been identified. Growers have largely adopted the practice of purchasing new seed each year and readily select new cultivars that enter the market. These cultivars have increased yield but unless they contain specific SCN resistance traits they do not provide improved SCN control. Resistant cultivars provided a consistent 14% yield increase compared with susceptible cultivars at all locations. A potential problem in the near future is the adaptation of SCN populations that allow their successful reproduction on cultivars that contain PI 88788 resistance. Cultivars resistant to SCN should be grown as soon as SCN has been identified and at locations that include HG Type 2 as part of the SCN population, cultivars must be selected carefully. When new high-yielding cultivars are available with other sources of SCN resistance these could provide greater yields and improved SCN management for these populations.

ACKNOWLEDGMENTS

The authors thank Jodee Stuart and Adriana Murillo-Williams for their technical assistance and Gregory Tylka for his review of the manuscript before submission. This research was funded by the Iowa Soybean Association.

REFERENCES

Alston, D.G., and D.P. Schmitt. 1987. Population density and spatial pattern of *Heterodera glycines* in relation to soybean phenology. J. Nematol. 19:336–345.

Appel, J.A., and S.A. Lewis. 1984. Pathogenicity and reproduction of *Hoplolaimus Columbus* and *Meloidogyne incognita* on 'Davis' soybean. J. Nematol. 16:349–355.

Board, J.E., and H. Modali. 2005. Dry matter accumulation predictors for optimal yield in soybean. Crop Sci. 45:1790–1799.

Chen, S. 2007. Tillage and crop sequence effects on *Heterodera glycines* and soybean yields. Agron. J. 99:797–807.

Chen, S.Y., P.M. Porter, J.H. Orf, C.D. Reese, W.C. Stienstra, N.D. Young, D.D. Walgenbach, P.J. Schaus, T.J. Arlt, and F.R. Breitenbach. 2001a. Soybean cyst nematode population development and associated soybean yields of resistant and susceptible cultivars in Minnesota. Plant Dis. 85:760–766.

Chen, S., P.M. Porter, C.D. Reese, and W.C. Stienstra. 2001b. Crop sequence effects on soybean cyst nematode and soybean and corn yields. Crop Sci. 41:1843–1849.

Concibido, V.C., B.W. Diers, and P.R. Arelli. 2004. A decade of QTL mapping for cyst nematode resistance in soybean. Crop Sci. 44:1121–1131.

Cook, R.J. 2000. Advances in plant health management in the twentieth century. Annu. Rev. Phytopathol. 38:95–116.

Cooper, R.L. 2003. A delayed flowering barrier to higher soybean yields. Field Crops Res. 82:27–35.

Edwards, D.I. 1988. The soybean cyst nematode. p. 81–86. *In* T.D. Wyllie and D.H. Scott (ed.) Soybean diseases of the North Central Region. Am. Phytopathol. Soc., St. Paul, MN.

Evans, L.T., and R.A. Fischer. 1999. Yield potential: Its definition, measurement, and significance. Crop Sci. 39:1544–1551.

Fallick, J.B., W.D. Batchelor, G.L. Tylka, T.L. Niblack, and J.O. Paz. 2002. Coupling soybean cyst nematode damage to CROPGRO-soybean. Trans. ASAE 45:433–441.

Francl, L.J., and V.H. Dropkin. 1986. *Heterodera glycines* population dynamics and relation of initial population to soybean yield. Plant Dis. 70:791–795.

Glover, K.D., D. Wang, P.R. Arelli, S.R. Carlson, S.R. Cianzio, and B.W. Diers. 2004. Near isogenic lines confirm a soybean cyst nematode resistance gene from PI 88788 on linkage group J. Crop Sci. 44:936–941.

Golden, A.M., J.M. Epps, R.D. Riggs, L.A. Duclos, J.A. Fox, and R.L. Bernard. 1970. Terminology and identity of infraspecific forms of the soybean cyst nematode (*Heterodera glycines*). Plant Dis. Rep. 54:544–546.

Koenning, S.R., D.P. Schmitt, K.R. Barker, and M.L. Gumpertz. 1995. Impact of crop rotation and tillage system on *Heterodera glycines* population density and soybean yield. Plant Dis. 79:282–286.

Kopisch-Obuch, F.J., R.L. McBroom, and B.W. Diers. 2005. Association between soybean cyst nematode resistance loci and yield in soybean. Crop Sci. 45:956–965.

Kull, L., E. Nafziger, R. Esgar, D. Stigberg, and C. Davis. 2007. Varietal information program for soybeans. Available at http://web.aces.uiuc.edu/VIPS/v4/vphome/vipshome_new.cfm?CFID=3219617&CFTOKEN=91368697(accessed 15 Dec. 2007; verified 18 July 2008). Univ. of Illinois, Urbana-Champaign, IL.

MacGuidwin, A.E., C.R. Grau, and E.S. Oplinger. 1995. Impact of planting 'bell', a soybean cultivar resistant to *Heterodera glycines*, in Wisconsin. J. Nematol. 27:78–85.

McIntosh, M.S. 1983. Analysis of combined experiments. Agron. J. 75:153–155.

Miller, D.R., S.Y. Chen, P.M. Porter, G.A. Johnson, D.L. Wyse, S.R. Stentina, L.D. Klossner, and G.A. Nelson. 2006. Rotation crop evaluation for management of the soybean cyst nematode in Minnesota. Agron. J. 98:569–578.

National Agriculture Statistics Service. 2007. Published estimates data base (PEDB). Available at http://usda.mannlib.cornell.edu/usda/nass/CropProd//2000s/2006/CropProd-11-09-2006.txt (accessed 12 Nov. 2006; verified 17 July 2008). USDA-NASS, Washington, DC.

Niblack, T.L. 2005. Soybean cyst nematode management reconsidered. Plant Dis. 89:1020–1025.

Niblack, T.L., P.R. Arelli, G.R. Noel, C.H. Opperman, J.H. Orf, D.P. Schmitt, J.G. Shannon, and G.L. Tylka. 2002. A revised classification scheme for genetically diverse populations of *Heterodera glycines*. J. Nematol. 34:279–288.

Niblack, T.L., N.K. Baker, and D.C. Norton. 1992. Soybean yield losses due to *Heterodera glycines* in Iowa. Plant Dis. 76:943–948.

Niblack, T.L., K.N. Lambert, and G.L. Tylka. 2006. A model plant pathogen from the kingdom animalia: *Heterodera glycines*, the soybean cyst nematode. Annu. Rev. Phytopathol. 44:283–303.

Riggs, R.D., and D.P. Schmitt. 1988. Complete characterization of the race scheme for *Heterodera glycines*. J. Nematol. 20:392–395.

SAS Institute. 2003. The SAS system for Windows. v. 9.1.3. SAS Inst., Cary, NC.

Sasser, J.N., and G. Uzzell, Jr. 1991. Control of the soybean cyst nematode by crop rotation in combination with nematicide. J. Nematol. 23:344–347.

Sinclair, T.R. 1993. Crop yield potential and fairy tails. p. 707–711. *In* D. Buxton et al. (ed.) International crop science I. CSSA, Madison, WI.

Specht, J.E., D.J. Hume, and S.V. Kumudini. 1999. Soybean yield potential—A genetic and physiological perspective. Crop Sci. 39:1560–1570.

Tabor, G.M., G.L. Tylka, J.E. Behm, and C.R. Bronson. 2003. *Heterodera glycines* infection increases incidence and severity of brown stem rot in both resistant and susceptible soybean. Plant Dis. 87:655–661.

Tylka, G.L. 2006. Soybean cyst nematode-resistant soybean varieties for Iowa. PM 1649. Iowa State Univ. Ext. Serv., Ames.

Tylka, G.L. 2007. Current status of the soybean cyst nematode as a threat to soybean production in the Midwest. p. 143–148. *In* Proc. 18th Annual Integrated Crop Management Conf., Ames, IA. 28–29 Nov. 2007. Iowa State Univ., Ames.

Tylka, G.L., G.D. Gebhart, and C.C. Marett. 2008. Evaluation of soybean varieties resistant to soybean cyst nematode in Iowa in 2007. Iowa State Univ., Ames.

Wang, J., T.L. Niblack, J.A. Tremain, W.J. Wiebold, G.L. Tylka, C.C. Marett, G.R. Noel, O. Meyers, and M.E. Schmidt. 2003. Soybean cyst nematode reduces soybean yield without causing obvious aboveground symptoms. Plant Dis. 87:623–628.

Wrather, J.A., and S.R. Koenning. 2006. Estimates of disease effects on soybean yields in the United States 2003 to 2005. J. Nematol. 38:173–180.