Yield Improvement and Stability for Soybean Cultivars with Resistance to *Heterodera Glycines* Ichinohe

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ABSTRACT

Cultivar selection is the most important management decision soybean [*Glycine max* (L.) Merr.] producers can make to achieve high yield. This experiment was conducted to evaluate the contributions to genetic gain and yield stability made by cultivar resistance to soybean cyst nematode (*Heterodera glycines* Ichinohe, SCN). Studies were established at three locations in Iowa during 2005 and 2006 in fields where SCN population densities ranged from 100 to 12,500 eggs 100-cm^{-3} soil of various Hg-Types. Twenty-three cultivars that varied by year of release and resistance to SCN were evaluated. Yield variability among environments was less for new SCN-resistant cultivars. Genetic gain was 14.9 kg ha^{-1} yr^{-1} greater for SCN-resistant cultivars compared with SCN-susceptible cultivars. Estimated genetic gain was similar for both high and low-yielding environments. Yield potential was greater for new cultivars but yield stability was similar to old cultivars. There was no evidence of a negative relationship between yield and yield stability. Cultivars resistant to SCN had greater yields in both high- and low-yielding environments and provided greater yield stability. These data support the selection of new cultivars that yield well at multiple locations and specifically cultivars with resistance to SCN for fields infested with SCN as a method to increase yield and yield stability.

An ideal soybean cultivar is one that achieves the greatest yield across many environments regardless of environmental conditions. It is expected that these types of cultivars will be produced as genes that control plant productivity, tolerance to abiotic and biotic stresses, and response to inputs are identified and integrated into breeding programs (Fasoula and Fasoula, 2002). Until that level of understanding exists, determination of environment × genotype interactions will remain important for cultivar selection (Bradley et al., 1988).

Soybean yield has increased over time in response to improved genetics and agronomic practices. In side-by-side comparisons, genetic gain was estimated to be 19 to 23 kg ha^{-1} yr^{-1} for cultivars released before 1977 (Specht and Williams, 1984). More recent estimation of privately released lines indicates genetic gain was 30 kg ha^{-1} yr^{-1} (Specht et al., 1999) and today the yield potential of many modern cultivars is greater than 6700 kg ha^{-1} (Cooper, 2003). Yield improvement is the result of greater leaf area duration (Kumudini et al., 2001) harvest index (Kumudini et al., 2001; Morrison et al., 1999) and carbon exchange rate (Morrison et al., 1999), but independent of N source or the level of absorbed radiation (Kumudini et al., 2008).

Average soybean yield among Iowa counties during 2006 ranged from 2822 to 4086 kg ha^{-1} and represented the yield variability within the state (National Agriculture Statistics Service, 2007). This yield variability can be attributed to differences in soil type, fertility, soilborne pathogens, insect infestations, and agronomic practices. A problem in Iowa and much of the north central United States soybean-producing regions is SCN (Workneh et al., 1999). This pathogen has been identified as causing the greatest yield losses each year in Iowa, estimated at 872,787 and 1,222,680 Mg during 2003 and 2004, respectively (Wrather and Koenning, 2006). By 2007, SCN had been identified in all but three Iowa counties (Tylka, 2007) and contributes to cultivar yield variability seen among locations (Tylka et al., 2008). More than 700 SCN resistant cultivars are available today (Tylka, 2006). When SCN resistant cultivars were first marketed, there was evidence of a 5 to 10% yield reduction (Noel, 1986). For this reason there has been hesitation by producers to use these cultivars due to the perception of "yield drag" associated with the resistance trait. In the presence of SCN, plant resistance should improve yield and reduce environmental variability of a cultivar; however, in environments where SCN is not present or when SCN population densities are low, the resistant trait may not provide any yield benefit (Chen et al., 2001). Addition of a resistance trait can come with a metabolic cost to a cultivar reducing the yield potential (Bergelson and Purrington, 1995). In the cases of resistance to Phytophthora root rot, caused by *Phytophthora megasperma* (Caviness and Walters, 1971; Singh and Lambert, 1985), and soybean mosaic virus (Ross, 1977) this has not occurred.

Tollenaar and Lee (2002) determined that corn (*Zea mays* L.) hybrids from record-setting yield trials had both high yield and yield stability. Their data indicated that yield stability and high yield potential are not mutually exclusive. Studies in soybean have also determined that yield can be increased without reducing yield stability (Voldeng et al., 1997; Wilcox et al., 1979). Neither of these studies addressed the contribution of resistance traits to yield potential and stability.

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Abbreviations: SCN, soybean cyst nematode.

Finlay and Wilkinson (1963) developed a method of analysis for determining cultivar stability by regressing the average yield of a specific cultivar against the mean of all cultivars for a specific environment. Regression coefficients greater than one indicate below-average stability and adaptation to specific, highly productive environments. Regression coefficients less than one indicate above-average stability and adaptation to unfavorable environments. Tollenaar and Lee (2002) termed cultivars with slopes greater than one "race horses" and those with slopes less than one "work horses." While this terminology is suitable, more commonly used terms to describe soybean cultivars have been "offensive" and "defensive" cultivars. Two studies have evaluated yield stability of various soybean cultivars. Wilcox et al. (1979) determined that yield of modern cultivars increased 25% but stability did not change. Voldeng et al. (1997) found that group 0, 00, and 000 maturity groups showed genetic yield increase for newer cultivars with no reduction in stability.

Cultivar resistance to SCN first appeared during the 1960s with the development of 'Pickett' (Brim and Ross, 1966). Since then many new cultivars have been bred for resistance to SCN using three main sources of resistance, PI 88788, Peking, and PI437654 (Shannon et al., 2004) with PI 88788 being the predominate source (Tylka, 2006). Addition of SCN-resistance has consistently provided improved yield in locations where SCN is present (Chen et al., 2001; Tylka et al., 2008).

The hypotheses for this work are (i) the addition of a "defensive" trait such as SCN-resistance must be considered when addressing genetic gain as it potentially inflates genetic gain and (ii) a defensive trait's presence in new cultivars improves both yield and yield stability making these cultivars less risky options for producers. The objectives for this research were to determine genetic gain and yield stability for three distinct classes of soybean cultivars that vary by year of release and resistance to SCN.

MATERIALS AND METHODS

Field research was conducted at three Iowa locations during 2005 and 2006. The three locations were near De Witt (eastern), Nevada (central), and Whiting (western). Soil type in De Witt is a well-drained fine-silty, mixed mesic, Typic Argiudolls. The Nevada location is a poorly-drained fine-loamy, mixed mesic, Typic Halpludolls. Soil at Whiting is a well-drained, fine-silty, mixed mesic, Typic Hapludolls. Plots were established on different fields each year of the study.

The experiment used a randomized complete block arrangement of treatments with four replications. Twenty-three cultivars were evaluated and were separated into three groups based on year of release and SCN-resistance (Table 1). Before

Table 1. Stability regression coefficients (b_l), maximum, minimum, and average yield for 23 cultivars grown at five environments in Iowa during 2005 and 2006.

Cultivar	Year of release	De Witt		Nevada		Whiting		b1	SE†
		2005	2006	2005	2006	2005	2006		
		kg ha^{-1}							
Old, soybean cyst nematode (SCN)-susceptible									
Hardin	1983	2696	3221	3825	1975	4982	3981	1.37‡	0.13
Harosoy	1951	2067	2618	3263	1533	3722	2798	1.00	0.16
Hawkeye	1948	2596	2832	2883	1649	3419	2648	0.71	0.14
Lincoln	1944	2270	2775	3434	1513	3150	2734	0.79	0.22
Richland	1938	2466	2849	2909	1519	3932	2976	1.01	0.11
Williams 82	1981	3128	2873	3221	1119	3497	2306	0.86	0.38
Mean		2537	2861	3256	1551	3783	2907		
New, SCN-resistant									
2509CN (PI 88788)	2003	4206	3828	4446	3201	6159	4637	1.16	0.31
Ag2801 (PI 88788)	2003	3866	4875	4429	3488	5544	5531	1.04	0.22
Dwight (PI 88788)	1997	3653	4186	4869	2718	5205	4559	1.16	0.13
E2620RX (PI 437654	2003	4351	4759	4575	4184	5015	5097	0.43*	0.10
IA2068 (PI 88788)	2003	4467	4989	4426	3461	4945	5675	0.78	0.29
L2811RX (PI 437654)	2003	3700	4137	4219	3746	5460	4669	0.76	0.21
P91M90 (Peking)	2003	3281	3945	4188	2662	5408	4938	1.31	0.14
PB291N (PI 88788)	2003	4766	4574	4149	2613	5462	4705	1.09	0.33
S-3012-4 (PI 88788)	2004	4528	3994	4323	3716	5074	4773	0.54	0.19
SOI2642NRR (PI 88788)	2003	2827	4648	4158	3511	4709	4618	0.75	0.34
SOI2858NRR (PI 88788)	2003	4223	4651	4450	3598	5622	5101	0.89	0.12
Mean		3988	4417	4385	3354	5327	4937		
New, SCN-susceptible									
Ag2403	2004	2180	3489	4272	1735	4949	4582	1.67‡	0.25
NE3001	2001	2956	3280	4319	902	4097	3521	1.46	0.35
NK S32-G5	2003	3577	3989	3847	2322	4088	4171	0.83	0.19
P92M91	2004	3200	4074	3895	2655	4703	4435	0.99	0.11
S25J5	2003	2890	3615	4059	1897	4499	3912	1.22	0.11
S-2743-4	2004	2659	3782	3958	2882	5224	4642	1.19	0.27
Mean		2910	3705	4058	2066	4593	4211		
Environment mean		3328	3825	4005	2548	4733	4218		
HSD (0.05)		789	492	602	460	856	508		

† Standard error of the regression coefficient B_l.

‡ Significantly different from a B_l = 1 at $P \leq 0.05$.

planting, the pre-emergent herbicides s-metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl) acetamide] (180 g a.i. ha^{-1}) and metribuzin [4-amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one] (40 g a.i. ha^{-1}) were applied 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.

Before planting each plot was sampled for SCN. Population densities were 3980 (Hg-Type 0) and 12,590 eggs 100-cm^{-3} of soil (Hg-Type 7) at De Witt in 2005 and 2006, respectively. At Nevada population densities were 3980 eggs 100-cm^{-3} of soil (Hg-Type 1.2.5.7) in 2005 and 630 eggs 100 cm^{-3} of soil (Hg-Type 2.5.7) in 2006. At Whiting population densities were 100 and 1000 eggs 100 cm^{-3} of soil in 2005 and 2006, respectively, and Hg-Type each year was 2.7.

Planting occurred the last week of April, except at Nevada in 2005, which was planted the second week of May. Plots were planted using an Almaco grain drill (Almaco, Nevada, Iowa) at a row spacing of 38 cm and a seeding rate of 432,400 seeds ha^{-1}. All seeds were inoculated with *Bradyrhizobium japonicum* (EMD Crop BioScience, Brookfield, WI). Glyphosate was applied twice during the season at a rate of 865 g a.e. ha^{-1} to the glyphosate resistant cultivars. The combination of acifluorfen [5-[2-chloro-4-(trifluoromethyl) phenoxy]-2-nitrobenzoic acid] at a rate of 30 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 40 g a.i. ha^{-1} was applied once to non-glyphosate resistant soybean cultivars. Plots were kept weed-free by hand-weeding during the rest of the growing season. Management practices to control insects were implemented as necessary throughout the season.

Data were analyzed separately by year and location using Proc Mixed in SAS (SAS Institute, 2003) treating blocks as a random effect. Cultivar yield differences were separated using the Tukey honest significant difference at $P = 0.05$ to control the comparisonwise error rate. Stability analysis was conducted based on the method of Finlay and Wilkinson (1963). Environmental means were plotted by cultivar means for new (SCN-resistant and SCN-susceptible) and old cultivars as well as for new SCN-resistant and new-SCN-susceptible cultivars. Proc Reg in SAS was used to determine the linear slope (b_1) for each cultivar between the lowest and highest yielding environment. Coefficients were tested to determine if they differed from a value of one or if differences existed between coefficients for all cultivars or groups.

Genetic gain was determined by regressing yield by year of cultivar release using Proc Reg in SAS. Analysis was conducted in three ways. The first approach was to estimate the average gain over time for new cultivars by regressing yield for all cultivars by year of release. The second approach was to estimate the genetic gain for cultivars without SCN-resistance by regressing the yield for all SCN-susceptible cultivars (old and new) cultivars by year of release. The third approach estimated the gain associated with the addition of the SCN resistance trait by regressing the yield of old SCN-susceptible cultivars and new SCN-resistant cultivars (excluding modern SCN-susceptible cultivars) by year of cultivar release. For each of these regressions means represent least-squares means that was obtained from an analysis using Proc Mixed in SAS where blocks and years were treated as random effects for determining the expected mean squares.

RESULTS AND DISCUSSION

Genetic Gain

Average genetic gain across all cultivars was 25.4 kg ha^{-1} yr^{-1} and is in line with previous reports (Specht and Williams, 1984; Voldeng et al., 1997; Wilcox, 2001). Genetic gain was greater for SCN-resistant cultivars at 30.3 kg ha^{-1} yr^{-1} than SCN-susceptible cultivars at 15.4 kg ha^{-1} yr^{-1} ($P = 0.005$) (Fig. 1). Evans and Fischer (1999) indicated that genetic gain can be inflated by genetic resistance to biotic stresses since older cultivars were not selected in the presence of the pathogen. In our evaluation, new SCN-susceptible cultivars and old SCN-susceptible cultivars showed a similar response to SCN as reproduction rates (final SCN population density/initial SCN population density) were similar (De Bruin and Pedersen, 2008). Addition of SCN-resistance increased the estimated genetic gain by 14.9 kg ha^{-1} yr^{-1}.

The estimated genetic gain for SCN-susceptible cultivars is less than values previously published for MG II and III cultivars (Specht and Williams, 1984; Wilcox, 2001) and indicates the slowing of genetic gain when cultivars do not have resistance to SCN and SCN is present in the production environment. From our data we can conclude that the addition of a defensive trait like SCN-resistance to a cultivar reduces stress, allows greater expression of genetic yield potential, and accounts for nearly 50% of the genetic gain (30.3 vs. 15.4 kg ha^{-1} yr^{-1}). As trials are established in the future to estimate genetic gain, cultivar resistant traits such as resistance to SCN must be taken into consideration to fully account for the contribution from time of selection and introduction of resistance traits.

Using all cultivars, the genetic gain at high-yielding environments (Whiting) was similar to that at low-yielding environments (Nevada) (Fig. 1). In high yield environments with limited amounts of abiotic and biotic stress, new cultivars continued to perform better than older cultivars and the genetic gain was similar to previous reports for modern cultivars (Specht et al., 1999). Our results were different from those reported by Salado-Navarro et al. (1993) who reported genetic gain as zero for trials conducted in high-yielding environments in Argentina.

There was no indication at the high yield, low SCN population density location (Whiting) that the addition of the SCN resistance trait was a cost to the new cultivars, as genetic gain was estimated at 34.3 and 27.3 kg ha^{-1} yr^{-1} for the SCN-resistant and SCN-susceptible cultivars, respectively (data not shown). At Nevada, a high SCN population density location, SCN-resistance was important and there was evidence for greater genetic gain for SCN-resistant cultivars at 21.1 kg ha^{-1} yr^{-1} compared with 12.9 kg ha^{-1} yr^{-1} without SCN-resistance ($P = 0.1$) (data not shown).

Yield Stability

Cultivars tested in this trial did not respond consistently among environments and there was a strong interaction among environments and cultivars ($P = 0.001$). The highest-yielding environment for all cultivars was Whiting in 2005 and the lowest-yielding environment for all cultivars was Nevada in

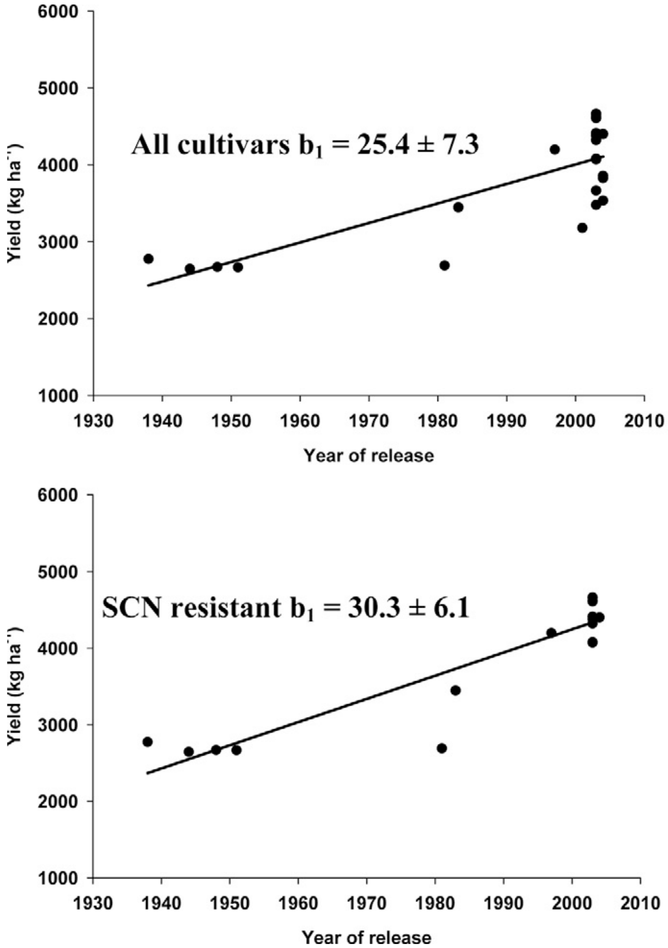

Fig. 1. Yearly genetic gain (B_1) ± 95% confidence interval. Top left: average yearly genetic gain for all cultivars tested. Top right: average yearly genetic gain between old, mid, and modern soybean cyst nematode (SCN) susceptible cultivars. Bottom left: yearly genetic gain between old, mid, and SCN resistant cultivars. Bottom right: yearly genetic gain between all cultivars tested in a high yield (Whiting) and low yield (Nevada) environment.

2006 (Table 1). Taking into account both year and location differences, yield of old SCN-susceptible cultivars increased 143% between the lowest and highest yielding environment. This was similar to the response for new SCN-susceptible cultivars where yield improvement was 122% but was much greater than the 59% yield improvement for SCN-resistant cultivars (Table 1).

Eleven cultivars had slopes above one and 11 cultivars had slopes less than one, with one cultivar having a slope equal to one, indicating the yields for this cultivar fit the environmental means. AG2403 had a slope of 1.67 and was significantly greater than one, classifying it as a "race horse" or "offensive" cultivar (Table 1). The other extreme was E2620RX, which had a slope significantly less than one at 0.43, classifying it as a "work horse" or "defensive" cultivar.

Comparison of new cultivars with old cultivars identified that the stability of these cultivars were identical with slopes of 1.03 and 0.93, respectively (Fig. 2). The yield potential of the new cultivars was consistently superior to the old cultivars, but there was no yield stability sacrificed to achieve the greater yield potential an outcome that is in agreement with (Voldeng et al., 1997; Wilcox et al., 1979).

A regression coefficient of 0.87 for new SCN-resistant cultivars compared with 1.20 ($P < 0.01$) for SCN-susceptible cultivars indicated that SCN-resistant cultivars had greater yield stability (Fig. 3). The slope of each line was largely controlled by the lower-yielding environments and provides some evidence that in lower-yielding environments where SCN is present, SCN-resistance provides greater yield benefit. As environmental mean yield increased beyond 5400 kg ha^{-1} the yields of susceptible cultivars would surpass those of resistant cultivars. This would imply a potential yield penalty for SCN-resistance in high-yielding low-SCN density environments. However, the highest environmental mean in this

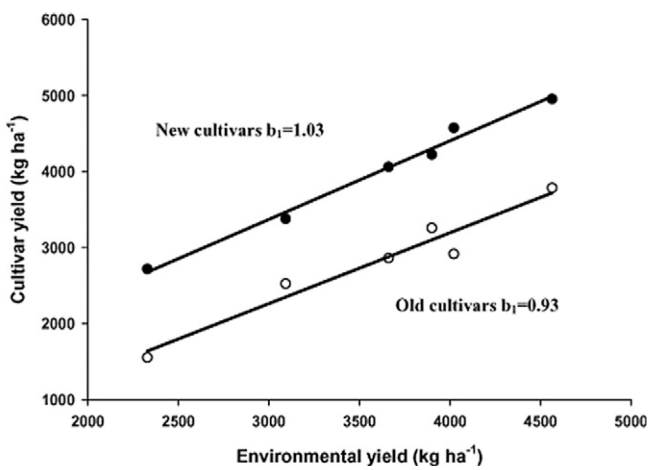

Fig. 2. Stability analysis of modern and old cultivars. The slopes of the lines are not significantly different $P \leq 0.05$.

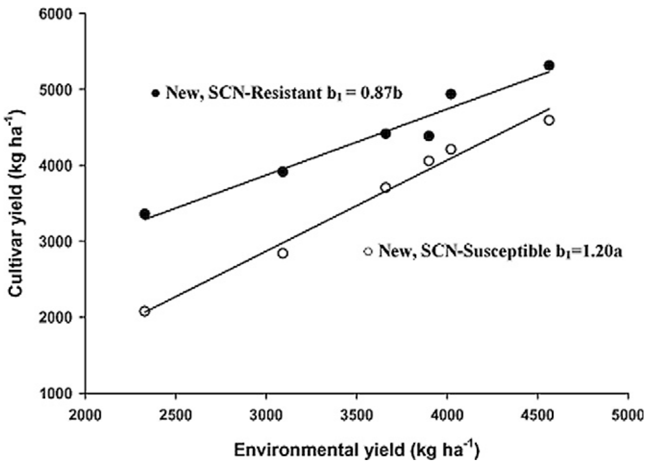

Fig. 3. Stability analysis of modern soybean cyst nematode (SCN) resistant and modern SCN susceptible cultivars. Values followed by the same letter are not significantly different at $P \leq 0.05$.

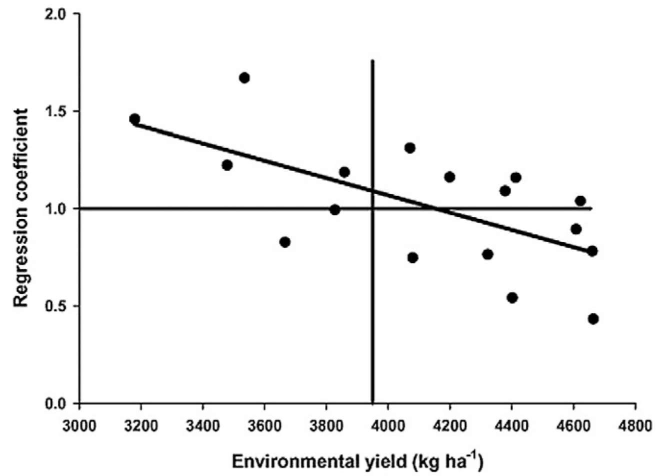

Fig. 4. Stability regression coefficients plotted against the average environmental means for 23 cultivars grown at six environments in Iowa during 2005 and 2006. Vertical line represents the average environmental yield and the horizontal line indicates cultivar yields equal to the environmental mean ($b_I = 1$). Stability regression coefficients of all new cultivars were negatively associated with yield ($P = 0.006$, $R^2 = 0.40$).

study was 4885 kg ha^{-1}, 1500 kg ha^{-1} greater than the state average in 2006 (National Agriculture Statistics, 2007). Environmental means greater than those achieved in this study are rarely reached on an annual basis and certainly not on a state wide basis. This finding provides continued support for the use of SCN-resistance for SCN-infested fields regardless of environmental yield potential and is in agreement with cultivar trials that continually document yield improvement from SCN-resistant cultivars in various testing environments (Tylka et al., 2008).

Following the method of Finlay and Wilkinson (1963) the environmental mean of each new cultivar was placed on the x axis and the regression coefficient (yield stability) was placed on the y axis to determine the relationship among yield and yield stability. Understanding this relationship may be important for cultivar selection. Old cultivars were not included in this analysis because (i) their yields were much lower than all other cultivars and (ii) theses cultivars are no longer grown and the focus must be placed on new cultivars. As yield increased stability increased ($P = 0.006$) because as environmental mean yield increased the regression coefficient decreased indicating greater stability (Fig. 4). Data presented here agrees with the ability of high-yielding corn hybrids to also produce stable yields (Tollenaar and Lee, 2002). Because yield increased with greater yield stability, evaluation of yield trial data from multiple locations will provide the greatest opportunity of selecting the highest yielding cultivar. This supports the conclusion of Hicks et al. (1992) that cultivar selection should be conducted by choosing high-yielding cultivars from trials that are conducted at multiple locations.

Only six of the 23 cultivars tested produced yields greater than the environment average and had stability coefficients less than one (i.e., high yield and high stability) (Fig. 4). Each of these cultivars was resistant to SCN. Our data provide evidence that addition of SCN resistance to cultivars provides a benefit by increasing yield potential and stability for new cultivars across various environments. Due to the presence of SCN in almost all Iowa counties and the majority of the soybean producing regions in the United States (Riggs, 2004) the increased yield and stability of new SCN-resistant cultivars is a good method for producers who detect SCN in their fields to minimize yield risk.

CONCLUSIONS

Soybean yields have increased over time and cultivars planted today have a yield potential superior to older cultivars, regardless of the presence or absence of SCN resistance. The addition of resistance to SCN provides the producer with greater yield, greater yield stability, and reduces exposure to economic risk. Our experiments confirm that high yields can be achieved along with improved yield stability and that the terms "defensive" and "offensive" do not adequately describe a cultivar, as new SCN-resistant cultivars appear to offer both traits. Through evaluation of multi-location cultivar trial data, we concluded that producers with SCN confirmed in their fields can minimize risk and increase the probability of increasing yield by selecting cultivars with SCN resistance.

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