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Performance of Blends of Soybean Cyst Nematode Resistant and Susceptible Cultivars

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ABSTRACT

Use of soybean cyst nematode (SCN), (Heterodera glycines Ichinohe), resistant cultivars of soybean [*Glycine max* (L.) Merr.] is a common practice to control losses due to this pest. The experiment was conducted to compare blends of resistant and susceptible cultivars with their yield response when grown in pure monoculture stands. Two SCN-resistant cultivars Bedford and Bradley, three susceptible cultivars or breeding lines, Essex, York, and N79-491, and blends of resistant and susceptible cultivars (50:50 ratio) were tested against soybean monoculture in a SCN Race 14-infested field. The mean yield (over 5 yr) of Bedford, Bradley, Essex, York, and N79-491 grown in monoculture was 1707, 1703, 903, 1063, and 1379 kg ha^{-1}, respectively. Yield of blends were generally similar to their resistant cultivar components in monoculture but they were always greater ($P = 0.05$) than the susceptible cultivar components. The Bedford and Essex blend resulted in the greatest yield, which was 672 kg ha^{-1} (51%) greater than the mean of component crop yields in pure stand. The race designation of the SCN population changed from Race 14 to Race 5 when resistant Bedford and Bradley were grown, from Race 14 to 9 when susceptible cultivars were grown, and from Race 14 to 2 in plots containing blends of resistant and susceptible cultivars or lines. Resistant cultivars grown with susceptible cultivars or lines in blends had lower numbers of cysts on the roots 30 d after planting than resistant cultivars grown in pure stands. Blends of resistant and susceptible cultivars can maintain soybean yields at acceptable levels by minimizing the selection pressure on the nematode population for their ability to parasitize resistant cultivars.

Soybean cyst nematode is an important soybean pest in the USA. Use of SCN-resistant cultivars and rotation of soybean with non-host crops are common management tools to limit SCN-caused losses (13). More than 130 soybean cultivars with resistance to SCN have been released in the USA (1), but resistance in most of these cultivars is not durable because of the genetic diversity in SCN and its ability to develop new races that will parasitize resistant cultivars. Continuous use of resistant cultivars exerts selection pressure in the nematode population that changes the frequency of genes for the ability to parasitize resistant cultivars (18). Young et al. (19) suggested a 2-yr rotation with a non-host crop to prolong the usefulness of an SCN-resistant genotype. Inclusion of an SCN-susceptible soybean in the rotation sequence has also been suggested to reduce the selection pressure on the nematode population (18). Maintaining a high proportion of the population which is unable to parasitize resistant cultivars should reduce the risk of race shifts and enhance the usefulness of resistant cultivars (16). In some cases, however, monocropping of SCN-resistant cultivars even for a period of 10 yr did not result in development of resistance-breaking nematode populations (10). Blends of resistant and susceptible soybean cultivars have been studied for the management of damage caused by SCN (9, 17, 19). The susceptible component of a blend is expected to reduce the selection pressure imposed by the resistant component, and this is expected to maintain the yield advantage.

Borlaug (4) suggested multi-line mixtures of blends of wheat (*Triticum aestivum L.*) genotypes as a protection against crop losses from pests and diseases. Multilines have been successfully used to increase the genetic diversity of small grains with respect to resisting rust (*Puccinia* spp.) fungi (22). This type of spatial deployment of resistance genes served to preserve the usefulness of resistance genes in these pathosystems, but limited information is available about the effectiveness of this approach with soilborne diseases and pests, including nematodes. Former studies with soybean and SCN were not generally comprehensive in covering all aspects of this complex pathosystem including the influence of blending resistant and susceptible cultivars.

The purpose of this 5-yr field study was to compare yields of resistant and susceptible cultivar blends with their component cultivars grown in pure stand, and to study changes in the ability of SCN populations to parasitize resistant cultivars in response to use of those blends.

MATERIALS AND METHODS

Field trials were conducted from 1984 through 1988 at the Rhodes Farm of the University of Missouri-Columbia, Delta Center, near Portageville, MO. The soil was a Brosley fine sandy loam (loamy, mixed thermic, arenic hapludalf), that was heavily infested with SCN Race 14 in 1984. Essex (15), a SCN-susceptible cultivar was planted in the entire field in 1983. Five monoculture treatments were two SCN Race 3 and 14 resistant cultivars, Bedford (8), and Bradley (3), and three SCN-susceptible cultivars, Essex (15), York (14), and N79-491. Six additional treatments were 50:50 blends of each resistant and susceptible cultivar. All cultivars were determinate maturity group (MG) V, except Bradley and N79-491, which are MG VI. Cultivars could be distinguished from each other by their flower and pubescence color. Test plots consisting of four, 6.1-m rows spaced 96 cm apart were planted in May each year. Both monoculture treatments and blends were planted at a seeding rate of 10 seeds per 30-cm row length.

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Abbreviations: SCN, soybean cyst nematode; MG, maturity group; PI, plant introduction.

Crop treatments were arranged in a randomized complete block design with four replications. Each treatment was planted in the same plot for each of the 5 yr. Test plots were irrigated when necessary.

Eight cores of soil, approximately 20 cm deep, were collected from the middle two rows of each plot at planting and at harvest each year to determine the SCN cyst population density. Cysts were extracted from 250 cm^3 of soil with a semi-automatic elutriator (5). At harvest, additional soil from each plot was taken, throughly mixed and added to 7.5-cm-diam clay pots. Seeds of standard SCN race differentials 'Pickett', 'Peking', PI 88788, and PI 90763, and the susceptible check cultivar Essex were sown in the pots and maintained in a greenhouse for race determination (11). Ten plants of each differential were studied. The number of white female cysts on the roots of each of the five differentials were counted 30 d after sowing and the index of parasitism for each cultivar was calculated as (number of cysts per plant/mean number of cysts on susceptible Essex) × 100. The SCN population in each plot was described by the predominant race as suggested by Riggs and Schmitt (11).

A month after planting every year, six plants from the border rows of each plot were carefully extracted along with their roots with the aid of a shovel to assess the number of cysts on roots. From blends, 12 plants (six of each component cultivar) were removed to assess the cyst number on roots. Resistant and susceptible plants could be separated at this time by their hypocotyl color.

The general linear models procedure of SAS was used for data analyses (12). Treatment means were compared using Duncan's Multiple Range Test. Blend yields were compared with both component monoculture yields and with the mean of component monoculture yields over 5 yr and statistically analyzed.

RESULTS

Yield Differences

Resistant cultivars Bedford and Bradley produced greater yields ($P = 0.05$) than the six blends and three susceptible cultivars in 1984 (Table 1). Yields of the blends did not differ significantly from each other (data not presented). The mean yield of blend treatments was 71% greater than that of the mean yield of susceptible cultivars. Yield differences between resistant cultivars and blends were not significant in 1985, but susceptible cultivars yielded significantly less than blends and resistant cultivars. The mean yield of susceptible cultivars was about half that of the mean yield of blends and resistant cultivars in 1985. Performance of blends in 1986 was better than that for resistant or susceptible cultivars grown in monoculture. The mean yield of susceptible cultivars was about 58% of the mean yield of the resistant cultivars, and 52% of the mean yield for blends. In 1987, the mean yield of resistant cultivars and blends was significantly greater than that of susceptible cultivars. Differences in soybean yield among resistant cultivars, blends, and susceptible cultivars were not significant in 1988.

Blends consistently yielded more than the mean of their component cultivars in pure-line stands except for the Bradley and York blend (Table 2). Yields of the various blends were similar to that of their resistant cultivar component and were significantly greater than that of their susceptible cultivar component every year except 1988. Blends always yielded more than the mean yield of their component monoculture in pure stand. Among the susceptible cultivars, N79-491 produced the greatest yield and Essex produced the lowest yield, but blends with Essex as a component cultivar produced greater yields than blends with N79-491 as a component cultivar (Table 2).

Table 1. Mean seed yields of SCN-resistant and susceptible cultivars and their blends, 1984 through 1988.

Cultivar	Year 1984	1985	1986	1987	1988	Mean
	kg ha^{-1}					
Resistant†	2232a‡	1731a	1280b	1488a	1794a	1705a
Susceptible	1135c	945b	747c	945b	1793a	1114b
Blends	1939b	1848a	1440a	1441a	1968a	1727a

† Bedford and Bradley were the resistant, and Essex, York, and N79-491 were susceptible cultivars. Blends were 50:50 combinations of resistant and susceptible cultivars.
‡ Means followed by the same letter in a column do not differ significantly ($P = 0.05$).

Table 2. Mean seed yields of 50:50 blends of SCN-resistant and susceptible cultivars, 1984 through 1988.

Blends	Actual yield	Expected yield†	Difference
	kg ha^{-1}		
Bedford + N79-491	1769	1543	+226*
Bedford + Essex	1977	1305	+672*
Bedford + York	1693	1385	+308*
Bradley + N79-471	1769	1541	+228*
Bradley + Essex	1642	1303	+339*
Bradley + York	1513	1383	+130

* Yield significantly ($P = 0.05$) better than the expected yield.
† Expected yield = average of the yield of component crops in pure stand.

SCN Population Analysis

The SCN cyst densities did not differ significantly between treatments at planting in 1984 (Table 3). The mean density of SCN cysts at planting increased through 1986 and then declined. The SCN cyst densities were significantly ($P = 0.05$) lower in plots receiving blends than in plots receiving monoculture treatments at the end of the 1985 and 1987 growing season as well as at the

Table 3. Soybean cyst nematode populations in the soil at planting and at harvest for resistant and susceptible cultivars, and their 50:50 blends in 1984 through 1988.

Treatment	Year 1984	1985	1986	1987	1988
At planting	cysts L^{-1}				
Susceptible	195a†	352a	622a	376a	235a
Resistant	161a	204b	489ab	358a	265a
Blends	169a	206b	366b	205b	148b
At harvest					
Susceptible	402a	775a	525a	275a	72a
Resistant	268b	499b	452ab	271a	54ab
Blends	296b	436b	378b	175b	40b

† Means with same letter in a column at planting or at harvest do not differ significantly ($P = 0.05$).

Table 4. Number of soybean cyst nematodes on roots of cultivars 30 d after planting, 1984 through 1988.

Treatment	1984	1985	1986	1987	1988
	cysts plant^{-1}				
Bedford	21c†	61b	107bcde	421cd	266bcd
Bradley	22c	27b	70bcde	239def	220cdef
Essex	703a	253a	468a	551bc	192cdef
York	462b	257a	351a	794a	546a
N79-491	384b	220a	187bcd	503bc	276bc
Bedford + Essex‡	356b	185a	355a	403cde	167cdef
Bedford + York	350b	221a	409a	778a	434ab
Bedford + N79-	423b	220a	196bc	533bc	233cde
Bedford + Essex	14c	16b	44e	172f	107cdef
Bedford + York	27c	36b	62cde	177f	110cdef
Bedford + N79-	24c	27b	32e	119f	67ef
Bradley + Essex	467b	200a	372a	419cd	118cdef
Bradley + York	510b	253a	352a	699ab	233cde
Bradley + N79-	410b	181a	206b	503bc	172cdef
Bradley + Essex	15c	29b	55de	211ef	80def
Bradley + York	13c	12b	30e	67f	37f
Bradley + N79-	23c	17b	22e	143f	104cdef

† Means followed by the same letter in a column do not differ significantly ($P = 0.05$).
‡ Cysts on roots of underlined cultivar in a blend.

beginning of the 1987 and 1988 growing season. SCN cyst densities at harvest were significantly lower on blends than on susceptible cultivars every year (Table 3).

Susceptible cultivars grown in monoculture or in blends had the greatest number of SCN cysts on roots 30 d after planting through 1986 (Tables 4 and 5). Numbers of cysts on the roots of resistant cultivars grown in monoculture did not differ significantly from those on roots of susceptible cultivars in 1987 and 1988. Significantly lower numbers of cysts were found on roots of resistant cultivars grown in blends (Tables 4 and 5) than on resistant cultivars grown in pure lines after 1986. The index of parasitism based on field data increased from 4.1 to 78.6 on resistant cultivars grown in monoculture versus an increase from 3.7 to 24.8 on resistant cultivars grown in blends (Fig. 1).

The index of parasitism on Peking increased in all the blend treatments except in the Bedford and Essex blend (Table 6). Conversely, the index of parasitism on PI 88788 decreased in all blends except in the Bradley and Essex blend. This blend increased the index of parasitism on all the differential soybean genotypes. Blending of Bedford with the susceptible cultivars generally tended to reduce the level of parasitism. A gradual change in race structure in the resistant, susceptible, and blend treatments was observed (Table 7). In 1984, the SCN population was characterized as Race 14 in this field which subsequently changed to Race 4 in 1987 and Race 9 in 1988 in the plots with susceptible cultivars. Race

Table 5. Number of soybean cyst nematodes on roots of resistant and susceptible cultivars and their 50:50 blends at 30 d after planting, 1984 through 1988.

Treatment	1984	1985	1986	1987	1988
	cysts plant^{-1}				
Resistant	21b†	44b	88b	333b	243a
Susceptible	516a	243a	335a	616a	338a
Blends-S‡	419a	210a	315a	556ab	226a
Blends-R‡	18b	23b	41b	148c	84b

† Means with same letter in a column do not differ significantly ($P = 0.05$).
‡ Blends-S and Blends-R refer to susceptible and resistant components of the blends.

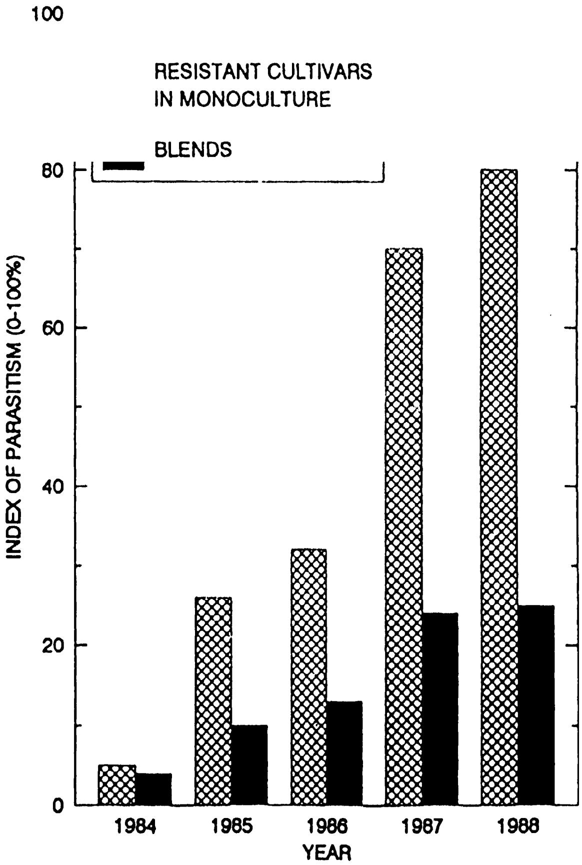

Fig. 1. Changes in the index of parasitism of *Heterodera glycines* at harvest in field plots over 5 yr (1984-1988).

Table 6. Effects of 50:50 blends of soybean genotypes on the index of parasitism on soybean cyst nematode race differentials, expressed as the difference between the index of parasitism in soils from blends and mean index of parasitism in soils from the component cultivars in pure stand.

	SCN race differential			
Blends	Peking	Pickett	PI 88788	PI 90763
Bedford + N79-491	+5.5	−25.3	−2.8	−0.2
Bedford + Essex	−2.4	+1.7	−4.1	−2.0
Bedford + York	+3.0	−10.7	−2.6	−0.2
Bradley + N79-491	+1.5	−1.8	−4.1	+1.5
Bradley + Essex	+14.6	+48.6	+5.3	+1.2
Bradley + York	+4.1	+14.5	−4.9	+6.7

4 was detected in resistant and blend treatments at planting in 1985, and after 1 yr Race 2 was found in these treatments. This population changed to Race 5 in the pure stand resistant cultivar treatment in 1988.

Indices of parasitism calculated at the end of each season on resistant host differentials changed over the course of this study in response to the various treatments (Table 7). Continuous culture of the resistant cultivars in pure line stands resulted in a decrease in the ability of these populations to parasitize PI 90763 compared to populations from continuous monoculture of susceptible cultivars. A similar trend was observed in the blends. But indices of parasitism on PI 88788 were significantly lower in soil from plots containing blends than from plots with resistant cultivars grown in pure line stand in 1985 and 1988 (Table 7).

DISCUSSION

Resistant cultivars showed an obvious yield advantage over the susceptible cultivars in these studies. Yield of the blends of resistant and susceptible cultivars, however, compared favorably with resistant cultivars grown in pure stand. Several reasons account for the greater than expected yield of the blends. Population densities of SCN on resistant cultivars increased to higher levels in plots planted in monoculture compared to the blends. Since the level of SCN resistance had declined in response to the selection pressure induced by continued culture of the same type of SCN resistance, the effectiveness of this type of resistance was reduced. Concurrent with the increased ability of these SCN populations to parasitize resistant cultivars was an increase in the SCN population densities which would result in significantly more damage to these cultivars because soybean yield is inversely proportional to the preplant SCN density (13).

The most important advantage of blends of resistant and susceptible cultivars may be through the improved management of SCN population density and population dynamics. Resistant cultivars have a competitive advantage over susceptible cultivars from two perspectives. Resistant cultivars will yield more than susceptible cultivars because they suffer less damage due to subsequent SCN infection. A second perspective is that they minimize SCN reproduction during the cropping season which will affect subsequent soybean crops, provided the resistance has not broken down. The blends of resistant and susceptible cultivars in this research minimized SCN reproduction compared to both susceptible and resistant cultivars, and prevented a shift from Race 14 to Race 5. The blends served to maintain yields and prolong the usefulness of the resistant cultivar.

The change in race status of these populations over the course of this study may need some explanation. The only difference between Races 2 and 5 is in their ability to parasitize the cultivar Peking at a level equal to or greater than 10% of a susceptible cultivar. For example, the index of parasitism on Peking was 9.8 and 10.9 for the resistant cultivar and susceptible cultivar, respectively, at the end of the experiment. These differences are not significant, but these populations are rated as 2 and 5 because one is greater than 10 and the other less than 10. It is possible that these differences would be reversed if the race determinations were performed a second time (21). The important differences between these two populations is in their ability to parasitize the line PI 88788 from which Bedford and Bradley derived most of their resistance. The population from plots with blends had a lower frequency of genes for parasitizing PI 88788 than the population from resistant cultivars in pure stand. This is evident in the race determination and cyst counts taken 30 d after planting. The resistant cultivar in monoculture is susceptible to that population, whereas the resistant cultivar in the blends may be moderately resistant to that population.

The high yield of Essex in blends was unexpected since this cultivar had the lowest yield among the susceptible

Table 7. Index of parasitism and cyst nematode race differentiation in resistant and susceptible cultivars and their 50:50 blends.

		Index of parasitism on				
Year	Treatment	Peking	Pickett	PI 88788	PI 90763	Race†
1985	Resistant	13.9b‡	92.2a	26.3a	10.9a	4
	Susceptible	21.1a	96.1a	8.1b	13.2a	14
	Blend	18.9ab	102.1a	13.2b	11.1a	4
1986	Resistant	14.6a	87.9a	20.5a	4.7b	2
	Susceptible	22.6a	100.9a	9.6a	11.9a	14
	Blend	33.2a	123.6a	17.4a	8.6a	2
1987	Resistant	12.8b	69.6a	17.1a	5.5b	2
	Susceptible	27.3a	95.0a	13.1a	14.3a	4
	Blend	17.2ab	91.1a	12.9a	9.1ab	2
1988	Resistant	9.8b	83.5a	28.8a	1.8c	5
	Susceptible	19.7a	88.5a	5.4c	8.0a	9
	Blend	10.9b	86.7a	15.9b	4.6b	2

† Race characterization as described by Riggs and Schmitt (10).
‡ Means followed by the same letter in a column in a year do not differ significantly ($P = 0.05$).

cultivars when evaluated as a pure line. Other research has shown that cultivars vary in their ability to contribute to the overall yield of blends (7). Bedford and Essex may be better suited for blends than were the other cultivars used in this research. Although Bedford, Essex, and York are MG V, Essex and York mature 7 to 10 d earlier than Bedford. Maturity differences probably did not result in higher yields of the blends in our research since different maturity groups in blends of southern determinate soybean types had little effect on the effectiveness of blends in North Carolina research (6).

Blends of SCN-resistant and susceptible cultivars at a 50:50 ratio were effective in maintaining soybean yields equivalent to a resistant cultivar in the presence of SCN. Our data suggest that use of SCN resistant and susceptible soybean blends could be an effective practice to manage SCN-caused economic losses because of the slower development of SCN populations capable of reproducing on the resistant cultivars. This is a major consideration for expanding the longevity of resistant cultivars. Earlier studies did not find blends of 70 to 80% resistant and 20 to 30% susceptible soybean cultivars superior to growing a resistant cultivar (10, 20). Tinius et al. (17) reported that a 50.50 mixture of resistant and susceptible soybean cultivars showed a yield response greater than expected from yields of component cultivars in a SCN-infested field in North Carolina. Additional investigations to determine the blending ability of resistant and susceptible cultivars will be useful. Future research should focus on combining two or three resistant cultivars with different sources of resistance to improve the level of resistance in a blend. An additional improvement might be the inclusion of tolerant cultivars (2) in blends to enhance yield performance. It is, however, evident that blending could have a broad spectrum effect on the rhizosphere, chemical, and biological environments; greater yield advantage will be the consequence of a comprehensive effect rather than that on SCN alone.

The research in this paper is unique in that it represents a new approach to managing nematode resistance genes in a spatial context. Multi-line approaches have been used for foliar pathogens (22), but the utility of this management tactic for soilborne pathogens and nematodes, in particular, has received only limited attention. Cultivar blends would serve to broaden the range of control tactics available for managing SCN. Combining blends of resistant and susceptible cultivars, rotation, and new sources of SCN resistance in a multifaceted strategy should ultimately prove to be a more successful approach to this complex problem.

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