JA1720

Reprinted from the Journal of Production Agriculture
Volume 8, no 1 January-March 1995
677 South Segoe Rd Madison WI 53711 USA

1165

2446

Effect of Temporal Deployment of Different Sources of Resistance to Soybean Cyst Nematode

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Crop rotation is an important management practice to reduce disease losses caused by soybean [*Glycine max* (L.) Merr.] cyst nematode (SCN, *Heterodera glycine* Ichinohe). Thirteen rotation treatments consisting of 'Bedford', a soybean cultivar resistant to SCN races 3 and 14, 'Forrest' resistant to races 1 and 3, susceptible 'Essex', and a nonhost crop (*cotton [Gossypium hirsutum* L.]) were evaluated in an SCN infested field for 4 yr. Yields of soybean cultivars in continuous production systems were compared with those in rotation with the nonhost, resistant, and susceptible cultivars. Bedford and Forrest yields, over the 4 yr, were less variable than Essex yields. Forrest and Essex produced similar yields in 3 out of 4 yr, and yields of Essex were significantly lower than Bedford yields in 2 out of 4 yr. Beneficial effects of different rotations on cultivar performance were not very conspicuous, however, yields of Essex were increased with rotation in five of the six comparisons compared with continuous Essex, whereas Bedford in rotation was significantly higher than continuous Bedford in two of the five comparisons. Grain yields of Forrest were not affected by rotation systems. The nematode density, after 4 yr, was lowest in cotton-Forrest-Bedford-cotton system and greatest in Bedford-cotton-Essex-Forrest system. The preceding crop had a greater influence on the nematode population density than the rotation system per se. Treatments with cotton as the preceding crop had lower nematode population densities than resistant or susceptible soybean. Rotating cultivars caused changes in SCN race structure. SCN race 14 was present in almost all rotations including Essex and Forrest. Bedford tended to increase the population with genes for parasitism on PI 88788, resulting in a shift to race 4. The shift to highly pathogenic race was slower in rotations that included susceptible Essex and Forrest as a component crop. Inclusion of susceptible soybean lines in rotations may delay, but not prevent, the development of highly virulent races of SCN. Rotation of soybean cultivars was found to be a useful practice in the management of SCN-caused losses.

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Published in J. Prod. Agric. 8:119-123 (1995).

RESISTANCE TO SCN in most of the released soybean cultivars is not durable due to genetic variability in SCN populations which enables them to parasitize resistant cultivars (Triantaphyllou, 1975). Populations of SCN differ in the frequency of occurrence of genes for parasitism of resistant soybean cultivars. Deployment of resistance genes in cultivars generally results in selection pressure, which affects a change in the frequency of corresponding genes in the nematode population and is termed a race shift. Continuous cultivation of a resistant cultivar usually results in development of SCN populations that can overcome the host resistance (Triantaphyllou, 1987). Nevertheless, cultivation of SCN resistant cultivars and rotation of soybeans with nonhost crops are common management tactics to contain SCN-caused yield suppression. The inherent variability and shifts in the ability of SCN populations to reproduce on cultivars with resistance genes accentuate the need to develop management strategies that minimize race specific selection

Table 1. Crop rotation sequences followed in soil infested with *Heterodera glycines*, Portageville, MO, 1983-1986.

Treatment	1983	1984	1985	1986
1	Essex†	Essex	Essex	Essex
2	Forrest	Forrest	Forrest	Forrest
3	Bedford	Bedford	Bedford	Bedford
4	Essex	Forrest	Bedford	Essex
5	Forrest	Bedford	Essex	Forrest
6	Bedford	Essex	Forrest	Bedford
7	Cotton	Essex	Forrest	Bedford
8	Essex	Forrest	Bedford	Cotton
9	Forrest	Bedford	Cotton	Essex
10	Bedford	Cotton	Essex	Forrest
11	Cotton	Forrest	Bedford	Cotton
12	Forrest	Bedford	Cotton	Forrest
13	Bedford	Cotton	Forrest	Bedford

† Essex, Forrest, and Bedford are soybean cultivars, and cotton cultivar Delcot 344 was used.

Table 2. Grain yield of soybean cultivars in continuous cropping, rotation with other soybean cultivars, and a nonhost crop, 1983-1986.

1983	1984	1985	1986
E† 26.3C*	E-E 39.7a	E-E-E 28.7f	E-E-E-E 25.8d
	B-E 35.6b	F-B-E 37.2abcd	F-B-C-E 30.2bcd
	C-E 35.2b	B-C-E 39 9ab	E-F-B-E 33.3bc
F 31.5b	F-F 38.4ab	F-F-F 33.1f	F-F-F-F 38.0ab
	E-F 39.5ab	C-E-F 31.9f	B-C-E-F 32.0ab
	C-F 36.6ab	B-C-F 38.1abc	F-B-E-F 38.6ab
		B-E-F 36.2cd	F-B-C-F 37.0ab
B 33.4a	B-B 36.6ab	B-B-B 35.2cde	B-B-B-B 37.8ab
	F-B 40.0a	C-F-B 39.9ab	C-E-F-B 41.9a
		E-F-B 40.4a	B-C-F-B 36.7ab

* Means with same letter in a column do not differ significantly ($P = 0.05$).
† E = Essex, F = Forrest, and B = Bedford are soybean cultivars, and C = cotton cultivar Delcot 344. Data indicate cropping sequences followed in preceding years and grain yield (bu/acre) of the last crop in the sequence.

pressure, and supplement the durability of resistant cultivars. Ideally, such strategies to manage SCN-caused losses would serve to stabilize soybean yield. Incorporation of SCN susceptible soybean cultivars in the rotation program is sometimes recommended to reduce selection pressure on the nematode population by maintaining the gene frequencies for parasitism close to the original levels with reduced risk of race shifts (Young and Hartwig, 1988; Young et al, 1986). The objective of this 4-yr field study was to examine the effects of selected rotations of SCN resistant and susceptible soybean cultivars with or without a nonhost crop on soybean yields and on SCN race structure.

MATERIAL AND METHODS

Field trials were conducted between 1983 and 1986 at the Lee Farm of the University of Missouri's Delta Center in Portageville. The test plot had Tiptonville fine sandy loam soil (fine sandy to silty, mixed, thermic Typic Arguidolls) with 59.5% sand, 34.3% silt, 6.2% clay, 1.4% OM, a pH of 5.6, and a heavy infestation of SCN. The susceptible cultivar Essex was grown in the field plot in 1982 prior to initiation of the study. Thirteen crop rotation treatments included 3-yr rotation cycles of SCN susceptible and resistant soybean cultivars and a nonhost crop, cotton (Table 1). Three treatments were continuous cultivations of the SCN susceptible cultivar, Essex, and resistant cultivars Forrest, resistant to races 1 and 3 derived from Peking (Hartwig and Epps, 1973), and Bedford, resistant to races 3 and 14 derived from PI 88788 (Hartwig and Epps, 1978). These cultivars are determinate and belong to maturity group V. In 1986, crop treatments of 1983 were repeated except in treatments 7, 8, 9, and 10 (Table 1). Cotton cultivar Delcot 344 was included in the trial to compare effects of rotation with a nonhost crop and resistant cultivars on yield of the susceptible cultivar. The soybean and cotton cultivars were planted every year in May in eight rows, 40 ft long and 30 in. apart. The crop treatments were in a randomized complete block design with four replications.

Soil samples were collected within six rows of each plot at planting and at harvest each year to determine the SCN population density and level of parasitism. Cysts were extracted from 1 pt of soil with a semi-automatic elutriator (Byrd et al., 1976). The soil samples from each plot, at planting in 1983 and at harvest in 1983 and 1984, were placed in 3-in. diameter pots. Seeds of each standard SCN race differentials—Pickett, Peking, PI 88788, and PI 90763—and a susceptible check cultivar—Lee 68—were sown individually in six pots. At 30 d after sowing, cysts on the roots of each of the six plants were counted and level of parasitism on each differential was calculated by multiplying the number of cysts per plant by 100 and then dividing by the number of cysts on Lee 68. The races were identified as per the scheme of Riggs and Schmitt (1988).

The general linear model procedure on SAS was used with the randomized complete block design model. Treatment means were compared using Duncan's Multiple Range Test (SAS Institute, 1985).

RESULTS

Bedford and Forrest produced 17 to 22% greater yields than Essex in 1983. Seed yield of Bedford was significantly ($P = 0.05$) greater than the two other cultivars (Table 2). Essex yields in 1984 were significantly lower in plots that had been rotated to the soybean cultivar Bedford or cotton than in plots with Essex in 1983. Soybean seed yields in 1984 were greater than in 1983. Essex, grown in rotation with a nonhost or following cultivar rotations, yielded significantly ($P = 0.05$) less than Essex grown in a continuous Essex system in 1984. Yields of Bedford or Forrest were similar, whether these cultivars were grown in rotation or in continuous culture in 1984. Bedford, grown in the cotton-Forrest-Bedford, sequence yielded more in 1985 than any other treatment (Table 2). Continuous culture of Essex soybean resulted in the lowest yield of any treatments in 1985. The seed yield of Essex grown in rotation was significantly greater ($P = 0.05$) than continuous Essex. Yields of Forrest grown in a rotation with cotton as the previous crop were greater than the yields of Forrest grown in a cotton-Essex-Forrest sequence or continuous Forrest. Continuous cultivation of Bedford resulted in lower soybean yield than Bedford grown in rotation in 1985. Yield trends in 1986 were similar to those encountered in 1985 (Table 2), although there was little significance associated with yield differences.

For most rotation sequences, population densities of SCN cysts peaked in 1985 after drought conditions in

Table 3. Cyst count of soybean cyst nematode per pint of soil following each cultivar in different rotations.

Rotation	1983	1984	1985	1986
EEEE†	E 120a‡*	E 201a	E 379a	E 193b
FFFF	F 102a	F 249a	F 467a	F 295a
BBBB	B 60b	B 102b	B 236a	B 129b
EFBE	E 126a	F 267a	B 85b	E 128b
FBEF	F 120a	B 39c	E 312a	F 280a
BEFB	B 66ab	E 198a	F 437a	B 52bc
CEFB	C 30b	E 291a	F 440a	B 49bc
EFBC	E 122a	F 297a	B 90b	C 24bc
FBCE	F 139a	B 51c	C 15c	E 153b
BCEF	B 62ab	C 9c	E 644a	F 430a
CFBC	C 37b	F 292a	B 78b	C 15c
FBCF	F 103a	B 70b	C 25c	F 150b
BCFB	B 55b	C 6c	F 590a	B 87bc

* Means with same letter in a column do not differ significantly ($P = 0.05$).
† B = Bedford, E = Essex, and F = Forrest are all soybean cultivars; C = cotton cultivar Delcot 344.
‡ Initial cyst count 35-40/pint of soil.

Table 4. Parasitism of race differential soybean genotypes by *Heterodera glycines* populations in different crop rotation sequences, Portageville, MO, 1983-1985.

	Level of parasitism on				
Treatment	Pickett	Peking	PI 88788	PI 90763	Race†
			At 1983 harvest		
Essex (E)	93b*	17b	2NS	14a	14
Forrest (F)	132a	23a	3	17a	14
Bedford (B)	78b	13b	6	7b	9
Cotton (C)	51c	5c	1	5b	6
			At 1984 harvest		
B-B‡	91NS	17NS	19a	9NS	2
B-E	72	24	6b	9	9
C-E	88	23	7b	13	14
C-F	92	22	5b	13	14
E-E	96	27	5b	12	14
E-F	93	27	6b	17	14
F-B	74	24	15ab	13	4
F-F	92	29	8b	18	14
			At 1985 harvest		
B-B-B	86ab	29NS	29a	13NS	4
C-F-B	75b	19a	15bc	14	4
E-F-B	94ab	31	16b	17	4
E-E-E	112ab	33	10bc	16	4
B-C-E	89ab	26	11bc	14	4
F-B-E	128a	41	11bc	18	4
F-F-F	91ab	26	10bc	13	4
B-C-F	90ab	23	8c	12	14
B-E-F	94ab	29	11bc	16	4
C-E-F	93ab	31	10bc	12	14

* Means with same letter in a column and year do not differ significantly ($P = 0.05$); NS = means in the column do not differ significantly ($P = 0.05$).
† Race designation as described by Riggs and Schmitt, 1988.
‡ B = Bedford, E = Essex, and F = Forrest are all soybean cultivars; C = cotton cultivar Delcot 344.

1983 and declined in 1986 (Table 3). The mean preplant cyst count was 40 cysts/pt of soil and did not differ significantly among treatments at experiment initiation in 1983. Cyst densities at soybean harvest were always lowest following a cotton crop and were generally highest when a soybean crop followed cotton (Table 3). Essex and Forrest maintained higher cyst population densities than Bedford at the end of study.

The race status of the nematode population was affected by the rotations employed in this research. Race determinations conducted in 1983 indicated that growing the soybean cultivar Bedford for 1 yr affected a change from race 14 to race 9, whereas the race changed from 14 to 6 when cotton was grown. Cultivation of Bedford soybean for 2 yr resulted in a change in the race designation of the population from race 9 to race 2 in 1984. The population in plots where Essex was planted in 1984 after Bedford in 1983 remained as race 9, but Bedford following Forrest produced a shift from race 9 to race 4. When Forrest or Essex were grown in rotation with each other or following cotton in 1984, the populations were classified as race 14. Race determinations conducted in 1985 resulted in all populations being designated as either race 14 or 4. The Bedford-cotton-Forrest and cotton-Essex-Forrest sequences had populations classified as race 14, whereas populations in the other sequences were classified as race 4. The ability of the SCN populations to parasitize Peking or PI 90763 was unaffected by any of the cultivar sequences employed in this research (Table 4). Any changes in the abilities of these populations to parasitize Pickett were small. Selected cropping sequences were effective in preventing a shift in the populations' ability to parasitize PI 88788 when compared with continuous cultivation of Bedford. Over the course of the study, there was an apparent increase in the ability of these populations to parasitize PI 90763, but this change is probably a result of random variation between years.

DISCUSSION

Yields of all cultivars were relatively low in 1983 as a result of drought stress. The greater yield of Bedford than Essex and Forrest in 1983 can be attributed to high level of resistance possessed by this cultivar to the SCN population present at the initiation of the experiment. Only relatively small differences in soybean yield occurred as a result of rotations in 1984. The higher yield of Essex in monoculture compared with the Bedford-Essex or cotton-Essex sequence may be a result of the low population densities of SCN following the 1983 season, since soybean yield is largely determined by preplant nematode density. Cotton and Bedford are nonhost and a resistant host, respectively. Cyst densities, however, may not have been reduced below the damage threshold in some plots following these crops, whereas cyst densities and the inoculum potential of the SCN eggs may have been suppressed in continuous Essex plots because of biological control organisms or damage caused to soybean in the preceding year. Francl and Dropkin (1986) found that 2 yr of a nonhost crop may be necessary to reduce nematode populations below damaging levels in Missouri.

Rotations of Essex with Forrest and Bedford or Bedford and cotton resulted in higher yields than continuous Essex in 1985, demonstrating that the yield of this susceptible cultivar was stabilized by rotation. The Bedford-cotton-Forrest sequence resulted in the highest yield of Forrest during 1985 compared with other sequences. The cotton-Essex-Forrest and Bedford-Essex-Forrest sequences did not differ from continuous Forrest in 1985 because of high cyst densities following cultivation of Essex in the preceding year. Population densities of SCN were much higher following a susceptible host if a nonhost preceded the susceptible host than in soybean monoculture (Koenning et al., 1993). A cultivar like Forrest should not follow Essex in rotation unless it possesses a moderate-to-high level of resistance to the SCN population present. The yield of Bedford grown in rotation with cotton and Forrest or Essex and Forrest was superior to that of continuous Bedford in 1985. Although the SCN population density was high following these rotational crops/cultivars, the temporal deployment of the resistance genes maintained the population as race 14, to which Bedford is resistant. Cropping sequences tended to stabilize soybean seed yield in Essex relative to monocultivar treatment in 1986, but the differences were not significant.

Other researchers (Hartwig et al., 1987, Young and Hartwig, 1988) have challenged the utility of the inclusion of susceptible cultivars in rotation with resistant cultivars since the resistant cultivars generally outyield the susceptible cultivars. Our research indicates that rotating resistant and susceptible cultivars tends to stabilize the yields of all cultivars. Part of the discrepancy between the current work and previous research may be a result of interactions with soil type and experimental design. The research conducted by Hartwig et al. (1987) and Young and Hartwig (1988) in Tennessee used three replications and was conducted in a silt loam soil. Damage caused by SCN is known to be influenced by soil texture (Koenning et al., 1988). Differences in soil texture between the sites may have resulted in reduced effects of SCN on soybean yields in Tennessee, masking differences between rotations.

Population densities of SCN cysts were greatest following a susceptible Essex or Forrest treatment each year. Inclusion of both Forrest and Essex in this type of rotation is not a suitable practice since both were susceptible to the present SCN population in this field. The yield of Forrest soybean following Essex was suppressed because it was not resistant to races 2, 6, 9, or 14. Cyst densities were high following cultivation of Forrest soybean, which may have had a slight detrimental effect on the yield of Bedford when this crop followed Forrest in an Essex-Forrest-Bedford sequence. When Bedford was grown in selected plots, it had the desired effect of preventing SCN buildup.

The shifts that occurred in the race status of the SCN populations affected by these cultivar sequences are somewhat problematical. Considerable variation occurs in race determinations (Riggs et al., 1988). The race classification of a population changes as the reproduction on a differential goes above or below 10% of the susceptible. The same population can be classified as one race or another with a slight change in test conditions due to the arbitrary nature of the classification. For example, in 1984, the population following the Bedford-Essex sequence was classified as race 9, whereas the populations following cotton-Essex, cotton-Forrest, continuous Essex or Forrest, and Essex-Forrest were all classified as race 14. The basis for this difference in classification is that the level of parasitism on PI 90763 was 9 for the Bedford-Essex sequence, but 13 to 18 for other combinations, even though these levels of parasitism are not significantly different. A similar problem is encountered with the race classification at the end of the experiment; 8 of the 10 treatments resulted in classification as race 4 while two were race 14. It is important to examine the data on levels of parasitism as influenced by the cropping sequences. The higher level of parasitism on PI 88788 following continuous culture of Bedford shows that the rotation sequences were beneficial in delaying a shift in the nematode populations' ability to parasitize PI 88788. In general, the ability of the population to parasitize PI 88788 seems to be related to the frequency and the time interval since that population was exposed to Bedford in the rotation. This last factor suggests that rotation, as opposed to continuous culture of Bedford, will delay but not prevent a shift in gene frequencies for parasitism in the nematode population. The inclusion of a nonhost in the rotation tended to maintain the populations closer to the original race 14. None of the rotations were effective in causing a shift in the population from race 14 to a less virulent race 3. Evidence for this conclusion lies in the fact that indices of parasitism on the Peking or Pickett differentials were not affected by these rotations. Although this conclusion is tenuous, the data show that once a population has shifted to a more virulent form, selection for a less virulent form may be ineffective or require many years.

An unexpected result was the shift from race 14 to race 6 in 1983 following cultivation of cotton. This may have been caused by the fact that the population density was lower following cotton, which resulted in levels of parasitism on differentials lower than expected. It is possible, however, that SCN biotypes may differ in their ability to survive in the absence of a host. Data from North Carolina (Sipes, 1990), showed that parasitic biotypes differed in rates of survival.

In summary, while inclusion of a susceptible variety will slow or delay a shift in the race of SCN, it is unlikely to effect a shift to a less virulent type.

The current research indicates that rotation systems that incorporate resistant and susceptible cultivars can stabilize soybean yield and delay a shift in the pathogen population toward parasitism of resistant cultivars. Yields of the resistant cultivar Bedford remained high during the course of this study. Inclusion of a susceptible cultivar did not result in a shift in the pathogen population to a form that could no longer affect resistant cultivars. Future research should focus on incorporating more sources of resistance to SCN in rotations to manage this pathogen.

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Effect of Temporal Deployment of Different Sources of Resistance to Soybean Cyst Nematode

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Research Question

The soybean cyst nematode (SCN) is an important pest of soybean in the USA. Rotation, resistant cultivars, and cultural practices are used to manage the population density of this nematode and associated soybean yield losses. Rotations of resistant soybean with susceptible soybean, with or without a nonhost crop, have been recommended for management of this pest. This research evaluated the effects of selected rotational sequences on (i) the population densities of SCN, (ii) the race structure of SCN populations, and (iii) the effects of these rotations in stabilizing soybean yields in the presence of this pest.

Literature Summary

The deployment of resistant cultivars for management of soybean cyst nematode is problematical due to the genetic diversity of this pest in field populations. Resistance breaking biotypes or races of this nematode are selected when resistant cultivars using Peking or PI 88788 as a source of resistance are deployed. Several schemes for minimizing selection pressure on this pest, which will also result in higher soybean yield, have been proposed. The basis of these strategies is: (i) a nonhost crop or a resistant cultivar are used to minimize SCN density so that a susceptible soybean cultivar can be grown with minimal yield loss, (ii) inclusion of the susceptible cultivar should reduce selection pressure on the pathogen population, and (iii) reducing the frequency with which a particular source of SCN resistance is deployed will also prevent the development of populations of the pest that can parasitize the resistant cultivar. Research to demonstrate the benefits of the approach are generally lacking. Some researchers have suggested that, while these rotations may delay development of resistance-breaking biotypes of SCN, a monoculture of the resistant cultivar resulted in superior yields.

Study Description

The experiment was constructed from 1983 to 1986 at the Lee Farm of the University of Missouri Delta Center near Portageville, in a field infested with race 14 of the soybean cyst nematode. Thirteen rotational sequences were evaluated for their effects on soybean grain yield, for SCN population density at the end of the soybean growing season, and for their effect on the race structure of the SCN populations. Rotations included the susceptible cultivar Essex, the race 1- and 3-resistant cultivar Forrest, and the race 3- and 14-resistant soybean cultivar Bedford in rotations with or without a nonhost crop cotton. Soybean yield and final SCN cyst densities were determined every year. The races of the nematode populations were determined in 1983, 1984, and 1985 using the soybean differentials Pickett, Peking, PI 88788, and PI 90763, and susceptible Lee 68.

Applied Questions

Is the inclusion of a nonhost in the rotation necessary to prevent SCN race shifts?

A nonhost in the rotation will help delay a shift in the SCN population but probably not prevent it. Similarly, inclusion of a susceptible soybean cultivar tended to retard selection of SCN races that can damage Bedford soybean. Growing a cultivar resistant to the SCN population in a particular field as infrequently as possible is the best way to preserve the usefulness of resistant cultivars.

Full scientific article from which this summary was written begins on page 119 of this issue.

Which rotations are superior for maintaining soybean yields at high levels—those that include a nonhost crop or rotated cultivars with different types of SCN resistance?

Soybean yield was generally improved following a cotton crop, but the SCN cyst density increased to greater than 200 cysts/pt when a susceptible soybean cultivar was grown after cotton. This often resulted in lower yields for the second soybean crop following cotton. Growing a nonhost crop every other year could prevent this yield loss. The time at which the rotation is started may also determine the best rotation to use. The resistance of Forrest soybean was no longer useful against the SCN population in these fields. The Essex-Forrest-Bedford rotation would probably provide better yields than Bedford monoculture if race 3 or race 1 were present, whereas with race 14, a rotation with a nonhost should be included every second or third year.