

Influence of Soybean Cropping Sequences on Seed Yield and Female Index of the Soybean Cyst Nematode

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ABSTRACT

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Several soybean (*Glycine max*) cropping sequences were planted for 12 years in a field that, at the beginning of the test, was infested with race 14 of the soybean cyst nematode, *Heterodera glycines*. Continuous soybean cropping sequences included *H. glycines*-susceptible cultivars Forrest, J82-21, Peking × Centennial breeding line, and moderately resistant cultivars Bedford and J81-116. Forrest treated with aldicarb or pentachloronitrobenzene (PCNB) plus metalaxyl and resistant breeding line JS83-236 followed by resistant cultivars Cordell and Hartwig were additional continuous soybean sequences. Rotations included two sequences each of Bedford with J81-116 or J82-21, and three sequences of Bedford with corn (*Zea mays*) and susceptible Essex soybean. Rotations of Bedford, corn, and Essex had 12-year mean yields significantly greater than continuous Bedford or Forrest. The female index (FI) of *H. glycines* on five cultivars and lines was used to bioassay changes in parasitic potential in each cropping sequence. The FI on Bedford bioassay plants increased significantly over time for all field treatments involving Bedford. When J82-21 was the bioassay plant, FI decreased significantly in treatments involving Bedford. There were no significant changes in FI for any treatment when Forrest, J81-16, and Peking were used as bioassays. Rotations of soybean cultivars with different sources of resistance and rotations of resistant and susceptible cultivars with a nonhost crop were not successful practices to manage the nematode's ability to parasitize the resistant cultivar Bedford. However, rotation of resistant and susceptible cultivars with a nonhost crop produced greater mean soybean yields and slowed the shift toward greater parasitism of the resistant cultivar sufficiently to warrant adoption of this practice.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, is a serious pest of soybean in the United States. It caused an estimated average annual yield reduction valued at \$177.82 million in the southern region (12) in 1992 to 1993 and \$267.36 million in the north central region in 1989 to 1991 (4). Planting resistant cultivars and rotating soybean with nonhost crops are the primary methods of suppressing damage by this nematode. However, control practices are complicated by the occurrence of physiological races of the nematode (8).

Frequent planting of resistant cultivars can lead to selection of *H. glycines* populations that can reproduce in abundance on the resistant cultivars (13,15,16). Inclusion of a susceptible cultivar in rotations with resistant cultivars and nonhost crops has been recommended to slow this change in the nematode populations (10). Rotations of resistant cultivars derived from different

sources of resistance have also been proposed as a means of managing genetic change in *H. glycines* populations (6,14). These latter rotations are based on the grouping of resistant plant introductions (PI) into two genetic groups in greenhouse selection experiments (1,2,6,7,13,14). As the number of *H. glycines* females increased on PIs in one genetic group through applied selection pressure, the number of females on PIs in the other genetic group decreased. Partial confirmation of the greenhouse experiments was observed in a field experiment conducted for 10 years (14).

The objectives of this study were to compare changes in soybean yield and soybean cyst nematode populations under continuous culture of soybean lines derived from different PIs, rotations involving lines derived from different PIs, and rotations of resistant and susceptible lines with a nonhost crop.

MATERIALS AND METHODS

Fifteen cropping sequences were established in 1985 in a field infested with *H. glycines* race 14. The soil was primarily a Lexington silt loam (fine-silty, mixed, thermic, typic Paleudalf; 62% silt, 32% sand, and 6% clay). The field had been planted in 1983 to 1984 with Forrest soybean (susceptible to race 14 but resistant to race 3); and in the 10 years prior to 1983,

Forrest was planted in alternate years with soybean germ plasm with race 14 resistance derived from PI 88788. Each sequence was replicated three times in randomized complete blocks. Five sequences were continuous plantings of soybean lines as follows: Bedford (moderately resistant to races 3 and 14), Forrest, J81-116 (moderately resistant to races 3, 5, and 14), J82-21 (susceptible), and an F₅ selection from the cross Peking × Centennial (susceptible). Two treatments were continuous plantings of Forrest treated with either aldicarb at 1.7 kg a.i./ha or PCNB at 2.8 kg a.i./ha plus metalaxyl at 0.3 kg a.i./ha in a 16-cm band over the row. The applications of pesticides were discontinued in 1995. The eighth treatment was continuous planting of soybean lines with broad resistance to *H. glycines*, JS83-236 (resistant to races 3 and 5 and moderately resistant to race 14) in 1985 to 1987, Cordell (resistant to races 3 and 5 and moderately resistant to races 2 and 14) in 1988 to 1991, and Hartwig (resistant to all races) in 1992 to 1996. Seven sequences were rotation sets involving Bedford: two of Bedford in rotation with J81-116, two of Bedford in rotation with J82-21, and three of Bedford in rotation with corn (*Zea mays*) and Essex (susceptible) soybean. Sets involving the same soybeans or crops differed by which phase initiated the rotation. Sources of resistance for the cultivars or breeding lines planted in the field are listed in Table 1.

Individual plots were eight rows wide and 10 m long, with 90-cm spacing between rows. The end of one plot was separated from the beginning of another by a 2-m-wide alley. Plots were planted between 2 May and 4 June of each year. Yield and soil samples were collected from the four

Table 1. Sources of resistance to *Heterodera glycines* in soybean lines used in cropping sequence treatments at Jackson, Tennessee, 1985 to 1996

Soybean	Sources of resistance
Bedford	Peking, PI 88788
Cordell	Peking, PI 88788, PI 90763
Essex	None
Hartwig	Peking, PI 437654
J81-116	Peking, PI 88788, PI 89772
J82-21	Peking, PI 90763
JS83-236	Peking, PI 88788, PI 89772, PI 90763
Peking × Centennial	Peking

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middle rows of each plot. Beginning in 1989, plots were drip-irrigated from onset of flowering to maturity as needed to maintain soil water potential at the 30-cm depth wetter than -60 J/kg. Twelve 2-cm-diameter soil cores were collected each year at 65 to 75 days after planting and again in September or October from each plot. Cysts were extracted by elutriation (3), placed in a gridded dish, and counted with the aid of a stereoscopic microscope. Eight liters of soil were collected in October each year with a small shovel from 15 places in each plot and mixed. The mixed soil was placed in pots in the greenhouse and planted with either Essex, Bedford, Forrest, Peking, J81-116, or J82-21. Three pots (subsamples) of each soybean were grown in the greenhouse for each treatment

replication in the field. After 35 days, *H. glycines* females were extracted from the roots and soil as follows: the root ball was crumbled over the funnel of an elutriator, and females were dislodged by hand while the roots were submerged in water in the elutriator funnel. A female index (FI) was calculated as follows: FI = (number of females on Bedford, Forrest, Peking, J81-116, or J82-21 ÷ number of females on Essex) × 100. The maximum value of FI allowed was 100 to reduce distortion due to a few large numbers (31 of 540 observations had FI values greater than 200; 26 of the 31 observations were associated with Forrest as bioassay plant).

After the bioassays with Essex, Bedford, Forrest, Peking, J81-116, and J82-21 were completed after the 1996 growing season,

remnant soil collected from the three replications of each treatment in the field was composited, and five pots each of Lee 68, Pickett, Peking, PI 88788, and PI 90763 were grown for each treatment to identify the nematode race present. Females were extracted as described for the bioassays.

Data for individual years were subjected to analysis of variance. Data combined across years were analyzed with a mixed linear model using a split-plot design with years as a subplot stripped across the main plots (SAS Institute, Cary, NC). This analysis was chosen as best for efficiency and description of error structure after comparing it with models using years as regular subplots or as a repeated measure. Replications and interactions involving replications with treatments and years were

Table 2. Yields of soybean lines in cropping treatments in a field infested with *Heterodera glycines* at Jackson, Tennessee, 1985 to 1996

	Yield (kg/ha) ^b												
Treatment ^a	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	Mean
FFFFFFFFFFFF	1,748	2,141	2,639	2,824	2,045	2,653	2,532	2,200	2,424	3,025	1,836	2,462	2,377
TTTTTTTTTTTF	1,951	2,317	2,906	2,699	2,280	2,637	2,371	2,178	2,653	2,781	1,868	2,673	2,443
RRRRRRRRRRFF	1,653	2,317	2,800	2,450	2,316	2,826	2,367	1,939	2,766	2,890	1,910	2,552	2,399
BBBBBBBBBBBB	1,626	2,182	2,933	2,678	2,398	3,160	2,628	1,964	2,768	2,691	1,965	2,765	2,480
111111111111	2,371	2,547	1,635	1,897	2,149	2,782	2,551	2,032	2,232	2,930	2,209	2,580	2,326
222222222222	1,870	1,802	2,488	2,672	2,226	2,584	2,512	2,116	2,802	3,145	2,518	3,236	2,498
PPPPPPPPPPPP	1,884	2,019	2,352	1,946	1,796	2,388	2,239	1,956	2,463	2,224	1,479	2,451	2,100
BB22BB22BB22	1,707	2,344	2,566	2,607	2,411	2,950	2,361	2,298	2,925	2,890	2,136	3,281	2,539
22BBB22BB22B	1,978	1,585	2,739	2,547	2,443	2,870	2,507	2,421	3,004	3,129	2,454	3,246	2,581
BB11BB11BB11	1,992	1,884	1,491	1,995	2,542	2,853	2,537	2,052	3,007	2,808	2,329	2,656	2,346
11BBB11BB11B	2,344	2,656	2,644	2,726	2,307	2,992	2,623	2,472	2,871	3,098	2,245	3,498	2,706
MEBMEBMEBMEB	... ^c	3,385	2,981	...	3,208	3,111	...	2,990	2,949	...	3,121	2,977	3,090
EBMEBMEBMEBM	2,412	2,331	...	2,341	2,533	...	3,327	2,452	...	4,070	2,403	...	2,734
BMEBMEBMEBME	2,182	...	2,649	2,632	...	3,185	2,710	...	2,457	3,393	...	3,474	2,834
333CCCCHHHHH	2,005	1,490	2,288	2,618	2,312	3,062	2,842	2,366	2,594	2,857	2,164	2,832	2,452
LSD, <i>P</i> < 0.05	NS	534	810	353	527	332	365	394	382	485	462	364	145

^a B = Bedford, C = Cordell, E = Essex, F = Forrest, H = Hartwig, P = Peking × Centennial selection, R = Forrest treated with PCNB at 2.8 kg a.i./ha + metalaxyl at 0.3 kg a.i./ha, T = Forrest treated with aldicarb at 1.7 kg a.i./ha, 1 = J81-116, 2 = J82-21, and 3 = JS83-236 soybean lines, and M = corn (*Zea mays*) grown in sequence as indicated. Each letter represents the soybean or corn grown for 1 year.

^b Means of three replicates.

^c Corn grown and yield was not measured.

Table 3. Numbers of cysts in soil sampled near harvest time from soybean cropping treatments in a field infested with *Heterodera glycines* at Jackson, Tennessee, 1985 to 1996

	Cysts per 450 cm ³ of soil ^b												
Treatment ^a	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	Mean
FFFFFFFFFFFF	203	38	112	75	78	67	40	100	33	175	27	33	82
TTTTTTTTTTTF	192	100	88	72	147	195	63	87	33	193	32	35	103
RRRRRRRRRRFF	263	162	235	68	130	158	95	122	60	170	77	68	134
BBBBBBBBBBBB	67	10	38	85	115	88	35	68	47	100	72	78	67
111111111111	82	13	75	60	65	68	42	52	13	60	45	38	51
222222222222	113	32	77	33	68	37	23	62	15	47	25	37	47
PPPPPPPPPPPP	132	30	82	53	120	52	38	60	38	90	38	55	66
BB22BB22BB22	53	5	78	42	40	68	13	63	15	72	23	32	42
22BBB22BB22B	108	20	25	32	85	57	13	27	23	42	25	25	40
BB11BB11BB11	52	3	42	135	32	60	27	42	47	147	35	30	54
11BBB11BB11B	50	18	15	8	73	40	13	50	15	67	42	65	38
MEBMEBMEBMEB	83	62	12	2	318	60	2	122	32	0	78	53	69
EBMEBMEBMEBM	193	0	2	48	45	7	67	27	3	62	20	2	40
BMEBMEBMEBME	32	5	87	8	0	132	7	3	25	28	2	43	31
333CCCCHHHHH	85	18	105	170	82	48	23	8	0	3	5	12	47
LSD, <i>P</i> < 0.05	105	51	87	70	61	55	33	47	26	79	34	37	25

^a B = Bedford, C = Cordell, E = Essex, F = Forrest, H = Hartwig, P = Peking × Centennial selection, R = Forrest treated with PCNB at 2.8 kg a.i./ha + metalaxyl at 0.3 kg a.i./ha, T = Forrest treated with aldicarb at 1.7 kg a.i./ha, 1 = J81-116, 2 = J82-21, and 3 = JS83-236 soybean lines, and M = corn (*Zea mays*) grown in sequence as indicated. Each letter represents the soybean or corn grown for 1 year.

^b Means of three replicates.

considered random terms for the mixed linear model. Orthogonal contrasts were used to compare different years within a treatment.

RESULTS

Yields of the continuously planted soybean lines were not significantly different in most years (Table 2). Four treatments, the three rotations involving Bedford with corn and Essex and one rotation involving Bedford and J81-116, had 12-year mean yields significantly greater than that of continuous Bedford. Yield of Essex following corn in the Bedford-corn-Essex rotations was significantly greater than yield of continuous Bedford in 7 of 12 years and was greater in all but one of the last 6 years of the test.

Numbers of cysts were not particularly high in any of the treatments throughout the study (Table 3), and numbers of cysts at 65 to 75 days after planting (data not shown) were similar to numbers of cysts at harvest. Application of fungicides to Forrest led to significantly higher numbers of cysts than on Forrest without fungicides in 6 of the 12 years. In most years, the numbers of cysts following a crop of corn were significantly less than numbers of cysts in plots of continuous Forrest. The number of cysts rebounded on Essex following the decreased numbers with corn. Introduction of the Hartwig cultivar also reduced cyst numbers. The increase in the FI on Bedford bioassay plants following rotations did not correspond with greater numbers of cysts when Bedford was grown in the field.

The FI increased significantly over time for all field treatments involving Bedford

when the greenhouse bioassay plant was also Bedford. After the second year of the study, the FI on Bedford bioassay plants was 66 (Table 4). An FI value greater than 60 indicates that Bedford had become susceptible to the nematode population in that treatment (9). The FI on Bedford bioassay plants for the continuous Bedford field plot did not increase significantly after the first 3 years of the test. The FI for continuous Bedford plots with Bedford as the bioassay plant was significantly greater than the corresponding FI for continuous Forrest plots after the third year of the study and remained significantly different until 1996, when the FI increased dramatically in the Forrest plots. The FI on Bedford also increased in each of the rotations such that FI was significantly greater in the last 4 years of the test than in the first 4 years for the rotations involving J81-116 or J82-21. In rotations involving Bedford, corn, and Essex, the mean FI increased for each of the first three cycles (3-year period) but not for the fourth cycle.

There were no major changes in FI for any field treatment when Forrest, J81-116, and Peking were used as bioassay plants, except there was a small (from 55 to 78, $P = 0.01$) increase in FI on the J81-116 bioassay plant when it was planted in soil from the continuous J81-116 field plots. Also, the FI on the Bedford bioassay plants doubled from 18 to 36 ($P = 0.05$) in the soil from continuous J81-116 field plots. When J82-21 was the bioassay plant, FI decreased significantly in field treatments involving Bedford (Table 5). There was no significant change in FI on Bedford bioassay plants grown in soil from the J82-21 field plots.

Races 4, 5, and 6 were found in continuous J81-116, continuous Bedford, and Forrest plus aldicarb treatments, respectively. Race 2 occurred in two sets of Bedford-corn-Essex rotation, one set of the Bedford-J81-116 rotation, and both sets of the Bedford-J82-21 rotation. Race 9 was found in plots of continuous Forrest, Forrest plus fungicides, continuous J82-21, continuous Peking \times Centennial selection, sequence of JS83-236, Cordell, and Hartwig, and one set each of the rotations involving Bedford with J82-21 or corn and Essex.

DISCUSSION

Differences in yield between continuous Bedford and Essex in the Bedford-corn-Essex rotations may be attributed to the higher yield potential of Essex or to the suppression of Bedford yield by the nematode as its parasitic potential increased in the continuous Bedford treatment. The yield potential of Essex could be fully expressed in the rotation because it followed the nonhost crop and was exposed to few nematodes. Yield suppression caused by the nematode is indicated because in the first 6 years of the rotation Bedford in the rotation had a yield significantly lower than that of Essex only twice; whereas in the last 6 years of the study, after the FI had increased, yield of Bedford was significantly less than that of Essex in 5 of the years.

Yield of Bedford in the rotations with J81-116 or J82-21 seldom differed significantly from yield of continuous Bedford; however, overall mean yield for three of the four sets of these rotations was signifi-

Table 4. Mean female indices when Bedford soybean was grown in the greenhouse in soil from soybean cropping treatments in a field infested with *Heterodera glycines* at Jackson, Tennessee, 1985 to 1996

Treatment ^a	Female index ^b												Mean
	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	
FFFFFFFFFFFF	8	35	18	15	32	24	23	24	21	28	21	59	26
TTTTTTTTTTTF	15	21	9	14	15	34	13	24	30	20	11	28	19
RRRRRRRRRRFF	15	20	19	20	33	25	26	20	17	27	17	31	22
BBBBBBBBBBBB	18	66	64	67	83	94	100	84	77	80	84	91	76
111111111111	14	29	12	19	31	38	23	27	32	32	38	37	28
222222222222	14	10	10	14	18	22	31	16	34	17	18	20	19
PPPPPPPPPPPP	11	24	13	23	17	34	28	19	22	23	19	39	23
BB22BB22BB22	16	69	18	27	36	62	50	32	72	81	75	84	52
22BBB22BB22B	17	27	28	49	63	61	56	56	100	66	55	76	54
BB11BB11BB11	18	51	19	28	42	54	79	74	83	76	76	57	55
11BBB11BB11B	9	21	6	55	50	65	40	66	65	75	70	97	52
MEBMEBMEBMEB	11	20	46	17	33	77	46	52	73	80	68	86	51
EBMEBMEBMEBM	15	19	57	38	73	62	60	86	76	65	71	77	58
BMEBMEBMEBME	13	13	14	31	48	51	77	73	39	74	53	94	48
333CCCCHHHHH	16	13	9	13	23	46	36	49	19	75	42	56	33
LSD, $P < 0.05$	NS	37	34	26	24	26	26	28	39	35	38	36	7

^a B = Bedford, C = Cordell, E = Essex, F = Forrest, H = Hartwig, P = Peking \times Centennial selection, R = Forrest treated with PCNB at 2.8 kg a.i./ha + metalaxyl at 0.3 kg a.i./ha, T = Forrest treated with aldicarb at 1.7 kg a.i./ha, 1 = J81-116, 2 = J82-21, and 3 = JS83-236 soybean lines, and M = corn (*Zea mays*) grown in sequence indicated. Each letter represents the soybean or corn grown for 1 year. Orthogonal contrasts: FFFFFFFFFFFFFF 1985 to 1987 vs. 1994 to 1996, $P < 0.0799$; BBBBBBBBBBBB 1985 to 1987 vs. 1994 to 1996, $P < 0.0001$; 111111111111 1985 to 1987 vs. 1994 to 1996, $P < 0.0503$; 222222222222 1985 to 1987 vs. 1994 to 1996, $P < 0.4187$; mean (BB22BB22BB22 + 22BBB22BB22B) 1985 to 1988 vs. 1993 to 1996, $P < 0.0001$; mean (BB11BB11BB11 + 11BBB11BB11B) 1985 to 1988 vs. 1993 to 1996, $P < 0.0001$; mean (MEBMEBMEBMEB + EBMEBMEBMEBM + BMEBMEBMEBME) 1985 to 1987 vs. 1994 to 1996, $P < 0.0001$.

^b Female index equals number of soybean cyst nematode females developing on Bedford expressed as percentage of number of females developing on Essex in a greenhouse bioassay. Means of three replicates.

cantly greater than overall mean yield of continuous Bedford. The change in FI was more rapid for continuous Bedford than for the rotations with J81-116 or J82-21.

It is unknown why the FI doubled on the Bedford bioassay plants in soil from continuous Forrest plots in 1996 over the value obtained for 1995. However, the FI value was 69 in two of the three replications. It is possible that the plots were contaminated with soil from adjoining plots, because several of these had high FI values, particularly the plots that lay in the direction of tillage. The FI did not increase in bioassays of soil from the continuous Forrest plantings treated with aldicarb or fungicides.

Results of this study agree with findings in previous field and greenhouse studies. Young and Hartwig (15) found at the end of a 10-year study that continuous susceptible Tracy plots contained race 3; whereas plots planted with rotations of Centennial (resistant to race 3) with Tracy contained either race 2 or 14. Anand et al. (2) found, in a 4-year study, increased FI on PI 88788 bioassay plants over time in a rotation involving Bedford, Forrest, and cotton. Change in FI was more rapid for continuous Bedford than for the rotation. Young and Hartwig (16) found FI increased over time on Bedford bioassay plants in soil from continuous Bedford plots and rotations of Bedford with corn or Forrest and Essex. They found an increase in Bedford bioassay FI for plots planted with a blend of Bedford and Forrest in the last year of an 11-year test. Average yield of Bedford in one of two rotation sequences with corn was significantly greater than mean yield of continuous Bedford. The FI decreased over time with PI 89772 and PI 90763 bioassays grown in soil from plots of continuous Bedford and rotations of Bedford and corn (14). Reciprocal changes in FI were observed in greenhouse studies be-

tween nematodes cultured on Bedford and those cultured on PI 89772 or PI 90763 (6,13). In the current study, FI decreased on J82-21 bioassay plants as FI increased on Bedford bioassay plants in soil from field plots involving Bedford. PI 90763 is one of the sources of resistance in J82-21. In continuous J82-21 field plots, no changes in FI on either Bedford or J82-21 bioassays plants were observed. This lack of change was probably due to the small amount of reproduction occurring on Bedford with the original population and J82-21 being susceptible to the original nematode population. The increase in FI with Bedford bioassay plants in soil from continuous J81-116 plots was unexpected because greenhouse studies indicated that reciprocal changes in FI with Bedford and PI 89972 bioassays occurred. PI 89972 is one source of resistance in J81-116. However, Bedford was also a parent, and genes passed from Bedford to J81-116 may account for the observed increase in FI on Bedford bioassay plants in continuous J81-116 plots.

Apparently, selection pressure exerted on the nematode population by Bedford was much stronger than the opposing selection pressure exerted by J82-21. There was not the equal mutually incompatible reaction (5) for nematode development required for effective rotations between the two soybeans, resulting in primarily unidirectional selection pressure on the nematode population. It may be possible to devise rotations with cultivars with different sources of resistance that are more effective than those in this study. Nearly equal selection pressure in opposite directions will be needed. Even if such cultivars could be developed, the system could be difficult to sustain in an environment of rapidly changing cultivars and with many heterogeneous nematode populations in infested fields that could react quite differ-

ently than the populations studied. Soybean producers need to be induced to sample more frequently to effectively utilize such rotations.

Although rotations of resistant and susceptible cultivars with nonhost crops may only slow the change in FI, there are benefits of increased yield and longevity of resistance that make these rotations worthwhile. Soybean growers should be encouraged to use them because changes can occur in the nematode populations much faster than new sources of resistance can be identified and incorporated into productive cultivars.

Blends of resistant and susceptible soybeans were not tested in this study, but additional research is needed on them because they may be more effective in slowing selection pressure exerted by resistant cultivars (11,16) than rotations involving susceptible cultivars. Effectiveness of blends may be due to simultaneous application of a stabilizing influence with the selection pressure exerted on the nematode population by the resistant cultivar. More study and monitoring of nematode populations will be needed to improve management practices to increase longevity of resistance to the soybean cyst nematode. Until management practices that enhance longevity of resistance are developed, additional research is needed to locate and incorporate new genes for resistance into cultivars.

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Table 5. Mean female indices when J82-21 soybean was grown in the greenhouse in soil from soybean cropping treatments in a field infested with *Heterodera glycines* at Jackson, Tennessee, 1985 to 1996

	Female index ^b												
Treatment ^a	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	Mean
FFFFFFFFFFFF	61	69	91	50	71	51	58	73	55	59	82	78	67
BBBBBBBBBBBB	65	83	65	48	54	57	24	26	15	18	10	28	41
222222222222	84	33	79	46	82	58	62	64	72	54	59	72	64
BB22BB22BB22	64	83	65	89	84	49	74	37	30	40	59	59	61
22BBB22BB22B	44	54	62	71	50	67	62	31	44	44	47	59	53
BB11BB11BB11	70	100	63	90	76	41	51	56	33	29	20	30	55
11BBB11BB11B	71	49	44	53	40	50	40	35	26	35	57	36	45
MEBMEBMEBMEB	58	67	63	32	52	57	58	42	50	29	49	45	50
EBMEBMEBMEBM	57	77	11	64	61	75	46	37	13	56	23	48	47
BMEBMEBMEBME	65	64	53	78	61	67	56	39	67	33	48	47	56
LSD, <i>P</i> < 0.05	NS	NS	35	32	NS	34	NS	NS	38	32	NS	NS	10

^a B = Bedford, E = Essex, F = Forrest, 1 = J81-116, and 2 = J82-21 soybean lines, and M = corn (*Zea mays*) grown in sequence indicated. Each letter represents the soybean or corn grown for 1 year. Orthogonal contrasts: FFFFFFFFFFFFFF 1985 to 1987 vs. 1994 to 1996, *P* < 0.947; BBBBBBBBBBBBBB 1985 to 1987 vs. 1994 to 1996, *P* < 0.0001; 222222222222 1985 to 1987 vs. 1994 to 1996, *P* < 0.8675; mean (BB22BB22BB22 + 22BBBB22BB22B) 1985 to 1988 vs. 1993 to 1996, *P* < 0.0037; mean (BB11BB11BB11 + 11BBB11BB11B), *P* < 0.0001; mean (MEBMEBMEBMEB + EBMEBMEBMEBM + BMEBMEBMEBME) 1985 to 1987 vs. 1994 to 1996, *P* < 0.0143.

^b Female index equals number of soybean cyst nematode females developing on J82-21 expressed as percentage of number of females developing on Essex in a greenhouse bioassay. Means of three replicates.

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