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Field Interrelationships among *Heterodera glycines*, *Pratylenchus scribneri*, and Three Other Nematode Species Associated with Soybean[1]

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Abstract: Field experiments were conducted in 1982 and 1983 to assess interactions between *Heterodera glycines* and *Pratylenchus scribneri* on soybean in southern Illinois. Soybean cyst nematode susceptible cultivar Williams 79 and resistant cultivar Fayette were treated or not treated with aldicarb 15G. Initial population densities were 35 *H. glycines* cysts containing eggs, 100 *P. scribneri*, 30 *Helicotylenchus pseudorobustus*, 225 *Paratylenchus projectus*, and 85 *Tylenchorhynchus martini* per 250 cm^3 soil in 1982, whereas in 1983 populations were 11 *H. glycines* cysts, 330 *P. scribneri*, and 620 *H. pseudorobustus*. In both years *H. glycines* populations increased on nontreated Williams 79, decreased on both treated and nontreated Fayette, and remained at initial levels on treated Williams 79. Recovery of *P. scribneri* per gram dry root was different between nontreated cultivars in 1982 but not in 1983. Aldicarb treatment suppressed soil and root populations of *P. scribneri* on both cultivars in both years. Populations of *H. pseudorobustus*, *P. projectus*, and *T. martini* at harvest indicated little population increase on either nontreated cultivar. In 1982 *H. glycines* caused yield suppression but *P. scribneri* did not, as differences in yield occurred between cultivars but not between aldicarb treatments. In 1983, however, there were no yield differences between cultivars, but aldicarb application resulted in yield increase in both cultivars. In 1983 the yield increase resulting from *P. scribneri* control was approximately 25%. No synergistic effect on yield was observed between *H. glycines* and *P. scribneri*.

Key words: population dynamics, soybean cyst nematode, lesion nematode, *Helicotylenchus pseudorobustus*, *Tylenchorhynchus martini*, *Paratylenchus projectus*, *Glycine max*, crop loss.

Agricultural soils are typically inhabited with polyspecific communities of plant parasitic nematodes. In much of Illinois, *Pratylenchus scribneri* Steiner and *Heterodera glycines* Ichinohe frequently cohabit agricultural fields. Previous studies involving lesion nematodes showed that, in nematode–nematode interactions, nematode population dynamics and effects on hosts varied, depending on the species of nematode, initial densities, host plants, and environmental conditions (8,13,14,20). A study of concomitant populations of *Pratylenchus penetrans* Cobb and *Meloidogyne incognita* (Kofoid and White) Chitwood on tomato (*Lycopersicon esculentum* Mill.) indicated an antagonistic competition resulting in a depression of population densities of both nematodes (8). Penetration of *M. incognita* into alfalfa roots was suppressed when roots were inoculated simultaneously with *P. penetrans* and *M. incognita* (20). On tobacco, populations of *P. brachyurus* (Godfrey) Filipjev and Schuurmans Stekhoven increased on *M. incognita* resistant cultivars and were suppressed on susceptible ones when plants were also infected with *M. incognita* (13). Heavy infestations of *Heterodera tabacum* Lownsbery and Lownsbery suppressed *P. penetrans* populations on tobacco, whereas large numbers of *P. penetrans* suppressed *H. tabacum* population increase (14).

Pratylenchus scribneri was pathogenic on soybean (*Glycine max* (L.) Merr.) in the greenhouse (1), but this has not been reported in the field. *P. scribneri* is parthenogenetic with an optimum temperature range of 30–34 C for reproduction (2). In contrast, *H. glycines* is amphimictic, with a temperature range of 19–27 C (11), and cannot penetrate roots and mature if temperatures exceed 34 C (18). Although both nematodes are endoparasitic, *P. scribneri* feeds primarily in the root cortex causing only secondary injury to the endodermis (4), whereas *H. glycines* penetrates the developing vascular cylinder producing syncytia that may extend into the endodermis (7).

Although *P. scribneri* is widely distributed in Illinois and other midwestern states, its potential as a soybean pest is poorly

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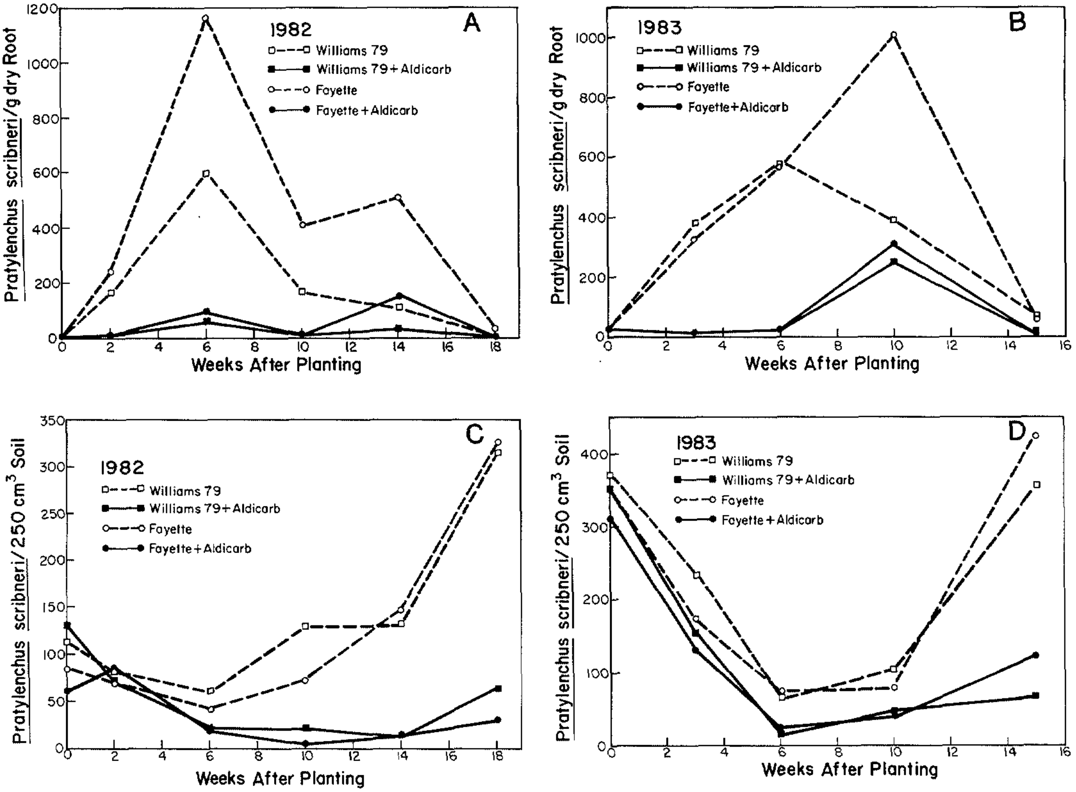

FIG. 1. Population dynamics of *Pratylenchus scribneri.* A, B) *Pratylenchus scribneri* in roots of *Heterodera glycines* susceptible Williams 79 or resistant Fayette soybeans treated with aldicarb or nontreated in 1982 and 1983. C, D) *Pratylenchus scribneri* in soil treated with aldicarb or nontreated and planted with *H. glycines* susceptible Williams 79 or resistant Fayette soybeans in 1982 and 1983.

understood. The objectives of this research were to determine 1) the dynamics of concomitant populations of *P. scribneri* and *H. glycines* on soybean under field conditions, 2) the potential for yield reduction by *P. scribneri* alone, and 3) any influence on yield resulting from interactions between these two and other concomitant nematodes.

MATERIALS AND METHODS

Experimental plots were established in 1982 at Vergennes and in 1983 at Bogota, Illinois. Both sites were infested with *P. scribneri* and *H. glycines* race 3. Other phytoparasitic nematode species present were *Helicotylenchus pseudorobustus* (Steiner) Golden, *Paratylenchus projectus* Jenkins, and *Tylenchorhynchus martini* Fielding at Vergennes and *H. pseudorobustus* at Bogota. Preceding crops were double-cropped winter wheat (*Triticum aestivum* L.) and sorghum (*Sorghum bicolor* L.) in 1982 and maize (*Zea mays* L.) in 1983. Soil types were a Wynoose silt loam (Typic Albaqualf; 14.1% sand, 74.1% silt, and 11.8% clay) at Vergennes and a Cisne silt loam (Typic Mollic Albaqualf; 7.9% sand, 76.1% silt, and 16.0% clay) at Bogota. Both soils contained approximately 2% organic matter.

The herbicides trifluralin and metribuzin were tank mixed and preplant incorporated according to recommended rates and standard cultural practices. Plots were cultivated and hand weeded as necessary. Semideterminate soybean cultivars Williams 79 (susceptible to *H. glycines*) and Fayette (resistant to *H. glycines* races 3 and 4) were planted in nontreated soil and soil treated with aldicarb 15G, thus establishing different levels of nematode primary inoculum. Both soybean cultivars are agronomically similar, differing mainly in their response to *H. glycines,* with only 2 days difference in maturity and 2 cm difference in height. Yield in absence of *H.*

TABLE 1. Analysis of variance for effect of aldicarb, cultivar (Williams 79 or Fayette), and sample date of *Pratylenchus scribneri* soil and root populations in 1982 and 1983.

	1982			1983		
		Mean squares			Mean squares	
Source of variation	df	g dry root	Soil	df	g dry root	Soil
Block	7	478,469.26	115,921.68*	7	167,761.80	77,001.40
Aldicarb (AL)	1	2,997,750.42*	359,623.91*	1	2,199,938.31*	373,987.25*
Error A	7	430,644.83	38,789.22	7	32,953.75	29,424.27
Cultivar (CU)	1	706,524.01*	12,829.84	1	377,291.78	447.23
AL × CU	1	439,014.38	74.38	1	300,640.92	81.94
Error B	14	101,726.99	4,467.13	14	351,331.25	13,570.93
Sample date (SD)	5	575,876.26*	85,902.28*	4	1,116,066.00*	497,692.03*
SD × AL	5	685,876.80*	89,499.43*	4	301,660.10*	99,372.08*
SD × CU	5	136,780.84	3,964.26	4	201,735.99	13,429.49
SD × AL × CU	5	81,889.39	2,692.18	4	146,596.16	1,050.48
Error C	140	152,360.56	6,394.21	112	102,847.09	19,621.32
CV (%)		250.7	91.2		168.9	80.1

* $P < 0.05$.

glycines is the same. Aldicarb was applied in a 15-cm band at 22 g a.i./100 m of row and incorporated 2–3 cm deep. Treatments were applied to four-row plots 5.6 m long with 76-cm row spacing in 1982 and 97-cm row spacing in 1983. Planting dates were 20 May 1982 and 14 June 1983. The experimental design was a split-plot with eight replications. Data were analyzed as a split-split-plot with aldicarb treatment as main plots, cultivars as subplots, and sampling dates as sub-subplots. Yield was determined by harvesting 4.7 m of each of the two center rows of the four-row plots.

Soil sampling dates were 0, 2, 6, 10, 14, and 18 (harvest) weeks after planting (WAP) in 1982, and 0, 3, 6, 10, and 15 (harvest) WAP in 1983. Using a 2-cm-d soil sampler, 15–20 cores were collected in a zig-zag pattern from the two center rows of each plot 3–7 cm from the base of plants and to a depth of 15 cm. Soil samples at 10 WAP in 1983 were taken with a trowel because of dry field conditions.

After kneading the samples to mix the soil, 250-cm^3 aliquants from 0, 2, or 3 WAP and harvest samples were processed to extract nematodes, whereas 500-cm^3 aliquants were processed from soil samples collected at other sampling dates. Water was added to each aliquant and the suspension agitated on a rotary shaker for 30 minutes. Nematodes were extracted by Cobb's gravity sieving technique (5) using 850-, 180-, and 38-μm-pore sieves. Cysts and white females were washed from the 180-μm-pore sieve. Vermiform nematodes collected on the 38-μm-pore sieve were separated from the residue using the rapid centrifugal-flotation technique (12). Populations of vermiform nematodes were estimated by counting two 1-ml aliquots.

Root samples at 2 or 3 WAP and at harvest were obtained from 10 plants uprooted at random from border rows. Debris from the previous crop, collected on the 850-μm-pore sieve, substituted for soybean roots at 0 WAP. Root samples for the other sampling dates were restricted to roots of less than 3 mm d and were collected from the 850-μm-pore sieve. All root samples were incubated in a mist chamber for 7 days at 22 C (17). Population estimates of *H. glycines* in soil at planting and harvest represented total cysts containing eggs, whereas those at the other sampling dates included only white and yellow females, and light brown cysts with attached egg masses. Populations determined in this manner provided for an estimate of females that matured since the previous sampling.

RESULTS

Differences ($P < 0.05$) in root and soil population densities of *P. scribneri* occurred between aldicarb-treated and nontreated plots in both 1982 and 1983 (Fig. 1, Table 1). Differences occurred in root population densities of *P. scribneri* between cultivars in 1982 but not in 1983. In 1982 numbers of *P. scribneri* recovered from

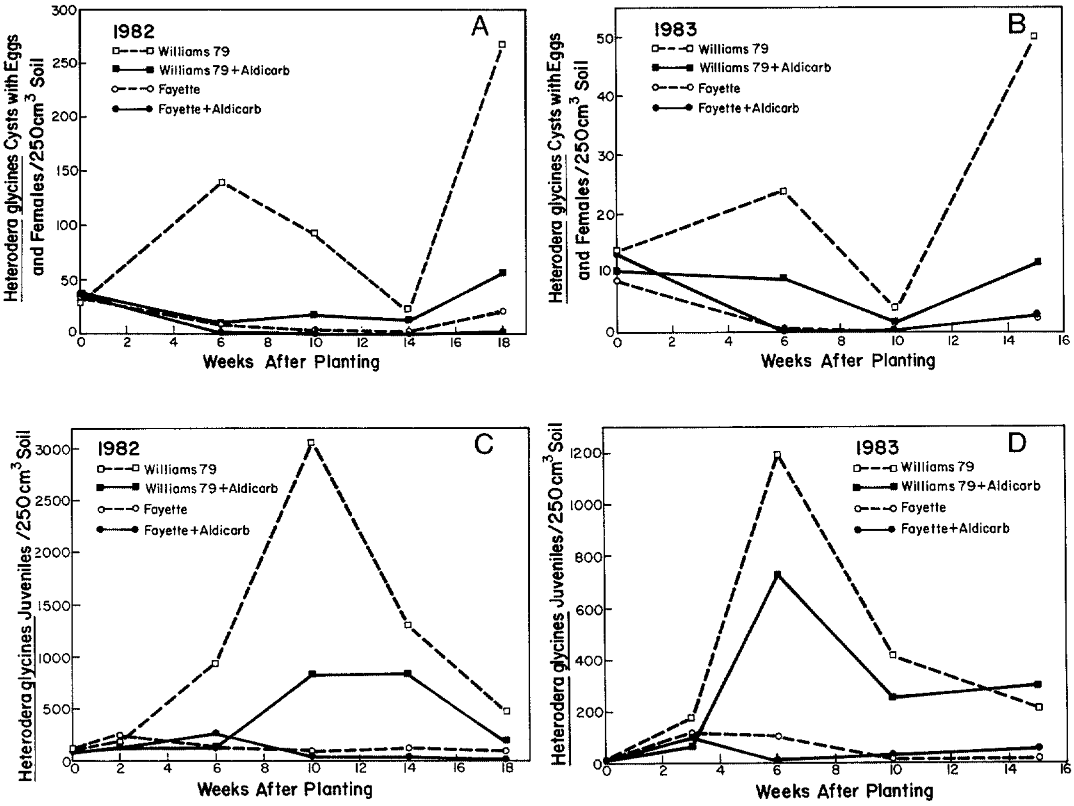

FIG. 2. Population dynamics of *Heterodera glycines*. A, B) *Heterodera glycines* egg containing cysts and females in soil treated with aldicarb or nontreated and planted with *H. glycines* susceptible Williams 79 and resistant soybeans in 1982 and 1983. Cyst and female counts at 0 weeks after planting and at harvest are the total number of cysts and females, whereas all other counts are of total females. C, D) *Heterodera glycines* juveniles in soil treated with aldicarb or nontreated and planted with *H. glycines* susceptible Williams 79 or resistant Fayette soybeans in 1982 and 1983.

roots peaked at 6 WAP then generally declined (Fig. 1A). In 1983 root population density peaks were at 6 WAP for nontreated Williams 79 and 10 WAP for Fayette nontreated, Fayette treated, and Williams 79 treated (Fig. 1B). Following the population peak in roots at 6 WAP during 1982, populations in the soil increased by 279% on nontreated Williams 79 and 392% on Fayette by harvest (Fig. 1C). A similar late-season population increase also occurred in 1983, but final population densities in soil were similar to those at planting (Fig. 1D). Final soil populations in 1982 had decreased slightly from at-planting levels for Williams 79 and Fayette growing in aldicarb-treated soil, but were 530% lower for Williams 79 and 250% lower for Fayette growing in treated soil in 1983. Soil nematode population differences between cultivars did not occur in either year (Table 1). In both years there was an effect ($P < 0.05$) of sample date and a sample date × aldicarb interaction for both soil nematode populations and nematode populations per gram of dry roots.

At both locations, soil population densities of *H. glycines* cysts containing eggs increased on Williams 79, decreased on Fayette, and remained near at-planting levels on both cultivars grown in soil treated with aldicarb (Fig. 2A, B). Brown cyst population densities in soil were different ($P < 0.05$) between cultivars and in the aldicarb treatment in 1982 when initial cyst levels averaged 35/250 cm^3 soil (Table 2). Additionally, in 1982 there were effects ($P < 0.05$) of sample date, aldicarb × cultivar, and sample date × aldicarb × cultivar interactions. In 1983 the only significant effects were the sample date × aldicarb and sample date × cultivar inter-

TABLE 2. Analysis of variance for effects of aldicarb, cultivar (Williams 79 or Fayette), and sample date upon *Heterodera glycines* mature cysts in 1982 and 1983.

		Mean squares	
Source of variation	df	1982	1983
Block	7	3,461.07	3,443.78
Aldicarb (AL)	1	47,524.00*	1,378.27
Error A	7	3,576.10	1,392.91
Cultivar (CU)	1	88,060.56*	3,291.89
AL × CU	1	34,503.06*	2,127.52
Error B	14	26,102.88	1,178.09
Sample date (SD)	1	43,576.56*	478.52
SD × AL	1	58,685.06*	1,530.77*
SD × CU	1	94,556.25*	2,848.89*
SD × AL × CU	1	40,200.25*	937.89
Error C	28	2,102.25	356.34
CV (%)		75.6	132.0

* $P < 0.05$.

actions. Female population densities in soil peaked at 6 WAP in both years. Female population densities in 1982 were affected by the same parameters that affected brown cyst population densities (Table 3). In 1983, however, there were no significant differences in the effects of aldicarb, cultivar, sample date, or interactions on female population densities. Population densities of *H. glycines* second-stage juveniles (J2) in soil followed similar trends in both years, but populations peaked 4 weeks later and reached higher levels in 1982 than in 1983 (Fig. 2C, D). J2 populations associated with Williams 79 growing in soil treated with aldicarb more closely followed populations on Williams 79 growing in nontreated soil in 1983 than in 1982 (Table 4). Effects on J2 populations in 1982 were significant ($P < 0.05$) for aldicarb, cultivar, aldicarb × cultivar interaction, sample date, sample date × aldicarb, sample date × cultivar, and sample date × aldicarb × cultivar interactions (Table 4). Only sample date caused an effect ($P < 0.05$) in 1983.

Initial *H. pseudorobustus* population densities of 30 and 620/250 cm^3 soil in 1982 and 1983, respectively, were maintained at harvest on both nontreated cultivars but decreased when aldicarb was applied to the soil (Fig. 3). In 1982 soil population densities in all four treatments declined at 6 WAP but recovered in nontreated soil. A similar population decline did not occur in 1983. Population densities differed significantly ($P < 0.05$) between treated and nontreated plots at 18 WAP (harvest) in 1982 and at 6, 10, and 15 WAP (harvest) in 1983 (Table 5). In addition to the aldicarb effect on population densities in 1983, there were significant ($P < 0.05$) effects of sample date and the sample date × aldicarb interaction.

Other phytoparasitic nematode species present in the 1982 plot were *P. projectus* (primarily fourth-stage juveniles) and *T. martini*, averaging 255 and 85/250 cm^3 soil, respectively. *Paratylenchus projectus* population densities declined in soil treated and not treated with aldicarb during most of the growing season but recovered to at-planting levels between 14 and 18 WAP (Fig. 4). Analysis of individual sample dates

TABLE 3. Analysis of variance for effects of aldicarb, cultivar (Williams 79 or Fayette), and sample date upon *Heterodera glycines* females in 1982 and 1983.

	1982		1983	
Source of variation	df	Mean squares	df	Mean squares
Block	7	660.36	7	2,658.59
Aldicarb (AL)	1	34,827.21*	1	217.56
Error A	7	589.52	7	992.08
Cultivar (CU)	1	52,196.69*	1	763.14
AL × CU	1	28,479.82*	1	798.06
Error B	14	473.81	14	731.30
Sample date (SD)	2	8,101.46*	1	15.01
SD × AL	2	8,398.15*	1	22.56
SD × CU	2	6,327.40*	1	23.76
SD × AL × CU	2	6,785.11*	1	0.25
Error C	56	679.98	28	11.89
CV (%)		100.9		35.7

* $P < 0.05$.

TABLE 4. Analysis of variance for effects of aldicarb, cultivar (Williams 79 or Fayette), and sample date upon *Heterodera glycines* second-stage juveniles in soil during 1982 and 1983.

	1982		1983	
Source of variation	df	Mean squares	df	Mean squares
Block	7	371,363.27	7	1,983,300.70
Aldicarb (AL)	1	5,505,534.67*	1	206,317.31
Error A	7	219,179.36	7	930,597.61
Cultivar (CU)	1	15,602,895.95*	1	3,251,137.85
AL × CU	1	4,466,572.61*	1	143,310.83
Error B	14	197,437.96	14	853,225.86
Sample date (SD)	5	3,800,989.80*	4	1,137,708.50*
SD × AL	5	1,371,586.80*	4	131,413.53
SD × CU	5	4,422,526.60*	4	1,088,162.10
SD × AL × CU	5	1,437,344.4*	4	54,753.08
Error C	140	275,659.24	112	462,589.63
CV (%)		130.2		352.8

* $P < 0.05$.

showed significant ($P < 0.05$) differences between treated and nontreated populations at 2 and 6 WAP. *Tylenchorhynchus martini* populations decreased during the growing season, but nontreated populations recovered to at-planting levels between 14 and 18 WAP (Fig. 5). Significant differences in *T. martini* population densities occurred between aldicarb-treated and nontreated populations ($P < 0.05$; $P < 0.06$) at 14 and 18 WAP.

Yield differences in 1982 were significant ($P < 0.05$) between *H. glycines* resistant and susceptible cultivars but not between aldicarb-treated and nontreated plots (Table 6). Mean yields of Fayette (treated and nontreated) in 1982 were 30% greater than Williams 79 (treated and nontreated). Yields in 1983 differed significantly ($P < 0.05$) between aldicarb treatments but not between cultivars. A 20% yield suppression occurred with nontreated Fayette and 25% for nontreated Williams 79 compared with these cultivars grown in soil treated with aldicarb.

DISCUSSION

During both 1982 and 1983 soil population densities of *P. scribneri* decreased simultaneously with increases of root population densities, and a gradual migration from roots into soil followed as the growing season progressed. Under greenhouse conditions, *P. scribneri* populations were concentrated in the top 10–15 cm of the soybean root system and decreased with depth of tap root and distance of lateral roots from the tap root (1). When rainfall was near normal (32.1 cm) and daily mean temperature 1.6 C below normal during the 1982 growing season, nematode pop-

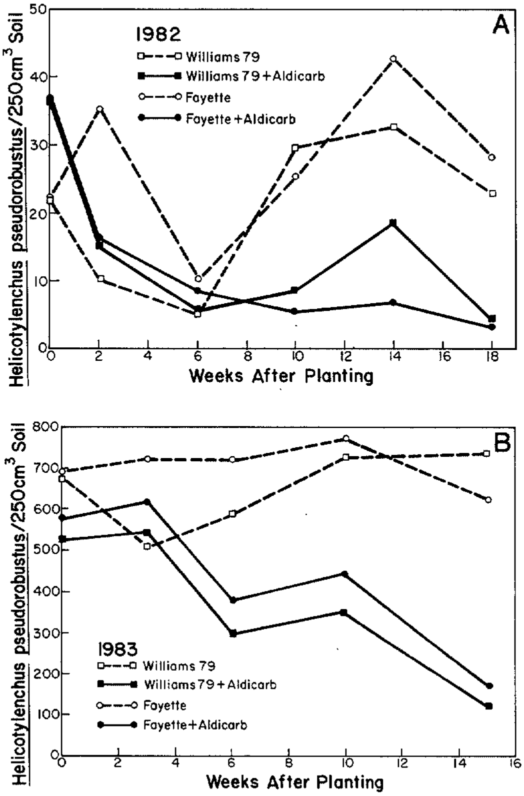

FIG. 3. Population dynamics of *Helicotylenchus pseudorobustus* in soil treated with aldicarb or nontreated and planted with *Heterodera glycines* susceptible Williams 79 and resistant Fayette soybeans in 1982 and 1983.

TABLE 5. Analysis of variance for effects of aldicarb, cultivar (Williams 79 or Fayette), and sample date upon *Helicotylenchus pseudorobustus* in 1982 and 1983.

Source of variation	1982		1983	
	df	Mean squares	df	Mean squares
Block	7	7,937.20	7	96,671.80
Aldicarb (AL)	1	4,880.33	1	3,007,974.03*
Error A	7	2,586.26	7	32,953.75
Cultivar (CU)	1	285.19	1	377,291.78
AL × CU	1	888.38	1	300,640.92
Error B	14	519.62	14	100,380.36
Sample date (SD)	5	1,983.79*	4	1,116,066.10*
SD × AL	5	1,910.72	4	301,660.10*
SD × CU	5	265.16	4	201,735.99
SD × AL × CU	5	257.11	4	146,596.16
Error C	140	851.84	112	102,847.08
CV (%)		154.5		168.9

* $P < 0.05$.

ulation increases to the 15-cm depth were observed on both nontreated Williams 79 and Fayette. Under the drier and hotter conditions (16.0 cm rainfall and daily mean temperatures 1.0 C above normal) of 1983, no increase in nematode populations occurred to a depth of 15 cm. Irrigation has been shown to affect soybean root dry matter (15). Soybean root dry matter from nonirrigated plots at depths greater than 45 cm exceeded that from irrigated plants in July, August, and September (15). The 0–15-cm layer contained 67% of irrigated soybean root dry matter, compared with 51% in the nonirrigated soil. It is likely that the nematodes migrated with the expanding root system below the 15-cm depth sampled in this study. Deeper migration would also explain greater *P. scribneri* root population maxima in 1982 than in 1983, when warmer temperatures should have enhanced *P. scribneri* reproduction.

In both years of this field study, recovery of *P. scribneri* from roots was greater for *H. glycines* resistant Fayette than for *H. glycines* susceptible Williams 79. At high initial cyst levels, numbers of *P. scribneri* recovered from soybean roots peaked at 6 WAP and were not cultivar dependent. When cyst populations were low, the *P. scribneri* population peak was delayed until 10 WAP on Fayette only, indicating that *H. glycines* suppressed *P. scribneri* reproduction. This depressive effect may have resulted from a reduction in number of feeding sites available to *P. scribneri.* A similar host–nematode response between root-knot nematodes and *P. brachyurus* in cotton

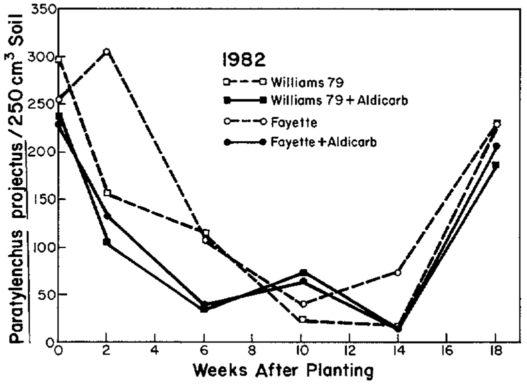

FIG. 4. Population dynamics of *Paratylenchus projectus* in soil treated with aldicarb or nontreated and planted with *Heterodera glycines* susceptible Williams 79 and resistant Fayette soybeans in 1982.

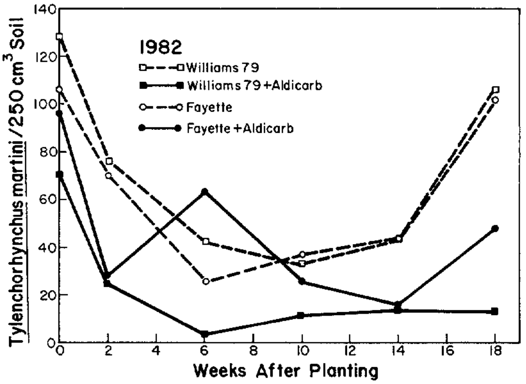

FIG. 5. Population dynamics of *Tylenchorhynchus martini* in soil treated with aldicarb or nontreated and planted with *Heterodera glycines* susceptible Williams 79 and resistant Fayette soybeans in 1982.

TABLE 6. Yield of *Heterodera glycines* susceptible Williams 79 and resistant Fayette treated (+) with aldicarb 15G at 22 g a.i./100 m of row or nontreated (−) in 1982 and 1983.

Treatment	Yield (kg/ha)	
	1982	1983
Williams 79 (−)	1,238	1,174
Williams 79 (+)	1,307	1,467*
Fayette (−)	1,690*	1,177
Fayette (+)	1,625*	1,415*
CV (%)	6.3	8.3

* Significant difference at $P < 0.05$ using orthogonal comparisons: 1982 = Williams 79 vs. Fayette; 1983 = aldicarb vs. no aldicarb.

was reported (10); populations of *P. brachyurus* were enhanced in concomitant situations on a host relatively resistant to the *Meloidogyne* species. Our findings suggest this type of competitive antagonism between *H. glycines* and *P. scribneri.*

Significant differences in *H. glycines* populations between cultivars in 1982 but not in 1983 indicated some reduction in *H. glycines* reproduction in 1983. This reduction possibly resulted from the higher *P. scribneri* populations suppressing *H. glycines* reproduction; however, the shorter growing season and more stressful environmental conditions of 1983 probably were more important factors in suppressing *H. glycines* population increase.

Differences in yield between *H. glycines* resistant and susceptible cultivars in 1982 indicated that *H. glycines* suppressed yield at initial levels of 35 cysts containing eggs/250 cm^3 soil. Lack of a yield response from aldicarb application suggests that *P. scribneri, H. pseudorobustus, P. projectus,* and *T. martini* were not pathogenic under those field conditions. This suggestion is supported by earlier studies, in which soybeans appeared tolerant of *T. martini* feeding (6) and *P. projectus* preferred lighter textured, dry soils for population increases (9). In contrast, yield differences occurred between aldicarb-treated and nontreated plots but not between cultivars in 1983 when *H. glycines* populations were lower (11 egg-containing cysts/250 cm^3 soil) and *P. scribneri* populations higher (330/250 cm^3 soil) than in 1982, suggesting that *P. scribneri* caused yield loss during dry, hot field conditions. Significant yield interactions did not occur between treatments in either 1982 or 1983, indicating no synergism due to concomitant feeding of *P. scribneri* and *H. glycines* on soybean. At planting, *H. pseudorobustus* field population densities of 1,289/250 cm^3 soil did not suppress yield (Noel, unpubl.). Other evidence indicates that *H. pseudorobustus* is not pathogenic to soybean (16). Thus it is unlikely that *H. pseudorobustus* interacted with *P. scribneri* to suppress yield.

Fayette, developed from a Williams × PI 88788 cross, is a maturity group III soybean with resistance to *H. glycines* races 3 and 4. PI 88788 was reported as an intermediate host for *P. scribneri* (3). Since maize (19) and Fayette are good hosts for *P. scribneri* and *P. scribneri* was associated with yield loss in Fayette, planting of this cultivar for *H. glycines* control could result in damaging *P. scribneri* population levels on both maize and soybean grown in rotation.

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