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Overwinter Population Dynamics of *Heterodera glycines*[1]

R. D. Riggs,[2] T. L. Niblack,[4] R. A. Kinloch,[5] A. E. MacGuidwin,[6] A. Mauromoustakos,[3] and L. Rakes[2]

Abstract: The purpose of this research was to compare the overwinter survival of populations of *Heterodera glycines* at different latitudes in the United States and the effect of changing latitudes before and after the initiation of dormancy. Soil samples infested with *H. glycines* were collected in August or October in 1992 to 1994 from soybean fields in two to four states (combinations of Arkansas, Florida, Minnesota, Missouri, and Wisconsin). The samples were mixed thoroughly, divided into subsamples, shipped to an overwinter location, and buried until time for processing. To determine survival, cysts, eggs, and second-stage juveniles were extracted from replicated subsamples and counted each month from December to May. Survival generally was between 50% and 100%, and often was best in the state of origin. In Florida, survival was at the 50 to 100% level in soil from most locations, and in Wisconsin was near 100%. Survival of *H. glycines* in Arkansas and Missouri varied more than at the other locations. In a separate test, survival in microplots in Arkansas, in a more natural environment than that of buried samples, was 70 to 94% for field isolates from Arkansas, Minnesota, and Missouri and 100% for isolates of races 1, 3, and 14 that had been maintained in a greenhouse for several years. Survival appears to be better than previous tests had indicated. High survival rates require cultivars with high levels of resistance and long-term rotations for management.

Key words: Heterodera glycines, nematode, overwintering, soybean cyst nematode, survival.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, is one of the most destructive pests of soybean, *Glycine max* (L.) Merr., worldwide (Noel, 1992; Wrather, 1998). This nematode can reproduce quickly and abundantly (Francl and Dropkin, 1986), and its eggs are capable of dormancy and delayed egg-hatch for short (overwintering) or long (absence of host) periods of time (Ross, 1963). Dormancy is characteristic of several species of cyst-forming nematodes (Evans, 1987). In some species, only one generation is produced in a year and the eggs are dormant until they undergo a period of undetermined low temperatures (Evans, 1987). In other species, such as *H. glycines*, several generations may be produced in a growing season and dormancy initiation is not well understood (Hill and Schmitt, 1989; Yen et al., 1995).

Research has suggested that survival of *H. glycines* in the southern states is poor (Slack et al., 1981), but in northern areas, where soil may stay frozen all winter, survival may be close to 100% (Niblack, unpubl.). Southern and northern populations of *H. glycines* differ in overwinter survival rates, but the reasons have not been delineated. The objectives of this research were to verify differences in overwinter survival between northern (colder) and southern (warmer) populations of soybean cyst nematode and to determine whether survival rate can be influenced by changing the overwintering latitude.

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[2] Department of Plant Pathology, and [3] Agricultural Statistics Laboratory, University of Arkansas, Fayetteville, AR 72701.

[4] Department of Plant Pathology, University of Missouri, Columbia, MO 65211.

[5] West Florida Research and Education Center, University of Florida, Rt. 3, Jay, FL 32565.

[6] Department of Plant Pathology, University of Wisconsin, Madison, WI 53706.

E-mail: rdriggs@comp.uark.edu

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Materials and Methods

Soil collection and storage: In 1992, *H. glycines*-infested soil was collected only in October for study. In 1993 and 1994, soil was collected in late August and in October. Arkansas and Missouri participated all 3 years, Florida in 1993 and 1994, Wisconsin in 1994, and some samples from Minnesota were included in 1992 and 1993. The soil characteristics of the Arkansas soil were: organic matter (OM) = 2.0%, sand = 2.5%, silt = 83.9%, and clay = 13.6%; of the Florida soil were: sand = 84.0%, silt = 9.0%, and clay = 7.0%; of the Missouri soil were: OM = 1.2%, sand = 18.0%, silt = 52.0%, and clay = 30.0%; and was not available for the Minnesota and Wisconsin soil.

All soil samples from a location were mixed thoroughly to ensure uniform distribution of the cysts. The mixed soil was separated into sufficient 250-cm^3 subsamples to provide 60 samples for each storage location. Each sample was placed in a plastic bag. At each storage location, all samples were buried 30 to 40 cm deep in a field. The storage locations were at 35° 23″ North Latitude, 94° 14″ West Longitude in Arkansas; 30° 46″ North Latitude, 87° 09″ West Longitude in Florida; and 40° 01″ North Latitude, 92° 11″ West Longitude in Missouri. The mean high and low temperatures were highest in Florida and lowest in Missouri, as would be expected (Table 1). Geographical coordinates and temperatures were not available for the other locations.

Sample processing: Soil samples were retrieved at monthly intervals from December to May for nematode extraction. Of 10 samples retrieved each month, five were processed by sieving and centrifugal flotation for the extraction and enumeration of cysts, eggs, and second-stage juveniles (J2), and five were used for bioassay on seedlings of susceptible soybean cultivars. In Arkansas, bioassay subsamples were placed in 7.5-cm-diam. clay pots and planted with soybean cv. Lee 74 and maintained on a greenhouse bench at 82 °C for 28 to 35 days. In Missouri, subsamples were placed in 2.5-cm-diam. × 20-cm-deep polyvinylchloride tubes, planted

TABLE 1. Mean high and low temperatures for Arkansas, Florida, and Missouri storage locations for December through May 1992–93, 1993–94, and 1994–95 near the locations[a] for the overwinter storage of the soil samples containing cysts of *Heterodera glycines*.

Year and location	December		January		February		March		April		May	
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
1992–93												
Arkansas	8.1	0.1	7.1	−1.6	8.3	−1.7	13.5	2.8	18.2	7.0	23.9	13.7
Missouri	3.4	−4.0	0.1	−7.2	0.1	−8.3	6.9	−1.8	14.9	5.9	22.2	12.2
1993–94												
Arkansas	11.5	0.5	6.5	−2.1	11.8	−0.1	19.1	4.2	23.8	9.4	25.4	14.3
Florida	15.9	3.3	14.3	1.8	20.1	6.4	22.6	9.2	26.1	12.8	29.1	16.5
Missouri	3.8	−4.2	−3.1	−11.4	2.6	−8.6	12.2	−0.3	17.7	4.7	24.1	10.6
1994–95												
Arkansas	11.2	2.6	10.1	−0.4	14.1	1.0	18.3	6.1	22.3	8.8	24.9	16.1
Florida	18.2	6.4	16.3	4.5	18.8	5.4	21.9	11.0	25.1	12.7	30.5	18.7
Missouri	6.4	−2.7	−0.4	−8.5	4.6	−5.9	12.5	0.1	15.7	3.8	19.8	10.4

[a] Information not available for Minnesota and Wisconsin.

with soybean cv. Essex, and the tubes embedded in sand in a plastic bucket that was maintained in a water bath at 28 °C for 30 days. At all locations, roots and soil were processed for the extraction of cysts and females (hereafter collectively referred to as cysts). For graphic presentation, the nematode count for the samples processed in December was used as the basis for comparison of subsequent counts within each group of samples.

Microplot test: In a separate test, *H. glycines* isolates that had been collected in 1992 from soybean fields in Arkansas, Minnesota, and Missouri were used to infest field microplots in Arkansas during May 1993. Microplots were made from 17.5 × 40 × 75-cm-deep clay fluetiles. In addition, isolates of *H. glycines* races 1, 3, and 14 that had been maintained in a greenhouse for several years were placed in similar microplots at the same time. Approximately 250 cysts were placed in each microplot. Each *H. glycines* isolate was replicated five times, and six seeds of Lee 74 were planted in each microplot. The tops were removed when the plants matured in October. The soil was left undisturbed except for monthly sampling, which coincided with the time the buried samples of the primary study were retrieved. Samples were processed, bioassayed, and analyzed as described for the buried samples.

Data and analyses: Data were recorded as numbers of cysts, eggs + J2, and number of cysts from bioassay plants. Survival indices were calculated, based on the numbers of eggs + J2 and numbers of eggs/cyst and bioassay units (numbers of bioassay cysts as a percentage of the total eggs + J2), as the number of a unit for May divided by the number of the same unit in December and expressed as a percentage. Means for each set of indices were compared by ANOVA, and means of paired sets, such as August and October samples, were compared using *t* tests by SAS (SAS Institute, Cary, NC) methods. Graphical presentations of survival differences were prepared with JMP software (SAS Institute, Cary, NC). Screening models with main effects and two-factor interactions accounted for approximately 70% of the variability of all three indices.

RESULTS

General pattern of survival: In general, survival of the Florida nematodes follows a similar pattern in the August and October samples, with survival in the October samples being slightly higher than in the August samples (Fig. 1A). Departures from this pattern were in the August sample in 1993 stored in Florida and the October sample in 1993 stored in Arkansas when the survival was much higher than in the matching sample. Survival of Missouri nematodes followed a similar pattern for 1993 and 1994 in three locations except that survival in the October 1993 sample in Arkansas was higher than in the comparable samples in Florida and Missouri (Fig. 1A). Survival of Wisconsin nematodes was similar in all three locations but was higher in Wisconsin than in Arkansas or Florida. Survival of Arkansas and Minnesota nematodes followed no regular pattern.

Survival of SCN in 1992 was variable among locations, but the survival trend was similar whether based on eggs + J2 or on eggs/cyst except in Minnesota samples (Fig. 1B). The range was from about 11% to 89% survival. Nematodes in the 1993 samples appeared to have similar patterns in the August and October samples, but those taken in October had survival generally ≥70% and survival in the August samples was somewhat lower (Fig. 1B). In 1994, survival in the August samples was higher, with most having a survival rate >70% whereas several October samples had survival rates of <70% (Fig. 1B). A more precise survival comparison is presented in the next section.

Survival in buried soil using different indices: Survival of *H. glycines* during the winter of 1992–93 was lowest (40.6%) when bioassay was used to determine survival and highest (90.6%) when the eggs/cyst was used (Table 2). In the winter of 1993–94, survival was highest when the eggs + J2 was used, whether samples were collected in August or October, and lowest when the bioassay and eggs/cyst were used to determine survival in samples collected in August and October, respectively. In samples collected in August 1994, survival was

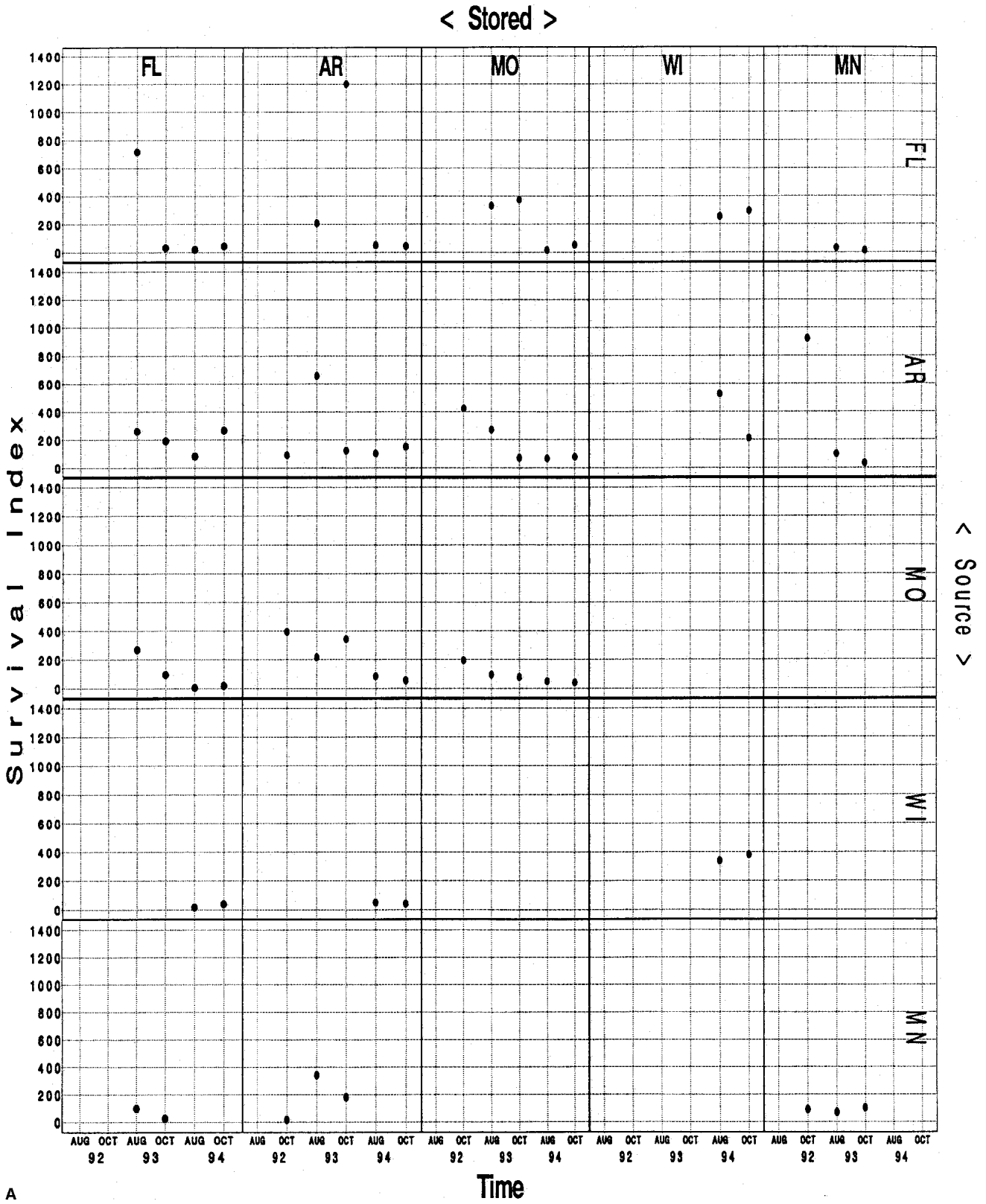

FIG. 1. Survival indices for *Heterodera glycines* from Arkansas (AR), Florida (FL), Minnesota (MN), Missouri (MO), and Wisconsin (WI) when stored at the source location or one of the other locations in 1992, 1993, or 1994; A) when soil was collected in August or October, and B) when survival is based on eggs + J2 compared to survival based on eggs/cyst. (These figures show the general trends of survival. For a more detailed record, see Tables 1–3.)

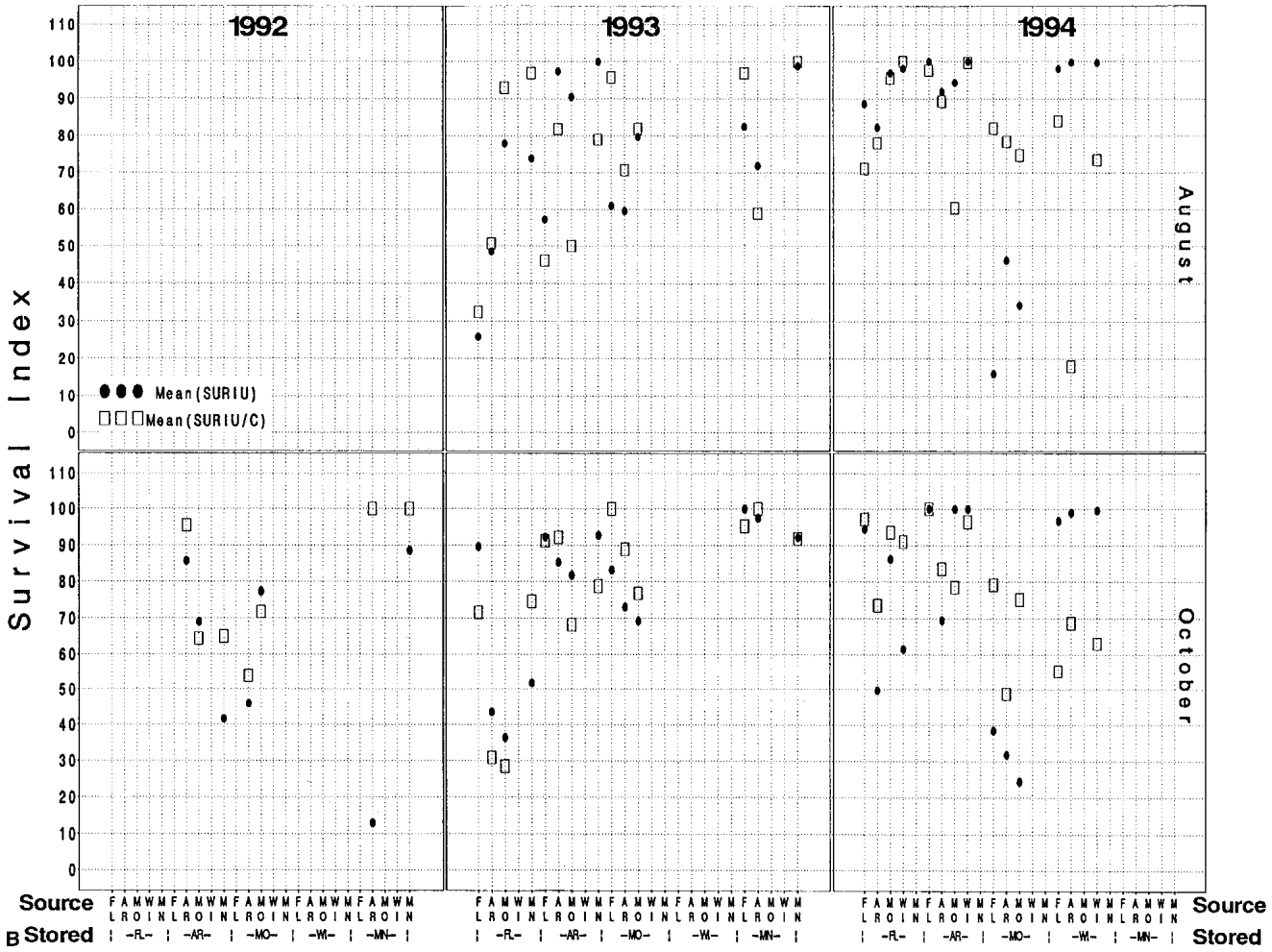

FIG. 1. Continued.

highest when the eggs + J2 was used and lowest when the bioassay was used to calculate survival; but in samples collected in October, the highest survival was obtained when the bioassay was used and lowest when the eggs/cyst was used. Over all years, survival was better in samples collected in October (102.4%) than in those collected in August (87.4%), and survival based on eggs + J2 (123.6%) was better than eggs/cyst (90.2%) or bioassay (75.4%) for determining survival.

Survival and latitude: To better examine the effects of latitude on survival, a table was constructed to show the latitude that was best for survival for all combinations of sample collection dates, year, and storage location (Table 3). Based on the combinations when eggs + J2 were used to determine survival, the Arkansas latitude was best for survival of *H. glycines* in samples from Arkansas and Florida and was equal to Florida for survival in samples from Missouri and Wisconsin (Table 3). Using the same survival criteria, survival was least at the Missouri latitude for *H. glycines* from Arkansas, Florida, and Missouri and was least in Florida and Wisconsin for *H. glycines* from Wisconsin. If eggs/cyst was the criterion for survival of *H. glycines*, the Missouri latitude was best for *H. glycines* from Florida, the Florida latitude was best for *H. glycines* from Arkansas, the Arkansas latitude was best for *H. glycines* from Wisconsin, and the Arkansas and Florida latitudes were best for *H. glycines* from Missouri (Table 3). The worst survival latitude, when eggs/cyst was the criterion, was the Florida latitude for Florida *H. glycines*, the Missouri latitude for Arkansas *H. glycines*, the Florida and Missouri latitudes for Missouri *H. glycines*, and the Wisconsin latitude for the Wisconsin *H. glycines*. Using the indication above that eggs + J2 is the best criterion for determining survival, the latitude of Arkansas was best for survival of the largest number of combinations followed by Florida, Missouri, and Wisconsin. The lowest survival for all combinations was the latitude of Missouri followed by Florida, Arkansas, and Wisconsin.

Microplot tests: The numbers of eggs + J2 were lower in May than in December in populations from Arkansas, Minnesota, and Missouri following one season in microplots in Arkansas (Table 4). The same was true for numbers of eggs/cyst except for the Missouri population. Survival was not different among the populations even though some differences were observed (Table 4). Among the races 1, 3, and 14 populations, May eggs + J2 levels were lower than the December levels in races 1

and 14 and eggs/cyst levels were lower in May in the race 3 population (Table 4). Survival was similar in all three race populations based on both eggs + J2 and on eggs/cyst.

When all six populations were considered together, survival was similar even though numbers of eggs + J2 and eggs/cyst showed significant differences (Table 4). When all of the field populations were compared to all of the greenhouse populations, no difference in survival was found. Survival during the winter of 1998–99, based on eggs + J2 only, was similar to that in 1992–93 (data not presented). Survival of the Arkansas population was somewhat lower than in 1992–93, and survival of the other two field populations was somewhat higher than in 1992–93. Similarly, survival of the race 1 population was lower in 1998–99 than in 1992–93, but survival of the other two race populations was as good or better than in 1992–93.

The number of J2 in each microplot sample was a very small percentage of the total eggs + J2 population level in both December and May ranging from 0.02% to 0.49% of the population in December (data not shown). In May the J2 population level ranged from 0.01% to 0.25%. For comparison, the highest J2 numbers were found in January, when the percentage ranged from 0.05% to 1.89% of the total eggs + J2 population.

Effect of various factors on survival: An analysis of variance that accounted for main effects and two-factor interaction for the effects of the source of samples, storage location of samples, month counts were made, year test was run, and time of year sample was taken on survival revealed few significant differences. When results were analyzed for the Arkansas, Florida, and Missouri samples run in 1993 and 1994, source had a significant effect on survival of eggs + J2 and cysts, but survival did not follow the expected pattern of a decline in population during the period measured. Storage location also had a significant effect on survival of eggs + J2 and cysts, but it was confounded by an interaction with the month counts were made and an interaction with time sample was collected (in the case of cysts). The only other factor that had a significant effect on the survival of eggs + J2 was the year tests were run, and no single factor had a significant effect on survival index. When the ANOVA was run on the data from each year, source of sample had a significant effect only in 1994. Storage location had a significant effect in all 3 years, but the effect was confounded by another factor each year. The only other factor that had a significant effect on survival was month counts were made, but again the effect was confounded by another factor.

Discussion

Results of these overwintering studies help clarify the survival of *H. glycines* in the different latitudes of the United States. Survival sometimes was best when the samples were stored in the state of origin, but exceptions were common. In addition, survival rate appears to have changed compared to earlier observations (Bonner and Schmitt, 1985; Riggs, 1982; Ross, 1963; Slack et al., 1981). Ross (1963) reported a survival rate of 67% in North Carolina early in his work with *H. glycines*, whereas in later studies the survival rate was estimated at 27% (Bonner and Schmitt, 1985). In earlier Arkansas studies over a period of 8 years the survival rate was about 50% based on cyst and juvenile counts (Slack et al., 1981), but in later rotation studies the survival rate was 57% following a susceptible soybean cultivar in rotation, 60% after the same cultivar not rotated, 66% after a moderately resistant cultivar in rotation, 99% after a resistant cultivar not rotated, 126% after the same cultivar in rotation, and 173% after a non-host crop, based on egg counts (Riggs, unpubl.). How can survival be more than 100%? If the base for comparison had been the month of collection, some females may not have been mature and continued to produce eggs after removal of the host. Miller (pers. comm.) found that females could be mated on agar and would produce eggs without feeding on a host. However, the base for comparison was December, 2 to 4 months after the host had been removed. The likelihood of egg production at that time is very low. The only conclusions are that: (i) not all of the eggs were counted in the December extraction or (ii) the samples were extremely variable. The survival rate on a susceptible cultivar in Arkansas did not change much even though the nematode stage counted was J2 in one case and eggs + J2 in another (Riggs, unpubl.).

Survival of *H. glycines* in Florida soybean fields appeared to be <10%, hardly maintaining the infestation from one year to the next (Kinloch, unpubl.). However, in the present study, survival of populations, taken from Florida soybean fields and stored in plastic bags buried in soil, ranged from an average of 40% when stored in Missouri to 82% in Arkansas. This survival may indicate that the factors responsible for the natural decline of the population in Florida (e.g., natural fungal parasites) are not active inside the plastic bags even though the soil was untreated in any way. However, the soil was mixed thoroughly, placed in a plastic bag, and placed at a colder temperature; except for populations stored in Florida, survival ranged from 25% to 95% in Florida soil based on eggs + J2 counts and was up to 97% based on eggs/cyst. Survival could not have been much better at other locations. In contrast, survival of eggs + J2 and eggs/cyst was 100% and 95%, respectively, for Wisconsin nematodes stored in Florida.

In Missouri, survival rates at or near 100% had been reported (Niblack, unpubl.). In the present study, survival of Missouri nematodes ranged from 62% to 79% in Missouri and from 32% to 99% in Florida. In Missouri, differing survival rates have been observed in southeastern and northern Missouri (Niblack and Donald, unpubl.). The apparent increase in survival rate

TABLE 2. Numbers of *Heterodera glycines* (December counts/May counts) obtained by extraction or bioassay[a] for soil collected in Arkansas, Florida, Missouri, or Wisconsin.[b]

Survival parameter	Year	Sample origin	FL	AR	MO	WI	Mean	Survival (%) FL	AR	MO	WI	Mean
					Soil collected in late August							
	1993	AR	77/35	829/585	1,101/642	—	669/421	45.5	70.6	58.3	—	62.9
		FL	131/33	1,036/445	2,320/1,178	—	1,162/552	25.2	43.0	50.8	—	47.5
		MN	136/104	6,262/6,262	—	—	3,199/3,183	76.5	100.0	—	—	99.5
		MO	650/488	11,606/11,606	11,304/8,885	—	7,853/6,993	75.0	100.0	78.6	—	89.0
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	249/165	4,933/4,725	4,908/3,568	—	3,363/2,819	66.3	95.8	72.7	—	83.8
	1994	AR	261/197	1,930/1,730	820/380	668/666	920/743	75.5	89.6	46.3	99.7	80.8
		FL	2,160/1,838	17,160/17,160	882/128	8,565/8,420	7,192/6,887	85.1	100.0	14.5	98.3	95.8
		MO	590/584	5,861/5,410	1,632/501	—	2,694/2,165	99.0	92.3	30.7	—	80.4
		WI	1,924/1,884	27,504/27,504	—	8,924/8,900	12,784/12,763	97.9	100.0	—	99.7	99.8
		Mean	1,234/1,126	13,113/12,957	1,111/336	6,052/5,995	5,378/5,102	91.2	98.8	30.2	99.1	94.9
Eggs/cyst	1993	AR	21/12	44/38	11/8	—	25/19	57.1	86.4	72.7	—	76.0
		FL	114/33	16/49	61/58	—	104/47	28.9	36.0	95.1	—	45.2
		MN	49/15	194/148	—	—	122/82	30.6	76.3	—	—	67.2
		MO	36/34	119/54	24/20	—	60/36	94.4	45.4	83.3	—	60.0
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	55/24	123/72	32/29	—	70/42	43.6	58.5	90.6	—	60.0
	1994	AR	52/31	28/21	7/5	114/20	50/19	59.6	75.0	71.4	17.5	38.0
		FL	92/62	104/103	69/55	135/110	100/83	67.4	99.0	79.7	81.5	83.0
		MO	57/55	59/35	10/8	—	42/33	96.5	44.3	80.0	—	78.6
		WI	107/107	102/102	—	149/107	119/105	100.0	100.0	—	71.8	88.2
		Mean	77/64	73/65	30/24	133/79	78/58	83.1	89.0	80.0	59.3	74.4
Bioassay units	1993	AR	3.6/9.6	1.7/7.9	31.5/61.6	—	12.3/26.4	266.7	464.7	195.2	—	214.6
		FL	0.8/5.4	72.6/112.5	11.1/35.4	—	28.2/51.1	675.0	155.0	318.9	—	181.2
		MN	—	1.0/2.4	—	—	1.0/2.4	—	240.0	—	—	240.0
		MO	0.2/0.4	1.0/2.4	38.4/37.1	—	14.9/15.7	200.0	155.7	96.7	—	105.4
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	1.5/5.1	20.4/33.1	27.0/44.7	—	16.3/27.6	340.0	162.3	165.6	—	169.3
	1994	AR	6.4/3.4	2.4/2.3	24.5/15.8	11.6/49.6	11.2/17.8	53.1	95.8	64.5	427.6	158.9
		FL	0.9/0.1	0.3/0.1	12.0/1.5	0.9/1.4	3.5/0.8	11.1	33.3	12.5	155.6	22.9
		MO	3.4/0.2	0.9/0.7	57.3/31.3	—	20.5/10.7	5.9	77.8	54.6	—	52.2
		WI	4.3/0.3	0.2/0.1	—	1.6/3.5	2.0/1.3	7.0	50.0	—	218.8	65.0
		Mean	3.8/1.0	1.0/0.8	31.3/16.2	4.7/18.2	10.2/9.1	26.3	80.0	51.8	387.2	193.6
					Soil Collected in October							
Eggs +J2	1992	AR	—	30,956/26,514	38,022/16,301	—	34,489/21,408	—	857.0	42.9	—	62.1
		MO	—	21,744/13,938	12,037/9,029	—	16,891/11,484	—	64.1	75.0	—	68.3
		MN	—	35,232/13,232	—	—	35,232/13,232	—	37.6	—	—	37.6
		Mean	—	29,311/17,895	25,030/12,665	—	27,170/15,280	—	61.1	50.6	—	56.2
	1993	AR	1,352/548	32,623/27,346	21,746/15,666	—	18,574/14,520	40.5	83.8	72.0	—	78.2
		FL	76/62	4,750/4,054	2,887/2,398	—	2,571/2,171	81.5	85.3	83.1	—	84.4
		MN	494/104	7,507/6,629	—	—	4,001/3,367	21.1	88.3	—	—	84.2
		MO	2,750/888	20,136/18,751	12,756/7,854	—	11,881/9,164	32.3	93.1	61.6	—	77.1
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	1,168/401	16,254/14,195	12,463/8,573	—	9,962/7,723	34.3	87.3	68.8	—	77.5
	1994	AR	266/101	3,026/3,042	451/72	913/907	1,164/1,031	38.0	67.5	16.0	99.3	88.6
		FL	2,560/2,218	17,280/17,280	1,538/546	10,227/9,893	7,901/7,484	86.6	100.0	35.5	96.7	94.7
		MO	654/594	2,695/2,695	2,293/584	—	1,881/1,291	90.8	100.0	25.5	—	68.6
		WI	3,814/2,112	10,836/10,836	—	5,437/5,413	6,696/6,120	55.4	100.0	—	99.6	91.4
		Mean	1,824/1,005	8,459/6,571	1,427/401	5,526/5,404	4,309/3,345	55.1	77.6	28.1	97.8	77.6
Eggs/cyst	1992	AR	—	128/122	75/39	—	102/81	—	95.3	52.0	—	79.4
		MO	—	167/108	56/38	—	112/73	—	64.7	67.9	—	65.2
		MN	—	157/98	239/239	—	198/169	—	62.4	100.0	—	85.4
		Mean	—	150/109	123/105	—	137/107	—	72.7	85.4	—	78.1
	1993	AR	103/26	84/78	29/25	—	72/43	25.2	92.9	86.2	—	59.7
		FL	43/29	67/60	37/37	—	49/42	67.4	89.6	100.0	—	85.7
		MN	74/14	150/108	—	—	112/61	18.9	72.0	—	—	54.5
		MO	152/29	171/114	30/22	—	118/55	19.1	66.7	73.3	—	46.6
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	93/25	118/90	32/28	—	81/48	26.9	76.3	87.5	—	59.3
	1994	AR	47/38	43/35	8/3	31/20	32/24	80.9	81.4	37.5	64.5	75.0

TABLE 2. *Continued*

Survival parameter	Year	Sample origin	FL	AR	MO	WI	Mean	Survival (%) FL	AR	MO	WI	Mean
		FL	78/77	97/97	71/57	146/80	98/78	98.7	100.0	80.3	54.8	79.6
		MO	42/39	41/31	10/7	—	31/26	92.9	76.4	70.0	—	83.8
		WI	84/78	145/140	—	175/113	135/110	92.9	96.6	—	64.6	81.5
		Mean	63/58	82/76	30/24	117/73	64/63	92.4	92.7	80.0	62.4	98.4
Bioassay units	1992	AR	0.9/0.4	2.0/2.0	—	—	1.5/1.2	44.4	100.0	—	—	80.0
		MO	5.0/4.9	4.7/3.5	—	—	4.9/4.2	98.0	74.4	—	—	85.7
		MN	5.1/0.9	10.6/10.6	—	—	7.9/5.8	17.6	100.0	—	—	73.4
		Mean	3.7/2.1	5.8/5.3	—	—	4.8/3.7	58.6	91.6	—	—	79.7
	1993	AR	2.3/4.0	1.3/1.4	3.7/1.8	—	2.4/2.4	173.9	107.7	48.6	—	100.0
		FL	4.9/1.3	1.2/8.5	6.3/13.0	—	4.1/7.6	26.5	708.3	206.3	—	185.4
		MN	—	1.1/1.7	—	—	1.1/1.7	—	154.5	—	—	154.5
		MO	1.2/1.1	2.4/8.2	22.5/18.5	—	8.7/9.3	91.7	341.7	82.2	—	106.9
		WI	—	—	—	—	—	—	—	—	—	—
		Mean	2.8/2.1	1.5/5.0	10.8/11.1	—	5.0/6.1	75.0	333.3	102.8	—	122.0
	1994	AR	1.0/2.2	1.5/2.2	23.8/8.1	10.1/15.3	9.1/7.0	220.0	146.7	34.0	151.5	76.9
		FL	0.7/0.04	0.3/0.1	8.0/4.2	0.7/2.3	2.4/1.7	5.7	33.3	52.2	328.5	70.8
		MO	5.8/0.7	2.9/1.1	91.6/35.3	—	33.4/12.4	12.1	37.9	38.5	—	37.1
		WI	1.0/0.4	0.5/0.2	—	1.9/7.2	1.1/2.6	40.0	40.0	—	378.9	236.4
		Mean	2.1/0.8	1.3/0.9	41.1/15.9	4.2/8.3	11.6/5.9	38.1	69.2	38.8	197.6	50.8

Data are means of five replications.
[a] Bioassay data are the numbers of females on bioassay plants as percentages of the total eggs + J2.
[b] Samples were subdivided into 250-cm^3 subsamples, placed in plastic bags, and buried at the origin or shipped to other states for burial from October to May at 35° 23″ N Latitude 90° 14″ W Longitude in Arkansas (AR), 30° 46″ N Latitude 87° 09″ West Longitude in Florida (FL), 40° 01″ N Latitude 92° 11″ W Longitude in Missouri (MO), and in Wisconsin[c] (WI).
[c] Geographic coordinates not available.

may be related to changes in extraction techniques or changes in the stage used to determine survival. In early research, population levels of *H. glycines* were based on numbers of cysts or J2 (Ross, 1963; Slack et al., 1981). In more recent years and in the present study, population levels were based on egg or egg and J2 numbers. Instead of sieving and Baermann funnel extractions, sieving and centrifugal-flotation techniques were used. The Baermann funnel method was not an efficient extraction method, and egg counts were seldom made in early studies. However the thorough mixing of soil, before transporting and burial prior to overwintering, could have altered edaphic factors that influenced the nematode. These could include physical interference of biotic factors (e.g., destruction of mycelial networks) detrimental to the nematode. In addition, increased soil aeration from soil mixing may have promoted nematode survival.

Microplot tests: Survival of the Arkansas population in the microplots was only slightly higher than had been observed when the population was taken from the field based on eggs + J2. Survival of the Missouri population was about 14% higher in the microplot study than had been observed when the field population was stored in Arkansas and about the same as when it was stored in Missouri the previous year.

TABLE 3. Latitudes with the best and poorest survival by populations of *Heterodera glycines* from Arkansas (AR), Florida (FL), Missouri (MO), and Wisconsin (WI)

Survival parameter	Year	Sample collection time[a]	Latitude: Best survival (°N) FL	AR	MO	WI	Worst survival (°N) FL	AR	MO	WI
Eggs + J2	1992	Late	—	35[b]	40	—	—	40	35	—
	1993	Early	40	35	35	—	30	30	40	—
		Late	30	35	35	—	40	30	30	—
	1994	Early	35	30	30	30	40	40	40	43
		Late	35	43	30	35	40	40	40	30
Eggs per cyst	1992	Late	—	35	35	—	—	40	40	—
	1993	Early	40	30	35	—	30	40	30	—
		Late	40	35	40	—	30	30	30	—
	1994	Early	40	30	30	35	30	40	35	43
		Late	35	30	30	35	43	40	40	43

[a] Early samples were collected in late August or early September; late samples were collected in October.
[b] Soil was collected in each state, subdivided into 250-cm^3 subsamples, placed in plastic bags, and either kept or shipped to each of the other states for burial to check overwinter survival at 35°23″ (AR), 30° 46″ (FL), 40° 01″ (MO), and unknown (near 43°) N latitude (WI). To save space, only the degrees N Latitude are given in the table.

TABLE 4. Comparisons of December and May population levels of six populations of *Heterodera glycines* in microplots.

Population[a]	No. cysts Dec./May	No. egg + J2 Dec./May	Eggs/cyst Dec./May	Survival %			
				Cysts	Eggs + J2	Eggs/cysts	Mean
AR	634/556	51,796/47,050	82/85	87.7	90.8	103.6	94.0
MN	721/484	53,041/39,676	74/82	67.1	74.8	110.8	84.2
MO	578/442	40,417/31,450	70/71	76.5	77.8	101.4	85.2
Mean	678/494	48,418/39,392	71/80	72.9	81.4	112.7	89.0
Race 1	244/191	33,652/23,615	138/124	78.3	70.2	89.9	79.5
Race 3	247/230	25,205/18,422	102/80	93.1	73.1	78.4	81.5
Race 14	174/148	19,854/19,851	114/134	85.1	100.0	117.5	100.9
Mean	222/190	26,237/20,629	118/109	85.6	78.6	110.2	91.5
Overall mean	—	—	—	81.3	81.1	100.3	104.5

Data are means of 5 replications.
[a] AR = Arkansas, MN = Minnesota, MO = Missouri.

Survival of the three races of *H. glycines* taken from the greenhouse was better than expected due to the length of time they had been cultured in the greenhouse. However, these populations might have had fewer natural enemies because they had been grown in pasteurized soil in the greenhouse and were placed in pasteurized soil in the microplots. The average survival of the three race populations was very similar to that of the three field populations, whether based on eggs + J2 or eggs/cyst.

The low level of J2 in all extractions indicated that dormancy may not have broken even in the May samples. However, the general increase in females produced on bioassay plants in the stored sample tests indicates that dormancy had been broken in those samples in May.

If survival rates have increased, more effective management strategies will be necessary to get the level of control that would result in the desired yield levels. At the lower survival rate, cultivars with a moderate level of resistance reduced the nematode population densities below damage thresholds, or those with good tolerance were able to tolerate the lower population densities and produce satisfactory yields. However, at the higher survival rates, cultivars with high levels of resistance or very high tolerance and longer-term rotations will be needed to maintain or increase the high yield levels expected and needed.

These studies have not resulted in definitive proof that changing the latitude of overwintering of cysts of soybean cyst nematodes can influence the dormancy of the eggs inside the cysts. Changing locations resulted in changes in the survival rate in some cases, but latitude was not necessarily a factor. Dormancy in soybean cyst nematodes may be related to factors other than temperature or temperature may be only one of many factors that affect dormancy. Gintis et al. (1983) demonstrated that many fungi infest the cysts of soybean cyst nematodes and some may parasitize the eggs if the temperature is favorable. Parasitism would reduce the number of eggs that hatched and would affect the number surviving the winter, although it would not be related to dormancy. The differences in environment inside the plastic bag, even though the bags allowed some air exchange, may have affected the eggs or the biota surrounding the eggs to change the dormancy of the eggs. If the soil biota are responsible for the low survival rate of *H. glycines* in southern areas, especially Florida, the use of a plastic bag or thorough soil mixing may inhibit the growth of the biota and its activity or may provide a micro-environment in which the biota is inhibited.

LITERATURE CITED

Bonner, M. J., and D. P. Schmitt. 1985. Population dynamics of *Heterodera glycines* life stages on soybean. Journal of Nematology 17: 153–157.

Evans, A. A. F. 1987. Diapause in nematodes as a survival strategy. Pp. 180–187 *in* J. A. Veech and D. W. Dickson, eds. Vistas on nematology. Hyattsville, MD: Society of Nematologists.

Francl, L. J., and V. H. Dropkin. 1986. *Heterodera glycines* population dynamics and relation of initial population to soybean yield. Plant Disease 70:791–795.

Gintis, B. O., G. Morgan-Jones, and R. Rodríguez-Kábana. 1983. Fungi associated with several developmental stages of *Heterodera glycines* from an Alabama soybean field. Nematropica 13:181–200.

Hill, N. S., and D. P. Schmitt. 1989. Influence of temperature and soybean phenology on dormancy induction in *Heterodera glycines*. Journal of Nematology 21:361–369.

Morgan-Jones, G., B. O. Gintis, and R. Rodríguez-Kábana. 1981. Fungal colonization of *Heterodera glycines* cysts in Arkansas, Florida, Mississippi, and Missouri soils. Nematropica 11:155–163.

Noel, G. R. 1992. History, distribution, and economics. Pp. 1–14 *in* R. D. Riggs and J. A. Wrather, eds. Biology and management of soybean cyst nematode. St. Paul, MN: APS Press.

Riggs, R. D. 1982. Cyst nematodes in the southern USA. Pp. 77–95 *in* R. D. Riggs, ed. Nematology in the southern region of the United States. Southern Cooperative Series Bulletin 276:1–206.

Ross, J. P. 1963. Seasonal variation of larval emergence from cysts of the soybean cyst nematode, *Heterodera glycines*. Phytopathology 53: 608–609.

Slack, D. A., R. D. Riggs, and M. L. Hamblen. 1981. Nematode control in soybeans: Rotation and population dynamics of soybean cyst and other nematodes. Arkansas Agricultural Experiment Station Report Series 263.

Wrather, J. A. 1998. Yield-robbing soybean diseases. Proceedings of the Midwest Soybean Research Conference, 1998. Davenport, IA.

Yen, J. H., T. L., Niblack, and W. J. Wiebold. 1995. Dormancy of *Heterodera glycines* in Missouri. Journal of Nematology 27:153–163.