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Dormancy of *Heterodera glycines* in Missouri[1]

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Abstract: A 2-year study was conducted in field microplots to determine the relative importance of soybean phenology and soil temperature on induction of dormancy in *Heterodera glycines* in Missouri. Four near-isogenic soybean lines differing for maturity date were planted in microplots infested with a race 5 isolate of *H. glycines*. Soil temperature was monitored at a depth of 15 cm. Eggs of *H. glycines*, extracted from cysts collected monthly from each microplot, were used in hatching tests and bioassays to determine dormancy. Egg hatching and second-stage juvenile (J2) infectivity rates decreased sharply from their highest levels in midsummer (July–August) to a low level by October of each year and remained low (< 10% hatching and < 0.2 J2/cm root) until May or June of the following year. The patterns of numbers of females and eggs in the bioassays were similar. The decreases were not related to soil temperature and did not differ consistently among soybean isolines. The monophasic changes in all nematode responses with peak midsummer rates suggest that *H. glycines* produces one primary generation per year in central Missouri. Changes in hatching rates and the timing of minimum and maximum rates suggested that *H. glycines* eggs exhibit more than one type of dormancy.

Key words: diapause, dormancy, *Glycine max*, hatching, infectivity, *Heterodera glycines*, nematode, soybean cyst nematode, survival, viability.

Yield suppression due to the soybean cyst nematode, *Heterodera glycines* Ichinohe, is dependent on the nematode's initial population density (Pi), which is in turn dependent on crop history and the nematode's overwinter survival rate (8,21,26). Determination of this rate is important in the development of population models for the practical application of predicting Pi from data collected in the fall in order to give soybean producers adequate time to make cultivar or nonhost crop choices. In addition, the ability to survive adverse environmental conditions (e.g., overwinter) is as important as host relations in determining the nematode's distribution and adaptation to new environments.

To survive in the absence of a host, many plant-pathogenic nematodes exhibit seasonal metabolic depression or arrested development (2). Such dormancy may be referred to as quiescence or diapause, and either type may be facultative or obligate, depending primarily on the cause of dormancy. Recent reviews presented detailed explanations of the differences among categories as they apply to nematodes (2,7, 19). The categories are not mutually exclusive; different types of dormancy may be exhibited within species (2), or even within populations, as shown for *H. schachtii* (27).

Dormancy of *H. glycines* eggs in North Carolina was induced by "conditions prevailing at the end of a growing season" (9) and characterized by low hatching rates, even when temperatures were suitable for hatching (20). Slack et al. (24) observed low hatching rates of eggs collected from field populations in Arkansas beginning in September. Hill and Schmitt (9) observed that a decrease in soil temperature to below 22 C in North Carolina was critical to dormancy induction, but postulated a cumulative conditioning effect due to gradually decreasing temperatures. In contrast, we have observed the decreased hatching indicative of *H. glycines* dormancy beginning in midsummer in Iowa and north Missouri (Niblack and Yen, unpubl.). Whereas populations of *H. glycines* had overwinter survival rates of 30–100% in North Carolina (9), the rates were 60–100% in central Missouri (Niblack, unpubl.), and overwintering populations had "little mortality" in Illinois (G. R. Noel, cited in 21). Thus, it appeared that conditions resulting in dormancy induction of *H. glycines* populations

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adapted to more northerly environments might differ from those of southern populations.

Although temperature is a primary factor in *H. glycines* dormancy, host phenology also may play a role (9). Our observation that dormancy may be induced before the occurrence of "dormancy-inducing temperatures" suggested that perhaps host phenology had a larger role in dormancy induction than had been shown. Our objectives were to determine the relative importance of host phenology and soil temperature on induction of dormancy in *H. glycines* in central Missouri.

Materials and Methods

Experiments were conducted in field microplots at the University of Missouri Agronomy Research Farm near Columbia, Missouri, from June 1991 to February 1993. The microplots were 1 m^2 with fiberglass barriers at the perimeter extending 0.53 m below and 0.15 m above the soil surface. In May 1989, the microplots were infested with a race 5 isolate of *H. glycines* and planted to either 'Williams 82' or 'Fayette' soybean. Both cultivars are susceptible to race 5, but Fayette is a less suitable host than Williams 82. Initial population (Pi) densities in May 1991 were either 149 ± 39 eggs/100 cm^3 soil ("low" Pi, planted with Fayette in 1989–90) or 12,147 ± 810 eggs/100 cm^3 soil (high Pi, planted with Williams 82 in 1989–90). In May 1992, the low Pi microplots had 5,315 ± 520 eggs/100 cm^3 soil, and the high Pi had 22,353 ± 4,035 eggs/100 cm^3 soil. Microplots designated low and high Pi were the same ones in 1992 as in 1991; treatment in 1991 had no effect on final population densities within Pi classes.

Seeds of near-isogenic soybean lines ("isolines") differing for date of maturity were provided by Dr. R. S. Nelson (USDA Soybean Germplasm Collection, Urbana, IL). Microplots were planted to the cultivar Clark (Maturity Group III) or one of three isolines differing from Clark for maturity: e_2, 10 days earlier than Clark; E_1e_3, 10 days later; and E_1, 20 days later. Clark is susceptible to all races of *H. glycines*. Forty-five seeds were planted in a row through the center of each microplot and thinned to 24 seedlings 5 days after emergence. The same isoline was planted between microplots to extend the microplot row beyond the fiberglass boundary, and rows of the same isoline were planted 0.76 m on either side of the microplot row, to provide canopy conditions within the microplot that were similar to those within a field.

The treatment design was a 4 (soybean isolines) × 2 (Pi class) factorial replicated four times in complete blocks. Isolines were assigned randomly within Pi classes. The planting dates were 3 June 1991 and 15 May 1992, and harvest dates were 20 October 1991 and 26 October 1992. Growth-stage data were collected for a concurrent study in the same microplots of soybean growth and yield components (Wilcox, Wiebold, and Niblack, unpubl.) to verify the differences in isoline maturity dates. Soil temperature was monitored with a thermocouple and recorded with a datalogger (LI-COR Inc., Lincoln, NE); the sensors were placed 15 cm deep in the soil.

Soil samples were collected at monthly intervals, except for October 1991, from each microplot. Six 2.5-cm-d × 20-cm deep cores were taken from within 20 cm of the row. Each sample was mixed thoroughly, and cysts were extracted from a 100-cm^3 subsample (measured by water displacement) with a semi-automatic soil elutriator (5). Eggs were freed from the cysts by a mechanical method (16) and collected on a 25-μm-pore sieve. For comparison with eggs from the microplots, and as a control for the effects of laboratory and greenhouse conditions during the hatching tests and bioassays described below, each test included eggs from a race 5 greenhouse-grown isolate that did not exhibit seasonal dormancy, hereafter referred to as the check isolate. The check isolate, originally a composite of several field populations, was maintained on 'Essex' soybean for 14 years. Eggs from the

check isolate were extracted at the same time and in the same manner as eggs from the microplots.

Hatching was determined for approximately 1,000 eggs from each treatment (the actual number of eggs was recorded for each observation). Eggs were placed on sterilized 25-μm-pore microsieves immersed in glass-distilled water in petri dishes and held at 27 C in covered, sterilized chambers. At 14 days, the number of emerged second-stage juveniles (J2) was counted and recorded as a percentage of the original number of eggs placed on the microsieve.

Infectivity and the numbers of females and eggs produced by the nematodes were determined in greenhouse bioassays on Williams 82 soybean. Infectivity studies were conducted from November 1991 through February 1993. Studies to determine the number of females and eggs produced were conducted from July 1991 through February 1993. For each bioassay, Williams 82 seeds were rolled in moist, sterilized germination paper and maintained for 3 days at 28 C. Seedlings were transplanted singly into 3-cm-d × 15 cm polyvinylchloride tubes containing 100 cm^3 sterilized field sand (74% sand, 16% silt, 10% clay) infested with ca. 1,000 eggs freshly collected from the microplots, and maintained in a 28 C water bath in the greenhouse under 16-hour illumination at an average 0.71 microeinsteins/m^2/sec.

To determine the nematodes' infectivity, plants were removed 5 days after soil infestation, and the J2 within roots were stained with acid fuchsin (6) and counted at ×60 magnification. Root length was determined by a modified line intersect method (25); infectivity was recorded as the number of J2 per cm root.

Plants were grown for 30 days to allow females to develop and produce eggs. Females were removed from the roots with a high-pressure water spray, counted, and the eggs extracted as described for microplot soil samples. Roots were dried for 1 week at 60 C and weighed. Female and egg data were recorded as numbers per gram dry root and eggs per cyst, respectively.

Response data were subjected to analysis with PC/SAS (SAS Institute, SAS Circle, Cary, NC) procedures: general linear models (GLM) for analysis of variance and CORR for product-moment correlations. Protected least significant differences were calculated for means of treatments having significant ($P < 0.05$) effects.

Results

Hatching of eggs collected from Clark soybean and the three isolines followed a similar pattern throughout the experiment (Fig. 1). The only deviations were: i) hatching of eggs from the low Pi treatments was greater ($P < 0.05$) than that from the high Pi treatments in July 1991; and ii) hatching of eggs differed ($P < 0.05$) in some months among soybean isolines, but the differences were not consistent across months. No significant Pi × isoline interaction was detected. The check isolate of *H. glycines* varied between 32 and 50% hatching during the entire experiment and did not follow a seasonal pattern.

In both years, the mean daily temperature at 15 cm deep in the soil was between 20 and 25 C from July to October. This period was followed with decreasing temperatures to 0 C from October to February, and then increasing temperatures through June (Fig. 2). There was no correlation between hatching rate and temperature for time periods during which hatching was increasing or decreasing.

Infectivity of J2 from eggs collected from the microplots followed the same pattern as hatching (Fig. 3). More variation occurred with the low Pi treatment than with the high Pi treatment. Differences in infectivity due to isoline or isoline × Pi interaction were not significant. Infectivity in the check treatment tended to be low from December 1991 through March 1992; however, infectivity during the same period in 1992–93 was consistent with values obtained in June through September 1992.

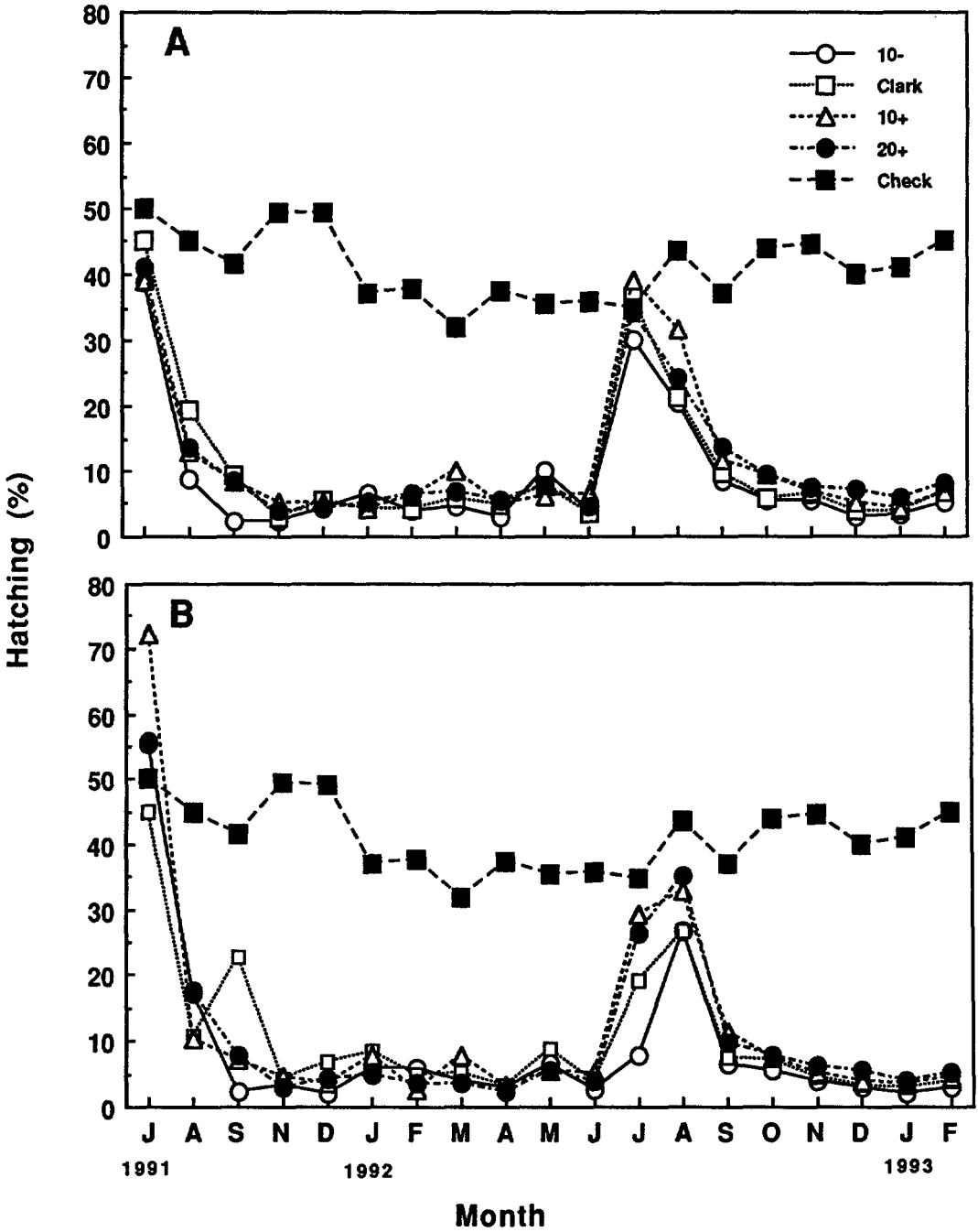

FIG. 1. Percentages of second-stage *Heterodera glycines* juveniles that emerged from eggs extracted from cysts that developed on near-isogenic soybean lines in field microplots. The soybean isolines differed only for date of maturity: Clark; 10− = 10 days earlier than Clark; 10+ = 10 days later; and 20+ = 20 days later. Check refers to an isolate of *H. glycines* produced on Essex soybean in the greenhouse. Data are means of four replications. A) "High" initial population of *H. glycines*. B) "Low" initial population of *H. glycines*.

The number of females per g dry root produced on the bioassay plant, Williams 82, was not affected by treatments of soybean isolines, Pi class, or isoline × Pi interaction, but results were somewhat more variable for *H. glycines* originating from the low Pi treatment than from the high Pi treatment (Fig. 4). The number of *H. gly-*

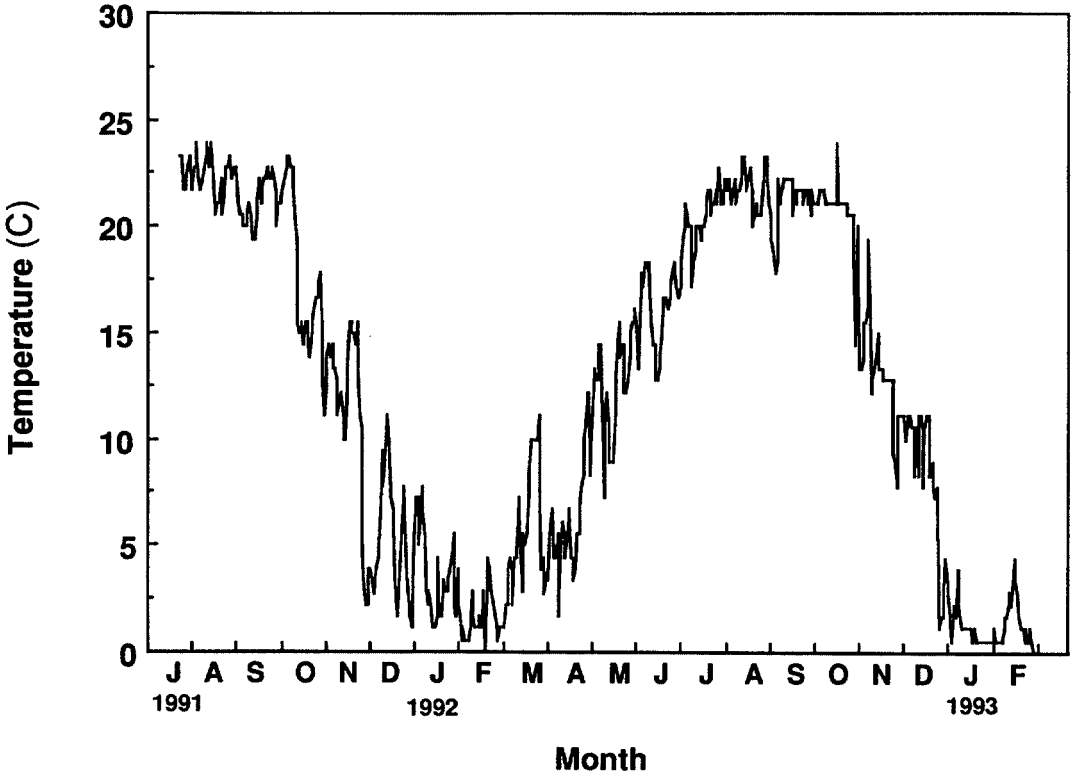

FIG. 2. Mean daily soil temperatures, measured 15 cm deep, in field microplots at the University of Missouri Agronomy Research Farm in central Missouri.

cines eggs per g dry root followed the same pattern as numbers of females (data not shown).

In contrast to the results for female development and reproduction expressed as a function of root weight, the number of eggs per cyst produced in the microplots frequently exceeded ($P < 0.05$) those produced by the check isolate from June through October (Fig. 5). Egg production per cyst was higher ($P < 0.05$) for the low Pi treatment than for the high Pi treatment. No consistent differences due to isoline or isoline × Pi interaction were detected.

DISCUSSION

To the question of whether the induction of dormancy in *H. glycines* in central Missouri is more dependent on soil temperature or host phenology, we have no simple answer. According to our results, and those of others (9,15,20,24), dormancy of *H. glycines* is complex and may not be explained by a single external "cause." In addition, several types of dormancy may be expressed within cyst nematode populations, as has been described for *H. schachtii* (27) and *G. rostochiensis* (10,11).

Measuring dormancy is the first consideration in evaluating it. Dormancy in *H. glycines* eggs is a requirement for overwinter survival because the J2, like those of *G. rostochiensis* (19) and *H. zeae* (14), do not survive freezing without the protection provided by the eggshell and perivitelline fluid (Niblack, unpubl.). Generally, the hatching rate of cyst nematode eggs is used to assess dormancy (19) due to the absence of other reliable indicators. For example, hatching of *G. rostochiensis* was central to Hominick's (11) study of the interaction between photoperiod and nematode diapause, and Zheng and Ferris' (27) study using hatching of *H. schachtii* to differentiate types of dormancy exhibited by eggs. Because a nematode's ability to hatch does

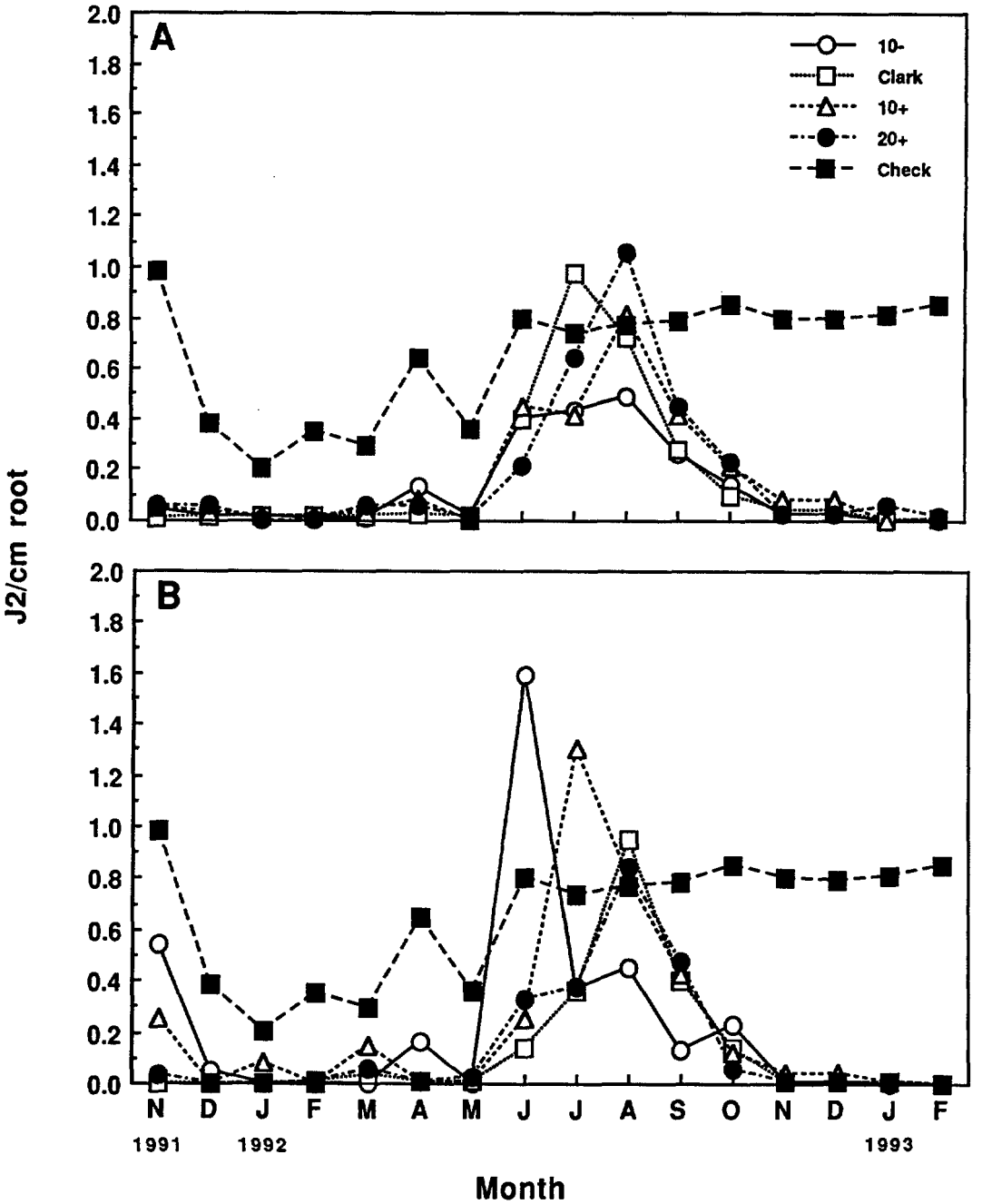

FIG. 3. Number of *Heterodera glycines* second-stage juveniles (J2) per cm root of Williams 82 soybean seedlings at 14 days after soil infestation with 1,000 eggs collected from near-isogenic soybean lines in field microplots. The soybean isolines differed only for date of maturity: Clark; 10− = 10 days earlier than Clark; 10+ = 10 days later; and 20+ = 20 days later. Check refers to an isolate of *H. glycines* produced on Essex soybean in the greenhouse. Data are means of four replications. A) "High" initial population of *H. glycines*. B) "Low" initial population of *H. glycines*.

not necessarily imply viability, infectivity can also be used as a dormancy indicator; infectivity may also help to define the type of dormancy involved. Egg hatching and J2 infectivity were used to study survival of *H. zeae* (14) and the effects of temperature on diapause of *Meloidogyne naasi* (3). In our experiments, dormancy of *H. glycines* was

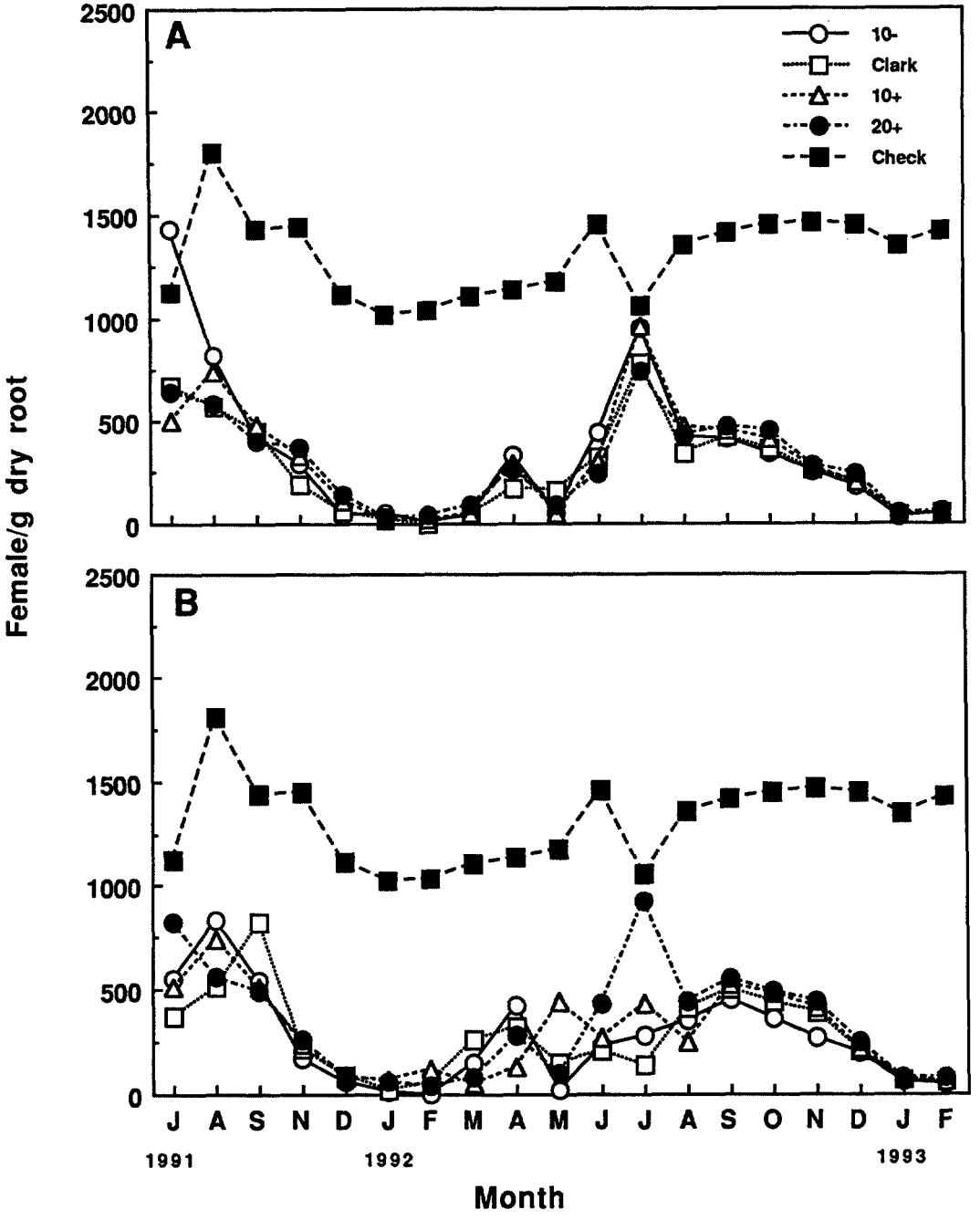

FIG. 4. Number of *Heterodera glycines* females on Williams 82 soybean, 30 days after soil infestation with 1,000 eggs produced on near-isogenic soybean lines in field microplots. The soybean isolines differed only for date of maturity: Clark; 10− = 10 days earlier than Clark; 10+ = 10 days later; and 20+ = 20 days later. Check refers to an isolate of *H. glycines* produced on Essex soybean in the greenhouse. Roots were oven-dried for 1 week at 60 C before weighing. Data are means of four replications. A) "High" initial population of *H. glycines*. B) "Low" initial population of *H. glycines*.

inferred from egg hatching, J2 infectivity, and the numbers of females and eggs produced on a bioassay plant. Nonetheless, the data must be interpreted with caution because our measurements were taken only from eggs that were removed from cysts. Ishibashi et al. (12) found that *H. glycines* eggs produced in the gelatinous

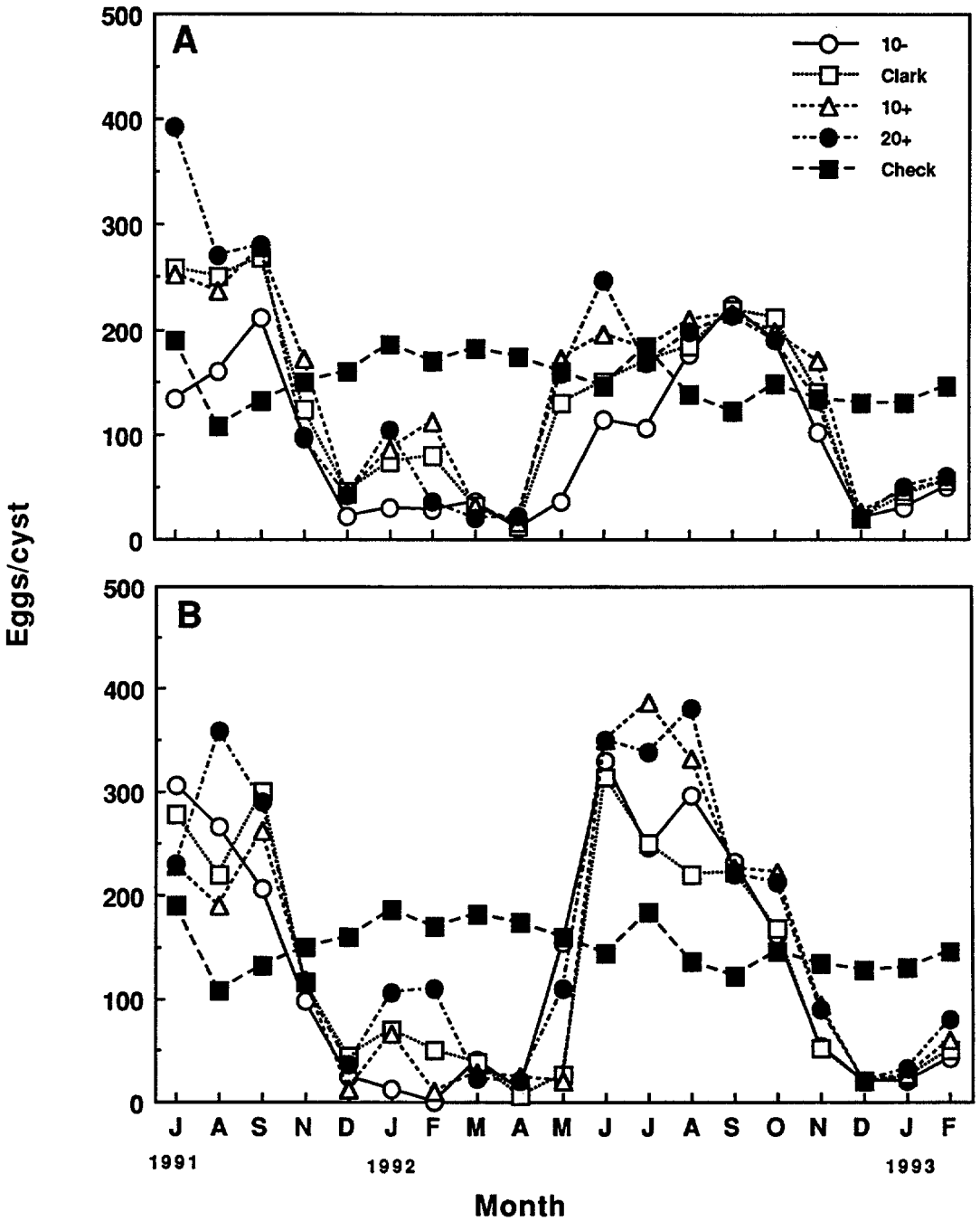

FIG. 5. Egg production of *Heterodera glycines* females on Williams 82 soybean at 30 days after soil infestation with 1,000 eggs collected from near-isogenic soybean lines in field microplots. The soybean isolines differed only for date of maturity: Clark; 10− = 10 days earlier than Clark; 10+ = 10 days later; and 20+ = 20 days later. Check refers to an isolate of *H. glycines* produced on Essex soybean in the greenhouse. Roots were oven-dried for 1 week at 60 C before weighing. Data are means of four replications. A) "High" initial population of *H. glycines*. B) "Low" initial population of *H. glycines*.

matrix hatched at a higher rate than those retained within the cyst. They suggested that eggs retained within the cyst were the source of inoculum for the subsequent year, whereas eggs produced in the gelatinous matrix were the source of inoculum for the current year. The cyst was also reported to contain a hatching inhibitor, but the inhibition was thought to be effective only on nondormant eggs (18).

The decline in hatching in August is evidence that dormancy is induced in July–August following planting in May–June. Assuming a life cycle of approximately 40 days in the field based on our soil temperatures (1), the timing of decreased hatching corresponded to the production of the first generation from J2 that would have begun hatching after planting and continued hatching and infecting for the next 30 days (4). If only one primary generation is produced, then dormancy may be an obligate condition for eggs retained within cysts of the first generation. Additional, smaller generations may be produced by nondormant J2 hatched from eggs produced in the gelatinous matrix; however, in other studies, we have observed that numbers of cysts and eggs in the soil rise only slightly from 60 days after planting to harvest (Niblack, unpubl.). Lawn and Noel (15) observed that most of the population increase in Illinois occurred in the first generation. In addition, we collected soil samples in 1993 for a follow-up study with an experimental design similar to that in the present study, in which the number of J2 in the soil peaked in June–July and decreased sharply through October (Yen and Niblack, unpubl.). These monophasic changes in population densities of cysts, eggs, and J2 support the interpretation of a single primary generation.

If *H. glycines* produces up to six or seven generations in the south (17), then a reduction in the number of generations may be an adaptation of northern populations for survival in colder winter conditions. Similarly, viability of the eggs surviving colder conditions may be reduced; for example, in our study, the microplot populations produced fewer females than did the check isolate. This reduction may be partly ameliorated by an increase in fecundity, shown by the higher numbers of eggs per cyst for the microplot populations collected during the growing season than those for the check isolate. But, as fecundity was apparently negatively related to population density, the differences were confounded with differences due to population density. Nonetheless, induction of dormancy in July in the first generation produced during a growing season suggests that the use of early maturing cultivars to reduce population densities (13) would not be an applicable strategy for *H. glycines* management in northern environments.

It is possible that timing of dormancy induction in our microplot populations is a response to photoperiod mediated through the host, as for *G. rostochiensis* (11). Dormancy induction did correspond temporally to the shift in soybean phenology from vegetative to reproductive stages; however, if the signal inducing dormancy came primarily from the host plant, then the 30-day difference in date of flowering between our early and late isolines should have been sufficient to allow detection of the effects of the signal. Our bioassays showed that the hatching rate, J2 per cm root, females and eggs per gram dry root, and eggs per cyst from the early isoline were lower than from the late isoline, but the differences were not consistently significant. Hominick et al. (10) showed that *G. rostochiensis* eggs from cysts from a single source population, which developed on the same cultivar grown in two locations 440 km apart in a north–south direction, hatched at different rates. In a subsequent study, Hominick (11) concluded that the length of diapause was negatively correlated with the daylength to which the host was exposed, but that the response was probably mediated by the maturity date of the potato cultivar. Likewise, Hill and Schmitt (9) suggested that soybean phenology affected dormancy of a North Carolina population of *H. glycines*. Thus, dor-

mancy is an intrinsic capability of populations, subject to modification by the environment, including the host plant. Characterization of dormancy as the result of a single mechanism or influence would be a gross oversimplification.

In the southern United States, *H. glycines* hatching may continue throughout the winter (26). In North Carolina studies, decreased hatching interpreted as dormancy occurred late in the growing season (20), and soil temperature was more important than soybean phenology in dormancy induction (9). In our studies, *H. glycines* dormancy was not induced by decreasing soil temperature but occurred in mid-summer. Population characteristics of *H. glycines* have changed as the nematode adapted to environments with colder winter temperatures; in fact, Sipes et al. (22,23) demonstrated that genetic differences related to dormancy exist among and within populations of *H. glycines*. Such differences should be exploited to characterize dormancy in *H. glycines* more completely.

Our data on the termination of dormancy were perhaps clearer than those on its induction, based on the categories detailed in the work of Zheng and Ferris (27). They considered that *H. schachtii* eggs that had not been subjected to any physical stress and hatched at a rate of 40–50% in water to be nondormant (facultatively quiescent), and the remaining eggs to be in one of three categories of dormancy: host-mediated obligate quiescence, host-mediated diapause, and time-mediated diapause. (Diapause and quiescence are differentiated based on the nature of the cause [2,19].) In our study, the percentage of eggs in host- and time-mediated dormancy can be inferred from the difference in hatching rates of eggs extracted from cysts collected on the pre- and postplanting sampling dates. A small proportion (<10%) of the eggs collected preplant hatched in water and thus were in a facultative quiescent state, and an average of ca. 40% hatched after planting and thus were probably in host-mediated dormancy, either quiescence or diapause. The remainder, up to 50%, were in time-mediated diapause. This type of diapause especially deserves further study in light of efforts to develop "hatching factors" to reduce population densities.

Several types of dormancy are exhibited by *H. glycines*. Development of biochemical or genetic markers for dormancy would be useful. At present, only the trehalose content of plant-parasitic nematode eggs has been used as a marker for dormancy (19), but whether trehalose has a role in dormancy of *H. glycines* has not been demonstrated. The possibility that some time-mediated dormancy is due to developmental arrest at an early embryological stage has not been borne out, according to flow cytometrical analyses of eggs in Iowa (G. L. Tylka, pers. comm.). Continuing studies in Missouri are focused on clarifying dormancy induction.

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