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Influence of Temperature and Soybean Phenology on Dormancy Induction of *Heterodera glycines*[1]

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Abstract: Growth room and field experiments were conducted to determine the influence of soil temperature and soybean phenology on dormancy induction of a North Carolina population of *Heterodera glycines* race 1. Three temperature regimes and two photoperiods to regulate plant phenology were investigated in growth rooms. *H. glycines* hatch was greatest from the 26 and 22 C (day and night) temperature treatment, intermediate at 22 and 18 C, and least from the decreasing regime (26 and 22 C, 22 and 18 C, and 18 and 14 C). More eggs hatched and greater nematode reproduction occurred on pod-producing soybeans than on those that remained vegetative. In the field study, hatching patterns were not different between depodded and naturally senescing soybeans nor between the different maturity groups of soybean cultivars (groups V through VIII). Egg hatch (9–16%) was greatest in August and September when mean soil temperatures were between 25 and 29 C. Hatch declined to 1% in vitro and was not detectable in the bioassay in November. Greatest nematode numbers were observed on the latest maturing cultivar (group VIII) and fewest on the cultivar which matured earliest (group V). Decreasing temperature appears to be more important than soybean phenology in dormancy induction of *H. glycines.*

Key words: Glycine max, Heterodera glycines, population dynamics, soybean cyst nematode, soybean, survival.

Heterodera glycines Ichinohe, the soybean cyst nematode, survives many years in the soil as encysted eggs (35). This serious pest of soybean, *Glycine max* (L.) Merr., is widely distributed in many soybean-growing regions of the world. Populations of *H. glycines* have an overwinter survival rate of 30–100% (10,35). Soybeans are planted mid-May through mid-July in North Carolina, and numbers of *H. glycines* increase during the growing season to a maximum in the fall near harvest (10,34). Eggs hatch during the growing season if soil temperature and moisture conditions are suitable (24,35,38). In late September or early October, *H. glycines* eggs become dormant and little or no hatch occurs even at temperatures optimal for hatch (32,33,44). Eggs that have overwintered usually hatch readily at planting time (10).

Dormancy induction in *H. glycines* and other nematodes is essential for overwinter survival. Environmentally induced dormancy may be caused by low temperature, lack of oxygen or moisture, or high salt levels (14). Normal hatching activity usually resumes when favorable conditions return. Additionally, some species of *Heterodera, Globodera,* and *Meloidogyne* exhibit seasonal hatch inhibition or facultative dormancy (14,30,36). These species include *H. glycines* (24,33), *H. avenae* Wollenweber (3,25), *H. cruciferae* Franklin (37), *Globodera rostochiensis* Wollenweber (36,37), and *Meloidogyne naasi* Franklin (19). Dormancy may be broken by a period of chilling (19) or fluctuating temperatures (4).

Temperature is an important aspect of dormancy induction in many nematode species (19,40). Summer dormancy occurs for *H. avenae* in Australia when temperatures exceed 20 C (3). Hatching resumes when autumn soil temperatures drop below 20 C. Warm-temperature dormancy can be induced in vitro (3). Alternating temperatures from 5 to 20 C daily, or at 4-day intervals in vitro, prevents this dormancy (4). *H. avenae* exhibits a cold-temperature dormancy in Europe when soil temperatures fall to 5 C (25). Exposure to natural autumn soil conditions induces dormancy in *G. rostochiensis* (36).

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Winter dormancy for *H. glycines* (24,33), other cyst nematodes (19,36,42), and for *M. naasi* (30) is probably temperature induced; however, hatch also varies throughout the season for *H. glycines* (33). Minimum hatch in November corresponds to lower temperatures after the crop matures. Juvenile emergence from newly developed, yellow females is delayed, but it is increased from brown cysts when they are exposed to prolonged low temperatures (24).

Host plant condition may also affect nematode dormancy and development. Cysts of *H. avenae* form earlier and eggs hatch faster on early maturing than on later maturing barley cultivars (5). Host condition, as affected by day length, influence abundance and hatching rate of *G. rostochiensis* on potato (18,20). *H. glycines* juveniles develop faster on photoperiod-induced, early-flowering soybean plants than on later flowering plants (24). Hatch rate of *H. glycines* eggs varies with the physiological age of host plants (39). Hatching enhancement by soybean root diffusate increases during the vegetative and reproductive stages of host development and declines with plant senescence. The greatest stimulation of egg hatching is by early reproductive plants (39).

Population levels of *H. glycines* in soil at planting give the best relationship to yield loss (10,29,35). Soil samples for nematode analysis for advisory purposes are routinely taken in the fall when nematode populations are highest. The following spring population levels are then extrapolated from fall samples (8). Nematode mortality rate differs annually, however, and numbers of eggs and juveniles in the soil at harvest are poorly related to eggs and juveniles that overwinter (10). Overwinter survival also varies considerably from one winter to the next (11). Identifying those factors which induce dormancy and enhance overwinter survival should increase the precision of estimates for spring population levels. The objective of this research was to determine the effects of soil temperature and soybean phenology on the induction of winter dormancy in *H. glycines.*

Materials and Methods

Growth room experiment: Tests were conducted in walk-in growth rooms (3.0 or 8.9 m^3) in the Phytotron at the Southeastern Plant Environment Laboratory, Raleigh, North Carolina (17). For each set of 10 pots, an aliquant of 150,000 eggs of a Clayton, North Carolina, population of *H. glycines* race 1 eggs, cultured on 'Ransom' soybeans, was pipetted into 2,500 cm^3 steamed soil (92% sand, 6% silt, 2% clay) and hand mixed in a large plastic bag for 30–60 seconds. A 250-cm^3 portion of infested soil containing approximately 15,000 eggs was distributed equally to the transplant hole in each 25-cm-d clay pot filled with the steamed soil. Uniform sized Ransom soybean seedlings with 3-cm-long radicles were selected after germination in a growth room set at 25 C for days and 22 C for nights on moist paper towels or in vermiculite. One seedling was transplanted to the center of the infested soil in each pot immediately after infestation.

Plants were grown in the infested soil in growth rooms for 4 weeks at alternating day and night temperature of 26 and 22 C with a 9 + 3-hour photoperiod for host–parasite establishment. During the day, 9 hours of light from cool-white fluorescent and incandescent lamps at 10:3 wattage ratio provided a photosynthetic photon flux density (PPFD) of 700 ± 30/μmol^2/sec at wavelengths of 400–700 nm and 10 ± 1 W/m^2 of photomorphogenic radiation (PR) at wavelengths of 700–850 nm (17). Between 11:00 p.m. and 2:00 a.m., light was from incandescent lamps providing a PPFD of 69/μmol^2/sec and PR of 9 ± 1 W/m^2 (17). Relative humidity was maintained at or above 70%. Day to night transition of temperature and light was abrupt and coincident. Water and nutrients were supplied as needed with the Phytotron nutrient solution, a modified half-strength Hoagland's solution (17).

Three temperature treatments were employed for 6 weeks in three growth rooms

with a 9-hour photoperiod: 1) 26 and 22 C, 2) 22 and 18 C, and 3) a decreasing temperature treatment of 26 and 22, 22 and 18, and 18 and 14 C for 2 weeks each. Treatments consisted of 10 infested pots and two uninfested controls. The study was repeated once; however, the 26 and 22 C treatment had five infested pots in the second test.

Photoperiod treatments were conducted at day and night temperatures of 26 and 22 C. A 9-hour photoperiod (9 hours light and 15 hours continuous dark) was provided to induce flowering and pod formation. A 9 + 3-hour photoperiod (9 hours light and a dark period interrupted with 3 hours light) was used to keep soybeans vegetative. Each photoperiod was maintained for 10 weeks with five infested pots and one uninfested control. Dicofol (Kelthane) was used to control spider mites.

Numbers of eggs and percentage of hatch were determined at termination of each test. A composite soil sample of 10–15 soil cores (2.5 cm d) was taken from each pot. Cysts and juveniles from 500 cm^3 soil were extracted by elutriation and centrifugal flotation (6). Eggs were released from cysts by crushing with a 40-ml Ten-Broeck tissue grinder. Nematode hatch was determined in vitro and in bioassay. Aliquants of 1,000 eggs were pipetted into a hatching chamber constructed of plastic and 26-μm-pore nylon screen placed in a 50-mm-d petri dish. Tap water was added to cover the eggs. Hatched juveniles were counted after 5 days at 24 C. For the bioassay, an aliquant of 1,000 eggs was mixed into 400 cm^3 steamed soil which was placed in a 7.5-cm-d clay pot, and a 3-day-old Ransom soybean seedling was transplanted into the pot. Roots were removed after 5 days and stained with acid fuchsin (12). The number of juveniles penetrating each root was determined by microscopic examination. Shoot, root, and pod weights were determined at the end of each test. Number of nematodes per gram dry root was calculated to standardize nematode numbers per root biomass. Data were subjected to analysis of variance.

Field experiment: Field plots were established at the Central Crops Research Station, near Clayton, in a soil (86% sand, 9% silt, 5% clay) naturally infested with *H. glycines* race 1. Four soybean cultivars—'Deltapine 105' (maturity group V), 'Coker 156' (group VI), Ransom (group VII), and 'Hutton' (group VIII)—were planted 1 June 1984. Plots were six rows (55-cm row spacing) 2.5 m long. Flowers and pods were removed weekly from 19 July to 4 October from half the plots to delay or prevent senescence. Treatments were arranged in a 2 (phenological stage) × 4 (cultivar) factorial and replicated six times.

A composite soil sample of 10–12 soil cores (2.5 cm d) was taken from the center four rows of each plot at monthly intervals from planting through November for nematode analysis. Numbers of nematodes per 500-cm^3 soil subsamples and percentage of egg hatch were determined as described in the growth room experiment, except 'Lee 68' soybean was used in the bioassay and the cysts collected from the roots after 28–30 days were counted. Soil temperature at 15 cm deep was continuously recorded at two points with a thermograph (Weathertronics, Inc.). Mean, maximum, and minimum daily temperatures were calculated and averaged into weekly values. Data were subjected to analysis of variance for a 2 × 4 factorial for soybean phenological stage versus soybean cultivar.

Results

Growth room temperature study: Egg hatch and all parameters of reproduction were inhibited in temperature treatments less than 26 and 22 C (Table 1). In vitro egg hatch averaged 75% less after 6 weeks exposure to 26 and 22, 22 and 18, and 18 and 14 C and 68% less at 22 and 18 C than at 26 and 22 C. The trend in the bioassay was similar, with an average of 75% fewer juveniles recovered in the roots at 26 and 22, 22 and 18, and 18 and 14 C and 58% fewer at 22 and 18 C than at 26 and 22 C. Nematode reproduction was greatly reduced by the lower temperature treat-

TABLE 1. Influence of temperature treatment for 6 weeks on population density and egg hatching of *Heterodera glycines* on soybean.

Temperature (C) (day–night)	Hatch†	Bioassay†	Cysts/g dry root	Eggs/g dry root	Eggs/cyst	Juveniles/ 500 cm³ soil	Juveniles/g dry root
			Test 1				
26–22	118	175	46	6,215	127	1,734	105
22–18	33	50	6	397	69	42	2
26–22, 22–18, 18–14	12	17	21	950	51	24	1
LSD (0.05)	25	43	13	1,494	22	606	41
			Test 2				
26–22	128	156	139	10,771	92	2,546	610
22–18	48	91	37	4,919	131	218	23
26–22, 22–18, 18–14	49	70	34	4,186	127	171	16
LSD (0.05)	29	44	41	3,209	NS	502	191

Data in test 1 are means of 10 pots unless otherwise noted. Data in test 2 are means of five pots. Analysis of variance performed among pots within individual tests.

† Number of juveniles hatching from 1,000 eggs after 5 days in vitro or penetrating soybean seedlings.

ments in this study (Table 1). Numbers of cysts and eggs per gram dry root were lowest at 22 and 18 C. Few juveniles were found at the two lower temperatures, whereas an average (tests 1 and 2) of 2,140/500 cm³ were detected at 26 and 22 C.

Growth room photoperiod study: More eggs hatched in vitro (27% average for tests 1 and 2) from soybeans in the reproductive phase than from those in the vegetative stage ($P = 0.15$ and 0.08 for tests 1 and 2) (Table 2). Numbers of juveniles detected in the roots of the bioassay plants were 23% greater from soybeans producing seed than from plants remaining vegetative.

Nematode reproduction was greater on soybeans that produced pods (short-day treatment) than on those that were kept vegetative by a long photoperiod (Table 2). Cysts and eggs per gram dry root averaged 4.4 and 3.4 times greater ($P = 0.03$ and 0.01, respectively) on plants in the reproductive stage than on those that were vegetative. Juveniles increased 13 times more in the soil and were 11-fold greater per gram dry root from reproductive plants as well.

Field experiment: Deltapine 105 began to flower 19 July. Dates of 50% flowering were Deltapine 105, 25 July; Coker 156, 29 July; Ransom, 2 August; and Hutton, 6 August. Deflowered, depodded plants held green leaves until frost, 8 November. Naturally maturing soybeans in the group VIII cul-

TABLE 2. Effects of vegetative versus reproductive soybean plants on egg hatching and reproduction of *Heterodera glycines*.

Phenological stage	Hatch†	Bioassay†	Cysts/g dry root	Eggs/g dry root	Eggs/cyst	Juveniles/ 500 cm³ soil	Juveniles/g dry root
			Test 1				
Vegetative	89	83	83	8,568	95	7,501	1,115
Reproductive	129	128	387	18,478	54	128,790	12,016
$P =$	0.15	0.21	0.03	0.03	0.01	0.21	0.17
			Test 2				
Vegetative	39	169	33	4,881	146	3,034	120
Reproductive	47	197	128	27,107	208	6,691	1,089
$P =$	0.08	0.48	0.01	0.01	0.06	0.08	0.04

Data in test 1 are means of five pots unless otherwise noted. Data in test 2 are means of four pots. Analysis of variance performed among pots within individual tests.

† Number of juveniles from 1,000 eggs hatching after 5 days in vitro or penetrating seedlings. Tests were conducted for 10 weeks.

tivar Hutton matured 3 weeks later than the group V cultivar Deltapine 105. Dates of 95% brown pods for naturally maturing treatments were Deltapine 105, 17 October; Coker 156, 22 October; Ransom, 30 October; and Hutton, 6 November.

Mean soil temperature fluctuated between 22 and 29 C from mid-June through mid-September (Fig. 1A). Throughout the season, maximum soil temperature exceeded 31 C for only 2 weeks in June. From mid-September to early October, mean soil temperature dropped from 25 to 17 C, whereas daily minimums ranged from 22 to 16 C. Daily minimum was between 17 and 15 C in November.

Nematode hatch as measured in vitro and with a bioassay had a similar pattern for all cultivars and so is combined for cultivars (Fig. 1B). Hatch in vitro was 5–10% from eggs collected at planting in June and 1–2% in the bioassay. Hatch was greater from eggs collected in August and September, with the bioassay giving a higher percentage hatch than in vitro. Hatch declined to about 1% in vitro and was not detected in the bioassay in November.

Nematode population density, as measured by number of eggs, was low from June (planting) through September and increased to a maximum level in November (Fig. 2). Fluctuation of numbers of cysts and juveniles paralleled that of eggs.

Numbers of *H. glycines* cysts and eggs recovered in October and November were slightly greater on podded soybeans than on depodded plants from all cultivars except Hutton (Fig. 2, egg data). Cultivar effects on nematode reproduction were associated with maturity group (Fig. 2). Nematode density was greater ($P = 0.05$) on the late-maturing Hutton than on Coker 156 and the early-maturing Deltapine 105.

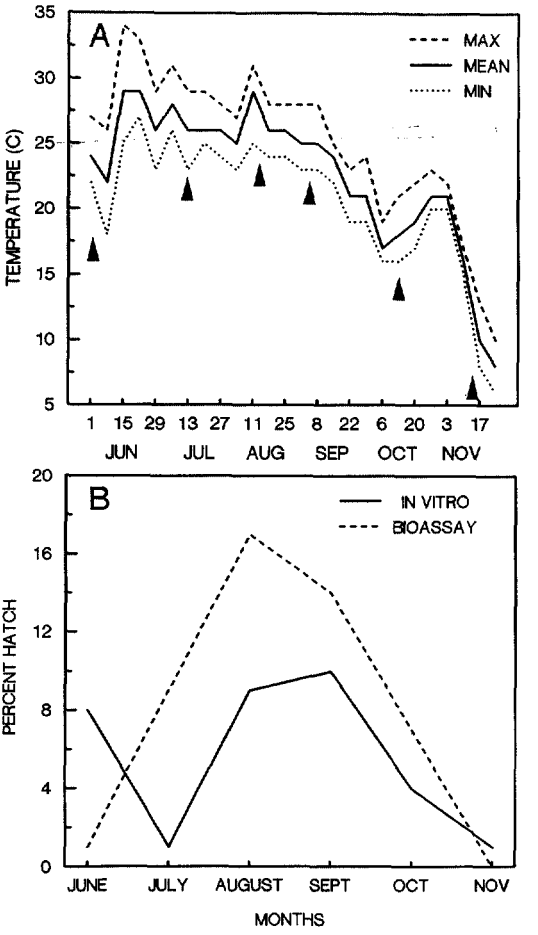

FIG. 1. Soil temperatures and egg hatching of *Heterodera glycines* at Central Crops Research Station, Clayton, North Carolina, 1984. A) Mean, maximum, and minimum soil temperatures at 15 cm deep. Each point is the mean of 7 days. Arrows indicate time of nematode sampling. B) Hatch percentage of 1,000 *H. glycines* eggs in vitro (5 days in water at 24 C) and in bioassay (number of cysts developing on Lee 68 soybean seedling from 1,000 eggs after 28–30 days. Each point is the average of 24 samples. Bioassay value at 11 July is predicted based on points above and below.

DISCUSSION

Temperature influenced egg hatch more than plant phenology. Hatch inhibition at low temperatures is considered to be caused by the induction of dormancy in this North Carolina population of *H. glycines* race 1. Temperatures of ca. 22 C, or lower, appeared to be critical for induction of dormancy, since hatching in the field declined in September and October and at less than 22 C in the growth-room experiment. Eggs collected in November, when the daily mean temperature had been 16–19 C for about 6 weeks preceding sampling, did not hatch. These results confirm previous reports of decreasing hatch of *H. glycines* in North Carolina in September through No-

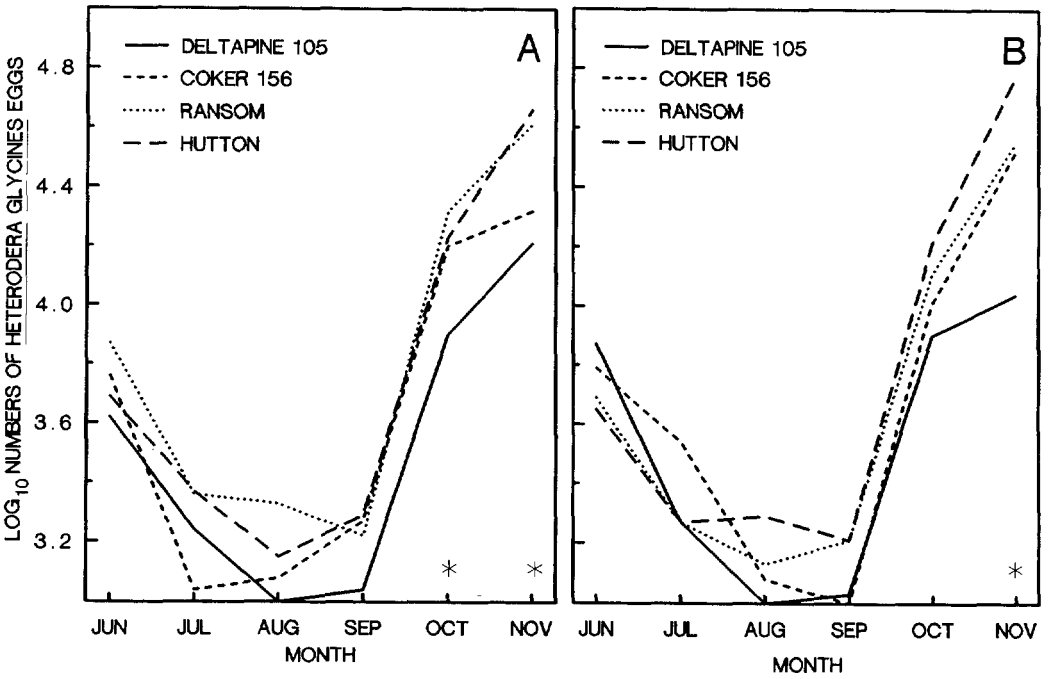

FIG. 2. Numbers of *Heterodera glycines* eggs from four soybean cultivars. Values are the mean of six replications. Asterisks below points represent significant differences ($P < 0.05$) among mean values. A) Podded plants. $LSD_{0.05}$ value is 119 for November. B) Depodded plants. $LSD_{0.05}$ values are 52 for October and 102 for November.

vember (33), and similarly for *G. rostochiensis* in England in August through November (36). The induction mechanism of winter dormancy in *G. rostochiensis* may not be totally related to temperature because hatch inhibition began before temperature conditions became unfavorable (36), although temperature has been associated with induction of dormancy in other cyst nematodes (3,25,42).

Reproductive soybeans did not inhibit hatch more than did nonreproductive plants in either field or growth room studies. This result conflicts with the hypothesis that as soybeans mature, the physiology of pod-bearing and senescing plants induces dormancy of *H. glycines*. In fact, hatching was slightly greater from reproductive soybeans when plant phenology was regulated by photoperiod. This trend agrees with a report that soybean root diffusate has peak hatching activity in vitro from soybeans during the R3 stage of pod development (21) and then declines as soybeans approach harvest maturity (39). Such hatch stimulation would account for greater nematode abundance from maturing plants compared with plants that remained vegetative.

The physiological status of a maturing soybean seems especially conducive to *H. glycines* reproduction. Stored carbon and nitrogen, which are mobilized within the plant during seed fill (15), may become more available to the feeding nematode. As nitrogen-fixing nodules senesce and nitrogenase activity declines (26), lower concentrations of *H. glycines*-inhibitory nitrogenous compounds (7,9) may provide a more favorable environment for nematode development. Changing composition and concentration of carbohydrates, amino acids, and plant growth regulators that vary with soybean phenology (15,23,27) may be beneficial for nematode feeding and reproduction.

The failure of flower and pod removal in the field to influence hatch may be caused by continued flower production which may create physiological conditions similar to

normally fruiting plants. Pod removal affects partitioning of plant constituents by altering the source–sink relationship for accumulation of dry matter, soluble protein, phosphorus, and nonstructural carbohydrates (15,28,43). Pod removal, however, has little effect on net photosynthesis and root senescence (15). Moreover, the impact of decreasing temperature in the field may mask any subtle effect of host phenology that might have been observed if sampling had been more frequent.

Cultivar effects on nematode hatching did not follow a pattern consistent with soybean maturity groups, which adds support that phenology per se may have only a slight effect, if any, on dormancy induction. The rate of hatching of *H. avenae* on barley was greater on early maturing barley cultivars than on those that matured later (5).

Nematode reproduction, however, was clearly related to the soybean maturity group with production of progeny increasing with later maturing cultivars. Significant differences in root production and distribution have been observed among soybean cultivars (31). The later maturing cultivars have root activity for a longer period and provide additional days of living host tissue (13). Early maturing barley cultivars have a similar effect on *H. avenae* (5).

Soybean yields are negatively correlated with *H. glycines* population densities in the previous fall (11). Because early maturing cultivars in this study did not permit final populations as high as the later maturing cultivars, subsequent preplant inoculum should be lower. Early maturing cultivars may be a potential pest management tool, especially in double cropping rotations.

A late season surge in abundance of cysts and eggs occurs in North Carolina (1,10,11). The low temperature-induced hatch inhibition and increased rate of reproduction may account for this phenomenon because unhatched eggs accumulate in the soil. Fewer degree days are required for *H. glycines* to complete a life cycle late in the season than at midseason (2). Egg development and maturity could alter survival through differential egg sensitivity to environmental stimuli. Early embryonic stages of *H. glycines* have a higher mortality level than do juveniles within the egg (2). Juvenile stages in the egg of *Meloidogyne* spp. are more resistant to cold because of inherent tolerance or conditioning by previous exposure to a range of temperatures (22).

Temperature-induced dormancy may be activated at a critical threshold or, more likely, by a conditioning effect that accompanies gradually decreasing temperatures. Perhaps temperature acts directly on the nematode by restricting enzyme activity or muscle movement necessary for eclosion or by affecting egg shell permeability or phase transition of membrane lipids and thereby limiting metabolic functions (41). Conversely, temperature may alter nematode activity indirectly by altering host growth (16). Whatever the mechanism, without the ability to acheive dormancy, overwinter survival would probably be poor. Overwintered eggs provide infective juveniles for the next season for 30 days or more after planting (10). Where dormancy-inducing temperatures do not occur, hatching probably continues throughout the winter as in the southernmost United States (44), thus depleting inoculum levels at planting. Identification of the actual mechanisms of temperature-induced dormancy will allow better understanding of the variation in annual nematode mortality rates and will facilitate more precise prediction of spring population levels.

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