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Factors Influencing Emergence of Juveniles from Cysts of *Heterodera zeae*[1]

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Abstract: Several factors were studied to determine their effects on hatch and emergence of second-stage juveniles (J2) from cysts of *Heterodera zeae.* The optimum temperature for emergence of J2 from cysts of *H. zeae* was 30 C. No juveniles emerged from cysts at 10 or 40 C. Immersion of cysts in 4 mM zinc chloride solution stimulated 10% greater emergence of J2 than occurred in tap water controls during 28 days. Fresh corn rhizosphere leachates from 25-day and older plants growing in sand or sandy field soil stimulated 22–24% greater emergence of J2 from cysts than occurred in tap water after 28 days. Rhizosphere leachates stored for 30 days at 4 C and leachates of sand, sandy field soil, and silty field soil inhibited emergence of J2 from cysts by 7–12% compared to tap water. Rhizosphere leachates from corn plants aged 20, 30, 40, 50, or 60 days growing in sandy field soil stimulated emergence of J2 from cysts. Similar numbers of J2 emerged from cysts regardless of whether the source of cysts was field microplot cultures, greenhouse cultures, or growth chamber cultures. Fertilizing growth chamber cultures of *H. zeae* on corn plants resulted in a doubling of the numbers of cysts produced in the cultures, and those cysts yielded 2–3 times as many emerged J2 in hatching tests compared to cysts from similar unfertilized cultures.

Key words: corn, corn cyst nematode, culturing, emergence, *Heterodera zeae,* soil leachate, soil type, *Zea mays,* zinc chloride.

In 1981, the corn cyst nematode *Heterodera zeae* was found in Kent County, Maryland, for the first time in the Western Hemisphere (22). This economically important nematode is distributed widely in most corn-growing areas in India (15) and Egypt (1), and it also occurs in Pakistan (2). In 1992, *H. zeae* was reported from a corn field in Cumberland County, Virginia, and was associated with severely stunted plants (10). Suppression of corn growth by a Maryland population of *H. zeae* was demonstrated in microplot (17) and growth chamber (11) tests.

Temperature influences the development (12) and reproduction (11) of *H. zeae.* However, there is little information on factors influencing egg hatch and emergence of second-stage juveniles (J2) from cysts of *H. zeae.* Egg hatch in nematode cysts and subsequent emergence of juveniles of various species from the cysts are affected by temperature (9). The optimum temperature for emergence of J2 from cysts of *H. avenae* was 15 C, although emergence occurred at constant temperature up to 20 C (3). Second-stage juveniles emerged from cysts of *H. cajani* at temperatures between 15 C and 37 C with an optimum at 29 C (16); the optimum for an Indian population of *H. zeae* was 30 C (28).

Host root leachates stimulate egg hatch in many cyst nematodes (19,20). For instance, hatch of eggs inside cysts of *H. schachtii* (31), *H. humuli* (31), *Globodera rostochiensis* (31), and *H. goettingiana* (4) was stimulated by root leachates from host plants and certain related non-host plants. Most studies with *H. glycines* cysts have shown that hatching of eggs is enhanced by soybean root leachates (7,23,26,27), but not in all studies (24,25). Corn rhizosphere leachate obtained from an Indian cultivar of corn susceptible to *H. zeae* reportedly did not increase hatch of eggs or emergence of J2 from cysts (28).

Information on environmental and cultural factors influencing the behavior and survival of *H. zeae* should prove useful for the development of methods for managing this pest. The objective of our study was to investigate the influence of temperature, host root leachates, and culturing environ-

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ment of *Heterodera zeae* on the emergence of juveniles from cysts.

Materials and Methods

Culturing of Heterodera zeae: Heterodera zeae was cultured in field microplots and in pots in the greenhouse and growth chamber. All cultures were maintained on Pioneer 3184 corn (*Zea mays* L.). Field cultures were maintained in methyl bromide-fumigated loamy sand soil contained in 45-cm-d × 60-cm-deep microplots constructed of fiberglass cylinders. Greenhouse cultures were maintained in pots containing 5,000 cm^3 autoclaved washed sand. Pots were situated on plant propagation mats to maintain a sand temperature of about 30 C. Pots were irrigated with tap water, and plants were fertilized once a week with a complete soluble fertilizer solution. Subcultures were initiated every 3 to 4 months. Growth chamber cultures were maintained in pots containing 100 cm^3 autoclaved washed sand at 30 C under a 12-hour photoperiod with a light intensity of 100 $\mu watts/m^2/sec$. Pots were irrigated with tap water, and plants were fertilized once a week. Subcultures were initiated every 2 months.

Nematode inoculum for initiating a culture was prepared as described by Hashmi et al. (11). When cultures were used as the source of nematodes for an experiment, shoots of 90- to 100-day-old plants from the greenhouse and 50-day-old plants from the growth chamber were excised at the sand surface and the pots were held in the laboratory at 25 C for 12 to 15 days to allow females on the roots to mature. Cysts were extracted by washing and decanting using a 250-μm-pore sieve. Several thousand cysts were collected and stored in tap water at 4 C for 4 to 5 days. *H. zeae* cysts were hand picked from water suspension, and only those cysts that appeared full of eggs were used in the tests.

Effect of temperature and incubation media on percentage emergence of J2: Corn rhizosphere leachate was obtained from 25-day-old corn plants (Pioneer 3184). Because corn leachate loses effectiveness after 15 days (data not shown), additional fresh leachate was obtained from the same pot of plants as needed. Ten plants in a single plastic pot were grown in 1,000 cm^3 autoclaved sand at 27 C in a growth chamber under a 12-hour photoperiod with a light intensity of 100 $\mu watts/m^2/sec$. Plants were watered but not fertilized. Corn rhizosphere leachate was obtained by pouring 300 ml of tap water into a pot and collecting the first 100 ml of liquid that drained from the bottom of the pot (23). Leachates were passed through No. 5 Whatman filter paper and used immediately or stored at 4 C. In addition to fresh corn rhizosphere leachate, leachate also was aged by storing at 4 C for 30 days. Aqueous 4 mM zinc chloride solution was prepared fresh. Tap water controls were included in each hatching test.

Cysts containing eggs, obtained from 3- to 4-month-old greenhouse cultures, were selected individually from a water suspension of cysts with a Pasteur pipet using a dissecting microscope and stored in tap water at 4 C for 4 to 5 days or until used in hatching tests. Hatching tests were performed on five samples of 25 cysts each for each treatment. Each sample of 25 cysts was incubated in a 5-cm-d plastic, grid petri dish containing 5 ml of test solution at 10, 15, 24, 27, 30, 33, 36, or 40 C in controlled temperature incubators in the dark. Temperatures were assigned randomly to growth chambers for each experiment. Counts on emerged juveniles were made at 4-day intervals, at which times old test solutions were removed and fresh test solutions added. At the end of 28 days and after the emerged J2 were counted, cysts were broken open and the numbers of unhatched eggs and juveniles were counted. The experiment was repeated twice and data were subjected to analysis with ANOVA as a 9 × 4 factorial arranged in a completely randomized design (18). The significance ($P < 0.05$) of main effects and interactions was determined.

Influence of soil type on the hatch-stimulating activity of soil leachates: Corn rhizosphere

leachate was obtained from 25-day-old corn plants (Pioneer 3184). As needed, additional fresh leachate was obtained from the same pot of plants. Ten plants in a single plastic pot were grown at 27 C and under a 12-hour photoperiod in the following 1,000 cm^3 of the potting media: 1) autoclaved sand, 2) methyl bromide-fumigated sandy field soil (Norfolk loamy sand, fine-loamy, silicaceous, thermic, Typic Paleudult consisting of 87% sand, 7% silt, 6% clay, 0.5% organic matter), or 3) methyl bromide-fumigated silty field soil (Matapeake silt loam, Typic Hapludults, fine-silty, mixed mesic consisting of 14% sand, 62% silt, 24% clay, 1.8% organic matter). Pots of the three planting media without plants were kept in the growth chamber to serve as controls. All pots were irrigated with tap water, and leachates were prepared as described in the temperature and incubation experiment.

Cysts containing eggs were obtained from 3- to 4-month-old greenhouse cultures. Hatching tests were performed on five replicates of 25 cysts for each treatment incubated at 30 C. The experiment was repeated once. Data from two tests were combined and subjected to analysis with ANOVA as a 2×3 factorial in a completely randomized design. The significance ($P < 0.05$) of main effects and interactions was determined.

The influence of different culturing environments and incubation media on percentage emergence of J2: Corn rhizosphere leachate was obtained as described for the temperature and incubation experiment, except that in this experiment the corn plants were grown in methyl bromide fumigated, sandy field soil (Norfolk loamy sand). Pots containing the same sandy field soil, but without plants, were kept in the same growth chamber to serve as controls. Cysts were obtained from 3- to 4-month-old microplot, greenhouse, and growth chamber cultures. Hatching tests were performed on five replicates of 25 cysts each at 30 C. The experiment was repeated once. Data from two tests were combined and subjected to analysis with ANOVA as a 3×2 factorial arranged in a completely randomized design. The significance ($P < 0.05$) of main effects and interactions was determined.

Influence of fertilizer application to corn plant cultures of H. zeae on plant growth, nematode reproduction, and percentage emergence of J2: Corn rhizosphere leachate was obtained as described for the temperature and incubation experiments using methyl bromide-fumigated Norfolk loamy sand. Cultures of *H. zeae* from plant growth chambers were used. Nematode inoculum was prepared as described in the culturing of *H. zeae*. Twenty ml of aqueous suspension containing 5,000 ± 250 mixed eggs and J2 were pipeted onto the surface of 100 cm^3 of autoclaved sand contained in each 10-cm-square pot. Four seeds of Pioneer 3184 corn were placed onto the sand in each pot and covered 2 cm deep with another 100 cm^3 of sand. All pots were then placed in plant growth chambers at 30 C under a 12-hour photoperiod. After the corn seedlings were about 10 cm tall, pots were divided into four groups. Each group contained three pots. Pots were fertilized weekly with 100 ml of a solution containing 0, 5, 10, and 20 ml of 20-20-20 fertilizer per liter of water. The undiluted fertilizer contained 473 ppm nitrogen.

After 8 weeks, plants were harvested and data were collected on fresh weight of roots, total numbers of cysts, and total numbers of females per pot. Cysts recovered by washing and decanting from three replicate pots of a treatment were combined and used for hatching tests. Hatching tests were performed on five replicates of 25 cysts each for each treatment incubated at 30 C. The final count on emerged J2 was made after 7 days of incubation. Experimental units were arranged in a completely randomized design. The experiment was repeated once. Data from two tests were combined and subjected to analysis with ANOVA. Emergence of J2 was analyzed as a 3×4 factorial arranged in a completely randomized design. Means on root weights and numbers of cysts plus females were compared at $P < 0.05$ using

the LSD. The significance ($P < 0.05$) of main effects and interactions was determined.

Influence of corn rhizosphere leachates from plants of different ages on the percentage emergence of J2: Rhizosphere leachates were obtained from different-age corn plants. Four plants of corn (Pioneer brand 3184) in each 10-cm-square plastic pot were grown in methyl bromide-fumigated sandy field soil at 27 C under a 12-hour photoperiod. Three pots of corn were planted at 0, 10, 20, 30, 40, and 50 days. At the same time, three similar pots containing the same soil, but without plants, were placed at each planting date in the same growth chamber to serve as controls. Soil in all pots was watered as required for good plant growth and to keep the soil moist, and unfertilized. At 60 days, rhizosphere leachates from pots with plants and leachates from pots of soil without plants were obtained by pouring 100 ml of tap water into a pot and collecting 25 ml of liquid that drained from the bottoms of the pots. Leachates were passed through No. 5 Whatman filter paper and used immediately. Then the plants were harvested and data collected on fresh weights of roots.

The source of *H. zeae* cysts for the hatching test was 3- to 4-month-old greenhouse cultures. Hatching tests were performed on three replicates of 25 cysts each for each treatment incubated at 30 C. The final count on emerged J2 was made after 7 days of incubation. Experimental units were arranged in a completely randomized design. The experiment was repeated once. Data from two tests were combined and subjected to analysis with ANOVA, and means were compared at $P < 0.05$ using LSD. Emergence was analyzed as a 2 × 5 factorial in a completely randomized design. The significance ($P < 0.05$) of main effects and interaction was determined.

Results

Effect of temperature and incubation media on percentage emergence of J2: Maximum percentage of J2 emerged from cysts of *H. zeae* at 30 C and in the presence of fresh corn rhizosphere leachate (Fig. 1). No J2 emerged at either 10 or 40 C. Few J2 emerged from cysts in any of the four incubation media at 15 C, and there were no differences between liquids in stimulating emergence at that temperature. Except at 15 C, fresh corn rhizosphere leachate stimulated greater percentage emergence of J2 from cysts than the other three media within any of the other temperatures at which hatch occurred. The descending order ($P < 0.05$) of the four media in their stimulation of J2 emergence were: fresh corn rhizosphere leachate > 4.0 mM zinc chloride > tap water > aged corn rhizosphere leachate. At most temperatures, fresh corn rhizosphere leachate resulted in at least twice as many J2 emerged from cysts as emerged in tap water, and usually 20-40% more than emerged in zinc chloride solution. Aged corn rhizosphere leachate inhibited emergence of J2 from cysts when compared to tap water. No J2 emerged from cysts in any incubation medium at 10 or 40 C.

Influence of soil type on the hatch-stimulating activity of soil leachates: Emergence of J2 in leachates of silty and sandy field soils with growing corn plants was higher ($P < 0.05$) than emergence in similar leachates of sand (Table 1). Leachates of all three soils with growing corn plants resulted in more

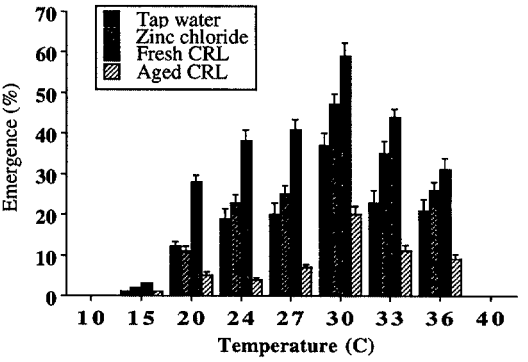

FIG. 1. Effect of temperature and incubation medium on emergence of second-stage juveniles (J2) from cysts of *Heterodera zeae*. Percentage of cyst contents emerged as J2 from 25 cysts (average 158 eggs per cyst) after 28 days. Vertical bars 1 SE.

TABLE 1. Percentage emergence of second-stage juveniles (J2) from cysts of *Heterodera zeae* in several leachates obtained from different soils planted with corn or fallow.

Source of leachate	Cyst contents emerged as J2 (%)[a]	
	+corn	−corn
Silty field soil	69	24
Sandy field soil	69	21
Washed builder's sand	57	26
Mean	65	24

Values are the means of two tests with five replications in each test.

[a] Percentage of cyst contents emerged as J2 from 25 cysts (average 155 eggs per cyst) after 28 days at 30 C. Data on percentage hatch were transformed using the arcsin transformation.

Main effect of corn leachate was significant ($P < 0.05$); however, the main effect of leachate source was not significant, and there was no interaction.

than twice as many J2 emerged from cysts as emerged in leachates of all three soil types not planted to corn.

Influence of different culturing environments and incubation media on percentage emergence of J2: There were no differences ($P < 0.05$) in percentages of J2 emerging from cysts collected from greenhouse cultures, field microplot cultures, or growth chamber cultures (Table 2); more J2 emerged from cysts in fresh corn rhizosphere leachate than in tap water or soil leachate.

Influence of fertilizer application to corn plant cultures of H. zeae on plant growth, nematode reproduction, and percentage emergence of J2: Application of fertilizer to cultures of *H. zeae* on corn plants growing in pots in growth chambers resulted in large increases in both plant growth and nematode reproduction (Table 3). Adding fertilizer greatly increased the fresh weight of corn plant roots; fresh root weight of corn plants increased incrementally with increased rates of fertilization. The lowest level of fertilizer application almost doubled number of cyst plus females of *H. zeae* compared to no fertilizer, but additional increases in fertilizer levels did not increase nematode reproduction.

A larger percentage of J2 emerged from cysts obtained from fertilized cultures than from cysts obtained from unfertilized cultures ($P < 0.05$), regardless of the hatching medium in which the cysts were incubated (Table 3). However, there was no increase in the percentage of J2 emerging from cysts as fertilizer level was increased above the lowest level. The percentage of J2 emerged from cysts was highest in fresh corn rhizosphere leachate, intermediate in distilled water, and lowest in tap water ($P < 0.05$) for each level of fertilizer applied to cultures.

Influence of corn rhizosphere leachates from plants of different ages on the percentage emergence of J2: Age or size of corn root systems had no influence on the percentage emergence of J2 from cysts incubated in rhizosphere plant leachates (Table 4). Only corn rhizosphere leachate stimulated emergence of greater percentage of J2 from cysts ($P < 0.05$) than occurred in tap water.

DISCUSSION

The optimum temperature for emergence of J2 from cysts of *H. zeae* differs from the closely related cyst nematode species *H. glycines* and *H. schachtii*. Slack and Hamblen (25) showed that maximum emergence of J2 from cysts of *H. glycines* occurred at 24 C, with no emergence of J2 below 16 C or above 36 C. Maximum emergence of J2 from cysts of *H. schachtii*

TABLE 2. Effect of growth chamber, greenhouse, and field microplot culturing environments, and incubation solutions, on the percentage emergence of second-stage juveniles (J2) from cysts of *Heterodera zeae*.

Source of cysts	Emergence of J2 (%)[a]		
	Tap water	Corn leachate	Soil leachate
Growth chamber	42	66	35
Greenhouse	41	66	33
Microplot	42	67	34
Mean	42	66	33

Values are the means of two tests with five replications in each test.

[a] Percentage of cyst contents emerged as J2 from 25 cysts (average 161 eggs per cyst) after 28 days at 30 C. Data on percentage hatch were transformed using the arcsin transformation.

Main effect of leachate was significant ($P < 0.05$); however, the main effect of cyst source was not significant and there was no interaction.

TABLE 3. Effect of different levels of soluble fertilizer on plant growth and on numbers of cysts plus females per 300 cm^3 soil per pot of *H. zeae* on Pioneer 3184 corn plants after 8 weeks in growth chambers at 30 C and emergence of second-stage juveniles (J2) from *Heterodera zeae* cysts in three media.

Fertilizer levels (ml/liter water)[a]	Root fresh wt (g)[b]	Cysts + females[c]	Emergence of J2 (%)[d]		
			Tap water	Distilled water	Corn leachate
0	3.0	7,680	15	23	39
5	10.4	13,400	42	59	77
10	16.9	14,420	42	58	76
20	22.1	14,315	45	58	78
Mean			36	50	68

Values are the means of two tests with three replications in each test.
[a] A 20-20-20 fertilizer at the original concentration of 473 ppm of nitrogen.
[b] LSD 0.05 = 2.7 for root fresh weight.
[c] LSD 0.05 = 1,850 for cysts plus females.
Main effects of fertilizer levels and hatching media, and the fertilizer levels × hatching media interaction were significant ($P < 0.05$).
[d] Influence of fertilizer application to corn plant cultures on percentage emergence of cyst contents emerged as J2 from 25 cysts (average 150 eggs per cyst) after 7 days at 30 C. Data on percentage hatch were transformed using the arcsin transformation.

occurred at 25 C; however, juveniles failed to emerge at or below 10 C or at 35 C (29,30). Although juveniles emerged from cysts of *H. zeae* at constant temperatures between 20 C and 36 C, the greatest emergence was at 30 C. Similarly, 30 C was the most favorable temperature for emergence of juveniles from cysts of an Indian population of *H. zeae* (28). The optimum temperature for hatch of eggs and emergence of juveniles from cysts of many species of *Heterodera* is between 15 C and 29 C (6,30). Juveniles failed to emerge from cysts of *H. zeae* at or below 10 C, or at or above 40 C in this study.

Zinc chloride at 4 mM was used in our hatching tests with *H. zeae* because this concentration was reported to be the best for stimulating hatch of eggs of other cyst nematodes, including *H. carotae, H. cruciferae, H. glycines, H. goettingiana, H. schachtii, G. rostochiensis,* and *G. tabacum* (8, 13,26). At 30 C, 4 mM zinc chloride stimulated 47% emergence of J2 from cysts of *H. zeae* as compared to 37% emergence in tap water over 4 weeks. Although 4 mM zinc chloride was reported as the optimum for stimulating emergence of J2 from cysts of several other nematodes, it was only weakly stimulatory for hatch of *H. zeae* eggs. Further study using lower and higher concentrations of zinc chloride is needed with *H. zeae.*

In *H. zeae* cysts, fresh corn rhizosphere leachate in the various experiments enhanced emergence of J2 by an average of 66% compared to tap water at 7 days. On the other hand, 47% inhibition of emergence of J2 from cysts occurred in corn rhizosphere leachate stored for 30 days at 4 C compared to tap water. Verma and Yadav (28) reported that corn rhizosphere leachate obtained from an Indian cultivar

TABLE 4. Fresh weights of shoots and roots of Pioneer 3184 corn and plants used as the sources of rhizosphere leachates at 20, 30, 40, 50, and 60 days of age, and emergence of second-stage juveniles (J2) from *Heterodera zeae* cysts.

Plant age (days)	Root fresh[b] weight (g)	Cyst contents emerged as J2 (%)[a]	
		Corn leachate	Soil leachate
20	6.8	23	10
30	6.9	23	9
40	8.5	23	10
50	7.7	24	10
60	7.7	24	9
Mean		23	10

Values are the means of two tests with three replications in each test.
Percentage emergence of cyst contents from 25 cysts (average 162 eggs per cyst) after 7 days at 30 C in corn rhizosphere leachate from plants of different ages. Percentage data on juvenile emergence were transformed using the arcsin transformation.
[a] Main effect of leachate was significant at $P < 0.05$; however, there was no effect on plant age, and there was no interaction.
[b] LSD 0.05 = 1.2 for root fresh weight.

of corn (hybrid not known) susceptible to *H. zeae* did not increase hatch of eggs or emergence of J2 from cysts.

Age of the host plant at the time rhizosphere leachate is collected can affect its potency as a hatching agent toward eggs in cysts of some species of *Heterodera*. For example, emergence of more than 40% was obtained with cysts of *H. goettingiana* immersed in leachate from 4- and 6-week-old pea plants compared to less than 10% emergence of J2 from cysts placed in leachate from 2- or 10-week-old pea plants at 15 C over 5 weeks (21). In these experiments, rhizosphere leachate was obtained from various aged plants and used as a stock solution for hatching tests. Although there is no report of loss of hatching activity for either potato or pea rhizosphere leachates even after several months of storage, we have found that refrigerated corn rhizosphere leachate began to lose its hatching activity after 15 days of storage (data not shown). Age of corn plants from 20 to 60 days when used as the source of rhizosphere leachate had no effect on emergence of J2 from cysts of *H. zeae*.

Soil leachates from pots of fallow, washed sand, sandy field soil, and silty field soil suppressed emergence of J2 from cysts of *H. zeae*. However, we do not know what agent(s) in the soil leachates was responsible for the reduced emergence of J2. In contrast, Verma and Yadav (28) reported that leachates from fallow sandy field soil increased emergence of J2 from cysts of an Indian population of *H. zeae*. There was an average 69% emergence of J2 from cysts of a Maryland population in rhizosphere leachate obtained from corn plants grown in pots of sandy field soil or silty field soil compared to 57% in leachate from corn plants grown in washed builder's sand. This difference may have resulted from the effect of fertilizer on the size of the root systems of the corn plants. Even without adding fertilizer during corn plant growth, sandy field soil contained almost 4-fold greater fertilizer levels than did washed sand (data not included).

Similar numbers of J2 emerged from cysts of *H. zeae* regardless of whether the cysts were from field microplot cultures, greenhouse cultures using large pots, or growth chamber cultures using small pots. Obviously, *H. zeae* can adapt to a range of environmental conditions. The source of cysts has been reported to influence hatch of eggs and the numbers of J2 emerging from cysts in other species of cyst nematodes. Berney and Bird (5) reported that hatch of eggs of *H. carotae* was greater in cysts obtained from field plots than in cysts obtained from greenhouse cultures. Our results with *H. zeae* indicated that laboratory-propagated nematodes were not greatly different from nematodes living under field conditions. For experimental purposes, this is important because we can propagate millions of uniform *H. zeae* in a small growth chamber. We obtain an average of about 14,000 cysts (data not shown) from each 7.5-cm-square area of growth chamber space every 8 weeks.

Supplying fertilizer to corn plant cultures of *H. zeae* resulted in a doubling of the numbers of cysts plus females produced, and when used in hatching tests 2–3 times as many J2 emerged from cysts propagated on fertilized as compared to unfertilized plants. As the rate of fertilizer application increased, corn plant fresh root and shoot weights increased incrementally. However, compared to the unfertilized corn plants, nematode reproduction doubled with the lowest rate of fertilizer application and remained at that level at the higher fertilization rates. We suggest that even the lowest rate of fertilizer application resulted in production of more corn roots, and therefore more nematode infection sites, than required by the amount of *H. zeae* inoculum applied. Withholding fertilizer was also reported to suppress the numbers of eggs produced on susceptible soybean plants by *H. glycines* and to promote early nematode maturation (14). Our findings thus far suggest that additional research on the influence of soil fertility on the reproduction of *H. zeae* may lead to even more efficient methods for producing large quantities of this nematode.

The specific hatching mechanisms are a major adaptation to parasitism in cyst nematodes. Eggs in diapause are capable of surviving for prolonged periods under conditions that would be unfavorable to hatched juveniles. Although similarities exist between *H. zeae* and other *Heterodera* species, there also are differences in the influence of environmental factors on the emergence of juveniles from cysts. Therefore, the general behavior patterns of one cyst nematode species do not necessarily relate to other species.

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