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Population Changes in *Heterodera glycines* and Its Bacterial Parasite *Pasteuria* sp. in Naturally Infested Soil[1]

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Abstract: A two-year soil sampling study was conducted on four microplots naturally infested with *Heterodera glycines* and an undescribed species of *Pasteuria*. The objectives of the study were to investigate the population dynamics of both organisms and to assess the potential of *Pasteuria* sp. as a biological control agent of *H. glycines*. Seasonal fluctuations were observed in numbers of cysts, eggs per cyst, second-stage juveniles (J2) of *H. glycines*, number of *Pasteuria* endospores attached per J2, and percentages of endospore-encumbered J2. Percentages of endospore-encumbered J2, Y, increased with the mean numbers of endospores per J2, X, according to the equation $Y = 87.0(1 - e^{-0.53X})$. In contrast, numbers of J2 per 250 cm^3 soil, Y, decreased with the numbers of endospores per J2, X, according to the exponential decay model $Y = 67.4 + 220.1e^{-1.2X}$. The equilibrium J2 density (67.4 ± 3.3) derived from this function was consistent with the predictions of the Lotka-Volterra model of population dynamics based on the equation $0.0195\ln(y) - 0.000336y = 0.000049x - 0.00285\ln(x) + 0.06589$, where x and y represent the biweekly means of J2 densities and the percentages of endospore-encumbered J2, respectively. In all cases, predicted equilibrium densities of J2 were below the damage threshold reported from field studies. These results indicate that, given sufficient time following introduction into a field, *Pasteuria* may increase to levels that would be effective as one component in an integrated pest management program to control *H. glycines*.

Key words: biological control, *Glycine max*, *Heterodera glycines*, modeling, nematode, *Pasteuria*, population dynamics, soybean, soybean cyst nematode.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, is the most economically damaging pathogen of soybean, *Glycine max* (L.) Merr., in the United States (Niblack, 1993). In the north-central and southern regions, the loss in average annual production is estimated at 1.3 million metric tons ($279.5 million) and 0.6 million metric tons ($127.7 million), respectively (Doupnik, 1993; Wrather et al., 1995). Planting resistant cultivars and cultural practices are the tactics used most often to manage the soybean cyst nematode. However, persistent crop losses indicate that additional management strategies are needed.

Species of *Pasteuria*, a gram-positive, mycelial, and endospore-forming bacterium of the order Actinomycetales (Starr and Sayre, 1988), are promising candidates for the biological control of several plant-parasitic nematodes (Brown et al., 1985; Chen et al., 1996, 1997; Nishizawa, 1987; Weibelzahl-Fulton et al., 1996). In spite of this potential, large-scale exploitation of *Pasteuria* spp. as biological control agents of nematodes has not been accomplished due to the lack of suitable procedures for in vitro mass cultivation (Bishop and Ellar, 1991; Williams et al., 1989) and to limited knowledge of the population dynamics of these parasites and the relationships with host populations in nature. Some studies have related low nematode densities to the suppressive action of *Pasteuria* (Bird and Brisbane, 1988; Oostendorp et al., 1991). However, the bacterium was associated with high nematode densities in one instance (Spaull, 1984), and in other instances no direct effect of *Pasteuria* was observed despite high percentages of infected nematodes (Ciancio et al., 1992; Giblin-Davis et al., 1990). Rates of parasitism were correlated with temporal fluctuations of the nematode population in only one of two

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kiwi orchards infested with both *Meloidogyne* spp. and *P. penetrans* (Thorne) Sayre & Starr (Verdejo-Lucas, 1992). In Italy, where parasitism of *Xiphinema diversicaudatum* (Micoletzky) Thorne by *P. penetrans* was investigated, nematode densities and rates of parasitism remained constant over time (Ciancio, 1995). Clearly, more data are needed to unveil the mechanisms that govern the *Pasteuria*-nematode interrelationships in nature. Understanding these mechanisms will assist in implementing biological control of nematodes as a component of integrated pest management.

An undescribed species of *Pasteuria* that infects *H. glycines* has been reported in North America (Noel and Stanger, 1994). Preliminary observations have shown that this isolate is not *P. nishizawae* Sayre, Wergin, Schmidt & Starr, the only species previously known to infect *H. glycines* (Sayre et al., 1991). The objectives of this study were to investigate the population dynamics of both *H. glycines* and *Pasteuria* sp. and to assess the potential of *Pasteuria* sp. as biological control agent of the soybean cyst nematode.

Materials and Methods

During the 1994 and 1995 growing seasons, experiments were established in four 5-m × 5-m microplots on the USDA nematology farm at Urbana, Illinois. Microplots were infested for several years before initiation of the experiments with *H. glycines*, two with race 3 and two with race 4. *Pasteuria* sp. was present in all four microplots. The soil was a series Watseka (sandy, mixed, mesic Aquic Hapludolls), with the upper 20 cm containing 73.8% to 79.0% sand, 10.8% to 18.0% silt, 7.0% to 11.4% clay, 4% organic matter, and with pH ranging from 5.9 to 6.4. Microplots were planted with the *H. glycines*-susceptible soybean cultivar Williams 82 on 15 May 1994 and 31 May 1995. Two soil samples, each consisting of 30 1.7-cm-diam. × 15 to 20-cm-deep cores, were collected randomly every 2 weeks from each microplot from 10 May to 4 October 1994 and from 5 April to 26 October 1995. White females and cysts of *H. glycines* (collectively referred to as cysts) were extracted from 250 cm^3 soil with gravity sieving (Cobb, 1918) onto a 180-µm-pore sieve. Second-stage juveniles (J2) and males of *H. glycines* were extracted from the same soil suspension with centrifugal flotation (Jenkins, 1964) and collected on a 38-µm-pore sieve. Cysts were crushed in a tissue grinder, and the numbers of eggs were determined with a Hawksley counting slide (Hawksley and Son, Lancing, England). All J2 and males of *H. glycines* were selected individually with the help of a stereomicroscope, mounted on temporary slides in 2.5% formalin, and examined under a compound microscope (×400) to determine the number of *Pasteuria* endospores attached to each nematode.

Poisson (PROC GENMOD, SAS Institute, Cary, NC) and negative binomial (LIMDEP, Econometric Software, Bellport, NY) models were used to estimate the frequency distribution of the numbers of endospores per J2. Both models involved three dummy variables (race, block, and year) and one continuous variable (date, expressed as number of weeks from the beginning of each sampling season) as covariates. The number of J2 from each 250-cm^3 soil sample was the exposure variable. Numbers of cysts, eggs per cyst, J2, endospores per J2, and percentages of endospore-encumbered J2 in each 250-cm^3 soil sample were analyzed with PROC GLM (SAS Institute, Cary, NC) for a split-split plot design with the race of *H. glycines* as the main plot, year as the split-plot, and sampling date as the split-split-plot. The biweekly means of each of the factors were interpolated with a cubic spline method (SigmaPlot, SPSS, Chicago, IL). A randomization test (Pollard and Lakhani, 1987) was used to detect density-dependent trends in the biweekly fluctuations of numbers of J2, endospores per J2, and percentages of endospore-encumbered J2. The test was based on Pearson's correlation coefficients, r_{xd}, between $x_{ij} = \ln(\overline{X}_{ij})$ and the corresponding differences, $d_{ij} = x_{ij+1} - x_{ij}$, where $\overline{X}_{ij}$ = the mean of variable X on date i and year j, $i = 1, \ldots, n_j - 1$; $j = 1, 2$; and n_j = the number of sampling dates in year j. Since the time series was discontinued from 4 October

1994 to 5 April 1995, the test was applied separately to the data from each year. However, when the date × year interaction was not significant, the $\overline{X}_{ij}$ were pooled over years. Conversely, when the race × year interaction was significant, the test was carried out on the data from each race × year combination. Each run of the test consisted of 2,000 simulations (Marriot, 1979) performed with a random number generator and a personal computer. Regression analyses also were conducted with nonlinear curve-fitting procedures PROC NLIN (SAS Institute, Cary, NC) and TableCurve (SPSS, Chicago, IL). Two predator-prey models of population dynamics were estimated from the biweekly means of J2 densities and the percentages of endospore-encumbered J2. The two models included the Lotka-Volterra model (Lotka, 1925; Volterra, 1926) and a modification of the Nicholson-Bailey model (Nicholson and Bailey, 1935) proposed by Hassel and May (1973). The considerations for the use of the Lotka-Volterra model to describe the *Pasteuria*-nematode interrelationship, the estimation procedure, and the biological significance of each of the parameters involved were outlined by Ciancio (1995). Specifically, the differential equation,

$$a\ln(y) - by = cx - d\ln(x) + k \qquad (1),$$

was estimated from the system of equations,

$$x_{t+1} = x_t + ax_t - bx_t y_t \qquad (2)$$

and

$$y_{t+1} = y_t + cx_t y_t - dy_t \qquad (3),$$

where x_t and y_t are the biweekly means of J2 densities and the percentages of endospore-encumbered J2 at time t, respectively; whereas a, b, c, d, and k are the model parameters. On a per-capita basis, a represents the host growth rate in the absence of other limiting factors, b accounts for the host decrease due to parasitism, c is the parasite growth rate in relation to the host density, d indicates the parasite death rate, and k is an integration constant. For the Nicholson-Bailey model, the host-parasite interrelationship was represented by the system of equations,

$$x_{t+1} = \lambda(1 - \gamma)x_t + \lambda\gamma x_t e^{-\alpha Y_t} \qquad (4)$$

and

$$y_{t+1} = \gamma x_t(1 - e^{-\alpha Y_t}) \qquad (5),$$

under the assumption that only a proportion, γ, of J2 may contact endospores at a given generation, t, with a probability α (Hassel, 1978; Hassel and May, 1973). The parameter λ represents the host rate of increase. The two models were fitted with Mathcad computer software (MathSoft, Cambridge, MA) by iteratively assigning values to the parameters and the initial values x_o and y_o so as to maximize the correlation between the observed and the interpolated values of y at each of the observed x values. Student's t-test was used to compare the observed and the predicted percentages of endospore-encumbered J2.

Results

During the 2 years of experimentation, 9,606 J2 and a few males of *H. glycines* were examined for the attachment of *Pasteuria* endospores. On average, 64.4% of the J2 had endospores adhering to their cuticle, but none showed evidence of internal proliferation of the parasite. The highest J2 densities and the lowest rates of endospore attachment were observed in one of the microplots infested with race 3 of *H. glycines* (Table 1).

Temporal fluctuations of the H. glycines population: Over both years, population densities of *H. glycines* ranged from 0 to 41 cysts, 0 to 262 eggs/cyst, and 2 to 552 J2/250 cm^3 soil. Means and standard errors of the means were 7.9 ± 0.6, 89.5 ± 4.4, and 57.2 ± 7.1, respectively. The effect of sampling dates was significant ($P \leq 0.05$) for the numbers of cysts (Table 2). Specifically, mean numbers of cysts declined from 19.8 ± 4.2 on 10 May to 4.8 ± 0.6 on 1 September 1994 (Fig. 1). A similar trend was observed in 1995 when numbers of cysts declined from 12.0 ± 3.9 on 25 April to 2.3 ± 0.6 on 21 September, although they subsequently increased to 8.6

TABLE 1. Mean numbers of *Heterodera glycines* cysts, eggs per cyst, second-stage juveniles (J2), *Pasteuria* endospores per J2, and percentages of endospore-encumbered J2 per 250 cm^3 of naturally infested microplot soil.[a]

Year	Race	Plot	Number of cysts	Eggs per cyst	Number of J2	Spores per J2	Percent J2 with spores
1994	3	1	8.8	94.7	100.5	0.4	15.1
		2	8.4	137.7	26.1	4.7	75.9
	4	3	15.3	101.0	49.1	3.7	74.3
		4	7.9	76.5	26.9	3.6	70.5
1995	3	1	12.3	87.1	161.3	1.7	31.1
		2	2.4	86.0	26.6	9.7	79.0
	4	3	5.6	72.9	37.0	13.6	83.6
		4	4.5	69.7	23.5	8.0	80.1

[a] Two soil samples were collected at 2-week intervals from each of four 5-m × 5-m microplots, from 10 May to 4 October 1994 and from 5 April to 26 October 1995, resulting in 18 and 24 samples per microplot in 1994 and 1995, respectively.

± 4.3 by the end of the season. For mean numbers of cysts, there were no significant differences between race 3 (7.9 ± 0.8) and race 4 (7.9 ± 0.9), or between 1994 (10.1 ± 1.0) and 1995 (6.2 ± 0.7).

Mean numbers of eggs per cyst decreased gradually from 133.1 ± 26.3 on 10 May to 69.9 ± 10.8 on 7 July 1994, then increased and peaked at 120.3 ± 15.4 on 19 September 1994 (Fig. 1). In 1995, the numbers of eggs per cyst oscillated with a decreasing amplitude and a regular periodicity of about 1 month from 5 April (153.6 ± 24.6) through mid-August (49.3 ± 14.9). Thereafter, the numbers of eggs per cyst increased and peaked at 101.3 ± 15.5 on 6 October. The effect of sampling dates was not significant ($P > 0.05$) for the numbers of eggs per cyst, nor were there significant differences between race 3 (99.4 ± 6.6) and race 4 (79.2 ± 5.7) or between 1994 (102.5 ± 6.3) and 1995 (79.2 ± 6.0).

TABLE 2. Analysis of variance summary.

		Sum of squares				
Effects	df	Number of cysts[a]	Eggs per cyst[b]	Number of J2[b]	Spores per J2[a]	Percent J2 with spores
Block (B)	1	12.91*	3.84	35.96*	141.60*	2.55*
Race (R)	1	0.01	10.32	6.60	162.28	2.88
R × B	1	1.04	6.97*	5.61	233.65*	3.23**
Microplot (M) [R B][c]	4	5.15**	2.78	12.20***	28.24***	0.31***
Year (Y)	1	17.12	20.56	0.76	141.70*	0.46
Y × R	1	2.41	3.49	2.03	2.01	0.00
Y × R ×B	2	6.23*	5.38	3.90	5.36	0.07
Y × M [R B]	4	1.36	14.50*	1.93	28.55***	0.12*
Date (D)	11	21.56*	27.30	21.01	307.20***	1.45***
D × B	11	6.87*	—	11.69***	—	—
D × R	11	5.38	16.21	4.34	30.33	0.27*
D × R × B	11	3.79	33.15	19.58***	48.43	0.23
D × M [R B]	44	10.63	48.56	10.46	153.56***	1.09*
D × Y	8	1.63	10.05	17.65	143.94***	0.91***
D × Y × B	8	—	—	10.21**	—	—
D × Y × R	8	1.61	9.08	6.42	18.63	0.17
D × Y × R × B	8	2.60	15.97	8.18*	42.28	0.26
D × Y × M [R B]	32	7.10	24.40	11.84	71.10***	0.36
Nema [D Y M R B]	9438	—	—	—	5382.77	—
C.V. (%)		25.23	22.83	17.95	101.13	16.52

[a] $\ln(x + 1)$.
[b] $\ln(x)$.
[c] Effect nested within those enclosed by brackets.

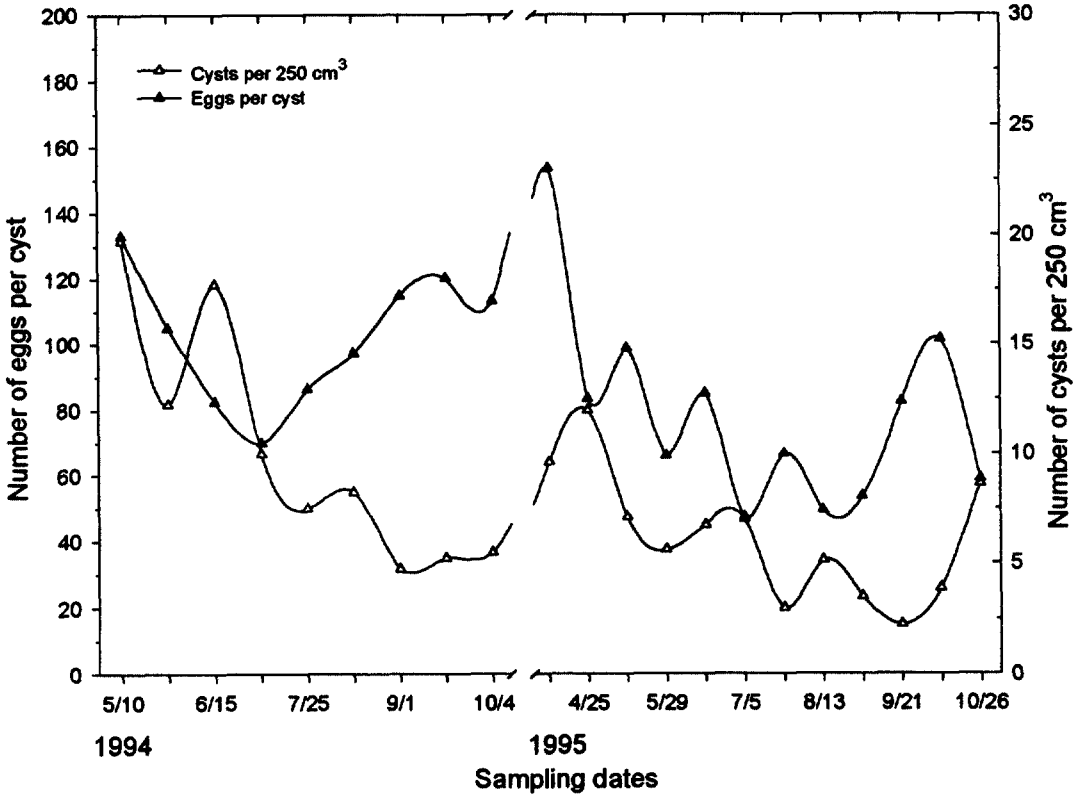

FIG. 1. Numbers of cysts and eggs per cyst of *Heterodera glycines* per 250 cm^3 of naturally infested microplot soil. Each observation represents the mean of eight samples, and points are connected with a cubic spline curve.

Numbers of J2 peaked at 157.3 ± 73.3 on 25 July 1994, and at 130.4 ± 74.1 on 21 September 1995 (Fig. 2). Other less pronounced peaks were observed on 12 May (65.6 ± 11.1) and 5 July (68.8 ± 11.8) of the second year. However, the analysis of variance (Table 2) indicated that none of the effects of sampling dates, race ($\overline{X}$ = 80.8 ± 13.3 and 33.5 ± 3.0 for races 3 and 4, respectively), and year ($\overline{X}$ = 50.6 ± 9.8 and 62.1 ± 9.9 for 1994 and 1995, respectively) was significant ($P > 0.05$) for numbers of J2. Also, no density-dependent trend was detected in the fluctuations of J2 numbers either in 1994 ($P = 0.417$) or in 1995 ($P = 0.156$), although the likelihood of density-dependence was significant ($P = 0.016$) when mean numbers of J2 were pooled over years.

Attachment of Pasteuria endospores: The numbers of *Pasteuria* endospores per J2 ranged from 0 to 133 ($\overline{X}$ = 3.9 ± 0.1), and the percentages of endospore-encumbered J2 ranged from 0 to 100% ($\overline{X}$ = 64.4% ± 2.3). The frequency distribution of the numbers of endospores per J2 was best described by a negative binomial distribution (expected mean $\mu = 2.1$ and clumping index $\theta = 0.2384$) rather than a Poisson distribution (X^2 = 403,037 and 1,070,200, respectively, for the saturated models). Based on the negative binomial distribution, the probability of a J2 being encumbered with at least one *Pasteuria* endospore was $P = 0.42$ (Fig. 3). However, the numbers of endospores per J2 were significantly affected by the race of *H. glycines,* the year, the date, and the interactions among these factors (results not shown). Specifically, the marginal effect of race on the expected mean number of endospores per J2 was an increase of 9.6 for race 4 ($\mu = 10.8$) compared to race 3 ($\mu = 1.2$), and the probability of having at least one endospore per J2 was 25% higher for race 4 ($P = 0.60$) than for race 3 ($P = 0.35$).

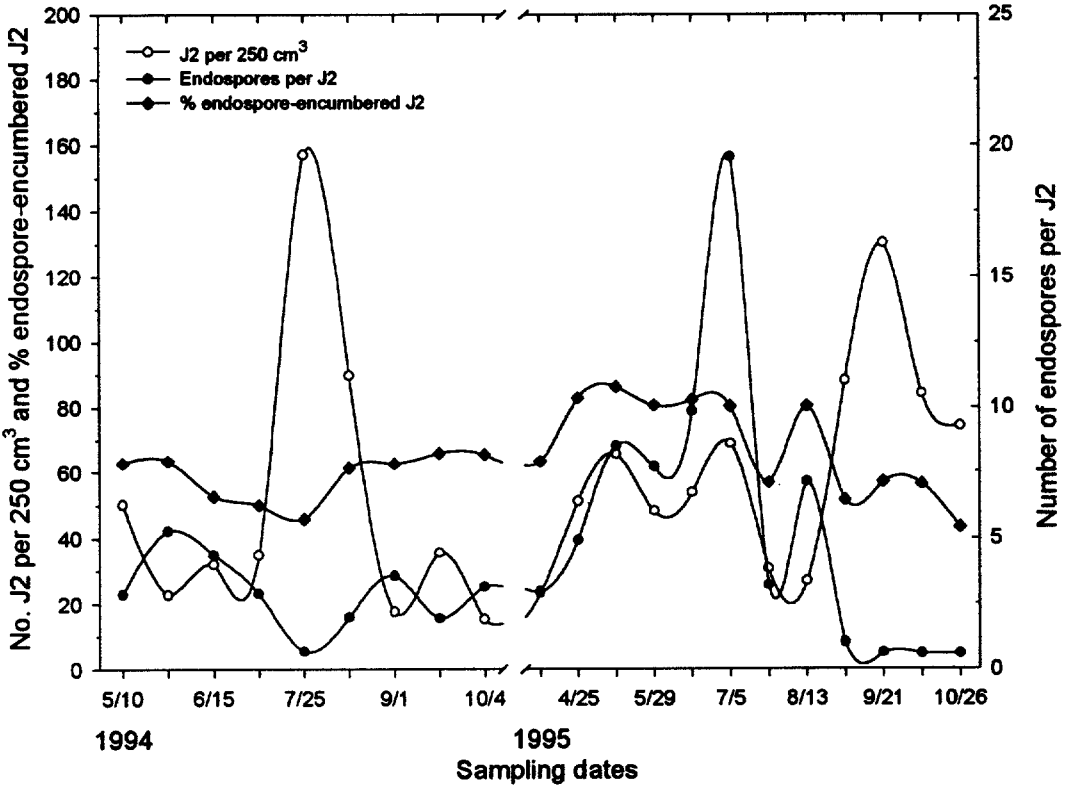

FIG. 2. Numbers of second-stage juveniles (J2) of *Heterodera glycines* and of *Pasteuria* endospores per J2, and percentages of endospore-encumbered J2 per 250 cm^3 of naturally infested microplot soil. Each observation represents the mean of eight samples, and points are connected with a cubic spline curve.

Similarly, the likelihood of having at least one endospore per J2 was higher in 1995 (P = 0.59) than in 1994 (P = 0.45), resulting in a greater expected mean number of endospores per J2 in 1995 (μ = 9.5) than in 1994 (μ = 2.6).

The analysis of variance (Table 2) also revealed significant ($P < 0.001$) seasonal fluctuations in the numbers of endospores per J2, and the percentages of endospore-encumbered J2. Fluctuations in numbers of endospores per J2 were affected by year, whereas both year and race of *H. glycines* had a significant effect on the fluctuations of the percentages of endospore-encumbered J2. In 1994, the numbers of endospores per J2 declined progressively from 5.3 ± 0.5 on 27 May to 0.7 ± 0.1 on 25 July, and thereafter increased to 3.6 ± 1.0 on 1 September (Fig. 2). In contrast, the numbers of endospores per J2 increased markedly during the first half of the 1995 growing season, from 3.0 ± 0.4 on 5 April to 19.6 ± 1.1 on 5 July, and subsequently declined to 0.6 ± 0.1 by the end of the season. For sampling dates where observations were made in both years, mean numbers of endospores per J2 were higher in 1995 than in 1994, except for the last three sampling dates (Fig. 2). The fluctuations in mean numbers of endospores per J2 were density-independent in both years (P = 0.368 and 0.898, respectively, for 1994 and 1995).

The percentages of endospore-encumbered J2 followed a trend similar to that of the numbers of endospores per J2. The mean percentages of endospore-encumbered J2 initially decreased from 62.9% ± 10.2 on 10 May to 45.9% ± 10.9 on 25 July, and then increased to 65.9% ± 11.0 by the end of the 1994 growing season (Fig. 2). In 1995, the percentages of endospore-encumbered J2 increased rapidly at the beginning of the growing season from 63.3% ± 11.0 on

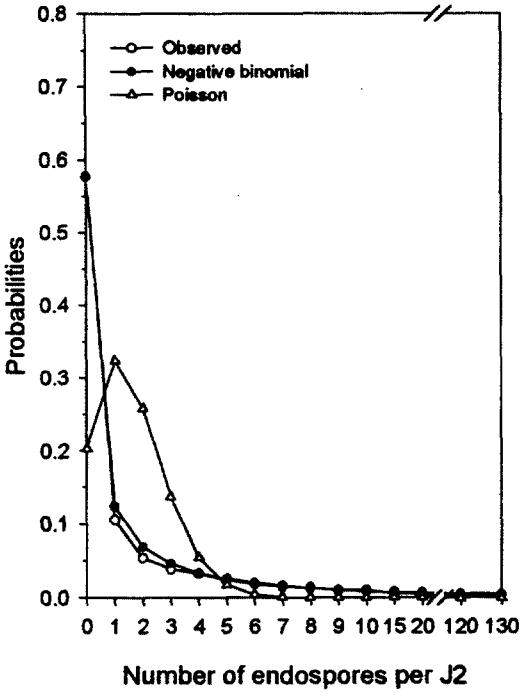

FIG. 3. Observed and predicted (negative binomial and Poisson distributions) probabilities for the attachment of *Pasteuria* endospores to second-stage juveniles (J2) of *Heterodera glycines* in a naturally infested microplot soil.

5 April to 86.3% ± 7.8 on 12 May. They leveled off at values ⩾ 80.3% ± 8.3 until 5 July, after which they declined to 43.4% ± 11.4 on 26 October. Percentages of endospore-encumbered J2 were higher in 1995 than in 1994 throughout the time period from 10 May to mid-August (Fig. 2). Likewise percentages of endospore-encumbered J2 were significantly higher for race 4 than for race 3, except in July (results not shown), with ranges of variation of 58.3% ± 11.2 to 90.6% ± 2.3, and 28.5% ± 18.4 to 75.2% ± 11.4, respectively. No density-dependent trend was observed in the fluctuations of mean percentages of endospore-encumbered J2 for both races of *H. glycines* ($P = 0.128$ and 0.712 for race 3, $P = 0.737$ and 0.468 for race 4 in 1994 and 1995, respectively), even when the data were pooled over years ($P = 0.636$ and 0.311, respecively, for race 3 and race 4).

Heterodera glycines-Pasteuria interrelationship: The relationship between J2 densities, Y, and the numbers of endospores per J2, X, was described by an exponential decay model, $Y = 67.4 + 220.1e^{-1.2X}$ (Fig. 4). According to this model, J2 densities declined with increasing numbers of endospores per J2 from 287.5 ± 5.2 to 67.4 ± 3.3 at a relative rate of 1.2 ± 0.1 units J2 density per endospore per J2 per unit J2 density, which was an absolute decrease of 220.1 ± 4.0 units J2 density attributed to the attachment of endospores. No further reduction in J2 densities occurred after 39.9 endospores had attached to every individual J2. This model accounted for the totality of the explainable variation in J2 densities, after allowance for pure error (72% total variation). A regression curve, $Y = 87.0(1 - e^{-0.53X})$, similar to the "competition curve" (Nicholson, 1933), provided a good fit ($r^2 = 0.75$; $P < 0.0001$) to the relationship between the percentages of endospore-encumbered J2, Y, and the mean numbers of endospores per J2, X (Fig. 5). Based on this equation, the percentages of endospore-encumbered J2 increased with the mean numbers of endospores per J2 at a relative rate of 0.53 ± 0.04 percent units per unit increase in mean numbers of endospores per J2 per percent unit until 87.0% ± 2.0 of the J2 were each encumbered with an average of 36.1 endospores.

The parameters of the Lotka-Volterra model (eq. 1) were estimated as $a = 0.0195$, $b = 0.000336$, $c = 0.000049$, $d = 0.00285$, and $k = 0.06589$ (Fig. 6). The model was fitted after 917 iterative solutions of the system of equations 2 and 3, starting from the initial values $x_0 = 11.250$ and $y_0 = 65.478$, respectively, for J2 densities and percentages of endospore-encumbered J2. The predicted equilibrium values for J2 densities (d/c) and the percentages of endospore-encumbered J2 (a/b) were 58.2 and 58.0, respectively. The corresponding ranges of variation were 10.5 to 175.3 and 33.1 to 93.6. A significant correlation ($r = 0.62$; $P < 0.01$) was obtained between the actual and predicted values of the percentages of endospore-encumbered J2, and the differences between these two sets of data were not significant ($t = 1.82$; $P > 0.05$). For the Nicholson-Bailey model, the

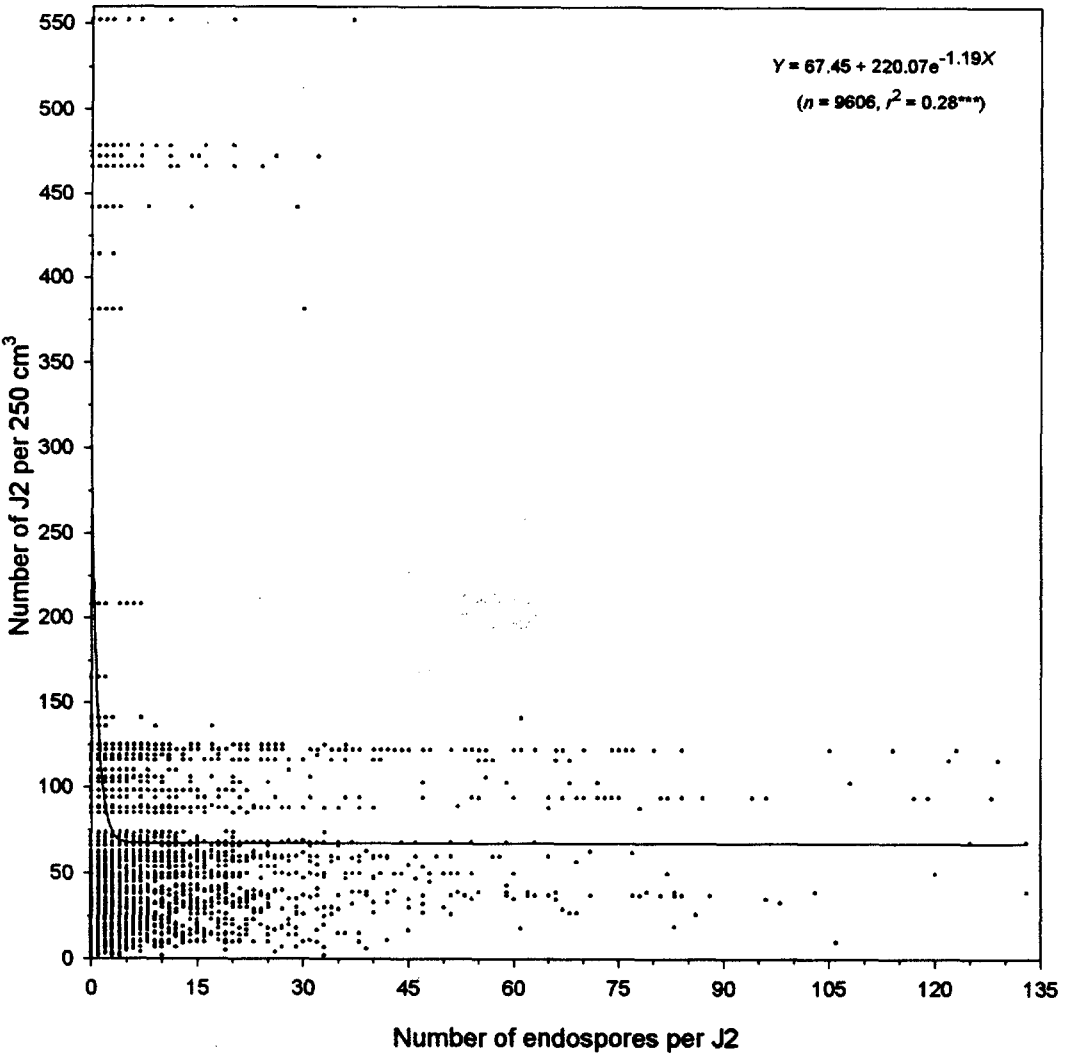

FIG. 4. Exponential decay of numbers of second-stage juveniles (J2) of *Heterodera glycines* with the numbers of *Pasteuria* endospores per J2 per 250 cm^3 of naturally infested microplot soil.

parameter estimates were $\lambda = 1.955$, $\gamma = 0.7978$, and $\alpha = 0.0789$ (Fig. 6). These values were obtained after 21 iterative solutions of the system of equations 4 and 5, beginning from $x_0 = 24.9$ and $y_0 = 68.7$. The steady values were calculated as 24.6 and 12.0, and the ranges of variation were 7.2 to 118.7 and 1.3 to 86.6, respectively, for J2 densities and percentages of endospore-encumbered J2. The actual and predicted values of the percentages of endospore-encumbered J2 were correlated ($r = 0.61$; $P \leq 0.01$), although they differed significantly according to Student's *t*-test ($t = 5.22$; $P < 0.01$). No correlation was found between numbers of cysts and numbers of endospores per J2, or percentages of endospore-encumbered J2. In contrast, a significant but low correlation ($r = -0.24$; $P < 0.01$) was observed between the numbers of eggs per cyst and the numbers of endospores per J2.

DISCUSSION

The *Pasteuria* spp. that parasitize cyst nematodes are separated into two groups, depending on their life history. The first group includes those that infect the oat and

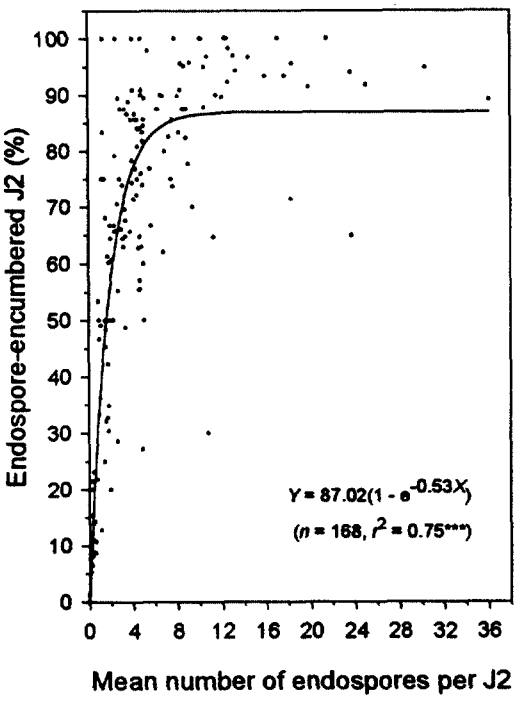

FIG. 5. Effect of the mean numbers of *Pasteuria* endospores per second-stage juvenile (J2) of *Heterodera glycines* on the percentages of endospore-encumbered J2 per 250 cm^3 of naturally infested microplot soil.

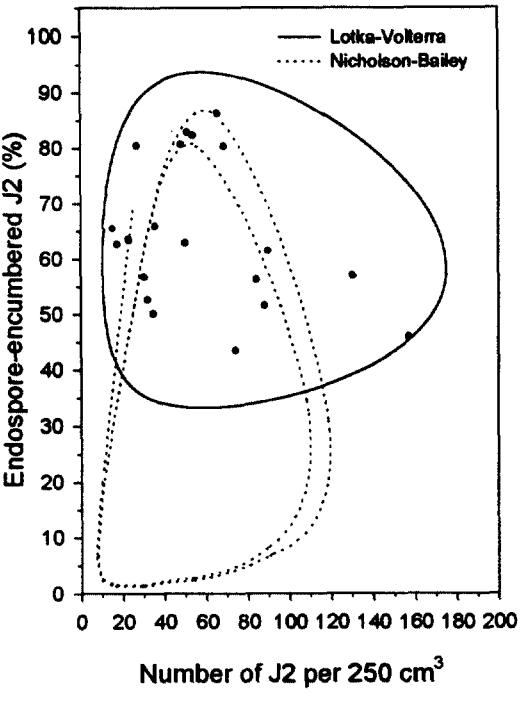

FIG. 6. Phase space diagram showing the relationship between densities of second-stage juveniles (J2) of *Heterodera glycines* and percentages of J2 encumbered with *Pasteuria* endospores in a naturally infested microplot soil. Each observation represents the mean of eight samples. The predictions for the Lotka-Volterra model were based on the system of equations

$$x_{t+1} = x_t + 0.0195x_t - 0.000336x_t y_t \text{ and}$$

$$y_{t+1} = y_t + 0.000049x_t y_t - 0.00285y_t;$$

where x_t and y_t are the numbers of J2 per 250 cm^3 soil and the percentages of endospore-encumbered J2 at time t, respectively; $t = 0, \ldots, 916$; $x_0 = 11.250$, and $y_0 = 65.478$. For the Nicholson-Bailey model, calculated values were obtained from the system of equations

$$x_{t+1} = 0.3953x_t + 1.55970x_t e^{-0.0789y_t} \text{ and}$$

$$y_{t+1} = 0.7978x_t(1 - e^{-0.0789y_t});$$

where x and y_t are the numbers of J2 per 250 cm^3 soil and the percentages of endospore-encumbered J2 at generation t, respectively; $t = 0, \ldots, 20$; $x_0 = 24.9$, and $y_0 = 68.7$.

pea cyst nematodes, *H. avenae* Wollenweber and *H. goettingiana* Liebscher. In these species the bacterium develops and completes its life cycle in the J2 (Davies et al., 1990; Sturhan et al., 1994). In the second group invasion of the host root by the endospore-encumbered J2 occurs prior to the germination of the bacterium, e.g. *P. nishizawae* on *H. glycines* (Sayre et al., 1991).

The life history of the Illinois isolate of *Pasteuria* was not known at the time the study was conducted. Therefore, its population dynamics and that of its host were investigated using attachment data of endospores to J2. Subsequent examinations of all life stages of *H. glycines* and cysts extracted from the rhizosphere of soybean plants revealed that the life history of this *Pasteuria* is similar to that of *P. nishizawae* (Atibalentja and Noel, 1997). Germ tubes develop from the endospores and penetrate the body of the nematode soon after the encumbered J2 invades the soybean root. The bacterium then proliferates and matures in the females, which ultimately become filled with an average of 3 × 10^5 endospores. Parasitized females normally do not produce eggs but, occasionally, a female may produce very few eggs. The life cycle is completed when endospores are liberated into the soil upon disintegration of the diseased female.

Seasonal fluctuations of irregular ampli-

tude and periodicity were observed in both the *Pasteuria* and the *H. glycines* populations. Typically, the greatest peaks in J2 densities coincided with the decline in the numbers of endospores per J2 and the percentages of endospore-encumbered J2. Such an observation suggests a regulation of the *H. glycines* population by *Pasteuria* sp., a hypothesis that has been substantiated by the fit of an exponential decay model to the relationship between J2 densities and numbers of endospores per J2. This model demonstrated a reduction of J2 densities with increasing numbers of endospores per J2, and a stable equilibrium density consistent with the obligately parasitic nature of *Pasteuria* sp. A similar conclusion was obtained from the analysis of variance, which showed that densities of J2 remained stable about their mean value. The steady density of J2 predicted by the Lotka-Volterra model also was consistent with that derived from the exponential decay model. In addition, the Lotka-Volterra model allowed the estimation of such biologically significant parameters as the host and parasite growth and death rates upon which the equilibrium of the host-parasite interrelationship hinges. The knowledge of these parameters may provide important clues about how the *H. glycines-Pasteuria* pathosystem could be manipulated to achieve effective control of the nematode by the bacterium.

The choice of the modified Nicholson-Bailey model (Hassel and May, 1973) was indicated by the form of the equation describing the relationship between the percentages of endospore-encumbered J2 and the mean numbers of endospores per J2. The similarity between this equation and the "random contact" equation (Jaffee et al., 1992; Nicholson, 1933; Perry, 1978) is apparent if the mean number of endospores per J2 is assumed to reflect the density, *S*, of endospores in the soil. In such a case, our equation gives the percentage of endospore-encumbered J2 as the product of two quantities: γ = the probability of a J2 being susceptible to infection, equal to 0.87 ± 0.02, and $P_s = 1 - e^{-0.53S}$ = the probability of having at least one endospore within the critical distance of a J2 (Perry, 1978). The critical distance, equal to 0.53, is the fraction of the soil pore volume covered per J2 per unit time, and is equivalent in concept to the transmission efficiency parameter of pathogen propagules (Anderson and May, 1981; Jaffee et al., 1992). These two terms are preferred to the term "searching efficiency" (Nicholson, 1933) since endospores are nonmotile and do not seek out their prey. However, unlike the spores of the nematophagous fungus *Hirsutella rhossiliensis* Minter & Brady (Jaffee et al., 1992; Perry, 1978), *Pasteuria* endospores are not transmitted directly through contact between parasitized and healthy nematodes (Ciancio, 1995). Lack of motility and of direct endospore transmission may explain why, despite the stabilizing effect of the refuge (Hassel and May, 1973) in which 11% to 20% of the J2 escape infection at each generation, the Nicholson-Bailey model did not fit the data as well as did the Lotka-Volterra model. In addition, the Nicholson-Bailey model and its variants (Hassel, 1978; Hassel and May, 1973; Jaffee et al., 1992; Perry, 1978) assume that encounters between the host and the parasite follow a Poisson distribution. We have shown that, for the *H. glycines-Pasteuria* pathosystem, the negative binomial distribution is more appropriate than the Poisson distribution.

This study indicated that the race of *H. glycines*, alone or in conjunction with other factors such as the date and the year, could have a significant effect on the numbers of endospores per J2 and the percentages of endospore-encumbered J2. Such results would imply that either the two races of *H. glycines* exhibit differential susceptibility to this *Pasteuria* or two distinct strains of the bacterium exist. Microscopic examinations of endospores from both races did not provide evidence to support the second of these hypotheses (Noel and Stanger, 1994). On the other hand, the results from individual microplots showed that the race effect could have originated from spatial and(or) temporal variations of *Pasteuria* inoculum densities in the soil. Further, these data suggest that the *Pasteuria* infestation of one of the race 3

microplots may have occurred later than that of the other three microplots.

The obligate nature and host specificity of *Pasteuria* spp. suggest density-dependent relationships with their hosts (Ciancio, 1995). The failure of the Pollard's test to detect any density-dependent trend in either the *H. glycines* or the *Pasteuria* populations does not rule out the existence of such relationships in these populations. In fact, the negative results obtained with the Pollard's test could be attributed to the small size of our time series, since the chance of detecting density dependence increases with the number of observations in the time series (Bulmer, 1975).

The research presented herein demonstrates that *Pasteuria* sp. is capable of maintaining *H. glycines* populations at equilibrium densities that are below the damage threshold reported from field studies (Noel, 1984). Whether fungi (Chen et al., 1996; McLean and Lawrence, 1995; Meyer and Meyer, 1996) contributed to this phenomenon is not known. Stiles et al. (1993) evaluated the pathogenicity of several fungi isolated from *H. glycines* in Illinois. Those fungi did not reduce either the numbers of cysts or numbers of eggs and J2. The soil used in that study originated from the same field that provided the soil for the microplots utilized in the current investigation. If other factors did affect the *H. glycines* population, their action may then explain the inflation of the pure error (variation in J2 densities at fixed levels of endospores per J2) observed and accounted for during the fitting of the exponential decay model. It is not known whether the equilibrium densities observed in this study can provide adequate control of *H. glycines* in commercial soybean fields. Nevertheless, these results are encouraging in that, given sufficient time following introduction into a field, this *Pasteuria* sp. may increase to levels that would be effective as one component in an integrated pest management program to control *H. glycines*.

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