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Effect of Initial Nematode Density on Managing *Globodera rostochiensis* with Resistant Cultivars and Nonhosts[1]

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Abstract: Cropping systems in which resistant potato cultivars were grown at different frequencies in rotation with susceptible cultivars and a nonhost (oats) were evaluated at four initial nematode population densities (Pi) for their ability to maintain *Globodera rostochiensis* at a target level of <0.2 egg/cm^3 of soil. At a Pi of 0.1 to 1 egg/cm^3 of soil, cropping systems with 2 successive years of a resistant cultivar every 3 years of potato production reduced and maintained *G. rostochiensis* at <0.2 egg/cm^3 of soil. At a Pi of 1 to 4 eggs/cm^3 of soil, 2 successive years of a resistant cultivar followed by 1 year of oats for every 4 years of production were necessary to reduce and maintain *G. rostochiensis* populations at <0.2 egg/cm^3 of soil. At a Pi greater than 4 eggs/cm^3 of soil, 2 successive years of a resistant cultivar plus 1 year of oats reduced *G. rostochiensis* densities to <0.2 egg/cm^3 of soil, but the population increased above that density after cropping 1 year to a susceptible cultivar. The numbers of cysts and eggs per cyst in the final population (Pf) of *G. rostochiensis* were influenced by initial density and the frequency of growing a susceptible cultivar in a cropping system. The lowest number of cysts and eggs per cyst in the final *G. rostochiensis* population occurred with a cropping system consisting of 2 successive years of a resistant cultivar followed by oats with a susceptible cultivar grown the fourth year of production.

Key words: cropping system, density, ecology, *Globodera rostochiensis,* golden nematode, integrated control, potato, potato cyst nematode, rotation.

Potato cyst nematodes, *Globodera rostochiensis* (Woll.) Behrens and *G. pallida* (Stone) Behrens, are the most economically important nematode parasites of potato (*Solanum tuberosum* L.) worldwide (9,12). In most countries where one or both species occur, some type of regulatory action is imposed to lessen their impact on potato production (4,6). Only *G. rostochiensis* (golden nematode) occurs in the United States and, although limited in distribution, it poses a serious threat to the U.S. potato industry (4,6).

Control of potato cyst nematodes in most countries is concerned with control of crop damage (7,9,22–24). In the United States, where stringent regulatory and quarantine activities do not allow population densities to reach crop-damaging levels, control of the golden nematode is concerned with control of nematode spread (4). Spread of *G. rostochiensis* is significantly limited at population densities <0.2 egg/cm^3 of soil (2). To minimize its spread, research on the golden nematode in the United States is aimed at developing strategies to manage its multiplication rates below unity (where the ratio of final population to initial population (Pf/Pi) is less than 1).

Managing potato cyst nematode multiplication rates below unity is much more difficult than managing population densities below crop-damaging levels (1). The decision to discontinue the use of chemical pesticides in the golden nematode control program made management of golden nematode multiplication rates below unity even more difficult. This decision placed total reliance on the use of host plant resistance and nonhost to control the golden nematode in the United States (4). The influence of host status on golden nematode population dynamics is well documented (7,11,13–15,18,23). Depending on initial density, decline in *G. rostochiensis* populations ranges from 85% to 95% each season that resistant potato cultivars are grown (11,20,21). Also, depending on initial nematode density, *G. rostochiensis* population densities increase from 2 to 35 times when susceptible cultivars are grown (9,11, 19). Decline of *G. rostochiensis* in the presence of a nonhost is density independent and, depending on environmental factors, ranges from 30% to 45% each season

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(9,11). Although the effects of individual cropping practices on *G. rostochiensis* population dynamics are known (5,8,17,26, 27), few studies have addressed their combined effects in different cropping systems on *G. rostochiensis* population dynamics (16).

In an earlier study, mathematical equations were developed to predict *G. rostochiensis* population density changes under resistant and susceptible potato cultivars (11). Cropping systems were identified involving resistant and susceptible cultivars and nonhost crops that these equations predicted would manage the golden nematode at various densities. The objective of the present study was to validate the efficacy of these cropping systems in managing *G. rostochiensis*. Specifically, this study was made to determine the influence of initial nematode density on the frequency at which resistant potato cultivars must be grown in rotation with susceptible cultivars and nonhost crops to reduce and manage *G. rostochiensis* at levels that minimize its potential for spread.

Materials and Methods

Studies were conducted at Prattsburg, New York, in field plots (10 m × 15 m) naturally infested with *G. rostochiensis* pathotype Ro1. The soil in these plots was a silty clay with 9.1% sand, 46.9% silt, and 44% clay. Different nematode population densities in the plots resulted from previous experiments involving combinations of crop rotations and nematicide application. Plots were divided into four groups of 20 plots each, representing four initial nematode population density ranges. The initial density ranges were 0.1–1.0 egg, 2–4 eggs, 5–15 eggs, and 16–35 eggs/cm^3 of soil.

Four different cropping systems were imposed on the different initial nematode densities. The cropping systems consisted of (i) alternating 1 year of golden-nematode resistant potato cv. Kanona with 1 year of a susceptible potato cv. Monona (R–S), (ii) 1 year of the resistant cultivar followed by 1 year of a nonhost crop of oats (*Avena sativa* cv. Porter) plus the susceptible cultivar in the third year (R-NH-S), (iii) alternating 2 successive years of the resistant cultivar with 1 year of the susceptible cultivar (R-R-S), and iv) 2 successive years of the resistant cultivar followed by 1 year of oats plus the susceptible cultivar in the fourth year (R-R-NH-S). These cropping systems represented a 2-, 3-, and 4-year rotation cycle. Each rotation cycle was repeated at least once. Five plots of each of the four nematode densities were assigned at random to each cropping system. Each set of assigned plots was planted only to its designated cropping system during the course of the experiment. The experimental design was a split plot with nematode densities as main plots and cropping systems as subplots arranged in a randomized complete block with five replications. The crops were planted in May and harvested in September of each year. In order to repeat each cropping system at least once, the experiment ran for 8 years.

The initial *G. rostochiensis* density ranges were determined from soil samples taken in September prior to the beginning of the experiment the following May. Changes in population density and structure (number of cysts with viable eggs and number of eggs per cyst) due to cropping system were determined from soil samples taken in September of each year immediately after harvest. Soil samples were taken with a sampling trowel inserted 8 cm deep on 0.37-m centers. A total of 50 subsamples consisting of 50 g each were taken from each plot. Subsamples from individual plots were bulked and air dried for 30 days. Afterwards, each bulked sample was thoroughly mixed and a 1.8 kg sample was processed using a U.S. Department of Agriculture cyst extractor (11). The number of cysts recovered from each sample was recorded and the cysts were saved. The number of cysts with viable eggs and the number of viable eggs per cyst were then determined by crushing 100 individual cysts selected at random from each sample. These data were used to calculate numbers of viable eggs per cubic centimeter of soil (population density) and to determine changes in the number of cysts with viable eggs and the number of viable eggs per cyst over time (population structure).

Data analysis consisted of a 1-way ANOVA for each of the 8 years. Means were compared using Fisher's protected LSD at $P \leqslant 0.05$.

Results

Population densities (eggs/cm^3 of soil) of *G. rostochiensis* varied widely in response to the host status of the crop grown each growing season (Figs. 1,2). Population densities declined up to 95% when a resistant host was grown but only 30% to 40% when a nonhost was grown. The magnitude of nematode population decline when a resistant host was grown depended upon the initial nematode density (Pi) with the greatest decline occurring at a high Pi (Figs. 1,2). Increase in *G. rostochiensis* population density in response to growing a susceptible potato cultivar was inversely related to Pi. The greatest increase occurred at a low Pi, except at extremely low densities (Fig. 1C,D). When population densities were reduced to less than 0.1 egg/cm^3 of soil, increase in density was essentially negligible after growing a susceptible cultivar (Fig. 1D).

The ability of cropping systems to reduce and maintain *G. rostochiensis* at desired population densities was variable and was influenced by Pi. At a Pi of 0.1–1.0 egg/cm^3 of soil and 2–4 eggs/cm^3 of soil, cropping systems without 2 successive years of a resistant potato cultivar reduced *G. rostochiensis* densities to less than 0.2 egg/cm^3 of soil but did not maintain them below that level (Fig. 1A,B). Cropping systems with 2 successive years of a resistant cultivar reduced a Pi of 0.1–1.0 egg/cm^3 of soil of *G. rostochiensis* to <0.2 egg/cm^3 of soil and maintained it below that level (Fig. 1C,D). At a Pi of 2–4 eggs/cm^3 of soil, the cropping system R-R-S reduced *G. rostochiensis* densities to <0.2 egg/cm^3 of soil but did not maintain it below that level (Fig. 1C). However, the cropping system R-R-NH-S reduce the *G. rostochiensis* Pi of 2–4 eggs/cm^3 of soil to <0.2 egg/cm^3 of soil and maintained it below that level (Fig. 1D).

None of the cropping systems tested reduced and maintained *G. rostochiensis* at the desired <0.2 egg/cm^3 of soil when the Pi was greater than 4 eggs/cm^3 of soil (Fig. 2A–D). At this Pi, population densities fluctuated annually and were dependent on the host status of the crop grown. The magnitude of annual population fluctuation increased as Pi increased, with the greatest fluctuations in population density occurring at a Pi of 16–35 eggs/cm^3 of soil (Fig. 2A–D).

Assessment of population density following a susceptible cultivar at the end of a rotation cycle was used to measure the effectiveness of a particular cropping system in managing *G. rostochiensis*. After one rotation cycle, cropping systems with a minimum of 2 successive years of a resistant cultivar had reduced the *G. rostochiensis* Pi of 0.1–1.0 egg/cm^3 of soil to <0.2 egg/cm^3 of soil and maintained it below that level (Fig. 3A). Cropping systems with only 1 year of a resistant cultivar per rotation cycle did not reduce the *G. rostochiensis* Pi of 0.1–1.0 egg/cm^3 of soil to <0.2 egg/cm^3 of soil after one cycle. Similar results were obtained after two rotation cycles at a Pi of 0.1–1.0 egg/cm^3 of soil (Fig. 3A).

The cropping system R-R-NH-S reduced the *G. rostochiensis* Pi of 2–4 eggs/cm^3 of soil to <0.2 egg/cm^3 of soil after one rotation cycle and maintained it below that level (Fig. 3B). At a Pi of 2–4 eggs/cm^3, none of the other cropping systems tested reduced *G. rostochiensis* populations to the desired density of <0.2 egg/cm^3 of soil even after two rotation cycles. However, the cropping systems R-R-S and R-S reduced the *G. rostochiensis* Pi of 2–4 eggs/cm^3 of soil after one rotation cycle but not to the desired level of <0.2 eggs/cm^3 of soil (Fig. 3B) ($P = 0.05$).

None of the cropping systems evaluated reduced the *G. rostochiensis* Pi of >5.0 eggs/cm^3 of soil to <0.2 egg/cm^3 of soil after one

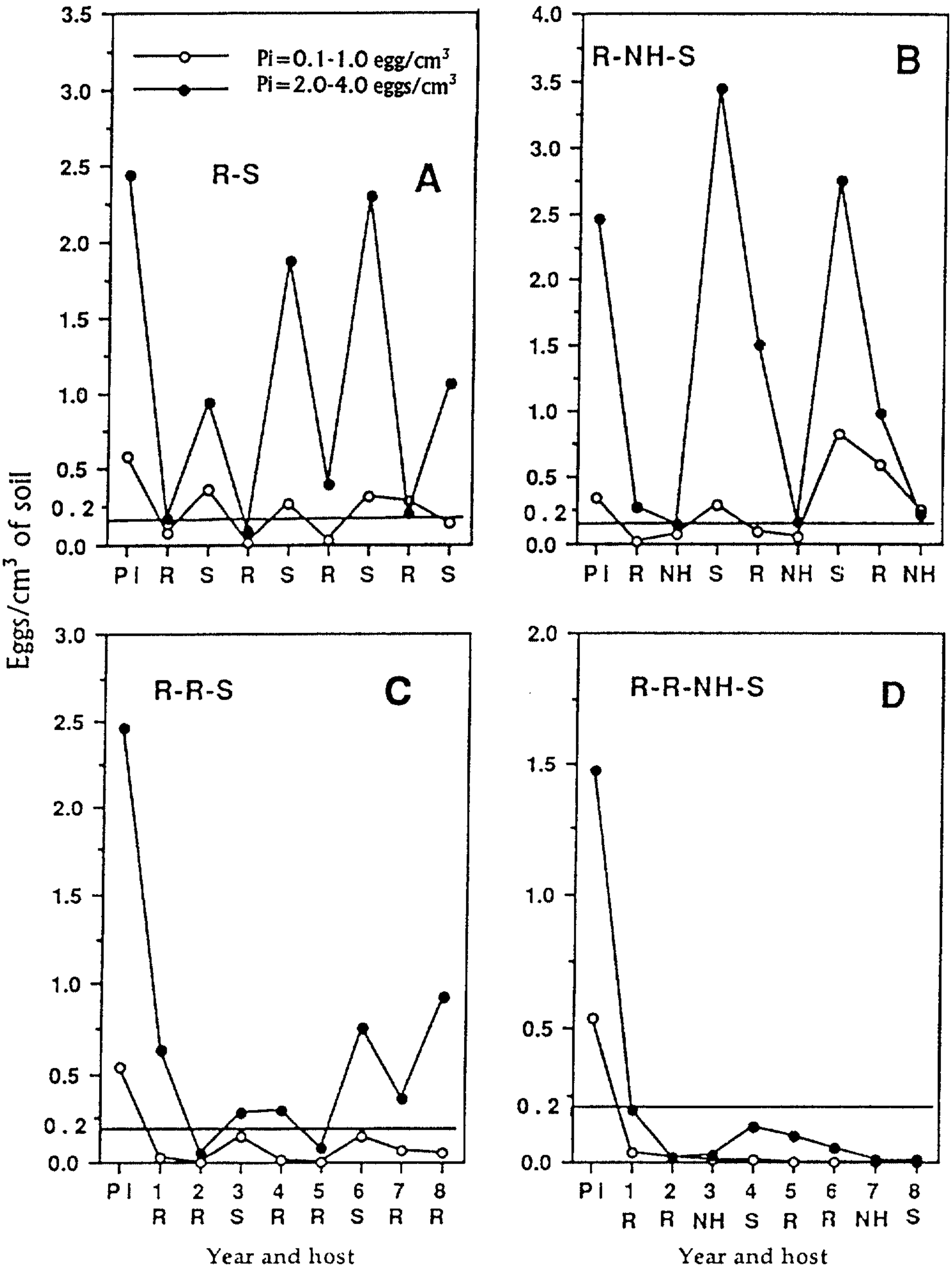

FIG. 1. *Globodera rostochiensis* population density changes following four cropping systems at a Pi of 0.1–1.0 and 2–4 eggs/cm^3 of soil. The cropping systems were: A) alternating resistant (R) and susceptible (S) cultivars; B) 1 year of R followed by oats, a nonhost (NH), the second year with S the third year; C) alternating 2 successive years of R with 1 year of S; D) 2 successive years of R followed by NH with S the fourth year. The horizontal line on a graph represents the desired Pf of below 0.2 egg/cm^3 of soil.

rotation cycle (Fig. 3C,D). However, after two rotation cycles, the cropping system R-R-NH-S reduced the Pi of 5–15 eggs/cm^3 of soil to <0.2 egg/cm^3 of soil (Fig. 3C). Also, after two rotation cycles, cropping systems with at least 2 successive years of a resistant cultivar reduced the *G. rostochiensis* Pi of >5.0 eggs/cm^3 of soil but not to the desired level of <0.2 eggs/cm^3 of soil (P = 0.05). This population reduction was

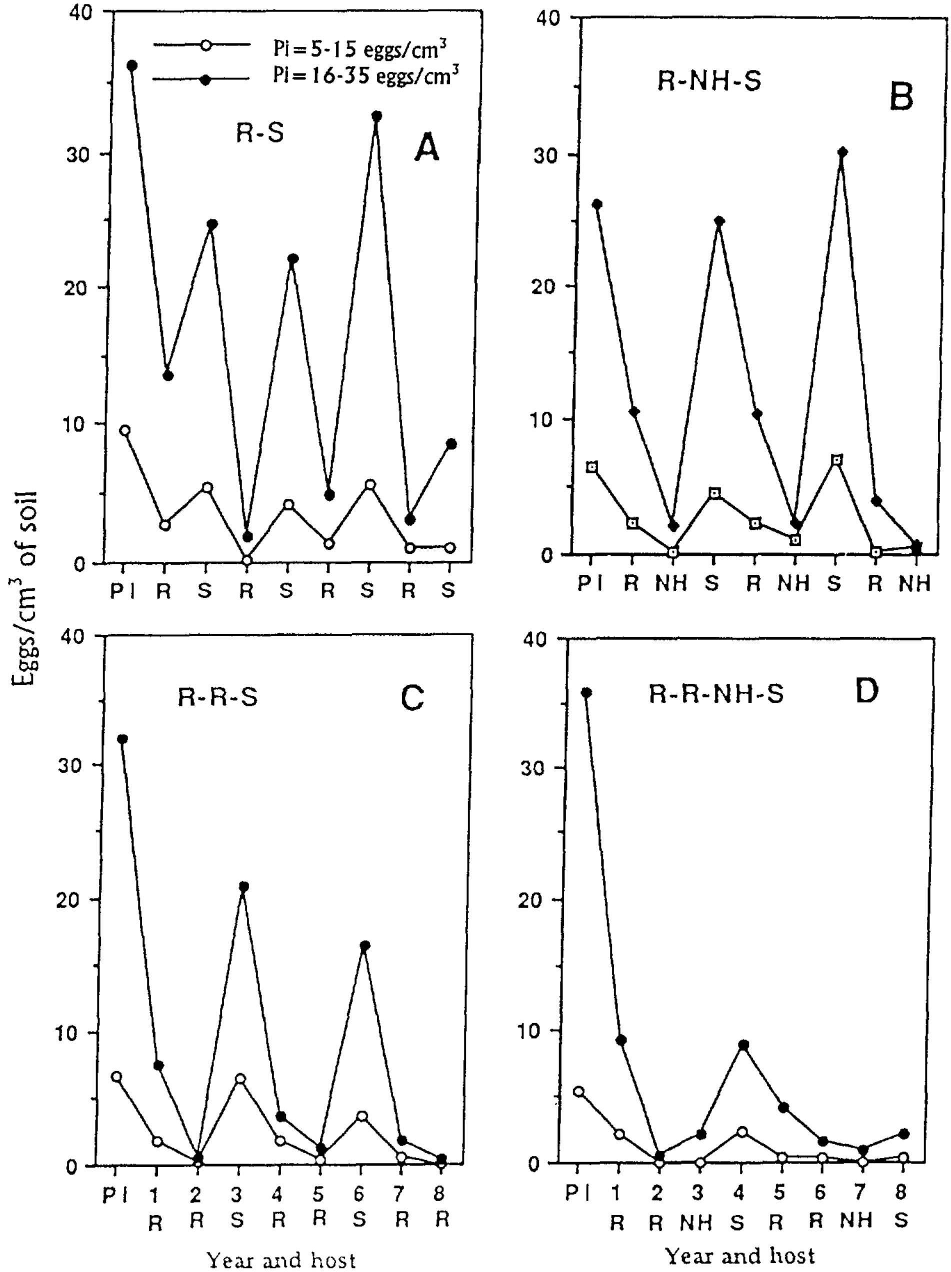

FIG. 2. *Globodera rostochiensis* population density changes following four cropping systems at a Pi of 5–15 and 16–35 eggs/cm^3 of soil. The croppingsystems were: A) alternating a resistant (R) and susceptible (S) cultivar; B) 1 year of R followed by oats, a nonhost (NH), the second year with S the third year; C) alternating 2 successive years of R with 1 year of S; D) 2 successive years of R followed by NH with S the fourth year.

greatest with the R-R-NH-S cropping system (Fig. 3C,D).

The structure (number of cysts with viable eggs and number of viable eggs per cyst) of the final *G. rostochiensis* population (Pf) was influenced by Pi and cropping systems. Regardless of cropping system, the largest numbers of cysts with viable eggs (viable cysts) in the Pf occurred in plots with the greatest Pi (Fig. 4). Also, regardless of Pi, the fewest number of viable cysts in the Pf occurred in plots in which the

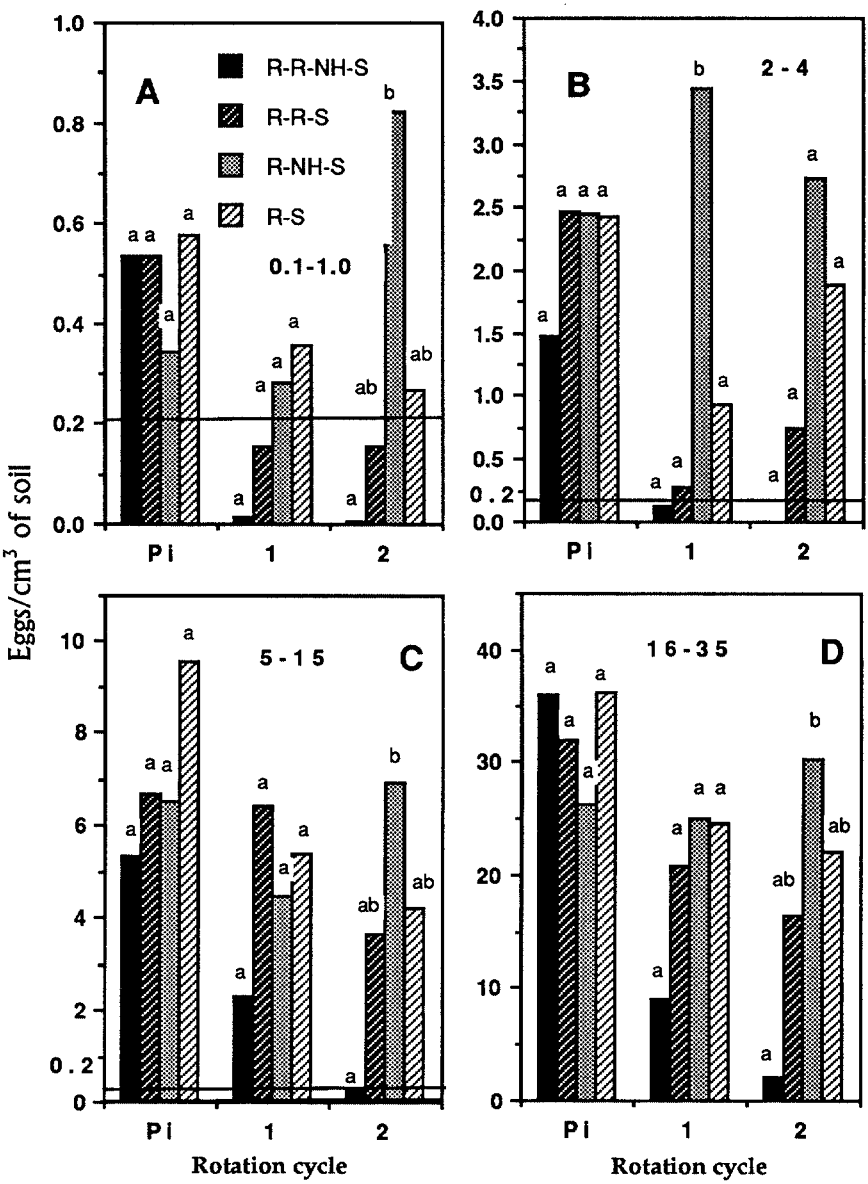

FIG. 3. Population densities of *Globodera rostochiensis* after one and two rotation cycles of four cropping systems at four Pi levels. A) Pi of 0.1–1.0 egg/cm^3 of soil, B) Pi of 2–4 eggs/cm^3 of soil; C) Pi of 5–15 eggs/cm^3 of soil, and D) Pi of 16–35 eggs/cm^3 of soil. Cropping systems consisted of 1) 2 successive years of a resistant cultivar (R) followed by the nonhost oats (NH), with a susceptible cultivar (S) the fourth year (R-R-NH-S; 2) alternating 2 successive years of R with 1 year of S (R-R-S; 3) 1 year of R followed by 1 year of NH with S the third year (R-NH-S; and 4) alternating R with S (R–S). The horizontal line on a graph represents the desired Pf of 0.2 egg/cm^3 of soil. Columns with different letters are significantly different (P = 0.05) according to Fisher's protected LSD.

cropping system R-R-NH-S was grown. At each Pi, the Pf consisted of fewer viable cysts in plots where the R-R-NH-S cropping system was grown than where the R-R-S, R-S, or R-NH-S cropping systems were grown (P = 0.05).

The number of viable eggs per cyst in the final *G. rostochiensis* population also was influenced by Pi and cropping system. At each Pi the Pf consisted of fewer viable eggs per cyst following the cropping system R-R-NH-S (P = 0.05) (Fig. 5). The cropping system R-R-S reduced the number of viable eggs per cyst in the final population at a Pi of 5–15 eggs/cm^3 of soil (P = 0.05). Cysts in the final population that contained the largest number of viable eggs occurred in plots with a Pi of 16–35 eggs/cm^3 of soil and in which a susceptible cultivar was grown at least once in 3 years (R-R-S, R-NH-S, and R-S).

Discussion

Several studies have reported a negative correlation between initial nematode density and *G. rostochiensis* population increase on susceptible potatoes (9,11,13,20). However, Kort (10) reported a positive correlation between Pi and cyst production at low densities. Further, LaMondia and Brodie (11) suggested that at some unknown low density the negative correlation between Pi and reproduction on both susceptible and resistant cultivars would change to a positive correlation. These studies confirmed both of these aspects of *G. rostochiensis* population dynamics. At high densities, *G. rostochiensis* increase was negatively correlated with Pi. At extremely low densities of 0.01 egg/cm^3 of soil or lower, *G. rostochiensis* population increase after 1 year of a susceptible cultivar was negligible. This phenomenon fits with the suggestion of Jones (9) that, at extremely low densities, *G. rostochiensis* may experience difficulties with host or mate finding, or both, resulting in little or no multiplication.

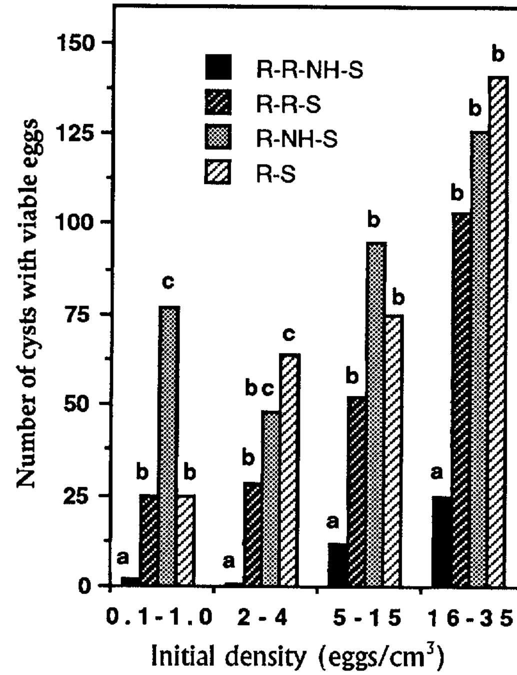

FIG. 5. Number of viable eggs per cyst in the final population of *Globodera rostochiensis* after two rotation cycles of four cropping systems at four initial densities. The cropping systems consisted of 1) 2 successive years of a resistant cultivar (R) followed by 1 year of the nonhost oats (NH) with a susceptible cultivar (S) the fourth year (R-R-NH-S), 2) alternating 2 successive years of R with 1 year of S (R-R-S), 3) 1 year of R followed by 1 year of NH with S the third year (R-NH-S), and 4) alternating R and S (R-S). Columns with different letters are significantly different (P = 0.05) according to Fisher's protected LSD.

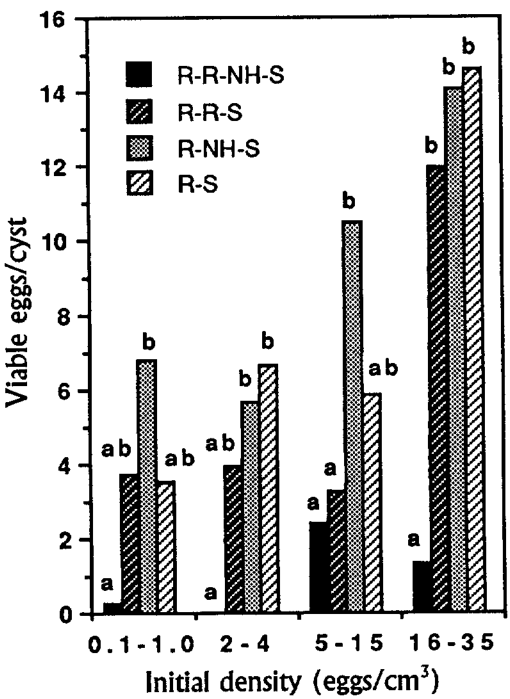

FIG. 4. Number of *Globodera rostochiensis* cysts with viable eggs in the final population after two rotation cycles of four cropping systems at four Pi levels. The cropping systems consisted of 1) 2 successive years of a resistant cultivar (R) followed by the nonhost oats (NH) with a susceptible cultivar (S) the fourth year (R-R-NH-S), 2) alternating 2 successive years of R with 1 year of S (R-R-S), 3) 1 year of R followed by 1 year of NH with S the third year (R-NH-S), and 4) alternating R with S (R-S). Columns with different letters are significantly different (P = 0.05) according to Fisher's protected LSD.

We reported earlier from this laboratory that *G. rostochiensis* population density decline in response to growing a resistant cultivar with the H_1 gene was density dependent with a greater decline at higher densities (11). In this study, percentage decline in *G. rostochiensis* population densities was consistent over several different densities. The average decline in *G. rostochiensis* population densities after growing a resistant cultivar was 76% at an average Pi of 27 eggs/cm^3 of soil, 75% at an average Pi of 6.7 eggs/cm^3 of soil, 78% at an average Pi of 2.5 eggs/cm^3 of soil, and 80% at an average Pi of 0.5 egg/cm^3 of soil. These experiments were conducted in soil naturally infested with *G. rostochiensis*, whereas previous studies relied on changes in population densities inside nylon bags buried around plants. Because of the need for a hatching stimulant, population changes in total soil mass are probably more reflective of the true population dynamics of *G. rostochiensis* than are changes in the number of viable eggs in cysts placed in the immediate vicinity of roots.

The growing of a susceptible cultivar at the end of each rotation cycle was a good indicator of the efficacy of a cropping system in terms of maintaining *G. rostochiensis* at the desired population level. If *G. rostochiensis* population density increased above 0.2 egg/cm^3 of soil when the susceptible cultivar was grown, the cropping system was judged to present too great a risk of nematode spread. Except at extremely low densities, *G. rostochiensis* populations increased when a susceptible cultivar was grown. One exception involved the cropping system with 2 successive years of a resistant cultivar followed by a susceptible cultivar grown at a Pi of 2–4 eggs/cm^3 of soil. During the eighth year of this cropping system, *G. rostochiensis* population density increased instead of decreased when a resistant cultivar was grown. This type of response indicates the presence of a race or pathotype of the nematode that can overcome resistance conferred by the H_1 gene (28). The populations of *G. rostochiensis* in the United States are believed to consist solely of pathotype Ro1, which is avirulent against the H_1 gene (4). However, the possible existence of other pathotypes or species of potato cyst nematode in these experimental plots is being examined. Another exception where *G. rostochiensis* did not behave as anticipated involved the cropping system in which resistant and susceptible cultivars were grown alternately. In this case, *G. rostochiensis* population did not increase when a susceptible cultivar was grown during the eighth year of the cropping system. Other than sampling error, no plausible explanation exists for this type of response.

Because spread of *G. rostochiensis* is severely limited at population densities of 0.2 egg/cm^3 of soil or lower (2), the objective of this research was to identify cropping systems that would maintain *G. rostochiensis* below that level. The ability of a cropping system to reduce and maintain *G. rostochiensis* densities below 0.2 egg/cm^3 of soil was related to both Pi and the frequency at which resistant and susceptible cultivars were grown in the cropping system. When the Pi exceeded 4 eggs/cm^3 of soil, none of the cropping systems tested in these studies reduced *G. rostochiensis* population densities and maintained them below 0.2 egg/cm^3 of soil. Because of strict regulatory activities against *G. rostochiensis* in the United States, population density rarely, if ever, exceeded 4 eggs/cm^3 of soil. Current soil survey techniques can detect *G. rostochiensis* population densities of 1–4 eggs/cm^3 of soil (3). At this Pi, *G. rostochiensis* was successfully managed at <0.2 egg/cm^3 of soil with cropping system of at least 2 successive years of a resistant cultivar followed by 1 year of oats with a susceptible cultivar grown no more frequently than once in 4 years. When the Pi was <1.0 egg/cm^3 of soil, *G. rostochiensis* was successfully managed with 2 successive years of a resistant cultivar with a susceptible cultivar grown once in 3 years of potato production.

Spread of *G. rostochiensis* is a function of both the number of cysts with viable eggs per unit volume of soil and the number of viable eggs per cyst. In earlier studies, we found that at a Pi of 0.05–0.20 egg/cm^3 of soil there was 12% probability of spread of *G. rostochiensis* cysts on potato tubers (2). Further studies indicated that the probability of population establishment after spread was a function of the number of viable eggs per cysts with 5% probability of establishment with three viable eggs per cyst and 20% probability of establishment with up to five eggs per cyst (3). In the present study, the cropping system in which a susceptible potato cultivar was grown only once in 4 years (R-R-NH-S) resulted in a fewer number of cysts with viable eggs and a fewer number of viable eggs per cysts than did other cropping systems. These differences were particularly evident at a Pi of 0.1–1.0 and 2–4 eggs/cm^3 of soil. Because the use of this cropping system in infested soil results in an acceptable risk of spreading *G. rostochiensis,* regulatory officials have approved and implemented it in the *G. rostochiensis* control program. Although the use of this cropping system to manage *G. rostochiensis* has proven successful, the source of resistance (H_1 gene) in the potato cultivars used in this system is effective against only *G. rostochiensis* pathotypes Ro1 and Ro4. This cropping system would not effectively manage other pathotypes of *G. rostochiensis* or *G. pallida* (25).

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