

## Effects of Initial Nematode Density on Population Dynamics of *Globodera rostochiensis* on Resistant and Susceptible Potatoes<sup>1</sup>

J. A. LAMONDIA AND B. B. BRODIE<sup>2</sup>

**Abstract:** The influence of resistant and susceptible potato cultivars on *Globodera rostochiensis* population density changes was studied at different nematode inoculum levels (Pi) in the greenhouse and field. Soil in which one susceptible and two resistant cultivars were grown and fallow soil in pots was infested with cysts to result in densities of 0.04–75 eggs/cm<sup>3</sup> soil. A resistant cultivar was grown in an infested field with Pi of 0.7–16.7 eggs/cm<sup>3</sup> soil. Pi was positively correlated with decline of soil population densities due to hatch where resistant potatoes were grown in the greenhouse and in the field but not in fallow soil. However, Pi was not correlated with in vitro hatch of *G. rostochiensis* cysts in water or potato root diffusate. Under continuous culture of a resistant cultivar, viable eggs per cyst declined 60–90% per plant growth cycle (4 weeks) and the number of cysts containing viable eggs had decreased by 77% after five cycles. The rate of *G. rostochiensis* reproduction on both resistant and susceptible cultivars was negatively correlated with Pi. These data were used to predict the effect of resistant and susceptible potato cultivars on *G. rostochiensis* soil population dynamics.

**Key words:** *Globodera rostochiensis*, golden nematode, modeling, plant resistance, population dynamics, *Solanum tuberosum*, potato.

The H<sub>1</sub> gene from *Solanum tuberosum* subsp. *andigena* Juz. & Buk. has been widely used as a source of resistance to Race 1 (pathotype Ro1 or R1A) of *Globodera rostochiensis* Behrens (16). Root diffusates from potato plants resistant to *G. rostochiensis* stimulate hatch and emergence of second-stage juveniles (J2) from cysts. Roots of resistant plants are invaded, but nematode development is limited by necrotic degeneration of syncytial feeding cells (7) usually resulting in death of the J2. This resistance mechanism is not absolute, as a few J2 successfully induce syncytia and develop into adult females. This is reflected in the procedure used to evaluate potato clones for *G. rostochiensis* resistance. Any plant on which more than five cysts develop is considered susceptible, and plants with fewer than five cysts are resistant (15).

The existence of resistance-breaking biotypes of *G. rostochiensis* has been demonstrated (3,20). It was originally proposed that any *G. rostochiensis* female that developed and reproduced on resistant plants had the genetic capability to overcome host resistance (9,10). Additional testing of the

few cysts produced in the Race 1/H<sub>1</sub> combination in the United States and Europe indicated that not all reproduction on resistant cultivars was due to resistance-breaking biotypes of the nematode. After 7 years of resistant cultivar monoculture, Harrison (5) did not detect resistance-breaking biotypes of *G. rostochiensis* in the United States. Populations of *G. rostochiensis* that reproduce poorly on resistant plants often produce a few females (14,20). The progeny of these females do not possess the capacity to reproduce abundantly on resistant plants. The reason for their limited reproduction is not known. This limited reproduction, sufficient to maintain populations at a low level (2,8), has recently been shown to be density dependent (17).

Resistant potato cultivars have been used to suppress *G. rostochiensis* soil population densities, achieving about 80% population reduction (2,3,19). Distribution of the nematode mirrors that of potato root systems in soil and may result in fairly uniform distribution of cysts to 40 cm deep in some soils (22). Such deep infestations may be more effectively managed by planting resistant cultivars than by applying nematicides. Potato root distribution in soil depends on growing conditions and is not uniform throughout the plow layer of the soil (12). Recent work indicates that about 70% of the soil in the plow layer contains the roots in which *G. rostochiensis* repro-

Received for publication 19 April 1985.

<sup>1</sup> Cooperative investigations of USDA ARS and Cornell University Agricultural Experiment Station.

<sup>2</sup> Postdoctoral Associate and Research Plant Pathologist, USDA ARS, Department of Plant Pathology, Cornell University, Ithaca, NY 14853.

TABLE 1. Percentage decline in *Globodera rostochiensis* juveniles per cyst as influenced by initial nematode density, cultivar, and fallow after 14 weeks.

Initial nematode density (eggs/cm <sup>3</sup> soil)	Fallow	Hudson	Rosa	Katahdin
0.04			64.5	64.5
0.07			64.9	64.0
0.18			77.6	86.7
0.36			82.6	84.4
0.72			76.0	84.6
0.75	12.2	81.4	63.5	82.0
3.75	39.2	91.2	84.6	85.0
7.50	44.9	92.9	81.9	85.0
37.50	42.0	95.4	83.8	90.6
75.00	45.9	94.6	96.8	90.6

ANOVA: 0.04–75.00,  $F = 7.98$ ; 0.75–75.00,  $F = 6.59$ ;  $r = 0.76$ .

Linear contrasts: Fallow decline less than under potatoes. Decline under Hudson and Rosa equal to Katahdin. Decline at lowest densities less than at greater densities. Decline at 75.00 eggs/cm<sup>3</sup> soil greater than at lower densities.

duces. The remaining 30% of the soil volume either lacks roots or does not contain roots until very late in the growing season and is therefore subject to nematode population decline, even with a susceptible cultivar (D. Rawsthorne, pers. comm.).

The golden nematode is a quarantined pest in the United States; its management consists primarily of maintaining soil population densities below levels at which spread might occur (4). Our objectives were to investigate 1) the influence of growing resistant potato cultivars on decline of *G. rostochiensis* soil populations, 2) the influence of low initial densities (Pi) on *G. rostochiensis* reproduction on resistant and susceptible potato cultivars, and 3) the effect of continuous planting of resistant cultivars on the final soil population densities (Pf) of *G. rostochiensis*.

#### MATERIALS AND METHODS

The decrease in numbers of juveniles in cysts from hatch and increase in cyst numbers from nematode reproduction on resistant and susceptible cultivars were determined in a greenhouse. Cysts of uniform size and age (0.35–0.45-mm-d, produced in 1981) with known viable contents of 151.0 eggs/cyst were mixed with 1 cm<sup>3</sup> soil and enclosed in nylon bags (11). Bags containing 1, 5, 10, 50, or 100 cysts were placed

1–2 cm below single-eye seed pieces of the resistant cultivars 'Rosa' and 'Hudson' and the susceptible cultivar 'Katahdin' planted in 7.5-cm-d clay plots. Similar bags with cysts were buried in pots without potatoes. The inoculum levels constituted densities of 0.75, 3.75, 7.50 or 37.50, and 75.00 eggs/cm<sup>3</sup> soil in pots. All treatments were replicated 10 times. Inoculum levels of 0.04, 0.07, 0.18, 0.36, and 0.72 eggs/cm<sup>3</sup> soil were achieved by inoculating pots with bags containing 1, 2, 5, 10, or 20 cysts per bag. These cysts were of uniform size and age and had been previously exposed to potato to lower content to 7.2 eggs per cyst. After 14 weeks, the bags were recovered from the pots and the cysts extracted. Cysts were crushed, and viable eggs per cyst were determined. All soil in each pot was processed by Fenwick can flotation to recover cysts.

Field experiments to determine the effect of Pi on *G. rostochiensis* population dynamics were performed in a naturally infested field on Long Island, New York, in 1984. Twenty-eight plots 16.5 × 9.9 meters with Pi ranging from 0.5 to 22.7 eggs/cm<sup>3</sup> soil were planted to the resistant cultivar 'Yankee Chipper'. Plant emergence was about 90%. Each plot was bulk sampled for nematodes by collecting and combining 100 50-cm<sup>3</sup> soil cores before planting and after harvest. A 250-cm<sup>3</sup> aliquot was processed for cysts which were crushed to determine the number of viable juveniles per cm<sup>3</sup> soil. Plots were grouped into nine classes by Pi. Pi and Pf were each averaged within classes before determining the percentage decline of population densities. This conservative statistical technique was used to reduce error due to the large variation in nematode counts at low Pi (21).

The effect of successive plantings of resistant potato cultivars on nematode population dynamics was determined by subjecting cysts of uniform size and age (0.45–0.84 mm, produced in 1983) and known viable contents to the resistant Rosa. Fifty replicate batches of 25 cysts each were enclosed in nylon bags and buried 1–2 cm below single eye seed pieces planted in 7.5-cm-d clay pots. Plants were killed and the bags were removed 4 weeks after potato shoot emergence. The viable eggs remaining inside cysts after one planting (4 weeks)

TABLE 2. Reproduction of *Globodera rostochiensis* on resistant and susceptible potato cultivars as influenced by initial nematode density.

Initial nematode density (eggs/cm <sup>3</sup> soil)	Resistant		Susceptible	
	Rate of increase*	Eggs/cyst	Rate of increase*	Eggs/cyst
0.04	0.00		16.9	90.7
0.07	0.00		18.8	176.7
0.18	0.00		7.5	113.2
0.36	0.00		12.6	185.4
0.72	0.14	227.0	10.6	123.3
0.75	0.10	54.0	34.7	156.0
3.75	0.06	169.0	30.5	129.9
7.50	0.04	252.0	26.6	168.1
37.50	0.02	116.6	17.7	132.6
75.00	0.016	152.5	12.7	145.0

\* New eggs produced per egg of inoculum (multiplication rate).

Regression: Resistant: new eggs/cm<sup>3</sup> soil = 0.0655 + 0.0159Pi eggs/cm<sup>3</sup> soil, R<sup>2</sup> = 0.96, F = 205.4. Susceptible: new eggs/cm<sup>3</sup> soil = 29.6 + 13.3Pi eggs/cm<sup>3</sup> soil, R<sup>2</sup> = 0.96, F = 225.0.

of Rosa were determined by individually crushing 10 cysts from each of 10 replications. Cysts from the remaining 40 replications were stored at 10 C for 1 week after which the experiment was repeated by subjecting the remaining cysts to a second 4-week planting of Rosa. After the second cycle, the eggs remaining unhatched in cysts were determined as before. The remaining 30 bags of cysts were again stored at 10 C for 1 week, and the procedure was repeated for five successive 4-week plantings of Rosa.

To investigate the influence of cyst density on emergence of juveniles from eggs in cysts in vitro, 1 or 25 cysts (0.35–0.45 mm, produced in 1981) were exposed to distilled water or potato root diffusate (PRD) for 4 weeks at 21 C. The one cyst per hatching chamber treatment was replicated 15 times, and the 25 cysts per chamber treatment was replicated 10 times. The numbers of juveniles emerging per week in each chamber were counted.

RESULTS

Decline in numbers of viable juveniles recovered from nylon bags containing cysts placed under potato plants was significantly influenced by initial density (Table 1). Reduction in the number of viable juveniles recovered was correlated with initial

TABLE 3. *Globodera rostochiensis* population dynamics (eggs/cm<sup>3</sup> soil) on resistant and susceptible potatoes as affected by initial nematode population density (Pi).

Pi	Un-hatched	Reproduction*		Final density	
		Resistant	Susceptible	Resistant	Susceptible
0.04	0.01	0.00	0.48	0.01†	0.49‡
0.07	0.02	0.00	0.92	0.02	0.94
0.18	0.03	0.00	0.95	0.03	0.98
0.36	0.06	0.00	3.18	0.06	3.24
0.72	0.14	0.07	5.34	0.21	5.48
0.75	0.18	0.06	18.22	0.24	18.40
3.75	0.49	0.16	80.07	0.65	80.56
7.50	1.01	0.21	139.65	1.22	140.66
37.50	3.79	0.53	464.63	4.32	468.42
75.00	4.50	0.84	666.75	5.34	671.25

\* New eggs/cm<sup>3</sup> soil resulting from reproduction × 0.7 to adjust for the 70% soil volume in which reproduction occurs.

† Log Pf = 0.743 + 0.829 log Pi, R<sup>2</sup> = 0.975, F = 316.0.

‡ Log Pf = 1.08 + 1.03 log Pi, R<sup>2</sup> = 0.969, F = 247.9.

nematode density. Decline in the number of recovered viable juveniles in the fallow pots was not affected by initial density. Hatch and subsequent nematode population decline was similar under resistant and susceptible cultivars. Decline in numbers of viable juveniles in cysts was much greater under potatoes than in fallow soil at all initial densities.

The number of cysts produced on both resistant and susceptible cultivars was influenced by initial density (P = 0.05) (Table 2). The rate of cyst production decreased as the initial inoculum increased. Neither initial densities nor cultivar affected the number of viable eggs per cyst.

The inoculum eggs remaining unhatched and the new eggs produced by nematode reproduction on both susceptible and resistant cultivars were regressed against initial density. Equations generated were

- 1) log Presidual = -0.786 + 0.834 log Pi (R<sup>2</sup> = 0.99),
- 2) log Psusceptible = 1.23 + 1.03 log Pi (R<sup>2</sup> = 0.97),
- 3) log Presistant = -0.970 + 0.527 log Pi (R<sup>2</sup> = 0.99).

Pi represents initial nematode density in eggs per cm<sup>3</sup> soil and Pf represents final population density. The residual population remaining unhatched (Presidual) and

TABLE 4. Projected and actual *Globodera rostochiensis* population density changes as influenced by resistant and susceptible potatoes.

Resistant		Susceptible	
Projected*	Actual†	Projected	Actual
5.00	5.00	0.01	0.01
0.69	0.90	0.10	0.20
0.13	0.22	1.18	1.75
0.03	0.07	14.21	8.38
0.01	0.03		
0.00	0.01		

\* Projected population changes calculated from equations in Table 3.

† Data taken from 10 years of experimental field data: Resistant:  $\log Pf = 0.624 + 0.83 \log Pi$ ,  $R^2 = 0.56$ ,  $F = 229.3$ ,  $df = 184$ . Susceptible:  $\log Pf = 0.748 + 0.723 \log Pi$ ,  $R^2 = 0.69$ ,  $F = 436.4$ ,  $df = 200$ .

new eggs produced by reproduction on either resistant or susceptible potatoes (Presistant and Psusceptible) at each initial density were used to determine final *G. rostochiensis* population densities after one season of potatoes (Table 3). To estimate projected *G. rostochiensis* decline under resistant and susceptible potatoes, the regression equations for population increase generated from pot experiments were considered representative of the 70% field soil volume in which reproduction occurs. The remaining 30% of soil was subject to *G. rostochiensis* decrease only. Final nematode population densities are a summation of the eggs remaining unhatched and new eggs produced at each initial density. Density changes under resistant potatoes are described by

$$4) \log Pf = -0.743 + 0.829Pi (R^2 = 0.98).$$

Density changes under susceptible potatoes are described by

$$5) \log Pf = 1.08 + 1.03 \log Pi (R^2 = 0.97).$$

Projected *G. rostochiensis* population dynamics on resistant and susceptible potatoes were similar to actual population changes observed in 10 years of experimental field results (Table 4).

Initial *G. rostochiensis* population density was positively correlated ( $r = 0.70$ ,  $P = 0.05$ ) with percentage of *G. rostochiensis* population density decline in response to the resistant potato cultivar Yankee Chipper (Table 5). Percentage of population decline ranged from 94.6% with 16.7 eggs/cm<sup>3</sup> soil to 85.7% at an initial population density of 0.7 eggs/cm<sup>3</sup> soil.

In greenhouse tests, successive plantings of resistant Rosa suppressed the number of eggs per cyst by 60–90% per planting (Table 6). Numbers of viable eggs per cyst were suppressed 99% after 2–5 plantings of Rosa. The percentage of cysts with viable contents was suppressed 77% after five plantings.

Emergence of juveniles from cysts in distilled water or potato root diffusate (PRD) in vitro was not influenced by population density (Table 7). However, total hatch after 4 weeks was 10 times greater in PRD than in water.

## DISCUSSION

The effect of resistant potatoes on *G. rostochiensis* population dynamics has been determined primarily at high nematode densities which cause economic loss and are easy to study. Initial population densities in our experiments ranged from 0.04 to 75.00 eggs/cm<sup>3</sup> soil. Because nematode decline ratios determined for higher population densities may not be transferable

TABLE 5. Effect of initial population density on *Globodera rostochiensis* population decline with the resistant cultivar 'Yankee Chipper'.

Low density		Medium density		High density	
Pi*	Decline (%)	Pi	Decline (%)	Pi	Decline (%)
0.7†	85.7	6.5	93.8	11.3	92.9
2.1	85.7	8.9	90.0	12.4	88.7
4.8	87.5	10.7	84.9	16.7	94.6
$\bar{x}$ 2.5	86.3 (84.6)‡	$\bar{x}$ 8.7	89.6 (87.5)	$\bar{x}$ 13.5	92.1 (88.4)

Linear regression:  $\log Pf = -0.8832 + 0.772 \log Pi$ ,  $R^2 = 0.88$ ,  $F = 51.86$ ,  $df = 8$ .

Correlation of Pi and % decline,  $r = 0.70$ .

\* Pi = initial density of viable juveniles per cm<sup>3</sup> soil.

† Each Pi data point combination is the average of three field plots classed by similar initial density.

‡ Projected decline at this initial population density.

TABLE 6. Effect of successive cycles of resistant cultivars on the number of viable eggs per cyst of *Globodera rostochiensis*.

Cycle	Cysts with viable contents (%) (Pi* = 100)	Viable juveniles per cyst (Pi* = 462.0)	Reduction from previous cycle (%)	Reduction from Pi (%)
1	99	135.8	70.6	70.6
2	88	14.7	89.2	96.8
3	71	5.5	62.6	98.8
4	59	3.2	41.8	99.3
5	23	0.9	71.4	99.8

\* Pi = initial inoculum.

to lower densities, the reduction in numbers of viable juveniles per cyst should be more critically studied at low population densities.

Initial nematode population density was not correlated with emergence of encysted juveniles from cysts in water or PRD. This lack of correlation differs from the positive correlation between initial nematode density and decline in numbers of juveniles emerging from cysts exposed to potato roots in pots. These data suggest that the density dependent decrease of juveniles in cysts exposed to potato roots is not caused by a within-cyst phenomenon. Wounding of potato roots and (or) stress on the plant resulting from nematode invasion may affect the quantity and (or) quality of PRD production and deserves further study.

Concentrating *G. rostochiensis* cyst inoculum in bags should not have affected cyst production. Hesling (6) reported that dispersion of cysts in soil or dispersion of the same number of eggs within cysts of different sizes had no effect on nematode reproduction. The number of cysts produced on both resistant and susceptible cultivars in this experiment was positively correlated with initial nematode density. The rate of reproduction per unit of inoculum was higher at low densities on both resistant and susceptible cultivars. Until recently this pattern of reproduction had been demonstrated for potato cyst nematodes on susceptible cultivars only (9,10,17). Although the reproduction rate of *G. rostochiensis* on resistant cultivars is more efficient at low population densities, only a few new cysts were produced and no new cysts were recovered from pots with Pi below 0.72 eggs/

TABLE 7. Effect of *Globodera rostochiensis* population density on in vitro hatch in water and potato root diffusate after 4 weeks at 21 C.

	No. juveniles hatched per cyst	
	1 cyst*	25 cysts
Distilled H <sub>2</sub> O	8.9† a	8.7 a
Potato root diffusate	100.1 b	97.9 b

\* Average of 15 replications.

† Average of 10 replications.

Linear contrasts: Hatch in potato root diffusate greater than in water. Hatch in chambers containing one cyst equal to hatch in chambers containing 25 cysts.

cm<sup>3</sup> soil. Cysts per volume of soil may increase slightly over time when resistant cultivars are grown. Cysts depleted of viable contents remain in the soil, and some new cysts are produced on resistant cultivars. However, numbers of viable eggs produced in these new cysts are few, compared with those hatched from cysts in the presence of a resistant cultivar. The majority of *G. rostochiensis* juveniles that hatch and emerge from cysts in response to stimulation by potato root exudates do so within the first 3 weeks of plant growth (1). Greenhouse experiments utilizing successive 4-week plantings of resistant cultivars resulted in a minimum decline in number of juveniles of 60–90% per planting. Successive plantings of resistant cultivars result in an increasing number of empty cysts, whereas total cysts remain relatively constant with each successive planting.

*G. rostochiensis*, a quarantined pest in the United States, is managed at very low population densities in infested fields. Therefore the model simulating population dynamics under a susceptible cultivar (equation 5) was generated without concern for rate limiting factors which limit reproduction at high densities to maintenance of an equilibrium density. This model should be used to simulate *G. rostochiensis* increase on susceptible cultivars only at low population densities.

For predictive purposes, we considered all cysts to contain 150 eggs, the average number of eggs per cyst produced on both susceptible and resistant cultivars in these experiments. Projected population decline caused by monoculture of resistant cultivars (equation 4) indicates that initial population densities of 5.00 eggs/cm<sup>3</sup> soil

would be reduced to 0.01 eggs/cm<sup>3</sup> soil after 4 years and after 5 years would be virtually undetectable (< 0.01 eggs/cm<sup>3</sup>) (Table 3). Because of the limited reproduction of *G. rostochiensis* on resistant cultivars and the slow degradation of cysts in soil (< 4% per year) (13), numbers of cysts would increase. Populations of encysted juveniles would decline after 5 years of resistant cultivars, as eggs per cyst would be drastically decreased due to hatching in response to the plants.

The actual population decline over time caused by resistant cultivars was similar to the projected decline. The actual decline is the result of regression of 184 field plots subjected to potato cultivars at different initial population densities (B. B. Brodie, unpubl.).

Projected *G. rostochiensis* population increase on successive crops of susceptible cultivars (equation 5) indicates that populations would increase from 0.01 eggs/cm<sup>3</sup> soil to 14.21 eggs/cm<sup>3</sup> soil in 3 years. The actual increase determined from regression of 200 field plots was from 0.01 eggs/cm<sup>3</sup> to 8.38 eggs/cm<sup>3</sup> soil in 3 years (Brodie, unpubl.).

Although projected *G. rostochiensis* decline was similar to that observed in field plots with initial densities as low as 0.01 eggs/cm<sup>3</sup> soil, reproduction of *G. rostochiensis* at very low population densities on resistant and susceptible cultivars would probably be much less in an agricultural setting than that determined by this study. Although cyst nematode populations tend to clump in nature, at very low populations problems associated with fertilization might exist (18). Kort (11) reported a positive correlation between initial density and cyst production at very low densities primarily because of increasing difficulty in finding mates.

At some population density, currently unknown, the negative correlation between population density and reproduction on susceptible and resistant cultivars would change to a positive correlation, as described by Kort (11). Since our data considered only the negative correlation, any prediction of population changes below this changeover point in population density would be subject to error. This error would be especially evident with susceptible cultivars, because reproduction on these cul-

tivars is many orders of magnitude greater than reproduction on resistant cultivars. Further study of population changes at very low population densities to define this changeover point are warranted.

#### LITERATURE CITED

1. Brodie, B. B. 1982. Possible use of potato as a trap crop for controlling *Globodera rostochiensis* populations. *Journal of Nematology* 14:432 (Abstr.).
2. Brodie, B. B. 1976. Managing population densities of *Heterodera rostochiensis*. *Journal of Nematology* 8:280 (Abstr.).
3. Cole, C. S., and H. W. Howard. 1962. Further results from a field experiment on the effect of growing resistant potatoes on a potato root eelworm (*Heterodera rostochiensis*) population. *Nematologica* 7:52-61.
4. Evans, K., and B. B. Brodie. 1980. The origin and distribution of the golden nematode and its potential in the USA. *American Potato Journal* 57:79-89.
5. Harrison, M. B. 1968. Control of golden nematode with resistant potato varieties. Proceedings of the North West Nematology Workshop, 16-18 April, Vancouver, B.C., Canada. P. 39.
6. Hesling, J. J. 1961. *Heterodera rostochiensis* (Woll. 1923) on *Solanum demissum*—a population study. *Annals of Applied Biology* 49:350-359.
7. Hoopes, R. W., R. E. Anderson, and W. F. Mai. 1978. Internal response of resistant and susceptible potato clones to invasion by potato cyst nematode *Heterodera rostochiensis*. *Nematropica* 8:13-20.
8. Huisman, C. A. 1961. The influence of resistant potato varieties on the soil population of *Heterodera rostochiensis* Woll. *Nematologica* 6:177-180.
9. Jones, F. G. W. 1966. The population dynamics and population genetics of the potato cyst-nematode *Heterodera rostochiensis* Woll. on susceptible and resistant potatoes. Report of the Rothamsted Experiment Station for 1965. Pp. 301-316.
10. Jones, F. G. W., and D. M. Parrott. 1965. The genetic relationships of pathotypes of *Heterodera rostochiensis* Woll. which reproduce on hybrid potatoes with genes for resistance. *Annals of Applied Biology* 56:27-35.
11. Kort, J. 1962. Effect of population density on cyst production in *Heterodera rostochiensis* Woll. *Nematologica* 7:305-308.
12. Lesczynski, D. B., and C. B. Tanner. 1976. Seasonal variation of root distribution of irrigated, field-grown Russet Burbank potato. *American Potato Journal* 53:69-78.
13. Oydvin, J. 1978. Studies on potato cyst-nematodes, *Globodera* spp. (Skarbilovich), and the use of plant resistance against *G. rostochiensis* (Woll.) in Norway. Växtskyddsrapporter. Avhandlingar 2.
14. Parrott, D. M. 1981. Evidence for gene-for-gene relationships between resistance gene H<sub>1</sub> from *Solanum tuberosum* ssp. *andigena* and a gene in *Globodera rostochiensis*, and between H<sub>2</sub> from *S. multidissectum* and a gene in *G. pallida*. *Nematologica* 27:372-384.
15. Plaisted, R. L., H. D. Thurston, B. B. Brodie, and R. W. Hoopes. 1984. Selecting for resistance to diseases in early generations. *American Potato Journal* 61:395-403.

16. Plaisted, R. L., H. D. Thurston, L. C. Peterson, D. H. Fricke, R. C. Cetas, M. B. Harrison, J. B. Sieczka, and E. D. Jones. 1973. Hudson, a high yielding variety resistant to golden nematode. *American Potato Journal* 50:212-215.

17. Seinhorst, J. W. 1984. Relation between population density of potato cyst nematode and measured degrees of susceptibility (resistance) of resistant potato cultivars and between this density and cyst content in the new generation. *Nematologica* 30:66-76.

18. Seinhorst, J. W. 1968. Underpopulation in plant parasitic nematodes. *Nematologica* 14:549-553.

19. Storey, G. W. 1984. The effect of oxamyl and the growing of susceptible and resistant potato cul-

tivars on the population dynamics of *Globodera rostochiensis* throughout the soil profile. *Annals of Applied Biology* 104:131-141.

20. Trudgill, D. L., and D. M. Parrott. 1973. Effects of growing resistant potatoes with gene H<sub>1</sub> from *Solanum tuberosum* ssp. *andigena* on a population of *Heterodera rostochiensis* British pathotype A. *Annals of Applied Biology* 73:67-75.

21. Wald, A. 1940. The fitting of straight lines if both variables are subject to error. *Annals of Mathematical Statistics* 11:284-300.

22. Whitehead, A. G. 1977. Vertical distribution of potato, beet and pea cyst nematodes in some heavily infested soils. *Plant Pathology* 26:85-90.