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Effects of Host Resistance on the Fecundity of *Globodera rostochiensis*[1]

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Abstract: The fecundity of *Globodera rostochiensis* (R_1A) females that developed on resistant Rosa and susceptible Katahdin potato cultivars were compared. Cysts collected from each cultivar were bulked, separated into four sizes (> 500 μm, 355–500 μm, 250–355 μm, and < 250 μm), and crushed to determine fecundity as measured by viable egg content (VEC). Fewer and generally smaller cysts developed on Rosa than on Katahdin. Although cyst size significantly ($P = 0.01$) influenced VEC, cyst age (8 or 13 weeks) had no effect. Regardless of size, cysts produced on Rosa contained significantly fewer viable eggs than did cysts produced on Katahdin. The fecundity of progeny from cysts produced on Rosa was significantly reduced compared with that of progeny from cysts produced on Katahdin. After two generations on Katahdin, the VEC of cysts from a population originating from Rosa was significantly less than that of cysts from a population originating from Katahdin, indicating that in the presence of a pure population of *G. rostochiensis* R_1A, the females that develop on the resistant cultivar Rosa represent a diminished rather than a superior selected population.

Key words: female fecundity, *Globodera rostochiensis,* host resistance, potato, *Solanum tuberosum.*

Resistance in some potato cultivars to *Globodera rostochiensis* (Wollenweber, 1923) Behrens, 1975 R_1A (= Ro1) is conditioned by the single dominant gene, H_1 (11). Females of *G. rostochiensis* occasionally develop in roots of potato plants bearing this gene (3,8,13). According to Brodie (pers. comm.), one to five females may develop in ca. 20% of the plants of such resistant cultivars, while zero females develop on the remaining 80%. These females appeared to possess a superior genetic constitution conferring such a capability (5,6). If that were true, the progeny of these females probably also possessed the ability to readily develop in resistant plants (5). Repeated growing of H_1-bearing potato cultivars where mixtures of potato-cyst nematode (PCN) species and races exist favored the increase of PCN populations with the ability to overcome this resistance (2,13). There is no evidence, however, that repeatedly growing H_1-bearing cultivars in the presence of only race R_1A of *G. rostochiensis* favors the development of nematode populations with such ability (1,4,7).

Populations of *G. rostochiensis* that developed in resistant potatoes were examined for their ability to establish on resistant and susceptible hosts (1,4), but the fate of individual females developing in resistant hosts has not been assessed. There are conflicting reports regarding the fecundity of such females. These females were reported to contain few viable eggs (4), but a later report indicated that some contained as many viable eggs as did those produced on a susceptible host (8). The reduced fecundity of females in resistant plants might be a function of delayed development in relation to that on a susceptible plant (Mullin, unpubl.). The fate of the progeny of females that develop in resistant plants has not been studied, primarily because of extremely limited reproduction in the resistant host. We examined the New York population of *G. rostochiensis* 1) to compare the fecundity of females that develop in resistant potatoes with the fecundity of those that develop in susceptible potatoes and 2) to determine if the progeny of females from resistant potatoes are equally as capable of reproducing in susceptible or resistant potatoes as the progeny of females from susceptible potatoes.

Materials and Methods

Fecundity of females: Susceptible (S) potato (*Solanum tuberosum* ssp. *tuberosum*) cultivar Katahdin and resistant (R) cultivar

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Rosa were used in these studies. Katahdin was derived totally from North American cultivated tetraploid potatoes. In addition to the H_1 gene that confers resistance to *Globodera rostochiensis,* one-half of Rosa's pedigree consists of South American cultivated tetraploid potatoes, and one-quarter of its genome was derived from Katahdin. Rosa bears no other major resistance genes as determined by progeny tests (R. L. Plaisted, pers. comm.). Sixty sprouted tubers of Katahdin and 425 of Rosa were planted individually in 7.5-cm-d clay pots containing a 1:1 (v:v) mixture of pasteurized loam and sand. The pots were then embedded in sand beds that had been fumigated previously with methyl bromide. Second-stage juveniles (J2) of *G. rostochiensis* were obtained by exposing pot-grown cysts to potato root diffusate for 3 weeks. When the plants were 10 cm tall, ca. 5,000 J2 were added to each pot via syringe in a depression made in the soil near the plant stem.

Half of the plants of each cultivar were harvested at 8 or 13 weeks after inoculation. Shoots were removed, and the contents of each pot were emptied into a paper bag and allowed to air dry. Each sample was then processed for cysts via elutriation (12). Cysts were further separated from debris by immersing filters containing the flotsam in acetone. To reduce variability between cysts, they were separated by host into four sizes: > 500 μm, 355–500 μm, 250–355 μm, and < 250 μm by screening through sieves with the respective pore openings. Cysts were hydrated overnight before crushing to determine fecundity as measured by viable egg content (VEC).

Reproductive potential of progeny: This experiment spanned three generations of *G. rostochiensis* reproduction on different sequences of susceptible and resistant potato cultivars. Twenty-five sprouted tubers of Katahdin and 100 of Rosa were planted and inoculated as described for the fecundity study. After 12 weeks, the plants were harvested and cysts were collected via elutriation as before, but not subjected to acetone. A total of 20 cysts were recovered from the 100 resistant plants, and ca. 100 cysts were collected from the susceptible plants to represent the first generation. Cysts obtained from each cultivar were divided in half, and each half was sewn into a separate nylon mesh bag that retained the cysts but allowed J2 to pass. Each bag was planted beneath a Katahdin tuber to produce the second generation. Cysts were harvested from this generation via elutriation 15 weeks later. Approximately 100 cysts were recovered from the two pots that had been inoculated with cysts derived from the resistant cultivar. Cysts from this treatment (R–S) were standardized by size, and about 70 relatively uniform cysts remained. Mean VEC of these cysts was 124.2. Many cysts were obtained from susceptible–susceptible (S–S) treatment; they were larger and contained more eggs. These were standardized by screening for the intermediate size (355–500 μm) to serve as parents for the third generation. Mean VEC of these cysts was 164.4 and not significantly different ($P = 0.05$) from those obtained from the R–S treatment.

To produce the third generation, second-generation cysts were sewn into nylon mesh bags (three cysts per bag) and one bag was placed in each pot planted to either Katahdin or Rosa. The uneven production of cysts resulted in uneven replication in the third generation. Progeny from the S–S treatment were replicated 18 times on each cultivar in the third generation. Progeny from the R–S treatment were replicated three times on the susceptible cultivar and 15 times on the resistant cultivar in the third generation. The pots were embedded in sand beds, and the resultant cysts were extracted via elutriation 12 weeks later and crushed individually to determine VEC. Cysts produced from each of the four treatments were designated as SSS, SSR, RSS, or RSR, with the letters representing the first, second, and third generations on potato cultivars Katahdin or Rosa.

Results

Fecundity of females: Regardless of size, cysts produced on the resistant cultivar Rosa contained significantly ($P = < 0.01$)

fewer viable eggs than did cysts produced on the susceptible cultivar Katahdin at both harvests (Table 1). Analysis of variance indicated significant differences in VEC due to cultivar ($P < 0.01$) and cyst size ($P = 0.01$), but not harvest date ($P = 0.05$). Despite the far greater number of Rosa plants inoculated in this experiment, only nine cysts of the largest size (> 500 μm) and fewer than 30 of the smaller sizes were recovered, compared with hundreds from Katahdin. All cysts of the smallest size (< 250 μm) recovered from Rosa were empty; no cysts of this size were recovered from Katahdin. The trend was the production of smaller cysts containing fewer viable eggs on the resistant host relative to cysts produced on the susceptible host.

Fecundity of progeny: Resistance in either the first or last host or both in a three-generation cycle of potato cultivars significantly reduced the fecundity of *G. rostochiensis*. The mean VEC of cysts derived from SSS, SSR, RSS, and RSR host sequences was 82.6, 32.4, 34.8, and 6.7, respectively. The ANOVA indicated a very highly significant ($P < 0.01$) effect of the first and third host, and interaction on viable egg production in the third generation. VEC was reduced in cysts derived immediately from a resistant host (SSR), reduced similarly in cysts produced on a susceptible host two generations removed from a resistant host (RSS), and further reduced in cysts derived from two cycles on a resistant host interrupted by one cycle of a susceptible host (RSR).

Discussion

These studies indicate that the fecundity of *G. rostochiensis* females that develop on the resistant potato cultivar Rosa is reduced relative to the fecundity of females that develop on the susceptible cultivar Katahdin. On a per female basis, viable egg production (fecundity) in the resistant host was sharply suppressed relative to that in the susceptible host. Suppression of egg production did not appear to be related to a delay in cyst maturity, as fecundity was not different when assessed at 8 or 13 weeks after inoculation (Table 1).

Table 1. Viable egg content of *Globodera rostochiensis* cysts harvested from the potato cultivars Katahdin (susceptible) and Rosa (resistant) at 8 or 13 weeks after inoculation (w.a.i.).

Cyst size (μm)	w.a.i.	Viable eggs/cyst (VEC)	
		Katahdin	Rosa
> 50	8	404.6**	137.3
	13	355.3**	104.7
355–500	8	213.3**	43.5
	13	229.7**	39.7
250–355	8	71.8**	45.7
	13	76.2	0†
< 250	8	‡	0
	13	‡	0

** Tests of mean VEC from Katahdin vs. Rosa highly significantly different within and between cyst sizes but not harvest dates.
† All data values zero, no analysis performed.
‡ No cysts of this size recovered from Katahdin.

Further, some effects of host resistance on the reproduction of *G. rostochiensis* were expressed two generations later on a susceptible cultivar in the progeny of females that originally developed on a resistant cultivar. That is, fecundity was significantly reduced in females whose grandmothers had developed on resistant hosts relative to that of females whose pedigree did not include a resistant host. Two generations on a resistant host, even though interrupted by one cycle on a susceptible host (treatment RSR), exaggerated this phenomenon.

M. B. Harrison (pers. comm.) observed that little or no increase of a *G. rostochiensis* population occurred when nematodes that had been produced on resistant potatoes were left in field plots planted with susceptible potatoes for several years. Some cysts that develop in resistant plants may contain a large number of viable eggs, and juveniles from such cysts might be expected to reproduce normally on a susceptible host (9). The results of our experiments indicate that this is not always the case. Although some cysts that develop on resistant plants may contain progeny capable of reproducing normally on susceptible plants, this does not appear to be a characteristic of the majority of the progeny.

We have observed that the single-gene resistance in the cultivar Rosa is expressed in different ways affecting different stages

of *Globodera rostochiensis* pleiotropically (10). The current experiments suggest that resistance might also influence the reproductive potential of the nematode. Although the plant's resistance is conditioned by one major gene (R. L. Plaisted, pers. comm.), the nematode's ability to overcome all resistance mechanisms is not necessarily conditioned by a single virulence gene. We suspect that the development of virulent races of *G. rostochiensis* in the United States has not yet occurred because 1) population levels of *G. rostochiensis* are kept extremely low, 2) the original infestation was very small and hence somewhat homogeneous, and 3) as shown in these and other experiments (10), resistance appears to operate on the nematode pleiotropically. There is no evidence that the races and species of potato-cyst nematodes found elsewhere have evolved in New York as a consequence of the commercialization of ex *andigena* resistance (14). If other races and species were not included in the original introduction of PCN into the United States, new races or species that might be detected probably would have been introduced rather than having developed from the existing population which appears to possess a very narrow and homogeneous gene pool for parasitism.

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