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Penetration and Post-infectional Development and Reproduction of *Meloidogyne arenaria* Races 1 and 2 on Susceptible and Resistant Soybean Genotypes[1]

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Abstract: Penetration, post-infectional development, reproduction, and fecundity of *Meloidogyne arenaria* races 1 and 2 were studied on susceptible (CNS), partially resistant (Jackson), and highly resistant (PI 200538 and PI 230977) soybean genotypes in the greenhouse. The ability to locate and invade roots was similar between races, but more juveniles penetrated roots of susceptible CNS than the resistant genotypes. At 10 days after inoculation, 56% and 99% to 100% of race 1 second-stage juveniles were vermiform or sexually undifferentiated in CNS and the resistant genotypes, respectively. In contrast, only 2%, 42%, 44%, and 62% of race 2 juveniles had not initiated development in CNS, Jackson, PI 200538, and PI 230977, respectively. By 20 days after inoculation, 88% to 100% of race 2 nematodes in roots of all genotypes were females, whereas only 25% and 1% of race 1 were females in CNS and the resistant genotypes, respectively. For all four genotypes, race 1 produce 85% to 96% fewer eggs per root system 45 days after inoculation than race 2. At 45 days after inoculation race 2 produced more eggs on CNS than the other genotypes.

Key words: Glycine max, Meloidogyne arenaria, pathogenicity, plant introduction, race, resistance, root-knot nematode, soybean.

The peanut root-knot nematode *Meloidogyne arenaria* (Neal) Chitwood is pathogenic to many important economic crops throughout the world. In the southeastern United States this nematode has become increasingly important on soybean, *Glycine max* (L.) Merr., because of its reproductive capabilities and damage potential on this crop (2,3). Planting of soybean cultivars resistant to *M. incognita* (Kofoid & White) Chitwood and *Heterodera glycines* Ichinohe (15) that exhibit only partial resistance to *M. arenaria* (10,30) could have selected for *M. arenaria* populations previously undetected (3,13,15). Furthermore, the genetic variability of *M. arenaria* (2,3) may have played an important role in the population shifts and contributed to its adaptability and stability in the soybean-*M. arenaria* relationship.

Besides the three chromosomal forms, which may coexist in a single population of *M. arenaria* (2), two races of this nematode are recognized: race 1, which reproduces on peanut (*Arachis hypogaea* L.), and race 2, which does not. These races, however, cannot be separated by any cytological, biochemical, morphological, or morphometric characteristics (4,27).

Despite reproducing exclusively by obligatory mitotic parthenogenesis (27), variability among field populations of *M. arenaria* has been reported, even within the two races. For example, reproduction and disease induction on soybean differed between race 1 (21) and race 2 (2,12) populations, although race 2 caused more damage and was more fecund on resistant soybean cultivars than race 1 (14,22).

The lack of a cost-effective nematicide (25) and the limitations of rotation crops (29) require that management of *M. arenaria* be based primarily on soybean cultivar resistance. However, few soybean cultivars have resistance to *M. arenaria* and the resistance level available is not adequate to permit profitable production on heavily infested soils (15,16). Resistance in soybean to *M. arenaria* has been evaluated based on nematode reproduction, juvenile densities in the soil, and plant damage (root galling and[or] yield suppression) at a determined developmental stage of the

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plant (2,10,12–16). Development and more effective use of *M. arenaria*-resistant soybean cultivars will be enhanced by a basic understanding of the resistance mechanisms involved.

New sources of resistance to *M. arenaria* race 2 were identified in the Southern Soybean Germplasm Collection (17), and their response to *M. arenaria* has been determined at different initial population densities of races 1 and 2 in field microplots (22). In the present study we investigated three factors that may determine the ability of *M. arenaria* to become established in susceptible and resistant soybean: rates of penetration, post-infectional development, and reproduction of both races of the nematode.

Material and Methods

Three *M. arenaria*-resistant soybean genotypes (Jackson, PI 200538, and PI 230977) and the susceptible genotype (CNS), all from Maturity Group VII, were used in these experiments (17,22). Two races of *M. arenaria,* race 1 (GA-7, Georgia isolate) (20) and race 2 (Govan, South Carolina isolate) (2), were cultured on greenhouse-grown tomato, *Lycopersicon esculentum* Mill. cv. Rutgers. Eggs from infected tomato roots were collected with the NaOCl (0.5%) procedure (11). Inoculum was obtained by hatching second-stage juveniles (J2) from eggs for a 48-hour period, after discarding J2 emerging during the first 24 hours. All experiments were conducted under greenhouse conditions (temperature range 21 to 35°C) with supplemental light from 400-watt multi-vapor phosphor coated lamps to provide a 16-hour photoperiod.

Penetration: Four seeds of each soybean genotype were planted in 474-cm^3 styrofoam cups filled with 420 cm^3 of soil mix (80% sand, 12% silt, 8% clay), previously fumigated with methyl bromide. After 5 days the seedlings were thinned to one plant per cup and inoculated with a 4-ml suspension of 3,000 J2/cup applied into four shallow depressions around the base of the seedling. Root systems of plants, harvested at 2, 4, 10, and 16 days after inoculation, were washed free of the soil, weighed, and stained with acid fuchsin (1). Penetration and early development of *M. arenaria* were determined by enumeration of J2 in the stained roots observed with a stereomicroscope. The four soybean genotypes, two nematode races, and four harvest intervals were arranged factorially in a randomized complete block design with six replications. The experiment was carried out twice and statistically analyzed separately. Since results were similar, data of only one experiment are presented.

Development and reproduction: Four seeds of each soybean genotype were planted in 474-cm^3 styrofoam cups as described above. After 5 days, the seedlings were thinned to one plant per cup, and 7 days later were inoculated with a 4-ml suspension of 2,000 J2/cup applied into four shallow depressions around the base of the plant. Two days after inoculation, the seedlings were removed from the cups and their root systems washed with tap water to limit penetration to a 48-hour period. Then the seedlings were transplanted into plastic pots containing the same type of soil. Plants of each genotype were harvested at 10, 20, 30, and 45 days after inoculation. The four soybean genotypes, two nematode races, and four harvest intervals were factorially arranged in a randomized complete block design with four replications. After root systems were washed free of soil, they were stained with acid fuchsin (1), and 20 nematodes were arbitrarily dissected from each root system. Only infection sites containing a single nematode were selected to eliminate the influence of competition on nematode development. The developmental stage of each nematode was recorded as outlined by Triantaphyllou and Hirschman (28) as follows: vermiform J2; swollen, sexually undifferentiated J2; late second-stage female juvenile; late second-stage male juvenile; third- or fourth-stage female juvenile; third- or fourth-stage male juvenile; female; early adult male (inside the cuticle). Migrating males were not considered in the enumeration of life stages.

Reproduction was assessed through the number of eggs per egg mass and total number of eggs per root system at 30 and 45 days after inoculation. Five egg masses were arbitrarily chosen from each root system and their gelatinous matrices dissolved in 1% NaOCl contained in a 1.5-ml microcentrifuge tube. Total eggs were collected from whole root systems with 1% NaOCl (11) and counted with the aid of a stereomicroscope.

Statistical analysis: Data from each experiment were analyzed separately. Chi-square analysis was used to compare rates of nematode development and analysis of variance by the SAS GLM procedure (SAS Institute, Cary NC) followed by mean separation with Fisher's protected LSD ($P = 0.05$) to compare rates of penetration and reproduction. Penetration and reproduction data (x) were transformed to $\log_{10}(x + 1)$ values prior to statistical analysis and are reported as antilogs.

Results

Penetration: Meloidogyne arenaria penetrated roots of all soybean genotypes. The number of nematodes per root system was affected by soybean genotype and time, but did not differ between races (Table 1). Fewer nematodes penetrated root systems of the resistant genotypes than CNS at all observation dates (Table 2). By 2 days after inoculation, about twice the number of J2 had penetrated roots of CNS than the other genotypes but juvenile development was not evident even at 4 days after inoculation. The greatest number of swollen juveniles were detected in CNS roots at both 10 and 16 days after inoculation.

The number of nematodes in soybean roots (per root system) usually increased throughout the 16 days, but there were exceptions. Maximum penetration of race 2 in PI 200538 and race 1 in PI 230977 occurred at 4 and 10 days after inoculation, respectively (Fig. 1). Even though the total number of *M. arenaria* per root system increased, the number of nematodes per gram of root decreased (Fig. 1). Significant difference in number of juveniles (vermiform and swollen) per gram of root was observed within genotypes, races, and days after inoculation, but their effects were independent, except for the genotype × day interaction ($P \leq 0.05$) (Table 1). Root fresh weights were affected by genotype, race, and time (data not shown) and were reflected in penetration and early develop-

Table 1. Main effects and interactions of races 1 and 2 of *Meloidogyne arenaria*, soybean genotypes, and days after inoculation (DAI) on root penetration and early development of *M. arenaria*.

		F values					
		Nematode per root system			Nematode per gram of root		
Source	DF	Vermiform[a]	Swollen	Total	Vermiform	Swollen	Total
Block	5	8*[b]	3*	10*	ns	ns	ns
DAI	3	28*	1,350*	15*	189*	1,641*	43*
Race (R)	1	ns	ns	ns	7*	10*	9*
DAI × R	3	ns	ns	ns	ns	4*	ns
Genotype (G)	3	7*	5*	13*	4*	6*	12*
DAI × G	9	ns	3*	ns	2*	5*	4*
Cont. 1[c]	1	ns	15*	9*	ns	12*	8*
Cont. 2	1	ns	ns	ns	ns	ns	ns
Cont. 3	1	ns	ns	ns	ns	10*	5*
R × G	3	ns	ns	ns	ns	ns	ns
DAI × R × G	9	ns	ns	ns	ns	ns	ns
ERROR	155						

Data (x) were analyzed as $\log_{10}(x + 1)$ values.

[a] Growth category: vermiform = not swollen; swollen = slightly swollen to partially globose.

[b] * Indicates significant F value ($\alpha = 0.05$).

[c] Contrasts: Cont. 1 = CNS vs. others at 16 days after inoculation; Cont. 2 = Jackson vs. PIs at 16 days after inoculation; Cont. 3 = PI 200538 vs. PI 230977 at 16 days after inoculation.

TABLE 2. Root penetration and early development by *Meloidogyne arenaria* races 1 and 2 in root systems and per gram of root of susceptible (CNS) and resistant (Jackson, PI 200538, and PI 230977) genotypes at 2, 4, 10, and 16 days after inoculation (DAI).

	Nematode per root system				Nematode per gram of root			
	Vermiform[a]		Swollen		Vermiform		Swollen	
DAI	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2
				CNS				
2	281	263	0	0	429	389	0	0
4	270	196	0	0	261	262	0	0
10	133	162	192	154	65	122	94	116
16	37	66	394	429	8	18	75	113
				Jackson				
2	120	82	0	0	207	187	0	0
4	145	118	0	0	153	194	0	0
10	125	138	50	85	68	88	26	54
16	19	39	245	243	5	11	61	71
				PI 200538				
2	155	127	0	0	260	292	0	0
4	139	175	0	0	178	270	0	0
10	79	86	101	97	51	71	66	82
16	35	25	178	139	8	8	40	41
				PI 230977				
2	149	64	0	0	219	196	0	0
4	34	81	0	0	51	134	0	0
10	185	102	62	98	136	86	44	82
16	21	43	156	287	8	16	49	96

Data are averages of six replications each inoculated with 3,000 *M. arenaria* juveniles.
Data were transformed to $\log_{10}(x + 1)$ values prior to statistical analysis and are reported as antilogs.
[a] Growth category: vermiform = not swollen; swollen = slightly swollen to partially globose.

ment of *M. arenaria* per gram of root. The number of vermiform or swollen race 2 was greater than race 1 per gram of root ($P \leq 0.05$) (Table 1), although inoculum efficiency (initial penetration) varied little between the two races. The percentage of race 1 and race 2 J2 infecting roots ranged from 6.3% and 6.2% to 12.8% and 12.4%, respectively.

No difference in number of juveniles (vermiform and swollen), either per root system or per gram of root at 16 days after inoculation, was observed among Jackson, PI 200538, and PI 230977 (Table 1). However, PI 200538 usually had lower and less variable rates of penetration per root system as well as lower numbers of nematodes per gram of root at the end of the experiment. In addition, 64%, 52%, and 39% fewer race 2 juveniles were present in roots of PI 200538 at 16 days after inoculation than in roots of CNS, PI 230977, and Jackson, respectively (Fig. 1).

Development: Development of *M. arenaria* race 1 was slower than race 2 and varied among soybean genotypes at all observation dates ($P \leq 0.05$) (Table 3). Slow development of race 1 resulted in 56% and 99% to 100% of juveniles being vermiform or sexually undifferentiated in CNS and the resistant genotypes, respectively, at 10 days after inoculation. Development of race 2, on the other hand, differed ($P \leq 0.05$) within soybean genotypes at 10 days after inoculation, when 98%, 58%, 56%, and 38% of the nematodes had developed to sexually differentiated juveniles in CNS, Jackson, PI 200538, and PI 230977, respectively.

As early as 20 days after inoculation, 88% to 100% of race 2 nematodes in roots of all genotypes were females, but 25% and 3% of race 1 were females in CNS and the resistant genotypes, respectively. By 30 days, all race 2 juveniles had matured to the adult stage. On the other hand, at 45

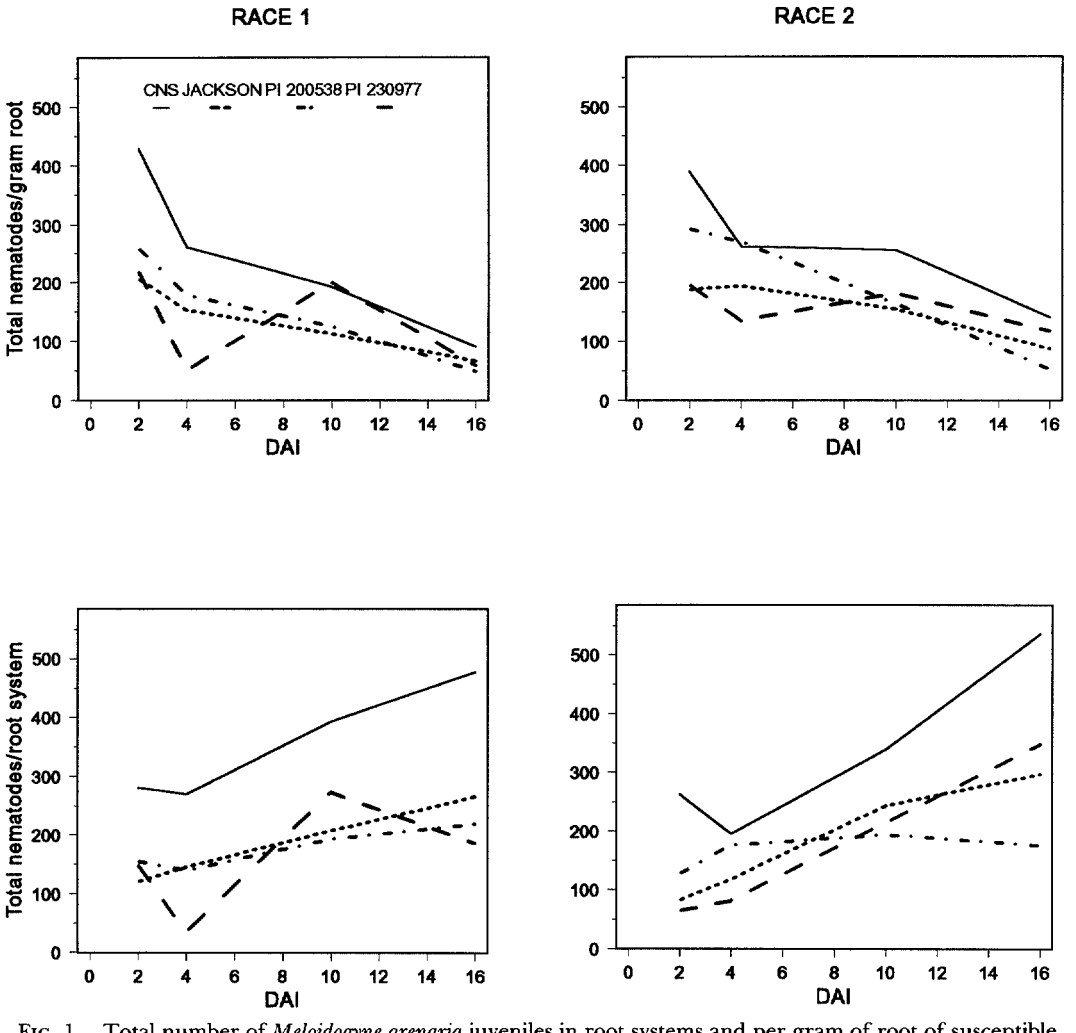

FIG. 1. Total number of *Meloidogyne arenaria* juveniles in root systems and per gram of root of susceptible CNS and resistant (Jackson, PI 200538, and PI 230977) soybean genotypes at 2, 4, 10, and 16 days after inoculation. Data are means of six replications and reported as antilogs.

days, 16% of race 1 individuals had not developed to maturity. At 30 and 45 days, 26%, 45%, 28%, 21%, and 11%, 29%, 39%, 36% of race 1 nematodes within root systems of CNS, Jackson, PI 200538, and PI 230977, respectively, were differentiated as males. The male:female ratio (%) at 30 and 45 days after inoculation was considerably higher for race 1 (35% and 25%) than race 2 (5% and 2%).

Reproduction: Meloidogyne arenaria reproduction and fecundity, expressed by egg production per female, were affected by genotype and race, but there was no genotype × race interaction (Table 4). Race 1 nematodes produced fewer eggs per egg mass and eggs per root system than race 2 on all genotypes at both observation dates ($P \leq 0.05$). Reproductive factors (RF = final density ÷ initial density) ranged from 8 to 24 in genotypes inoculated with race 2 but were less than 1 in genotypes with race 1. The ratio of eggs produced by race 2 to those produced by race 1 on each genotype was 60:1 or greater and 13:1 or greater at 30 and 45 days after inoculation, respectively. Differences within genotypes were less evident, even at 30 days after inoculation when CNS tended to support at least three times more eggs than each plant

TABLE 3. Distribution of developmental stages of *Meloidogyne arenaria* races 1 and 2 on susceptible CNS and resistant (Jackson, PI 200538, and PI 230977) soybean genotypes at 10, 20, 30, and 45 days after inoculation (DAI).

		Second-stage juvenile (J2)								Developed beyond J2							
				Swollen													
						Sexually differentiated				J3 or J4				Adult			
		Vermiform		Sexually undifferentiated		Female		Male		Female		Male		Female		Male	
Genotype	DAI	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2	Race 1	Race 2
CNS	10	–[1]	–[1]	45	2	34	78	1	–	–	–	–	–	–	–	–	–
	20	–	–	8	–	5	–	6	–	9	–	17	–	19	80	16	–
	30	–	–	2	–	–	–	–	–	–	–	–	–	57	80	21	–
	45	–	–	–	–	–	–	1	–	–	–	1	–	70	80	8	–
Jackson	10	39	–	41	34	–	46	–	–	–	–	–	–	–	–	–	–
	20	–	–	41	–	18	–	17	4	2	–	2	–	–	76	–	–
	30	–	–	2	–	2	–	7	–	–	–	3	–	33	73	33	7
	45	–	–	–	–	–	–	1	–	–	–	6	–	56	80	17	–
PI 200538	10	58	20	21	15	1	45	–	–	–	–	–	–	–	–	–	–
	20	–	–	27	–	13	–	14	1	7	2	11	–	2	77	6	–
	30	–	–	2	–	2	–	8	–	8	–	7	–	34	75	15	5
	45	–	–	–	–	–	–	–	–	1	–	11	–	48	78	20	2
PI 230977	10	50	23	30	23	–	30	–	4	–	–	–	–	–	–	–	–
	20	–	–	39	–	6	–	17	3	9	6	4	1	4	70	1	–
	30	–	–	19	–	5	–	6	–	4	–	1	–	29	77	16	3
	45	–	–	–	–	1	–	19	–	2	–	6	–	29	80	23	–

Race 1 development at 10, 20, 30, and 45 days after inoculation differed in all four genotypes ($P \leq 0.05$) by Chi-square analysis. Race 2 development at 10 days after inoculation differed in all four genotypes ($P \leq 0.05$) by Chi-square analysis. For each genotype, 20 nematodes of both races from each of four plants were examined on each date.

[1] No nematodes of the developmental stage indicated were observed for the genotypes on that date.

TABLE 4. Reproduction and fecundity of *Meloidogyne arenaria* races 1 and 2 on four soybean genotypes at 30 and 45 days after inoculation.

Genotype	Eggs per root system		Eggs per female	
	Race 1	Race 2	Race 1	Race 2
		Day 30		
CNS	176 aB	16,246 aB	6 aB	140 aA
Jackson	86 aB	5,152 aA	4 aB	54 aA
PI 200538	24 abB	5,174 aA	2 aB	58 aA
PI 230977	10 bB	5,168 aA	2 aB	54 aA
		Day 45		
CNS	1,687 aB	47,746 aA	80 aB	525 aA
Jackson	1,109 aB	25,085 bA	9 bB	248 abA
PI 200538	927 aB	18,306 bA	14 bB	168 bA
PI 230977	1,234 aB	16,009 bA	8 bB	148 bA

Data are means of four replications each inoculated with 3,000 *M. arenaria* juveniles. Means within columns followed by different lowercase letters and means within rows followed by different uppercase letters indicate significant difference based on Fisher's (protected) LSD ($P \leq 0.05$) for comparisons between genotypes and races, respectively, at the same day after inoculation.

Data were transformed to $\log_{10}(x + 1)$ values prior to statistical analysis and are reported as antilogs.

introduction. By 45 days, however, race 2 nematodes produced more eggs on CNS than on any other genotype ($P \leq 0.05$). The number of eggs per egg mass produced by each race was greatest in CNS and similar in Jackson and plant introductions at 45 days after inoculation ($P \leq 0.05$).

DISCUSSION

Successful long-lasting interactions of root-knot nematodes with host plants depend on their ability to locate and invade roots, establish feeding sites, and develop into mature females that produce progeny. Host resistance suppresses nematode development and(or) reproduction. Host penetration by *Meloidogyne* spp. J2 is usually similar in susceptible and resistant cultivars of soybean and other crops (7,18, 19). However, fewer nematodes may be present in roots of resistant than in roots of susceptible cultivars within a few days following the initial penetration. Reynolds et al. (23) and Herman et al. (8) related the reduction in number of *M. incognita* J2 in roots of resistant alfalfa and soybean, respectively, to J2 emerging soon after penetration. In our study, at 2 days after inoculation more J2 had penetrated the susceptible CNS than the resistant soybean genotypes. Similarly, in microplots 14 days after planting (22) usually fewer *M. arenaria* races 1 and 2 were present in soybean roots of the resistant genotypes compared to CNS.

Penetration of soybean roots by J2 varies among species of root-knot nematode. Penetration of soybean roots by *M. incognita* and *M. javanica* was rapid and increased little after 2 days, in contrast to *M. arenaria,* which continued to penetrate roots for 10 days (5). Also, even though race 1 of *M. arenaria* develops more rapidly on peanut than on soybean, a greater rate of root penetration occurs on soybean (20). In the present study, *M. arenaria* penetration of roots usually increased over 16 days, but after 4 days the rate of penetration per gram of root decreased in most genotype-race combinations. Because of the similar penetration rate of races 1 and 2 in soybean root systems, the greater number of race 2 juveniles per gram of root may result from a decreased root growth rate likely induced by this more aggressive race.

Even though more J2 penetrated CNS than resistant genotypes, resistance clearly is not so much related to penetration of the roots as it is to factors affecting the development of J2 following penetration. Nematode developmental rate and fecun-

dity were consistently greater on the susceptible CNS than the resistant genotypes, resulting in greater total egg production on CNS than the other genotypes. In addition, resistance of PI 200538 and PI 230977 to *M. arenaria,* reported previously (17,22), is supported by our data, which also suggest that the mechanism(s) of resistance to race 1 differs from that for race 2 on soybean. Development of race 1 J2 was slow on soybean, delaying completion of its life cycle. Besides an unbalanced sex ratio, the few females that developed were smaller and produced fewer eggs than race 2. These data help explain previous results indicating higher reproductive and damage potential of race 2 than race 1 on soybean (2,10,14,22). The observed shift in the sex ratio toward males affects not only the potential rate of population increase but also the extent of host damage, which most often is proportional to the female population due to their increase in nutritional requirements for reproduction (26). It is not clear, however, that race 2 of *M. arenaria* has greater inherent reproductive capacities than race 1. If it is true that individual females have the capacity to produce a fixed number of eggs (6), the higher fecundity of race 2 may reflect a shorter, but intensive, reproductive period.

Individual J2 of race 1 did not progress through the developmental stages as uniformly as did race 2, suggesting some genetic diversity in the race 1 population. Intrapopulation variation among single egg mass lines of *M. arenaria* has been observed by RFLP analysis, and variant forms have been detected even within individual lines (9). On the other hand, the diversity within the race 1 population agrees well with the fact that not all progeny of a parthenogenetic female able to reproduce on resistant plants inherit the same ability (24) or, if they do, that it has an adverse cost to fitness.

The extent of differences between races is critical for management strategies because it may affect crop-rotation sequences as well as the inherent tolerance of the crop to the damage potential of the nematode. Although our results support the use of resistant soybean genotypes in rotation with peanut in fields infested with *M. arenaria* race 1, continuous use of resistant cultivars should be avoided since some reproduction does occur on the resistant genotypes. Resistance genes in Jackson, PI 200538, and PI 230977 confer a superior level of resistance to race 1 than race 2, expressed through "rate reduction" of nematode development and reproduction.

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