Journal of Nematology 31(3):283–290. 1999.

Genetics and Mechanism of Resistance to *Meloidogyne arenaria* in Peanut Germplasm

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Abstract: Segregation of resistance to *Meloidogyne arenaria* in six BC_5F_2 peanut breeding populations was examined in greenhouse tests. Chi-square analysis indicated that segregation of resistance was consistent with resistance being conditioned by a single gene in three breeding populations (TP259-3, TP262-3, and TP271-2), whereas two resistance genes may be present in the breeding populations TP259-2, TP263-2, and TP268-3. Nematode development in clonally propagated lines of resistant individuals of TP262-3 and TP263-2 was compared to that of the susceptible cultivar Florunner. Juvenile nematodes readily penetrated roots of all peanut genotypes, but rate of development was slower ($P = 0.05$) in the resistant genotypes than in Florunner. Host cell necrosis indicative of a hypersensitive response was not consistently observed in resistant genotypes of either population. Three RFLP loci linked to resistance at distances of 4.2 to 11.0 centiMorgans were identified. Resistant and susceptible alleles for RFLP loci R2430E and R2545E were quite distinct and are useful for identifying individuals homozygous for resistance in segregating populations.

Key words: Arachis hypogaea, genetics, host resistance, *Meloidogyne arenaria,* molecular markers, nematode, peanut, RFLP, root-knot nematode.

The root-knot nematode *Meloidogyne arenaria* is an important pathogen of peanut (Minton and Baujard, 1990). No peanut (*Arachis hypogaea* L.) cultivar has resistance to *M. arenaria,* but resistance has been reported from several wild *Arachis* spp. (Baltensperger et al., 1986; Holbrook and Noe, 1990; Nelson et al., 1989). Resistance to root-knot nematodes from wild *Arachis* species has been introgressed into *A. hypogaea.* Stalker et al. (1995) identified *M. arenaria*-resistant genotypes where resistance was introgressed into *A. hypogaea* from *A. cardenasii* using a hexaploid pathway. Garcia et al. (1996) reported that this resistance was conditioned by two dominant genes, one gene (Mag) inhibiting root galling and another gene (Mae) inhibiting egg production by *M. arenaria.* Resistance to *M. arenaria* also has been introgressed into *A. hypogaea* by a diploid pathway (Simpson, 1991). TxAG-6 is an F1 from [*A. batizocoi* × (*A. cardenasii* × *A. diogoi*)]$^{4\times}$ and each of these species is resistant to *M. arenaria* (Nelson et al., 1989). TxAG-7 is from the first backcross generation of *A. hypogaea* 'Florunner' × TxAG-6 (Simpson et al., 1993). In addition to resistance to *M. arenaria,* TxAG-6 and TxAG-7 also have resistance to *M. javanica* and an undescribed *Meloidogyne* sp. (Abdel-Momen et al., 1998). TxAG-7 has been used for introgression of resistance to root-knot nematodes into peanut breeding populations using a backcross breeding program (Starr et al., 1995).

Resistance to *M. arenaria* in *A. cardenasii* was reported to completely inhibit nematode development and was accompanied by an apparent necrotic, hypersensitive host reaction (Nelson et al., 1990). The resistance of *A. batizocoi* caused a reduction in the total number of invading nematodes that reached maturity and produced eggs, and increased the time required for *M. arenaria* to complete its life cycle. No hypersensitive reaction was observed in *A. batizocoi* (Nelson et al., 1990). The resistance of TxAG-7 was similar to that of *A. cardenasii,* except that no host-cell necrosis characteristic of a hypersensitive reaction was associated with invading second-stage juveniles (J2) (Starr et al., 1990).

Burow et al. (1996) identified three RAPD markers linked to resistance to *M. arenaria* in several peanut breeding populations from the fifth backcross generation (BC_5) where TxAG-7 was the initial resistant par-

Received for publication 5 February 1999.
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This paper was edited by L. D. Young.

ent and Florunner was the recurrent susceptible parent. The resistance in each of the populations appeared to have been derived from *A. cardenasii* and was mostly likely due to a single gene. However, due to the few individuals examined per BC_5F_2 population, it was not possible to unequivocally determine the numbers of genes conditioning resistance in each population. Three objectives of this study were to: (i) test the hypothesis that resistance in several BC_5 breeding lines was due to a single gene; (ii) determine the effects of resistance conditioned by a single gene on nematode development; and (iii) determine if the mechanism of resistance conditioned by that gene involves a necrotic, hypersensitive host reaction.

Burow, Paterson, Simpson, and Starr (unpubl. data) have developed a genetic map of *A. hypogaea* based on 350 RFLP loci mapped to 22 linkage groups. The RAPD marker RKN440 linked to resistance to *M. arenaria* in several BC_5 breeding populations (Burow et al., 1996) was used as an RFLP probe and mapped to linkage group 1, indicating that at least one locus for resistance also maps to linkage group 1. Because the codominance of RFLP theoretically allows one to distinguish between homozygotes and heterozygotes, a further objective of this study was to determine the utility of RFLP loci from linkage group 1 to identify individuals homozygous for resistance.

Materials and Methods

Genetics of resistance: Meloidogyne arenaria isolate no. 82-4 from peanut was maintained on *Lycopersicon esculentum* Mill. 'Rutgers'. Nematode inoculum was prepared by extracting eggs from infected tomato roots with 0.5% NaOCl (Hussey and Barker, 1973). Esterase and malate dehydrogenase phenotypes were used to confirm the identity of *M. arenaria* (Esbenshade and Triantaphyllou, 1985).

Segregation of resistance was examined in six breeding populations from the BC_5F_2 generation of *A. hypogaea* × TxAg-7, with Florunner the recurrent parent for TP259-2, TP259-3, TP262-3, TP263-2, and TP271-2; and with NC7 the recurrent parent for TP268-3. Florunner was used as the standard susceptible control for all tests. The six BC_5F_2 populations were divided into two groups and each group was tested separately: TP259-2, TP259-3, and TP262-3 in test 1 and TP263-2, TP268-3, and TP271-2 in test 2. Fifty seeds of each line were dusted with the fungicide captan; placed into moist, rolled germination paper; and incubated at 25 °C. Four-day-old seedlings were transplanted singly into 12.7-cm-diam. pots filled with a 6:1 (v/v) mixture of pasteurized coarse sand and peat. All pots were kept in a greenhouse at 25 to 32 °C, watered daily, and fertilized with N-P-K. Each plant was inoculated with 10,000 eggs of *M. arenaria* 5 days after transplanting by pipetting the eggs into four holes (0.4-cm diam. × 3-cm depth) distributed equally from the base of the plants.

Eight weeks after inoculation, the plants were harvested and the soil was washed from the roots with water. Eggs were extracted from roots with 1.0% NaOCl (Hussey and Barker, 1973) and counted at ×20 with a dissecting microscope to determine the numbers of eggs per gram of fresh root weight. Plants having less than 10% of the number of nematode eggs per gram of root of the susceptible Florunner were classified as resistant (Starr et al., 1995). Chi-square analysis was used to determine if observed ratios of resistant to susceptible individuals for each population fit expected values for resistance being governed by one (AA) or two (AABB, AABb, or AaBb) genes.

Nematode development in resistant plants: Resistant individuals of TP262-3 and TP263-2, identified from the experiment above, were vegetatively propagated and used to determine if the resistance genes caused a hypersensitive host response to nematode infection and the effect of the resistance genes on nematode development. Florunner stem cuttings (test 1) or Florunner seeds (test 2) were the susceptible controls.

Thirty stem cuttings of each resistant line and 30 Florunner cuttings were transplanted to peat pellets after dipping the cut stems in a commercial preparation of 0.02%

1-naphthaleneacetamide and 4.04% thiram (Rootone, Green Light, San Antonio, TX) and maintained in a growth chamber with 100% relative humidity at 25 °C. After 4 weeks, cuttings with well-developed root systems were removed from the peat pellets and transplanted into a coarse sand and peat mix (6:1, v/v) in 250-cm^3 cups.

Plants were inoculated with 2,000 freshly hatched J2 (Vrain, 1977) 6 days after transplanting or 10 days after germination of Florunner seeds. The inoculation method was the same as that of the previous experiment. Inoculated plants were then placed in the growth chamber maintained at 26 °C day (14 hours) and 24 °C night, with 646 umol $sec^{-1}m^{-2}$ of photosynthetically active light energy.

The roots of inoculated plants were harvested at 2, 4, 8, 16, and 24 days after inoculation (DAI). The harvested roots were cleared with 1.0% NaOCl, weighed, and then stained with acid fuchsin (Byrd et al., 1982) for observation of nematode development (Triantaphyllou and Hirschmann, 1960). Total number of nematodes in roots and the number of nematodes in each developmental stage were recorded. Analysis of variance with general linear models (SAS Institute, Cary, NC) was used to determine significant treatment effects with mean separation by Fisher's protected LSD.

RFLP loci linked to resistance: Unexpanded tetrafoliate leaves were collected from BC_5F_2 and $BC_5F_{2:4}$ individuals from the breeding populations TP260-1-9, TP261-1-2, and TP262-3-5 that were determined to be resistant or susceptible to *M. arenaria* as described above. Each of these populations originated from the same Florunner × TxAG-7 cross described above and had Florunner as the recurrent parent. One tetrafoliate leaf was placed in each 1.5-ml microcentrifuge tube, frozen in liquid N2, and stored at -80 °C. To extract genomic DNA, the frozen samples were first coarsely ground with a small spatula, then 0.5 ml of extraction buffer (0.05 M citric acid, pH 5.0 with 0.10 M disodium EDTA, 0.5 M glucose, 0.06 M ascorbic acid, 0.4M $NHSO_3$, 0.06 M Na-diethyldithiocarbamate, 2% polyvinylpyrrolidone-40 and 5% Triton X-100) was added to each sample and they were further homogenized with a micro-pestle mounted in a hand drill for 3 minutes at 0 °C. The homogenates were centrifuged at 2,040g for 10 minutes, and the supernatant was discarded. Each pellet was re-suspended in 0.375 ml of a nuclear lysis buffer (0.05 M citric acid, pH 5.0, 0.05 M sodium EDTA, 0.14 M NaCl, 0.06 M ascorbic acid, 0.4M $NaHSO_3$, 0.06 M Na-diethyldithiocarbamate, and 20 g/liter each of polyvinylpyrrolidone-40 and sodium dodecylsulfate) and incubated for 20 minutes at 65 °C. The supernatant was collected following centrifugation at 5,220g for 5 minutes and transferred to sterile 1.5-ml micro-centrifuge tubes. Proteins and polysaccharides were precipitated by addition of 0.125 ml of 5 M potassium acetate pH 5.2 and incubation at 0 °C for 20 minutes, followed by centrifugation at 5,220g for 10 minutes. The supernatant was transferred to a sterile 1.5-ml microcentrifuge tube, the DNA was precipitated with 1 ml ethanol, and the viscous DNA was transferred with a hooked glass rod to another micro-centrifuge tube containing 0.5 ml of 70% ethanol and 0.5 M sodium acetate. The DNA was pelleted by centrifugation at 5,220g for 5 minutes, air-dried, and then dissolved in 0.03 ml of 0.05 M tris buffer pH 8.0 containing 0.001 M disodium EDTA. Each sample routinely yielded 2 to 4 μg of DNA of sufficient purity for Southern analysis.

Approximately 2 μg of DNA from each sample was digested with EcoR I (New England Biolabs, Beverly, MA) according to the manufacturer's directions. The digested samples were separated on 0.8% agarose gels and transferred to Hybond N+ membrane (Amersham, Arlington Heights, IL) (Chittenden et al., 1994). Membranes were probed with *A. hypogaea* cDNA clones from linkage group 1 (Burrow, Paterson, Simpson, and Starr, unpubl. data). Based on a preliminary screen of DNA from BC_5F_2 individuals, the clones S11137E, R2430E, and R2545E were selected to probe DNA from $BC_5F_{2:4}$ individuals.

Results

Genetics of resistance: Mean numbers of eggs produced by *M. arenaria* on Florunner were 4,150 and 2,810/g fresh root weight in test 1 and test 2, respectively. Reproduction of *M. arenaria* on each of the six BC_5F_2 breeding populations was highly variable (Fig. 1), and ranged from 0 to > 1,000 eggs/g fresh root weight. Each population had numerous individuals that were classified as resistant, based on having less than 10% of the number of eggs per gram of root than that produced on Florunner.

The ratio of resistant to susceptible individuals in each of the six BC_5F_2 populations was not different ($P > 0.05$) from that predicted for a single dominant gene (Table 1). No line had a segregation ratio that was consistent with two dominant genes, with the resistant parent homozygous for each gene (AABB). Segregation ratios for TP259-2, TP263-2, and TP268-3, however, were consistent also with two dominant genes, both heterozygous (AaBb). The segregation ratio for TP268-3 also was consistent with resistance being governed by two dominant genes, homozygous for one and heterozygous for the second (AABb.)

Nematode development in resistant plants: In all but one comparison, root weight of Florunner was greater ($P = 0.05$) than that of the resistant genotypes (data not shown). Second-stage juveniles were observed in the roots of the resistant genotypes and Florunner at 2 DAI in both tests. Whereas numbers of nematodes per gram of root were different between the resistant genotypes and Flo-

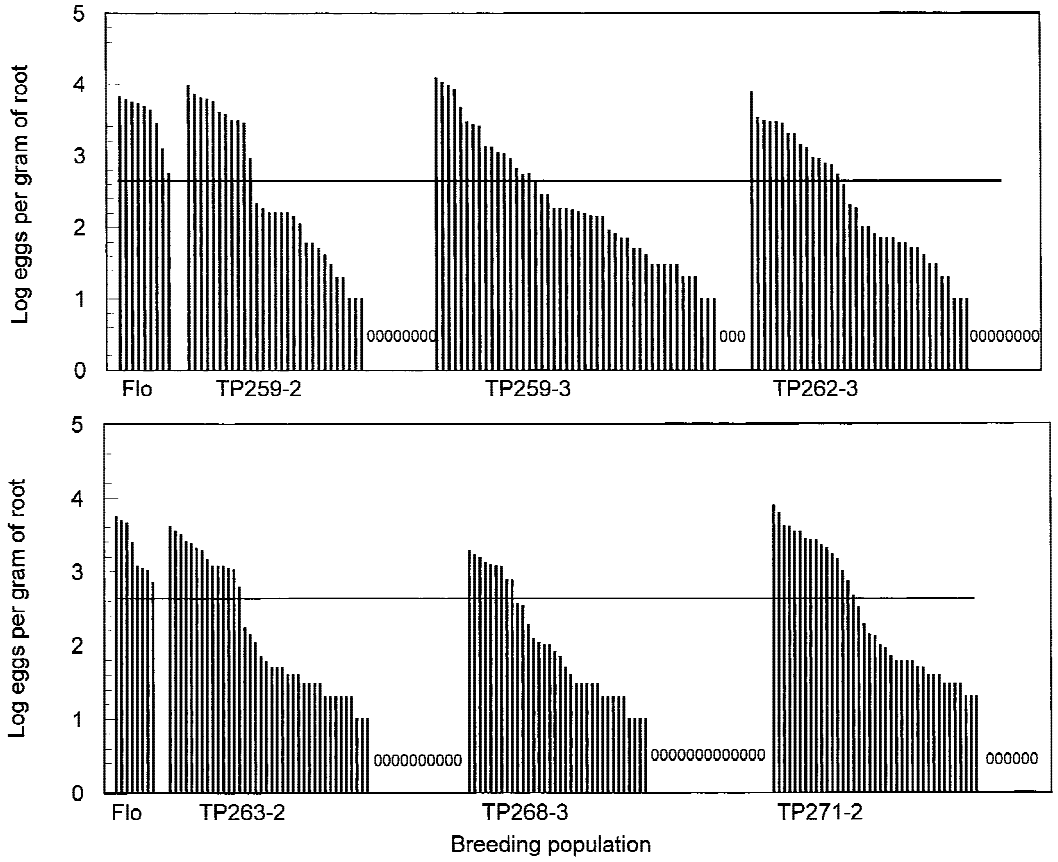

Fig. 1. Variation in eggs per gram of root produced by *Meloidogyne arenaria* on individual plants of six BC_5F_2 breeding populations of peanut developed for resistance to *M. arenaria*. Each population was derived from Florunner × TxAG-7, with Florunner as the recurrent parent for each population, except TP268-3 for which NC7 was the recurrent parent. The horizontal line represents 10% of the mean numbers of eggs produced on the susceptible Florunner. No eggs were produced on individuals marked with 0.

TABLE 1. Chi-square analysis of segregation for resistance to *Meloidogyne arenaria* in six BC_5F_2 peanut breeding populations.[a]

BC_5F_2 population	Genotype for resistance[b]	Resistant/Susceptible		χ^2 value[c]
		Observed	Expected	
	Test 1			
TP259-2	AA	29:11	30:10	0.13
	AABB	29:11	38:2	30.83*
	AABb	29:11	34:6	4.28*
	AaBb	29:11	33:7	2.01
TP259-3	AA	33:17	38:12	2.16
	AABB	33:17	47:3	65.72*
	AABb	33:17	42:8	12.91*
	AaBb	33:17	41:9	7.62*
TP262-3	AA	29:16	34:11	2.67
	AABB	29:16	42:3	65.96*
	AABb	29:16	38:7	13.56*
	AaBb	29:16	37:8	8.33*
	Test 2			
TP263-2	AA	35:14	37:12	0.44
	AABB	35:14	46:3	41.67*
	AABb	35:14	41:8	6.23*
	AaBb	35:14	40:9	3.09
TP268-3	AA	37:11	36:12	0.32
	AABB	37:11	45:3	22.76*
	AABb	37:11	41:7	1.94
	AaBb	37:11	39:9	0.54
TP271-2	AA	33:17	38:12	2.16
	AABB	33:17	47:3	65.71*
	AABb	33:17	42:8	12.81*
	AaBb	33:17	41:9	3.84*

[a] Each breeding population was derived from Florunner × TxAG-7 with Florunner as the recurrent parent for each population, except for TP268-3 for which NC7 was the recurrent parent.
[b] Expected ratios of resistant to susceptible individuals were AA = 3:1, AABB = 15:1, AABb = 27:5, and AaBb = 39.9.
[c] Values with asterisks are significantly different from the expected ratio at $P = 0.05$.

TABLE 2. Comparison of development of *Meloidogyne arenaria* in the two resistant BC_5F_2 peanut breeding populations (PBP) TP262-3 and TP263-2 and the susceptible cultivar Florunner (F1) at different days after inoculation (DAI). Each breeding population was derived from Florunner × TxAG-7, with Florunner as the recurrent parent.

	Nematodes/g root		Percent J2		Percent Adv. J2		Percent J3+J4		Percent females		Percent females with eggs	
DAI	PBP	Fl	PBP	Fl	PBP	Fl	PBP	Fl	PBP	Fl	PBP	Fl
	Peanut breeding population TP262-3 (Test 1)											
2	138a	409a	100a	100a	0	0	0	0	0	0	0	0
4	190a	646b	100a	100a	0	0	0	0	0	0	0	0
8	79a	153b	98.7a	80.6b	1.3a	19.4b	0	0	0	0	0	0
16	93b	77a	77.5a	46.0b	20.0a	48.0b	2.5a	5.1b	0	0	0	0
24	46a	84b	57.8b	16.1a	41.4a	45.0a	2.9a	0.1a	0a	15.6b	0a	5.6b
	Peanut breeding population TP263-2 (Test 2)											
2	13a	186b	100a	100a	0	0	0	0	0	0	0	0
4	11a	179b	100a	100a	0	0	0	0	0	0	0	0
8	295b	78a	100b	89.6a	0a	10.4b	0	0	0	0	0	0
16	250b	50a	96.6b	80.1a	3.5a	18.1b	0a	1.8b	0	0	0	0
24	402b	198a	89.3b	54.0a	9.2a	21.5a	1.3a	9.3b	0.2a	15.2b	0	0

Mean values in columns for each parameter in each test followed by a common letter are not significantly different ($P = 0.05$). J2 = second-stage juveniles; Adv. J2 = swollen, advanced second-stage juveniles; J3+J4 = third- and fourth-stage juveniles.

runner at several observation times, no consistent trend was detected. Distinctly swollen, advanced J2 were observed in resistant and susceptible roots at 8 DAI, with Florunner having a greater percentage ($P = 0.05$) of the nematodes in this stage of development than the resistant genotypes (Table 2). By 24 DAI, mature females with a small egg mass and a few eggs were observed in roots of Florunner in both tests, whereas no adult females were observed in TP262-3 and only a few females without eggs were observed in TP263-2. Conversely, in the resistant genotypes the majority of the nematodes in the roots were still unswollen J2 at 24 DAI. Necrosis of host cells surrounding invading nematodes was observed occasionally in the resistant genotypes but was absent from more that 60% of the encounter sites examined in resistant plants.

RFLP loci linked to resistance: Each of the three RFLP probes tested was linked to resistance. The resistant and susceptible alleles for loci R2430E and R2545 were quite distinct and easy to score, whereas the susceptible allele at S1137E was indistinct and more difficult to score (Fig. 2). The total numbers of individuals that were correctly scored for resistance using each of the markers did not differ ($P = 0.05$) from that predicted by the phenotype determined from nematode reproduction (Table 3). Recombination between the RFLP loci and resistance was observed, indicating that none of the markers was derived directly from the resistance gene. Analysis of segregation of resistance and the RFLP loci using MapMaker (Lander et al., 1987) at LOD 3.0 indicated that R2430 was 4.2 centiMorgans (cM) from the resistance gene, followed by R2545E at 5 cM, and S1137E at 11 cM from the resistance gene (Fig. 3).

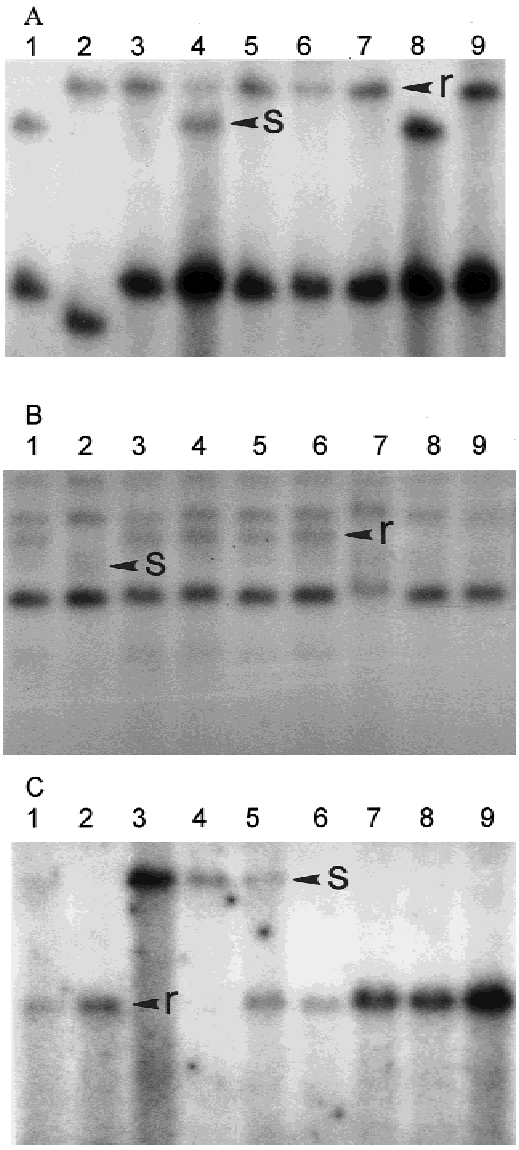

FIG. 2. RFLP loci linked to resistance to *Meloidogyne arenaria* in individuals from $BC_5F_{2:4}$ peanut breeding populations. Each population was derived from Florunner × TxAG-7, with Florunner as the recurrent parent. Both resistant (r) and susceptible (s) alleles are shown. A) Locus R2430E; lane 1 is susceptible Florunner, lane 2 is the resistant interspecific hybrid TxAG-6, and lanes 3 to 9 are segregating individuals of TP262-3. Lane 4 shows the heterozygous condition. B) Locus S1137E; lanes 1 to 9 are individuals from TP262-3. The susceptible allele is indistinct. C) Locus R2545E; lanes 1 to 9 are individuals of TP259-3; lane 5 shows the heterozygous condition.

DISCUSSION

In a study to identify RAPD markers linked to resistance to *M. arenaria* in several BC_5F_2 peanut breeding populations derived from the interspecific hybrids TxAG-6 and TxAG-7, Burow et al. (1996) estimated that resistance was conditioned by one or two genes. Further, this resistance was found to be derived from *A. cardenasii*. However, because those data were derived from a total of 63 individuals from 17 BC_5F_2 peanut breeding populations, and because each popula-

TABLE 3. Linkage of three RFLP loci to resistance to *Meloidogyne arenaria* in three $BC_5F_{2:4}$ breeding populations of peanut derived from Florunner × TxAG-7, with Florunner as the recurrent parent.

Breeding line	S1137E			R2545E			R2430E		
	R	S	X2	R	S	X2	R	S	X2
TP260-1-9	1/0	11/12	nd	6/2	20/24	nd	5/2	23/26	nd
TP261-1-2	14/14	8/8	0.00	15/15	8/8	0.00	15/16	9/8	0.19
TP262-3-5	26/26	7/7	0.00	38/38	9/9	0.00	42/42	9/9	0.00
Total	41/40	26/27	0.02	59/55	37/41	0.38	62/60	41/43	0.37

Values are numbers of observed individuals scored as resistant (R) or susceptible (S) based on RFLP alleles observed over expected phenotypes determined from analysis of nematode reproduction. Chi-square values for TP260-1-9 were not determined (nd) because there were insufficient expected numbers of resistant individuals for a valid test. In no comparison did chi-square values exceed the critical value ($P = 0.05$) of 3.84.

tion could have different numbers of resistance genes, it was not possible to determine the number of resistance genes present in each separate breeding population. In the present study, by examining a larger number of individuals from each of six BC_5F_2 breeding populations, it was possible to confirm the hypothesis that resistance in at least some BC_5F_2 peanut breeding populations is conditioned by a single dominant gene. However, it is also possible that a second resistance gene is present in some lines.

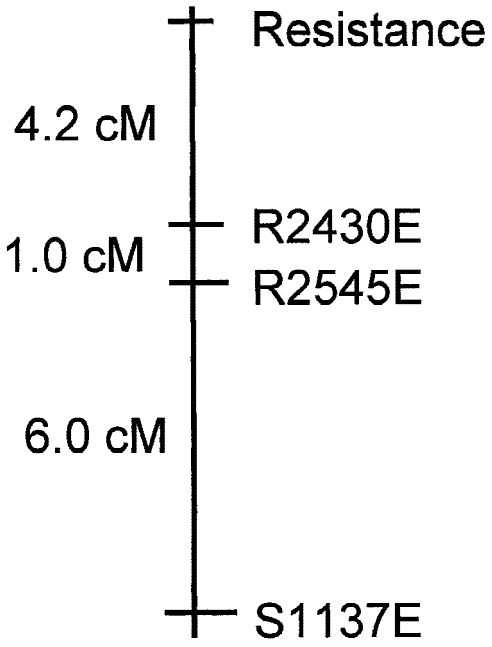

FIG. 3. Linkage of three RFLP loci to a gene for resistance to *Meloidogyne arenaria* in $BC_5F_{2:4}$ peanut breeding populations. Each population was derived from Florunner × TxAG-7, with Florunner as the recurrent parent.

That some breeding populations may have two genes for resistance is consistent with the resistance being derived from *A. cardenasii* (Burow et al., 1996), which has multiple resistance genes (Starr and Simpson, 1991). Further, Garcia et al. (1996) reported two genes for resistance to *M. arenaria* were introgressed from *A. cardenasii* into *A. hypogaea* by a hexaploid introgression pathway. Additionally, because the complex diploid introgression pathway used to develop the initial resistant hybrids in our breeding program utilized a complex hybrid of three wild *Arachis* spp. (Simpson, 1991), each of which is resistant to *M. arenaria,* it is also possible that a second gene present was derived from either *A. batizocoi* or *A. diogoi.* The single gene for resistance in TP259-3, TP262-3, and TP271-2 probably originated from *A. cardenasii* (Burow et al., 1996). The origin of the putative second gene for resistance in the other breeding populations is unknown and may have originated from any of the three wild species used to develop TxAG-6.

In a previous report, Nelson et al. (1990) suggested the possibility that resistance of *A. cardenasii* to *M. arenaria* was due to a hypersensitive response, similar to that conditioned by the Mi gene in tomato (Williamson and Hussey, 1996) and many other resistance genes (Bent, 1996). However, Starr et al. (1990) did not observe any evidence of a hypersensitive response in TxAG-7, which was the donor parent for resistance in these BC_5F_2 peanut breeding populations. The resistance of TP262-3 and TP263-2 appears identical to that of TxAG-7 and did not in-

volve a necrotic, hypersensitive response. In previous studies of the mechanism of resistance (Nelson et al., 1990; Starr et al., 1990), the genotypes being studied had multiple resistance genes. In the present study we confirmed that a single gene in TP262-3 conditions a similar resistance response. Although resistance to pathogens that is conditioned by single, major effect genes is usually believed to involve a hypersensitive host response, another case of a non-hypersensitive response resistance condition by a single gene is the Lr34 gene that confers resistance to leaf rust in wheat (Rubiales and Niks, 1995).

Of the three RFLP probes tested for use in identifying individuals homozygous for resistance in a segregating population, both R2545 and R2430E were relatively easy to score and both were sufficiently close to the resistance allele to be used with a high level of confidence. The third locus, S1137E, will have less utility as it is difficult to score the susceptible allele and is more distant from the resistance gene.

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