Resistance in Peanut Cultivars and Breeding Lines to Three Root-Knot Nematode Species

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ABSTRACT

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Three major species of root-knot nematode infect peanut: *Meloidogyne arenaria* race 1, *M. hapla*, and *M. javanica* race 3. Sources of resistance to all three nematodes are needed for developing novel peanut cultivars with broad resistance to *Meloidogyne* spp. Cultivars and breeding lines of peanut were evaluated for resistance to *M. arenaria*, *M. hapla*, and *M. javanica* in the greenhouse and in the laboratory. Twenty-six genotypes with some resistance to *M. arenaria*, *M. javanica*, or *M. hapla* were identified from 60 accessions based on average eggs per gram of root and gall index relative to a susceptible control. Among these, 14 genotypes were moderately to highly resistant to all three species, 5 genotypes were resistant to *M. arenaria* and *M. javanica*, 2 genotypes were resistant to *M. javanica* and *M. hapla*, 1 genotype was resistant to *M. arenaria* alone, and 4 genotypes were resistant to *M. hapla* alone. Reproduction of *M. arenaria* on lines NR 0817, C724-19-11, and D108 was highly variable, indicating that these genotypes likely were heterogeneous for resistance. COAN, NemaTAM, C724-25-8, and the *M. arenaria*-resistant plants of C724-19-11 contained the dominant sequence-characterized amplified region marker (197/909) for nematode resistance. Results with the molecular markers indicate that the high resistance to *M. arenaria* in GP-NC WS 6 may be different from the resistance in COAN, NemaTAM, and C724-25-8. Resistance to *M. arenaria* was correlated with resistance to *M. javanica* in peanut, whereas resistance to *M. hapla* was not correlated with the resistance to either *M. arenaria* or *M. javanica*. The resistant selections should be valuable sources for pyramiding resistance genes to develop new cultivars with broad and durable resistance to *Meloidogyne* spp.

Additional keywords: *Arachis hypogaea*, greenhouse screening

Root-knot nematodes (*Meloidogyne* spp.) are among the most serious plant pests in the world. Several species of root-knot nematodes are pathogenic on peanut (*Arachis hypogaea* L.) and cause considerable yield loss annually. Of these, *Meloidogyne arenaria* race 1 (Neal) Chitwood, *M. hapla* Chitwood, and *M. javanica* race 3 (Treub) Chitwood are the major pathogenic species of peanut (2,29). These three species are known to occur in many peanut-producing regions, including North, Central and South America, Africa, Asia, Europe, and Australia (34,39). *M. arenaria* and *M. javanica* are common in warm peanut-growing regions whereas *M. hapla* occurs mainly in cool regions. In the United States, *M. arenaria* and *M. hapla* exist throughout the peanut-producing

areas. *M. arenaria* is the predominant species parasitizing peanut in the southern regions, especially in Alabama, Florida, Georgia, Texas, and South Carolina, where up to 40% of the fields are infested and yield losses in heavily infested fields can exceed 30% (27,29,48). All three species may cause significant losses in yield and quality of peanut (2). *M. hapla* is the most prevalent species in more northerly states, including North Carolina, Virginia, and Oklahoma (4,26). Populations of *M. javanica* parasitic on peanut are common in Egypt (47) and India (35), but they are rare in the United States, having been described from only a few fields in Florida, Georgia, and Texas (28,30,48).

Developing cultivars with host resistance to nematodes, which can be defined as the suppression of nematode reproduction by the resistant plant relative to reproduction on a susceptible genotype of the same species (49), is a desirable approach to manage nematodes. Many sources of moderate resistance to *M. arenaria* have been identified from *A. hypogaea* in the United States germplasm collection (17,19). High levels of resistance to *M.*

arenaria exist in *Arachis* spp. (16,31), and resistance has been introgressed into *A. hypogaea*. Currently, there are six registered interspecific germplasm lines with resistance to *M. arenaria*: TxAG-6 and TxAG-7 (36), GP-NC WS 5 and GP-NC WS 6 (41), and NR 0812 and NR 0817 (3). A backcrossing program was used to introgress the root-knot nematode resistance from TxAG-7 into peanut breeding populations (43). This work resulted in the release of cvs. COAN and NemaTAM, which are highly resistant to *M. arenaria* and *M. javanica* (37,38). The resistance in the two cultivars is governed by a single dominant gene (8,42). However, neither COAN nor NemaTAM has been widely used in agricultural practice due to the low yield potentials relative to the recurrent parent Florunner in noninfested fields (44) and high susceptibility to *Tomato spotted wilt virus* (TSWV; 20). No peanut cultivars or interspecific germplasm have high levels of resistance to *M. hapla* (46), although resistance to *M. hapla* has been identified in *Arachis hypogaea* and related species (7,13,45).

Planting cultivars with currently available sources of nematode resistance may be effective in managing *M. arenaria* and *M. javanica*; but the presence of *M. hapla* throughout the peanut-growing region raises concerns about durability of resistance. Planting cultivars with resistance genes to *M. arenaria* and *M. javanica* may provide a competitive advantage to *M. hapla* and lead to a species shift. In an analogous situation, planting potato cultivars with resistance only to *Globodera rostochiensis* led to a rapid increase in *G. pallida*, a species unaffected by the resistance (12). Reliance on a single gene for resistance to nematodes also can lead to selection of virulent biotypes. Several populations of *M. incognita* recently have been identified as virulent on tomato with *Mi* in regions where tomato is a major crop (14,25). Additional sources of resistance to root-knot nematodes in peanut are needed to develop new cultivars with broad and durable resistance to *Meloidogyne* spp.

In order to expedite breeding for nematode resistance, several molecular markers have been developed (6,9,10,15). One random amplified polymorphic DNA (RAPD) marker, Z3/265, was developed from an F₂ population of GA6 (*A. hypo-*

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gaea (PI261942) × *A. cardenasii* Krapov. & W.C. Gregory) backcrossed with PI261942 (15). A 265-bp fragment derived from *A. cardenasii* was linked at 10 ± 2.5 and 14 ± 2.9 centimorgans from the putative nematode resistance genes *Mag* and *Mae*, respectively. It was converted suc-

cessfully into a sequence-characterized amplified region (SCAR) marker (15). Choi et al. (8) found that the single dominant resistance gene in COAN was linked to restriction fragment length polymorphism (RFLP) markers R2430E and R2545E. Burow et al. (6) identified three

RAPD markers (RKN 229, RKN 410, and RKN 440) linked to *M. arenaria* resistance in several breeding populations derived from TxAG-7 in the fifth backcross generation. Marker RKN 440 was identified in the backcross population with a 5.8 ± 2.1% recombination rate with the resistance gene derived from either *A. cardenasii* or *A. diogeni* Hoehne. Based on the sequence of the RAPD fragment that originated from COAN, a new SCAR marker, 197/909, recently was developed (9). This SCAR marker amplifies fragments from both susceptible and resistant plants but of different molecular weights, thus avoiding false negative classifications caused by failed reactions with dominant markers.

The objectives of this study were to (i) use greenhouse screening methods and molecular markers to identify new resistance sources to *M. arenaria*, *M. javanica*, and *M. hapla* and (ii) determine the correlations between the resistances to different species of *Meloidogyne*.

MATERIALS AND METHODS

Peanut genotypes. In all, 60 peanut genotypes were evaluated in this study. These included 9 cultivars from China; 9 cultivars from the United States; 12 and 5 breeding lines from China and the United States, respectively; 4 released germplasm lines from the United States; and 21 selections from Chinese peanut germplasm and local cultivars (Table 1). Of these, five accessions previously had been reported to have moderate resistance to *M. hapla* (D009, D029, D031, D040, and D099) (13,40); eight accessions (NR 0817 [3], GP-NC WS 5 and GP-NC WS 6 [41], COAN [37], NemaTAM [38], C209-6-37 [18], and C724-19-11 and C724-25-8 [C. C. Holbrook, unpublished]) had high or moderate resistance to *M. arenaria*; and COAN (37) and NemaTAM (38) were reported to be resistant to *M. javanica*.

Nematode inoculum. One isolate each of *M. arenaria*, *M. hapla*, and *M. javanica* was used to evaluate the peanut accessions for resistance. The isolate of *M. arenaria* originated from a peanut field in Tift County, GA. *M. javanica* and *M. hapla* were isolated from peanut in Texas. The nematodes were cultured alternately on tomato (*Lycopersicon esculentum* cv. Rutgers) or eggplant (*Solanum melongena* cv. Blackbeauty) and peanut cv. Georgia Green. Eggs used for inoculum were extracted from roots of tomato or eggplant by use of 0.05% NaOCl in water (24). Species identity of the isolates was confirmed by isozyme phenotyping and by a host differential test (33).

Greenhouse resistance screening. The peanut genotypes were evaluated for resistance to *M. arenaria*, *M. hapla*, and *M. javanica* in three separate experiments in a greenhouse with six replicates in each trial. Two seeds were planted in each 10-by-10-cm² pot filled with steam-pasteurized

Table 1. Peanut (*Arachis hypogaea*) genotypes evaluated for resistance to three species of *Meloidogyne*

Name/code ^a	Origin and type of line	Known resistance ^b	Parent species, resistance source
9509	China; breeding line	N	<i>A. hypogaea</i>
950213	China; breeding line	N	<i>A. hypogaea</i>
950404	China; breeding line	N	<i>A. hypogaea</i>
950521	China; breeding line	N	<i>A. hypogaea</i>
950530	China; breeding line	N	<i>A. hypogaea</i>
950536	China; breeding line	N	<i>A. hypogaea</i>
961308-1	China; breeding line	N	<i>A. hypogaea</i>
961308-2	China; breeding line	N	<i>A. hypogaea</i>
970101	China; breeding line	N	<i>A. hypogaea</i>
970105	China; breeding line	N	<i>A. hypogaea</i>
990304	China; breeding line	N	<i>A. hypogaea</i>
991219	China; breeding line	N	<i>A. hypogaea</i>
Baisha 1016	China; cultivar	N	<i>A. hypogaea</i>
C209-6-37	Georgia, USA; released germplasm line	Ma	<i>A. cardenasii</i>
C724-19-11	Georgia, USA; breeding line	Ma	COAN
C724-25-8	Georgia, USA; breeding line	Ma	COAN
C-99R	Florida, USA; cultivar	N	<i>A. hypogaea</i>
COAN	Texas, USA; cultivar	Ma & Mj	<i>A. cardenasii</i>
D002	China; selection	N	<i>A. hypogaea</i>
D009	China; selection	Mh	<i>A. hypogaea</i>
D013	China; selection	N	<i>A. hypogaea</i>
D0206	China; selection	N	<i>A. hypogaea</i>
D029	China; selection	Mh	<i>A. hypogaea</i>
D031	China; selection	Mh	<i>A. hypogaea</i>
D040	China; selection	Mh	<i>A. hypogaea</i>
D054	China; selection	N	<i>A. hypogaea</i>
D098	China; selection	N	<i>A. hypogaea</i>
D099	China; selection	Mh	<i>A. hypogaea</i>
D108	North Carolina, USA; breeding line	N	<i>A. cardenasii</i>
D122	China; selection	N	<i>A. hypogaea</i>
D129	China; selection	N	<i>A. hypogaea</i>
D131	China; selection	N	<i>A. hypogaea</i>
D132	China; selection	N	<i>A. hypogaea</i>
D133	China; selection	N	<i>A. hypogaea</i>
D134	North Carolina, USA; breeding line	N	<i>A. cardenasii</i>
D140	China; selection	N	<i>A. glabrata</i>
D142	China; selection	N	<i>A. hypogaea</i>
D143	China; selection	N	<i>A. hypogaea</i>
D169	China; selection	N	<i>A. hypogaea</i>
D998	China; selection	N	<i>A. hypogaea</i>
D999	China; selection	N	<i>A. hypogaea</i>
Florunner	Florida; cultivar	N	<i>A. hypogaea</i>
Georgia Green	Georgia, USA; cultivar	N	<i>A. hypogaea</i>
Georgia-01R	Georgia, USA; cultivar	N	<i>A. hypogaea</i>
Georgia-02C	Georgia, USA; cultivar	N	<i>A. hypogaea</i>
GP-NC WS 5	North Carolina, USA; released germplasm line	Ma	<i>A. cardenasii</i>
GP-NC WS 6	North Carolina, USA; released germplasm line	Ma	<i>A. cardenasii</i>
HT 02-01	North Carolina, USA; breeding line	N	GP-NC WS 5
Huayu 17	China; cultivar	N	<i>A. hypogaea</i>
Huayu 21	China; cultivar	N	<i>A. hypogaea</i>
Huayu 22	China; cultivar	N	<i>A. hypogaea</i>
Lianhua 2	China; cultivar	N	<i>A. hypogaea</i>
Luhua 9	China; cultivar	N	<i>A. hypogaea</i>
Luhua 11	China; cultivar	N	<i>A. hypogaea</i>
Luhua 14	China; cultivar	N	<i>A. hypogaea</i>
NemaTAM	Texas; cultivar	Ma & Mj	<i>A. cardenasii</i>
NR 0817	Georgia, USA; released germplasm line	Ma	GP-NC WS 5
Qinglan 2	China; cultivar	N	<i>A. hypogaea</i>
Southern runner	Florida, USA; cultivar	N	<i>A. hypogaea</i>
Tifrunner	Georgia, USA; cultivar	N	<i>A. hypogaea</i>

^a Numbers 95xxxx indicate that the cross was made in 1995 and numbers starting with a D were selections from Chinese germplasm and local cultivars.

^b N—unknown; Ma, Mj, and Mh = resistant to *Meloidogyne arenaria*, *M. javanica*, and *M. hapla*, respectively.

(steam heated at 100°C for 6 h) sandy soil (texture: 85% sand, 11% silt, and 4% clay) and thinned to one plant per pot after germination. Eight thousand nematode eggs were distributed into two holes (3 cm deep) at the base of each plant 2 weeks after planting and covered with soil. In the greenhouse, soil temperatures varied between 20 and 35°C; every experiment was arranged as a randomized complete block design on a bench.

Peanut plants were uprooted and washed clean of soil 60 days after inoculation. Each plant was assessed for root galling based on the following index: 0 = no galling, 1 = trace infection with a few small galls, 2 = ≤25%, 3 = 25 to 50%, 4 = 51 to 75%, and 5 = ≥75% of root galled. Roots then were cut into approximately 5-cm pieces, weighed, and agitated in 1% NaOCl solution for 5 min. Eggs were collected and rinsed with tap water on nested 150- and 25-μm-pore sieves, and a subsample was counted under ×10 magnification with an inverted microscope. The genotypes selected as resistant to nematodes, based on either gall index or egg number per gram of root, and the susceptible control (Georgia Green) were reevaluated at least one more time to confirm the resistance.

Gall index and egg number data were analyzed with the PROC GLM procedure of SAS (version 9.1; SAS Institute, Inc., Cary, NC). Means for each genotype within one nematode population were calculated with least-squares estimates of marginal means (LSMEANS), and an individual *t* test was used for mean separation. The correlation coefficients of resistance to different species of *Meloidogyne* were analyzed by the PROC CORR procedure of SAS.

SCAR marker screening. Newly expanded leaf tissue samples were collected from approximately 30-day-old peanut seedlings in the greenhouse. Total genomic DNA was extracted using the cetyltrimethylammonium bromide method according to Hopkins et al. (21), with several modifications. The DNA was dissolved in Tris-EDTA buffer (10 mM Tris and 0.1 mM EDTA, pH 8.0) with 1% RNase and stored at 4°C. SCAR makers Z3/265 (15) and 197/909 (9) were used to determine whether the resistance gene or genes were linked to the *M. arenaria*-resistant markers in selected genotypes. In all, 1 μl of the DNA extract was used for a 25-μl-volume polymerase chain reaction (PCR) reaction. Each PCR reaction was performed with 0.5 U of Hotmaster Taq DNA polymerase (Promega Corp., Madison, WI) using the buffer supplied by the manufacturer containing 25 mM Mg²⁺ (final reaction concentration, 2.5 mM). Amplification conditions for both sets of primers were similar: initial denaturation at 95°C for 5 min; 40 cycles of 95°C for 30 s, annealing temperature of 60.2°C for 30 s, and 72°C for

Table 2. Root galling, reproduction of *Meloidogyne arenaria*, and resistance classification for selected peanut genotypes tested in the greenhouse

Genotype	No. of replicates ^a	Gall index ^b	Eggs/g of root ^c	Resistance ^d
NemaTAM	17	0.64 ± 0.25	586 ± 1,041	HR
GP-NC WS 6	12	0.37 ± 0.31	875 ± 1,249	HR
COAN	16	1.15 ± 0.27	889 ± 1,074	HR
C724-25-8	18	0.78 ± 0.25	1,073 ± 1,011	HR
D054	16	1.92 ± 0.25	1,341 ± 1,074	MR
D031	16	1.42 ± 0.25	1,428 ± 1,074	MR
D040	16	1.47 ± 0.25	1,879 ± 1,074	MR
D998	16	1.50 ± 0.26	2,386 ± 1,074	MR
D099	16	0.95 ± 0.27	2,439 ± 1,074	MR
D009	16	1.79 ± 0.26	2,491 ± 1,073	MR
950530	12	2.23 ± 0.31	2,836 ± 1,248	MR
D108	18	1.00 ± 0.26	2,917 ± 1,041	MR
990304	15	1.69 ± 0.28	3,393 ± 1,110	MR
950521	11	1.16 ± 0.33	3,705 ± 1,304	MR
970101	10	1.97 ± 0.34	3,852 ± 1,367	MR
NR 0817	11	1.86 ± 0.33	4,166 ± 1,304	MR
C724-19-11	17	1.94 ± 0.25	4,597 ± 1,011	MR
C209-6-37	16	2.45 ± 0.26	4,609 ± 1,073	MR
D999	10	1.85 ± 0.31	4,611 ± 1,367	MR
HTS 02-01	10	2.34 ± 0.34	4,670 ± 1,369	MR
950213	10	3.89 ± 0.31	6,337 ± 1,367	S
GP-NC WS 5	11	3.45 ± 0.33	11,046 ± 1,304	S
Georgia Green	18	4.14 ± 0.25	11,069 ± 1,011	S

^a Data from three trials (six replicates/trial) were combined for analysis as unbalanced data.

^b Gall index, where 0 = no galling, 1 = trace infection with a few small galls, 2 = ≤25%, 3 = 25 to 50%, 4 = 51 to 75%, and 5 = ≥75% of roots galled. Data were least-squares estimates of marginal means (LSMEANS) ± standard errors.

^c Data were LSMEANS ± standard errors.

^d HR = highly resistant, eggs/g of root ≤10% of Georgia Green; MR = moderately resistant, eggs/g of root ≤50% of Georgia Green and gall index ≤3.00; and S = susceptible, eggs/g of root >50% of Georgia Green or gall index >3.00.

Fig. 1. Frequency of individuals with different levels of resistance to *Meloidogyne arenaria* in peanut genotypes. NemaTAM was classified as highly resistant (HR), C209-6-37 was classified as moderately resistant (MR), and Georgia Green was the susceptible (S) control.

30 s; and final extension at 72°C for 7 min. All PCR amplifications were performed with the GeneAmp PCR system 9700 (Applied Biosystems, Foster City, CA). PCR products were separated on 2% agarose gels (Invitrogen, Carlsbad, CA) and 8% polyacrylamide (PAGE) gels.

RESULTS

***M. arenaria*.** Fifty-seven genotypes were included in the first greenhouse screening trial for resistance to *M. arenaria*. The second greenhouse trial evaluated 28 accessions with low gall indices (≤ 3.0) or low egg numbers ($\leq 50\%$ of the susceptible control Georgia Green), as well as two genotypes that did not germinate in trial 1, three new collections, and susceptible control Georgia Green. Of these entries, 21 accessions with low gall

indices or low egg numbers were selected and advanced to the third trial with Georgia Green as the susceptible control. Genotype GP-NC WS 5 also was included in trial 3, although it had a high gall index and eggs per gram of root in the earlier trials. There were no significant interactions of genotype-trial for gall index and eggs per gram of root; thus, data for the genotypes included in all three trials or in the second and the third trials were pooled across trials. The data was analyzed with GLM of SAS as unbalanced data set (Table 2). Eggs per gram of root for all the selected genotypes, except GP-NC WS 5, were lower ($P \leq 0.05$) than the susceptible control Georgia Green. Reproduction of *M. arenaria* on genotypes NemaTAM, GP-NC WS 6, COAN, and C724-25-8 were less than 10% of Georgia Green, and they

were classified as highly resistant (HR). Sixteen genotypes were classified as moderately resistant (MR) because nematode reproduction was $<50\%$ of Georgia Green. The genotypes 950213 and GP-NC WS 5 were classified as susceptible (S). On all the HR and MR genotypes, gall indices were ≤ 3.00 .

The variability of egg numbers for NR 0817, C724-19-11, and D108 was extremely high, and the frequencies of individual plants with different resistance levels for these three genotypes were different from NemaTAM (highly resistant), C209-6-37 (MR), or Georgia Green (susceptible) (Fig. 1). Genotypes NR 0817, C724-19-11, and D108 showed high frequencies in both HR and S categories, and low in MR, although they were ranked in the MR group. This suggests that these three genotypes were segregating. The resistant phenotype of the SCAR marker Z3/265 was detected in five (62.5%), three (42.9%), and two (33.3%) individuals of NR 0817, C724-19-11, and D108, respectively. Those plants showing the marker were scored HR in the greenhouse screening, whereas the others showed a susceptible band pattern with one exception in C724-19-11 (Fig. 2).

***M. javanica*.** In all, 57, 34, and 24 genotypes were included in the *M. javanica* screening trials 1, 2, and 3, respectively. Trials 2 and 3 included resistant selections from the previous trial, new collections, and the susceptible control Georgia Green. Data for those genotypes that were tested in three or the last two trials were pooled and analyzed because there were no significant interactions between genotypes and trials for gall index and eggs per gram of root (Table 3). All the selected genotypes, except GP-NC WS 5, showed lower ($P \leq 0.05$) eggs per gram of root and gall indices than the S control Georgia Green. The eggs per gram of root for genotypes C724-25-8, NemaTAM, and COAN were less than 10% of the S control, and these three genotypes were classified as HR. Based on both eggs per gram of root and gall index, 18 genotypes were classified in the MR group. On genotypes HTS 02-01 and GP-NC WS 5, *M. javanica* produced over 50% of the eggs produced on Georgia Green; therefore, these two genotypes were classified as S.

***M. hapla*.** In all, 57, 37, and 26 genotypes were included in the *M. hapla* screening trials 1, 2, and 3, respectively. Trials 2 and 3 included resistant selections from the previous trial, new collections, and an S control, Georgia Green. Data for those genotypes, which were included in all three or in the last two trials, were combined for analysis. Compared with *M. arenaria* and *M. javanica*, the galls caused by *M. hapla* were smaller and the symptoms on root systems were less severe. Therefore, the gall index standard which was used to identify the resistant geno-

Fig. 2. Polymerase chain reaction (PCR) amplification by primer sets 400/401 and 199/200 for individuals of **A**, C724-19-11, **B**, NR 0817, and **C**, D108. Set 400/401 amplified actin depolymerizing factor an endogenous gene. It serves as a positive control for sources of PCR amplification. Set 199/200 was a *Meloidogyne arenaria*-resistant sequence-characterized amplified region marker (Z3/265). GG: Georgia Green (susceptible control), NM: NemaTAM (resistant control), R: highly resistant individual in greenhouse screening, and S: susceptible individual in greenhouse screening.

types to *M. hapla* was modified from that for *M. arenaria* and *M. javanica*. The gall indices for the genotypes that were classified as highly or moderately resistant to *M. hapla* were ≤ 2 rather than ≤ 3.0 for *M. arenaria* and *M. javanica*. The genotypes GP-NC WS 5, HTS 02-01, D108, and NemaTAM supported the same amount of *M. hapla* reproduction as the S control Georgia Green (Table 4). The genotypes D031, 970105, and 990304 were HR to *M. hapla*, with $<10\%$ of the eggs per gram of root of Georgia Green. Eighteen genotypes with $\leq 50\%$ of the eggs per gram of root on Georgia Green and low gall indices (≤ 2.0) were MR.

SCAR marker phenotypes. In total, 27 genotypes, including 26 selected genotypes with high or moderate resistance to one or more of the three *Meloidogyne* spp. and the susceptible control (Georgia Green), were evaluated with the SCAR markers Z3/265 and 197/909. On 2.5% agarose gel, the marker Z3/265 produced a strong resistance band at 265 bp on the genotypes COAN, NemaTAM, C724-25-8, GP-NC WS 6, and some individuals of C724-19-11, D108, and NR 0817 (Fig. 3). This set of primers also produced a faint resistance band on the genotypes 970105, 991219, D040, D031, HTS 02-01, and some individuals of C724-19-11, which were MR or S to *M. arenaria* in the greenhouse (Figs. 3 and 2A). The S control Georgia Green and the other genotypes did not show any specific bands.

On 8% polyacrylamide gel, the marker 197/909 amplified the *M. arenaria*-resistant band on NemaTAM, COAN, C724-25-8, and some individuals of C724-19-11 with high resistance to *M. arenaria* and *M. javanica*, but not on GP-NC WS 6 and some individuals of NR 0817 and D108 that also showed high resistance to *M. arenaria* in the greenhouse. The PCR product from NR 0817 was approximately 260 bp, even smaller than that from *M. arenaria*-susceptible genotype Georgia Green. The genotype 970105 showed two major bands, which might be an indication of heterozygosity. The other genotypes with moderate resistance to *M. arenaria* or with moderate to high resistance to *M. javanica* and *M. hapla* showed the *M. arenaria*-susceptible band pattern (Fig. 4).

Correlations for resistance to *M. arenaria*, *M. javanica*, and *M. hapla*. Of 60 genotypes, 26 were identified with some resistance to *M. arenaria*, *M. javanica*, or *M. hapla*. For the 26 resistance selections and Georgia Green, gall indices caused by *M. arenaria* were correlated with gall indices caused by *M. javanica* ($r = 0.7498$, $P = 0.0015$). However, the resistance to *M. hapla* did not show any significant correlations to resistance to either *M. arenaria* ($r = 0.2188$, $P > 0.05$) or *M. javanica* ($r = 0.3256$, $P > 0.05$).

Table 3. Root galling, reproduction of *Meloidogyne javanica*, and resistance classification for selected peanut genotypes tested in the greenhouse

Genotype	No. of replicates ^a	Gall index ^b	Eggs/g of root ^c	Resistance ^d
C724-25-8	15	0.59 $\pm$ 0.29	519 $\pm$ 939	HR
NemaTAM	16	0.62 $\pm$ 0.28	703 $\pm$ 908	HR
COAN	17	0.60 $\pm$ 0.27	899 $\pm$ 880	HR
991219	8	0.96 $\pm$ 0.40	1,560 $\pm$ 1,299	MR
950530	12	1.34 $\pm$ 0.32	1,757 $\pm$ 1,057	MR
D009	13	1.57 $\pm$ 0.31	1,782 $\pm$ 1,011	MR
D031	13	1.44 $\pm$ 0.30	2,204 $\pm$ 1,009	MR
950521	18	1.17 $\pm$ 0.26	2,497 $\pm$ 854	MR
D099	16	1.57 $\pm$ 0.28	2,657 $\pm$ 908	MR
D040	16	1.77 $\pm$ 0.27	2,996 $\pm$ 908	MR
D108	18	0.86 $\pm$ 0.26	3,000 $\pm$ 854	MR
D998	10	2.47 $\pm$ 0.32	3,013 $\pm$ 1,158	MR
990304	13	1.85 $\pm$ 0.31	3,050 $\pm$ 1,009	MR
D054	18	1.67 $\pm$ 0.26	3,283 $\pm$ 854	MR
D999	12	1.72 $\pm$ 0.32	3,343 $\pm$ 1,057	MR
GP-NC WS 6	10	1.29 $\pm$ 0.35	3,544 $\pm$ 1,161	MR
NR 0817	15	2.05 $\pm$ 0.29	3,624 $\pm$ 937	MR
970101	9	1.81 $\pm$ 0.37	3,841 $\pm$ 1,221	MR
C724-19-11	11	1.91 $\pm$ 0.33	4,070 $\pm$ 1,100	MR
D002	18	1.83 $\pm$ 0.26	4,237 $\pm$ 854	MR
C209-6-37	18	2.53 $\pm$ 0.26	4,804 $\pm$ 854	MR
HTS 02-01	12	2.58 $\pm$ 0.32	6,996 $\pm$ 1,057	S
GP-NC WS 5	10	2.88 $\pm$ 0.35	8,708 $\pm$ 1,160	S
Georgia Green	14	4.49 $\pm$ 0.28	10,318 $\pm$ 972	S

^a Data from three trials (six replicates/trial) were combined for analysis as unbalanced data.

^b Gall index, where 0 = no galling, 1 = trace infection with a few small galls, 2 = $\leq 25\%$, 3 = 25 to 50%, 4 = 51 to 75%, and 5 = $>75\%$ of roots galled. Data were least-squares estimates of marginal means (LSMEANs) $\pm$ standard errors.

^c Data were LSMEANs $\pm$ standard errors.

^d HR = highly resistant, eggs/g of root $\leq 10\%$ of Georgia Green; MR = moderately resistant, eggs/g of root $\leq 50\%$ of Georgia Green and gall index = ≤ 3.00 ; and S = susceptible, eggs/g of root $>50\%$ of Georgia Green or gall index >3.00 .

Table 4. Root galling, reproduction of *Meloidogyne hapla* reproduction, and resistance classification for selected peanut genotypes tested in the greenhouse

Genotype	No. of replicates ^a	Gall index ^b	Eggs/g of root ^c	Resistance ^d
970105	9	0.31 $\pm$ 0.39	550 $\pm$ 1,745	HR
D031	12	0.43 $\pm$ 0.34	631 $\pm$ 1,505	HR
990304	10	0.25 $\pm$ 0.37	811 $\pm$ 1,653	HR
950530	11	0.68 $\pm$ 0.35	985 $\pm$ 1,574	MR
D099	14	0.46 $\pm$ 0.34	1,087 $\pm$ 1,505	MR
D009	12	0.38 $\pm$ 0.34	1,149 $\pm$ 1,505	MR
COAN	9	0.87 $\pm$ 0.39	1,180 $\pm$ 1,745	MR
Luhua 14	12	1.88 $\pm$ 0.34	1,712 $\pm$ 1,505	MR
961308-1	11	0.71 $\pm$ 0.34	1,769 $\pm$ 1,574	MR
D999	12	0.87 $\pm$ 0.34	1,790 $\pm$ 1,505	MR
Huayu 21	11	0.91 $\pm$ 0.35	1,879 $\pm$ 1,574	MR
C724-19-11	11	1.54 $\pm$ 0.34	1,904 $\pm$ 1,574	MR
991219	16	0.50 $\pm$ 0.34	1,988 $\pm$ 1,505	MR
D054	11	0.51 $\pm$ 0.35	1,997 $\pm$ 1,574	MR
D040	12	0.38 $\pm$ 0.34	2,084 $\pm$ 1,505	MR
D998	14	0.50 $\pm$ 0.34	2,456 $\pm$ 1,505	MR
970101	12	0.87 $\pm$ 0.34	3,350 $\pm$ 1,505	MR
D002	12	0.83 $\pm$ 0.34	3,376 $\pm$ 1,505	MR
NR 0817	8	1.07 $\pm$ 0.41	4,074 $\pm$ 1,848	MR
GP-NC WS 6	12	1.50 $\pm$ 0.34	4,103 $\pm$ 1,505	MR
C724-25-8	13	1.25 $\pm$ 0.34	4,393 $\pm$ 1,505	S
D108	13	1.04 $\pm$ 0.34	7,695 $\pm$ 1,505	S
NemaTAM	12	2.17 $\pm$ 0.34	7,706 $\pm$ 1,505	S
Georgia Green	15	2.87 $\pm$ 0.34	8,739 $\pm$ 1,505	S
HTS 02-01	10	3.02 $\pm$ 0.37	9,192 $\pm$ 1,653	S
GP-NC WS 5	12	2.83 $\pm$ 0.34	11,348 $\pm$ 1,505	S

^a Data from three trials (six replicates/trial) were combined for analysis as unbalanced data.

^b Gall index, where 0 = no galling, 1 = trace infection with a few small galls, 2 = $\leq 25\%$, 3 = 25 to 50%, 4 = 51 to 75%, and 5 = $>75\%$ of roots galled. Data were least-squares estimates of marginal means (LSMEANs) $\pm$ standard errors.

^c Data were LSMEANs $\pm$ standard errors.

^d HR = highly resistant, eggs/g of root $\leq 10\%$ of Georgia Green; MR = moderately resistant, eggs/g of root $\leq 50\%$ of Georgia Green and gall index = ≤ 2.00 ; and S = susceptible, eggs/g of root $>50\%$ of Georgia Green or gall index >2.00 .

DISCUSSION

Some of the peanut genotypes evaluated in this study were known to be resistant to one or more *Meloidogyne* spp. For the most part, our results support previous findings, such as the high resistance to *M. arenaria* and *M. javanica* in COAN and NemaTAM (37,38), high resistance to *M. arenaria* in GP-NC WS 6 (41), and moderate resistance in C209-6-37 (18). Our results also indicated that there existed moderate resistance to *M. hapla* in COAN, which is consistent with the finding of Timper et al. (46). NemaTAM was classified as susceptible to *M. hapla*, although NemaTAM was derived from the same backcross introgression pathway as COAN and the same genes resistant to *M. arenaria* and *M. javanica*. The resistance to *M. hapla* in COAN may have been lost in NemaTAM during the two additional backcross generations with Florunner. We also obtained some conflicting results from previous reports. The genotype GP-NC WS 5 (41) was released as an *M. arenaria*-resistant breeding line, and has been used as the resistant parent to develop additional germplasm with nematode resistance (3). However, in our study, it was extremely susceptible. Perhaps GP-NC WS 5 was not completely homogeneous when it was released, and the seed that we used in this study were collected from susceptible plants. The genotype NR 0817 (3) also was released as an *M. arenaria*-resistant breeding line; however, in this study, it was clas-

sified as MR, mainly due to a mixture of resistant and susceptible individuals. The results indicate that the genotypes NR 0817, C724-19-11, and D108 are still segregating for resistance; therefore, further selection is needed before they would be good sources of nematode resistance for peanut breeding programs.

High levels of resistance to *M. arenaria* have been identified in wild *Arachis* spp. (31). The different mechanisms of resistance that exist in the wild *Arachis* spp. suggest that different genes for resistance exist in different wild species (32,42). High levels of resistance to *M. arenaria* in *A. cardenasii* were reported to be conditioned by at least two dominant genes (15) and are expressed as a hypersensitive-like reaction with few second-stage juveniles showing signs of development (31). The germplasm TxAG-6, an interspecific *Arachis* hybrid developed from a cross made in Texas between *A. batizocoi* Krapov. & W. C. Gregory and (*A. cardenasii* × *A. diogeni*), was the source of the resistance in COAN, NemaTAM, C724-25-8, and C724-19-11 (37,38; C. C. Holbrook, unpublished). The results of RFLP markers indicated that the resistance in COAN and NemaTAM was derived from *A. cardenasii* and segregates as a single dominant gene (8,10). However, the resistance in COAN does not appear to involve a necrotic hypersensitive response and may be due to constitutive factors in the roots (5). The gene or genes conditioning hypersensitive

response in *A. cardenasii* may not have been introgressed into COAN. In addition, a recessive gene for resistance to *M. arenaria* has been identified in TxAG-6 (11); however, it is not known if this recessive gene exists in COAN and NemaTAM. The resistance in GP-NC WS 6 and NR 0817 originated from a cross made in North Carolina between *A. cardenasii* and *A. hypogaea* (3,41). Two dominant genes conferring resistance to *M. arenaria* were identified in GP-NC WS 6: *Mae* conditions resistance to egg production and *Mag* conditions resistance to gall formation (15,41). There is no evidence that *Mae* is the same gene that suppresses egg production in COAN. We have shown the presence of SCAR marker Z3/265 in both COAN and GP-NC WS6 and the absence of SCAR marker 197/909 in GP-NC WS 6, suggesting that the resistant genes in the genotypes derived from the two different introgression pathways may be different. Moreover, resistance in other genotypes which were moderately resistant to *M. arenaria*, such as D054, D031, D040, D099, and so on, also may be conditioned by different genes because all these genotypes are *A. hypogaea* without any introgression from wild species.

The SCAR marker Z3/265 was developed from an F₂ population of GA6, which originated from a cross made in North Carolina. In our results, this marker exists in the genotypes with resistance genes derived from both the North Carolina cross

Fig. 3. Separation of amplicons from selected peanut genotypes with primers 199/200 on 2.5% agarose gel.

Fig. 4. Separation of amplicons from selected peanut genotypes with primers 197/909 on 8% polyacrylamide gel. C724-19-11(1) and C724-19-11(2) were two individuals of the same breeding line.

and Texas cross. It also is present in some *M. arenaria*-susceptible genotypes with or without any introgression from wild species. This confirmed a previous finding that Z3/265 can produce a false positive score (9). The SCAR marker 197/909 was developed based on the sequence of an RAPD fragment that originated from COAN (9). This marker shows a high correlation with the greenhouse phenotype data. It amplifies fragments from both susceptible and resistant samples but of different molecular weights, avoiding false negatives. However, this marker is present only in the genotypes directly related to the resistance gene derived from the TxAG-7.

In this study, we found that resistance to *M. arenaria* and *M. javanica* was highly correlated, indicating that, in many peanut genotypes, the same gene or genes may confer resistance to both species, or the resistance genes for each species are closely linked. This was different from the previous observations with the interspecific hybrid TxAG-7, in which the resistance to *Meloidogyne* spp. segregated independently (1). Our study also showed that resistance to *M. hapla* was not correlated with resistance to *M. arenaria* or *M. javanica*. The mechanisms of resistance to *M. hapla* may be different from that of *M. arenaria* and *M. javanica*. The difference between resistance to *M. arenaria* and resistance to *M. hapla* may not be caused by differences in their parasitism gene. Recent evidence suggests that *M. arenaria*, *M. javanica*, *M. hapla*, and *M. incognita* may have identical parasitism genes (22,23). Therefore, the resistance genes in peanut may be related to differential recognition by the plant of the three *Meloidogyne* spp.

In summary, the data presented in this report showed that resistance to all three *Meloidogyne* spp. exists within cultivated peanut (*A. hypogaea*), either with or without introgressed genes from wild species. We identified several additional genotypes with moderate resistance to *M. arenaria* and *M. javanica*, such as D009, D031, D040, D054, D099, D998, D999, 950521, 950530, 970101, and 990304. The level of resistance in these genotypes was as good as or better than the resistance in the MR genotype C209-6-37. These genotypes may have different resistance genes from released *M. arenaria*-resistant germplasm (3,36,41) because they do not have introgressed genes from wild species. We identified peanut genotypes with high and moderate resistance to *M. hapla*. The 3 HR genotypes and most of the 18 MR genotypes do not have introgressed genes from wild species, whereas some MR genotypes, such as C724-19-11, COAN, NR 0817, GP-NC WS 6, and C724-25-8, have introgressed genes. Although the genetics of the resistance to *M. hapla* in peanut has not been determined, we believe that the selected genotypes will be valuable for

developing new peanut cultivars with broad and durable resistances to *Meloidogyne* spp.

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