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Phenotypic and Molecular Evaluation of Interspecific Peanut (*Arachis*) Lines

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ABSTRACT

Peanut breeders are constantly in search of new sources of genes that confer tolerance or resistance to biotic and abiotic stresses to improve the production and quality. The objective of this study was to evaluate peanut lines generated from interspecific crosses for amounts of wild species introgression, including genes for resistance to peanut root-knot nematodes, tomato spotted wilt virus and leaf spot diseases. Nine diploid *Arachis* species were crossed with peanut breeding lines and 130 different interspecific hybrid lines were developed. These lines were evaluated for the amount of introgression using RFLP analyses, plant morphology, and disease resistant phenotypes. Based on RFLPs, 41 lines showed measurable introgression and 12 hexaploid-derived lines were polymorphic for at least four probes. Greenhouse and field evaluations indicated that resistance was not present in the lines tested for tomato spotted wilt virus, early leaf spot, or Cylindrocladium black rot. However, resistance approaching that of the wild species was found for the peanut root-knot nematode (*Meloidogyne arenaria*) among lines derived from crosses with *Arachis diogoi*, *A. correntina*, *A. batizocoi*, and *A. cardenasii*. Introgression lines were resistant (disease ratings of 1.5 to 4.5 and lesion numbers 8 to 63) compared to Southern Runner (ratings of 5.5 to 6 and lesion numbers of nearly 500) for late leaf spot (*Cercosporidium personatum*) in field evaluations performed in Gainesville, FL over 2 yr. The greatest resistance was found among lines from crosses with *A. batizocoi*, *A. duranensis*, *A. stenosperma*, *A. magma*, and *A. diogoi*. Results indicate that it should be possible to identify molecular markers to tag resistance genes for use in conventional breeding programs and stack these genes in highly productive peanut cultivars.

Key Words: Root-knot nematode, RFLP, AFLP, disease resistance.

Improvement of peanut (*Arachis hypogaea* L.) cultivars has historically been achieved by crossing elite by elite genotypes. This procedure often results in genotypes with higher yields, but may cause vulnerability to biotic and/or abiotic stresses. During the last few decades peanut breeding programs have attempted to incorporate genes for increased tolerance or resistance to known diseases of peanut. Primary and secondary gene pools have also been evaluated for disease resistance. Partial resistance to diseases such as tomato spotted wilt virus (TSWV) (Anderson *et al.*, 1996), leaf spot diseases (Holbrook and Anderson, 1995; Isleib *et al.*, 1995), peanut root-knot nematodes [*Meloidogyne arenaria* (Neal) Chitwood] (Holbrook *et al.*, 2000), and soil-borne diseases (Isleib *et al.*, 1995; Franke *et al.*, 1999) has been found. However, much higher levels of resistance are often observed in related *Arachis* species. Some wild species of peanut possess genes for extremely high resistance to the leaf spot diseases [*Cercospora arachidicola* Hori, and *Cercosporidium personatum* (Berk. et Curt.)], root-knot nematodes, and many insect pests (Stalker and Moss, 1987; Stalker and Simpson, 1995).

The *Arachis* species have extensive genetic diversity (Kochert *et al.*, 1991). However, molecular marker techniques such as isozymes (Grieshammer and Wynne, 1990), randomly amplified fragment length polymorphisms (RAPD) (Halward *et al.*, 1992; Garcia, 1995),

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restriction fragment length polymorphisms (RFLP) (Halward *et al.*, 1991; Kochert *et al.*, 1991), and amplified fragment length polymorphisms (AFLP) (He and Prakash, 1997) have failed to identify significant genetic polymorphisms among domesticated peanut varieties, and thus molecular-marker assisted breeding has little potential within *A. hypogaea*. Because a large amount of variation is present in *Arachis* species that has not been observed in the cultivated peanut, molecular markers should be useful for tracking introgression in a breeding program.

Although highly desirable genes are present in wild species accessions, it is difficult to introgress these genes into domesticated peanut (Simpson, 2001). The majority of the wild species are diploid ($2n = 2x = 20$), whereas domesticated peanut is tetraploid ($2n = 4x = 40$), and crossing results in sterile triploids ($2n = 3x = 30$). Various techniques such as cholchicine doubling have been used to restore fertility (Smartt and Gregory, 1967; Stalker *et al.*, 1979; Simpson, 1991). Few seed are produced in initial hybrids and backcross generations, and only when the interspecific lines revert to the tetraploid chromosome level do more normal numbers of seed occur on plants.

Interspecific peanut hybrids were produced by crossing *A. hypogaea* with diploid *Arachis* species and have been maintained at North Carolina State Univ. Lines have been self-pollinated for many generations and fertility restored to the tetraploid level (Stalker *et al.*, 1979). Analysis by Garcia *et al.* (1995) of 46 lines from one of these crosses (*A. hypogaea* × *A. cardenasii* Krap. and W.C. Gregory), indicated introgression of *A. cardenasii* in 10 of the 11 linkage groups of the diploid map. Introgression within these lines ranged from 0 to 16% of the *A. cardenasii* genome.

Garcia *et al.* (1996) and Burow *et al.* (1996) independently mapped genes for resistance to the peanut root-knot nematode. Simpson and Starr (2001) released a nematode-resistant cultivar (COAN) by first using a conventional breeding technique and then backcrossing with a second cultivar (NemaTAM) by using the marker-assisted selection (Simpson *et al.*, 2003). It also should be possible to map additional important genes from other introgressed lines. The purpose of this study was to evaluate 130 interspecific lines developed at North Carolina State Univ. for resistance to peanut root-knot nematode (*M. arenaria*), early (*C. arachidicola*) and late leaf spot (*C. personatum*), TSWV, and CBR (*Cylindrocladium crotalariae* (Loos) Bell and Sobers), as well as estimate the amount of introgression of phenotypic characteristics by using RFLP analysis. This is the beginning step in searching for traits that may be bred into elite peanut lines using molecular marker-assisted breeding techniques.

Materials and Methods

Interspecific Peanut Lines. The interspecific germplasm evaluated in this study originated from crosses of 13 diploid ($2n = 2x = 20$) wild species of peanut (Table 1) with *A. hypogaea* ($2n = 4x = 40$) lines. The triploid interspecific hybrids were colchicine-treated to restore fertility at the 60-chromosome level and resulting hexaploid (H) lines were maintained by selfing for 10 generations. Thirteen lines (H 15-19, H 21-25, H 66, H 68, and H 71) originated from the work of Smartt and Gregory (1967), all of which had *A. diogoi* Hoehne in the pedigree. The other 94 hexaploid-derived lines were obtained from crossing programs at N.C. State University during 1979, 1980, and 1983 (Stalker, unpubl. data). Pentaploid-derived lines (P) (Table 1) were obtained after backcrossing first-generation hexaploid plants with the respective *A. hypogaea* parent (as the female) during 1981, 1982, and 1984 (Stalker, unpubl. data) and then by selfing the pentaploids to obtain 40-chromosome progenies. The lines evaluated in this study were in the F_{10} to F_{12} generation.

RFLP Analysis. Three leaflets from 10 randomly selected plants of each interspecific line were collected from field plots grown in Ashburn, GA during the summer of 1994. DNA was extracted and RFLP analysis was performed as per Kochert *et al.* (1991). The DNA was digested first with restriction endonucleases (*Eco*RV, *Hind*III, *Hae*III, and *Dra*I) and then fragments were separated by gel electrophoresis. RFLP probes were selected and used based on known polymorphisms between the wild and allotetraploid parents of each line (Halward *et al.*, 1991).

Greenhouse Disease Evaluations. All interspecific peanut lines and checks were tested for resistance to peanut root-knot nematode (*M. arenaria*, Race 1) in the greenhouse during the winter of 1994. Seed of interspecific lines and checks (Florunner, GK7, and *Arachis* species parents) were planted in 200-cm^3 black plastic pots filled with sandy loam soil. Prior to planting the soil was autoclaved to eliminate all soil microbes. Two seed/pot were planted and were thinned to one plant per pot after emergence. The test consisted of eight replications in a randomized complete block design.

Meloidogyne arenaria Race 1 that had originated from a field in Tifton, GA was cultured on tomato (*Lycopersicon esculentum* Mill.) and peanut alternately. Nematode eggs used for inoculation were extracted from tomato roots, cleaned, and diluted as described by Holbrook *et al.* (1983). Each pot was inoculated with 3000 eggs at 10 d after planting. Plants were watered lightly each day, maintained at 20 to 25 C, and fertilized once (5-10-15 NPK) 4 wk after planting. Plants were harvested at 14 wk after planting. Roots were gently washed clean of soil, dyed with 0.05% phloxine-B solution, and rated for galling and egg masses as described by Holbrook and Noe (1990).

The interspecific lines were tested for resistance to *C. crotalariae* during the winter of 1994. Soil for the CBR tests was prepared by autoclaving 2:1 field soil (sandy

Table 1. Wild species parents of interspecific crosses evaluated in 1994-1996.

Species	Accession[a]	Hexaploid-derived lines	Pentaploid-derived lines
		no.	no.
A. batizocoi Krapov. & W.C. Gregory	K 9484	12	13
A. cardenasii Krapov. & W.C. Gregory	GKP 10017	8	5
A. correntina (Burkart) Krapov. & W.C. Gregory	K 9530	3	2
A. correntina	K 9548	13	0
A. diogoi Hoehne	GK 10602	25	7
A. diogoi	KG 30005	1	0
A. diogoi	GKPSc 30106	3	0
A. duranensis Krapov. & W.C. Gregory	K 7988	3	0
A. duranensis	GKP 10038	4	0
A. hoehnei Krapov. & W.C. Gregory	KG 30006	2	0
A. stenosperma Krapov. & W.C. Gregory	HLK 410	18	2
A. valida Krapov. & W.C. Gregory	KG 30011	6	0
A. villosa Benth.	Bu 22585	2	0

Bu = A. Burkhart; G = W.C. Gregory; H = R.O. Hammons; K = A. Krapovickas; L = W.R. Langford; P = J.R. Pietrarelli; Sc = A. Schinini.

loam)/MetroMix – 510 (Scott Co., Marysville, OH) and adding 25 microsclerotia/g soil. The microsclerotia were obtained from potato dextrose agar (PDA) cultures of *C. crotalariae*. One seed of each entry was placed in the infested soil that filled 3 × 25 cm cone tubes that were placed in racks. The bottom third of the tubes was submerged in water for the duration of the experiment to provide a conducive environment for the disease. The test included 10 randomized replications of each interspecific entry plus Florunner, NC 3033 (partially resistant check), and the *Arachis* species parents. Plants were maintained at 20 to 25 C. Plants were harvested after 10 wk; roots were washed and rated (0 = healthy to 5 = completely rotted) as described by Black and Beute (1984).

Field Evaluations. A field test was planted on 27 April 1995 in Ashburn, GA to evaluate susceptibility of the interspecific lines to early leaf spot (*C. arachidicola*) and TSWV. The two-row plots were 7.6 m in length with 15 cm spacing between plants in each row. Two replications were planted and were maintained using recommended agronomic practices; however, no pesticides were applied after planting. Early leaf spot susceptibility was evaluated by visually rating the disease (1 = no disease to 10 = total defoliation) using the Florida scale (Chiteka *et al.*, 1988). These evaluations were performed on 9 Sept. 1994, 28 July 1995, 22 Aug. 1995, and 11 Sept. 1995. The amount of early leaf spot sporulation was also rated on 28 July 1995 (1 = no spores to 5 = heavy sporulation). The amount of TSWV was measured by recording the number of plants with disease symptoms and calculating a percentage of disease within each plot. Yield potential and phenotypic notes were also recorded for the interspecific lines.

Field tests were planted on 1 June 1995 in Gainesville, FL to evaluate resistance to late leaf spot (*C. personatum*). Two replications each of all the interspecific lines were randomized and planted 15 cm apart in two-row plots 7.6 m in length. The plots were maintained using recommended agronomic practices except for fungicide sprays being omitted. The plots were visually rated for susceptibility to late leaf spot (1 = no disease; 10 = total defoliation) on 5 Sept., 23 Sept., 11 Oct., and 27 Oct. 1995 (Chiteka *et al.*, 1988). The amount of sporulation was rated (1 = no spores; 5 = very heavy sporulation) on 23 Sept. Four replications of the most resistant lines from 1995 and checks were planted at Gainesville, FL on 30 May 1996 as was done in 1995. Plots were rated on 23 Aug., 12 Sept., 23 Sept., 3 Oct., 12 Oct., and 24 Oct. 1996. The third and fourth leaves from the terminal of 10 random plants within each plot were sampled for lesion number and approximate lesion diameter. Notes were taken on growth habit and production potential at the field locations. Pod and seed characteristics were measured and recorded from harvested field plots. Analysis of variance was performed on all tests and genotypic means were compared using LSD (P = 0.05).

Results and Discussion

Introgression was measured using up to 24 RFLP probes from the peanut map and 41 of 130 lines were confirmed to have some introgression of the wild species parent (Table 2). The six lines from the pentaploid pathway showing introgression were from only one probe (four lines with *A. batizocoi* – 9484) or two probes (P21 from *A. correntina* – 9530 and P16 from *A. diogoi* – 10602). The lines derived from selfing hexaploids showed higher amounts of introgression. Lines derived from crosses with *Arachis correntina* – 9548 (H 32, H 69, H 87, H 84, H 85, H 89) and *Arachis diogoi* –10602 (H 21, H 24, H 71, H 75, H 78, and H 82) showed introgression by at least four probes (Fig. 1). Many of these highly introgressed lines displayed wild species characteristics.

Table 2. Introgression determined by RFLP probes from wild species map.

	Number of probes showing introgression				
	0	1	2	3	4 or more
Pentaploid-derived lines (no.)	23	4	2	0	0
Hexaploid-derived lines (no.)	65	9	10	3	13

All lines except H 32 and H 69 had a spreading growth habit with erect mainstems, prostrate lateral branches, and small leaves. H 21 and H 78 had severe pod constriction and very small pods. H 85 had only single-seeded pods. None of the lines produced high yields. Growth habits ranged from runner to bunch type, with some smaller plants potentially valuable for twin-row planting. Highly introgressed lines may have many genes of interest that would enhance domesticated peanut; however, extensive time and effort will be required to identify the genes and tag them. Although chromosome numbers were not determined for the selfed hexaploids, in most (if not all) cases it appeared that they had reverted back to tetraploid state. Most lines exhibited a predominance of *A. hypogaea* traits. Numerous backcrosses are required to extract the useful genes from the wild species genome and to eliminate DNA fragments that may otherwise confer detrimental effects on yield or seed quality.

Some of the lines derived by selfing hexaploids had very high levels of resistance to peanut root-knot nematodes (Table 3); however, none of the lines derived from backcrossing the hexaploids to create pentaploids expressed significant levels of resistance. Introgression was measured using RFLPs in all the most resistant lines except H 29 and H 95. However, these two lines appeared to be the most productive and were closer to having acceptable pod and seed characteristics. H 29 and H 95 were two lines identified for use in the breeding program due to the combination of high nematode resistance and close adaptability to domesticated peanut. Further testing using AFLP analysis (Anderson, unpubl. data) identified six and nine polymorphic bands, respectively, for H 29 and H 95, indicating potential marker genes for resistance to root-knot nematodes. Genes conferring resistance to root-knot nematodes from H 29 (*A. diogoi* – 10602) and H 95 (*A. batizocoi* – 9484) are expected to be different from the nematode resistance genes identified by Garcia *et al.* (1996) from *A. cardenasii*. Thus, peanut breeders should be able to stack resistance genes that would add stability to resistance to peanut root-knot nematodes.

None of the interspecific lines showed resistance to Cyclindrocladium black rot. The lowest mean root rot rating was 1.8 and 2.0 for H 48 and H 96, respectively (*A. cardenasii* – 10017), compared to 2.5 for NC Ac 3033 (resistant check). Means of TSWV were generally low in both 1994 (GK 7 = 10.3%) and 1995 (GK 7 = 14.2%) and means of lines were not significantly different. However, some lines had consistently low levels of TSWV. Line H 87 (*A. correntina* –10017) had TSWV symptoms of 0.0% and 2.3% for 1994 and 1995, respectively, while H 105 (*A. stenosperma* – 410) had symptoms of 0.0% and 4.2%.

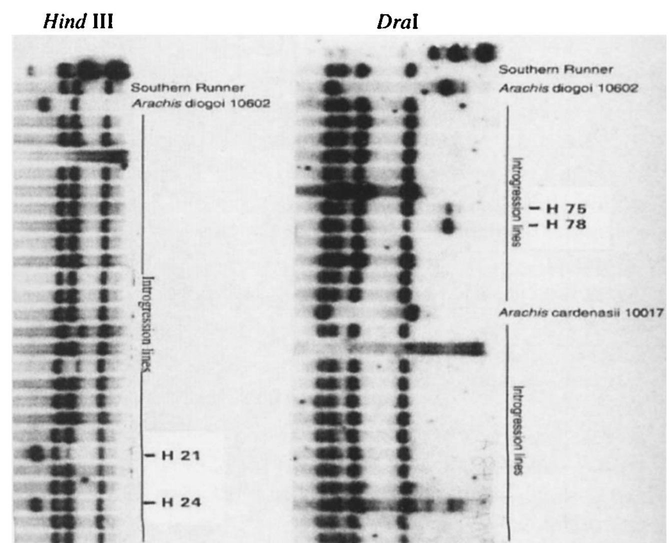

Fig 1. Southern blot measuring introgression of *Arachis diogoi* into *A. hypogaea*.

No resistance to early leaf spot was observed; however, a number of lines had high resistance to late leaf spot compared to the moderately resistant check cultivar Southern Runner. This resistance was identified in lines from different genetic sources adding to the potential of staking genes for resistance (Table 4). Resistance

Table 3. Interspecific peanut lines with *A. hypogaea* having the greatest levels of resistance to peanut root-knot nematode (*Meloidogyne arenaria*).

Genotype	*Arachis* species parent	Gall index[a]	Egg mass index[b]
Florunner (Check)		4.6	2.6
GK7 (Check)		4.5	3.0
H 87	*A. correntina* – 9548	3.7	2.1
H 86	*A. correntina* – 9548	3.4	2.1
H 61	*A. diogoi* – 30106	2.7	2.0
H 78	*A. diogoi* – 10602	2.2	1.9
H 95	*A. batizocoi* – 9484	2.4	1.0
H 97	*A. cardenasii* – 10017	2.0	0.7
H 29	*A. diogoi* – 10602	1.9	0.5
H 99	*A. correntina* – 9548	1.1	0.1
A. cardenasii – 10017 (check)		0.4	0.0
$LSD_{(0.05)}$		0.8	0.8

[a]Gall index: 0 = no galls; 1 = 1-2 galls; 2 = 3-10 galls; 3 = 11-30 galls; 4 = 31-100 galls; 5 = 101-200 galls; 6 = > 200 galls.

[b]Egg mass index: 0 = no egg masses; 1 = 1-2 egg masses; 2 = 3-10 egg masses; 3 = 11-30 egg masses; 4 = 31-100 egg masses; 5 = > 100 egg masses.

Table 4. Interspecific lines with resistance to late leaf spot (*Cercorsporidium personatum*) in Gainesville, FL in 1995 and 1996.

Genotype	*Arachis* parent species	Rating[a] 10/11/95	Sporulation rating[b] 9/23/95	Rating[a] 10/7/96	Lesions[c] 10/7/96	Lesion size[d] 9/27/96	Sporulation rating[b] 10/7/96
GK 7		9.0	3.0	8.2	658	2.62	3.87
Southern Runner		5.5	2.5	6.0	496	1.25	3.25
H 74	*A. diogoi* – 10602	4.0	2.0	4.5	61	1.25	2.25
H 58	*A. valida* – 30011	3.5	2.0	2.7	19	0.65	1.30
H 94	*A. batizocoi* – 9484	3.0	1.0	4.2	63	1.25	2.25
H 2	*A. batizocoi* – 9484	3.0	1.0	2.5	10	0.75	1.25
H 107	*A. stenosperma* – 410	2.2	1.5	2.7	58	1.62	2.62
H 76	*A. stenosperma* – 410	1.5	1.0	2.2	8	0.62	1.25
H 104	*A. duranensis* – 7988	1.5	1.0	3.2	10	0.65	1.13
$LSD_{(0.05)}$		2.0	1.2	1.1	90	0.85	0.62

[a]Disease rating: 1 = no disease to 10 = dead plant.
[b]Sporulation rating: 1 = no spores; 5 = very heavy sporulation.
[c]Lesion number: lesion count on leaves – third from terminal from 10 random plants.
[d]Lesion size: average diameter of 5 lesions on each of 10 random leaves/plant (mm).

appeared to be introgressed from *A. batizocoi* – 9484 (H 2 and H 94), *A. diogoi* – 10602 (H 74), *A. duranensis* – 7988 (H 104), *A. valida* – 30011 (H 58), and *A. stenosperma* – 410 (H 76 and H 107). Of these, introgression via RFLP probes was confirmed in only H 107. The use of AFLP analyses or other more sensitive molecular techniques may aid in determining markers for late leaf spot resistance. Although early and late leaf spot resistances are multi-genic, one or few genes may control the hypersensitive-type reactions that were observed in the most resistant lines. Markers for this hypersensitivity or to major genes responsible for specific components of resistance, such as sporulation or lesion expansion, may be found with more research.

genes for the same pathogen will only be possible with the aid of molecular markers (Nelson, 1978).

A high level of resistance to late leaf spot was found among some interspecific lines of this study. These provide an excellent source of newly accessible genetic materials for a breeding program. Although resistance to leaf spots in *A. hypogaea* is controlled by multiple genes, the hypersensitive-type reaction that was observed in some of the interspecifics (H 58, H 76, H 104) and the almost total lack of lesions in other lines (H 2, H 76, H 104), may be controlled by one or few genes from the resistant *Arachis* species parent. If this is the case, then a search for markers of these "major" genes would facilitate breeding efforts to eliminate deleterious genes.

Conclusions

Garcia *et al.* (1996) and Simpson and Starr (2001) gave examples of the ability to introgress useful wild species peanut genes into allotetraploid peanut and identify and use molecular markers in a conventional peanut breeding program. From the evaluation of the diverse interspecific lines of this study, it was shown that genes conferring resistance to peanut root-knot nematode have been introgressed from wild species such as *A. diogoi* and *A. batizocoi*. Continued work in identifying polymorphisms that tag these genes can reap tremendous rewards to breeders. Although resistance can be evaluated in the greenhouse and field, and pedigree selection can be performed through generations of selfing to obtain resistant cultivars, if molecular markers can be identified and linked to resistance genes, then selection will be more efficient. Identifying multiple tagged genes through molecular techniques is more efficient than identifying plants by extensive testing simultaneously for different diseases or pathologic strains. Further, stacking resistance

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