Pathways for Introgression of Pest Resistance into *Arachis hypogaea* L.[1]

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ABSTRACT

Four pathways for gene introgression into *Arachis hypogaea* L. were studied. Two "hexaploid routes" involved direct crosses of diploid *Arachis* species and diploid species hybrids with *A. hypogaea* (Pathways 1 and 2, respectively) and were followed by chromosome doubling with colchicine. A third pathway, a tetraploid route, involved chromosome doubling of a diploid hybrid before crossing with *A. hypogaea*. These first three routes involved only the A genome species, and all were unsuccessful because of lack of fertility. The fourth pathway, also a tetraploid route, utilized the B genome *A. batizocoi* Krap. et Greg. as a bridge species and brought about a successful (fertile) introgression. Genes from *A. cardenasii* Krap. et Greg. *nom. nud.* and *A. chacoensis* Krap et Greg. *nom. nud.* were combined into a hybrid and incorporated into *A. hypogaea* by using the B genome bridge species. Introgression of additional characters from these and other species through this pathway should be possible.

Key Words: Peanut, groundnut, *Arachis hypogaea* L., interspecific hybrids, introgression, leafspot, nematode, resistance, wild species.

The search for variability for use in improvement of the cultivated peanut, *Arachis hypogaea* L. (called groundnut in much of the world), has focused on plant introductions since the early stages of peanut breeding in the USA. In the mid-1940's the possibility of finding needed variability in other species came to the attention of Gregory (5, 6, 7) and Krapovickas (12). Considerable attention has been given to searching for, collecting, introducing, preserving, and evaluating germplasm in the form of wild *Arachis* species (8, 25), and effort has been directed toward utilization of the wild species in improvement of the cultigen (1, 2, 14, 28, 30, 31, 40, 42).

In *Arachis*, the most devastating diseases world wide include the leafspots, early (*Cercospora arachidicola* Hori) and late [*Cercosporidium personatum* (Berk. and Curt.) Deighton] (21, 41). Thousands of *A. hypogaea* lines have been evaluated for resistance to these two organisms, and some lines with resistance have been identified (13, 21, 35, 41). Attempts to utilize this resistance have been made by numerous breeders [13, and see reviews by Gregory (7), Norden (18), Norden *et al.* (19) Stalker and Moss (40), and Wynne and Halward (42)], with limited success. Recently the first cultivar with resistance to late leafspot was released by Gorbet and co-workers (3).

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Abdou *et al.* (1) determined that *A. chacoensis* Krap et Greg. *nom. nud.* (GKP-10602, PI-276235) had a high level of resistance to early leafspot, and *A. cardenasii* Krap et Greg. *nom. nud.* (GKP-10017, PI-262141) was immune to late leafspot. The results of Sharief et al. (22) indicated that the genes for the resistance to these two diseases were not at the same loci; thus, providing a possibility that the resistances could be combined into one genotype, as suggested by Smartt et al. (34).

Recently, Nelson *et al.* (15) identified high levels of resistance to root-knot nematode, *Meloidogyne arenaria* (Neal) Chitwood in twenty-one *Arachis* species. Within this group, the best resistance to *M. arenaria* was identified in *A. cardenasii* (GKP-10017) and *A. batizocoi* Krap. et. Greg. (K-9484) (PI-298639). These two species represent two different resistance mechanisms (15).

Smartt *et al.* (33) identified two genomes (A and B) in the section *Arachis*, both of which occur in the tetraploid *A. hypogaea*. Chromosome analyses by Stalker and Dalmacio (39) and by Singh and Moss (26) strongly support the two genome theory. Most diploid wild species which have been identified as section *Arachis* have the A genome, including *A. cardenasii* and *A. chacoensis*. Progeny from crosses within the A genome have varying levels of fertility (4, 26, 27, 32, 36, 38). *Arachis batizocoi* is the only diploid B genome species which has been identified to date.

When wild diploid *Arachis* species are crossed directly with the cultigen, *A. hypogaea*, triploids are produced which are essentially sterile. However, several studies have shown that triploids between many A genome diploids and *A. hypogaea* produce varying degrees of peg, pod, and seed set (22, 24, 27, 32, 34, 38).

Wild *Arachis* genes have been introgressed into *A. hypogaea*. See the review by Stalker and Moss (40) for a complete description of these reports. The objective of these studies was to develop a consistent pathway for introgressing wild *Arachis* genes for pest resistance into *A. hypogaea*. This paper reports on four attempted procedures.

The efforts began in 1970 (Table 1), and have continued to the present (Table 2).

Materials and Methods

The cultigens used in this research came from two of the four market classes. Spantex and Tamnut 74 (parent 82) represented the spanish market type, and UF-439-16-10-3-2 (parent 83), one of three sister lines comprising 'Florunner' (9, 16), represented the runner market type. Spantex was used as parent 82 until 1973, then Tamnut 74 was substituted for the old "landrace" variety. Tamnut 74 was derived from a crossing scheme which involved *A. monticola* Krap. et Rig., but the cultivar is classified as subspecies *fastigiata* var. *vulgare* (23). Florunner has some spanish germplasm in its pedigree but is classified as subspecies *hypogaea* var. *hypogaea* (16).

The wild species used in this program were collected in South America during the 1950's. *Arachis batizocoi* (K-9484)(parent 19) was collected in Southeast Bolivia and is thought by many to be one of the original parents of *A. hypogaea* (33). *Arachis cardenasii* (GKP-10017) (parent 34) was found near Robore in Eastern Bolivia and has been proposed as one of the parents of *A. hypogaea* (33). *Arachis chacoensis* (GKP-10602) (parent 37) was collected in north central Paraguay. All three species are diploid; *A. batizocoi* is annual and the other two are perennials.

Standard cross pollination techniques were used in hybridization work as described by Norden (17). Cytological material was fixed in 1:1 alcohol/acetic acid, modified (95% alcohol instead of 100%) Carnoy's or modified (added 5 mL chloroform/100 mL) FAA solutions (10). Chromosomes were stained in acetocarmine or aceto-orcein. Chromosome numbers were doubled by treating cuttings with 0.02% colchicine or by treating seedlings as described by Banks (2). Pollen was stained in a 1:1 mixture of acetocarmine/glycerin. Pollen counts were made by placing the pollen from one flower under a 22 mm^2 coverslip with acetocarmine/glycerin, taking the mean of five 100-grain counts made from random fields (maximum of ten grains per field), and making three flower counts per plant on separate days. These pollen counts were made on all plants which flowered, with the exceptions noted in Table 1.

Plants were grown in deep soil benches, clay pots, or lined fruit baskets. In the short days of winter, daylength was extended to 12 h by using incandescent plant growth bulbs. Plants were inoculated with a commerical *Rhizobium* inoculum. The soil was a mix of fine sandy loam top soil and builders sand or washed river sand mixed in a 1:1 ratio. Final sand content of the soil mix was approximately 92%.

Leafspot resistance was determined in laboratory experiments by using a modification of the detached leaf technique described by Melouk and Banks (13). Field screening was accomplished by using the ICRISAT scale (41) or the Florida scale (11) for late leafspot. Nematode studies were described by Nelson *et al.* (15).

Parent numbers used in these studies correspond to parent numbers cited by Gregory and Gregory (4) for parents 19, 34, and 37. However, parents 82 and 83 were not the same germplasm as those used by Gregory and Gregory (4). The four pathways studied are outlined in Tables 1 and 2.

Results and Discussion

Pathway 1

My first attempts to transfer leafspot resistance were made by crossing parents 34 and 37 directly to parent 82. Triploids from *A. hypogaea* X 34 and 37 were produced and treated with colchicine to obtain hexaploids. Table 1 shows the pollen counts and ploidy of these hybrids and amphiploids. Meiotic behavior of the triploids was similar to that reported for other triploids (14, 24, 29, 30, 32, 37). The hexaploids were backcrossed to the *A. hypogaea* parent to produce pentaploid progeny (Table 1); however, a high level of sterility was encountered in the subsequent backcross and the pentaploids produced no seed (Table 1). This pathway has been used with some success by others (40, 42).

Table 1. Four pathways in attempts to introgress wild Arachis genes into *A. hypogaea*.

Pathways	CROSS	Ploidy of hybrid	Year	Number* observed	Pollen Counts** average	Pollen Counts** range	Seed set yes/no
					%	%	
1	82X34 [1]	3x	1970	7(P)	5	2 to 7	Y
1	82X37	3x	1970	16(P)	6	.08 to 12	Y
1	(82X34)[c] [2]	6x	1971	10(P)	23	14 to 37	Y
1	(82X37)[c]	6x	1971	10(P)	7	4 to 12	Y
1	82X(82X34)[c]	5x	1972			sterile [3]	N
1	82X(82X37)[c]	5x	1972			sterile [3]	N
2	34X37	2x	1973	14(F)	59	53 to 62	Y
2	82X(34X37)	3x	1974	56(P)	18	1 to 93	Y
2	[82X(34X37)][c]	6x	1974	5(F)	10	6 to 12	Y
2	82X[82X(34X37)][c]	5x	1975	0 [4]			N
3	(34X37)[c]	4x	1975	61(P)	58	0 to 99	Y
3	82X(34X37)[c]	4x	1975	6(P)	31	17 to 42	Y
3	82X[82X(34X37)[c]]	4x	1976	27 [5](P)			N
4	19X(34X37)	2x	1976	29(P)	0.6	0 to 0.8	N
4	[19X(34X37)][c]	4x	1976	5(P)	78	70 to 92	Y
4	82X[19X(34X37)][c]	4x	1977	group 1(P) [6]	7	0 to 24	Y
4	82X[19X(34X37)][c]	4x	1978	group 2(P)	29	27 to 32	Y
4	83X[19X(34X37)][c]	4x	1977	group 1(P)	15	2 to 31	Y
4	83X[19X(34X37)][c]	4x	1977	group 2(P)	19	8 to 37	Y
4	83X[19X(34X37)][c]	4x	1978	group 3(P)	32	29 to 35	Y
4	82X[82X(19X(34X37))[c]] [7]	4x	1979	17(P)	30	14 to 68	Y
4	83X[83X(19X(34X37))[c]] [7]	4x	1979	37(P)	40	9 to 79	Y

*Number of flowers (F) on one plant, or number of plants (P) observed.
**Percentage of stained (viable) pollen, rounded to whole numbers.
1 Parental numbers used to identify parents in program.
19=Arachis batizocoi (K-9484).
34=A. cardenasii (GKP-10017).
37=A. chacoensis (GKP-10602).
82=A. hypogaea var. vulgare (Spantex through 1973).
82=A. hypogaea var. vulgare (Tamnut 74 after 1973).
83=A. hypogaea var. hypogaea (UF-439-16-10-3-2, component line of Florunner).
2 Treated with colchicine to double the chromosome number.
3 The only flowers produced were used for crossing attempts.
4 All embryos aborted.
5 All plants were weak, none produced viable seeds.
6 A group represents from 4 to 7 plants from one F_1.
7 Backcross one.

Pathway 2

Attempts to hybridize *A. cardenasii* (parent 34) and *A. chacoensis* (parent 37) to combine the two leafspot resistances met with complete failure when pollinations were made inside the greenhouse. Success was achieved by growing the female parent (parent 34) outdoors, where one seed was obtained after making 3500 pollinations. The resulting diploid hybrid plant was crossed (as a male parent) with Tamnut 74 (parent 82), producing triploids. Colchicine treatment of triploid seeds resulted in one partially fertile hexaploid (Table 1). The first backcross to parent 82 produced a pentaploid that closely resembled the *A. hypogaea* parent in phenotype. Pollen staining (Table 1) indicated no male fertility, selfed seed were not obtained, and no seed were produced from backcross pollination with parent 82, even though pegs and pods developed. No attempts were made to culture the aborted embryos. Use of this pathway for germplasm enhancement has not been reported.

Pathway 3

Cuttings and seeds from the 34 X 37 hybrid plant were treated with colchicine. Some of the resulting tetraploids had high levels of stainable pollen (Table 1), so crosses were attempted with parent 82. Resulting progeny were tetraploid with varying levels of pollen stainability (Table 1). The plants appeared somewhat intermediate between wild and cultivated peanuts in early growth stages, but as they grew they became progressively more like the wild type in appearance. Fertility was low on all plants and no seed were produced (Table 1).

These results on pathways 1 to 3 differ from those reported by others (40, 42). The difference is most likely due to the use of different *A. hypogaea* parents, although location (latitude, elevation, climate) may have more effect than realized at the time these crosses were made. Existence of effects of differences in location were pointed out by Stalker and Moss (40).

Pathway 4

The above approaches did not appear promising for the introgression of characters due to lack of fertility, so the 34 X 37 diploid hybrid was crossed with *A. batizocoi*. This approach (Pathway 4) had been proposed by Smartt et al (34) as a solution to overcoming the sterility barrier between *A. hypogaea* and diploid species. They hypothesized that use of the B genome parent might make the complex amphiploids more cross-compatible with *A. hypogaea*. The diploid three-way hybrid [19 X (34 X 37)] was sterile (anticipated), an ideal situation for colchicine doubling. The induced tetraploid expressed elevated hybrid vigor, had 92% pollen stainability (Table 1), and was highly female fertile.

The complex amphiploid was hybridized with Tamnut 74 and the Florunner component line. The progeny expressed considerable hybrid vigor, a moderate level of pollen stained (Table 1) and a low level of seed set. Backcrosses to the two *A. hypogaea* parents were accomplished readily. At this stage, the first backcross F_1's were evaluated for early and late leafspot resistance. High levels of resistance to both diseases were present in all plants evaluated, indicating that the gene groups can be combined into one plant. Others have confirmed this conclusion (14, 37, 38, 40, 42). Recombination of the genes for resistance into the *A. hypogaea* cytoplasm has been confirmed by Ouedraogo (20) in BC_5F_4's derived from these lines.

In an attempt to accelerate the introgression of disease resistance into *A. hypogaea*, the subsequent testing and backcrossing after the BC_1 generation was all done using greenhouse and laboratory techniques, whereby BC_nF_1's were tested for leafspot resistance and plants identified as resistant were again backcrossed to *A. hypogaea* (Table 2). The stainable pollen count data presented in Table 2 for the six backcross generations show that the stainablility of pollen increased from BC_1 to BC_4. The data for BC_5 and BC_6 do not appear to reflect increases; however, this may not be the case. Beginning in 1985 (last half of BC_4 cycle, i.e., parent 82 backcross) and continuing to date, an over-all suppression of pollen quality has been noted in our program. The reduction in stainable pollen (7 to 12%) was suspected at first, but has now been confirmed on cultivars, species, and hybrids analyzed before and after 1985. The reason for the lower counts has been identified and is being verified, but will not be presented here. If a conditions-induced reduction of 7 to 12% is assumed on the BC_5 and BC_6 pollen counts a continuous increase in pollen stain for the six backcrosses was observed. Although pollen stain counts are not necessarily the same as plant fertility, if used properly, they can be a relative measure of male fertility. In these studies the absolute percentage of pollen stained was not important because the fertility levels were high enough after the BC_3 generation to allow the germplasm to be used as a parent with *A. hypogaea* for introgression of desirable traits.

After five cycles of testing/backcrossing in the above manner, seeds of BC_5F_2 families were increased for field

Table 2. A successful pathway for introgression from *Arachis* species to *A. hypogaea*.

Cross or Backcross	Parent Number	Number Plants observed	Pollen Counts* average	Pollen Counts* range	Seed Set yes/no
			%	%	
Pathway 4					
82X[19X(34X37)] [c 1,2]		4 (group 3) [3]	27	24-32	Y
83X[19X(34X37)] [c]		4 (group 4)	30	27-31	Y
BC_1	82	17	30	14-68	Y
(1979-1982)	83	37	40	09-79	Y
BC_2	82	3	46	18-80	Y
(1982-1983)	83	14	48	11-95	Y
BC_3	82	18	74	59-85	Y
(1983-1984)	83	56	72	32-96	Y
BC_4	82	12	73	64-84	Y
(1984-1985)	83	70	82	13-92	Y
BC_5	82	18	69	54-77	Y
(1985-1986)	83	68	78	63-88	Y
BC_6	82	20	75	68-80	Y
(1986-1987)	83	44	74	65-84	Y

*Percentage of stained (viable) pollen, rounded to whole numbers.
1 Parental numbers used to identify parents in program.
19=Arachis batizocoi (K-9484).
34=A. cardenasii (GKP-10017).
37=A. chacoensis (GKP-10602).
82=A. hypogaea var. vulgare (Spantex through 1973).
82=A. hypogaea var. vulgare (Tamnut 74 after 1973).
83=A. hypogaea var. hypogaea (UF-439-16-10-3-2, component line of Florunner).
2 Plant treated with colchicine to double the chromosome number.
3 A group represents 4 plants from one F_1.

testing. Field evaluation of the BC_5F_2 families indicated that resistance to leafspot had been introgressed into *A. hypogaea*. Further evaluation of six of these lines (20) has confirmed introgression of leafspot resistance greater than that expressed by the *C. personatum* resistant cultivar, 'Southern Runner' (3).

Evaluating this program in light of the available literature (e.g., 40, 42) points out the reason for lack of high levels of leafspot resistance. The characters of early and late leafspot are apparently multigenic with the strong possibility that each character is controlled by two or more genes. Thus the testing and backcrossing should have been conducted on BC_nF_2's or BC_nF_3's rather than BC_nF_1's. The characters can be introgressed through pathway 4 (20), but the time factor will be important because selections for backcrossing will have to be made after testing and from later generations.

Cuttings were maintained of almost all generations (some cuttings died), and retesting of these materials indicated that the resistance to three diseases (early and late leafspot and southern root-knot nematode) was contained in the BC_1F_1 material (15, 20 and unpublished data). Backcrossing to that generation followed by testing of BC_nF_2's (or later generations) should result in development of leafspot resistant/root-knot nematode resistant germplasm that is highly compatible with *A. hypogaea*.

Conclusions

Conclusions drawn from these and the related studies are as follows:

1. Hybrids between A and B genome *Arachis* parents appear to be useful for introgressing characters into *A. hypogaea* from wild *Arachis* species.
2. B genome *A. batizocoi* can serve as an effective bridge species between A genome wild *Arachis* and *A. hypogaea*.
3. The results support the hypothesis that leafspot resistance is multigenic.
4. Leafspot resistant/root-knot nematode resistant cultivars of peanut should be possible by introgression of genes from wild peanut species into *A. hypogaea*.

Acknowledgments

The author thanks W.C. Gregory and M.P. Gregory for stimulating his interest in this program, and he gratefully acknowledges the technical assistance of Wm. H. Higgins, Jr., K.E. Woodard, D.L. Higgins, K.S. Davis, and numerous Tarleton State University students. Also, the encouragement and advise of O.D. Smith and J.S. Newman is acknowledged.

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Accepted February 8, 1991