

Genetic Introgression from Compatible Wild Species into Cultivated Groundnut

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Abstract

*The diploid wild species ($2n=20$) compatible with the cultivated tetraploid groundnut *A. hypogaea* ($2n=40$), are good sources of resistance to many diseases of groundnut.*

*The fertility observed in triploid hybrids of *A. hypogaea* and eight diploid species, and the recovery of progenies with diploid to hexaploid chromosome numbers have led to the identification of a rapid method for the production of tetraploid interspecific derivatives. The hexaploids raised from the triploid hybrids show intra- and intergenomic pairing in the form of bivalents and multivalents. Hexaploids and the progenies of the triploids were backcrossed with *A. hypogaea* and produced *A. hypogaea*-like derivatives.*

*Autotetraploids were crossed with *A. hypogaea* and some fertile F_1 progenies obtained*

*Forty-six of the 56 possible interspecific crosses among eight diploid wild species produced seeds. Amphiploids were established in 31 combinations, 23 have been crossed with *A. hypogaea**

Résumé

*Introgression génétique à partir d'espèces sauvages compatibles dans l'arachide cultivée Les espèces sauvages diploïdes ($2n=20$) compatibles avec l'arachide tétraploïde cultivée *A. hypogaea* ($2n=40$) se révèlent constituées des sources de résistance très appréciables à de nombreuses maladies de l'arachide.*

*La fertilité observée chez des hybrides triploïdes entre *A. hypogaea* et 8 espèces diploïdes, et la récupération de descendants à nombres chromosomiques diploïdes à hexaploïdes ont conduit à l'identification d'une méthode rapide permettant la production de tétraploïdes interspécifiques. Les hexaploïdes issus des hybrides triploïdes présentent un appariement intra- et inter-génomique sous forme de bivalents et de multivalents. Rétrocroisés avec *A. hypogaea*, les hexaploïdes et les descendances des triploïdes ont donné des descendants semblables à *A. hypogaea**

*Des autotétraploïdes ont été croisés avec *A. hypogaea* avec obtention de certains descendants F_1 , fertiles.*

*Quarante-six des 56 croisements interspécifiques possibles entre les 8 espèces sauvages diploïdes ont produit des graines. Des amphiploïdes ont été obtenus dans 31 combinaisons, 23 ont été croisés avec *A. hypogaea*.*

Introduction

Groundnut (*Arachis hypogaea* L.) suffers from many diseases and pests that cause serious yield losses. Wild relatives of crop species have been found to be potential sources of a number of desirable characters, especially resistance to diseases and pests (Watson 1970; Knott and Dvorak 1976). The genus *Arachis* contains a number of such wild species. Gregory et al. (1973) divided the genus

into seven sections based on morphological affinities and cross compatibility. The section *Arachis* Krap et Greg. nom. nud. comprises the cultivated tetraploid species, *A. hypogaea*, and a number of compatible diploid wild species. The diploid species are good sources of resistance to many groundnut diseases, such as rust (*Puccinia arachidis*) and leaf spots (*Cercospora arachidicola* Hori) and (*Cercosporidium personatum* (Berk. et Curt.) Deighton), and to insect pests, such as thrips (*Sci-*

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rotothrips dorsalis Wood), and aphids (*Aphis craccivora* Koch). (Abdou et al. 1974; Herbert and Stalker 1981; Subrahmanyam et al. 1980, 1983, 1985; Amin 1985). Thus they have immediate potential as sources for the genetic improvement of groundnut.

Recent investigations on genome relationships in section *Arachis* have led to the identification of two genomes, A and B, in the diploid species. There is evidence that the cultivated tetraploid species *A. hypogaea* is an amphiploid (AABB), involving these two genomes from the diploid species (Singh and Moss 1982, 1984a) (Fig. 1). These observations have led to the identification of certain routes for the introgression of desirable genes from the compatible wild diploid species of section *Arachis* into cultivated groundnut. This paper discusses the efficacy of different cytogenetic manipulations for transfer of desirable characters from the eight available

diploid wild species of section *Arachis* into *A. hypogaea*.

Materials and Methods

The source and identity of eight diploid ($2n=20$), namely *A. batizocoi* Krap. et Greg. nom. nud., *A. duranensis* Krap. et Greg. nom. nud., *Arachis* species GKP 10038 (PI 263133), *A. correntina* (Burk.) Krap. et Greg. nom. nud., *A. chacoense* Krap. et Greg. nom. nud., *A. villosa* Benth., *A. cardenasii* Krap. et Greg. nom. nud., *Arachis* sp HLK 410 (PI 338280) and the two subspecies of *A. hypogaea* ($2n=40$), *A. hypogaea* L. subspecies *hypogaea* Krap. et Greg. and *A. hypogaea* L. subspecies *fastigiata* Waldron, all in section *Arachis*, have been given earlier (Singh and Moss 1982, 1984a).

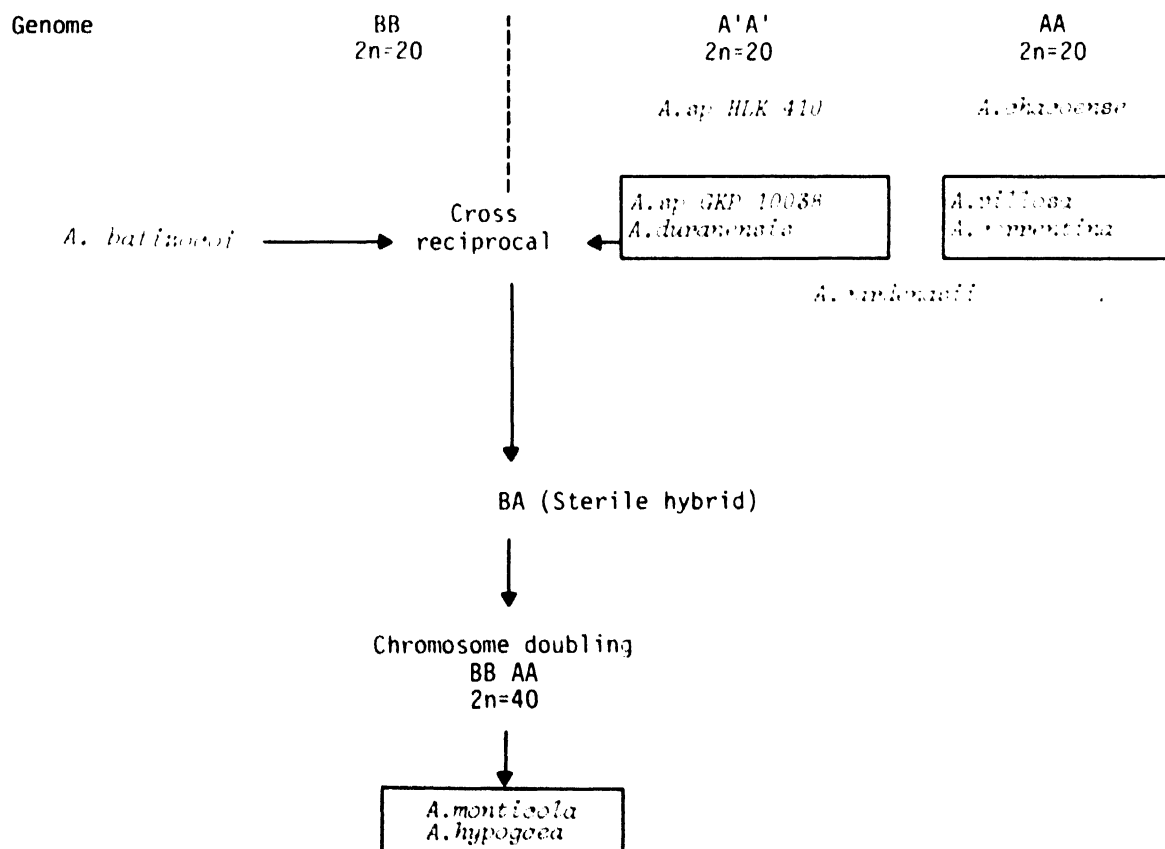


Figure 1. Genomic relationships in section *Arachis*, 'A' and 'B' genome/species have the same basic complement. Species have been arranged to indicate relative affinities based on geographical, morphological and cytogenetical evidence.

All the experiments were done in the screen-house, or in the field at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Center, Patancheru, near Hyderabad, India. The techniques followed for hybridization, cytological analysis, polyploid induction, and screening interspecific derivatives have been previously discussed (Subrahmanyam et al. 1980, Singh et al. 1983; Singh and Moss 1984a)

Results and Discussion

Based on the ploidy differences and genomic relationships between wild *Arachis* species and cultivated *A. hypogaea* (Fig. 1) the following cytogenetic manipulations were chosen for genetic introgression from the wild diploid species into *A. hypogaea*

Introgression through Amphiploids (Hexaploids)

In the section *Arachis* the most common way to incorporate desired characters from the diploid species into tetraploid *A. hypogaea* has been to cross the diploid species with tetraploid *A. hypo-*

gaea to produce triploid hybrids, and then to double their chromosome number by colchicine treatment to produce hexaploids and regain fertility (Smartt and Gregory 1967, Raman 1976, Moss 1980, Singh et al. 1980, Moss et al. 1981, Company et al. 1982). At ICRISAT, the triploid and hexaploid hybrids from crossing all eight available diploid species with *A. hypogaea* have been raised (ICRISAT 1982). Cytological analysis of hexaploids has revealed 10 to 30 bivalents, with means ranging from 20.3 to 23.9, and 0 to 8 multivalents, with means ranging from 1.1 to 3.2 per pollen mother cell (PMC) (Table 1, Fig. 2d). The multivalent associations in these hexaploids indicate that intergenomic (A-B) pairing occurs between the chromosomes of wild species and those of the cultivated species in all combinations, besides intragenomic or intraspecific (A-A or B-B) pairing of chromosomes. This suggests that the desired recombinants combining wild and cultivated species characters can be obtained through natural meiotic pairing and crossing over. However, the frequency of such recombinations is very low, as evidenced by low multivalent frequency due to preferential autosyndetic pairing between the homologous chromosomes of one species, giving a high bivalent frequency (Table 1). Hence, a very

Table 1. Chromosome associations, and pollen and pod fertilities in hexaploids from *A. hypogaea* (4x) × *Arachis* (2x) hybrids.

<i>A. hypogaea</i> cross	Cells analysed (no.)	Chromosome associations						Pollen stainability (%)	Pods produced (range)
		I	II	III	IV	V	VI		
<i>A. villosa</i>	7	8.3 ±1.83	23.9 ±0.63	0.2 ±0.14	0.9 ±0.34	0	0	60	0-200
<i>A. correntina</i>	43	6.7 ±0.44	22.2 ±0.47	1.1 ±0.16	1.1 ±0.19	0	0.5 ±0.02	26 ¹	0-110
<i>A. chacoense</i>	216	6.6 ±0.33	20.9 ±0.26	1.2 ±0.17	1.4 ±0.10	0.3 ±0.01	0.1 ±0.02	88	0-53
<i>Arachis</i> sp. HLK 410	88	7.1 ±0.52	20.6 ±0.45	1.1 ±0.26	1.5 ±0.17	0.5 ±0.01	0.1 ±0.04	61	0-180
<i>A. cardenasii</i>	160	6.9 ±0.35	20.3 ±0.29	1.3 ±0.20	1.5 ±0.10	0.1 ±0.01	0.1 ±0.02	62	0-113
<i>A. duranensis</i>	10	6.6 ±0.64	21.8 ±1.29	1.1 ±0.38	1.4 ±0.48	0.1 ±0.1	0	73	0-99
<i>A. batizocoi</i>	7	5.6 ±1.13	23.7 ±0.68	0.7 ±0.42	1.1 ±0.34	0	0	93	5-92

1. From two screenhouse plants.

Table 2. Pod production in backcrossing of *A. hypogaea* (4x) × wild species (2x), amphiploids (6x) with *A. hypogaea*, and number of fertile derivatives obtained by post-rainy season 1982-83.

	BC ₁			BC ₂			BC ₃			BC ₄			BC ₅			Fertile tetraploids (no.)
	Poll. (no.)	Pod (no.)	Poll./pod (%)	Poll. (no.)	Pod (no.)	Poll./pod (%)	Poll. (no.)	Pod (no.)	Poll./pod (%)	Poll. (no.)	Pod (no.)	Poll./pod (%)	Poll. (no.)	Pod (no.)	Poll./pod (%)	
<i>A. hypogaea</i> × <i>Arachis</i> sp (6x)																
<i>A. cardenasii</i>	1277	109	9	2516	464	18	709	80	11	432	95	22	94	15	16	23
		(2'×10) ²			(5'×1)			(5')								
<i>A. chacoense</i>	302	19	6	462	40	9	303	51	17	220	14	6	94	15	16	8
		(1)			(2)			(4)			(1)					
<i>Arachis</i> sp HLK 410	254	36	14	169	27	16	863	81	9	28	1	4				3
		(1)			(2)											
<i>A. correntina</i>	56	14	25	252	12	5										
<i>A. villosa</i>	224	16	7													
<i>A. balizocoi</i>	179	17	10													

1 From progenies of selfed triploids 2 Number of fertile tetraploid derivatives obtained

large population of interspecific derivatives is essential for the selection of desired recombinants. Backcrossing these hexaploids with *A. hypogaea*, either using the same, or different cultivars produced *A. hypogaea*-like derivatives in different backcross generations (Table 2) as a result of increased autosyndetic preferential pairing between chromosomes of *A. hypogaea* in backcross progenies. However, this pairing behaviour restricts further genetic exchange between cultivated and wild species chromosomes in subsequent generations, but has helped in the rapid production of tetraploid derivatives similar to *A. hypogaea*. At ICRISAT 22 *A. hypogaea*-like tetraploid lines involving three diploid species, *A. cardenasii*, *A. chacoense*, and *Arachis* sp HLK 410, resistant to rust and leaf spot diseases were obtained using this method in the post-rainy season 1982 (Table 2). From these interspecific derivatives a large number of segregates resistant to late leaf spot and rust have been selected (Fig. 3) (ICRISAT 1982; and Singh unpublished).

Introgression through Triploids

Recently the triploid hybrids between *A. hypogaea* and diploid species, which were hitherto reported sterile except by Smartt and Gregory (1967) for three combinations, and Simpson and Davis (1983) for a single plant from a complex triploid, have been found fertile across all combinations (Singh and Moss 1984b). Cytological analysis of these triploid hybrids revealed interspecific, and intragenomic pairing between the chromosomes of wild and cultivated species in the form of up to 10 bivalents with means ranging from 8.0 to 9.9/cell. Intergenomic pairing also occurred in cells with more than 10 bivalents or with multivalents (Table 3; Fig. 2a). The frequency of cells with multivalents and/or more than 10 bivalents indicates a high degree of genetic exchange (crossing over) between chromosomes of wild and cultivated species. At anaphase I (AI) and anaphase II (AII) unequal chromosome segregation results in the formation of haploid to hyperdiploid gametes, and spindle breakdown results in the formation of restitution nuclei and unreduced gametes. Fertilization between such viable gametes results in the fertility of triploids previously considered sterile. As this process was never observed in the triploids produced and maintained at Reading University, UK during the period 1973 to 78, but was observed at ICRISAT in plants grown

Table 3. Chromosome associations, pollen, and pod fertility in F₁ triploids of *A. hypogaea* (4x) × *Arachis* species (2x).

<i>A. hypogaea</i> cross	Cells analysed (no.)	Chromosome association				Pollen stainability (%)	Pods produced (range)
		I	II	III	IV		
<i>A. villosa</i>	25	9.1 ±0.52	8.6 ±0.37	1.0 ±0.22	0.2 ±0.1	19	0.7
<i>A. correntina</i>	21	8.3 ±0.43	9.9 ±0.31	0.6 ±0.16	0.1 ±0.05	20	0-25
<i>A. chacoense</i>	40	9.7 ±0.4	8.7 ±0.25	0.8 ±0.16	0.1 ±0.49	17	0-19
<i>Arachis</i> sp HLK 410	30	9.2 ±0.43	9.6 ±0.28	0.5 ±0.13	0.1 ±0.03	13	0-16
<i>A. cardenasii</i>	25	8.3 ±0.52	9.7 ±0.27	0.5 ±0.17	0.2 ±0.08	9	0-10
<i>Arachis</i> sp GKP 10038	25	10.0 ±0.44	8.0 ±0.26	1.2 ±0.18	0.1 ±0.06	11	2 ¹
<i>duranensis</i>	20	8.3 ±0.45	9.4 ±0.24	1.0 ±0.17	0.1 ±0.05	18	4 ¹
<i>A. batizocoi</i>	21	6.2 ±0.42	8.7 ±0.49	2.0 ±0.29	0.1 ±0.07	7	3-18

¹ Single plant

from rooted cuttings from the same triploids, it is probable that the phenomenon is affected by environment. The occurrence of 82% hexaploids in progenies of triploids suggests the greater success of unreduced gametes than other types of gametes in fertilization. These progenies are the product of fertilization between gametes resulting from pairing and crossing over between the chromosomes of wild and cultivated species at metaphase (MI), and therefore have a greater degree of recombination between wild and cultivated species characters than artificially-induced hexaploids. Many triploid progenies have fewer chromosomes than hexaploid, or even a few tetraploids, and have reduced the number of backcross cycles required for the production of tetraploid derivatives. At ICRISAT, following this method, 13 tetraploid *A. hypogaea*-like derivatives involving *A. cardenasii*, *A. chacoense*, and other species have been obtained and segregates resistant to insect pests, such as leaf miner (*Aproaerema modicella* Dev.), jassids (*Empoasca kerii* Pruthi) and thrips have been selected (Singh unpublished).

The gametic fertility of triploids suggests that they can also be used directly in backcrossing to

recipient cultivars to obtain pentaploids (Simpson and Davis 1983) and also tetraploid *A. hypogaea*-like progenies as in wheat (Kerber and Dyck 1973).

Introgression through Amphiploids (Tetraploids)

Identification of A and B genomes in wild diploid species of section *Arachis*, and the amphiploid origin of tetraploid *A. hypogaea* involving A and B genome species, suggest that maximum genetic exchange between wild and cultivated species chromosomes can be achieved when two wild species, with AA and BB genomes, are crossed, the chromosome number doubled, and the AABB amphiploid so produced crossed with *A. hypogaea* (Singh and Moss 1984a). The resultant hybrids are fertile. The evidence of chromosome pairing in the hybrids between *A. hypogaea* and these species at different ploidy levels suggests that both auto- and allosyndetic pairing will occur.

Amphiploids were raised from sterile or semi-sterile hybrids in 34 diploid species hybrid combinations (ICRISAT 1982). Cytological analysis

showed that amphiploids from hybrids between closely-related species with the A genome behaved like autotetraploids, with a high frequency of quadrivalents and low pod fertility. The amphiploids from hybrids between distantly-related species, with A and B genomes, showed higher bivalent associations (Fig 2c), and greater pod fertility (Singh unpublished). The hybrids between *A. hypogaea* and 23 of these amphiploids were established and ten hybrid combinations were cytologically analysed (Table 4). The hybrids between *A. hypogaea* and amphiploids involving *A. batizocoi* have higher bivalent association, (Fig. 2c), pollen, and pod fertility than others (Table 4). Subsequent backcrossing of these hybrid progenies with *A. hypogaea* has resulted in 26 tetraploid *A. hypogaea*-like derivatives (Table 5). However, the high susceptibility of *A. batizocoi*, to late leaf spot diseases the only B genome species, and of the related annual species, is a serious limitation. Therefore collection of B genome, resistant acces-

sions, or a very large interspecific population will be necessary to make this method effective. The method has been effective in transferring rust resistance from wild diploid species into *A. hypogaea*, and a number of *A. hypogaea*-like segregates resistant to rust have been selected.

Introgression through Autotetraploids

Another possibility for genetic introgression is to cross the autotetraploids of diploid species with *A. hypogaea*. As well as hybridization at the same ploidy level, this offers a few valuable advantages previously obtained in other crop species such as potato, *Solanum tuberosum* and tobacco, *Nicotiana tabacum* (Livermore and Johnstone 1940; Clayton 1947). *A. hypogaea* has greater genomic affinity with diploid *A. batizocoi*, (B genome) followed by annual and perennial species with th

Table 4. Chromosome associations and pollen and pod fertility in *A. hypogaea* × diploid species amphiploids (4x).

<i>A. hypogaea</i> × amphiploid	Crossability with <i>A. hypogaea</i> (%)	Cells analysed (no.)	Chromosome association				Pollen stainability (%, range)	Pods produced (no. range)
			I	II	III	IV		
(<i>A. batizocoi</i> × <i>A. correntina</i>)	18	11	7.9 ±1.18	13.3 ±0.57	1.5 ±0.34	0.3 ±0.14	37	2-4
(<i>A. batizocoi</i> × <i>A. duranensis</i>)	50	16	3.3 ±0.54	16.4 ±0.57	0.7 ±0.24	0.4 ±0.13	29-62	1-5
(<i>A. villosa</i> × <i>A. batizocoi</i>)	26	25	4.7 ±0.43	15.5 ±0.38	0.8 ±0.16	0.5 ±0.12	33-63	3-19
(<i>A. duranensis</i> × <i>A. chacoense</i>)	13	5	10.8 ±0.2	7.2 ±0.58	2.4 ±0.4	1.4 ±0.25	56	0
(<i>A. villosa</i> × <i>A. duranensis</i>)	19	3	10.0 ±0	13.0 ±1.16	0.0	1.0 ±0.58	63-57	12
(<i>A. duranensis</i> × <i>Arachis</i> sp GKP 10038)	26	20	9.5 ±0.42	10.8 ±0.56	1.1 ±0.24	1.4 ±0.27	43-53	3-5
(<i>Arachis</i> sp HLK 410 × <i>Arachis</i> sp GKP 10038)	9	25	10.1 ±0.54	11.5 ±0.6	0.8 ±0.19	0.9 ±0.19	18-35	34
(<i>Arachis</i> sp HLK 410 × <i>A. chacoense</i>)	9	15	11.3 ±0.62	11.0 ±0.54	1.2 ±0.34	0.9 ±0.22	37	0
(<i>A. villosa</i> × <i>Arachis</i> sp HLK 410)	13	11	9.5 ±0.96	11.9 ±0.39	1.3 ±0.3	0.7 ±0.2	55	0
(<i>A. correntina</i> × <i>A. villosa</i>)	22	12	11.1 ±1.0	11.3 ±0.66	0.4 ±0.19	1.3 ±0.33	51	1

Table 5. Pod production in backcrossing of *A. hypogaea* × diploid species amphiploids (4x) hybrids with *A. hypogaea*, and number of fertile derivatives obtained by postrainy season 1982-83.

<i>A. hypogaea</i> × amphiploid (4x)	BC ₁			BC ₂			BC ₃			BC ₄			Fertile tetraploids (no)
	Poll (no)	Pod (no)	Poll / pod (%)	Poll (no)	Pod (no)	Poll / pod (%)	Poll (no)	Pod (no)	Poll / pod (%)	Poll (no)	Pod (no)	Poll / pod (%)	
<i>A. villosa</i> × <i>A. batizocoi</i>	1024	89 (1) ¹	9	562	58 (1)	10	696	90	13				2
<i>A. correntina</i> × <i>A. batizocoi</i>	215	10	5	978	52 (2)	5	889	80 (1)	9	297	53	18	3
<i>A. batizocoi</i> × <i>A. correntina</i>	362	20	6	282	39 (1)	14							1
<i>A. batizocoi</i> × <i>A. chacoense</i>	217	36	17	76	17 (1)	22							1
<i>A. batizocoi</i> × <i>A. duranensis</i>	846	46	5	413	44 (1)	11	769	73 (1)	9	64	8	13	2
<i>A. duranensis</i> × <i>Arachis</i> sp GKP 10038	460	26 (1)	6	155	11	7							1
<i>Arachis</i> sp GKP 10038 <i>Arachis</i> sp HLK 410	232	5 (1)	2	537	42	8	452	53	12	261	29	11	1
<i>Arachis</i> sp HLK 410 <i>Arachis</i> sp GKP 10038	78	6 (1)	12	68	15	22							1
<i>Arachis</i> sp HLK 410 <i>A. chacoense</i>	310	44	14	131	17 (2)	8	527	47	9				2
<i>A. duranensis</i> × <i>Arachis</i> sp HLK 410	160	14	9										0
<i>A. villosa</i> × <i>Arachis</i> sp HLK 410	683	73 (2)	11	236	51	21							2
<i>A. villosa</i> × <i>A. duranensis</i>	195	19 (1)	10	73	5	7							1
<i>A. correntina</i> × <i>A. chacoense</i>	99	22 (2)	22	317	46	15	440	55	13				2
<i>A. duranensis</i> × <i>A. chacoense</i>	283	51 (2)	18	174	40 (1)	23	436	53	12	91	11	12	3
<i>A. correntina</i> × <i>A. villosa</i>	893	62 (3)	7	90	4	4							3
<i>A. correntina</i> × (<i>A. chacoense</i> × <i>A. cardenasii</i>)	404	33	8	697	114	16							1
<i>A. correntina</i> × <i>Arachis</i> sp GKP 10038	28	6	21										0

¹ Number of fertile tetraploids derivatives obtained shown in parentheses

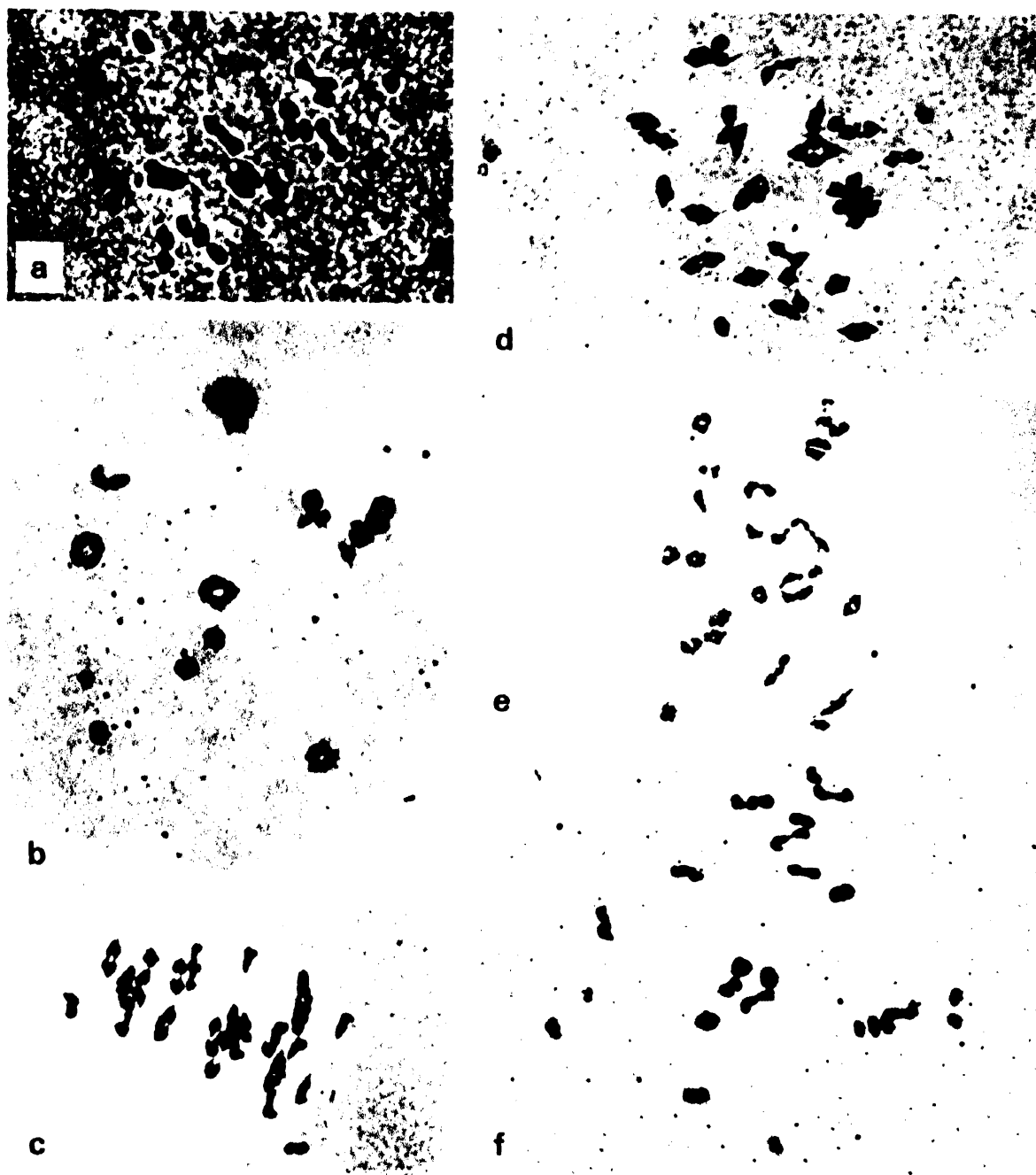


Figure 2. Pollen mother cells at metaphase I showing:

- a. $8I + 9II + 1IV$ in a triploid hybrid, *A. hypogaea* subsp *hypogaea* \times *A. correntina*
- b. In an autotetraploid, *A. correntina*, $2I + 9II + 5 IV$;
- c. in an amphiploid, *A. batizocoi* \times *A. villosa*, $2I + 17II + 1IV$;
- d. in an amphiploid, *A. hypogaea* \times *A. cardenasii*, $4I + 18II + 5 IV$;
- e. in a hybrid *A. hypogaea* subsp *fastigiata* \times (*A. batizocoi* \times *A. duranensis*) amphiploid, $1I + 14II + 1III + 2IV$;
- f. in a hybrid, *A. hypogaea* subsp *fastigiata* \times *A. batizocoi* autotetraploid, $8I + 14II + 1IV$.

Table 6. Chromosome associations, pollen and pod fertility in *A. hypogaea* × diploid species autotetraploids (4x).

<i>A. hypogaea</i> × autotetraploid (4x)	Crossability with <i>A. hypogaea</i> (%)	Cells analysed (no.)	Chromosome associations				Pollen stainability (%, range)	Pod produced (no. range)
			I	II	III	IV		
<i>A. batizocoi</i>	14	23	5.8 ±0.52	14.1 ±0.56	0.9 ±0.23	0.9 ±0.19	43-64	5-26
<i>Arachis</i> sp HLK 410	11	21	10.1 ±0.78	11.1 ±0.52	1.9 ±0.28	0.5 ±0.18		2-5
<i>A. villosa</i>	22	9	7.2 ±0.68	11.8 ±0.94	2.2 ±0.4	0.3 ±0.17	44-75	2-4

genome. The autotetraploids of these species do not differ significantly between each other in chromosome associations but the annual species autotetraploids have higher pollen and pod fertility (Singh unpublished). Crossabilities between *A. hypogaea* and the autotetraploids of section *Arachis* diploid species do not differ, but the fertility of the resulting first generation hybrids does differ. The hybrids with two annual species autotetraploids, *A. hypogaea* × *A. batizocoi* (4x) and *A. hypogaea* × *Arachis* sp 10038 (4x) produced most pods when backcrossed, *A. hypogaea* × *A. batizocoi* (4x) hybrid showed the highest mean bivalent associations (14.1) (Fig. 2f), and moderate pollen fertility (43 to 64%), and pod production (range 3 to 21)

(Table 6). It produced five *A. hypogaea*-like tetraploid progenies within two backcross generations and enabled incorporation of resistance to the rust pathogen from this species into *A. hypogaea* (Table 7, ICRISAT 1983).

The autotetraploids of other species in section *Arachis* with the A genome can also be of great value, as more than 10 bivalents and a few multivalent associations in PMCs of the hybrids between *A. hypogaea* and A genome species autotetraploids, were recorded (Table 6). Their first generation hybrids do not produce pods on selfing but this has been overcome by backcrossing to *A. hypogaea*. The genomic constitution of these hybrids (AAAB) is conducive to intergenomic A-B pairing, altering

Table 7. Pod production in backcrossing of *A. hypogaea* × diploid species autotetraploids (4x) hybrids with *A. hypogaea*, and number fertile derivatives obtained by postrainy season 1983-84

<i>A. hypogaea</i> × amphiploid (4x)	BC ₁			BC ₂			BC ₃			BC ₄			Fertile tetraploids (no.)
	Poll (no.)	Pod (no.)	Poll / pod (%)	Poll (no.)	Pod (no.)	Poll / pod (%)	Poll (no.)	Pod (no.)	Poll / pod (%)	Poll (no.)	Pod (no.)	Poll / pod (%)	
<i>A. batizocoi</i>	1012	59 (1) ¹	6	1563	110 (4)	7	346	47	14	182	19	10	5
<i>A. villosa</i>	368	20	5	31	2	6							0
<i>A. correntina</i>	50	1 (1)	2	209	61	29	7	1	14				1
<i>Arachis</i> sp HLK 410	301	9 (1)	3	103	13	14	51	2	4				1
<i>Arachis</i> sp GKP 10038	75	8	11										

¹ Number of fertile tetraploid derivatives obtained



Figure 3. A field view of some late leaf spot-resistant segregates from *A. cardenasii*.

the genetic constitution of chromosomes, such as those of the B genome carrying susceptibility to late leafspot.

Conclusions

The degree of genomic affinity between *A. hypogaea* and diploid species of section *Arachis* permits intergenomic and intragenomic pairing between chromosomes of wild and cultivated species. The production of hybrids at different ploidy levels through conventional interspecific hybridization and cytogenetic manipulations leads to incorporation of desired traits from wild species into *A. hypogaea*. The different pathways for gene transfer from wild into cultivated species can be adopted based on; phylogenetic relationships between species, an understanding of the cytogenetic behaviour of the two genomes involved at the different ploidy levels, and the nature of the gene(s) and their expression. With such an understanding, genes can be intro-

gressed from the wild diploid species into *A. hypogaea*.

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