# Incorporation of Rust Resistance from Wild *Arachis* Species into the Cultivated Groundnut

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## Abstract

*On the basis of genomic relationships in section* Arachis *in the genus* Arachis *several cytogenetic manipulations were adopted to aid gene transfer from the diploid wild species (2n = 20) into the cultivated tetraploid* A. hypogaea *(2n = 40). Triploid hybrids were produced between* A. hypogaea *and the eight diploid rust-resistant species of section* Arachis. *Chromosome numbers in these hybrids were doubled to produce hexaploids that were fertile and could be backcrossed with* A. hypogaea. *Some triploids did produce a few seeds and seedlings, these progenies had varying chromosome numbers (2n = 20 to 60) and produced a considerable range of recombinants. Synthetic autotetraploids and amphidiploids were produced from the diploid species. They were then crossed with* A. hypogaea. *This has bridged the ploidy gap between the diploid wild and the tetraploid cultivated species, and increased meiotic recombinations. Backcrossing the resultant hybrids with* A. hypogaea *with a few intervening selfing generations has produced a large number of* A. hypogaea*-like interspecific derivatives. Screening these derivatives identified segregants incorporating genes from the wild species* A. cardenasii, A. batizocoi, A. duranensis *and* A. *species GKP 10038 that confer resistance to rust.*

## Résumé

**Incorporation de la résistance à la rouille dans les arachides cultivées à partir des espèces sauvages d' Arachis :** *L'existence de relations génomiques à l'intérieur de la section* Arachis *du genre* Arachis *a permis de faire des manipulations cytogénétiques en vue d'un transfert des gènes à partir des espèces sauvages diploïdes (2n = 20) en tétraploïde cultivé* A. hypogaea *(2n = 40). Des hybrides triploïdes sont obtenus des croisements d'* A. hypogaea *avec les huit espèces résistantes diploïdes de la section* Arachis. *Les nombres chromosomiques chez ces hybrides sont doublés afin d'obtenir des hexaploïdes féconds permettant le rétrocroisement avec* A. hypogaea. *Certains triploïdes ont en effet produit quelques semences et de plantules, ces descendances possèdent des nombres chromosomiques variables (2n = 20 à 60) donnant une large gamme de recombinants. A partir des espèces diploïdes sont obtenus des autotétraploïdes et des amphidiploïdes de synthèse. Leur croisement avec* A. hypogaea *permet de rapprocher, du point de vue genomique, les diploïdes sauvages et les tétraploïdes cultivés tout en augmentant les recombinaisons méiotiques. Le rétrocroisement des hybrides avec* A. hypogaea *en passant par quelques generations autofécondées produit un grand nombre de dérivés interspécifiques d'* A. *hypogaea. Parmi ces dérivés, on a reperé des ségrégants qui comportent des gènes des espèces sauvages dont* A. cardenasii, A. batizocoi, A. duranensis *et l'espèce GKP 10038 d'*Arachis *responsables de la production de la résistance à la rouille*


Groundnut (*Arachis hypogaea* L.) rust caused by the fungus *Puccinia arachidis* Speg. often results in yield losses of over 50% (Subrahmanyam et al. 1979). The disease can be controlled with fungicides, but resource-poor groundnut farmers in the semi-arid tropics (SAT) need a groundnut cultivar that has genetic resistance. A wide range of groundnut germplasm, cultivated as well as wild, has been screened

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for resistance to rust and several rust-resistant accessions have been identified (Subrahmanyam et al 1980, 1982, 1983, 1985)

The cultivated species, *A hypogaea* (2n=40), has been grouped with a number of cross-compatible wild diploid species (2n=20) in the section *Arachis* (Gregory et al 1973) All these diploid species have a high degree of resistance to groundnut rust ranging from immunity (no visible symptoms) to hypersensitivity (a few small necrotic non-sporulating pustules on leaflets) These are good sources of rust resistance for use in genetic improvement of *A hypogaea*

Ploidy differences between wild and cultivated species in section *Arachis* are barriers to genetic introgression A basic understanding of genomic structure and interrelationships between the species has helped in the selection of procedures that can overcome these barriers The present paper reports the progress of work at ICRISAT on the transfer of genes conferring rust resistance from a few diploid wild species into the cultivated tetraploid species using different genomic and ploidy manipulations

## Materials and Methods

The sources and identities of the eight diploid wild species (2n=20) and the cultivars belonging to two subspecies of *A hypogaea* (2n=40), *A hypogaea* subspecies *hypogaea* Krap et Rig and *A hypogaea* subspecies *fastigiata* Waldron, all of section *Arachis*, are given in Table 1 Hybridization between the diploid species and cultivars of *A hypogaea* was done in a screenhouse at ICRISAT Center The techniques followed for hybridization, cytological analysis, polyploidy induction, and screening against rust in the field and under laboratory conditions have been described earlier (Subrahmanyam et al 1980, Singh et al 1983)

**Table 1 Sources and taxonomic status of parents used in transfer of rust resistance from wild species.**

| Species cultivar | Collector[1] | Coll No | ICG No [2] | Origin |
|---|---|---|---|---|
| Wild | | | | |
| *A villosa* (Benth) | - | - | 8144 | Uruguay |
| *A correntina* (Burk ) Krap et Greg | GKP | 9530 | 8140 | Argentina |
| *A chacoense* Krap et Greg | GKP | 10602 | 4983 | Argentina |
| *A cardenasii* Krap et Greg | GKP | 10017 | 8216 | Bolivia |
| *Arachis* species | HLK | 410 | 8126 | Brazil |
| *Arachis* species | GKP | 10038 | 8139 | Argentina |
| *A duranensis* Krap et Greg | K | 7988 | 8123 | Argentina |
| *A batizocoi* Krap et Greg | K | 9484 | 8124 | Argentina |
| Cultivated | | | | |
| *A hypogaea* L ssp *fastigiata* Waldron var *fastigiata* (valencia) | | | | |
| 1 Gangapuri | | - | 2738 | India |
| *A hypogaea* L ssp *fastigiata* Waldron var vulgaris (spanish) | | | | |
| 2 99-5 | | - | 1472 | Unknown |
| 3 Chico | | - | 476 | USA |
| 4 Tifspan | | - | 3497 | USA |
| 5 91176 | | - | 4117 | India |
| *A hypogaea* L ssp *hypogaea* Krap et Rig var *hypogaea* (virginia) | | | | |
| 6 Robut 33-1 | | - | 799 | India |
| 7 M 13 | | - | 156 | India |
| 8 Makulu Red | | - | 6391 | Zambia |

1 G = Gregory H = Hammons K = Krapovickas, L = Langford, P = Pietrarelli
2 ICG = ICRISAT Groundnut Accession

## Results and Discussion

### Transfer of rust resistance

Genome analysis in the section *Arachis* has revealed that *A hypogaea* is a segmental allotetraploid with two genomes "A" and "B" each with base number 10 Among the diploid species there are several species with the "AA" genomic constitution although grouped as "A" genome species, these differ in karyotype and there are genetic differences within "A" genome species (Singh and Moss 1982, 1984a), the "BB" genome is represented by a single species, *A batizocoi* (Husted, 1936, Smartt et al 1978, Stalker and Dalmacio 1981, Singh and Moss, 1982) Further studies have revealed that the two genomes "A" and "B" are closely related *A hypogaea* forms predominantly bivalents, suppressing A-B intergenomic pairing However, such a suppression of A-B pairing does not seem to occur at different levels of ploidy in its experimental hybrids with wild species (Smartt and Stalker 1983, Singh and Moss 1984a) Therefore, genetic introgression from wild diploid species of section *Arachis* into *A hypogaea* is possible provided suitable ploidy and genomic manipulations are adopted

The cytogenetic manipulations used at ICRISAT to facilitate transfer of rust resistance from wild diploid species into *A hypogaea* outlined in Figure 1 are discussed below

### Crosses between tetraploid *A hypogaea* and diploid species

*A hypogaea* is freely crossable with these diploid species and direct hybridization between them and *A hypogaea* for gene transfer is the first logical proposal Eight rust-resistant wild diploid species were crossed as male parents with cultivars belonging to two subspecies of *A hypogaea*, and triploid hybrids were established The hybrids were vigorous, with intermediate leaflet size and a trailing habit, and expressed the dominant morphological features of the wild species, they were also resistant to groundnut rust

Cytological analysis of these hybrids revealed that the 10 chromosomes contributed by the wild species paired with 10 corresponding chromosomes of the homologous genome of *A hypogaea* to form 10 bivalents The 10 chromosomes of the non-homologous genome of *A hypogaea* predominantly remained unpaired, as univalents Homoeology of wild species chromosomes with the non-homologous genome of *A hypogaea* resulted in intergenomic pairing and the formation of more than 10 bivalents, or of multivalents in some pollen mother cells (PMCs) (Singh 1985) Such a pairing behavior indicates that meiotic recombination between wild and cultivated species does occur, but the gametes so formed abort as a result of irregular meiosis caused by high frequency of univalents, thus rendering the triploid hybrids sterile

**Use of amphiploids (hexaploids) of triploid hybrids.** Sterile triploids were treated with colchicine to double the chromosome number and restore fertility This has been the most common method for genetic introgression from wild species and has been adopted by many workers (Smartt and Gregory 1967 Raman 1976, Moss et al 1981) At Reading University UK and at ICRISAT Center triploid hybrids between all 8 diploid species and 1 *hypogaea* were raised to hexaploids Cytologically, hexaploids formed mostly bivalents (range 10 to 30 mean 21 to 24) but a few multivalent associations (range 0 to 8, mean 1 1 to 2 7) have been observed (Singh 1985) involving the chromosomes of both wild and cultivated species (Spielman et al 1979) Consequently, recombinants with desirable traits of wild and cultivated species were formed, though at a very low frequency They were screened for resistance to foliar diseases under field conditions during the rainy seasons of 1978 and 1979 Segregants resistant to rust and late leaf spot were selected and backcrossed with *A hypogaea* to reduce their chromosome numbers and regain the agronomic traits of *A hypogaea*

Backcrossing of hexaploids with *A hypogaea* resulted in the production of 32 *A hypogaea*-like tetraploid derivatives incorporating genes from *A chacoense A cardenasii* and 1 species HLK 410 These have been screened for resistance to rust under natural field conditions during several rainy seasons, and a large number of resistant segregants have been selected (Table 2)

**Use of triploid progenies.** Although triploids were reported sterile they were found to produce some seeds and seedlings (Singh and Moss 1984b) Therefore, useful meiotic recombinations that occur in triploid hybrids are available for utilization Eighty-two percent of plants in progenies from triploids were hexaploid, 10% aneuploid, and 8% tetraploid The plants that have either 40, or less than 60, chromosomes are important, because their use redu-

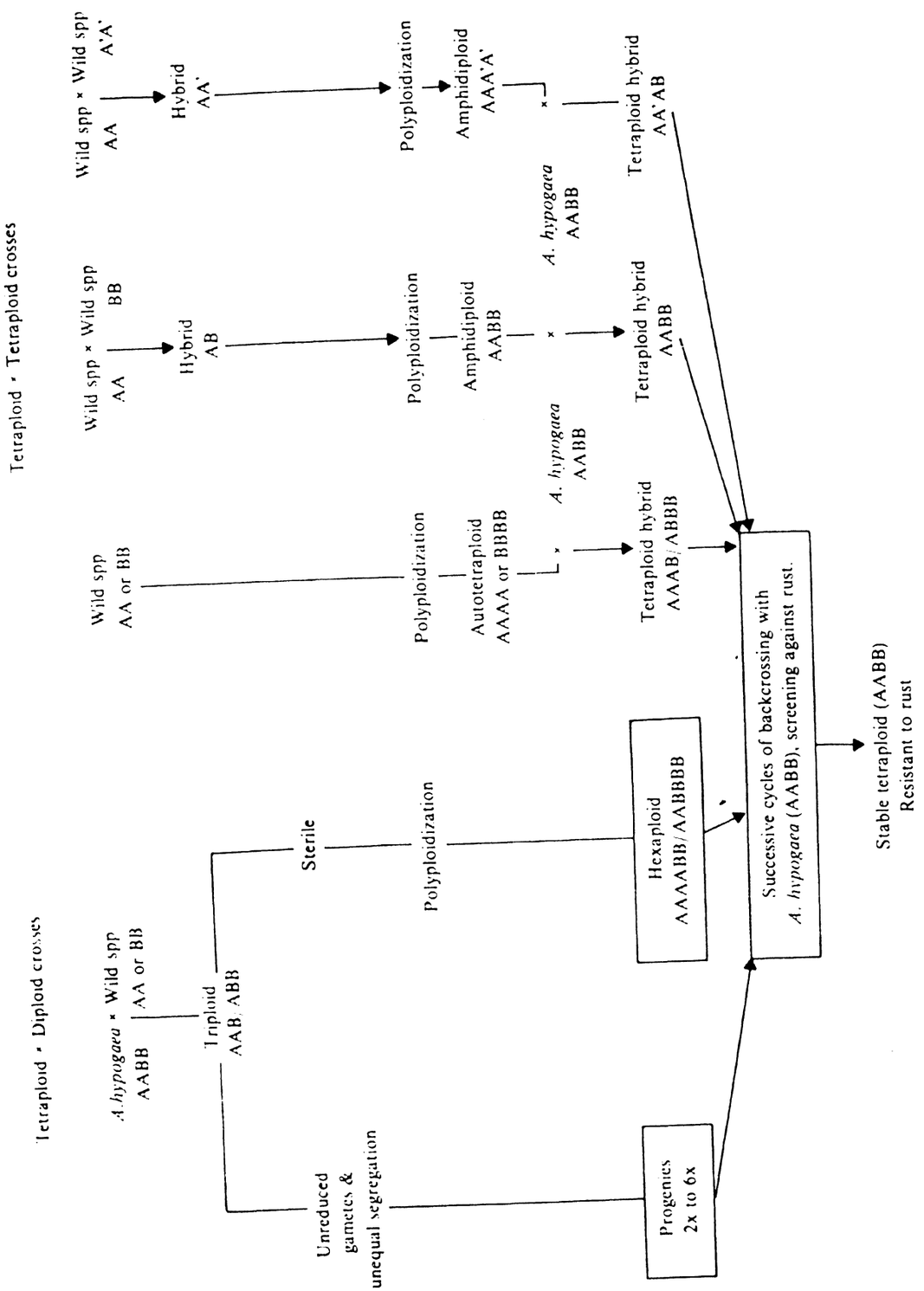


**Figure 1. Manipulations for gene transfer in *Arachis*.**

**Table 2. Number of stable interspecific tetraploid derivatives produced and number of plants selected from their populations for resistance to rust, ICRISAT Center, 1982, 1984.**

| Route | Species | 1982 | 1983 | 1984 | Total |
|---|---|---|---|---|---|
| Self Triploids | *A. cardenasii* | 5 (7)[1] | 8 (14) | 1 | 14 (21) |
| | *A. chacoense* | 2 | | 1 | 3 |
| Hexaploids | *A. cardenasii* | 11 (23) | 1 (229) | (6) | 12 (258) |
| | *A. chacoense* | 5 (9) | 2 (4) | (33) | 7 (46) |
| | *A.* sp HLK 410 | 1 (6) | 2 (1) | 10 | 13 (7) |
| Autotetraploids | *A. batizocoi* | 2 | 4 (1) | (2) | 6 (3) |
| | *A. correntina* | | 2 | | 2 |
| | *A.* sp GKP 10038 | 1 | | | 1 |
| | *A.* sp HLK 410 | 1 | | | 1 |
| | *A. villosa* | 1 | | | 1 |
| Amphidiploids | *A. batizocoi* × *A. chacoense* | | 1 | | 1 |
| | *A. batizocoi* × *A. correntina* | | 2 | | 2 |
| | *A. batizocoi* × *A. duranensis* | 1 | 2 (27) | (484) | 3 (511) |
| | *A. correntina* × *A. batizocoi* | 2 | 2 (1) | 11 | 15 (1) |
| | *A. correntina* × *A. chacoense* | | 4 | | 4 |
| | *A. correntina* × (*A. chacoense* × *A. cardenasii*) | 1 | | | 1 |
| | *A. correntina* × *A. villosa* | 2 | 2 | 1 | 5 |
| | *A. duranensis* × *A. cardenasii* | | 1 | | 1 |
| | *A. duranensis* × *A. chacoense* | 1 | 3 (1) | | 4 (1) |
| | *A. duranensis* × *A.* sp GKP 10038 | | 1 | | 1 |
| | *A. villosa* × *A. batizocoi* | 2 | 5 (18) | (1) | 7 (19) |
| | *A. villosa* × *A.* sp HLK 410 | 2 | | | 2 |
| | *A. villosa* × *A. duranensis* | | 1 | 3 | 4 |
| | *A.* sp GKP 10038 × *A.* sp HLK 410 | 1 | (1) | 16 | 17 (1) |
| | *A.* sp HLK 410 × *A. chacoense* | | 4 | | 4 |
| | *A.* sp HLK 410 × *A.* sp GKP 10038 | | 1 | | 1 |
| | Total | 41 (45) | 48 (297) | 43 (526) | 132 (868) |

1. Figures in parentheses are number of plants selected.

ces the number of backcross cycles required for the production of stable *A. hypogaea*-like tetraploid derivatives compared to the number of backcross cycles required from hexaploids.

Backcrossing the progenies from triploids with *A. hypogaea* has resulted in the production of 17 stable *A. hypogaea*-like tetraploids involving *A. chacoense* and *A. cardenasii*. Rust-resistant segregants were selected by field screening of these tetraploid derivatives (Table 2). Certain selections were also found resistant to late leaf spot (*Phaeoisariopsis personata* (Berk. & Curt.) v. Arx.)

The gametic (pollen) fertility of these triploids also indicates that they can be backcrossed with *A. hypogaea* to produce *A. hypogaea*-like tetraploid derivatives, as has been done in wheat (Kerber and Dyck 1973).

## Crosses between tetraploid *A. hypogaea* and synthetic tetraploids

The difference in ploidy levels between diploid wild *Arachis* species and tetraploid cultivated *A. hypogaea* restricts sexual genetic introgression, because of the low fertility of the triploid hybrids. Raising the ploidy level of the diploid species to that of *A. hypogaea* and then crossing with *A. hypogaea* at the tetraploid level is a useful option for gene transfer, as in cotton, potato and tobacco (Knight 1953, 1954, Wangenheim 1955, Stavely et al. 1973).

**Use of autotetraploids of diploid species.** The autotetraploids of diploid species not only facilitate crossing at the same ploidy level as the cultivated species, but also provide an additional dose of the

desired traits and may also permit a forced homoeologous intergenomic (A-B) pairing to effect genetic alteration in the non-homologous genome of *A. hypogaea*.

Autotetraploids of 6 wild diploid species have been crossed with *A. hypogaea*. The $F_1$ plants were vigorous, and resembled *A. hypogaea*. These hybrids can be either AAAB or ABBB depending on whether an AA or BB species autotetraploid was crossed with *A. hypogaea*. Homology of a genome of *A. hypogaea* with a diploid species can result in the formation of bivalents due to intragenomic (A-A or B-B) pairing. Homoeology with the other genome of *A. hypogaea* results in the formation of more than 10 bivalents (11.2 to 14.1) due to intergenomic (A-B) pairing or multivalents (1.8 to 2.5) due to intra- and intergenomic (A-A-B; A-B-B; A-A-A-B; A-B-B-B) pairing (Singh 1985). The hybrids between *A. hypogaea* and the autotetraploids of section *Arachis* species were resistant to rust (Singh et al. 1984c) and were backcrossed with *A. hypogaea*. Eleven stable *A. hypogaea*-like derivatives have been produced. Of these, six were derived from the hybrids between *A. hypogaea* and autotetraploid *A. batizocoi*. These have been screened during rainy seasons. Several rust-resistant segregants have been selected (Table 2), and are being advanced.

**Use of amphidiploids of diploid species.** The presence of two homoeologous genomes, "A" and "B", among diploid wild *Arachis* species, and the occurrence of both genomes in *A. hypogaea*, suggest that hybridization at the same ploidy level between tetraploid *A. hypogaea* and synthetic amphidiploids of diploid wild species can be a promising approach to provide a high degree of recombination and highly fertile hybrids.

Amphidiploids were produced from sterile or partially sterile interspecific hybrids, representing 34 combinations of the 8 diploid wild species of section *Arachis*. Of these, 22 (AABB and AAAA amphidiploids) have been crossed with *A. hypogaea*. All the $F_1$ hybrids between *A. hypogaea* and amphidiploids were resistant to rust. The hybrids between *A. hypogaea* and AABB amphidiploids had higher bivalent associations (14.4 to 16.4) and pollen and pod fertility, than the hybrids between *A. hypogaea* and AAAA amphidiploids (10.8 to 15.0). In *A. hypogaea* × AAAA amphidiploid hybrids (AAAB), homoeology between A and B genome results in the formation of more than 10 bivalents and a few multivalents as a result of intra and intergenomic pairing. Subsequent backcrossing with *A. hypogaea*, sometimes with intervening selfing generations, have resulted in the production of 72 stable *A. hypogaea*-like tetraploid progenies. These tetraploid progenies were screened for resistance to rust and late leaf spot during rainy seasons. In derivatives *A. hypogaea* × (*A. batizocoi* × *A. duranensis* amphidiploid) and *A. hypogaea* × (*A. villosa* × *A. batizocoi* amphidiploid) hybrid fertility has enabled the advancement of the progenies into subsequent generations even without backcrossing. Resistant segregants have been selected from these progenies (Table 2).

A large number of *A. hypogaea*-like interspecific derivatives incorporating genes from diploid wild *Arachis* species have been produced that confer a high degree of resistance against rust. The most advanced lines involve a perennial species such as *A. cardenasii*, (resistant to both rust and late leaf spot) and three annual species, *A. batizocoi*, *A.* species GKP 10038, and *A. duranensis* (resistant to rust and some groundnut pests). A number of been evaluated in replicated trials characters and for rust resistance (T quently several lines resistant to rust ior agronomic traits, e.g., ICG(C) ICG(C) 8, and ICG(C) 12, are being t many locations in the All Indi Research Project for Oil Seeds (AI In addition, a large number of deriv four other species that are resistant t other pathogens and pests are bein

## Genetics of rust resistance

Preliminary investigations on the ir resistance derived from diploid w shown that the $F_1$ hybrids between diploid species, their autotetraploi ploids, are resistant to rust, suggest tance is governed by a partially (Singh et al. 1984c). Identification loci is in progress. The interspecific *A. hypogaea*-like derivatives with wild species have been crossed susceptible and rust-resistant *A. hy*

*A. hypogaea* rust-resistant germplasm lines have also been crossed with susceptible cultivars. These studies should reveal the inheritance pattern of the two resistances and their relationships. These results have generated a great interest in the utilization of wild species as sources of rust resistance and in combining resistance of wild species with that of *A. hypogaea*.

**Table 3. Rust resistance (1-9 scale) and other agronomic characters of some of the advanced interspecific derivatives[1] (8 × 8 triple lattice, plot size 10.8 m²), ICRISAT Center, 1984 rainy season.**

| Code | Pedigree | Rust score | Yield (kg ha⁻¹) | Haulm weight (kg ha⁻¹) | Shelling % |
|---|---|---|---|---|---|
| CS 36 | *A. hypogaea* × *A. cardenasii* | 1.4 | 4470 | 8690 | 71 |
| 2403 | *A. hypogaea* × *A. cardenasii* | 1.6 | 3600 | 6150 | 71 |
| 2404/4 | *A. hypogaea* × *A. cardenasii* | 1.6 | 4770 | 7190 | 70 |
| CS 7 | *A. hypogaea* × *A. cardenasii* | 1.7 | 4280 | 8580 | 75 |
| CS 33 | *A. hypogaea* × *A. cardenasii* | 1.7 | 4200 | 9880 | 74 |
| 2245 | *A. hypogaea* × *A. cardenasii* | 1.9 | 4050 | 7410 | 69 |
| CS 2 | (*A. batizocoi* × *Arachis* sp GKP 10038) × *A. hypogaea* | 1.7 | 3510 | 5590 | 61 |
| CS 19 | *A. hypogaea* × (*A. batizocoi* × *Arachis* sp GKP 10038) | 1.7 | 2730 | 4840 | 66 |
| Checks | | | | | |
| Robut 3301 | | 8.9 | 2880 | 3600 | 54 |
| TMV 2 | | 8.9 | 2170 | 4940 | 40 |
| EC 76446 (292) | | 2.8 | 3620 | 5840 | 54 |
| NC Ac 17133-RF | | 7.2 | 4410 | 5000 | 61 |
| | CV (%) | 27 | 15 | 18 | 16 |
| | SE | ±0.7 | ±314.4 | ±764.7 | ±2.9 |

1 All the derivatives are virginia-bunch type

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