The Value of Diploid Peanut Relatives for Breeding and Genomics

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ABSTRACT

Collection, evaluation, and introgression research has been conducted with *Arachis* species for more than 60 years. Eighty species in the genus have been described and additional species will be named in the future. Extremely high levels of disease and insect resistances to immunity have been observed in many species of the genus as compared to the cultivated peanut, which makes them extremely important for crop improvement. Many thousands of interspecific hybrids have been produced in the genus, but introgression has been slow because of genomic incompatibilities and sterility of hybrids. Genomics research was initiated during the late 1980s to characterize species relationships and investigate more efficient methods to introgress genes from wild species to *A. hypogaea.* Relatively low density genetic maps have been created from inter- and intra-specific crosses, several of which have placed disease resistance genes into limited linkage groups. Of particular interest is associating molecular markers with traits of interest to enhance breeding for disease and insect resistances. Only recently have sufficiently large numbers of markers become available to effectively conduct marker assisted breeding in peanut. Future analyses of the diploid ancestors of the cultivated peanut, *A. duranensis* and *A. ipaensis*, will allow more detailed characterization of peanut genetics and the effects of *Arachis* species alleles on agronomic traits. Extensive efforts are being made to create populations for genomic analyses of peanut, and introgression of genes from wild to cultivated genotypes should become more efficient in the near future.

Key Words: *Arachis*, wild species, molecular genetics, introgression, peanut, genomics.

Wild species of *Arachis* are native to a large region of South America in tropical and subtropical areas. Eighty species have been named (Krapovickas and Gregory, 1994; Valls and Simpson, 2005) and others will likely be described from uncollected regions of South America. Wild peanut species have been important to man since before the cultivated peanut evolved, and they are still used as forages, for their esthetic value, and as sources of germplasm for crop improvement. For example, *A. glabrata* and *A. pintoi* are utilized for grazing (Mathews *et al.*, 2000; Hernandez-Garay *et al.*, 2004) and *A. repens* is used as a ground cover in residential areas and roadsides in tropical regions. Several species have been consumed for their seeds, but only *A. hypogaea* is economically important today as a human food source. The primary interest in wild species of *Arachis* for the past 50–60 years has been as sources of disease and insect resistances for crop improvement. Several species, including ones that will hybridize with the cultivated peanut, have extremely high levels of disease resistance and a few (e.g., *A. diogoi*) have virus resistance genes that are not present in the cultivated gene pool.

Cytology and Evolution of *Arachis*

Arachis hypogaea is an allotetraploid ($2n = 4x = 40$) with a very large and complex genome. Chromosome behavior and morphology were reported by Husted (1936) and Stalker and Dalmacio (1986). Gregory (1946) reported the first chromosome number of a wild species (*A. glabrata*) as $2n = 4x = 40$ and a year later Mendes (1947) reported diploid species ($2n = 2x = 20$). Not until 2005 were species with 18 chromosomes discovered (Penaloza and Valls, 2005). Most species in the genus are diploid, but tetraploids exist in sections *Arachis* and *Rhizomatosae*; and several species in sections *Arachis* and *Erectoides* are aneuploid ($2n = 2x = 18$) (Table 1). Polyploidy evolved independently in sections *Arachis* and *Rhizomatosae* (Smartt and Stalker, 1982); and Nelson *et al.* (2006) concluded that polyploidy evolved multiple times within section *Rhizomatosae*. Tallury *et al.* (2005) reported molecular evidence that the diploid section *Rhizomatosae* species (only one known) did not give rise to the tetraploids. Because *A. glabrata* will hybridize with species of both sections *Erectoides* and *Arachis*, Smartt and Stalker (1982) concluded that two diploids from sections *Erectoides* and *Arachis* likely hybridized and spontaneously doubled in chromosome number, evolving into the tetraploid species of section *Rhizomatosae.*

Krapovickas and Gregory (1994) concluded that *Erectoides*, *Extranervosae*, *Heteranthae*, *Trierectoides*

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and *Triseminatae* are "older" sections, while *Arachis*, *Caulorrhizae*, *Procumbentes*, and *Rhizomatosae* are more "recent" in origin. The largest subgeneric group is section *Arachis*, which includes the cultivated species, one other tetraploid (*A. monticola*), 26 diploid ($2n = 2x = 20$), and three aneuploid ($2n = 2x = 18$) species. These species are highly variable, and especially the annual species are continuing to differentiate. For example, *A. duranensis* has northern and southern groups which can be distinguished morphologically and with molecular markers (Stalker *et al.*, 1995).

The first published attempt at interspecific hybridization in the genus was between the two tetraploids *A. hypogaea* (section *Arachis*) and *A. glabrata* (section *Rhizomatosae*) (Hull and Carver, 1938), but no hybrids were obtained. Krapovickas and Rigoni (1951) later hybridized *A. hypogaea* with *A. villosa* var. *correntina* and the F_1s were vigorous, but sterile. The cultivated peanut has since been hybridized with most species in section *Arachis*. Similar to other genera which have a polyploid series, crosses are usually more successful when the species at the higher ploidy level (in this case *A. hypogaea*) is used as the female parent. Triploid interspecific hybrids usually have 10 bivalents and10 univalents, but trivalents are also observed in pollen mother cells which indicates that some chromosome homology exists between the A and B genomes (Stalker, 1985).

Early cytological research identified one pair of significantly smaller chromosomes (termed 'A' chromosome) in species of section *Arachis* and a unique chromosome pair that had a large secondary constriction (termed 'B' chromosome) in the species *A. batizocoi* (Husted, 1936). Hybridization between diploid species was first reported between *A. duranensis* and *A. villosa* var. *correntina* (Raman and Kesavan, 1962) and meiosis was regular. Later studies indicated that hybrids between species having the small chromosome pair were partially to fully fertile and most will produce F_2 seeds; however, hybrids between the species with the small chromosome and *A. batizocoi* are sterile (Stalker and Simpson, 1995). Thus, the terminology 'A' and 'B' genome has been used in peanut to describe the two cytological groups. Because the cultivated peanut has one pair of smaller chromosomes and one pair of chromosomes with a large secondary constriction, it was described as an allotetraploid with AABB genomes. Stalker *et al.* (1991) crossed a series of species designated as having the A genome with *A. batizocoi* and found that F_1s had many univalents, and bivalents were loosely associated. Hybrids between either A or B genome species with *A. glandulifera* (D genome) also have many univalents and are sterile (Stalker *et al.*, 1991). Thus, there is a considerable amount of cytological differentiation between the three genomes.

Gregory and Gregory (1979) conducted an extensive hybridization program using 91 *Arachis* collections and reported cross-compatibility relationships among species of the genus. Their results indicated that hybridization between species within the same section is more successful than crosses between sections; F_1s of intersectional crosses were highly sterile. To overcome crossing barriers, complex hybrids have been attempted (Gregory and Gregory, 1979; Stalker, 1981), but fertility has not been restored. Thus, introgression from wild *Arachis* species to *A. hypogaea* by conventional hybridization is believed to be restricted to members of section *Arachis.* Even within section *Arachis* there are many difficulties encountered to obtain hybrids due to genomic and/or ploidy differences.

Based on cross-compatibility data, Smartt and Stalker (1982) and Stalker (1991) concluded that genomic groups have evolved in the genus which mostly follow sectional designations (Am – *Ambinervosae*, T – *Triseminatae*, C – *Caulorrhizae*, EX – *Extranervosae*, and E – *Erectoides*, R – *Rhizomatosae*, and A, B and D – *Arachis*). The B genome was recently divided into B, F, and K genomes by Seijo *et al.* (2004) and Robledo and Seijo (2010). Based on rDNA loci and chromosomes with centromeric heterochromatin, Robledo *et al.* (2009) described three karyotypic subgroups within the A genome and grouped the cultivated peanut with *A. duranensis*, *A. villosa*, *A. schininii,* and *A. correntina*. Other studies support placing *A. hypogaea* closely with *A. duranensis* (Moretzsohn *et al.*, 2004; Milla *et al.*, 2005a; Bravo *et al.*, 2006; Koppolu *et al.*, 2010; Calbrix *et al.*, 2012). The chromosomes of B genome species are karyologically more diverse than those with an A genome (Fernandez and Krapovickas, 1994; Seijo *et al.*, 2004). The B genome species (as opposed to the F and K genomes) does not have centromeric heterochromatin and includes *A. ipaensis* (the B component of *A. hypogaea*), *A. magna, A. gregoryi, A. valida,* and *A. williamsii* (Seijo *et al.*, 2004; Robledo and Seijo, 2010). The D genome species *A. glandulifera* is more distantly related to *A. hypogaea* than other species of section *Arachis.* Also, molecular analysis has indicated that the aneuploids in section *Arachis* are more closely related to the B (now classified as the B, F, and K genomes) and D genome species than to A-genome species (Tallury *et al.*, 2005). Evolution is apparently continuing in section *Arachis* at a rapid pace and multiple translocations have been observed in diploid accessions of *A. duranensis* (Stalker *et al.*,

Table 1. *Arachis* species identities*.

Section and Species	2n	Type specimen		
		Genome	Collector[a]	No.
Section *Arachis*				
A. batizocoi Krapov. & W.C. Gregory	20	K	K	9505
A. benensis Krapov., W.C. Gregory & C.E. Simpson	20	F	KGSPSc	35005
A. cardenasii Krapov. & W.C. Gregory	20	A	KSSc	36015
A. correntina (Burkart) Krapov. & W.C. Gregory	20	A	Clos	5930
A. cruziana Krapov., W.C. Gregory & C.E. Simpson	20	K	KSSc	36024
A. decora Krapov., W.C. Gregory & Valls	18	–	VSW	9955
A. diogoi Hoehne	20	A	Diogo	317
A. duranensis Krapov. & W.C. Gregory	20	A	K	8010
A. glandulifera Stalker	20	D	St	90–40
A. gregoryi C.E. Simpson, Krapov, & Valls	20	B	VS	14960
A. helodes Martius ex Krapov. & Rigoni	20	A	Manso	588
A. herzogii Krapov., W.C. Gregory and C.E. Simpson	20	A	KSSc	36030
A. hoehnei Krapov. & W.C. Gregory	20	A	KG	30006
A. hypogaea L.	40	AB	Linn.	9091
A. ipaensis Krapov., W.C. Gregory	20	B	KMrFr	19455
A. kempff-mercadoi Krapov., W.C. Gregory & C.E. Simpson	20	A	KGPBSSc	30085
A. krapovickasii C.E. Simpson, D.E. Williams, Valls & I.G. Vargas	20	K	WiSVa	1291
A. kuhlmannii Krapov. & W.C. Gregory	20	A	KG	30034
A. linearifolia Valls, Krapov, & C.E. Simpson	20	A	VPoBi	9401
A. magna Krapov., W.C. Gregory & C.E. Simpson	20	B	KGSSc	30097
A. microsperma Krapov., W.C. Gregory & Valls	20	A	VKRSv	7681
A. monticola Krapov. & Rigoni	40	AB	K	8012
A. palustris Krapov., W.C. Gregory & Valls	18	–	VKRSv	6536
A. praecox Krapov., W.C. Gregory & Valls	18	–	VS	6416
A. schininii Valls & C.E. Simpson	20	A	VSW	9923
A. simpsonii Krapov. & W.C. Gregory	20	A	KSSc	36009
A. stenosperma Krapov. & W.C. Gregory	20	A	HLK	410
A. trinitensis Krapov. & W.C. Gregory	20	F	Wi	866
A. valida Krapov. & W.C. Gregory	20	B	KG	30011
A. villosa Benth.	20	A	Tweedi	1837
A. williamsii Krapov. & W.C. Gregory	20	B	WiCl	1118
Section *Caulorrhizae*				
A. pintoi Krapov. & W.C. Gregory	20	C	GK	12787
A. repens Handro	20	C	Otero	2999
Section Erectoides				
A. archeri Krapov. & W.C. Gregory	20	E	KCr	34340
A. benthamii Handro	20	E	Handro	682
A. brevipetiolata Krapov. & W.C. Gregory	20	E	GKP	10138
A. cryptopotamica Krapov. & W.C. Gregory	20	E	KG	30026
A. douradiana Krapov. & W.C. Gregory	20	E	GK	10556
A. gracilis Krapov. & W.C. Gregory	20	E	GKP	9788
A. hatschbachii Krapov. & W.C. Gregory	20	E	GKP	9848
A. hermannii Krapov. & W.C. Gregory	20	E	GKP	9841
A. major Krapov. & W.C. Gregory	20	E	Otero	423
A. martii Handro	20	E	Otero	174
A. oteroi Krapov. & W.C. Gregory	20	E	Otero	194
A. paraguariensis				
ssp. *paraguariensis* Chodat & Hassl.	20	E	Hassler	6358
ssp. *capibarensis* Krapov. & W.C. Gregory	20	E	HLKHe	565
A. porphyrocalyx Valls & C.E. Simpson	18	E	VSPtWiSv	7307
A. stenophylla Krapov. & W.C. Gregory	20	E	KHe	572
Section Extranervosae				
A. burchellii Krapov. & W.C. Gregory	20	EX	Irwin *et al.*	21163
A. lutescens Krapov. & Rigoni	20	EX	Stephens	255
A. macedoi Krapov. & W.C. Gregory	20	EX	GKP	10127

Table 1. Continued.

Section and Species	2n	Type specimen		
		Genome	Collector[a]	No.
A. marginata Gardner	20	EX	Gardner	3103
A. pietrarellii Krapov. & W.C. Gregory	20	EX	GKP	9923
A. prostrata Benth.	20	EX	Pohl	1836
A. retusa Krapov., W.C. Gregory & Valls	20	EX	VPtSv	12883
A. setinervosa Krapov. & W.C. Gregory	20	EX	Eiten & Eiten	9904
A. submarginata Valls, Krapov. & C.E. Simpson	20	EX	SiW	3729
A. villosulicarpa Hoehne	20	EX	Gehrt	SP47535
Section Heteranthae				
A. dardani Krapov. & W.C. Gregory	20	H	GK	12946
A. giacomettii Krapov., W.C. Gregory, Valls & C.E. Simpson	20	H	VPzV1W	13202
A. interrupta Valls & C.E. Simpson	20	H	VPiFaSv	13082
A. pusilla Benth.	20	H	Blanchet	2669
A. seridoensis Valls, C.E. Simpson, Krapov, & R. Veiga	20	H	VRSv	10969
A. sylvestris (A. Chev.) A. Chev.	20	H	Chevalier	486
Section Procumbentes				
A. appressipila Krapov. & W.C. Gregory	20	PR	GKP	9990
A. chiquitana Krapov., W.C. Gregory & C.E. Simpson	20	PR	KSSc	36027
A. hassleri Valls & C.E. Simpson	20	PR	SvPiHn	3818
A. kretschmeri Krapov. & W.C. Gregory	20	PR	KrRa	2273
A. lignosa (Chodat and Hassl.) Krapov. & W.C. Gregory	20	PR	Hassler	7476
A. matiensis Krapov., W.C. Gregory & C.E. Simpson	20	PR	KSSc	36014
A. pflugeae C.E. Simpson, Krapov, & Valls	20	PR	VOlSiS	13589
A. rigonii Krapov. & W.C. Gregory	20	PR	K	9459
A. subcoriacea Krapov. & W.C. Gregory	20	PR	KG	30037
A. vallsii Krapov. & W.C. Gregory	20	PR	VRGeSv	7635
Section Rhizomatosae				
Ser. *Prorhizomatosae*				
A. burkartii Handro	20	R_1	Archer	4439
Ser. *Rhizomatosae*				
A. glabrata	40			
var. *glabrata* Benth.		R_2	Riedel	1837
var. *hagenbeckii*[c] Benth. (Harms ex. Kuntze) F.J. Herm.		R_2	Hagenbeck	2255
A. nitida Valls, Krapov, & C.E. Simpson	40	R_2	VMPiW	14040
A. pseudovillosa (Chodat & Hassl.) Krapov. & W.C. Gregory	40	R_2	Hassler	5069
Section Trierectoides				
A. guaranitica Chodat & Hassl.	20	TE	Hassler	4975
A. tuberosa Bong. ex Benth	20	TE	Riedel	605
Section Triseminatae				
A. triseminata Krapov. & W.C. Gregory	20	T	GK	12881

[a]Collectors: B = Banks, Bi = Bianchetti, Cl = Claure, Cr =Cristobal, Fa = Faraco, Fr = Fernandez, G = Gregory, Ge = Gerin, H = Hammons, He = Hemsy, Hy = Hn = Heyn, K = Krapovickas, Kr = Kretchmere, L = Langford, M = Moss, Mr = Mroginski, Ol = Oliveira, P = Pietrarelli, Pi = Pizarro, Po = Pott, Pt = Pittman, R = Rao, Ra = Raymon, S = Simpson, Sc = Schinini, Si = Singh, St = Stalker, Sv = Silva, V = Valls, Va = Vargas, Ve = Veiga, Vl = Valente, W = Werneck, and Wi = Williams. Others = as listed.

*From Krapovickas, A., and W.C. Gregory. 1994. Taxonomy of the genus *Arachis* (Leguminosae). Bonplandia 8:1–186; and Valls, J.F.M., and C.E. Simpson. 2005. New species of *Arachis* (Leguminosae) from Brazil, Paraguay and Bolivia. Bonplandia 4:35–63.

1995) and *A. batizocoi* (Stalker *et al.*, 1991; Guo *et al.*, 2012). At least five different secondary constriction types have been observed in *A. hypogaea*, which were most likely from translocation events (Stalker and Dalmacio, 1986), and this species is also evolving cytologically.

Analyses of species outside section *Arachis* have been infrequent. Stalker (1985) reported that the two diploid section *Erectoides* species *A. rigonii* × *A. paraguariensis* hybrids had many univalents and Krapovickas and Gregory (1994) later placed these species in different sections. Intersectional hybrids also were reported by Mallikarjuna (2005) who used in vitro techniques to obtain F_1s.

In addition to morphological and cross-compatibility studies, molecular investigations have

been used to better clarify the phylogenetic relationships among peanut species. Most of these investigations have involved species in section *Arachis* because of their close association with *A. hypogaea*. Many molecular systems have been utilized, including isozymes (Lu and Pickersgill, 1993; Stalker *et al.*, 1994), seed storage proteins (Singh *et al.*, 1991; Bianchi-Hall *et al.*, 1993; Liang *et al.*, 2006), Restriction Fragment Length Polymorphisms (RFLPs) (Kochert *et al.*, 1991; Paik-Ro *et al.*, 1992), Amplified Fragment Length Polymorphisms (AFLPs) (Milla-Lewis *et al.*, 2005b); Simple Sequence Repeats (SSRs) (Hopkins *et al.*, 1999; He *et al.*, 2005; Hong *et al.*, 2010; Guo *et al.,* 2012; Nagy *et al.*, 2012). Randomly Amplified Polymorphic DNA (RAPDS) (Halward *et al.*, 1992; Lanham *et al.*, 1992; Hilu and Stalker, 1995), and *in situ* hybridization (Raina and Mukai, 1999; Seijo *et al.*, 2004). All of the studies have indicated that the cultivated peanut has significantly less molecular variation than diploid species, which supports the hypothesis that *A. hypogaea* originated from a single hybridization event. Additionally, there has been little or no apparent introgression from diploid species to *A. hypogaea* since its inception (Kochert *et al.*, 1996).

As opposed to the cultivated species, large amounts of molecular variation have been documented among wild species of the genus. Although there have been differences observed among marker systems regarding species relationships, and there remain questions about species positions in sectional groupings (Friend *et al.*, 2010), the molecular data generally fits the sectional relationship model proposed by Krapovickas and Gregory (1994). For example, Hoshino *et al.* (2006) used microsatellites to evaluate species in the nine peanut sections, and while most species grouped as expected, several species in the *Procumbentes* grouped with species from section *Erectoides*, and others clustered into sections *Trierectoides* and *Heteranthae*. Galgaro *et al.* (1998) also indicated that species in section *Heteranthae* did not group together. Friend *et al.* (2010) conducted a more comprehensive investigation of *Arachis* species and found that sections *Extranervosae*, *Triseminatae*, and *Caulorrhizae* each separated into distinct groups based on trnT-trnF sequences; but species in sections *Erectoides*, *Heteranthae*, *Procumbentes*, *Rhizomatosae*, and *Trierectoides* formed a major lineage. Species in section *Arachis* grouped into two major clades, with (i) the B (renamed the B, F, and K genomes), the D genome species, and 18-chromsome aneuploids being in one group and (ii) the A genome species being in the second group.

Desirable Traits in *Arachis* Species for Crop Improvement

As compared to lines of *A. hypogaea*, extremely high levels of resistance have been identified in *Arachis* species for many important peanut pathogens (Stalker and Moss, 1987; Dwivedi *et al.,* 2007) (Table 2). Mehan *et al.* (1986) identified four *Arachis* species that are resistant to aflatoxin production and Xue *et al*. (2004) found pre-harvest aflatoxin resistance in *A. duranensis.* Subrahmanyam *et al.* (2001) found 12 *Arachis* species accessions to be immune to groundnut rosette virus as opposed to none in the cultivated species. *Arachis diogoi* was the only species identified with no infection to peanut bud necrosis virus (Subrahmanyam *et al.*, 1985b); this species is also the only one with immunity to tomato spotted wilt virus (Lyerly *et al.*, 2002). None of 7,000 cultivated lines screened for peanut clump virus (PCV) had useful resistance whereas four *Arachis* accessions of *A. kuhlmannii*, *A. duranensis*, and *A. ipaensis* were immune (Dwivedi *et al.,* 2007). ICRISAT scientists also have evaluated *Arachis* species for late and early leaf spots and they identified highly resistant materials (Dwivedi *et al.,* 2007). Many *Arachis* species also have been evaluated for insect pests and extremely high levels of resistance observed as compared to the cultivated peanut (Table 3).

Introgressing Genes from *Arachis* Species to *A. hypogaea*

Because the domesticated peanut is an allotetraploid with two genomes and the species being utilized for introgression are diploids, sterility barriers result from ploidy differences and genomic incompatibilities between the species. Traits of interest from *Arachis* species have been difficult to follow in progenies of interspecific hybrids and disease and insect resistances in 40-chromosome progenies have been lost because of low population sizes and inadequate methods for selection in single plants. Utilizing molecular markers associated with traits of interest may help overcome many of these problems, but unfortunately, few molecular markers have been available to enhance selection efficiency. Molecular research to date indicates that introgression from *Arachis* species to *A. hypogaea* appears to be in large blocks (Garcia *et al.*, 1995; Nagy *et al.*, 2010) rather than as single genes or small chromosome segments. Thus, linkage drag of undesirable traits can restrict the use of genetic resources, and molecular markers also have great potential for selection against these characters.

The first peanut cultivars released from interspecific hybridization were from a cross between *A. hypogaea* and the second tetraploid species in

section *Arachis* (*A. monticola* Krapov. & Rigoni). Biologically, *A. monticola* could be considered a weedy subspecies of *A. hypogaea*. Spancross was released by Hammons (1970) and Tamnut 74 was later released by Simpson and Smith (1975). Neither of these cultivars had phenotypic traits that could be identified as being derived from the wild species, which is not surprising because *A. monticola* has most of the same disease and insect problems as found in *A. hypogaea*.

Several methods have been utilized to create populations of fertile *A. hypogaea* interspecific hybrids and to restore plants to the tetraploid level. First, crosses can be made by hybridizing *A. hypogaea* with diploids to produce triploid ($3x = 30$) F_1s, after which cuttings can be colchicine-treated to restore fertility at the hexaploid ($6x = 60$) level. Many triploids will also produce a few seeds through fusion of unreduced gametes, especially if they are left in the field or grown in the greenhouse for long periods of time (Singsit and Ozias-Akins, 1992). Backcrossing the hexaploids with *A. hypogaea* results in pentaploids ($5x = 50$) that are usually vigorous, but only partially fertile. Additionally, they produce few flowers and are difficult to use in crossing programs; but they sometimes yield a few seeds when selfed and the ploidy level stabilizes in progenies at the tetraploid level. A major problem with this scheme has been the few seeds produced at the hexaploid and pentaploid levels, and the lack of selection methods for traits of interest during the semi-sterile generations has resulted in many hundreds of tetraploid lines without traits of interest for crop improvement. To date, no useful germplasm has resulted from backcrossing hexaploids with *A. hypogaea*. Although backcrossing hexaploids with diploids will theoretically drop the chromosome number to the tetraploid level in one generation, these $6x \times 2x$ crosses (or reciprocals) have not produced viable progenies.

An alternative method to backcrossing hexaploids with the cultivated species is to allow $6x$ plants to self-pollinate and, by selecting fertile progenies, a few plants may spontaneously lose chromosomes and stabilize at the 40-chromosome level. The loss of chromosomes appears to be infrequent and random, but the advantage of this procedure is associating chromosomes in different species at a high ploidy level which can increase the frequency of recombination. For example, *A. hypogaea* × *A. cardenasii* hexaploids were selfed for five generations after which they produced 40-chromosome progenies that were highly variable for seed size, color and other morphological traits (Company *et al.*, 1982). Garcia *et al.* (1995) analyzed introgression from *A. cardenasii* to *A. hypogaea* with RFLPs and found wild species-specific markers on 10 of 11 linkage groups on the diploid RFLP map developed by Halward *et al.* (1993). Most of the introgression (88%) was apparently in the A genome of *A. hypogaea*, with the remaining 12% in the B genome. Germplasm lines have been released from this cross with resistance to early leaf spot, nematodes, and several insect pests (Stalker *et al.*, 2002a, b; Stalker and Lynch, 2002; Isleib *et al.*, 2006). The cultivar Bailey was released after utilizing these lines as sources of multiple disease resistances (Isleib *et al.*, 2010).

A second method to introgress germplasm from diploid species to *A. hypogaea* is to first double the chromosome number of the diploid species to the tetraploid level. This method has the advantage of avoiding several generations of mostly sterile hybrids and recovering tetraploids and is much faster than by going through the triploid – hexaploid procedure; but autotetraploids generally have low vigor, and when annual species are used as parents, they are short lived. Ideally, A and B genome species would be hybridized at the diploid level and then the chromosomes doubled to produce AABB genome allopolyploids to be crossed with the cultivated species. However, chromosome doubling of the sterile AB genome diploids can be highly problematic. Examples of success with this methodology are TXAg-6 and TX Ag-7 (Simpson *et al.*, 1993) which originated from the complex hybrid [*A. batizocoi* (B genome) × (*A. cardenasii* (A genome) × *A. diogoi* (A genome))]^{4x}. TxAG-6 had very good nematode resistance, but also significant linkage drag which resulted in low yields and poor seed and pod quality. RFLP markers linked to the nematode gene conferring resistance were used to select favorable genotypes (Church *et al.,* 2000). The nematode-resistant cultivars COAN (Simpson and Starr, 2001) and NemaTAM (Simpson *et al.*, 2003) were released after introgressing genes from TXAg-6 to *A. hypogaea*. By using SSR markers, Nagy *et al.* (2010) showed that recombination was greatly reduced in the chromosome region where the nematode-resistance gene is located because a large introgressed segment from the wild species comprised a third to half of a chromosome. This germplasm was used in the development of the nematode-resistant cultivar Tifguard (Holbrook *et al.*, 2008), which also has good resistance to tomato spotted wilt virus.

Tracking introgression from *Arachis* species to cultivated peanut would greatly facilitate selection of desirable progenies in advanced generations of interspecific hybrids. Molecular markers offer a method for following introgression from *Arachis*

Table 2. *Arachis* species resistant to peanut diseases[a].

Trait	Species	Citation
Aflatoxin – seed colonization and production		
	A. cardenasii	Nigam *et al.* (1991); Xue *et al.* (2004)
	A. duranensis	Nigam *et al.* (1991); Xue *et al.* (2004)
Cylindrocladium black rot (*Cylindrocladium parasiticum*)		
	A. cardenasii	Tallury *et al.* (2011)
	A. correntina	Tallury *et al.* (2011)
	A cruziana	Tallury *et al.* (2011)
	A. helodes	Tallury *et al.* (2011)
	A. kempff-mercades	Tallury *et al.* (2011)
	A. kuhlmannii	Tallury *et al.* (2011)
	A. microsperma	Tallury *et al.* (2011)
	A. monticola	Fitzner *et al*. (1985)
	A. valida	Tallury *et al.* (2011)
	A. williamsii	Tallury *et al.* (2011)
Early leaf spot (*Cercospora arachidicola*)		
	A. appressipila	ICRISAT (2000)
	A. batizocoi	Stalker (1992)
	A. cardenasii	Abdou *et al.* (1974); Nigam (1991); Stalker (1992); Stalker *et al.* (2002a, b);
	A. diogoi[b]	Abdou *et al.* (1974); Subranmanyam *et al.* (1980); Nigam *et al.* (1991)
	A. dardani	ICRISAT (2000)
	A. glabrata	Gibbons and Bailey (1967)
	A. hagenbeckii	Gibbons and Bailey (1967)
	A. kempff-mercadoi	Mallikarjuna *et al.* (2004)
	A. magna	ICRISAT (2000)
	A. monticola	Subrahmanyam *et al.* (1985c)
	A. pusilla	ICRISAT (2000)
	A. repens	Gibbons and Bailey (1967); Abdou *et al.* (1974)
	A. stenosperma	Kolawole (1976); Sharief *et al.* (1978); Subranmanyam *et al.* (1980); Nigam (1991)
	A. sylvestris	ICRISAT (2000)
	A. triseminata	ICRISAT (2000)
	A. valida	ICRISAT (2000)
	A. villosulicarpa	Abdou *et al.* (1974)
	A. sp. 10596	Subranmanyam *et al.* (1980)
Groundnut Rosette Disease		
	A. appressipila	Subrahmanyam *et al.* (2001)
	A. cardenasii	Subrahmanyam *et al.* (2001)
	A. decora	Subrahmanyam *et al.* (2001)
	A. diogoi	Subrahmanyam *et al.* (2001)
	A. glabrata	Gibbons (1969)
	A. hagenbeckii	Gibbons (1969)
	A. hoehnei	Subrahmanyam *et al.* (2001)
	A. kretschmeri	Subrahmanyam *et al.* (2001)
	A. kuhlmannii	Subrahmanyam *et al.* (2001)
	A. pintoi	Subrahmanyam *et al.* (2001)
	A. repens	Gibbons (1969)
	A. stenosperma	Subrahmanyam *et al.* (2001)
	A. triseminata	Subrahmanyam *et al.* (2001)
	A. villosa	Subrahmanyam *et al.* (2001)
Late leaf spot (*Cercosporidium personatum*)		
	A. appressipila	Subrahmanyam *et al.* (1983, 1985a)
	A. batizocoi	Subrahmanyam *et al.* (1983, 1985a); Stalker (1992)
	A. benensis	Pande and Rao (2001)
	A. burkartii	Subrahmanyam *et al*. (1985a);
	A. cardenasii	Abdou *et al.* (1974); Subrahmanyam *et al.* (1983, 1985a) Nigam *et al.* (1991); Stalker (1992); Sharma *et al.* (2003)
	A. chiquitana	Pande and Rao (2001)
	A. decora	Pande and Rao (2001)
	A. diogoi	Abdou *et al.* (1974); Subrahmanyam *et al.* (1983, 1985a); Nigam *et al.* (1991)
	A. correntina	Subrahmanyam *et al.* (1983, 1985a)
	A. duranensis	Subrahmanyam *et al.* (1983, 1985a); Pande and Rao (2001) Sharma *et al.* (2003)
	A. glabrata	Subrahmanyam *et al.* (1983, 1985a)
	A. hagenbeckii	Subrahmanyam *et al.* (1983, 1985a)
	A. hoehnei	Pande and Rao (2001)
	A. ipaensis	Pande and Rao (2001)
	A. kempff-mercadoi	Sharma *et al.* (2003); Mallikarjuna *et al.* (2004)
	A. kretschmeri	Subrahmanyam *et al*. (1985a); Pande and Rao (2001)
	A. kuhlmannii	Pande and Rao (2001)
	A. magna	Subrahmanyam *et al.* (1985a); Pande and Rao (2001)
	A. monticola	Sharma *et al*. (2003)
	A. paraguariensis	Subrahmanyam *et al.* (1983, 1985a); Sharma *et al*. (2003)
	A. pseudovillosa	Subrahmanyam *et al*. (1985a)
	A. pusilla	Subrahmanyam *et al.* (1983, 1985a); Sharma *et al*. (2003)
	A. repens	Subrahmanyam *et al.* (1983, 1985a)
	A. stenosperma	Kolawole (1976); Subrahmanyam *et al.* (1983, 1985a); Nigam *et al.* (1991); Stalker (1992); Sharma *et al.* (2003)
	A. triseminata	Sharma et al (2003)
	A. valida	Pande and Rao (2001)
	A. villosa	Subrahmanyam *et al.* (1983, 1985a)
	A. villosulicarpa	Subrahmanyam *et al.* (1983, 1985a)
Peanut Bud Necrosis Virus		
	A. appressipila	Reddy *et al.* (2000)
	A. benensis	Reddy *et al.* (2000)
	A. cardenasii	Reddy *et al.* (2000)
	A. diogoi	Subrahmanyam *et al.* (1985b)
	A. triseminata	Reddy *et al.* (2000)
	A. villosa	Reddy *et al.* (2000)

Table 2. Continued.

Trait	Species	Citation
Peanut Mottle Virus (PMV)		
	A. cardenasii	Subrahmanyam *et al.* (1985b)
	A. diogoi	Subrahmanyam *et al.* (1985b); Nigam *et al.* (1991)
	A. correntina	Subrahmanyam *et al.* (1985b)
	A. glabrata	Demski and Sowell (1981)
	A. pusilla	Subrahmanyam *et al.* (1985b); Nigam *et al.* (1991)
	A. sp. AM 3867	Demski and Sowell (1981)
	A. sp. PI 172223	Demski and Sowell (1981)
	A. subcoriacea	Melouk *et al.* (1984)
Peanut Clump Virus		
	A. helodes	ICRISAT (1985)
Peanut Ringspot Virus		
	A. diogoi	Klesser (1965)
	A. glabrata	Klesser (1965)
	A. prostrata	Klesser (1965)
Peanut rust (*Puccinia arachidis*)		
	A. appressipila	Subrahmanyam *et al.* (1983, 1985a)
	A. batizocoi	Subrahmanyam *et al.* (1983, 1985a)
	A. cardenasii	Subrahmanyam *et al.* (1983, 1985a); Nigam *et al.* (1991); Subranmanyam *et al.* (1980); Sharma *et al.* (2003)
	A. diogoi	Subrahmanyam *et al.* (1980, 1983, 1985a); Nigam *et al.* (1991)
	A. correntina	Subrahmanyam *et al.* (1983, 1985a)
	A. duranensis	Subrahmanyam *et al.* (1983, 1985a); Pande and Rao (2001) Sharma *et al.* (2003)
	A. glabrata	Subrahmanyam *et al.* (1983, 1985a)
	A. hagenbeckii	Subrahmanyam *et al.* (1983, 1985a)
	A. helodes	Subrahmanyam *et al.* (1983)
	A. hoehnei	Subrahmanyam *et al.* (1983); Pande and Rao (2001)
	A. ipaensis	Pande and Rao (2001)
	A. kempff-mercadoi	Subrahmanyam *et al*. (1983); Sharma *et al.* (2003)
	A. kuhlmannii	Subrahmanyam *et al.* (1983); Pande and Rao (2001)
	A. monticola	Pande and Rao (2001); Sharma *et al.* (2003)
	A. oteroi	Subrahmanyam *et al.* (1983)
	A. paraguariensis	Subrahmanyam *et al.* (1983, 1985a); Sharma *et al.* (2003)
	A. pusilla	Subrahmanyam *et al.* (1983, 1985a); Sharma *et al.* (2003)
	A. repens	Subrahmanyam *et al.* (1983, 1985a)
	A. pseudovillosa	Subrahmanyam *et al.* (1983)
	A. stenosperma	Subrahmanyam *et al.* (1983, 1985a); Nigam *et al.* (1991) Sharma *et al.* (2003)
	A. triseminata	Sharma *et al.* (2003)
	A. valida	Subrahmanyam *et al.* (1983, 1985a)
	A. villosa	Subrahmanyam *et al.* (1983, 1985a)
	A. villosulicarpa	Subrahmanyam *et al.* (1983, 1985a)
Peanut Stripe Virus (PStV)		
	A. cardenasii	Nigam *et al.* (1991)
	A. diogoi	Culver and Sherwood (1987)
	A. helodes	Culver and Sherwood (1987)
	A. glabrata	Culver and Sherwood (1987)
Peanut Stunt Virus		
	A. benthamii	Herbert and Stalker (1981)
	A. correntina-villosa	Herbert and Stalker (1981)
	A. duranensis	Herbert and Stalker (1981)
	A. glabrata	Herbert and Stalker (1981)
	A. lignosa	Herbert and Stalker (1981)
	A. major	Herbert and Stalker (1981)
	A. pseudovillsa	Herbert and Stalker (1981)
	A. oteroi	Herbert and Stalker (1981)
	A. repens	Herbert and Stalker (1981)
	A. villosa	Herbert and Stalker (1981)
Peanut Web Blotch (*Didymella arachidicoria*)		
	A. glabrata	Subrahmanyam *et al.* (1985c)
Sclerotinia Blight (*Sclerotinia minor*)		
	A. glandulifera	Tallury *et al.* (2011)
	A. helodes	Tallury *et al.* (2011)
	A. magna	Tallury *et al.* (2011)
Tomato-Spotted Wilt Virus (TSVW)		
	A. batizocoi	Lyerly *et al.* (2002)
	A. cardenasii	Subrahmanyam *et al.* (1985b); Lyerly *et al.* (2002)
	A. diogoi	Subrahmanyam *et al.* (1985b); Lyerly *et al.* (2002)
	A. correntina	Subrahmanyam *et al.* (1985b)
	A. pusilla	Subrahmanyam *et al.* (1985b)
	A. stenosperma	Lyerly *et al.* (2002)

[a]Not all accessions of species listed are resistant to the diseases in the table.
[b]Formerly published *A. chacoense* in the literature.

species to *A. hypogaea*. This is important because recombination between the cultivated genomes and those of other species is rare, thus restricting selection for desired traits in interspecific hybrid derivatives (Holbrook and Stalker, 2003). Guimarães *et al.* (2010, 2011) identified eight genes in *A. stenosperma* roots that correspond with resistance to *M. arenaria*, and QTLs for resistance to late leaf

Table 3. *Arachis* species resistant to peanut diseases[a].

Trait	Species	Citation
Insect-Pests		
	A. correntina	Nigam *et al.* (1991)
	A. diogoi[b]	Nigam *et al.* (1991)
	A. stenosperma	Nigam *et al.* (1991)
	A. villosulicarpa	Nigam *et al.* (1991)
Armyworm (*Spodoptera litura*)		
	A. appressipila	ICRISAT (1990)
	A. glabrata	ICRISAT (1990)
	A. kempff-mercadoi	ICRISAT (1990)
	A. major	ICRISAT (1990)
	A. paraguariensis	ICRISAT (1990)
	A. stenophylla	ICRISAT (1990)
	A. villosa	ICRISAT (1990)
Armyworm (*Spodoptera* spp.)		
	A. appressipila	Stevenson *et al.* (1993); Sharma *et al.* (2003)
	A. burkartii	Lynch *et al.* (1981)
	A. cardenasii	Lynch *et al.* (1981); Sharma *et al.* (2003)
	A. diogoi	Lynch *et al.* (1981); Stevenson *et al.* (1993)
	A. correntina	Lynch *et al.* (1981)
	A. duranensis	Sharma *et al*. (2003)
	A. glabrata	Stevenson *et al.* (1993)
	A. ipaensis	Sharma *et al.* (2003)
	A. kempff-mercadoi	Stevenson *et al.* (1993); Mallikarjuna *et al.* (2004)
	A. lignosa	Lynch *et al.* (1981)
	A. paraguariensis	Stevenson *et al.* (1993)
	A. pusilla	Sharma *et al.* (2003)
	A. pseudovillosa	Stevenson *et al.* (1993)
	A. repens	Lynch *et al.* (1981)
	A. stenophylla	Sharma *et al.* (2003)
	A. sylvestris	Sharma *et al.* (2003)
	A. triseminata	Sharma *et al.* (2003)
	A. villosa	Lynch *et al.* (1981)
	A. villosulicarpa	Lynch *et al.* (1981)
Corn Earworm (*Heloithis zea*)		
	A. batizocoi	Campbell *et al.* (1982)
	A. diogoi	Stalker and Campbell (1983)
	A. correntina	Stalker and Campbell (1983)
	A. duranensis	Stalker and Campbell (1983)
	A. paraguariensis	Stalker and Campbell (1983)
	A. repens	Stalker and Campbell (1983)
	A. rigonii	Stalker and Campbell (1983)
	A. stenosperma	Stalker and Campbell (1983)
	A.triseminata[c]	Stalker and Campbell (1983);
	A. villosa-correntina	Stalker and Campbell (1983)
Corn Earworm (*Helicoverpa armigera*)		
	A. appressipila	Sharma *et al.* (2003)
	A. benensis	Sharma *et al.* (2003)
	A. cardenasii	Sharma *et al.* (2003)
	A. duranensis	Sharma *et al.* (2003)
	A. hoehnei	Sharma *et al.* (2003)
	A. ipaensis	Sharma *et al.* (2003)
	A. kempff-mercadoi	Sharma *et al.* (2003)
	A. matiensis	Sharma *et al.* (2003)
	A. monticola	Sharma *et al.* (2003)
Corn Earworm (*Helicoverpa armigera*) (cont.)		
	A. paraguariensis	Sharma *et al.* (2003)
	A. pusilla	Sharma *et al.* (2003)
	A. rigonii	Sharma *et al.* (2003)
	A. stenosperma	Sharma *et al.* (2003)
	A. stenophylla	Sharma *et al.* (2003)
	A. sylvestris	Sharma *et al.* (2003)
	A. triseminata	Sharma *et al.* (2003)
Groundnut aphid (*Aphis craccivora*)		
	A. batizocoi	ICRISAT (1990)
	A. diogoi	Amin & Mohammad (1980, 1982); Amin (1985); ICRISAT (1990)
	A. correntina	Amin & Mohammad (1982); Amin (1985); ICRISAT (1990)
	A. duranensis	Amin & Mohammad (1982); Amin (1985)
	A. glabrata	Amin & Mohammad (1982); Amin (1985)
	A. kempff-mercadoi	ICRISAT (1990)
	A. marginata	Amin & Mohammad (1982); Amin (1985)
	A. paraguariensis	ICRISAT (1990)
	A. repens	Amin (198b)
	A. stenophyla	ICRISAT (1990)
	A. stenosperma	ICRISAT (1990)
	A. villosa	Amin (1985)
Leafminer (*Aproaerema modicella*)		
	A. benensis	Sharma *et al.* (2003)
	A. cardenasii	Sharma *et al.* (2003)
	A. duranensis	Sharma *et al.* (2003)
	A. kempff-mercadoi	Sharma *et al.* (2003)
	A. monticola	Sharma *et al.* (2003)
	A. paraguariensis	Sharma *et al.* (2003)
	A. pusilla	Sharma *et al.* (2003)
	A. stenosperma	Sharma *et al.* (2003)
	A. triseminata	Sharma *et al.* (2003)
Leafhoppers (*Empoasca fabae*)		
	A. appressipila	Sharma *et al.* (2003)
	A. batizocoi	Campbell and Wynne (1980)
	A. benensis	Sharma *et al.* (2003)
	A. diogoi	Stalker and Campbell (1983)
	A. cardenasii	Stalker (1992); Stalker *et al.* (2002a, b); Stalker and Lynch (2002); Sharma *et al.* (2003)
	A. correntina	Stalker and Campbell (1983)
	A. diogoi	Stalker (1992)
	A. duranensis	Stalker and Campbell (1983); Sharma *et al.* (2003)
	A. glabrata	Campbell and Wynne (1980)
	A. hoehnei	Sharma *et al.* (2003)
	A. ipaensis	Sharma *et al.* (2003)
	A. kempff-mercadoi	Sharma *et al.* (2003)
	A. macedoi	Campbell and Wynne (1980)
	A. matiensis	Sharma *et al.* (2003)
	A. monticola	Leuck *et al.* (1968); Campbell & Wynne (1980); Sharma *et al.* (2003)

Table 3. Continued.

Trait	Species	Citation
	A. paraguariensis	Stalker and Campbell (1983); Sharma *et al.* (2003)
	A. pusilla	Sharma *et al.* (2003)
Leafhoppers (*Empoasca fabae*) (cont.)		
	A. repens	Stalker and Campbell (1983)
	A. rigonii	Stalker and Campbell (1983)
	A. stenophylla	Sharma *et al.* (2003)
	A. stenosperma	Campbell and Wynne (1980); Stalker and Campbell; (1983); Sharma *et al.* (2003)
	A. sylvestris	Sharma *et al.* (2003)
	A. triseminata[c]	Stalker and Campbell (1983); Sharma *et al.* (2003)
	A. villosa	Campbell and Wynne (1980)
	A. villosa-correntina	Stalker and Campbell (1983)
Lesser Cornstalk Borer (*Elasmopalpus lignosellus*)		
	A. appressipila	Stalker *et al.* (1984)
	A. correntina	Stalker *et al.* (1984)
	A. paraguariensis	Stalker *et al.* (1984)
	A. triseminata[c]	Stalker *et al.* (1984)
	A. villosa	Stalker *et al.* (1984)
Mites (*Tetranychus tumidellus*)		
	A. repens	Leuck and Hammons (1968)
	A. villosulcarpa	Leuck and Hammons (1968)
Spider Mites (*Tetranychus urticae*)		
	A. correntina	Johnson *et al.* (1977)
	A. glabrata	Johnson *et al.* (1977)
	A. macedoi	Johnson *et al.* (1977)
	A. villosa	Johnson *et al.* (1977)
Nematodes (*Meloidogyne arenaria*)		
	A. batizocoi	Nelson *et al.* (1989); Holbrook & Noe (1990); Simpson *et al.* (1993)
	A. burkartii	Holbrook and Noe (1990)
	A. cardenasii	Nelson *et al.* (1989); Holbrook and Noe (1990); Simpson *et al.* (1993); Stalker *et al.* (2002a, b); Stalker and Lynch (2002)
	A. diogoi	Nelson *et al.* (1989)
	A. duranensis	Holbrook and Noe (1990)
	A. glabrata	Banks (1969); Castillo *et al.* (1973), Nelson *et al.* (1989); Holbrook and Noe (1990)
	A. hagenbeckii	Holbrook and Noe (1990)
	A. helodes	Holbrook and Noe (1990); Sharma *et al.* (1999)
	A. hermanii	Nelson *et al.* (1989)
	A. hoehnei	Nelson *et al.* (1989)
	A. kretschmeri	Sharma *et al.* (1999)
	A. kuhlmannii	Nelson *et al.* (1989); Sharma *et al.* (1999)
	A. major	Nelson *et al.* (1989)
	A. matiensis	Nelson *et al.* (1989)
	A. paraguariensis	Nelson *et al.* (1989)
	A. pintoi	Nelson *et al.* (1989); Carvalho and Quesenberry (2009)
	A. pusilla	Nelson *et al.* (1989)
	A. stenosperma	Nelson *et al.* (1989); Sharma *et al.* (1999)
	A. sylvestris	Nelson *et al.* (1989); Sharma *et al.* (1999)
	A. villosa	Holbrook and Noe (1990)
Nematodes (*Meloidogyne hapla*)		
	A. burchellii	Castillo *et al.* (1973)
	A. cardenasii	Nelson *et al.* (1989)
	A. diogoi	Nelson *et al.* (1989)
	A. stenosperma	Castillo *et al.* (1973); Nelson *et al.* (1989)
Nematodes (*Meloidogyne incognita* (nematodes)		
	A. pintoi	Carvalho and Quesenberry (2009)
Nematodes (*Meloidogyne javanica*)		
	A. helodes	Sharma *et al.* (1999
	A. kretschmeri	Sharma *et al.* (1999)
	A. kuhlmannii	Sharma *et al.* (1999)
	A. pintoi	Carvalho and Quesenberry (2009)
	A. stenosperma	Sharma *et al.* (1999)
	A. sylvestris	Sharma *et al.* (1999)
Southern Corn Rootworm (*Diabrotica undecimpunctata howardi*)		
	A. cardenasii	Stalker *et al.* (2002a, b); Stalker and Lynch (2002)
Thrips (*Enneothrips flavens*)		
	A. gregoryi	Janini *et al.* (2010)
	A. kuhlmanii	Janini *et al.* (2010)
	A. stenosperma	Janini *et al.* (2010)
	A. villosa	Janini *et al.* (2010)
Thrips (*Frankliniella fusca*)		
	A. batizocoi	Campbell and Wynne (1980)
	A. diogoi	Stalker and Campbell (1983); Stalker (1992)
	A. correntina	Stalker and Campbell (1983)
	A. duranensis	Stalker and Campbell (1983)
	A. glabrata	Campbell and Wynne (1980)
	A. macedoi	Campbell and Wynne (1980)
	A. monticola	Leuck *et al.* (1968); Campbell &Wynne (1980)
	A. paraguariensis	Stalker and Campbell (1983)
	A. repens	Stalker and Campbell (1983)
	A. rigonii	Stalker and Campbell (1983)
	A. stenosperma	Campbell and Wynne (1980); Stalker and Campbell (1983)
	A. triseminata[c]	Stalker and Campbell (1983)
	A. villosa	Campbell and Wynne (1980)
	A. villosa-correntina	Stalker and Campbell (1983)
	A. villosulicarpa	Leuck *et al.* (1968)
Thrips (*Frankliniella schultzei*)		
	A. diogoi	Amin and Mohammad (1980); Amin (1985)
	A. duranensis	Amin and Mohammad (1980)
	A. glabrata	Amin and Mohammad (1980)
Chilli Thrips (*Scirtothrips dorsalis*)		
	A. diogoi	Amin (1985)
	A. duranensis	Amin (1985)

Table 3. Continued.

[a]Not all accessions of species listed are resistant to the insect pests in the table.
[b]Formally published as *A. chacoense* in the literature.
[c]Formerly published as *A. pusilla* by Stalker and Campbell (1983).

spot also have been identified (Leal-Bertioli *et al.*, 2009) in section *Arachis* species.

For tracking introgressed segments from wild accessions into cultivated germplasm, markers that allow more agile assays would be ideal. A different type of marker, transposon-based, is being evaluated for their use for introgressed segments. For example, Shirasawa *et al.* (2012b) developed 535 markers derived from transposon-enriched genomic libraries. These markers show great potential and detect higher polymorphism levels than genomic microsatellite markers (Shirasawa *et al.*, 2012b). Also, Single Nucleotide Polymorphism (SNP) markers constitute the most abundant molecular markers in the genome and can be carried out with high throughput genotyping methods. SNP markers have been widely used in many plant species. However, they have had limited use in peanut due to the difficulties of their implementation in polyploid plants, and in *Arachis* it will require separation of A and B-genome sequences. A SNP-based map of diploid *Arachis* was developed by Nagy *et al.* (2012) wherein a high-density genetic map of the A genome was developed from an intra-species cross within *A. duranensis*, and 598 SSRs, 37 single-stranded DNA conformation polymorphism (SSCP) markers, and 1,054 SNPs were mapped. SNP-based markers have not yet been extensively used on the tetraploid *Arachis*, but they are expected to greatly accelerate genetic mapping and marker-assisted selection when genotyping-by-sequencing (Elshire *et al.*, 2011) can be routinely implemented.

Linking Agronomic Traits with Markers. The narrow genetic base of peanut makes the development of molecular markers a difficult task. The nature and the possibility of using molecular markers have been evolving as have all aspects of the agronomical sciences. The first molecular marker studies used for peanut were based on isozymes and proteins (Grieshammer and Wynne, 1990; Krishna and Mitra, 1988; Lu and Pickersgill, 1993), followed by Restriction Fragment Length Polymorphism - RFLPs (Kochert *et al.*, 1991; Kochert *et al.*, 1996; Paik-Ro *et al.*, 1992), Random Amplified Polymorphic DNA - RAPDs (Halward *et al.*, 1991; Halward *et al.*, 1992; Hilu and Stalker, 1995; Subramanian *et al.*, 2000; Dwivedi *et al.*, 2001; Raina *et al.*, 2001) and Amplified Fragment Length Polymorphism – AFLPs (He and Prakash, 1997; Gimenes *et al.*, 2000; Gimenes *et al.*, 2002; Herselman, 2003; Milla *et al.*, 2005a, 2005b; Tallury *et al.*, 2005).

In recent years, microsatellite or Simple Sequence Repeat (SSR) markers have become the assay of choice for genetic studies in *Arachis* since they are multiallelic, co-dominant, transferable among related species, PCR-based markers, and usable in tetraploid genomes. Efforts by several research groups to develop microsatellite markers for peanut have resulted in more than 5,000 SSRs (see Pandey *et al.*, 2011, 2012 for reviews). This large effort to produce and characterize SSRs has enabled the phylogenetic evaluation of the genus *Arachis* (Krishna *et al.*, 2004; Barkley *et al.*, 2007; Tang *et al.*, 2007; Varshney *et al.*, 2009b, Moretzsohn *et al.*, 2013) and production of moderately dense genetic maps for cultivated peanut, which will be described below.

To date, the number of genes associated with molecular markers in peanut is relatively small, but the large number of molecular markers becoming available has great potential for utilization in crop improvement programs. Bertioli *et al.* (2003) described numerous linkages of resistance genes in peanut. Pandey *et al.* (2012) listed QTLs for some of the important traits found in the cultivated peanut. Chu *et al.* (2011) outlined a breeding scheme to utilize marker-assisted selection to pyramid nematode resistance and the high oleic acid trait in peanut cultivars, and the system has greatly increased efficiency for developing breeding lines.

Introgression of QTLs with the Aid of Molecular Markers

By the use of molecular markers to map genetically structured populations, a number of Quantitative Trait Loci (QTLs) have been identified and some are already used for tracking wild segments introgressed into *A. hypogaea*.

Root-knot Nematode (*Meloidogyne *spp.). The first markers for an agronomically useful, wild species-derived trait in peanut were for resistance to root-knot nematode (*M. arenaria*) from *A. cardenasii*. Two closely-linked sequence characterized amplified region (SCAR) markers were identified for genes for reduced galling and egg number (Garcia *et al.*, 1996). Simultaneously, three RAPD markers were associated with nematode resistance in several backcross breeding populations derived from the interspecific hybrid TxAG-6 [*A. batizocoi* × (*A. cardenasii* × *A. diogoi*)]^{4x} (Burow *et al.*, 1996). Marker-assisted selection then was used to develop NemaTAM, a high yielding, nematode resistant

cultivar (Simpson *et al.*, 2003). In this case, it was demonstrated that use of markers was more efficient than phenotypic selection because plants selected with markers for the homozygous resistance gene have fewer escapes compared to plants from phenotypic selection. Marker-assisted selection and an accelerated backcross breeding program were also used in development of a high-oleic variety with nematode and tomato spotted wilt virus resistances, called high O/L Tifguard (Chu *et al*. 2011). The effectiveness of selection of nematode resistance has been the most successful use of MAS in peanut to date. However, in spite of the success of this work, it is now thought that the use of a single gene trait that confers near immunity may be subject to breakdown of resistance under high selection pressure, and is cause for concern. Therefore, new sources of resistance for nematodes, such as amphidiploids derived from *A. stenosperma*, which is highly resistant to fungi and nematodes (Leal-Bertioli *et al.*, 2010; Proite *et al.*, 2008; Santos *et al.*, 2011; Singsit *et al*., 1995), would be useful for peanut breeding.

Late Leaf Spot Resistance. Resistance to late leaf spot (LLS) (*Cercosporidium personatum*) has multiple components, including percent defoliation, incubation period, latency period, lesion number and diameter, sporulation, and pod yield (Green and Wynne, 1986; Chiteka *et al.*, 1988a, 1988b; Anderson *et al.*, 1993; Waliyar *et al.*, 1993, 1995). High levels of resistance have also been associated with low yield suggesting linkage or pleotropic effects (Iroume and Knauft, 1987), thus breeding for high yielding cultivars with resistance requires this linkage to be broken.

Stalker and Mozingo (2001) identified three RAPD markers associated with early leaf spot lesion diameter in a peanut population derived from a cross between an *A. hypogaea* × *A. cardenasii* introgression line with NC 7. Two breeding lines developed from this material have been placed into advanced line trials.

Mapping of RFLP markers on BC_3F_1 lines in greenhouse studies identified five markers for leaf spot resistance (Burow *et al.*, 2008), including three QTLs for incubation period, and one each for latency period, lesion number and diameter. Those QTLs for latency period and lesion number were overlapping, suggesting either linkage between the two or a QTL with pleiotropic effects.

Leal-Bertioli *et al.* (2009) reported the mapping of 34 resistance gene analogues (RGAs) and five QTLs for LLS resistance (% diseased leaf area) on detached leaves of the F_2 plants of the A-genome mapping population derived from *A. duranensis* × *A. stenosperma*, and suggested additive or partial dominance gene action. One QTL explained almost half of the phenotypic variance observed and some QTLs mapped near RGA markers. In another QTL study based on cultivated genotypes, with GPBD-4 as one parent, Khedikar *et al.* (2010) reported 11 QTLs for LLS; each QTL explained 2 to 7% of phenotypic variation in three environments, suggesting that the genes controlling LLS resistance in this cross are relatively minor. In maps from two other populations, again using GPBD-4 and a larger number (188 and 181) of markers and six trials, a major QTL for LLS was reported, which explained from 10% to 62% of phenotypic variance, depending on the environment (Sujay *et al.*, 2011). These are being used for marker assisted selection breeding at ICRISAT in India (Varshney, 2012, personal communication).

Rust. QTL analysis using a partial genetic map of a mapping population with 67 marker loci derived from the cross TAG 24 × GPBD-4 and multiple season phenotyping data on both rust and LLS detected 12 QTLs explaining between 1.70 and 55.20% of the phenotypic variation for each disease, respectively (Khedikar *et al.*, 2010). The SSR marker tightly linked to the major QTL (IPAHM103; QTLrust01), was then validated among a diverse set of genotypes as well as another mapping population (Sarvamangala *et al.*, 2011) derived from the cross TG 26 × GPBD-4. The SSR marker (IPAHM 103) was deployed to introgress the rust resistance QTL into three elite groundnut varieties (ICGV 91114, JL 24 and TAG 24) using the donor GPBD-4 through marker-assisted backcrossing. GPBD-4 was a common parent in all of these crosses, and since it was derived from the wild species *A. cardenasii,* resistance incorporated into cultivars was likely derived from wild species germplasm.

Groundnut Rosette Virus. The aphid-transmitted groundnut rosette virus is an important pathogen of peanut in Africa and Asia, causing severe stunting and loss of yield. Herselman *et al.* (2004) tested 308 AFLP primer combinations, and they were able to devise five linkage groups consisting of 12 markers with one marker linked to aphid resistance.

Tomato Spotted Wilt Virus (TSWV). Tomato spotted wilt virus is transmitted by tobacco thrips (*Frankliniella* spp.) and causes serious losses in the U.S.A. segregating population of F_2 plants of the A-genome diploid cross *A. kuhlmannii* × *A. diogoi* was screened for resistance to TSWV, and five linked AFLP markers on one chromosome were associated with resistance at a high statistical threshold (Milla *et al.*, 2004; Milla, 2003). In Brazil, interspecific populations and wild species

have also been found as promising for introgression of resistance to the thrips, *Enne-othrips flavens* (Janini *et al.*, 2010).

Domestication Traits. Mapping of RFLP markers on BC_3F_2 lines of the cross *A. hypogaea* × *A. cardenasii* (Burow *et al.*, 2011) identified 29 markers for the domestication-related traits of main stem length, number of lateral branches, pod size, and seed size. Foncéka *et al.* (2012) produced populations derived from crosses of cultivar Fleur 11 and an amphidiploid (*A. ipaensis* × *A. duranensis*)^{4x} (Fávero *et al.*, 2006) to investigate introgression of wild segments. A population composed of a mixture of BC_3F_1 and BC_2F_2 individuals, each self-pollinated to produce BC_3F_2 and BC_2F_3 families, was used for phenotyping and QTL detection. Domestication-related trait QTLs were found, including ones associated with days to flowering, plant architecture, pod and seed morphology, and yield components. Perhaps surprisingly, it was shown that wild alleles contributed positive variation to several agronomic traits such as flowering precocity, seed and pod number per plant, and length, size and maturity of pods. Moreover, the comparison of QTLs obtained under well-watered and water limited conditions revealed that QTLs for stress tolerance indices for pod and seed numbers with favorable alleles could be attributed to the wild parents. These could be involved in reproductive trade-offs between producing large seeds versus producing more, but smaller, seeds under water stress.

Genetic Maps

One of the main uses of molecular markers in peanut has been the construction of genetic linkage maps, which are used to study the genome structure and organization, identify regions of particular interest (e.g., resistance to diseases) and for marker-assisted selection in breeding programs. Due to the very low genetic variation in cultivated peanut, wild species were initially used for the construction of linkage maps in *Arachis* because of their simple genetic structure and higher polymorphism levels. The first map used RFLPs to analyze variation between the diploid species *A. stenosperma* and *A. cardenasii* where a total of 117 RFLP markers were mapped into 11 linkage groups (Halward *et al.*, 1993). An AFLP-based A-genome map was generated from an F_2 population developed from the cross *A. kuhlmannii* × *A. diogoi* (Milla, 2003), and a RAPD-based map of *A. stenosperma* × *A. cardenasii* also was developed by Garcia *et al.* (2005).

It was only with the large abundance of SSR markers that moderately saturated maps were created. The first SSR-based map was constructed for an F_2 population derived from a cross of two A-genome diploid species (*A. duranensis* and *A. stenosperma*) where 170 loci mapped into 11 linkage groups covering 1231 cM of total map distance (Moretzsohn *et al.*, 2005). Additional markers were subsequently included in the diploid A genome map, resulting in 369 markers (188 SSRs, 80 anchor markers, and 35 resistance gene analogues, among others), mapped into 10 linkage groups, which correspond to the 10 chromosomes of the haploid genome (Leal-Bertioli *et al.*, 2009). Nagy *et al.* (2012) published a more saturated map having 1724 SNP, SSR, and single stranded DNA conformation polymorphism (SSCP) makers from a cross between two *A. duranensis* accessions.

A diploid F_2 population derived from the cross *A. ipaënsis* × *A. magna* was used to develop a map for the B genome of *Arachis,* with 149 codominant markers (mostly microsatellites) mapped into 10 linkage groups covering of 1294.4 cM (Moretzsohn *et al.*, 2009). Fifty-one common markers presented evidence of the high synteny of the B and the A genomes. Guo *et al.* (2012) created a more dense map by crossing two accessions of *A. batizocoi.* They compared high density A and B genome maps and observed a large amount of synteny between the A and B genomes, but also several inversions and translocations.

The first tetraploid map also was created with RFLPs by using progenies of a cross between the cultivar Florunner × the synthetic amphidiploid TxAG-6 [*A. batizocoi* × (*A. cardenasii* × *A. diogoi*)]^{4x} where 383 markers were mapped (Burow *et al.*, 2001). A genetic map was created based on a population of 88 BC_1F_1 individuals of a cross of a synthetic amphidiploid (*A. ipaënsis* × *A. duranensis*) by Fávero *et al.* (2006) with *A. hypogaea* cv. Fleur11. This SSR-based linkage map for the tetraploid genome was composed of 298 markers and 21 linkage groups, spanning 1843.7 cM (Fonceka *et al.*, 2009). A comparative analysis of this map with the A genome map of Moretzsohn *et al.* (2005) suggested the occurrence of a chromosomal translocation event prior to the peanut's tetraploidization (Fonceka *et al.*, 2009).

The partial first linkage map from a cross between accessions of *A. hypogaea* was constructed using an F_2 population (Herselman *et al.*, 2004), in which five linkage groups with 12 markers spanned 139 cM of the genome. More complete maps were later reported, with the first being in 2008 by using 142 individuals of a recombinant inbred line (RIL) population derived from a cross between one accession of *A. hypogaea* subsp. *hypogaea* and one accession of the *fastigiata* subspecies (Hong *et al.*, 2008). New markers were added to this map and two additional maps were constructed based

on RIL populations having accessions of the subspecies *fastigiata* as parents (Hong *et al.*, 2010). A reference map was developed, with 175 loci and 22 linkage groups, covering a total distance of 885.4 cM. The marker order was in general collinear to the A genome map (Moretzsohn *et al.*, 2005). Another intraspecific map for peanut was developed using a RIL population composed of 318 F_8/F_9 plants (Varshney *et al.*, 2009a); and of the 1145 microsatellite markers screened, only 135 mapped in 22 linkage groups spanning 1270.5 cM. More recently, Wang *et al.* (2012) published a SSR map based on an F_2 population of 94 individuals derived from an *A. hypogaea* subsp. *hypogaea* × *A. hypogaea* subsp. *fastigiata* hybrid. This map consisted of 385 polymorphic SSRs covering 318 loci and 21 linkage groups that spanned 1674.4 cM. To date, there are 23 maps of peanut published using RFLPs, AFLPs, SSRs, SNP, SCAR and CAPS markers which are summarized in Pandey *et al.* (2012). A recent consensus map of *A. hypogaea* map comprised of 897 marker loci was constructed by Gautami *et al.* (2012).

These maps are very useful for breeding because they incorporate QTLs for agronomically important traits, such as disease resistance and drought related traits. They also have been used to develop markers closely associated with a nematode resistance gene (Nagy *et al.*, 2010). Further, as the cultivated genome is sequenced, the diploid maps will be of great importance for sorting out the chromosome and genetic organization of the tetraploid genome.

Map Synteny

In general, it is possible to map only limited numbers of molecular markers in a given mapping population due to polymorphism constraints, and this is especially true for peanuts. In order to improve the knowledge on the genetic and genomic structure, assignment of marker and QTL positions, genetic maps developed for different mapping populations can be used for creating consensus maps, which can be also be anchored to other species maps. Consensus maps allow investigators to (i) map a large number of marker loci onto a single map, (ii) determine relative position of common markers across different mapping populations, (iii) determine stability of marker locus position across the genomes, and (iv) provide evidence for chromosomal rearrangements, gene duplication and assists in the assignment of linkage groups to chromosomes (Gautami *et al.*, 2012).

With the present availability of markers, the international *Arachis* community has been striving towards developing a consensus genetic map. By integration of the eleven linkage maps of the artificial amphidiploids and cultivated tetraploid peanuts, a reference consensus map consisting of 897 marker loci has been constructed and given the consensus nomenclatures for the linkage groups (a01 to a10 and b01 to b10) (Gautami *et al.*, 2012).

Subsequently, Shirasawa *et al.* (2012a) created the most comprehensive consensus map to date. They mapped a large number of DNA markers from two cultivated peanut maps (Shirasawa *et al.*, 2012b) onto the previously reported linkage maps of the A and B genomes (Moretzsohn *et al.*, 2005) and the artificial amphidiploid map (Fonceka *et al.*, 2009), and integrated these with nine maps of cultivated peanut (Gautami *et al.*, 2012; Hong *et al.*, 2010; Khedikar *et al.*, 2010; Sarvamangala *et al.*, 2011; Qin *et al.*, 2012; Ravi *et al.*, 2011; Sujay *et al.*, 2011; Varshney *et al.*, 2009b; Shirasawa, 2012a, 2012b). This consensus map was then subjected to comparative analysis with four legume genomes (*Cajanus cajan, Glycine max, Lotus japonicus,* and *Medicago truncatula*) to clarify the feature of genome structure in the genus *Arachis*. The comparison of diploid and tetraploid maps revealed probable genome rearrangements within the *Arachis* genomes. Bertioli *et al.* (2009) used sequence characterized markers, and a high proportion of low or single copy gene markers to anchor the AA-diploid *Arachis* map onto the fully sequenced genomes of *L. japonicus* and *M. truncatula* (Sato *et al.*, 2008); www.medicago.org). This alignment was represented as "genome plots" (Bertioli *et al.*, 2009). Inspection of these plots shows surprising degrees of synteny considering the time of species divergence (estimated 55 million years). Although there are some regions of double affinities between *Arachis* and these model legumes, most synteny blocks have a single main affinity and not multiple affinities. Genome evolution (e.g., chromosomal translocations and inversions) progressively breaks down syntenic relationships between species over evolutionary time.

The comparative genomics of the legumes revealed that the *Arachis* genome structure was moderately divergent from those of the compared legumes. This information will be useful for selecting highly informative and uniformly distributed markers for developing new genetic maps, background selection and diversity analysis, aligning new genetic and physical maps, performing QTL analysis in a multi-populations design, evaluating the genetic background effect on QTL expression, and serving other genetic and molecular breeding activities in peanut.

Value of Diploids for Genomic Investigations

The chromosomes of *A. hypogaea* are highly diplodized which indicates that there may be little recombination between the A and B genomes except

when the infrequent quadrivalent is formed. To support this, genomic comparison of *A. duranensis* and *A. ipaensis* indicates that there is significant divergence in repetitive DNA; however, the repetitve DNA in the tetraploid species has not significantly recombined since *A. hypogaea* evolved (Araujo *et al*., 2012). Thus, genomic investigations of the progenitor diploid species should have direct application to the cultivated peanut. For example, sequencing the diploid genome of either *A. duranensis* or *A. ipaensis* could serve as a template for sequencing the genomes of the tetraploid species. This is important because developing a high quality diploid genetic sequence will be significantly less expensive than developing an entire sequence for the tetraploid genomes and trying to sort out the genetic duplications between the A and B genomes. Using a diploid progenitor species also will lead to fewer assembly errors. In addition, utilizing *A. duranensis* or *A. ipaensis* for sequencing templates will solve problems associated with chimeric contigs in de-novo assemblies of the tetraploid genomes.

Conclusions and Future Prospects

The incorporation of wild alleles into crops is a proven strategy for the development of improved varieties with pest and disease resistance, tolerance to abiotic stress, improved yield and quality, and even male fertility and fertility restoration. However, the extent of utilization of the useful allele reservoir in wild species and its impact on peanut breeding has been limited, mainly due to the restrictions of the plant itself in terms of crossability, multiplication rate, and, until recently, to the lack of appropriate molecular tools to analyze and follow traits in hybrids. *Arachis cardenasii* has been one of the most useful sources of genes from wild species to date, but crosses involving other species also have been used. The recent use of the two most probable ancestors of peanut *A. duranensis* and *A. ipaënsis* in a systematic introgression program opens the way for extensive and detailed characterization of the peanut genome and wild allele interactions for a wide range of traits. As new materials are being created and genotyping strategies are becoming more advanced, variability from the wild species is being harnessed to the benefit of world agriculture.

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