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Genetic Resources, Diversity and Association Mapping in Peanut

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ABSTRACT

Globally, peanut is an important crop, providing both oil and protein, and gene banks across the world have conserved a large collection of peanut germplasm including wild *Arachis* species. The key to the success in crop improvement depends on how effectively and efficiently the new genetic variation is introduced to broaden the genetic base of cultigens. The genus *Arachis* harbors considerable diversity for morpho-agronomic traits including resistance to abiotic and biotic stresses. Impressive progress have been made towards developing a large number of markers specific to peanut in addition to the technological breakthrough in developing high-throughput genotyping platforms for unlocking the genetic variation present in the germplasm collections. Using core and mini core collections and genomic tools, peanut researchers have identified a number of diverse germplasm possessing agronomically beneficial traits that are now being used in peanut breeding. Amphidiploids originating from distant wild *Arachis* species crosses are expected to unravel the variation not earlier available to peanut research community due to bottlenecks associated with peanut domestication.

Keywords: peanut, *Arachis*, germplasm, diversity, abiotic/biotic stresses, mapping

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2.1 Introduction

Peanut (groundnut) (*Arachis hypogaea* L.), an important food legume crop, grown in more than 108 countries representing tropical, subtropical and warm temperate regions of the world, extending cultivation between 40°N to 40°S. It ranks 6th among the oilseed crops and 13th among food crops of the world. Globally it is cultivated on 24.1 million ha area, with a total production of 37.6 million tons and average productivity of 1.6 t ha⁻¹ (FAO 2010: <http://www.faostat.fao.org>). Developing countries account for 96% of the global peanut area and 92% of the global production. Asia accounts for 64% of the global peanut production, while Africa only 28%. In Asia, India and China together produce 57% of the global peanut production. Other countries in Asia that produce substantial peanut include Indonesia, Myanmar and Vietnam. Peanut in Africa is widely distributed, grown over 50 countries across the continent. Nigeria, Sudan, Senegal, Chad and Ghana together account for 54% of the peanut production in the continent, with Nigeria the leading producer. North America contributes ~5% of the global peanut production, 80% of which is in the USA, the world's fourth-largest producer. Europe and Oceania contribute less than 1% peanut production.

Peanut seeds, rich in oil, protein, minerals and vitamins, are consumed in a variety of forms. About two-thirds of global peanut production is crushed for extracting vegetable oil, while the remaining is used in the form of edible products. Peanut cake obtained after oil extraction is used as protein-rich meal for livestock or for making other food products. The haulms are an important source of good quality animal fodder, especially in developing countries. Peanut helps improve soil fertility through biological nitrogen fixation

Peanut production is adversely affected by both biotic and abiotic stresses. Rust, early leaf spot and late leaf spot are the most common and widely distributed foliar diseases, while peanut bud necrosis virus in South Asia, rosette disease in Africa and bacterial wilt in Southeast Asia are the major diseases of peanut, impacting yield and quality. The pests are of localized importance, for example, leaf miner and *Spodoptera* in South and Southeast Asia, termites in Africa and corn earworm, lesser corn stock borer and southern corn rootworm in North America. Drought is one of the major abiotic stresses, potentially limiting the peanut productivity worldwide. Peanut quality is adversely affected by aflatoxin contamination. All these factors either alone or in combination cause substantial yield losses worldwide, which necessitates the utilization of host-plant resistance to ameliorate losses to peanut production caused by biotic and abiotic stresses (Dwivedi et al. 2003 and references therein).

Legumes, including peanut, has a narrow genetic base, particularly due to bottleneck associated with their evolution. Various studies have shown that the cultivated peanut originated by a single hybridization event between two wild diploid species with distinct genome giving rise to a sterile hybrid followed by a spontaneous duplication of chromosomes producing fertile tetraploid (peanut) that remain reproductively isolated from its wild ancestors (Kochert et al. 1991; Jung et al. 2003; Seijo et al. 2004). Both pre- and post-zygotic hybridization barriers have been shown to restrict crossing between cultivated peanut and wild *Arachis* species (Halward and Stalker 1987). Crop genetic resources are the reservoir of many useful genes but general reluctance of the breeders to use exotic germplasm has severely restricted the introgression of useful variation present in exotic germplasm including wild *Arachis* species. The main reason for such low use of germplasm is due to the difficulties in evaluating large sets of germplasm across multilocations to get information about the traits of economic importance. This chapter provides information about the nature and extent of peanut genetic resources preserved across gene banks globally, the pattern of diversity unearthed in cultivated and wild *Arachis* species and various approaches including genomic tools to promote utilization of genetic resources to broaden the genetic base for sustainable peanut production.

2.2 Origin, Dissemination and Gene Pools

The genus *Arachis* contains nine sections comprising 80 species. Most of these species are diploid with $2n = 2x = 20$ and $2n = 2x = 18$ (*A. praecox*, *A. palustris* and *A. decora* in section *Arachis* and *A. porphyrocalyx* in section *Erectoides*) except *A. pseudovillosa*, *A. glabrata* and *A. nitida* in section *Rhizomatosae* and *A. hypogaea* (cultivated peanut) and *A. monticola* in section *Arachis*, which are tetraploid with $2n = 4x = 40$ (reviewed in Upadhyaya et al. 2011a). The genus *Arachis* originated in South America, where it is widely distributed, mainly in Argentina, Brazil, Paraguay and Uruguay. The cultivated *A. hypogaea* probably originated in the region of southern Bolivia and northern Argentina, since its progenitor *A. monticola*, the only wild allotetraploid species that crosses with *A. hypogaea* is found in this area (Krapovickas 1969). The diploid species *A. duranensis* and *A. ipaensis*, the most likely donors of A and B genomes, are restricted to northwest Argentina and southeast Bolivia (Krapovickas and Gregory 1994, 2007) that overlap to the segmental allotetraploid, *A. monticola*/*A. hypogaea* and *A. monticola* (Seijo et al. 2004). This, together with evidence on archeological and morphological diversity, indicate that this region may be the center of origin and the primary center of diversity for *A. hypogaea* (Krapovickas and Rigoni 1957; Hammons 1994; Singh and Simpson 1994; Kochert et al.

1996). Archeological evidences suggest that peanut has been cultivated for over 3,500 years. Domestication probably first took place in northern Argentina and southern Bolivia and was subsequently introduced to Africa, India and the Far East by the Portuguese and from the west coast of South America to the western pacific to Indonesia and China by the Spaniards in the early 16th century; and later on from Asian countries to east Africa. By the middle of the 16th century, peanut was introduced to North America and other parts of the world. Subsequent spread of the crop to different agroclimatic zones brought further diversification and variability in growth habit and seed and pod characteristics, which resulted into evolution of a number of morphologically distinct botanical varieties that predominate and show high levels of diversity in some geographical areas (Singh 1995; Singh and Nigam 1997).

The four gene pools in genus *Arachis* include i) primary gene pool (*A. hypogaea* landraces and its wild form *A. monticola*), ii) secondary gene pool (diploid species from section *Arachis* that are cross-compatible with *A. hypogaea*), iii) tertiary gene pool (species of section *Procumbentes*, weakly cross-compatible with *A. hypogaea*), and iv) the remaining *Arachis* species from other seven sections, not easily cross-compatible with *A. hypogaea* (Singh and Simpson 1994).

2.3 Conserving *Arachis* Species Diversity

Crop genetic diversity is threatened by several factors such as replacement of traditional varieties and landraces with genetically uniform high yielding cultivars, changes in dietary habits, habitat loss, natural calamities, land and crop conversion, introduction of exotic crops, environmental pollution and above all global warming. These genetically uniform modern cultivars could become vulnerable to new pests and diseases resulting into epidemics as have been seen in the past (Tatum 1971). Such experiences necessitate the use of diverse sources in plant breeding programs with a view to broaden the genetic base of crop cultigens. The landraces, exotic germplasm and wild relatives are the repository of many useful genes/alleles and can be utilized in breeding programs to develop new high yielding climate resilient cultivars.

The Consultative Group on International Agricultural Research (CGIAR), comprising 16 centers, represents the largest concerted effort toward collecting, preserving and utilizing global agricultural resources and holds nearly 7,60,000 samples of the estimated 7.4 million accessions of different crops preserved globally (FAO 2009). There are a number of germplasm banks, which are conserving the peanut germplasm worldwide. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India has the global responsibility of collecting, conserving

and distributing the peanut germplasm comprising landraces, modern cultivars, genetic stocks, mutants and wild *Arachis* species. It contains 14,968 accessions of cultivated peanut and 477 accessions of 48 wild *Arachis* species representing eight sections from 93 countries. These accessions came from donations as well as from collecting missions launched in different countries. Other major gene banks holding peanut germplasm include the National Bureau of Plant Genetic Resources, New Delhi (14,593 accessions), India; the Directorate of Groundnut Research, Junagadh (8,934 accessions), India; the United States Department of Agriculture (9,964 accessions), USA; the Instituto Nacional de Tecnología Agropecuaria, Argentina (8,347 accessions); the Institute of Crop Germplasm Resources, Beijing (6,565 accessions), China; Institute of Oil Crops Research, Wuhan (5,688 accessions), China; Crop Science Department, North Carolina State University, Raleigh, USA (3,788 accessions) and Estación Experimental Agropecuaria Manfredi, EEA INTA Manfredi, Argentina (2,158 accessions) (<http://apps3.fao.org>). Other gene banks specialized in conservation and maintenance of wild *Arachis* species are Texas A&M University, USA and Centro de Investigaciones de Nataima, Instituto Colombiano Agropecuario, Colombia (<http://apps3.fao.org>).

2.4 Assessing Species Diversity

2.4.1 Wild Relatives

Besides resistance to biotic and abiotic stresses (Dwivedi et al. 2003, 2008), wild *Arachis* species also harbor novel sources of variation for morpho-agronomic and nutritional traits, which can be used to enhance the genetic base of cultivated peanut. Stalker (1990) reported substantial variation in leaflet size and shape, branching habit and flower size among 73 wild *Arachis* species accessions, while Singh et al. (1996) found that the height of the main axis, length of apical leaflet on the main stem, length of isthmus between pods, seed width, and reaction to rust accounted for the greater part of variation amongst 42 *A. duranensis* accessions. The *A. pinto* accessions from section *Caulorrhizae* also showed greater variability for most of the morphological traits (Carvalho and Quesenberry 2009). Nautiyal et al. (2008) based on relative injury identified NRCG 11824 (*A. glabrata*) as heat tolerant and NRCG 12042 (*A. paraguariensis*) as cold tolerant, while NRCG 11786 (*A. appresipila*) susceptible both to heat and cold. Their study indicated that the plants with thicker leaves were better protected from heat injuries and epi-cuticular wax load helped in maintaining stomatal regulation and leaf water relations, thus enabling these species to thrive under water-limited environments. More recently, Upadhyaya et al. (2011b) evaluated the largest collections of wild *Arachis* species accessions (269) from 20 wild

Arachis species representing six sections for 41 morpho-agronomic traits and 89 accessions for nutritional traits. The species accessions showed large variability for days to flowering, pod and seed characteristics, Specific Leaf Area (SLA) and for SPAD Chlorophyll Meter Reading (SCMR). For example, *A. pusilla* accessions, ICG 14898 and ICG 14906 flowered in 13–14 days, the earliest flowering accessions among the 20 wild *Arachis* species studied and were a week earlier than the earliest flowering cultivated groundnut germplasm, Chico. Further, *A. duranensis* had maximum intraspecific variability for 23 of the 41 traits. The other species with desirable traits was *A. villosa* (high SCMR at 60 and 80 days after sowing). The best 20 wild *Arachis* accessions, possessing one to five desirable agronomic, nutritional and drought related traits identified in this study were ICG 8144 (*A. villosa*) high in SCMR, low SLA, high sugar content; ICG 3223, 13244, 14868, 14872, 14874, 14884 (*A. stenosperma*) superior in pod length and width and/or seed length and width; ICG 13211 (*A. pusilla*) earliest to flower; ICG 13178 (*A. monticola*) and ICG 13189 (*A. duranensis*) high in sugar; ICG 15142 (*A. pusilla*) and ICG 13227 (*A. dardani*) high in protein), which may be exploited to broaden the genetic base of cultivated peanut (Upadhyaya et al. 2011b).

2.4.2 *Cultigens*

2.4.2.1 *Geographical Diversity*

Geographical pattern of diversity, involving 13,342 accessions from 92 countries and 14 regions conserved in ICRISAT gene bank, revealed that South America (where primary and seven secondary centers of diversity are located) and China (an important center of diversity) are under-represented, which necessitates the exploration and collection of germplasm from these regions (Upadhyaya et al. 2002a). This study further revealed that though South America is under-represented in terms of number of accessions (10.06% of total accessions) but contained adequate diversity for morphological and agronomic traits. Further, the principal component analysis grouped the 14 regions into three clusters—accessions from North America, Middle East, and East Asia in the first cluster; South America in the second cluster; and West Africa, Europe, Central Africa, South Asia, Oceania, South Africa, East Africa, Southeast Asia, Central Asia, and Caribbean in the third cluster.

2.4.2.2 *Biological Diversity*

Several studies in the past involving 22 to 125 genotypes were used to quantify variability for morpho-agronomic traits (Vaddoria and Patel 1990; Reddy and Gupta 1992; Pathirana 1993; Senapati and Roy 1998; Singh and

Chaubey 2003; John et al. 2005; Kotzamanidis et al. 2006; Sumathi and Muralidharan 2007; Korat et al. 2009; Sumathi et al. 2009; Sadeghi et al. 2011; Vekariya et al. 2011; Nautiyal et al. 2012).

Upadhyaya (2003) used morpho-agronomic traits to study phenotypic diversity in peanut core collection consisting of 1,704 accessions of which 910 belong to subsp. *fastigiata* (var. *fastigiata*, *vulgaris*, *aequatoriana*, *peruviana*) and 794 to subsp. *hypogaea* (var. *hypogaea*, *hirsuta*). The two groups, subsp. *fastigiata* and *hypogaea*, differed significantly for most of the traits with the *hypogaea* accessions having significantly greater mean pod length, pod width, seed length, seed width, yield per plant and 100-seed weight. The *fastigiata* accessions had higher plant height, leaflet length, leaflet width and shelling percentage. They detected maximum diversity between ICG 13479 and ICG 8422 in the *fastigiata* group and between ICG 13723 and ICG 20016 in the *hypogaea* group. Further, they found that 12–15 morpho-agronomic traits explained most of the phenotypic variability. The ICRISAT peanut mini core (182 accessions) also showed sufficient variability for most of the morphological traits (Madhura et al. 2011). Swamy et al. (2003) evaluated Asia-specific peanut core collection (544 accessions (Upadhyaya et al. 2001) for 20 agronomic traits for two seasons that detected sufficient variability (except pod yield) explaining multivariate polymorphism. Accessions with maximum diversity were ICG 9581 and ICG 9973 in the *fastigiata* group and ICG 4906 and ICG 15126 in the *hypogaea* group.

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2.4.2.3 Trait Diversity

2.4.2.3.1 Early maturity: Most breeding programs aim at developing early-maturing cultivars that matches with the available crop duration. Appropriate time to flowering is a major component of crop adaptation, particularly in the environments where the growing season is restricted by terminal drought and high temperature. In most breeding programs, Chico has been used as the source of early maturity, which resulted in a narrow genetic base of peanut cultivars of this early maturing source. In a study involving sources of early maturity germplasm revealed that 21 such germplasm had similar a maturity as of Chico but produced ~12 and ~8% greater pod yield at 75 and 90 days harvest including the control cultivars such as Gangapuri and JL 24 (Upadhyaya et al. 2006). These new sources of early maturity grouped into three distinct clusters—cluster I comprises of ICG 9930, ICG 4558, Gangapuri and Chico, cluster II 12 landraces and JL 24, while cluster III had seven landraces.

2.4.2.3.2 Yield and component traits: Evaluation of a peanut core collection for Asia across multilocations resulted in identification of 15 *fastigiata*, 20 *vulgaris*, and 25 *hypogaea* type peanut accessions for pod yield, total pods,

shelling percentage, 100-seed weight and oil content. Clustering of these accessions together with controls resulted in four clusters in *fastigiata* and three clusters each in *vulgaris* and *hypogaea*. The control cultivars, Gangapuri in *fastigiata*, ICGS 44 in *vulgaris* and ICGS 76 and S 230 in *hypogaea* clustered separately indicating that the selected accessions were diverse from the control cultivars (Upadhyaya et al. 2005).

2.4.2.3.3 Drought tolerance: Upadhyaya (2005) evaluated peanut mini core collection for SLA and SCMR, associated with drought tolerance. The five and 13 most promising *vulgaris* and *hypogaea* accessions identified in this study clustered into four groups, all *vulgaris* types (ICG 118, ICG 14985, ICG 2106, ICG 5236 and ICG 6654) clustering with controls (Gangapuri, ICGS 44 and ICGS 76) in Cluster I, most of the *hypogaea* accessions including control cultivar M 13 (*hypogaea*) in cluster II, while ICG 6766 and ICG 14523 forming separate clusters, indicating that these two are diverse and can be used in breeding to enhance drought tolerance in peanut cultivars. Ravindra et al. (1990) reported that GG 2 in comparison to J11, JL 24 and TMV 10 has an inherent ability to produce more under drought stress occurring at any growth stage, while Ratnakumar and Vadez (2011) suggested that genotypes with lower leaf area may use water more sparingly under intermittent drought stress, which will have less damaging consequences for reproductive and pod development than genotypes having larger leaf area.

2.4.2.3.4 Cold tolerance: Upadhyaya et al. (2009) studied the phenotypic diversity in 158 cold tolerant peanut germplasm, which reported substantial diversity for base-temperature tolerance at germination (12°C, as used by Bell et al. 1994) as well as for agronomic traits. The clustering pattern grouped the cold tolerant accessions into four clusters. The accessions in these four clusters differed in mean, variance and range for agronomic traits. The cold tolerant accessions were superior to control cultivars for several agronomic traits indicating the potential of these accessions in developing genetically diverse cold tolerant peanut cultivars.

2.4.2.3.5 Salinity: Srivastava (2010) evaluated 275 accessions representing mini core, high yielding breeding lines and landraces from salinity prone areas and identified ICG 5195, ICG 442, ICG 7283, ICG 1711, ICG 2106 and ICG 1519 as good sources of salinity tolerance.

2.4.2.3.6 Resistance to diseases: ICG 11426, ICG 13787 and ICG 8760 were identified as resistant to rust and late leaf spot, ICG 14985, ICG 3673, ICG 6025, ICG 12625, ICG 13787 and ICG 8760. Of these, ICG 13787 and ICG 8760 were resistant to all the three diseases (Kusuma et al. 2007); ICG 875, ICG 928, ICG 1668, and ICG 14466 resistant to the bud necrosis disease (Ahmed 2008). In another study, accessions from ICRISAT peanut mini core were

found more resistant to seed colonization by *Aspergillus flavus* and aflatoxin production from ICRISAT peanut mini core than those from Chinese peanut mini core, with ICG 6813, ICG 12370, ICG 4750, ICG 4156, ICG 12625, ICG 12697, ICG 14482 combining resistance to both seed invasion and aflatoxin production (Jiang et al. 2010a). Molecular profiling study further revealed that ICG 12625 (resistance to aflatoxin production) and ICG 4750 (resistance to seed invasion) were diverse from the rest of the accessions (Jiang et al. 2010a). ICG 36, ICG 118, ICG 1448, ICG 434, ICG 1415, ICG 5745, ICG 76, ICG 1668, ICG 14710, ICG 6057, ICG 6201, ICG 1455, ICG 397 and ICG 7633 were identified as resistance to bacterial wilt (rcg). US researchers identified a number of accessions tolerant to root-knot nematode, early leaf spot, pepper spot, tomato spotted wilt virus and soil borne fungal diseases, including pre-harvest aflatoxin contamination (Isleib et al. 1995; Anderson et al. 1996; Holbrook et al. 1998, 2000; Franke et al. 1999; Damicone et al. 2010; Chamberlin et al. 2010).

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2.4.2.3.7 Seed quality traits: Upadhyaya et al. (2012) found sufficient variation for protein, oil and fatty acid composition including oleic (O), linoleic (L) fatty acids and O/L ratio in peanut mini core collection. Subsp. *fastigiata* as a group has shown relatively high variation for protein, while subsp. *hypogaea* for high O/L ratio. They identified accessions with high protein and oil, and better O/L ratio. Cluster analysis delineated these accessions into three clusters: cluster 1 those with high oleic acid, high pod yield, and high 100-seed weight, cluster 2 with those having high O/L and early flowering, while cluster 3 had accessions with high protein and high shelling percentage.

2.5 Genetic and Genomic Resources to Promote Utilization of Germplasm in Breeding

2.5.1 Core/mini core Subsets to Identifying New Sources of Variation

The low use of germplasm accessions in breeding programs is mainly due to the lack of information on traits of economic importance such as yield, resistance to biotic and abiotic stresses and quality traits, which often show high genotype x environment interactions that require replicated multilocational evaluations. This is a costly and resource-demanding task owing to the large size of the germplasm collections. Thus, the collection needs to be sampled to get the size of the collections to a manageable level for meaningful evaluation. Frankel (1984) coined the term “core collection” to sample representative variability from the entire collection. A core collection contains 10% of the accessions from the entire collection that captures most of the available diversity in the species (Brown 1989a).

Frankel and Brown (1984) suggested that greater use of germplasm in crop improvement is possible if a small collection representing diversity is made available for characterization and utilization. Thus, core collection has a reduced size containing a diverse set of germplasm that represents the entire collection. Such a core collection can be evaluated extensively and the information derived could be used to guide more efficient utilization of the entire collection (Brown 1989b).

A number of reduced subsets in the form of core or mini core collections (Upadhyaya and Ortiz 2001) have been reported in peanut (Table 2-1), which researchers at ICRISAT have used to identify new sources of variation for important agronomic and nutritional traits (Table 2-2) or resistance to various biotic and abiotic stresses (Table 2-3). For example, 21 accessions combining early maturity with high yield (Upadhyaya et al. 2006), 60 accessions having greater pod yield, shelling percentage, 100-seed weight and oil content (Upadhyaya et al. 2005), or 12 accessions with 100-seed weight ≥ 60 g (Upadhyaya et al. 2010), Likewise, a number of accessions with high oil and protein contents or accessions with O/L ratio greater than 3.0 have been identified (Upadhyaya et al. 2012). Furthermore, accessions tolerant to drought (Upadhyaya 2005), low temperature (Upadhyaya et al. 2009), salinity (Srivastava 2010), aflatoxin (Kusuma et al. 2007; Jiang et al. 2010a) or resistant to bud necrosis disease (Ahmed 2008) have been reported. Few of these accessions have also shown multiple resistances—ICG 11426,

Table 2-1 Core and mini core collections as reported in peanut.

Reduced subset	# accessions used in forming reduced subset	# traits used in forming reduced subset	# accessions in constituted subset	% of accessions in reduced subset representing entire collection	Reference
US Valencia core	630	26	77	12.22	Dwivedi et al. 2008
US core	7,432	6	831	11.18	Holbrook et al. 1993
Chinese core	6,390	15	576	9.01	Jiang et al. 2008
Asian core	4738	15	504	10.64	Upadhyaya et al. 2001
Global core	14,310	14	1,704	11.91	Upadhyaya et al. 2003
USA mini core	831	16	111	13.36	Holbrook and Dong 2005
ICRISAT mini core	1,704	31	184	1.28	Upadhyaya et al. 2002b

Table 2-2 Promising germplasm accessions identified for agronomic and nutritional traits.

Traits	Few promising germplasm	Reference
Early maturity	ICG# 4558, 4890, 9930, and 11605 having early maturity and 3–4 seeds per pod	Upadhyaya et al. 2006
Large seed size	ICG# 2381, 5016, 5051, 5745, 5662, 6057, 6766, 8760, 11219, 11855, 11862, and 14482	Upadhyaya et al. 2010
Yield and component traits	60 accessions: ICG# 4, 29, 3443, 14161, 11188, 7140, 2918 and others	Upadhyaya et al. 2005
Protein content (>30%)	5 accessions: ICG# 36, 5779, 3421, 3584, and 2019	Upadhyaya et al. 2012
Oil content (>50%)	ICG 442	Upadhyaya et al. 2012
Oleic acid ($\geq 60\%$)	6 accessions: ICG# 2381, 10185, 15419, 12276, 7243, and 11088	Upadhyaya et al. 2012
O/L ratio (>3.0)	12 accessions: ICG# 2381 (O/L ratio of 7.0), 10185, 6022, 1274, 7243, 6766, 12625, 12276, 15419, PI 274193, PI 290594, PI 468271	Upadhyaya et al. 2012; Dean et al. 2009

Table 2-3 Promising germplasm accessions having tolerance/resistance to abiotic/biotic stresses.

Traits	Promising accessions	Reference
Drought	18 accessions: ICG# 14523, 6766, 7243, 862, 6654, 14985 and others	Upadhyaya 2005
	30 accessions: ICG# 11088, 12697, 8751, 3140, 3584 and others	Hamidou et al. 2012
Low temperature	15 accessions with superior pod yield: ICG# 12625, 7898, 11130, 6148, 7013, 6022, 7905, 7884, 4992, 9515, 10915, 10567, 1710, 11088 and 10945	Upadhyaya et al. 2009
Salinity	6 accessions: ICG# 5195, 442, 7283, 1711, 2106, and 1519	Srivastava 2010
Rhizoctonia limb rot resistant	6 accessions: PI# 343398, 343361, 288178, 331326, 497351 and 274193	Franke et al. 1999
Late leaf spot	7 accessions: ICG# 12625, 11426, 12672, 13787, 14475, 2857, and 8760	Kusuma et al. 2007
Rust	5 accessions: ICG# 9809, 11088, 11426, 13787, and 8760	Kusuma et al. 2007
<i>A. flavus</i>	12 accessions: ICG# 14985, 3673, 6025, 12625, 13787, 8760, 6813, 12370, 4750, 4156, 12697, and 14482	Kusuma et al. 2007; Jiang et al. 2010a
Bud necrosis	4 accessions: ICG# 875, 928, 1668, and 14466	Ahmed 2008
Combined resistance to Sclerotinia blight, pepper spot and web blotch	5 accessions: PI# 274193, 497599, 458619, 468195, and 259796	Damicone et al. 2010
Sclerotinia blight resistant	39 accessions	Chamberlin et al. 2010

ICG 13787 and ICG 8760 resistant to late leaf spot and rust or ICG 13787 and ICG 8760 resistant to late leaf spot, rust and *A. flavus* (Kusuma et al. 2007).

2.5.2 Assessing Population Structure and Diversity in Germplasm

Of late, a number of publications have come out detailing the allelic richness and diversity amongst the cultivated peanut germplasm. Most of these studies reported on an average 3–15 alleles per locus (Table 2-4), with Barkley et al. (2007) and Kottapalli et al. (2011) detecting 13–15 alleles. Furthermore, a few of these studies clearly separated accessions based on botanical groups or accessions within species into different clusters, clearly indicating diversity among accessions (Ferguson et al. 2004; Moretzsohn et al. 2004; He et al. 2005; Mace et al. 2007; Kottapalli et al. 2011). For example, 10 simple sequence repeat (SSR) loci separated South American landraces from African and Asian landraces (Ferguson et al. 2004); *hypogaea* and *fastigiata* forming distinct clusters (Mace et al. 2007); Valencia accessions clustering into different groups (Kottapalli et al. 2011); SSR loci contributing more variation to rust and/or late leaf spot (Mace et al. 2006) and bacterial wilt (Mace et al. 2007) or SSR loci detecting more diversity in *fastigiata* than those of *hypogaea* accessions (Jiang et al. 2007); Chinese peanut mini core contributing more diversity than that of ICRISAT mini core with accessions L 2 Gangguo (a Chinese genotype) and ICG 12625 (an ICRISAT genotype) revealing the highest genetic dissimilarity (Jiang et al. 2010b). Likewise, the South American landraces showed high allelic diversity than those from Africa and Asia (Ferguson et al. 2004), while a new marker (Ah-041) differentiated AA-genome species accessions with those from non-AA genome species accessions (Moretzsohn et al. 2004). These examples clearly demonstrate that marker-based information provides breeders critical inputs to plan future breeding strategies in peanut.

2.5.3 Molecular Markers and Genetic Maps

Molecular markers are important for germplasm characterization, to assess variability for identifying genetically diverse traits-specific germplasm and marker-trait association in crop improvement programs. DNA-based markers provide a reliable means of estimating the genetic relationships between genotypes and taxonomic groups as compared to morphological markers. Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) markers detected little variation among *A. hypogaea* cultivars and germplasm lines whereas abundant polymorphism amongst

Table 2-4 Allelic richness and diversity, and grouping of accessions based on allelic diversity in peanut.

# genotypes	# SSR	Allelic richness	Summarized findings	Reference
22 accessions including wild species	6	38 fragments, averaged 6 fragments per primer	Effective in detecting molecular variation in cultivated peanut	Hopkins et al. 1999
24 accessions	56	79 alleles, averaged 4 alleles per locus	Highlighted a simple and reliable way in obtaining polymorphic SSR markers from cultivated peanut	He et al. 2003
188 landraces	10	89 alleles, averaged 7 alleles per locus	Discriminated South American landraces than those from Africa and Asia	Ferguson et al. 2004
60 accessions	8	74 alleles, averaged 8.4 alleles per locus	Highlighted the usefulness of SSR markers for genetic diversity analysis of cultivated peanut	Moretsohn et al. 2004
60 cultivated and 36 wild species accessions	12	-	More diversity amongst the Brazilian germplasm; two major groups among <i>A. hypogaea</i> accessions; high marker transferability between <i>Arachis</i> species, Ah-041 showing 100% transferability across species	Moretsohn et al. 2004
48 accessions representing six botanical varieties	38	-	Differentiated six botanical types (<i>fastigiata</i> , <i>vulgaris</i> , <i>hypogaea</i> , <i>hirsuta</i> , <i>peruviana</i> and <i>aequatoriana</i>) into separate groups	He et al. 2005
22 accessions	23	135 alleles, averaged 6 alleles per locus	Few SSRs differentiated rust and/or late leaf spot resistant germplasm	Mace et al. 2006
46 accessions representing six botanical types	32	107 alleles, averaged 3 alleles per locus	Two distinct groups corresponding to subspecies <i>hypogaea</i> and <i>fastigiata</i> ; six alleles differentiated bacterial wilt resistant and susceptible accessions	Mace et al. 2007
31 bacterial wilt resistant accessions	SSR: 78; AFLP 126	91 loci (3.14 alleles per locus) with SSR and 72 loci (2.25 alleles per locus) with AFLP markers	14H06, 7G02, 3A8, 16C6, and P1M62 were effective in detecting polymorphism	Jiang et al. 2007
US peanut mini core and wild relatives	31	477 alleles, averaged 15.4 alleles per locus	13 transferable markers across all wild relative accessions	Barkley et al. 2007
114 Valencia peanut accessions	52	683 alleles, averaged 13 alleles per locus	Differentiated Valencia germplasm into five clusters with two distinct major groups	Kottapalli et al. 2011
466 accessions	26	-	Greater diversity among the Chinese mini core accessions; L2 Gangguo and ICG 12625 the most genetically diverse; among six botanical types, accessions of <i>fastigiata</i> and <i>hypogaea</i> were more diverse than other types	Jiang et al. 2010b

wild *Arachis* species (Halward et al. 1991; Halward et al. 1992; Paik-Ro et al. 1992; He and Prakash 1997; Subramanian et al. 2000; Gimenes et al. 2002).

The SSR (also known as microsatellites) and Single Nucleotide Polymorphism (SNP) markers are becoming important in molecular breeding of most crops including peanut because of their codominant nature, high polymorphism and transferability among related species. Concerted effort during the past decade has led to the development of >6,000 SSR markers and about >2,000 SNPs at the University of Georgia, USA (Pandey et al. 2012). The other marker system, a Diversity Array Technology (DArT) platform comprising of about 15,000 DArT clones has been developed at DArT Ptv. Ltd (Australia) in collaboration with ICRISAT (India), CIRAD (France), Catholic University of Brasilia and EMBRAPA (Brazil). Use of DArT arrays with a range of genotypes representing diploid (AA, BB) and tetraploid (AABB) genome species showed low polymorphism in tetraploids but more diversity among accessions from diploid species (Kilian 2008; Varshney et al. 2010), which indicate that DArT markers may not be very useful in peanut breeding and genetics; however, more useful in monitoring genome introgression from diploid to cultivated peanut (Pandey et al. 2012).

Moretzsohn et al. (2005) constructed A-genome based genetic map in *Arachis* by using an F_2 population derived from a cross between two diploid species with AA genome (*A. duranensis* × *A. stenosperma*). This genetic map placed 170 SSR loci on 11 linkage groups (LGs) covering 1,231 cM, with an average distance of 7.24 cM. Further, Gobbi et al. (2006) developed B-genome based F_2 map by crossing *A. ipaensis* and *A. magna*, which mapped 130 SSR loci into 10 LGs. However, these maps have limited value to cultivated peanut, a tetraploid, and hence there is a need to develop tetraploid-based genetic maps in cultivated peanut. Varshney et al. (2009) were probably the first to construct SSR-based genetic linkage map for the cultivated peanut that mapped 135 SSR loci into 22 LGs, which was further saturated with the current map having 191 SSR loci into 20 LGs and a total map distance of 1,785 cM (Ravi et al. 2011). Subsequently, several other genetic maps for cultivated peanut have become available (reviewed in Pandey et al. 2012).

2.5.4 Markers Associated with Agronomically Beneficial Traits

Using genetic mapping, a number of markers/QTLs (Quantitative Trait Loci) associated with useful traits have been reported and used to introgress beneficial traits to cultivated peanut. Introgression of nematode-resistant gene from *A. cardenasii* into *A. hypogaea* was reported in 10 of 11 linkage groups (Garcia et al. 1995), which were used to develop nematode-resistant germplasm (Garcia et al. 1996). Two dominant genes conferring resistance to root-knot nematode, *Meloidogyne arenaria* race 1 were mapped using RAPD

and Sequence-Characterized Amplified Region (SCAR) markers (Garcia et al. 1996). One marker, Z3/265, closely linked with *M. arenaria* resistance, was mapped to a linkage group on a backcross map in an area known to contain *A. cardenasii* introgression. This marker was cloned to make SCAR and RFLP probes, which further confirmed the linkage with nematode resistance. Subsequently, the RFLP markers linked to a locus for resistance to *M. arenaria* race 1 has been identified by various workers (Choi et al. 1999; Church et al. 2000; Seib et al. 2003) that provided a useful selection method for identifying resistance to the peanut root-knot nematode. Likewise, RAPD markers associated with nematode resistance in BC₄F₂ of the cross involving Florunner and TxAg-6 has been identified: *RKN410* and *RKN440* closely linked with each other identified a resistance gene derived from either *A. cardenasii* or *A. diogeni*, while *RKN229*, inherited from *A. cardenasii* or *A. diogeni* was 9 cM away from this locus (Burow et al. 1996). Herselman et al. (2004) identified 20 putative AFLP markers associated with aphid vector of peanut rosette disease, of which, 12 mapped to five linkage groups covering a map distance of 139.4 cM, while Varma et al. (2005) reported two to seven SSR alleles associated with rust resistance in two F₂ populations. A few SSR markers associated with yield and yield contributing traits were also reported (Liang et al. 2009; Selvaraj et al. 2009).

Molecular mapping of drought tolerance traits identified 153 main-effect and 25 epistatic QTLs (Varshney et al. 2009; Ravi et al. 2011; Gautami et al. 2012). A major QTL each for leaf rust (Khedikar et al. 2010; Sujay et al. 2012) and late leaf spot (Sujay et al. 2012) has been identified for use in peanut breeding. Likewise, QTLs associated with peanut nutritional traits such as oil and protein contents have been identified (Sarvamangala et al. 2011). Diagnostic markers for resistance to nematode (Nagy et al. 2010), leaf rust (Khedikar et al. 2010), late leaf spot (Sujay et al. 2012) and high-oleate trait (Chu et al. 2009; Chen et al. 2010) are available for use in molecular breeding of peanut.

2.5.5 Association Mapping

The phenotypic variation of agronomically important traits is influenced by multiple QTLs, their interaction, the environment and the QTL x environment interactions. Association mapping, also known as Linkage Disequilibrium (LD) mapping, is a relatively new and promising tool for dissecting complex traits. Association mapping in comparison to the traditional linkage mapping has major advantages due to increased mapping resolution through exploitation of historical and evolutionary recombination events at the population level (Risch and Merikangas 1996; Nordborg and Tavare 2002). The prerequisites to perform association mapping include a dense genetic linkage map, passport information and

phenotypic data, an understanding of population structure, and contrasting genotypes for beneficial traits (Kresovich et al. 2002). The marker-trait association approach relies on the assumption that an allele responsible for a phenotype and the associated flanking markers are inherited as a block, and therefore neutral marker-based selection will be predictive of allelic content at critical genes determining favorable phenotype. Such marker-trait associations in a collection of plant genetic resources would allow the assessment of the genetic potential of specific genotypes prior to phenotypic evaluation and identification of superior trait alleles in germplasm collection (Gebhardt et al. 2004).

Belamkar et al. (2010) used 32 highly-polymorphic SSRs to study population structure and LD in 96 peanut genotypes comprising 92 US peanut mini core accessions, the diploid progenitors *A. duranensis* (AA) and *A. ipaensis* (BB) and synthetic amphidiploid accession TxAG-6 and a widely grown US peanut cultivar, Florunner. The population structure revealed that the diploid progenitors and their synthetic amphidiploid grouped separately from most mini core accessions. UPGMA and model-based clustering divided the population into four subgroups, two major subgroups representing subspecies *fastigiata* and *hypogaea*, a third group containing mixed individuals, while the fourth containing diploid progenitors and TxAG-6. Unified mixed linear model analysis incorporating population structure and kinship identified several SSR loci associated with drought tolerance traits. This study revealed the importance of LD mapping in exploiting the natural variation present in cultivated peanut. Wang et al. (2011) studied the population structure and marker-trait association by genotyping 94 accessions with 81 SSRs and two functional SNPs from Fatty Acid Desaturase 2 (FAD2), which identified four major subpopulations, related to four botanical varieties. Candidate-gene association analysis verified that one functional SNP from the *FAD2A* gene is significantly associated with oleic acid (C18:1), linoleic acid (C18:2), and oleic-to-linoleic (O/L) ratio across this diverse collection.

2.5.6 Amphidiploids as Source of Agronomically Beneficial Traits

Utilization of wild *Arachis* species following interspecific hybridization has resulted in the development of many elite germplasm lines and cultivars with improved level of resistance to diseases and insect-pests (Dwivedi et al. 2008 and references cited therein). Varieties such as Spancross (Hammons 1970), Tamnut 74 (Simpson and Smith 1975), Coan (Simpson and Starr 2001), NemaTAM (Simpson et al. 2003), having a genetic base from wild *Arachis* species, were released for cultivation in the USA. Likewise, ICGV-SM 85048 and ICGV-SM 86715 have been released for cultivation in Mauritius (Nigam et al. 1998; Moss et al. 1998).

The development and utilization of synthetic amphidiploids such as TxAG-6 with high genetic variations (Simpson et al. 1993) in breeding programs has made possible the transfer of resistance genes from wild species into cultivated peanut. This amphidiploid has been synthesized using species that are not in the direct lineage of the cultigen. However, it is crossable with the cultivated peanut and produced fertile progenies thus proved useful for introducing genetic variability into the cultigen. Crosses involving TxAG-6 with cultivated peanut has resulted in the release of two cultivars (Coan and NemaTAM) carrying genes for root-knot nematode (*M. arenaria*) resistance from *A. cardenasii* (Simpson and Starr 2001, Simpson et al. 2003). TxAG-6 is a small-seeded (~12 g 100 seed weight) and low-yielding (2–5 g plant⁻¹), which when crossed with TMV 2 (32 g 100 seed weight) at ICRISAT produced backcrossed progenies with much higher seed weight and yielded 23 to 68% more than TMV 2 (3,343 kg ha⁻¹). These backcrossed progenies also out yielded by 10 to 50% the highest yielding control cultivar ICGV 91114 (3,741 kg ha⁻¹, 49 g 100-seed weight⁻¹) (Upadhyaya 2008). This demonstrated that the novel alleles of wild relatives, that were considered to be lost in evolution to cultivated types, could be used to enhance the trait value in peanut cultivar development. Encouraged with this, the researchers at ICRISAT have developed a number of amphidiploids that are being assessed for releasing novel variation for use in peanut breeding (Mallikarjuna et al. 2012).

2.6 Conclusions

Natural genetic variation and means to exploit such variability is the key to the success of crop improvement programs. Large collections of peanut germplasm including wild *Arachis* species have been preserved in gene banks worldwide, representing a large spectrum of diversity in the genus *Arachis*. Development and evaluation of small-sized subsets such as core and mini core have resulted in the identification of trait-specific germplasm accessions for agronomic traits including resistance to abiotic and biotic stresses and nutritional traits, which would result in the enhanced utilization of genetic resources to broaden the genetic base to face new challenges to peanut production. Considerable variability for some traits of interest exists in wild *Arachis* gene pools, which can be brought, using wide hybridization and applying novel tools, in crop cultigens for sustainable production of peanut globally. Several elite germplasm lines and the cultivars carrying resistances from wild *Arachis* species have been released for use as a resource in crop breeding or even for direct cultivation. More importantly, amphidiploids are now being developed using species that were earlier not easily crossable, and the work so far revealed that these amphidiploids have the potential to release hidden variability that was locked due to

bottlenecks associated with the origin of cultivated peanut, thus making available more variability to peanut research community. Unlike in the 80s and 90s, the availability of a large number of PCR-based markers (SSRs and SNPs), high-throughput genotyping platforms and bioinformatics resources have enabling effects towards identifying and tracking allelic variants associated with beneficial traits and identifying desirable recombinant plants with the traits of interest, thus accelerating molecular breeding in peanut improvement.

References

- Ahmed K (2008) Evaluation of groundnut (*Arachis hypogaea* L.) germplasm (Mini core collection). MSc Thesis, University of Agricultural Sciences, Dharwad, Bangalore, India.
- Anderson WF, Holbrook CC, Culbreath AK (1996) Screening the peanut core collection for resistance to tomato spotted wilt virus. *Peanut Sci* 23: 57–61.
- Barkley NA, Dean RE, Pittman RN, Wang ML, Holbrook CC, Pederson GA (2007) Genetic diversity of cultivated and wild-type peanuts evaluated with M13-tailed SSR markers and sequencing. *Genet Res Camb* 89: 93–106.
- Belamkar V, Selvaraj MG, Ayers JL, Payton PR, Puppala N, Burrow MD (2010) A first insight into population structure and linkage disequilibrium in peanut, and association mapping of drought tolerance-related traits in the US peanut minicore collection. In: Proceedings of Plant and Animal Genomes XVIII Conference, 9–13 January 2010, San Diego, USA, p 423.
- Bell MJ, Roy RC, Tollenaar M, Michaels TE (1994) Importance of variation in chilling tolerance for peanut genotypic adaptation to cool short-season environments. *Crop Sci* 34: 1030–1039.
- Brown AHD (1989a) Core collections: a practical approach to genetic resources management. *Genome* 31: 818–824.
- Brown AHD (1989b) The case for core collections. In: Brown AHD, Frankel OH, Marshall DR, Williams JT (eds) *The Use of Plant Genetic Resources*. Cambridge University Press, Cambridge, UK, pp 136–155.
- Burrow MD, Simpson CE, Paterson AH, Starr JL (1996) Identification of peanut (*Arachis hypogaea* L.) RAPD markers diagnostic of root-knot nematode (*Meloidogyne arenaria* (Neal) Chitwood) resistance. *Mol Breed* 2: 369–379.
- Carvalho MA, Quesenberry KH (2009) Morphological characterization of the USA *Arachis pinto* Krap. and Greg. collection. *Plant Syst Evol* 277: 1–11.
- Chamberlin KDC, Melouk HA, Payton ME (2010) Evaluation of the US peanut mini core collection using a molecular marker for resistance to *Sclerotinia minor* Jagger. *Euphytica* 172: 109–115.
- Chen CY, Guo B, Qin H, Feng S, Dang P, Culbreath A, Wang ML, Holbrook C (2010) Morphological and molecular marker characterization of two RIL mapping populations in cultivated peanuts. In: Proceedings of Plant and Animal Genome XIX Conference, 9–13 January 2010, San Diego, USA, p 422.
- Choi K, Burrow MD, Church G, Burrow G, Paterson AH, Simpson CE, Starr JL (1999) Genetics and mechanism of resistance to *Meloidogyne arenaria* in peanut germplasm. *J Nematol* 31: 283–290.
- Chu Y, Holbrook CC, Ozias-Akins P (2009) Two alleles of ahFAD2B control the high oleic acid trait in cultivated peanut. *Crop Sci* 49: 2029–2036.
- Church GT, Simpson CE, Burrow MD, Paterson AH, Starr JL (2000) Use of RFLP markers for identification of individuals homozygous for resistance to *Meloidogyne arenaria* in peanut. *Nematology* 2: 575–580.

- Damicone JP, Holbrook CC, Smith DL, Melouk HA, Chamberlin KD (2010) Reaction of the core collection of peanut germplasm to *Sclerotinia* blight and pepper spot. *Peanut Sci* 37: 1–11.
- Dean LL, Hendrix KW, Holbrook CC, Sanders TH (2009) Content of some nutrients in the core of the peanut germplasm collection. *Peanut Sci* 36: 104–120.
- Dwivedi SL, Crouch JH, Nigam SN, Ferguson ME, Paterson AH (2003) Molecular Breeding of groundnut for enhanced productivity and food security in the semi-arid tropics: Opportunities and challenges. *Adv Agron* 80: 153–221.
- Dwivedi SL, Upadhyaya HD, Blair MW, Bertioli DJ, Nielen S, Ortiz RO (2008) Enhancing crop gene pools with beneficial traits using wild relatives. *Plant Breed Rev* 30: 179–230.
- FAO (2009) The state of *ex situ* conservation. In: *The Second State of the World's Plant Genetic Resources for Food and Agriculture*. FAO, Rome, Italy, pp 51–87.
- FAO (2010) FAO (<http://apps.fao.org/page/collections?subset=agriculture>), Rome, Italy.
- Ferguson ME, Burrow MD, Schultze SR, Bramel PJ, Paterson AH, Kresovich S, Mitchell S (2004) Microsatellite identification and characterization in peanut (*A. hypogaea* L.). *Theor Appl Genet* 108: 1064–1070.
- Franke MD, Bennemen TB, Holbrook CC (1999) Identification of resistance to *Rhizoctonia* limb rot in a core collection of peanut germplasm. *Plant Dis* 83: 944–948.
- Frankel OH (1984) Genetic perspective of germplasm conservation. In: Arber W, Limensee K, Peacock WJ, Stralinger P (eds) *Genetic Manipulations: Impact on Man and Society*. Cambridge University Press, Cambridge, UK, pp 161–170.
- Frankel OH, Brown AHD (1984) Plant genetic resources today: a critical appraisal. In: Holden JHW, Williams JT (eds) *Crop Genetic Resources: Conservation and Evaluation*. George Allen and Unwin, London, UK, pp 249–257.
- Garcia GM, Stalker HT, Kochert G (1995) Introgression analysis of an interspecific hybrid population in peanuts (*Arachis hypogaea* L.) using RFLP and RAPD markers. *Genome* 38: 166–176.
- Garcia GM, Stalker HT, Shroeder E, Kochert G (1996) Identification of RAPD, SCAR and RFLP markers tightly linked to nematode resistance genes introgressed from *Arachis cardenasii* into *Arachis hypogaea*. *Genome* 39: 836–845.
- Gautami B, Pandey MK, Vadez V, Nigam SN, Ratnakumar P, Krishnamurthy L, Radhakrishnan T, Gowda MVC, Narasu ML, Hoisington DA, Knapp SJ, Varshney RK (2012) QTL analysis and consensus genetic map for drought tolerance traits based on three RIL populations of cultivated groundnut (*Arachis hypogaea* L.). *Mol Breed* 32: 757–772.
- Gebhardt C, Ballvora A, Walkemeier B, Oberhagemann P, Schuler K (2004) Assessing genetic potential in germplasm collections of crop plants by marker-trait association: a case study for potatoes with quantitative variation of resistance to late blight and maturity type. *Mol Breed* 13: 93–102.
- Gimenes MA, Lopes CR, Galgalo ML, Valls JFM, Kochert G (2002) RFLP analysis of genetic variation in species of section *Arachis*, genus *Arachis* (Leguminosae). *Euphytica* 123: 421–429.
- Gobbi A, Teixeira C, Moretzsohn M, Guimaraes P, Leal-Bertioli D, Lopes CR, Gimenes M (2006) Development of a linkage map to species of B genome related to the peanut (*Arachis hypogaea*-AABB). In: *Plant and Animal Genome XIV Conference*, 14–18th January 2006, San Diego, CA, USA, p 679.
- Halward T, Stalker HT (1987) Incompatibility mechanism in interspecific peanut hybrids. *Crop Sci* 27: 456–460.
- Halward T, Stalker HT, Larue E, Kochert G (1991) Genetic variation detectable with molecular markers among unadapted germplasm resources of cultivated peanut and related wild species. *Genome* 34: 1013–1020.
- Halward T, Stalker HT, Larue E, Kochert G (1992) Use of single-primer DNA amplification in genetic studies of peanut (*Arachis hypogaea* L.). *Plant Mol Biol* 18: 315–325.
- Hamidou F, Ratnakumar P, Halilou O, Mponda O, Kapewa T, Monyo E, Faye I, Ntare BR, Nigam SN, Upadhyaya HD, Vadez V (2012) Selection of intermittent drought tolerant

- lines across years and locations in the reference collection of groundnut (*Arachis hypogaea* L.). *Field Crops Res* 126: 189–199.
- Hammons RO (1970) Registration of Spangcross peanuts (Reg. No. 3). *Crop Sci* 10: 459–460.
- Hammons RO (1994) The origin and history of the groundnut. In: Smartt J (ed) *The Groundnut Crop: A Scientific Basis for Improvement*. Chapman Hall, London, UK, pp 24–39.
- He G, Prakash CS (1997) Identification of polymorphic DNA markers in cultivated peanut (*Arachis hypogaea* L.). *Euphytica* 97: 143–149.
- He G, Meng R, Newman M, Gao G, Pittman RN, Prakash CS (2003) Microsatellites as DNA markers in cultivated peanut (*Arachis hypogaea* L.). *BMC Plant Biol* 3: 3.
- He G, Meng R, Gao H, Gou B, Gao G, Newman M, Pittman RN, Prakash SH (2005) Simple sequence repeat markers for botanical varieties of cultivated peanut (*Arachis hypogaea* L.). *Euphytica* 142: 131–136.
- Herselman LR, Thwaites FM, Kimmins B, Courtois PJA, Merwe VD, Seal SE (2004) Identification and mapping of AFLP markers linked to peanut (*Arachis hypogaea* L.) resistance to the aphid vector of groundnut rosette disease. *Theor Appl Genet* 109: 1426–1433.
- Holbrook CC, Dong W (2005) Development and evaluation of a mini core collection for the U.S. peanut germplasm collection. *Crop Sci* 45: 1540–1544.
- Holbrook CC, Anderson WF, Pittman RN (1993) Selection of a core collection from the US germplasm collection of peanut. *Crop Sci* 33: 859–861.
- Holbrook CC, Bruniard J, Moore KM, Knauff DA (1998) Evaluation of the peanut core collection for oil content. In: *Agronomy Abstracts 1998*. American Society of Agronomy, Madison, WI, USA, p 159.
- Holbrook CC, Stephenson MG, Johnson AW (2000) Level and geographical distribution of resistance to *Meloidogyne arenaria* in the US peanut germplasm collection. *Crop Sci* 40: 1168–1171.
- Hopkins MS, Casa AM, Wang T, Michell SE, Dean RE, Kochert GD, Kresovich S (1999) Discovery and characterization of polymorphic simple sequence repeats (SSRs) in peanut. *Crop Sci* 39: 1243–1247.
- Isleib TG, Beute MK, Rice PW, Hollowell JE (1995) Screening the core collection for resistance to *Cylindrocladium* black rot and early leaf spot. *Proc Am Peanut Res Edu Soc* 27: 25.
- Jiang H, Liao B, Ren X, Lei Y, Mace E, Fu T, Crouch JH (2007) Comparative assessment of genetic diversity of peanut (*Arachis hypogaea* L.) genotypes with various levels of resistance to bacterial wilt through SSR and AFLP analyses. *J Genet Genom* 34: 544–554.
- Jiang HF, Ren XP, Liao BS, Huang JQ, Lei Y, Chen BY, Guo B, Holbrook CC, Upadhyaya HD (2008) Peanut core collection established in china and compared with ICRISAT mini core collection. *Acta Agron Sin* 34: 25–30.
- Jiang HF, Ren XP, Wang SY, Zhang XJ, Huang JQ, Liao BS, Holbrook CC, Upadhyaya HD (2010a) Development and evaluation of peanut germplasm with resistance to *Aspergillus flavus* from core collection. *Acta Agron Sin* 36: 428–434.
- Jiang HF, Ren XP, Zhang XJ, Huang JQ, Lei Y, Yan LY, Liao BS, Upadhyaya HD, Holbrook CC (2010b) Comparison of genetic diversity between peanut mini core collections from China and ICRISAT by SSR markers. *Acta Agron Sin* 36: 1084–1091.
- John K, Vasanthi RP, Venkateswarlu O, Naidu PH (2005) Variability and correlation studies for quantitative traits in Spanish bunch groundnut (*Arachis hypogaea* L.) genotypes. *Legume Res* 28: 189–193.
- Jung S, Tate PL, Horn R, Kochert G, Moore K, Abbott AG (2003) The phylogenetic relationship of possible progenitors of the cultivated peanut. *J Hered* 94: 334–340.
- Khedikar YP, Gowda MVC, Sarvamangala C, Patgar KV, Upadhyaya HD, Varshney RK (2010) A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 121: 971–984.
- Kilian A (2008) DArT-based whole genome profiling and novel information technologies in support system of modern breeding of groundnut. In: *Proceedings of 3rd International Conference for Peanut Genomics and Biotechnology on Advances in Arachis through Genomics and Biotechnology (AAGB)*, 4–8 November 2008, Hyderabad, India, p 02.

- Kocher G, Halward T, Branch WD, Simpson CE (1991) RFLP variability in peanut (*Arachis hypogaea* L.) cultivars and wild species. *Theor Appl Genet* 81: 565–570.
- Kochert G, Stalker HM, Gimense M, Galgaro L, Lopes CR, Moore K (1996) RFLP and cytogenetics evidence on the origin and evolution of allotetraploid domesticated peanut, *Arachis hypogaea* (Leguminosae). *Am J Bot* 83: 1282–1291.
- Korat VP, Pithia MS, Savaliya JJ, Pansuriya AG, Sodavadiya PR (2009) Studies on genetic variability in different genotypes of groundnut (*Arachis hypogaea* L.). *Legume Res* 32: 224–226.
- Kottapalli P, Upadhyaya HD, Kottapalli KR, Payton P, Dwivedi SL, Burow M, David KO, Sanogo S, Puppala N (2011) Population structure and diversity in Valencia peanut germplasm collection. *Crop Sci* 51: 1089–1100.
- Kotzamanidis ST, Stavropoulos N, Ipsilandis CG (2006) A systematic analysis for grouping Greek peanut (*Arachis hypogaea* L.) germplasm based on eight important phenotypic traits. *Asian J Plant Sci* 5: 481–486.
- Krapovickas A (1969) The origin, variability and spread of groundnut (*Arachis hypogaea* L.). In: Ucko PJ, Dimbley G (eds) *The Domestication and Exploitation of Plants and Animals*. Duckworth, London, UK, pp 135–151.
- Krapovickas A, Rigoni UA (1957) Nuevas especies de *Arachis* vinculadas al problema del origen del maní. *Darwinians* 11: 431–455.
- Krapovickas A, Gregory WC (1994) Taxonomía del género *Arachis* (Leguminosae). *Bonplandia* 8: 1–186 (in Spanish with English abstr).
- Krapovickas A, Gregory WC (2007) Taxonomy of the genus *Arachis* (Leguminosae) (Translated by DE Williams and CE Simpson). *Bonplandia* 16: 1205.
- Kresovich S, Luongo AJ, Schloss SJ (2002) Mining the gold: finding allelic variants for improved crop conservation and use. In: Engels JMM, Rao VR, Brown AHD, Jackson MT (eds) *Managing Plant Genetic Diversity*. CAB International, Wallingford, UK, pp 379–386.
- Kusuma VP, Yugandhar G, Ajay BC, Gowda MVC, Upadhyaya HD (2007) Identification of sources of multiple disease resistance in groundnut (*Arachis hypogaea* L.) mini core. In: *Proceedings of National Seminar by Indian Society of Oilseeds Research (ISOR)*, 29–31 January 2007, Directorate of Oilseeds Research, Rajendranagar, Hyderabad, India, pp 31–32.
- Liang X, Chen X, Hong Y, Liu H, Zhou G, Li S, Guo B (2009) Utility of EST-derived SSR in cultivated peanut (*Arachis hypogaea* L.) and *Arachis* wild species. *BMC Plant Biol* 9: 35.
- Mace ES, Phong DT, Upadhyaya HD, Chandra S, Crouch JH (2006) SSR analysis of cultivated groundnut (*Arachis hypogaea* L.) germplasm resistant to rust and late leaf spot diseases. *Euphytica* 152: 317–330.
- Mace ES, Yuejin W, Boshou L, Upadhyaya HD, Chandra S, Crouch JH (2007) Simple sequence repeat (SSR)-based diversity analysis of groundnut (*Arachis hypogaea* L.) germplasm resistant to bacterial wilt. *Plant Genet Resour Characteriz Utiliz* 5: 27–36.
- Madhura C, Kenchanagoudar, Basamma PV, Sujay V (2011) Morphological characterization of a minicore subset in different botanical types of groundnut (*Arachis hypogaea* L.). *Int J Plant Sci* 6: 280–284.
- Mallikarjuna N, Senthilvel S, Hoisington D (2012) Development of new sources of tetraploid *Arachis* to broaden the genetic base of cultivated groundnut (*Arachis hypogaea* L.). *Genet Resour Crop Evol* 58: 889–907.
- Moretzsohn MC, Hopkins MS, Mitchell SE, Kresovich S, Valls JFM, Ferreira ME (2004) Genetic diversity of peanut (*Arachis hypogaea* L.) and its wild relatives based on the analysis of hyper variable regions of the genome. *BMC Plant Biol* 4: 11.
- Moretzsohn MC, Leoi L, Proite K, Guimaraes PM, Leal-Bertioli SCM, Gimenes MA, Martins WS, Valls JFM, Grattapaglia D, Bertioli DJ (2005) A microsatellite-based, gene-rich linkage map for the AA genome of *Arachis* (Fabaceae). *Theor Appl Genet* 111: 1060–1071.
- Moss JP, Singh AK, Nigam SN, Hilderbrand GL, Govinden N, Ismael FM (1998) Registration of ICGV-SM 87165 peanut germplasm. *Crop Sci* 38: 572.

Initial missing

- Nagy E, Chu Y, Guo Y, Khanal S, Tang S, Li Y, Dong W, Timper P, Taylor C, Ozias-Akins P, Corley HC, Beilinson V, Nielsen N, Stalker H, Knapp S (2010) Recombination is suppressed in an alien introgression in peanut harboring *Rma*, a dominant root-knot nematode resistance gene. *Mol Breed* 26: 357–370.
- Nautiyal PC, Rajgopal K, Zala PV, Pujari DS, Basu M, Dhadhal BA, Nandre BM (2008) Evaluation of wild *Arachis* species for abiotic stress tolerance: I. Thermal stress and leaf water retentions. *Euphytica* 159: 43–57.
- Nautiyal PC, Ravindra V, Rathnakumar AL, Ajay BC, Zala PV (2012) Genetic variations in photosynthetic rate, pod yield and yield components in Spanish groundnut cultivars during three cropping seasons. *Field Crops Res* 125: 83–91.
- Nigam SN, Hildebrand GH, Bock KR, Ismael FM, Govinden N, Subrahmanyam P, Reddy LJ (1998) Registration of ICGV-SM 85048 peanut germplasm. *Crop Sci* 38: 572–573.
- Nordborg M, Tavare S (2002) Linkage disequilibrium: What history has to tell us. *Trends Genet* 18: 83–90.
- Paik-Ro OG, Smith RL, Knauff DA (1992) Restriction fragment length polymorphism evaluation of six peanut species within the *Arachis* section. *Theor Appl Genet* 84: 201–208.
- Pandey MK, Monyo E, Ozias-Akins P, Liang X, Guimarães P, Nigam SN, Upadhyaya HD, Janila P, Zhang X, Guo B, Cook DR, Bertioli DJ, Michelmore R, Varshney RK (2012) Advances in *Arachis* genomics for peanut improvement. *Biotechnol Adv* 30: 639–651.
- Pathirana R (1993) Yield component analysis of bunch groundnut (*Arachis hypogaea* L. ssp. *fastigiata*) germplasm in Sri Lanka. *Trop Agric* 70: 256–259.
- Ratnakumar P, Vadez V (2011) Groundnut (*Arachis hypogaea*) genotypes tolerant to intermittent drought maintain a high harvest index and have small leaf canopy under stress. *Funct Plant Biol* 38: 1016–1023.
- Ravi K, Vadez V, Isobe S, Mir RR, Guo Y, Nigam SN, Gowda MV, Radhakrishnan T, Bertioli DJ, Knapp SJ, Varshney RK (2011) Identification of several small effect main QTLs and large number of epistatic QTLs for drought tolerance in groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 122: 1119–1132.
- Ravindra V, Nautiyal PC, Joshi YC (1990) Physiological analysis of drought resistance and yield in groundnut (*Arachis hypogaea* L.). *Trop Agri* 67: 290–296.
- Reddy KR, Gupta RVS (1992) Variability and inter-relationship of yield and its component characters in groundnut. *J Maharashtra Agric Univ* 17: 224–226.
- Risch N, Merikangas K (1996) The future of genetic studies of complex human diseases. *Science* 273: 1516–1517.
- Sadeghi SM, Javid F, Niyaki SAN (2011) Assessment of genetic diversity in peanut (*Arachis hypogaea* L.) genotypes using quantitative traits by cluster analysis method. *Res J Biol Sci* 6: 293–297.
- Sarvamangala C, Gowda CLL, Varshney RK (2011) Identification of quantitative trait loci for protein content, oil content and oil quality for groundnut (*Arachis hypogaea* L.). *Field Crops Res* 122: 49–59.
- Seib JC, Wunder L, Gallo-Meagher M, Carpentieri-Pipolo V, Gobert DW, Dickson DW (2003) Marker-assisted selection in screening peanut for resistance to root-knot nematode. In: *Proc American Peanut Research Education Society*, July 8–11, 2003, Clearwater, Florida, 35: 90.
- Seijo JG, Lavia GI, Fernandez A, Krapovickas A, Ducasse D, Moscone EA (2004) Physical mapping of the 5S and 18S-25S rRNA genes by fish as evidence that *Arachis duranensis* and *A. ipaensis* are the wild diploid progenitors of *A. hypogaea*. *Am J Bot* 91: 1294–1303.
- Selvaraj MG, Narayana M, Schubert AM, Ayers JL, Baring MR, Burow MD (2009) Identification of QTLs for pod and kernel traits in cultivated peanut by bulked segregant analysis. *Elec J Biotechnol* 12: DOI: 10.2225/vol12.
- Senapati BK, Roy K (1998) Correlation coefficients among stability parameters of yield and yield contributing characters in groundnut (*Arachis hypogaea* L.). *Legume Res* 21: 37–40.
- Simpson CE, Smith OD (1975) Registration of Tamnut 74 peanut (Reg. No. 19). *Crop Sci* 15: 603–604.

- Simpson CE, Starr JL (2001) Registration of COAN peanut. *Crop Sci* 41: 918.
- Simpson CE, Starr JL, Nelson SC, Woodard KE, Smith OD (1993) Registration of TxAG-6 and TxAG-7 peanut germplasm. *Crop Sci* 33: 1418.
- Simpson CE, Starr JL, Church GT, Burrow MD, Paterson AH (2003) Registration of 'Nema TAM' peanut. *Crop Sci* 43: 1561.
- Singh AK (1995) Groundnut, *Arachis hypogaea* Lin. (Leguminosae-Papilionoideae). In: Simmonds NW, Smartt J (eds) *Evolution of Crop Plants*, 2nd ed. Longman Group Ltd., London, pp 246–250.
- Singh AK, Nigam SN (1997) Groundnut. In: Fuccillo D, Sears L, Stapleton P (eds) *Biodiversity in Trust. Conservation and Use of Plant Genetic Resources on CGIAR Centres*. Cambridge University Press, UK, pp 114–127.
- Singh AK, Simpson CE (1994) Biosystematics and genetic resources. In: Smartt J (ed) *The Groundnut Crop: A Scientific Basis for Improvement*. Chapman and Hall, London, UK, pp 96–137.
- Singh AK, Subrahmanyam P, Gurtu S (1996) Variation in a wild groundnut species, *Arachis duranensis* Krapov, Gregory WC. *Genet Resour Crop Evol* 43: 135–142.
- Singh SB, Chaubey AK (2003) Variability and association amongst quantitative characters in peanut (*Arachis hypogaea* L.). *New Agri* 14: 97–101.
- Srivastava N (2010) Identification of contrasting parental material for salinity tolerance based on morphological, physiological, and biochemical study and molecular diversity by SSR molecular markers in groundnut (*Arachis hypogaea*). PhD Thesis, Jawaharlal Nehru Technological University, Hyderabad, India.
- Stalker HT (1990) A morphological appraisal of wild species in section *Arachis* of peanuts. *Peanut Sci* 17: 117–122.
- Subramanian V, Gurtu S, Nageswara Rao RC, Nigam SN (2000) Identification of DNA polymorphism in cultivated groundnut using random amplified polymorphic DNA (RAPD) assay. *Genome* 43: 656–660.
- Sujay V, Gowda MVC, Pandey MK, Bhat RS, Khedikar YP, Nadaf HL, Gautami B, Sarvamangala C, Lingaraju S, Radhakrishnan T, Knapp SJ, Varshney RK (2012) QTL analysis and construction of consensus genetic map for foliar diseases resistance based on two RIL populations in cultivated groundnut (*Arachis hypogaea* L.). *Mol Breed* 32: 773–788.
- Sumathi P, Muralidharan V (2007) Character association and path coefficient analysis in confectionery type groundnut (*Arachis hypogaea* L.). *Madras Agri J* 94: 105–109.
- Sumathi P, Amalabalu P, Muralidharan V (2009) Genetic variability for pod characters in large seeded genotypes of groundnut (*Arachis hypogaea* L.). *Adv Plant Sci* 22: 281–283.
- Swamy BPM, Upadhyaya HD, Goudar PVK, Kullaiswamy BY, Singh S (2003) Phenotypic variation for agronomic characteristics in a groundnut core collection for Asia. *Field Crops Res* 84: 359–371.
- Tatum LA (1971) The southern corn leaf blight epidemic. *Science* 171: 1113–1116.
- Upadhyaya HD (2003) Phenotypic diversity in groundnut (*Arachis hypogaea* L.) core collection assessed by morphological and agronomical evaluations. *Genet Resour Crop Evol* 50: 539–550.
- Upadhyaya HD (2005) Variability for drought resistance related traits in the mini core collection of peanut. *Crop Sci* 45: 1432–1440.
- Upadhyaya HD (2008) Crop germplasm and wild relatives: a source of novel variation for crop improvement. *Kor J Crop Sci* 53: 12–17.
- Upadhyaya HD, Ortiz R (2001) A mini core collection for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. *Theor Appl Genet* 102: 1292–1298.
- Upadhyaya HD, Ortiz R, Bramel PJ, Singh S (2001) Development of Asia region groundnut core collection. In: *Diamond Jubilee Symposium on Hundred years of Post-Mendelian Genetics—Retrospect and Prospects*. 6–9 November 2001, Indian Agricultural Research Institute, New Delhi, India, pp 43–44.

- Upadhyaya HD, Bramel PJ, Ortiz R, Singh S (2002a) Geographical pattern of diversity for morphological and agronomic traits in the groundnut germplasm collection. *Euphytica* 128: 191–204.
- Upadhyaya HD, Bramel PJ, Ortiz R, Singh S (2002b) Developing a mini core of peanut for utilization of genetic resources. *Crop Sci.* 42: 2150–2156.
- Upadhyaya HD, Ortiz R, Bramel PJ, Singh S (2003) Development of a groundnut core collection using taxonomical, geographical and morphological descriptors. *Genet Resour Crop Evol* 50: 139–148.
- Upadhyaya HD, Mallikarjuna Swamy BP, Goudar PVK, Kullaiswamy BY, Singh S (2005) Identification of diverse groundnut germplasm through multienvironment evaluation of a core collection for Asia. *Field Crops Res* 93: 293–299.
- Upadhyaya HD, Reddy LJ, Gowda CLL, Singh S (2006) Identification of diverse groundnut germplasm: Sources of early-maturity in a core collection. *Field Crops Res* 97: 261–267.
- Upadhyaya HD, Reddy LJ, Gowda CLL, Singh S (2009) Phenotypic diversity in cold-tolerant peanut (*Arachis hypogaea* L.) germplasm. *Euphytica* 165: 279–291.
- Upadhyaya HD, Yadav D, Dronavalli N, Gowda CLL, Singh S (2010) Mini core germplasm collections for infusing genetic diversity in plant breeding programs. *Elec J Plant Breed* 1: 1294–1309.
- Upadhyaya HD, Sharma S, Dwivedi SL (2011) *Arachis*. In: Kole C (ed) *Wild Crop Relatives: Genomic and Breeding Resources*. Vol: Legume Crops and Forages. Springer Berlin, Heidelberg, Germany, pp 1–19.
- Upadhyaya HD, Dwivedi SL, Nadaf HL, Singh S (2011b) Phenotypic diversity and identification of wild *Arachis* accessions with useful agronomic and nutritional traits. *Euphytica* 182: 103–115.
- Upadhyaya HD, Mukri G, Nadaf HL, Singh S (2012) Variability and stability analysis for nutritional traits in the mini core collection of peanut. *Crop Sci* 52, doi: 10.2135/cropsci2011.05.0248.
- Vaddoria MA, Patel VJ (1990) Genetic variability in Virginia runner groundnut (*Arachis hypogaea* Linn.). *J Oilseeds Res* 7: 130–132.
- Varma TSN, Dwivedi SL, Pande S, Gowda MVC (2005) SSR markers associated with resistance to rust (*Puccinia arachidis* Speg.) in groundnut (*Arachis hypogaea* L.). *SABRAO J Breed Genet* 37: 107–119.
- Varshney RK, Bertioli DJ, Moretzsohn MC, Vadez V, Krishnamurthy L, Aruna R, Nigam SN, Moss BJ, Seetha K, Ravi K, He G, Knapp SJ, Hoisington DA (2009) The first SSR-based genetic linkage map for cultivated groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 118: 729–739.
- Varshney RK, Gowda MVC, Radhakrishnan T, Pandey MK, Gautami B, Sujay V, Koppolu R, Senthilvel S, Vadez V, Nigam SN, Upadhyaya HD, Isobe S, He G, Bertioli DJ, Knapp SJ, Cook DR (2010) Development and application of genomic resources for molecular breeding in groundnut (*Arachis hypogaea* L.). In: *Proceedings of the 3rd International Conference on Plant Molecular Breeding (ICPMB)*, 5–9th September 2010a, Beijing, China.
- Vekariya HB, Khanpara MD, Vachhani JH, Jivani LL, Vagadiya KJ, Revkar HJ (2011) Correlation and path analysis in bunch groundnut (*Arachis hypogaea* L.). *J Plant Sci (Muzzaffarnagar)* 6: 11–15.
- Wang ML, Sukumaran S, Barkley NA, Chen Z, Chen CY, Guo B, Pittman RN, Stalker HT, Holbrook CC, Pederson GA, Yu J (2011) Population structure and marker-trait association analysis of the US peanut (*Arachis hypogaea* L.) mini-core collection. *Theor Appl Genet* 123: 1307–1317.