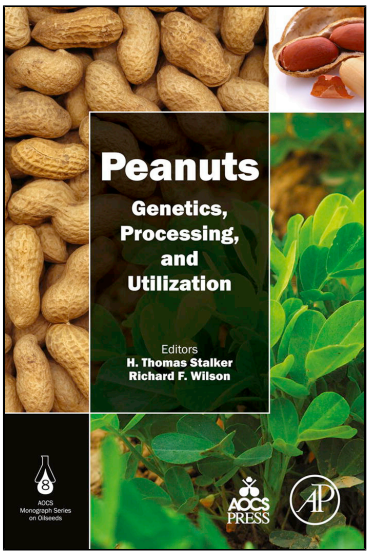

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Chapter 6

Annotation of Trait Loci on Integrated Genetic Maps of *Arachis* Species

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INTRODUCTION

Peanut or groundnut (*Arachis hypogaea* L.) is second, behind soybean, in the world's legume oilseed market. In 2012, global production was 41.2 metric tons from an area of 24.7 million hectares (FAOSTAT, 2014). Yield of peanut under stressed environments is an ultimate goal of improvement for enhanced production as it is usually susceptible to a range of abiotic and biotic stresses, such as drought, tomato spotted wilt virus (TSWV), early leaf spot (ELS) and late leaf spot (LLS), nematodes, rust, and aflatoxin contamination (Guo et al., 2012a). However, cultivated peanut is an allotetraploid ($2n=4x=40$) with a large genome, which greatly complicates interpretation of genomic data compared with the diploid wild relatives ($2n=2x=20$) (Guo et al., 2013). It is difficult to transfer alleles from wild species to cultivated peanuts (Simpson, 1991). For the last ten years, extensive efforts in the area of peanut genomics have resulted in a large number of genetic and genomic resources such as mapping populations, expressed sequence tags (ESTs), a wide range of molecular markers, transcriptome and proteomics (Guo et al., 2013; Katam et al., 2014; Varshney et al., 2013). These genetic and genomic resources have been successfully used to construct genetic maps, to identify quantitative trait loci (QTLs) of traits of

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interest, and to conduct marker-assisted selection and association mapping for peanut improvement (Pandey et al., 2014a).

Genetics and genomics will have the potential to enhance sustainable peanut production. The major contribution of these technologies for peanut will likely be improved disease resistance, oil quality, and enhanced productivity. Those attributes may be achieved more effectively through genomic biotechnology to utilize the genetic resources preserved in germplasm collections for maximizing the genetic potential in breeding. Superior cultivars will maximize desirable genetic traits and provide growers with cultivars that are locally adapted and highly productive. Genomics involves the study of the complete genetic makeup through mapping, sequencing, and functional studies to identify genes that regulate, control, or modify trait expression. With the development in sequencing technologies, next-generation sequencing (NGS) has opened the gateway to sequence the genomes in a fast, reliable, and cost-effective manner (Varshney et al., 2013). The international peanut genome sequencing project was discussed in the year of 2010 and launched in the year of 2012 after a long deliberation and strategic planning (Guo et al., 2013). The exciting news is that the Peanut Genome Consortium, representing a coalition of international scientists and stakeholders engaged in the International Peanut Genome Initiative, announced the public release of the first chromosomal-scale draft sequences of two peanut species (*Arachis duranensis* and *Arachis ipaënsis*) on April 2, 2014 (http://www.peanutbioscience.com/images/4-2-14_News_Release_Notice.pdf).

In this chapter, we update the information on the molecular markers, genetic linkage maps, and QTLs of traits mapped to date. Information of the preview of genome sequences, which would be available in peanut populations for high resolution genetic and trait mapping such as multiparent advanced generation intercross (MAGIC) and nested association mapping (NAM), is also discussed. Furthermore, an innovative method to identify a causal mutant single nucleotide polymorphism (SNP) or major allele for QTLs through NGS techniques such as MutMap and QTLseq is also discussed in the section on emerging trait mapping strategies. A special emphasis on Africa and China is given in different sections to update on the activities in peanut research and emerging issues. The goal of this chapter is to update the new progress in the development of genetic and genomic resources and technologies in peanuts.

GENETIC MARKER DEVELOPMENT

Genetic markers have proven to be a valuable tool in genetic mapping, marker-assisted selection (MAS), association analysis, genomic selection, and fine mapping (Hyten et al., 2010). Due to low levels of polymorphism detected (Kochert et al., 1991) and complex polyploidy genomes, genetic marker development in cultivated peanut has been slow compared with many other legume crops such as *Glycine max* (L.) Merr., *Medicago truncatula* Gaertn., and *Phaseolus*

vulgaris (L.). However, progress made since the mid-2000s has been reviewed (Pandey et al., 2012c; Guo et al., 2013; Varshney et al., 2013).

In the 1990s, a handful of isozyme markers were developed to evaluate the gene diversity in peanut (Lacks and Stalker, 1993). Soon after, restriction fragment length polymorphism (RFLP) (Kochert et al., 1996), random amplified polymorphic DNA (RAPD) (Subramanian et al., 2000), and amplified fragment length polymorphism (AFLP) (He and Prakash, 1997) were established. However, divergence was rarely detected in cultivated peanut. There are newer types of genetic markers developed for peanut genotyping, such as sequence-related amplified polymorphism (SRAP) (Wang et al., 2010b), single strand conformational polymorphism (SSCP) (Nagy et al., 2010), and miniature inverted-repeat transposable elements (MITEs) (Shirasawa et al., 2012a), but they are less commonly used. Several reports on diversity arrays technology (DArT) markers showed low levels of polymorphism and limited capability to be used for genetic and breeding activities in peanut (Varshney et al., 2010). With the rapid development of NGS technologies, efforts have been placed on simple sequence repeats (SSRs) and SNPs in peanut, which require the sequence information. SSR polymorphism between the individuals is generated as a result of "slip-strand mispairing" during DNA replication (Eisen, 1999).

SSR Development in *Arachis*

SSRs in *Arachis* were first reported in 1999 by Hopkins et al. (1999), with a total of 26 SSRs, of which six proved to be polymorphic. Until 2002, only one publication reported discovery of new SSRs (Palmieri et al., 2002); seven SSRs were discovered and only two proved to be polymorphic. However, since 2000, more than 15,000 SSRs have been detected in peanuts, though some SSRs are duplicate discoveries made by different laboratories (Guo et al., 2013). This increase is largely due to the substantial number of sequences generated from complementary DNA libraries, bacterial artificial chromosome (BAC) libraries, and NGS (Feng et al., 2012; Guimaraes et al., 2008; Guo et al., 2013; Song et al., 2010; Yüksel and Paterson, 2005). Zhang et al. (2012a) and Guimaraes et al. (2012) utilized RNAseq to discover 6244 SSRs, which account for more than 40% of the 15,000 SSRs.

ESTs are available to the public through the National Center for Biotechnology Information (NCBI) database (Feng et al., 2012). By April of 2014, a total of 178,962 ESTs of *A. hypogaea* were available to the public in NCBI, plus 75,579 ESTs from other *Arachis* species including *A. duranensis*, *A. ipaënsis*, *Arachis stenosperma*, and *Arachis magna*. Through investigation of 24,238 ESTs, 881 SSRs were identified and 251 were successfully designed with primer pairs. Twenty-two cultivated and 16 wild genotypes were then genotyped using the 251 SSR markers (Liang et al., 2009a). Guo et al. (2013) summarized a total of 12,190 EST–SSRs, or 78.5% of the SSRs currently available in peanut.

Pandey et al. (2012b) used a panel of 20 parental genotypes to screen a compilation of 4485 SSRs, of which 1351 were polymorphic markers. One hundred and ninety-nine SSRs showed polymorphism information content (PIC) greater than 0.50, and thus were deemed as highly informative SSRs. Zhao et al. (2012) created a summary of various reports on polymorphisms in peanuts. Among the compiled 9274 SSRs, 1343 were identified as polymorphic, which contained 142 SSRs with PIC >0.50. Another study characterized 146 SSRs using 22 genotypes of cultivated peanuts, which discovered 78 polymorphic SSRs including 66 that are highly informative (Macedo et al., 2012). The highly informative SSR markers have proven to be efficient in detecting genetic variation (Belamkar et al., 2011; Ren et al., 2014).

SNP Development in *Arachis*

SNPs are one of the most abundant sources of genetic variation and are widely distributed throughout the genome. The estimated SNP frequency in a plant genome is around one SNP every 100–300 bp (Gupta et al., 2001). The allotetraploid genome of peanuts hinders SNP marker development by providing the plethora of polymorphisms between homoeologous subgenomes. Different types of SNPs exist (Figure 1) with homoeologous polymorphism as the most frequent scenario indicating more divergence between the A and B subgenomes of the allotetraploid peanut than between genotypes of the same genome. This poses a problem during genotyping that would result in a mixture of sequences from

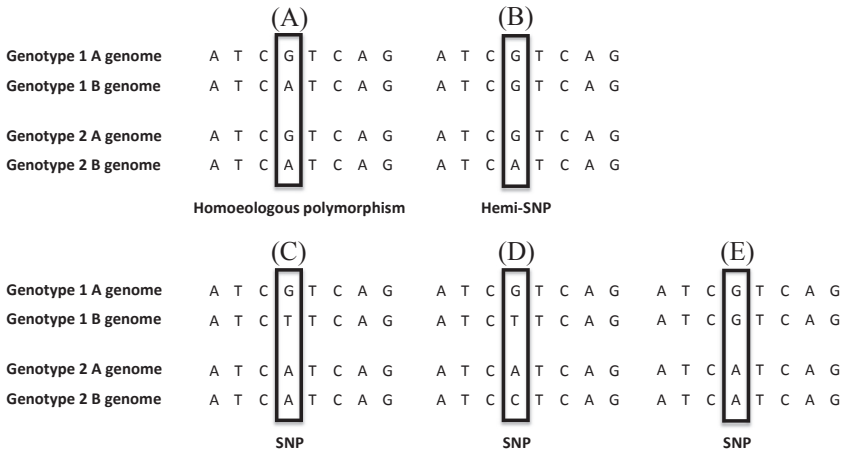

FIGURE 1 Single nucleotide polymorphism (SNP) types in cultivated peanut (A) homoeologous polymorphism between A and B genomes within genotypes. (B) HemiSNP between B genomes of different genotypes; (C) SNP between genotypes on both A and B genomes with hemihomoeologous polymorphism (D) SNP between genotypes on both A and B genomes with homoeologous polymorphism. (E) SNP between genotypes on both A and B genomes. Modified based on Trick et al. (2009).

multiple divergent loci (Dwivedi et al., 2007). A research group at the University of Georgia compiled the Illumina GoldenGate array containing 1536 SNPs by comparing sequences of 17 tetraploid genotypes with Tifrunner's transcriptome (Nagy et al., 2012). In peanut, a set of 90 informative groundnut kompetitive allele-specific polymerase chain reaction assay markers have been developed and its use in deciphering genetic diversity in the reference set was recently demonstrated (Khera et al., 2013). Another 768-SNP Illumina GoldenGate array developed at the University of California–Davis has been utilized solely for diploid genotypes (Mallikarjuna and Varshney, 2014). Zhou et al. (2014) reported the large-scale SNP marker development for tetraploid peanuts. Out of these SNP markers, 1621 were successfully utilized for constructing genetic linkage maps. Therefore, more efforts and technological innovation are necessary to increase the number of SNP markers in tetraploid peanuts; and the completion of whole genome sequences of cultivated peanuts will advance the application of SNP markers.

GENETIC LINKAGE MAPS FOR DIPLOID AND TETRAPLOID PEANUTS

Once molecular markers have been identified, the next effort is to develop genetic maps. This is an initial step toward identification of molecular markers linked to traits of interest. Particularly since 2000, many mapping populations have been generated which resulted in genetic maps for diploid (AA and BB) as well as the tetraploid (AABB) genomes (Guo et al., 2013; Pandey et al., 2014a). However, until recently, the genetic maps developed contain only few 100 genetic markers; but with the advent of NGS and discovery of SNPs, genetic maps with thousands of markers are now available in peanut (Table 1).

Genetic Maps with Early Generation Markers

With the early generation markers such as RFLP, AFLP, and RAPD, five genetic maps were developed, including three for diploid (AA) and two for tetraploid (AABB) peanuts. Halward et al. (1993) reported the first RFLP-based linkage map of AA genome by using an F_2 population from the cross between the diploid wild species *A. stenosperma* Krapov. and W. C. Gregory and *Arachis cardenasii* Krapov. and W. C. Gregory. Later there were two other AA genome-specific maps developed, one with 102 AFLP marker loci using an F_2 population of (*Arachis kuhlmanni* Krapov. and W. C. Gregory × *Arachis diogoi* Hoehne) (Milla, 2003) and the other with 206 RFLP and RAPD marker loci in a BC_1F_1 population of (*A. stenosperma* × (*A. stenosperma* × *A. cardenasii*)) (Garcia et al., 2005). Two tetraploid maps also were developed using early generation markers, one through utilization of 370 RFLP loci in a BC_1F_1 population, *A. hypogaea* × (*Arachis batizocoi* Krapov. and W. C. Gregory × (*A. cardenasii* × *A. diogoi*)) (Burow et al., 2001), and the other with only 12 AFLP marker loci in an F_2 population (Herselman et al., 2004).

TABLE 1 Comprehensive List of Genetic Maps Constructed in the *Arachis* Species Using a Range of Diverse Molecular Markers

Genome	Population Size	Marker Loci Mapped	Marker Type	Linkage Groups	Total Map Distance (cM)	References
Early Generation Markers						
AA	F_2	117	RFLP	11	1063.00	Halward et al. (1993)
AABB	78 BC1F1	370	RFLP	23	2210.00	Burow et al. (2001)
AA	179 F_2	102	AFLP	12	1068.10	Milla (2003)
AABB	200 F_2	12	AFLP	5	139.40	Herselman et al. (2004)
AA	44 BC1F1	206	RAPD, RFLP	11	800.00	Garcia et al. (2005)
SSR-Based Genetic Maps						
AA	93 F_2	170	SSR	11	1230.89	Moretzsohn et al. (2005)
BB	93 F_2	149	SSR	10	1294.00	Moretzsohn et al. (2009)
BB	94 F_2	449	SSR	16	1278.60	Guo et al. (2012b)
AABB	318 RILs	135	SSR	22	1270.50	Varshney et al. (2009)
AABB	318 RILs	191	SSR	20	1785.40	Ravi et al. (2011)
AABB	88 BC_1F_1	298	SSR	21	1843.70	Foncéka et al. (2009)
AABB	142 RILs	133	SSR	19	684.90	Hong et al. (2010)
AABB	84 RILs	109	SSR	21	540.69	Hong et al. (2010)
AABB	136 RILs	46	SSR	13	401.70	Hong et al. (2010)
AABB	266 RILs	188	SSR	20	1922.40	Khedikar et al. (2010) and Sujay et al. (2012)
AABB	188 RILs	82	SSR	15	831.40	Gautami et al. (2012b)
AABB	176 RIL	119	SSR	20	2208.20	Gautami et al. (2012b)

AABB	146 RILs	181	SSR	21	1963.00	Sarvamangala et al. (2011) and Sujay et al. (2012)
AABB	190 RILs	172	SSR, CAPS	22	1213.40	Qin et al. (2012)
AABB	158 RILs	239	SSR, CAPS	26	920.70	Qin et al. (2012)
AABB	94 F_2	318	SSR	21	1674.40	Wang et al. (2012, 2013c)
AA	93 F_2	369	SSR, AFLP, SNP, RFLP, SCAR	10	–	Leal-Bertioli et al. (2009)
AABB	164 RILs	109	SSR	24	882.90	Mondal et al. (2012)
AABB	94 F_2	1114	SSR, transposon	21	2166.40	Shirasawa et al. (2012b)
AABB	186 F_2	326	SSR, transposon	19	1332.90	Shirasawa et al. (2012)
AA	89 F_5	437	SSR, transposon	10	544.00	Shirasawa et al. (2013)
BB	94 F_6	680	SSR, transposon	10	461.00	Shirasawa et al. (2013)
AABB	91 F_6	1261	SSR, transposon	20	1442.00	Shirasawa et al. (2013)
AABB	352 F_9	206	SSR, SNP	20	1780.60	Pandey et al. (2014b)
AABB	248 F_9	378	SSR, SNP	20	2487.40	Pandey et al. (2014b)
AABB	162 F_9	426	SSR, SNP	24	1980.78	Wang et al. (2014)
AABB	352 RILs	248	SSR, SNP	21	1425.91	Khera et al. (2014)
AABB	215 RILs	61	SSR	18	504.18	Zhang (2011)

Continued

TABLE 1 Comprehensive List of Genetic Maps Constructed in the *Arachis* Species Using a Range of Diverse Molecular Markers—cont'd

Genome	Population Size	Marker Loci Mapped	Marker Type	Linkage Groups	Total Map Distance (cM)	References
AABB	160 RILs	73	SSR	16	448.28	Zhang (2011)
AABB	268 F_2	61	SSR	18	847.47	Zhang (2011)
AABB	217 RILs	277	SSR, transposon	23	1504.66	X. Zhang, person. commun.
AABB	128 F_2	223	SRAP	22	2129.4	Wang (2006) and Wang et al. (2010b)
SNP-Based Genetic Maps						
AA	94 F_2	1724	SNP, SSR, SSCP	10	1081.30	Nagy et al. (2012)
AABB	166 RILs	1685	SNP, SSR	20	1446.70	Zhou et al. (2014)
AA	89 F_5	384	SNP, SSR	10	705.10	Bertioli et al. (2014)
AABB	91 F_6	772	SNP, SSR	20	1487.30	Bertioli et al. (2014)
Consensus Genetic Maps						
–	–	175	–	22	885.40	Hong et al. (2010)
–	–	225	–	20	1152.90	Sujay et al. (2012)
–	–	293	–	20	2840.80	Gautami et al. (2012b)
–	–	324	–	21	1352.10	Qin et al. (2012)
–	–	897	–	20	3863.60	Gautami et al. (2012a)
–	–	3693	–	20	2651.00	Shirasawa et al. (2013)
–	–	101	–	17	953.88	Zhang (2011)

Genetic Maps with SSR Markers

SSRs developed from various sources such as expressed sequence tag-simple sequence repeat (EST–SSR), BAC-end sequences SSR (BES–SSR), *A. hypogaea* genomic SSR were used for development of genetic maps (Liang et al., 2009a; Shirasawa et al., 2012b; Wang et al., 2012). Several other markers such as resistance gene homologs, MITEs, sequence characterized amplified region (SCAR), and cleaved amplified polymorphic sequence (CAPS) were also used in combination with SSR markers (Leal-Bertioli et al., 2009; Liu et al., 2013a; Qin et al., 2012; Shirasawa et al., 2012a, 2013).

The first AA genome map was developed with 170 SSR marker loci in an F_2 population derived from *A. duranensis* (K 7988) and *A. stenosperma* (V 10309) (Moretzsohn et al., 2005). Later, the same map was enriched with AFLP, SNP, RFLP, and SCAR markers that led to 369 mapped loci (Leal-Bertioli et al., 2009). Furthermore, with the availability of more SSR and transposon markers, the map from an F_5 population derived from the above-mentioned cross was improved further containing 437 mapped loci (Shirasawa et al., 2013).

For the BB genome, the first SSR map was developed with 149 mapped loci in an F_2 population derived from the cross, *A.* ipaënsis (K 30076) × *A. magna* (K 30097) (Moretzsohn et al., 2009). The same map was improved further to 680 marker loci with SSR and transposon markers in an F_6 population (Shirasawa et al., 2013). Another BB genome specific map from the cross of *A. batizocoi* (PI 298639) and *A. batizocoi* (PI 468327) was developed containing 449 SSR mapped loci (Guo et al., 2012b).

The first SSR-based genetic map was developed with 135 loci using a recombinant inbred line (RIL) population by Varshney et al. (2009). Later the map was improved to 191 SSR mapped loci (Ravi et al., 2011). This was a significant landmark because it was made from the "true" tetraploid cross and the QTL identified could be directly used in peanut crop improvement. The next SSR-based genetic map contained 298 marker loci, but this was developed by using a backcross mapping population from the cross between a cultivar Fleur 11 and a synthetic amphidiploid (*A. duranensis* (AA genome) × *A.* ipaënsis (BB genome)) (Foncéka et al., 2009).

RIL populations have advantages over F_2 and backcross populations. Hong et al. (2010) reported three SSR-based genetic maps from three RIL populations with one common parental line. GPBD 4, a Spanish bunch cultivar with high resistance to rust and LLS, was used to develop two RIL populations at the University of Agricultural Sciences-Dharwad (UAS-D). The SSR-based genetic maps having only 56 marker loci for TAG 24 × GPBD 4 and 45 marker loci for TG 26 × GPBD 4 were developed initially (Khedikar et al., 2010; Sarvamangala et al., 2011). As more SSR markers were available in the public database, these maps were further improved to 188 and 181 marker loci, respectively (Sujay et al., 2012). Mondal et al. (2012) developed an SSR-based linkage map for the RIL population derived from VG 9514 and TAG 24. Furthermore, two other RIL

populations were developed from the cross of peanut lines ICGS 44×ICGS 76 and ICGS 76×CSMG 84-1 (Gautami et al., 2012b).

In the United States, genetic maps were developed from two RIL mapping populations including the T population (Tifrunner×GT-C20) and the S population (SunOleic 97R×NC 94022). Wang et al. (2012) reported a large set of BES–SSR markers used in a linkage map of F_2 T-population with 318 mapped loci. Qin et al. (2012) reported two maps using EST–SSR markers for the T and the S population at F_5 generation with 236 and 172 mapped loci, respectively, which were used to detect the first QTLs for TSWV. These maps were further improved to 377 and 206 mapped loci, respectively, and used for oil content and oil composition studies (Pandey et al., 2014b; Wang et al., 2015). Currently, these maps are being improved with 426 and 248 marker loci for major peanut foliar disease QTL studies, such as TSWV and leaf spots, respectively (Khera et al., 2014; Wang et al., 2014). We noted that the map generated using the T population has by far the most SSR markers from a single RIL population. It is noteworthy that whole genome sequence data for these two populations are being generated as part of the International Peanut Genomic Initiative.

In Japan, through the utilization of BES–SSR and transposon markers, Shirasawa et al. (2012b) developed two genetic maps using the F_2 populations. There were 1114 mapped loci in the cross of Satonoka×Kintoki, and 326 mapped loci in the cross of Nakateyutaka×YI-0311. This was the first study in which transposon markers were used for mapping in peanut. Recently, an F_6-based genetic map from a cross of *A. hypogaea* line "Runner IAC 886" and a synthetic amphidiploid (*A. ipaënsis*×*A. duranensis*) was developed with 1261 mapped loci. This is by far the densest genetic map based on SSR and transposon markers in a synthetic peanut mapping population (Shirasawa et al., 2013).

Genetic Maps with SNP Markers

Efforts have led to the identification of SNPs in peanut. A set of 1536 Illumina GoldenGate array for SNP genotyping was developed using the SNPs identified between two *A. duranensis* accessions (Nagy et al., 2012). These SNPs were then used for the first time to develop an SNP-based genetic map for the AA genome using an F_2 population derived from the cross of *A. duranensis* (PI 475887)×*A. duranensis* (Grif 15036). It anchored a total of 1724 mapped loci including 1054 EST–SNP markers, 598 EST–SSR markers, 37 disease-resistance gene candidates, and 35 other markers previously published (Nagy et al., 2012). Later, using the same 1536 GoldenGate SNP assay, Bertioli et al. (2014) developed two SNP-based maps, one for the AA genome *A. duranensis* (K 7988)×*A. stenosperma* (V10309) with 384 mapped loci which includes 326 SNPs and 58 SSRs and the other for the synthetic tetraploid genome "Runner IAC 886"×(*A.* ipaënsis (GK 30076)×*A. duranensis* (V 14167)) with 772 mapped loci including 366 SNPs and 406 SSRs. Zhou et al. (2014) reported an SNP-based map from a "true" tetraploid peanut RIL population of "Zhonghua

5"×"ICGV 86699," containing 1685 mapped loci which includes 1621 SNPs and 64 SSRs.

Consensus Maps

With the availability of large number of linkage maps in peanuts, efforts were made to construct the consensus map, which is important to understand the ploidy at the genome level. Individual genetic maps obtained for A and B genome can be integrated together with the tetraploid maps, and the linkage groups could be assigned in relation to the donor genomes. This effort has led to the development of high-density consensus maps in peanuts. In general, the consensus map has several advantages such as presence of a large number of markers onto one map, relative recombination frequency with other markers on the same linkage group (LG) across different maps, assigning a common name for different LGs across different maps, and providing insights into chromosomal rearrangements and gene duplication (Jackson et al., 2005; Wang et al., 2011a). Consensus maps for many legume and oilseed crops are available such as soybean (Hwang et al., 2009), chickpea (Millan et al., 2010), common bean (Galeano et al., 2011), pigeonpea (Bohra et al., 2012), and faba bean (Satovic et al., 2013).

Hong et al. (2010) reported the first consensus genetic map by integrating genetic maps from three RIL mapping populations in peanut. In 2012, three consensus maps were developed, the first from two RIL mapping populations containing 225 SSR mapped loci by Sujay et al. (2012), the second using three RIL populations possessing a total of 293 mapped marker loci by Gautami et al. (2012b), and the third from two RIL mapping populations resulting in 324 mapped marker loci by Qin et al. (2012). With the increase in the number of consensus maps, a joint international initiative made progress to combine all the four consensus genetic maps available from 10 RIL populations mentioned above along with one backcross population (Foncéka et al., 2009), resulting in the first international reference consensus genetic map with 897 marker loci on 20 LGs, spanning a map distance of 3863.6 cM with an average map density of 4.4 cM (Gautami et al., 2012a). This effort led to the development of another consensus genetic map, building on this map by adding another five mapping populations, resulting in a new integrated consensus map covering 2651 cM with 3693 marker loci which was anchored to 20 consensus LGs corresponding to the A and B genomes (Shirasawa et al., 2013).

TRAIT MAPPING USING FAMILY-BASED MAPPING POPULATIONS

Trait mapping includes the process of identification of statistically significant genomic regions related to traits of interest. The linkage between genetic markers, maps and agronomically important traits is an integral part of MAS. Breeding

programs facilitated with MAS have dramatically improved efficiency in selection of target traits, that otherwise would require labor-intensive and destructive measures. Garcia et al. (1996) and Burow et al. (1996) reported the linkage between RAPD markers and root-knot nematode resistance. Chu et al. (2007) reported the conversion of the RAPD markers into reproducible SCAR markers, which has a high correlation with phenotypic data and could be used in MAS (Chu et al., 2011). A few AFLP markers have been identified to be linked with resistance to aphid vector of rosette disease (Herselman et al., 2004), which accelerated the process of selecting rosette disease-resistant peanut lines. Potential linkage between an SSR marker and *Sclerotinia* blight resistance was identified by Chenault and Maas (2006). Two SNP markers have been identified to associate with a higher oleic acid and lower linoleic acid (Lopez et al., 2000; Pandey et al., 2014b). The initial QTL associated with TSWV resistance was reported by Qin et al. (2012). With the deployment of high throughput genotyping platforms such as genotyping by sequencing and exome-sequencing, more marker and important trait associations will be discovered.

The other challenge that breeders are facing is to improve yield. Yield is a quantitative trait and genetically controlled by multiple genes. The genotype-by-environment interactions for yield and market grade also exist in peanuts (Knauft and Wynne, 1995). The amount of emphasis that can be placed on yield improvement also depends on the numbers of other characters that must be considered, such as biotic and abiotic stresses. Nevertheless, breeding for resistance to different stresses is one of the key objectives. The availability of genetic maps has paved the way for trait mapping and QTL analysis. Comprehensive reviews are available wherein all the findings have been reported (Burow et al., 2013; Janila et al., 2013; Pandey et al., 2014a; Varshney et al., 2013). However, the majority of QTLs identified in these studies have minor phenotypic variance explained (PVE). Since it is very difficult to practically use these minor QTLs, this chapter focuses only on the major QTLs (>10% PVE) since 2009 wherein SSR markers have been used for mapping the traits of interest (Table 2).

Biotic Stress

Leal-Bertioli et al. (2009) reported 35 candidate genes and five QTLs for resistance to LLS using a 93 F_2 mapping population derived from a cross between *A. duranensis* K 7988 and *A. stenosperma* V 10309, the same population used by Moretzsohn et al. (2005). This study indicated several regions within the *Arachis* genome as being involved in controlling disease resistance. Sujay et al. (2012) identified 13 major QTLs for resistance to LLS with PVE in the range of 10.27–67.98% and seven major QTLs for resistance to rust with PVE up to 82.62% in two RIL populations of TAG 24×GPBD 4 and TG 26×GPBD 4, in which both the resistance traits come from the parental line GPBD 4. GPBD 4 is predominantly cultivated with some *A. cardenasii* parentage derived through doubling the chromosome number of triploid interspecific hybrids to produce

TABLE 2 Major QTLs Associated with Traits in Peanut

Traits Studied	Major QTLs Identified	Population	Phenotypic Variance Explained (%)	References
Resistance to Diseases				
Late leaf spot (LLS)	13	TAG 24 × GPBD4, TG 26 × GPBD 4	10.27–67.98	Sujay et al. (2012)
Leaf spot	2	Tifrunner × GT-C20	11.2–21.45	Wang et al. (2013c)
Leaf rust	1	TAG 24 × GPBD 4	55.2	Khedikar et al. (2010)
	7	TAG 24 × GPBD4, TG 26 × GPBD 4	10.68–82.96	Sujay et al. (2012)
Aspergillus flavus invasion	3		10.5–22.7	Liang et al. (2009b)
Aphid vector of groundnut rosette disease	4	ICG 12991 × ICGVSM-93541	10.05–76.1	Herselman et al. (2004)
Tomato spotted wilt virus (TSWV)	2	Tifrunner × GT-C20 and SunOleic × NC94022	12.9–35.8	Qin et al. (2012)
	3	Tifrunner × GT-C20	10.6–14.14	Wang et al. (2013c)
Root-knot nematode	7	Florunner × TxAG-6	11.9–22.1	Burow et al. (2014)
Bacteria wilt	3	Yuanza 9102 × Chico	21.62	Peng et al. (2010)
Drought Tolerance-Related Traits				
Transpiration (T)	1	TAG 24 × ICGV 86031	10.3	Varshney et al. (2009)
	1	TAG 24 × ICGV 86031	10.86	Ravi et al. (2011)
	3		10.3–18.17	Gautami et al. (2012b)

Continued

TABLE 2 Major QTLs Associated with Traits in Peanut—cont'd

Traits Studied	Major QTLs Identified	Population	Phenotypic Variance Explained (%)	References
Transpiration efficiency (TE)	1		12.3	Ravi et al. (2011)
	3		13.44–18.12	Gautami et al. (2012b)
Specific leaf area (SLA)	3	TAG 24 × ICGV 86031	13–17.6	Varshney et al. (2009)
	3		11.02–13.29	Ravi et al. (2011)
Leaf area (LA)	1		11.51	Ravi et al. (2011)
SPAD chlorophyll meter reading (SCMR)	2	TAG 24 × ICGV 86031	10.6–11	Varshney et al. (2009)
	10		10.11–19.53	Ravi et al. (2011)
Biomass	3		15.58–20.32	Ravi et al. (2011)
Canopy conductance (ISC)	3		11.92–22.24	Ravi et al. (2011)
Total dry matter (TDM)	1		22.39	Gautami et al. (2012b)
Harvest index	1		18.1	Fonceka et al. (2012)
Hundred pod weight	2		15–17	Fonceka et al. (2012)
Hundred seed weight	2		12.4–14.9	Fonceka et al. (2012)
Haulm weight	2		13.5–17.5	Fonceka et al. (2012)
Pod number	2		9.6–12.6	Fonceka et al. (2012)
Total biomass	2		11–16.6	Fonceka et al. (2012)
STI – hundred pod weight	2		13.9–16.8	Fonceka et al. (2012)
STI – hundred seed weight	2		15.5–16.2	Fonceka et al. (2012)

STI – haulm weight	2		16.4–17.1	Fonceka et al. (2012)
STI – pod number	2		10.4–19.4	Fonceka et al. (2012)
STI – pod weight	1		12.3	Fonceka et al. (2012)
STI – seed number	1		11	Fonceka et al. (2012)
STI – seed weight	1		11.5	Fonceka et al. (2012)
STI – total biomass	2		10.8–20.1	Fonceka et al. (2012)
Agronomic and Yield Component Traits				
Shoot dry weight (ShDW)	2		14.4–22.09	Gautami et al. (2012b)
Haulm weight	1		33.36	Ravi et al. (2011)
	1		10.4	Fonceka et al. (2012)
Harvest index	1		40.1	Gautami et al. (2012b)
	1		11	Fonceka et al. (2012)
Pod mass/plant	3		13.1–18.3	Liang et al. (2009b)
Mature pods/plant	2		11.9–12.3	Liang et al. (2009b)
Pod number	1		14.2	Fonceka et al. (2012)
Number of branches	3		10.2–17.3	Liang et al. (2009b)
Number of fruit branches	1		17.5	Liang et al. (2009b)
Height of main axis	3		10.3–12.8	Liang et al. (2009b)
Stem diameter	2		10.4–24.1	Liang et al. (2009b)
Leaf length, width and length/ width ratio	7		12.4–18.9	Liang et al. (2009b)
Length of main stem	2	Satonoka × Kintoki (SKF_2)	15.7–19.2	Shirasawa et al. (2012b)

Continued

TABLE 2 Major QTLs Associated with Traits in Peanut—cont'd

Traits Studied	Major QTLs Identified	Population	Phenotypic Variance Explained (%)	References
Length of the longest branch	2	Satonoka × Kintoki (SKF_2)	14.2–21.1	Shirasawa et al. (2012b)
Number of branches	1	Satonoka × Kintoki (SKF_2)	15.6	Shirasawa et al. (2012b)
Weight of plant	1	Satonoka × Kintoki (SKF_2)	11.8	Shirasawa et al. (2012b)
Weight of mature pod per a plant	1	Satonoka × Kintoki (SKF_2)	28.1	Shirasawa et al. (2012b)
Weight of seeds	1	Satonoka × Kintoki (SKF_2)	19.1	Shirasawa et al. (2012b)
Yield parameters	5		10.1–17.69	Selvaraj et al. (2009)
Hundred pod weight	2		15.1–20.6	Fonceka et al. (2012)
Hundred seed weight	2		15.7–16.3	Fonceka et al. (2012)
Pod weight	1		11.7	Fonceka et al. (2012)
Shell weight	1		12.6	Fonceka et al. (2012)
Seed number	1		14.5	Fonceka et al. (2012)
Seed weight	1		11	Fonceka et al. (2012)
Total biomass	1		13.2	Fonceka et al. (2012)
Height of main stem	1		11.41	Zhang (2011)
Length of first primary branch	1		11.06	Zhang (2011)
Number of branches	1		14.45	Zhang (2011)
Number of mature pods/plant	1		11.73	Zhang (2011)

Height of main stem	5		11.97–18.00	Liu et al. (2013b)
Length of first primary branch	4		10.67–25.12	Liu et al. (2013b)
Other Morphological Traits				
Flowering date	1	Satonoka × Kintoki (SKF_2)	19.5	Shirasawa et al. (2012b)
Angle of branch	2	Satonoka × Kintoki (SKF_2)	11.9–23.2	Shirasawa et al. (2012b)
Constriction of pod	1	Satonoka × Kintoki (SKF_2)	18.1	Shirasawa et al. (2012b)
	6		10–23.9	Fonceka et al. (2012)
Pod beak	5		11.6–17.4	Fonceka et al. (2012)
Length of pod	2	Satonoka × Kintoki (SKF_2)	20.5–28.2	Shirasawa et al. (2012b)
Thickness of pod	1	Satonoka × Kintoki (SKF_2)	21.7	Shirasawa et al. (2012b)
Width of pod	2	Satonoka × Kintoki (SKF_2)	15.2–25.5	Shirasawa et al. (2012b)
Pod width	5		12.2–20.1	Fonceka et al. (2012)
Seed length	1		12.5	Fonceka et al. (2012)
Seed width	2		14.2–23.7	Fonceka et al. (2012)
Growth habit	5		13.9–17.3	Fonceka et al. (2012)
Main stem height	4		10–26.7	Fonceka et al. (2012)
Seed and Oil Quality				
Oil content	1		11.03	Selvaraj et al. (2009)
	1		10.2	Sarvamangala et al. (2011)
	4		10.23–14.18	Pandey et al. (2014b)

Continued

TABLE 2 Major QTLs Associated with Traits in Peanut—cont'd

Traits Studied	Major QTLs Identified	Population	Phenotypic Variance Explained (%)	References
Protein content	1		13.4	Liang et al. (2009b)
	2		10.2–10.7	Sarvamangala et al. (2011)
Arachidic acid	1		18.32	Zhang (2011) and Zhang et al. (2012b)
Stearic acid	1		24.14	Zhang. (2011) and Zhang et al. (2012b)
Carbon discrimination ratio	1		12.15	Ravi et al. (2011)
Oleic acid	9		10.71–38.41	Pandey et al. (2014b)
Linoleic acid	8		11.98–39.5	Pandey et al. (2014b)
O/L ratio	3		10.82–45.63	Pandey et al. (2014b)
Palmitic acid	6		10.56–37.37	Wang et al. (2015)
Stearic acid	6		17.8–40.57	Wang et al. (2015)
Arachidic acid	4		28.32–36.93	Wang et al. (2015)
Gadoleic acid	9		11.17–26.14	Wang et al. (2015)
Behenic acid	2		12.37–13.56	Wang et al. (2015)
Lignoceric acid	3		10.03–12.61	Wang et al. (2015)

STI = stress tolerance indices.

hexaploids and then selfing through several generations to recover 40 chromosome progenies (Gowda et al., 2002). A great example of using the major rust QTL, with PVE up to 82.62%, is successfully used in MAS in breeding to transfer the rust resistance trait from donor cultivar GPBD 4 into three elite peanut rust-susceptible cultivars (ICGV 91114, JL 24, and TAG 24) using the marker-assisted backcrossing (MABC) approach (Varshney et al., 2014).

Another study using the two RIL populations from crosses of Tifrunner × GT-C20 and SunOleic 97R × NC 94022, respectively, identified two major QTLs for resistance to leaf spot disease with PVE up to 21.45% and five major QTLs for resistance to TSWV with PVE of up to 35.8% (Qin et al., 2012; Wang et al., 2013c). Major QTLs have been identified in these two populations for ELS, LLS, and TSWV with PVE of up to 15, 17, and 29%, respectively (Khera et al., 2014; Wang et al., 2014). Efforts in the direction of fine mapping these major QTLs and MABC program has been initiated at USDA-ARS and the University of Georgia, Tifton, Georgia.

Aflatoxin contamination caused by the fungus *Aspergillus flavus* (Link ex Fr.) poses major risk to human health. Only limited study has been done for genetic resistance. Liang et al. (2009b) reported three major QTLs with PVE in the range of 10.5–22.7%. Root-knot nematode infection is another major disease, and seven major QTLs have been identified from a cross between the cultivar line Florunner and an amphidiploid "TxAG-6" with PVE up to 22.1% (Burow et al., 2014).

Abiotic Tolerance

Abiotic stress is common throughout the peanut growing areas in the world. Drought stress is among the major abiotic stresses causing yield loss and quality issues. Other factors include salinity, acid soils, and aluminum toxicity (Janila et al., 2013). Drought tolerance is a complex trait and the yield loss in a drought-affected area depends primarily on the crop stage of drought, intensity, and duration of the drought. Scientists at the International Crops Research Institute for the Semiarid Tropics (ICRISAT), India along with the collaborators have done notable work in detecting QTLs for drought tolerance-related traits in three RIL populations, TAG 24 × ICGV 86031, ICGS 76 × CSMG 84-1, and ICGS 44 × ICGS 76 (Gautami et al., 2012b; Ravi et al., 2011; Varshney et al., 2009). The majority of the QTLs are minor with significant epistatic interactions. There are major QTLs identified for transpiration (5), transpiration efficiency (4), carbon discrimination ratio (1), specific leaf area (6), leaf area (1), soil plant analysis development (SPAD) chlorophyll meter reading (12), biomass (3), shoot dry weight (2), haulm weight (1), harvest index (1), canopy conductance (3), and total dry matter (1).

Oil and Nutritional Quality

Peanuts are a rich source of oil and protein. In Asian countries such as China and India, high-oil content is desirable for peanuts to be crushed primarily for oil.

In contrast, in the US low-oil content is desirable for peanuts which are mostly used for edible purposes such as roasted, salted, peanut butter, and confectionary. Peanut oil is predominantly composed of unsaturated oleic acid (C18:1) and linoleic acid (C18:2). A high ratio of oleic acid and linoleic acid (O/L) is a highly desired quality trait for consumers and manufacturers to reduce oxidation and off-flavors. Selvaraj et al. (2009) identified an SSR marker for oil content based on bulked segregant analysis (BSA). The first QTL study was done by Sarvamangala et al. (2011) in the RIL population of TG 26×GPBD 4 and identified one major QTL with PVE of 10.2%. Pandey et al. (2014b) identified four major QTLs for oil content in two RIL populations with PVE up to 14.18%.

The translation of oleic to linoleic acid is catalyzed by the fatty acid desaturase (FAD) enzyme by adding a double bond to C18:1 (oleic acid) (Ray et al., 1993). There are two copies of this gene each on the A and B genome as *FAD2A* and *FAD2B* (Yu et al., 2008b). The first mutant line F-435 was identified as a high oleic line with O/L ratio of more than 40 (Norden et al., 1987). Pandey et al. (2014b) reported major QTLs other than *FAD2A* and *FAD2B* for oleic acid, linoleic acid, and O/L ratio. Furthermore, there are other minor fatty acids in peanut and could affect peanut oil quality and composition, and the major QTLs have been reported for palmitic acid, stearic acid, arachidic acid, gadoleic acid, behenic acid, and lignoceric acid (Wang et al., 2015).

Protein content is another important trait in peanut. However, not much study has been done with this aspect. Only one major QTL with PVE up to 13.4% and two major QTLs with PVE up to 10.7% have been reported by Liang et al. (2009b) and Sarvmangala et al. (2011), respectively.

Agronomic Traits

Yield is the most important breeding objective for plant breeders and several studies decipher the QTLs for yield and yield component traits. Using the BSA approach Selvaraj et al. (2009) identified five markers with PVE up to 17.69%. Liang et al. (2009b) reported seven QTLs for leaf length, leaf width, and leaf length and width ratio; three QTLs each for pod weight per plant, number of reproductive branches, and height of main axis; two QTLs for mature pods per plant, and stem diameter; and one QTL for pod number and number of fruit branches. Under well-watered conditions, Foncéka et al. (2012) reported several QTLs for yield component traits in the advanced backcross population of Fleur 11 and amphidiploid "AiAd" (*A. ipaënsis* GK 30076×*A. duranensis* V 14167)$^{\times 4}$ with PVE up to 20.6%. Shirasawa et al. (2012b) identified a number of QTLs for yield and agronomic traits such as seed weight, mature pod weight, and number of branches with PVE up to 28.1% in an F_2 population derived from the cross of Satonoka and Kintoki. Pandey et al. (2014c) reported a marker-association study for traits including yield and its components using the ICRISAT mini core collection.

Morphological Traits

During the course of domestication many morphological differences arise between the cultivated peanuts from wild relatives. Identification of QTLs for these traits would assist the understanding of the evolutionary changes at the genome level. Major QTLs for flowering date, angle of branch, pod characteristics such as constriction, beak, length, thickness and width, seed width and length, growth habit, and main stem height were identified in two reported studies (Foncéka et al., 2012; Shirasawa et al., 2012b). Pandey et al. (2012a) also reported the preliminary data on morphological descriptors and identified seven markers for main axis, 13 markers for growth habit, and one marker for main stem.

TRAIT MAPPING USING GERMPLASM SETS

Large sets of peanut germplasm are available across the world. In order to use these resources, association mapping is a great approach toward studying the genetics of quantitative traits and identifying marker–trait associations (MTAs) from the diverse set of germplasm collections or breeding materials. There are several advantages of using this approach, such as utilization of stable germplasm sets which can be phenotyped for multilocations over years. Higher resolution maps could be achieved compared with biparental interval mapping due to strong linkage disequilibrium present and natural genetic variability, which could identify MTAs and validate the associated markers among breeding lines for faster application in genomics-assisted breeding (GAB) programs. However, there are some important considerations for designing an effective strategy for a successful association mapping project, much of which is extensively covered in the review by Gupta et al. (2014). Depending upon the use of markers and method of approach, association mapping can be categorized into candidate gene association mapping and genome-wide association mapping (GWAS) (Zhu et al., 2008).

The first attempt to study population structure in peanut and MTA was on a subset of the US mini core collection containing 94 accessions phenotyped for quality traits and genotyped with 81 SSRs and two functional SNP markers of *FAD2*. The population structure analysis revealed four subpopulations each related to the four botanical varieties of peanut and the experimental feasibility of the US mini core collection for their use in association mapping studies through re-discovery of association of SNP markers for *FAD2* genes with oleic acid, linoleic acid, and O/L ratio (Wang et al., 2011b).

The next study on association analysis was carried out on the Chinese mini core collection containing 298 accessions genotyped with 109 SSRs and phenotyped for 15 agronomic traits across three environments (Jiang et al., 2014). They identified a total of 89 SSR alleles associated with 15 agronomic traits with a low PVE (1.05–4.81%). There were also 15 alleles identified to be commonly associated with more than one agronomic trait. Pandey et al. (2014c) used the

ICRISAT "reference set" comprising 300 accessions in order to identify MTAs. High-resolution genotyping was carried out using 4597 polymorphic DArT loci, 154 SSR markers, and multiple season phenotyping data collected for 50 agronomic traits across 14 locations and eight countries. A total of 524 highly significant MTAs were identified with PVE of 5.81–90.09% for 36 traits. These traits include disease resistances, oil and nutritional quality, physiological traits, yield, and its components.

An international initiative for peanut GWAS started a few years ago and included a diverse peanut global germplasm sets, i.e., the ICRISAT mini core collection of 300 accessions, the US mini core collection of 112 accessions, and the Chinese mini core collection of 298 accessions. This initiative will compile and curate available phenotypic data, generate high-density genotyping data based on genotype-by-sequencing, conduct comprehensive statistical analysis, estimate diversity features, and undertake GWAS for traits of importance to breeders. Therefore, this initiative is expected to provide sequence-based markers and haplotypes associated with traits of agronomic importance, to identify accessions with superior alleles that can be used as donors in the breeding programs, and to provide the breeder-friendly toolbox with phenotyping and genotyping data (www.PeanutBase.org).

ADVANCED-BACKCROSS QTL MAPPING

Wild species in peanut contain large number of useful genes and alleles for biotic and abiotic stresses (Upadhyaya et al., 2012). During the course of evolution and domestication these useful alleles might have been lost. Although peanut possesses a large collection of germplasm, only a handful of accessions (1.1%) have actually being utilized to develop advanced breeding lines (Sharma et al., 2013). Efforts have been made toward utilization of wild species, resulting in the release of some elite cultivars with multiple disease and pest resistance from ICRISAT (Sharma et al., 2013) and from the US (Burow et al., 2013; Isleib et al., 2011).

Two introgression pathways termed as tetraploid and hexaploid routes have been employed for transferring genes from wild species to cultivated peanuts (Simpson, 1991), which has led to multiple germplasm lines with disease resistance to ELSs and LLSs, nematodes, and insect resistances. This paved the way for development and exploitation of synthetic amphiploid such as TxAG-6 from the cross of (*A. batizocoi* × (*A. cardenasii* × *A. diogoi*))$^{4\times}$ which has high resistance to *Meloidogyne arenaria*, *Phaeoisariopsis personata* (*Mycosphaerella berkeleyi*) and *Cercospora arachidicola* (*Mycosphaerella arachidic*) (Simpson et al., 1993). At the ICRISAT, efforts have led to the development of a set of 17 new synthetic amphiploid and autotetraploid populations, which would be helpful in broadening the genetic base of peanuts. Some of these synthetic amphiploids and autotetraploids have shown resistance to LLS (Mallikarjuna et al., 2012) and peanut bud necrosis disease (Shilpa et al., 2013).

With the availability of genomic resources in peanut, genomic introgression from wild species can be monitored in the introgression lines, and markers can be identified for useful alleles. Tanksley et al. (1996) first proposed a strategy termed as advanced-backcross QTL (AB-QTL) wherein markers for trait of interest and introgression can be simultaneously achieved. In peanut, using BC_3F_2 and BC_2F_3 populations from the cross between cultivar Fleur 11 and amphidiploid AiAd (*A. ipaënsis* GK 30076×*A. duranensis* V 14167)$^{4\times}$, 95 QTLs were identified under two water treatments (water-limited and well-watered) for physiological, agronomic, and morphological traits (Foncéka et al., 2012). In a BC_3 population from the cross of "Florunner" and the synthetic amphidiploid TxAG-6, 10 QTLs were identified for resistance to the root-knot nematode (Burow et al., 2014). At ICRISAT, two AB-QTL populations have been developed from the cross between ICGV 91114 (cultivated and) synthetic amphiploid ISATGR1212 (*A. duranensis* K 7988×*A. ipaënsis* GK 30076), and between ICGV 87846 (cultivated and) synthetic amphiploid ISATGR265-5A (*Arachis kempff-mercadoi* GKSPScGB 35001×*Arachis hoehnei* GK 30006). These populations have been genotyped with DArT markers and phenotyped for several disease resistance traits (Sharma et al., 2013).

HIGH RESOLUTION GENETIC AND TRAIT MAPPING

With the advent of NGS technologies, a large amount of genomic data can be generated in a relatively short time. A number of genomes have been sequenced using NGS, such as pigeon pea (Varshney et al., 2011), bread wheat (Brenchley et al., 2012), barley (IBGSC, 2012), and chickpea (Varshney et al., 2013). Many breeding activities in the past were limited by the extent of availability of genomic data in a crop, but with NGS technologies there is a new strategy to understand the genetics of traits of interest. Various new mapping populations have been proposed as next-generation populations which utilize multiparent individuals such as MAGIC and NAM, in which the recombinant inbred advanced intercross line (RIAIL) population fits into MAGIC scheme (Morrell et al., 2012). These populations have advantages of both biparental (high power of QTL detection) and association mapping (high resolution) (Gupta et al., 2014). Two diploid genomes of peanut, *A. duranensis* (A genome) and *A. ipaënsis* (B genome), have been sequenced (http://peanutbase.org/news_page_all); furthermore, the sequencing of tetraploid peanut is in progress. Hence, in the coming years, a large amount of genomic data will be available in peanut. In order to fully utilize the fruits of the genomic efforts, there is a need to develop these next-generation populations in peanuts.

MAGIC

MAGIC populations provide an increased level of recombination and mapping resolution by integrating multiple alleles from different parents (Cavanagh et al.,

2008). The MAGIC population is developed in many ways, in a "funnel" breeding scheme also termed as "classic MAGIC population," the multiple parents (founders) are intercrossed for n/2 generations (wherein "n" is the number of founders) until the founders are combined with equal proportions, followed by single seed descent (SSD) method to develop a RIL population (Rakshit et al., 2012). Another variant uses the half-diallele mating system for intercrossing the parents (two-way crosses) followed by intercrossing the F_1s until all the founders are represented in a single F_1 followed by SSD to the RIL population (Bandillo et al., 2013). A similar concept of crossing multiple parents has been used in the past. However, Rockman and Kruglyak (2008) proposed various breeding designs for development of RIAIL such as circular mating–RIAIL, circular pair mating–RIAIL, inbreeding avoidance–RIAIL, random mating–RIAIL, random mating with equal contributions of each parent–RIAIL, random pair mating–RIAIL, and random pair mating with equal contributions–RIAIL. In a simulation study in rice, Yamamoto et al. (2014) illustrated that the number of subsequent intercrossing dramatically increases the power of QTL detection. The current bottleneck is the QTL analysis in MAGIC populations. Verbyla et al. (2014) proposed a whole-genome average interval mapping (WGAIM) approach to simultaneously incorporate all founder probabilities at each marker for all individuals in the analysis, rather than using a genome scan in the R package "WGAIM," which could be useful in QTL analysis with multiple alleles.

The MAGIC scheme was first used in mice involving an eight-way cross using eight inbred strains and demonstrated that this population is efficient in fine mapping QTLs with small effects (Mott et al., 2000). Soon it was adapted in crops, and many populations in a wide range of species have been developed (Verbyla et al., 2014). Trebbi et al. (2008) developed a RIL population from a balanced four-way cross using four founders in durum wheat. In another study, two MAGIC populations were developed in wheat, one with four founders and the other with eight founders (Huang et al., 2012). In *Arabidopsis thaliana*, MAGIC population containing 19 founders was constructed (Kover et al., 2009). The most comprehensive MAGIC populations to date are in rice where four MAGIC populations have been developed for the two subspecies *indica* and *japonica*. For the *indica* subspecies, *indica* MAGIC and MAGIC plus were developed containing eight *indica* parents. However, for *japonica* subspecies, *japonica* MAGIC and Global MAGIC have been developed containing 8 *japonica* parents and 16 parents (eight *indica* and eight *japonica*), respectively (Bandillo et al., 2013). Development of a peanut MAGIC population is underway under the ambit of the Peanut Mycotoxin Innovation Lab project at ICRISAT, India, in collaboration with the University of Georgia, USA. However, MAGIC populations for different market types in peanut (runner, Spanish, Virginia, and Valencia types) should be initiated.

NAM

The NAM scheme is a proven strategy to dissect the genetic basis of complex traits in maize. The aim of the NAM deign was to capture genetic diversity by selecting

diverse parents (founders) and developing a large set of interrelated RIL mapping populations. The NGS platform then is used for generating dense genotyping data which helps in achieving high level of resolution by taking advantage of ancestral recombination. The NAM population has higher power QTL detection as compared with biparental mapping populations (McMullen et al., 2009; Yu et al., 2008a). In maize, the process of development of NAM populations involves individually crossing a set of 25 genetically diverse founders with a common parent "B73." The F_1s from each cross is forwarded through the SSD method to form a RIL population from each cross. The combined set of RILs arisen from each cross combination is called NAM (Yu et al., 2008a). The 5000 lines developed from this effort in maize has been successfully implemented in dissecting several complex traits, such as flowering time (Buckler et al., 2009), 13 morphological traits (Brown et al., 2011), southern leaf blight (Kump et al., 2011), northern leaf blight (Tian et al., 2011), and kernel composition traits (Cook et al., 2012).

However, in the case of sorghum, backcross (BC)-NAM populations were developed by using 100 diverse unadapted germplasm lines with the elite line "R931945-2-2." The F_1s were then backcrossed to the male sterile version of "R931945-2-2" to produce BC_1F_1 and followed by selfing of 50–100 individuals until BC_1F_4 population (Jordan et al., 2011). Forty QTLs for flowering time were identified in a subset of this population (Mace et al., 2013). At the ICRISAT, efforts are underway toward the development of NAM populations in peanut. In the United States, the development of 16 structured RIL populations has been accomplished by crossing two common parental lines to eight unique lines (2 × 8), factorial nested association mapping populations (Holbrook et al., 2013). The common parents are "Tifrunner" and "Florida-07" while the eight unique parents are "N08082olJCT," "C76-16," "NC 3033," "SPT 06-06," "SSD 6," "Olin," "New Mexico Valencia A," and "Florunner." The parents represent a wide range of disease resistance, agronomic, and morphological traits.

EMERGING TRAIT MAPPING STRATEGIES

Many economically important agricultural traits do not segregate in a qualitative manner. They are mostly quantitatively inherited with alleles having minor effects. The conventional way of identifying such variations is through QTL analysis where statistical association is made between genetic markers and phenotypic traits. It is required to have a large set of mapping populations in order to obtain recombination between QTL alleles. The population required is even larger if more than one QTL is present on the same linkage group. However, it has been discovered that a high level of resolution can be achieved with the help of high-density genotyping by using NGS methods (Huang et al., 2009). Mapping by sequencing has emerged as an important strategy for identifying major QTLs with high phenotypic variance (Schneeberger and Weigel, 2011). In this section we discuss some of these emerging strategies for faster identification of alleles by using new sequencing technologies.

MutMap

A method called MutMap was developed to combine cross-breeding with NGS in order to speed up the identification of genes that cause agronomically important traits in mutant lines (Abe et al., 2012). This innovative strategy was first demonstrated in rice to rapidly identify the locations of genes associated with desirable traits in mutants of an elite rice cultivar. In MutMap, whole-genome resequencing (WGRS) is done with the pooled DNA samples from an F_2 segregating progeny of a cross between a mutant and its wild type (WT). The process involves a mutagen, which is used to mutagenize a line that has a reference genome sequence. The first mutant generation (M_1) plants are then selfed to generate M_2 plants. These M_2 plants are phenotyped for the trait of interest and the desirable mutant is crossed with the WT. This F_1 is selfed to the F_2 generation and then phenotyped for the trait of interest. The extreme phenotypes are then pooled to form the two bulks which are then subjected to WGRS for identification of SNPs. The concept of SNP identification is based on the SNP index, and the sequence data of bulked DNA is aligned with the reference sequence. The SNPs with sequence reads containing only the mutant sequences (SNP index = 1) are considered to be linked to the causal SNP for the mutant phenotype. The MutMap is theoretically similar to some of the other related methods such as SHOREmap (Schneeberger et al., 2009) and next-generation mapping (Austin et al., 2011). The same group has updated MutMap to MutMap plus where the same concept of identification of causative SNP for the mutant phenotype can be achieved without crossing the mutant with WT line. Therefore, the DNA of M_3 progenies with extreme phenotypes are bulked to get the SNP index (Fekih et al., 2013). To overcome the difficulty of mutations in the missing genomic regions from the reference (gap) genome when the reference genome is aligned to the re-sequenced lines, Takagi et al. (2013b) proposed a MutMap-Gap strategy where MutMap is used to identify the causal SNP followed by de novo assembly, alignment, and identification of the causal mutation within the genome gaps. In peanut, this strategy can be implemented to identify agronomic traits of interest, such as peanut TILLING (targeting induced local lesions in genomes) population (Guo et al., 2012a).

QTL-seq

In the QTL-seq technique, the MutMap strategy was conceptually integrated to the normal F_2 and RIL population (Takagi et al., 2013a). The principle involves a combination of bulked segregant analysis and whole genome re-sequencing for rapid identification of agronomically important QTLs. A mapping population is developed by crossing plants with contrasting phenotypes for the trait of interest. The most preferred mapping population are RIL or doubled haploid for possible generating replicated data. But an F_2 population can also be used as it requires less time to develop than does RIL. However,

minor QTLs cannot be detected in this population. Once the population is generated and phenotyped, the DNAs of extreme phenotypes (20–50 individuals) are bulked together for whole genome re-sequencing. After alignment of the sequence with reference sequence, an SNP index is derived to narrow down to the causal SNP (Takagi et al., 2013a). This strategy has been used to identify an early flowering QTL in cucumber (Lu et al., 2014). In peanut, there are many RIL populations available (Table 1). Due to the availability of genome sequence of tetraploid peanut in the near future, we believe that QTL-seq technique can be applied for identification of causal SNPs for agronomically important traits.

Genetic Mapping, QTLs, and Molecular Breeding in China

China is the largest peanut producer in the world with about 4.7 million hectares in the regions from north latitude 18–46° and east longitude 80–131°. Due to the great differences in climate and soil types in the growing regions, there are many issues that the scientists and growers are facing, such as sustainable production, improving yield and quality, and abiotic stresses and disease resistances. In addition to the conventional technologies for peanut improvement, biotechnological approaches have been employed with notable success in peanut research and production in recent years in China.

The first genetic linkage map developed in China for cultivated peanut was reported in China at the International Conference on Groundnut Aflatoxin Management and Genomics held in Guangzhou 2006 (Wang, 2006) and published by Wang et al. (2010b), which was based on an F_2 population and SRAP makers and the map spanned a genomic distance of 2129.4 cM with 223 SRAP makers distributed on 22 linkage groups. Since then at least 14 other genetic maps have been developed by various research institutions. Yueyou 13 and Zhenzhuhei were used to develop RILs for linkage map construction. More than 1000 genomic-SSRs and EST–SSRs were screened for polymorphisms between these two parents. A total of 144 SSR markers that could detect polymorphisms were used to analyze the population. A genetic linkage map consisting of 131 SSR loci in 20 linkage groups was constructed. The map covered 679 cM with an average distance of 6.12 cM between adjacent markers (Hong et al., 2008). The same group constructed another map using a RIL population derived from the cross between Yuyou 13 and Fu 95-5. In this map, 114 SSR markers were mapped on 20 linkage groups which covered 568 cM with an average distance of 6.45 cM between adjacent markers (Hong et al., 2009). Later, Hong et al. (2010) constructed another genetic map using another RIL population derived from "Yueyou 13" and "J11." The length of this map was 401.7 cM containing 46 SSR markers on 13 linkage groups.

In collaboration with colleagues in the United States, Hong et al. (2010) reported a composite map to integrate these three maps. The length of this map was 885.4 cM and the average distance between adjacent markers was 5.8 cM.

Henan Academy of Agricultural Sciences (HAAS) developed four genetic maps based on the four mapping populations including two RILs and two F_2 populations, and a composite genetic map was also developed by integrating these four genetic maps (Zhang, 2011). A RIL population derived from an interspecific cross between a widely grown cultivar Baisha 1016 and the tetraploid species *Arachis monticola* was developed by HAAS. Both SSR markers and transposon elements (TE) were employed in the development of a genetic map. A total of 344 markers including 277 SSRs and 67 TEs were mapped onto 23 linkage groups covering a genomic distance of 1504.66 cM (X. Zhang, person. commun.). An SNP-based genetic linkage map was constructed using F_9 RIL population derived from "Zhonghua 5" × "ICGV 86699" (Zhou et al., 2014). "Zhonghua 5" is a cultivar of early maturing, high yield but susceptible to LLS disease. "ICGV 86699" is a breeding line that showed resistance to LLS disease. In this study, 35,257 SNPs were developed using next-generation double-digest restriction site-associated DNA sequencing approach. A map comprising 1685 marker loci (1621 SNPs and 64 SSRs) on 20 linkage groups was constructed with map length of 1466.7 cM and an average distance of 0.9 cM between adjacent markers (Zhou et al., 2014).

Trait mapping has been extensively carried out in China despite the paucity of dense genetic maps. Bacterial wilt (BW) is a severe disease in peanut production, especially in southern China. Several BW-resistant cultivars have been developed, for example, Yuanza 9102 which was derived from a cross between a cultivated peanut and a wild species, *A. diogoi*. A RIL population was developed from the cross of Yuanza 9102 and Chico (very susceptible to BW) and a linkage map was constructed using SSR markers. Two SSR markers that associated with BW resistance were mapped. The distance of these two markers to the disease resistance locus was 10.9 and 13.8 cM, respectively (Jiang et al., 2007). Based on an AFLP-based map constructed by the same research group, three QTLs related to BW resistance, qBW1, qBW2, and qBW3, were identified (Peng et al., 2010). Three BW resistance QTLs were detected with PVE of 21.62% (Peng et al., 2010). Web blotch caused by *Phoma arachidicola* Marass, Pauer & Boerema is an increasingly important foliar disease in major northern peanut growing regions in China. HAAS identified one QTL for web blotch resistance, which was located between SSR markers ARS313~ARS120, very close to ARS313 (0.42 cM), with PVE of 5.76% (Zhang, 2011). Through correlation analysis, Guangdong Academy of Agricultural Sciences (GAAS) detected five SSR markers having correlation with host plant resistance to *A. flavus* infection. A marker, pPGSseq19D9, with the highest correlation coefficient of 0.913 can differentiate the resistant varieties from susceptible ones, indicating a tight association with one major gene conditioning host resistance to *A. flavus* (Hong et al., 2009).The same research group reported one SSR marker linked to peanut testa color (Hong et al., 2007). A total of 42 QTLs were detected and could explain 7.0–24.1% of the variation for different traits (Hong et al., 2010; Liang et al., 2009b).

Using different RIL populations under two different environments, Zhang (2011) detected 66 QTLs that related to peanut yield, quality traits (lipid, protein, and fatty acid composition), and resistance to peanut web blotch (Zhang, 2011; Zhang et al., 2012b). Liu et al. (2013b) reported QTLs associated with stem height (PVE 5.81–18.0%) and the length of first primary lateral branch (PVE 5.61–25.12%). HAAS further found that QTLs for the number of total branches, 100 pod weight followed by the number of fruiting branches and 100 seed weight usually have higher PVE among the agronomic traits investigated, and QTLs for stearic acid and arachidic acid have much higher PVE (X. Zhang, person. commun.). Hebei Academy of Agricultural Sciences identified 13 additive QTLs for oil content with PVE 5.01–20.03% based on a RIL population derived from the cross SW9721-3×TE21 based on phenotypic data collected under 10 environments (L. Liu, person. commun.).

Association mapping was also conducted by Chinese institutions. HAAS selected 136 peanut varieties released in China and 64 SSR makers were employed for genotyping, and the phenotyping traits include oil content, protein content, and oleic acid content for three consecutive years (2010–2012). The study identified 18, 26, 31 SSR makers to be associated with the above-mentioned traits in the year 2010, 2011, and 2012, respectively, with PVE ranging from 2.7 to 35.4%. Four SSR markers, three associated with oleic acid content and one with protein content, were repeatedly detected in three years (Yan et al., 2013). The Oil Crops Research Institute conducted a similar study with Chinese peanut mini core collection of 289 germplasm lines. Genotyping was conducted with 109 SSR markers, and phenotyping performed in three environments. A total of 89 SSR alleles were identified to be associated with 15 agronomic traits. Eight alleles were repeatedly detected in two or three environments with PVE ranging between 1.05 and 2.98%, and 15 alleles were detected to be associated with multiple agronomic traits (Jiang et al., 2014).

MAS has thus far not been widely used in peanut breeding in China. However, the successful MAS example is selection for high oleic acid content. SSR markers were used in genetic diversity studies of high oleic acid peanut lines (Hu et al., 2013), and CAPS markers were used to genotype *FAD2A* and *FAD2B* of high oleic acid peanut breeding lines and cultivars (Chen et al., 2013a). High oleic acid markers such as SNPs (Wang et al., 2010a) or SSRs (Chen et al., 2009) were used to identify true hybrids. Wang et al. (2013a) reported the results from a multiple linear regression analysis, indicating that the *FAD2B* had more effect on high oleic acid content than *FAD2A* in peanut using an F_2 population derived from a cross between a normal oleic and a high oleic parental line. C.T. Wang's team at the Shandong Peanut Research Institute is investigating the possible role of other genetic modifier factors in additional to the well-documented *FAD2A* and *FAD2B* genes in conditioning oleic acid content, using a bulk segregant analysis strategy. Progress has been made in identification of candidate SNP markers associated with high oleic acid traits.

So far, several high oleic peanut cultivars have been released using traditional hybridization together with MAS. Kaifeng Academy of Agricultural and Forestry Sciences registered five high oleic acid peanut cultivars, Kainong H03-3 (81.6% oleic acid) in 2007, Kainong 61 (77.7%) in 2012, Kainong 176 (76.8%) in 2013, and Kainong 1514 (75.6%) and Kainong 58 (79.4%) in 2014 (Jian Zhong Gu, person. commun.). Since the release of Huayu 32 (77.8%) in 2009 by the Shandong Peanut Research Institute, five additional high oleic acid peanut cultivars have been registered in China, including Huayu 51 (80.31%), Huayu 52 (81.45%), Huayu 662 (80.80%), Huayu 951 (80.63%), and Huayu 961 (81.20%). High oleic acid peanut with cold tolerance also has been selected for regional evaluation (Wang et al., 2013b). Promising lines out-yielding the local check Huayu 33 (large-seeded peanut cultivar) or Huayu 20 (small-seeded cultivar) by 6–8% have also been developed. In 2013, Jihua 11 was registered as a high oleic acid (80.7%) peanut by Hebei Academy of Agricultural and Forestry Sciences (Chen et al., 2013b). There have been additional high oleic acid peanut cultivars registered in China. In 2013, Mars, Inc. launched a high oleic peanut breeding project in China with the five research institutions, Henan Academy of Agricultural Sciences (Zhengzhou), Oil Crops Research Institute of Chinese Academy of Agricultural Sciences (Wuhan), Shandong Academy of Agricultural Sciences (Jinan), Qiongzhou University (Sanya), and Qingdao Agricultural University (Qingdao). The project goal is to develop high oleic acid peanut cultivars using MAS to transfer the trait to local elite peanut lines in a three-year breeding scheme.

ISSUES AND TRAITS, GENETICS, AND GENOMICS IN WEST AND CENTRAL AFRICA (WCA)

Peanut production in WCA faces several important challenges. The crop is grown mainly in poor soils often deficient in many nutrients, particularly phosphorus and calcium. Soils are also frequently exposed to intermittent drought due to erratic rainfall patterns in the region. Climate change models predict increased variability in precipitation (IFPRI, 2013), with increasing water shortage worldwide (Bernstein et al., 2007). Reduced overall rainfall, coupled with increases in precipitation events, will result in increased runoff, soil erosion, and reduced soil fertility (IFPRI, 2013; St Clair and Lynch, 2012). Several biotic constraints lower the yield and trade prospects of peanut in the WCA region, and many smallholder farmers in Africa lack access to improved seed due to weak national seed systems. ICRISAT and a wide range of partners have been working to improve peanut production in the WCA region through development of options for improved crop management and genetic enhancement.

Challenges and Opportunities for Peanut Production in WCA

Among the biotic constraints, foliar diseases, such as ELS, LLS, and rust; aflatoxin contamination; groundnut rosette disease (GRD); and soil-borne diseases

such as stem rot (*Sclerotium rolfsii* Sacc.) and collar rot (*Aspergillus niger* (Tiegh.) Speg.) are important constraints for which research for developing resistant peanut cultivar is underway in WCA. Among the insect pests, lepidopterans, aphids, thrips, and bruchids cause the greatest losses to the peanut crop. *Aphis craccivora* Koch plays a role in transmission of a number of viruses, including GRD known as a major viral disease of peanut and can cause up to 100% yield losses (Naidu et al., 1999).

Based on the relative importance of the various constraints in the WCA region, agreed priorities have led to emphasis on genetic improvement to challenge foliar diseases, aflatoxin, GRD, and drought. Among the important foliar diseases in WCA ELS and LLS are common and cause yield losses varying from 20 to 50%, and if combined with rust, the losses could be in excess of 50% (Waliyar et al., 1994).

Over 15 closely related *Aspergillus* spp. are known to produce aflatoxins, but *A. flavus* and *Aspergillus parasiticus* are the most important in the colonization of peanuts and other agricultural crops (Torres et al., 2014). Toxin-producing strains occur in high frequencies in West Africa with specific reports from Nigeria (Donner et al., 2010); Senegal (Diedhiou et al., 2011; Waliyar, 1978), Ghana (Perrone et al., 2014), Burkina Faso, Ivory Coast, and Sierra Leone (Probst et al., 2014). Others suggest that all West African countries are endemic with the presence of toxin-producing strains in their cropping fields. Both fungal species produce a highly toxic group of mycotoxins known as aflatoxins. Health effects in humans and livestock due to consumption of aflatoxin-contaminated foods include impaired growth, liver and other cancers, immunosuppression, synergisms with hepatitis B and C virus infection, and death. Aflatoxin contamination in peanuts and other food crops have contributed to significant trade losses to West African countries, but these losses have been difficult to quantify. Dohlman (2003) suggested that global trade would decline by US$3 billion if countries were to adopt European Union standards on aflatoxin.

Breeding and Genetics in WCA

Peanut research in WCA is currently focused on genetic improvement and broadening the genetic base for major biotic and abiotic stresses. Specifically, emphasis is in the areas of identification of short duration aflatoxin-free germplasm lines through systematic laboratory and field screening, breeding programs for incorporating resistance, and evolving cultivable resistance to these stresses and in characterization of biotic constraints. Other key thrusts include analyzing demand for information research priorities on an ongoing basis; facilitating peanut seed and technology delivery systems; enhancing postharvest processing and market opportunities; and fostering innovation and knowledge management. Identification of resistant sources for foliar diseases such as rust, LLS, and ELS is currently through field evaluation by infector rows under artificial epiphytotic conditions. The elite breeding lines with consistency in rust and leaf

spot resistance are being used in regional breeding programs. Several sources of resistance have been identified, and breeding lines and varieties have been developed and deployed. Improved peanut genotypes resistant to debilitating diseases have been released and adopted in many countries in the region such as groundnut lines ICGV 92093, ICGV 92088, ICGV 92082, ICGV 91225, ICGV 86124, and ICGV 96894 (Ndjeunga et al., 2013; Ntare et al., 2007).

GRD epidemics are known to cause up to 100% yield losses (Naidu et al., 1999). Following initial reports in Tanzania in 1907 (Zimmerman, 1907), GRD has been confirmed in many countries throughout Sub-Saharan Africa (Naidu et al., 1997, 1999). GRD is known to be caused by three causal agents: the groundnut rosette assistor virus, groundnut rosette virus, and a satellite-RNA (SatRNA) (Waliyar et al., 2007). Current thrust areas for GRD include the development of cultivar resistance include standardizing various screening techniques for resistance screening, vector-ecology studies, germplasm screening, determining the inheritance of resistance to GRD, factors governing GRD resistance, disease epidemiology, and management by vector control (*A. craccivora*) (Waliyar et al., 2007). In collaboration with the Institute of Agricultural Research, Zaria, Nigeria, several cultivars (Samnut 22, Samnut 23, and Samnut 24) were released with very high level of resistance to GRD.

Aflatoxin research comprised evaluating various germplasm sets such as the core collection, mini core, advanced breeding lines, and synthetics at the field level for preharvest resistance in hot spot locations and for in vitro seed colonization (IVSC) at the laboratory level (Waliyar et al., 1994). The accessions, ICGs 4888 and 9407 were found to be resistant to in vitro seed colonization by *A. flavus*. Further, groundnut accessions ICG 1326, 3263, 3336, 3700, 4749, and 7633 were resistant to both IVSC and seed aflatoxin contamination and so are important in breeding programs for aflatoxin resistance. In another study during 1999–2001, the accessions, ICG 9610, 1323, 10094, 9407, 3263, 4749, 1859, 4589, and 7633 have shown consistent resistant reaction to preharvest aflatoxin contamination at Indian and African conditions. Altogether, 29 genotypes have recorded resistance to aflatoxins ranging from 0.4 to 3.5 $\mu g\,kg^{-1}$ (Nigam et al., 2009). Relationships between drought stress and aflatoxin contamination in Sahelian environment have also been investigated (Hamidou et al., 2014). These authors found that groundnut accessions ICG 5891, ICG 4729, and ICG 6813 revealed resistance to aflatoxin contamination and tolerance to intermittent drought stress.

Genomics and molecular breeding research and its application is limited for peanut improvement in African countries and has yet to take momentum due to various reasons such as inadequate infrastructure, high genotyping costs, and inadequate human capacities (Janila et al., 2013).

Peanut Improvement for Drought Adaptation in WCA

Drought stress limits peanut productivity in Sub-Saharan Africa, but drought scenarios vary across time and geographical scales. The extent of this variation

and, more importantly, the consequence on crop yields has not been described. Also, over the past decades, the peanut plant type cultivated in Africa has evolved from predominantly spreading types of medium to long duration with quite profuse foliage to now mostly erect types of early duration with much smaller foliage. However, the recommended seeding rate of 60 kg seed ha^{-1} (20 plants m^{-2}) has remained unchanged with this change in plant characteristics. Therefore, the number one priority for peanut productivity improvement is to ensure that the agronomic practices currently recommended are optimal for the plant types, and to carry out a proper characterization of the stress environments to better target crop improvement efforts, where needed. Crop simulation studies are actually showing that a rate of 40 plant m^{-2} would increase crop productivity by about 20% and be optimal (V. Vadez, person. commun.).

With regards to the genetic improvement efforts, the past few years have identified a number of highly tolerant Spanish germplasm sources (Hamidou et al., 2012), some of which (e.g., ICGV 11088 and ICGV 97183) coming ahead of drought-adapted ICGV 91114. In parallel, research efforts have shown that adaptation to drought was in part lying in adjusting the crop canopy size to water availability (Ratnakumar and Vadez, 2011), and in the capacity of plants to restrict transpiration under high vapor pressure deficit (VPD) conditions (Devi et al., 2010). Both traits control the plant water budget, and the latter one allows plants to save water when the evaporative demand is high (a feature of the growing conditions in the semiarid tropics) and when the water cost of producing biomass is high. Crop simulation studies indicate indeed possible yield increases with that trait in the range of 20–30% under drought stress conditions (V. Vadez, person. commun.). In parallel, several potential donor parents for these traits are being used in the development of genetic population. The ultimate objective is to decipher the genetics of these traits in order to manipulate and "tailor" the leaf canopy size and the VPD response trait to specific stress scenario. Considerable progress also has been made in the phenotyping protocols to assess drought response in peanut (Ratnakumar and Vadez, 2011; Vadez et al., 2014), and in particular using a lysimeter system to assess transpiration efficiency against improper indirect screening methods for transpiration efficiency like SPAD chlorophyll meter readings (SCMR) or specific leaf area (SLA) measurements (Devi et al., 2011).

Drought is a recurrent problem for WCA. Peanut is part of cropping systems and it is important to view the crop improvement efforts from this perspective of two areas that require future investments (Sinclair and Vadez, 2012). First, peanut has a very efficient symbiotic nitrogen fixation system but there is likely very large genetic variation, something that was indirectly suggested from a study on the forage nutritional quality of peanut haulm (Blummel et al., 2012). Therefore, highly efficient germplasm for symbiotic nitrogen fixation should be screened and used in breeding because N-rich haulm would be an outstanding source of animal feed and N-rich underground residue could bring substantial N benefit to subsequent cereals. Especially as in peanut grown area of WCA,

agriculture and livestock are tightly linked. Second, low soil P is a feature of WCA and legumes such as peanut or cowpea do better than cereals like sorghum and pearl millet and can contribute to the system in the form of P-rich crop residue. Here also we could expect large genotypic variations in the capacity to adapt to these low soil P conditions, which would require the development of screening facilities to harness this potential. In recent work, P availability in Sahelian poor soil is crucial for nitrogen fixation in groundnut (F. Hamidou, person. commun.). For drought and low nutrient (low P) adaptation in peanut, great emphasis must be on roots traits contributing to efficient capture of water/nutrients in sandy soil as the recurrence and duration of occurring intermittent drought during seedling and/or vegetative stage lead to early plant death.

CONCLUSIONS

From lack of availability of molecular markers to the release of genome sequence of two of its diploid wild relative, the international peanut community has come a long way and, particularly since 2010. However, there still is long way to go when genomics-assisted breeding would be a routine implementation in crop improvement like in rice, maize, and other crops. Nevertheless, the stage is now set to harvest the fruits of genomics research for peanut improvement. It is expected that with the increasing effort toward SNP-based markers there will be an increased use of GAB in peanuts. It has been already proven to be efficient in developing high oleic acid, resistance to root-knot nematode, and rust resistance in peanuts. Nevertheless, it will contribute to the peanut community in whole and global food supply and human health in general and to fight the malnutrition.

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