8 History and Impact of the International Peanut Genome Initiative: The Exciting Journey Toward Peanut Whole-Genome Sequencing

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Abstract

Peanut is one of the major oilseed crops in the world and is a staple food crop for much of the world. It also faces many challenges in production and possesses many opportunities in advancing science. The U.S. Peanut Genome Initiative (PGI) was launched in 2004, and brought to the international stage in 2006 to meet these challenges through coordination of international efforts in genome research beginning with molecular marker development and the improvement of genetic map resolution and coverage. The International Peanut Genome Initiative (IPGI) was the first committed step by the global peanut research community toward meeting these needs and challenges. Ultimately, a peanut genome sequencing project was initiated in 2010 by the Peanut Genome Consortium (PGC) and the genome sequences of two diploid peanut progenitors were published in 2016. During this time, IPGI and PGC have been guiding and leading demand-driven innovations in peanut genome research and translating the information into practical research and breeding. In this chapter, we review the background and history of IPGI and its achievement in developing improved genotypes using marker-assisted breeding. We also reviewed the development of peanut populations for high-resolution genetic and trait mapping, highlighting the transition to and preparation for next-generation, multi-parental genetic mapping populations from individual bi-parental populations.

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8.1 Introduction

A major milestone in biological science was the sequencing of the human genome which provided fundamentally novel methods of studying the human body (Lander et al. 2001; Subramanian et al. 2001; Venter et al. 2001). Likewise, plant genome sequencing is impacting our understanding of crops and their interactions with the environment. The complete decoding of the three billion letter human genetic codes marked an important milestone in biomedical research, suggesting that the human genome may contain fewer than the expected 50–100,000 genes (Lander et al. 2001). No matter how many genes are encoded in the human genome, only a fraction of them are expressed at any given time in any given cell within the human body. This is also true in the plant genome. To better understand plant genetic improvement of crop yields and plant responses to stress, more information is needed on the dynamics of gene activities in plants, and how their expression is controlled in the context of a cell as a function of time and space. By 2050, the human population on the earth is expected to reach nine billion (Nature Editorial 2010), with demands for food, feed, and fiber continuing to grow. Therefore, there is an urgent need to develop new technology to produce improved cultivars of crop plants, such as peanuts, that contribute toward feeding the increasing global population. Advances in food production will also require greater efforts in agricultural research to increase crop yield with improved genetics for plant protection from biotic and abiotic stresses.

Peanut (*Arachis hypogaea* L.) is one of the major economically important legumes cultivated worldwide for its ability to grow in semi-arid environments with relatively low inputs of chemical fertilizers. On a global basis, peanut is also a major source of protein and vegetable oil for human nutrition, containing about 28% protein, 50% oil, and 18% carbohydrates. Peanut is cultivated in more than 100 countries in Asia, Africa, and the Americas, grown mostly by resource-limited farmers of the semi-arid regions. India and China together produce almost two-thirds of the world's peanuts, and the U.S. produces about 6% (Guo et al. 2012).

Farmers face many challenges to increasing peanut productivity. Low productivity of peanut in several countries is ascribed to several stress factors including biotic and abiotic stresses in the cultivation of the crop (Khedikar et al. 2010; Pandey et al. 2014a, b, c). Among the biotic stresses, diseases are the major constraints that limit peanut productivity including yield and quality. Major peanut diseases include early leaf spot (ELS, *Cercospora arachidicola*), late leaf spot (LLS, *Phaeoisariopsis personata* Berk. and Curt.), rust (*Puccinia arachidis* Speg.), *Peanut mottle virus* (PMV), *Groundnut rosette virus* (GRV), *Tomato spotted wilt virus* (TSWV), and root-knot nematode (Pandey et al. 2014a, b, c). Rust, stem rot (*Sclerotium rolfsii*), collar rot (*Aspergillus niger* Van Teighem), and leaf spots often occur together and cause pod yield loss up to 50–70% (Subrahmanyam et al. 1989; Mishra et al. 2015). Because of the frequent occurrences of multiple diseases, peanut yields are often significantly lower than their potential production (Holbrook and Stalker 2003).

Another challenge to enhancing peanut production is polyploidy ($2n = 4x = 40$) and a large genome size, which greatly complicates interpretation of genomic data as compared to the diploid wild relatives ($2n = 2x = 20$) (Guo et al. 2013). It is also difficult to transfer alleles from wild species to cultivated peanuts (Simpson 1991). During the past decade, extensive efforts in 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, transcriptomes, and proteomics analyses (Guo et al. 2013; Varshney et al. 2013; Katam et al. 2014), which were reviewed by Feng et al. (2012) and Guo et al. (2016). These genetic and genomic resources have been successfully used to construct genetic maps, to identify quantitative trait loci (QTL) of traits of interest, and to conduct marker-assisted selection and association mapping for peanut improvement (Pandey et al. 2014a, b, c; Guo et al. 2016).

Recognizing the challenges and importance of this crop and the benefits of enhancing our understanding of the peanut genome, the international peanut research community established the International Peanut Genomics Initiative (IPGI) in order to pool resources to meet these needs. In this chapter, we focus on the history and accomplishments of the IPGI in three areas: (1) brief background of the IPGI and a chronology of recent efforts in the peanut genome sequencing project; (2) recent developments in molecular markers, particularly molecular markers associated with disease resistance traits and current progress in marker-assisted breeding; and (3) recent efforts in developing next-generation populations for high-resolution genetic and trait mapping in peanut. Advances in each area over the years have come as the result of the initiative and international cooperative efforts of the scientific research community.

8.2 A Brief History and an Overview of the Peanut Genome Project

As early as 2001, the efforts were initiated at a meeting in Hunt Valley, MD on July 30–31, in light of the challenges and opportunities facing cool and warm season legume crops, and international research cooperation to develop new genomic technologies for legume crop improvement. Twenty-six legume scientists with knowledge of structural and functional genomics, DNA markers, transformation, bioinformatics, and legume crop improvement participated in a workshop hosted by the United Soybean Board, the National Peanut Foundation, the USA Dry Pea and Lentil Council, and the USDA-ARS to develop a strategy to advance genomics research across five economically important legume species. The group of scientists published the *U.S. Legume Crops Genomics White Paper* (Boerma et al. 2001) that outlined six areas where progress was needed across all legume crops. This meeting was followed by the Cross-Legume Advances through Genomics (CATG) Conference in Santa Fe, NM on December 14–15, 2004, where nearly 50 legume researchers and funding agency representatives met and developed a plan for cross-legume genomics research and to develop an action plan for legume research (Gepts et al. 2005). The peanut scientific community participated in both workshops. A book, *Legume Crop Genomics*, which documented the status of genomic resources for each legume crop including peanut (Wilson et al. 2004) was published under the auspices of the U.S. Legume Crop Genome Initiative (LCGI).

In 2004, 26 U.S. peanut scientists participated in a workshop hosted by the Peanut Foundation and American Peanut Council in Atlanta, GA on March 22–23. A *National Strategic Plan for the Peanut Genome Initiative* (PGI) (Wilson 2006b) was developed that outlined six objectives for the years 2004–2008: (1) improve the utility of genetic tools for peanut genomic research and develop useful molecular markers and genetic maps for peanut; (2) improve the efficacy of technology for gene manipulation in genomes and develop useful transformation methods for functional genomic research in peanut; (3) develop a framework for assembling the peanut genetic blueprint and locate abundant and rarely expressed genes, using genetic and physical approaches to integrate diverse data types; (4) improve knowledge of gene identification and regulation; (5) provide bioinformatics management of peanut biological information resources; and (6) determine the allergenic potential of peanut proteins. An action plan summarized in the white paper *National Program Action Plan for the Peanut Genome Initiative* soon followed (Wilson 2006a); and in 2006 an assessment of costs associated with genomic research was presented in the *Biotech Peanut White Paper "Benefits and Issues"* (Valentine et al. 2006) (http://www.peanutbioscience.com/images/PeanutWhitePaper.pdf).

In 2006, the PGI sought to expand its mission through outreach to the international peanut research community. The foundation for this effort was established in November 2006 in Guangzhou, China at the *International Conference on Aflatoxin Management and Genomics* where delegates from nine countries voted to maintain an open dialog to explore opportunities

for cooperative research, and to take steps toward achieving that goal with annual meetings. Therefore, the second conference of the international peanut research community was hosted on October 24–26, 2007 in Atlanta, GA, and it was the first conference to use the name Advances *in Arachis through Genomics & Biotechnology (AAGB): An International Strategic Planning Workshop* (credited to Varshney and ICRISAT team), which was another step toward bringing members of the international peanut community together to foster research collaboration on high priority issues. The *International Strategic Plan for the Peanut Genome Initiative 2008–2012 (IPGI): Improving Crop Productivity, Protection, and Product Safety & Quality* was developed at this workshop (http://www.peanutbioscience.com/images/Peanut_Genome_Intitative-StratPlan_DRAFT_v1.2_Mar08.pdf).

Since then the tradition of excellence that was established in Guangzhou and in Atlanta has been upheld at subsequent meetings including the *Third Advances in Arachis through Genomics & Biotechnology* (III AAGB-2008) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India, IV AAGB-2009 in Bamako, Mali, V AAGB-2011 in Brasilia, Brazil, VI AAGB-2013 in Zhengzhou, China, VII AAGB-2014 in Savannah, Georgia, U.S., VIII AAGB-2015 in Brisbane, Australia, and IX AAGB-2017 in Cordoba, Argentina.

With the progress made by IPGI and the need to move on to the whole-genome sequencing discussion, the Peanut Foundation and the American Peanut Council on behalf of international peanut research community initiated the discussion of pursuing a peanut whole-genome sequencing project and related issues on July 12, 2010, at Clearwater, FL, as reported by Baozhu Guo, the liaison to China, that Chinese collaborators had been discussing a plan for peanut whole-genome sequencing. The executive committee of IPGI made the decision to send a delegation to China to initiate discussions with Chinese peanut collaborators for a possible joint sequencing project along with other international partners. Two members from the executive committee Victor Nwosu, Plant Science Program Manager, Global Chocolate Science & Technology of Mars Chocolate, NA, and Baozhu Guo, Plant Pathologist, USDA-ARS Crop Protection and Management Research Unit, traveled to China from September 2 to 12, 2010. The local host Xinyou Zhang, Henan Academy of Agricultural Sciences and Peanut Breeder, made the plan and arranged a meeting with Chairman Fuhe Luo who was then President of Guangdong Academy of Agricultural Sciences in 2006, and who had moved up to be national leader in Beijing since early 1998, along with other scientists, including Xingjun Wang of Shandong Academy of Agricultural Sciences and Da Luo of Sun Yat-Sen University. A proposal was made to collaborate and pool resources together to sequence both the tetraploid and diploid peanut genomes.

This trip report was sent to the IPGI executive committee, which started the ball rolling, resulting in the Peanut Genome Project Inaugural Meeting (http://www.peanutbioscience.com/peanutgenomeproject.html) on December 8 2010 in Atlanta, where Howard Shapiro of Mars also reported his meeting with BGI (Beijing Genomics Institute) concerning the peanut whole-genome sequencing. The Executive Committee of the IPGI agreed in principle to move the sequencing project forward to sequence peanut whole genomes with international collaborative effort. The IPGI Executive Committee called another meeting to continue the discussion of pursuing a peanut whole-genome sequencing project and related issues on January 12, 2011 at the Plant and Animal Genome (PAG) Conference, San Diego, CA, organized by Howard Shapiro and Rich Wilson, and tentatively decided to sequence four peanut cultivars (Tifrunner and GT-C20, SunOleic 97R, and NC94022) and their 200 recombinant inbred line (RIL) progenies (Qin et al. 2012) in collaboration with Chinese peanut researchers, in addition to the two diploid peanut progenitors. Nwosu and Guo made another trip to China from March 18 to 31, 2011 to discuss technical strategies and cost-sharing with Chinese collaborators, Xinyou Zhang, Suoyi Han, Wenyue Ma, Xingjun Wang,

Jiaquan Huang, Ronghua Tang, and Xuanqiang Liang along with Xiaoping Chen (on conference call). The group unanimously agreed to join the peanut genome sequencing projects and signed a Memorandum of Understanding.

A third trip was made by U.S. delegation to China (September 19–30, 2011) for meetings with Chinese collaborators and the China Ministry of Science and Technology, and discussed the time for launching the peanut genome sequencing project. The members were Victor Nwosu, Kim Moore, Howard Valentine, and Baozhu Guo. The sequencing and assembly strategies as proposed by BGI were adopting an integrated strategy combining whole-genome sequencing (WGS) plus bacterial artificial chromosomes (BACs) by BAC sequencing with Hiseq 2000 technology, and then resequencing and calling SNPs according to alignment to the developed reference genome with the aforementioned 200 RILs of the two mapping populations (Qin et al. 2012). The SNPs will then be used as markers to construct a genetic map for chromosome-level assembly.

In 2012, the sequencing and assembly strategies were discussed and adopted on March 28, in Atlanta. The Peanut Genome Consortium (PGC) was formally established as an extension of the IPGI and was embodied by a coalition of international scientists and stakeholders engaged in the Peanut Genome Project (PGP). PGP is an international collaborative research program whose goal is the complete mapping and understanding of all the genes of peanuts. PGC scientists have been deciphering the peanut genome in three major ways: developing polymorphic markers and producing genetic linkage maps; mapping the locations of genes/markers associated or linked with inherited traits such as disease resistance, yield, and quality; and determining the correct order or "sequence" of all the bases in peanut genome's DNA. Finally, the IPGI and PGC released the two diploid sequences for public use in April 2014 (http://www.peanutbase.org/node/618) and published the two genome sequences of the diploid ancestors of cultivated peanut in the journal *Nature Biotechnology* in February 2016 (Bertioli et al. 2016). The amazing findings of this publication were that these two genomes are very similar to the A and B subgenomes of allotetraploid cultivated peanut and could be used to identify candidate disease resistance genes, and to guide tetraploid transcript assemblies. Based on the high DNA identity of the *A. ipaensis* genome and the B subgenome of cultivated peanut and biogeographic evidence, the conclusion could be reached that *A. ipaensis* may be a direct descendant of the same population that contributed the B subgenome to cultivated peanut (Bertioli et al. 2016).

Another significant publication for *Arachis duranensis*, the peanut A-genome progenitor, a draft genome, was published in May 2016 in the journal of Proceedings of the National Academy of Sciences of the United States of America (PNAS) (Chen et al. 2016). This genome analysis suggests that the peanut lineage was affected by at least three polyploidizations since the origin of eudicots. Further resequencing of synthetic *Arachis* tetraploids also revealed extensive gene conversion since their formation by human hands. The *A. duranensis* genome provides a major source of candidate genes for fructification, oil biosynthesis, and allergens, expanding knowledge of understudied areas of plant biology and human health impacts of plants. This study also provides millions of structural variations that can be used as genetic markers for the development of improved peanut varieties through genomics-assisted breeding.

8.3 Major Contributions of IPGI in Trait Mapping and Molecular Breeding

During the years, much effort has been made to develop genetic and genomic tools and resources for cultivated peanut, such as construction of BAC libraries (Yuksel and Paterson 2005; Guimarães et al. 2008), cDNA libraries (Luo et al. 2005; Proite et al. 2007; Guo et al. 2008, 2009), RNAseq using next-generation sequencing technology (Guimaraes et al. 2012; Zhang et al. 2012), and development of DNA markers (see

reviews of Feng et al. 2012; Zhao et al. 2012; Varshney et al. 2013). Several reviews have recently been published in summarizing the achievements made in peanut genetics and genomics tool and resource development (see reviews of Feng et al. 2012; Zhao et al. 2012; Varshney et al. 2013; Guo et al. 2013, 2016).

Development of disease-resistant genotypes involves a series of processes including selection of ideal parents, generation of a large segregating population, and subsequent selection of desirable plants. Those are the essential steps of traditional interspecific hybridization breeding. Since 1960s, progress has been made in interspecific hybridization in peanuts because some wild *Arachis* species show a very high level of resistance to many diseases, such as ELS, LLS, rust, and stem rot (Holbrook and Stalker 2003). However, attempts to utilize these wild species as sources and the process of transferring the resistance and desired alleles to cultivated peanut has been severely hampered because of many factors, such as genomic (A and B genomes) and ploidy (diploid and tetraploid) barriers, restricted gene flow due to differences in ploidy level, the long period required for developing stable tetraploid interspecific derivatives, cross compatibility barriers, and a complicated inheritance mechanism (Burow et al. 2013). Meanwhile, conventional methods of screening germplasm in the field are time and resource consuming. Several factors contribute to the development of uniform occurrence of diseases in field conditions, which usually makes it difficult to achieve uniform distribution of disease pressure on populations and can lead to misclassification of lines (Yol et al. 2015). Moreover, the partial and polygenic nature of disease resistances makes the selection of ideal cross parents and the identification of resistant and susceptible lines in different generations very tedious using the traditional screening techniques (Leal-Bertioli et al. 2009).

Therefore, more efforts have been made to achieve progress in the area of crop genomics applied to breeding in recent years (Varshney et al. 2005; Guo et al. 2016). Combining genomics tools with conventional breeding can lead to more rapid development of resistant cultivars. Particularly, the advances in molecular marker technologies have provided techniques to improve crop breeding, which would be cost-effective and faster for selection, such as marker-assisted selection (MAS), which offers great promise for increasing the efficiency of conventional plant breeding, including the potential to pyramid resistance genes in peanut (Guo et al. 2012; Pandey et al. 2014a, b, c). Significant progress has been made for resistance to nematodes, rust, and leaf spots in addition to oil content and quality, and MAS has been applied into breeding programs for these traits (Simpson et al. 2003; Chu et al. 2011; Varshney et al. 2014; Khera et al. 2017).

8.3.1 Resistance to Root-Knot Nematode

Among the many pathogens of peanut, root-knot nematodes are among the most serious damaging and widespread (Dickson 1998). In many peanut production areas all over the world, root-knot nematodes are the most important factors that limit the yield of peanut and cause significant economic losses every year (Holbrook and Stalker 2003). There are three nematode species which can infect peanut, *Meloidogyne arenaria* (Neal) Chitwood, *M. hapla* Chitwood, and *M. javanica* (Treub) Chitwood. *Meloidogyne arenaria* is the predominant pathogenic species in the peanut areas of southern United States. About 40% fields in some areas can be infected resulting in yield losses in excess of 30% (Burow et al. 2014). Quantitative sources of resistance to root-knot nematodes have been identified in germplasm, even in *A. hypogaea*, and molecular work has been done to find the linked markers, genes, and QTLs.

Two dominant genes conferring resistance to *M. arenaria* were identified in an F_2 population, *Mae* and *Mag*. *Mae* is the gene restricting egg number, while *Mag* restricts galling. Meanwhile, a RAPD marker (Z3/265) which was linked to these genes was also identified (Garcia et al. 1996). These were the first molecular markers linked with a resistance gene for an

agronomically useful trait in peanut. Three more RAPD markers RKN410, RKN440, and KKN229 were found to be associated with nematode resistance in several backcross populations (Burow et al. 1996). These markers were all tightly linked and were all for the same gene. Two RFLP markers ca. 4 cM from the resistant gene were identified by bulked segregate analysis (Church et al. 2000). A sequence characterized amplified region (SCAR) marker, 197/909, was a new nematode resistance dominant marker. It was developed from the published sequence of a RAPD marker RKN440 and was found to be tightly linked with the resistance locus in populations derived from two tetraploid crosses (Burow et al. 1996; Chu et al. 2007). Two SSR markers with the genetic distance of 4.42 cM and 7.40 cM to root-knot nematode (*M. hapla*) resistance were discovered by analysis of an F_2 population derived from Huayu-22 and D099 (Wang et al. 2008). Nagy et al. (2010) developed a codominant SSR marker, GM565, through high-resolution mapping for nematode resistance, which could be used to identify heterozygotes for nematode resistance. These markers were then been examined for accuracy through field tests for root-knot nematode resistance in peanut (Branch et al. 2014). A new RFLP marker, R2430E, was found to be linked to the locus for the resistance to peanut root-knot nematode (*M. arenaria* race 1) (Pipolo et al. 2014).

Marker-assisted selection (MAS) has been demonstrated to be more efficient than phenotypic selection in use of markers for development of the nematode-resistant cultivars. Since Simpson et al. (1991) developed a root-knot nematode-resistant, synthetic allotetraploid line (TxAG-6), the first nematode-resistant peanut cultivar COAN was developed which contained a distinct trait donated from wild species (Simpson and Starr 2001). The second nematode-resistant peanut cultivar was then released with two generations of backcrossing of COAN-derived materials, and was developed by the use of RFLP markers (Simpson et al. 2003). These two resistant cultivars were found to carry the same dominant resistance gene for two root-knot nematode species (*M. arenaria* and *M. javanica*), and both have been widely used as important sources of resistance to root-knot nematode (Chu et al. 2007). For example, another nematode-resistant cultivar Tifguard was developed based on the improved nematode-resistant markers (Holbrook et al. 2008). This cultivar also was successfully converted into the Tifguard High O/L cultivar using MAS backcrossing selection (Chu et al. 2011). During the breeding process, three markers were involved including the dominant SCAR marker 197/199 (resistant allele), another dominant CAPS marker 1169/1170 (susceptible allele), and the codominant marker GM565 (Chu et al. 2011). This allowed for the identification of homozygous resistant, homozygous susceptible, and heterozygous individuals, respectively.

The previously mentioned markers for root-knot nematode resistance were mostly identified by using bulked segregate analysis. This method is efficient for identifying the markers with major effects but is less efficient for identifying the markers with minor effects (Burow et al. 2013). To improve sensitivity for small-effect QTLs, an advanced backcross population was screened for response to root-knot nematode infection. Composite interval mapping results suggested a total of seven QTLs plus three putative QTLs. These included the known major resistance gene plus the second QTL on LG1, and a potentially homeologous B-genome QTL on LG11. Additional potential homeologs were on LG8 and LG18, another QTL on LG9.2, and putative QTLs on LG9.1 and 19. Two introgressed QTLs were associated with susceptibility, and QTLs at some homeologous loci were found to confer opposite phenotypic responses (Burow et al. 2014).

8.3.2 Resistance to Leaf Spots and Rust

The foliar diseases early and late leaf spot are major destructive diseases of peanut worldwide (Shokes and Culbreath 1997). Epidemics of leaf spot diseases cause nearly complete defoliation

and yield losses of 50% or more through reduction of photosynthesis, death of the plant, and pod loss. Rust also is one of the severest diseases in peanut and can cause significant defoliation resulting in yield losses up to 50% (Subrahmanyam et al. 1989). Rust frequently occurs in combination with leaf spots, but one may predominate at different times (Burow et al. 2013). Although these diseases can be controlled by multiple applications of fungicides, long-term fungicide application could cause a slow erosion in disease control due to the gradual losses of sensitivity in the target population, environmental pollution, and economic impacts due to their application costs (Luo et al. 2005).

Because of the economic importance of these diseases, several studies in the area of molecular genetics and breeding have been performed, such as the application of different types of molecular markers, and the construction of peanut linkage maps (Mishra et al. 2015). Three RAPD markers associated with early leaf spot lesion diameter were identified through a population derived from the cross between an *A. cardenasii* introgression line and an *A. hypogaea* cultivated variety. Two breeding lines were developed from this genetic cross (Stalker and Mozingo 2001). A total of nine SSR markers were identified to be associated with rust resistance in two F_2 populations (Varma et al. 2005). Varman (1999) developed a rust-resistant line (VG9514) from the cross between the cultivar CO 1 and an *A. cardenasii* line to generate a mapping population. Using this population and a modified bulk segregate analysis, two RAPD markers, $J7_{1300}$ and $J7_{1350}$, linked to rust resistance were identified (Mondal et al. 2007). In the same lab, based on the Kruskal–Wallis one-way ANOVA and simple regression analysis, three and four SSR alleles were found associated with rust and late leaf spot, respectively (Mondal and Badigannavar 2010). Two genomic SSR markers (pPGPseq 4A05 and gi56931710) and a genic SSR marker (SSR-GO340445) for rust resistance in peanut were developed from the same mapping population mentioned previously (Mondal et al. 2012a, b). An F_2 population derived from Yuanza 9102 (a rust-susceptible line) and ICGV86699 (a rust-resistant cultivar) were applied to screen AFLP markers linked to rust resistance (Hou et al. 2007). By analysis of an F_2-segregating population derived from the cross of ICGV86699 and Zhonghua-5, three AFLP markers linked to late leaf spot resistance were identified (Xia et al. 2007). Using bulked segregate analysis, an SSR marker (PM384) was identified to have association with late leaf spot resistance. This marker could be utilized in marker-assisted breeding program (Shoba et al. 2012).

Burow et al. (2008) reported five markers for leaf spot resistance based on a mapping using RFLP markers, including three QTLs for incubation period and one each for latency period, lesion number, and diameter. Five QTLs were detected based on a mapping of 34 RGAs for late leaf spot disease resistance on detached leaves of the F_2 plants of the A-genome mapping population derived from *A. duranensis* × *A. stenosperma* (Leal-Bertioli et al. 2009), and suggested additive or partial dominance gene action. One QTL explained almost half of the phenotypic variance observed and two QTLs mapped near RGA markers. The first detailed study conducted in cultivated peanut was based on a partial genetic map comprising 56 SSR loci for the TAG24 × GPBD4 recombinant inbred line (Khedikar et al. 2010). This study reported 12 QTLs for rust (explaining 1.70–55.20% phenotypic variation). The SSR marker tightly linked to the major QTL (IPAHM103; QTLrust01) was then validated among a diverse set of genotypes as well as another population (Sarvamangala et al. 2011). This marker has been used for introgressing the major QTL for rust in peanut breeding program (Varshney et al. 2014). Using the same population mentioned previously and another RIL population, a consensus map with 225 SSR loci was developed. QTL analysis detected a total of 28 QTLs for late leaf spot and 15 QTLs for rust. A major QTL for late leaf spot ($QTL_{LLS}01$; linked markers GM1573 and Seq 8D09) with 10.27–62.34% phenotypic variance explained was detected across all the environments. Four new markers showed significant association with the major QTL (82.96% PVE) for rust resistance (Sujay et al. 2012). Validation of linked markers would accelerate the process of introgression of

rust and leaf spots resistance gene into preferred peanut genotypes. Gajjar et al. (2014) have attempted to validate the linkage of 22 SSR markers for rust and late leaf spot as reported by different workers, and 16 SSRs could be validated. QTL analysis based on an F_2 population derived from Tifrunner and GT-C20 had identified 37 QTLs for leaf spots, while in the F_5 map, 14 QTLs were found linked to leaf spots resistance (Wang et al. 2013). By using microarray analysis and real-time PCR, Luo et al. (2005) found genes were more greatly expressed in the resistant genotype as a response to *C. personatum* than in the susceptible genotype.

Another successful story of using MAS in peanut breeding was reported by Varshney et al. (2014) for rust resistance in addition to high oleic acid content and nematode resistance (Chu et al. 2011). Introgression of a major QTL for rust resistance through marker-assisted backcrossing has been successful in three popular Indian peanut cultivars, and generated several promising introgression lines with enhanced rust resistance and higher yield. One QTL explaining about 83% phenotypic variation for resistance to rust was validated and introgressed from the donor parent "GPBD 4" to three other peanut cultivars ("ICGV 91114", "JL 24", and "TAG 24") through marker-assisted breeding. There were a total of four markers used in the MAS breeding including one dominant (IPAHM103) and three codominant (GM2079, GM1536, GM2301) markers present in the QTL region (Varshney et al. 2014).

8.3.3 Resistance to Tomato Spotted Wilt Virus (TSWV)

Tomato spotted wilt virus is generally spread by thrips (*Frankinellia* spp.) and people usually control TSWV indirectly by applying insecticides. However, planting-resistant cultivars still is the best control strategy, which is effective and eco-friendly (Wang et al. 2013). Two major QTLs for TSWV resistance were identified for two RIL populations derived from the crosses of Tifrunner × GT-C20 and SunOleic 97R × NC94022, respectively, which explained 12.9% and 35.8% phenotypic variance (Qin et al. 2012). Recently, further study done in the different generations of the two populations identified 15 QTLs for TSWV resistance in F_2 map and nine QTLs in F_5 map, which explained 4.4–34.92% and 5.20–14.14% phenotypic variance, respectively (Wang et al. 2013). These were the only studies reporting QTL for TSWV resistance; however, it still provides hope for marker-assisted improvement of resistance to this disease (Burow et al. 2013). As a runner-type peanut cultivar, Tifrunner was released in 2005 with significantly higher resistance to TSWV than the moderately resistant cultivar Georgia Green (Holbrook and Culbreath 2007). Recently, Khera et al. (2017) reported an improved genetic linkage map for a recombinant inbred line (RIL) population derived from the cross between SunOleic 97R and NC94022. Multi-season (2010–2013) phenotypic data collected for the same population allowed for the identification of 16 major QTLs with more than 10% phenotypic variance explained, including four for resistance to TSWV, and six each for early spot and late leaf spot.

8.3.4 High Oleic Oil Peanuts

Oleic to linoleic acid ratios (O/L) in wild-type peanut are 1.0–4.0, whereas the O/L ratio in high oleic acid mutants is 35–40 (Norden et al. 1987). High O/L is desirable for healthy cholesterol-lowering benefits and the oxidative stability of the oil (Wilson et al. 2006a). The rate-limiting enzyme for the conversion of oleic to linoleic acid is oleoyl-PC desaturase (ahFAD2) (Ray et al. 1993). The two homoeologous genes encoding oleoyl-PC desaturase are *ahFAD2*A and *ahFAD2*B which are localized to the A and B subgenomes of *A. hypogaea*, respectively (Jung et al. 2000a, b). As an example of MAS in a breeding program for peanut cultivar improvement, an intensive backcross schedule has been developed to pyramid the high O/L trait with nematode resistance in the cultivar "Tifguard" (Holbrook et al. 2008). Crosses with

two high O/L cultivars, "Georgia 02C" (GAO2C) and "Florida 07", were made with "Tifguard". The markers used for nematode resistance were S197 and GM565 to detect the inheritance of the introgressed segment carrying *Rma*. Both high O/L donor parents possess the 441_442insA mutation which could be identified by CAPS marker *Hpy*188I, and all three parents carry the A-genome 448G → A transitional mutation in *ahFAD*2A allele; therefore, the only marker used for high O/L was *Hpy*188I-CAPS in order to track inheritance of high O/L. These markers can identify true hybrids at each stage of backcrossing. Therefore, the backcross and selection could be accelerated by using heterozygous F_1 hybrids as donor parents. In contrast to conventional breeding, which takes 8–10 years for a new cultivar release, this MAS approach is expected to produce a high O/L "Tifguard" within 26 months (Chu et al. 2011). Since then, efforts have been taken in ICRISAT and China and progress has been made significantly (Guo et al. 2016).

8.4 Recent Advancement in the Development of Next-Generation Mapping Populations for High-Resolution Genetic and Trait Mapping in Peanut

The primary goals of plant breeding for breeders are to improve yields, qualities, and other traits of commercial value suited to the needs of farmers and consumers (Moose and Mumm 2008). In practice, plant breeding mainly covers three processes: useful genetic variation is created or assembled; individuals with superior phenotypes are chosen; and improved cultivars are developed from selected individuals. The creation of experimental populations is a crucial step for plant breeders or geneticists (Varshney et al. 2006). However, during the initial period, breeder only depends on direct phenotypic selection, which is easily affected by genetic and environmental factors (Poormohammad Kiani et al. 2009). Thus, breeding methods depending only on phenotypic selection result in decreased accuracy and efficiency due to the fact that the majority of phenotypic variation in both natural populations and agricultural environments is determined by quantitative genetic traits (Mackay 2001).

With the advent of molecular marker, traditional breeding and genetics research is transitioning from a data-poor to a data-rich environment. Since the linkage mapping was developed using marker systems and crop traits (Edward et al. 1987; Paterson et al. 1988), the populations utilized for linkage mapping have included F_2, backcross (BC) or recombinant inbred (RI) populations and remain the primary methods used for plant QTL mapping studies (Huang et al. 2009). Recently, some researchers have applied genome-wide association study (GWAS) and single nucleotide polymorphism (SNP) genotyping markers into association analyses for crop genetic improvement (Rafalski 2010; Zhao et al. 2011; Riedelsheimer et al. 2012). Combined with next-generation sequencing technology, multi-parental mapping populations such as multi-parent advanced generation intercross (MAGIC) and nested association mapping (NAM) populations have become popular due to the high-resolution trait mapping obtained by combining the advantages of linkage analysis and association mapping (Zhang et al. 2005; Cavanagh et al. 2008; Yu et al. 2008). Recently, Huang et al. (2015) reviewed the current status and future prospects of multi-parent breeding populations, and here we summarize the efforts in the peanut community in developing next-generation multi-parental populations. We also compare the advantages and disadvantages of bi- and multi-parental mapping populations providing a frame of reference for choosing breeding populations in the future.

8.4.1 Bi-parental Breeding Populations

Bi-parental breeding populations, such as F_2, backcross (BC), and recombinant inbred line (RIL) populations, result from crosses between just two parents and may be effectively applied to

quantitative trait loci (QTL) analysis and linkage mapping (Verbyla et al. 2014). Among the bi-parental populations, the F_2 population is the easiest and most common population developed because it only requires a simple cross between two parents and the resulting progeny exhibits an obvious Mendelian segregation (Li et al. 2010). Genetic linkage map and QTL analyses with F_2 mapping populations have successfully been employed in peanut (Wang et al. 2013). However, the F_2 population still has two major limitations. First, the genetic structure of the F_2 population is easily affected by the environment resulting in difficulty of long-term preservation. Second, F_2 populations are the narrow genetic base of the population. For the dominant markers, the homozygous-dominant genotype and heterozygous genotypes could not be distinguished (Huang et al. 2015). To reduce these limitations and improve mapping resolution, recombinant inbred lines (RIL) populations are extensively utilized to map QTLs in peanuts (Qin et al. 2012; Pandey et al. 2014a, b, c; Wang et al. 2015; Guo et al. 2016). Compared to F_2 populations, RILs are permanent but cost time to create. With the development of next-generation sequencing technologies, RIL populations are easy to use in map construction and QTL mapping analysis for agronomic and morphological traits (Huang et al. 2009; Wang et al. 2010). Using peanut as an example, two major QTLs were detected in two related recombinant inbred line (RIL) populations (TAG 24 × GPBD 4 and TG 26 × GPBD 4) for rust resistance explaining up to 82.27% and 82.96% of phenotypic variance (PV), respectively (Sujay et al. 2012).

8.4.2 Multi-parent Advanced Generation Inter-Cross (MAGIC) Population

Multi-parent advanced generation intercross (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 can be developed using several different techniques. One method begins with a "funnel" breeding scheme also termed as a "classic MAGIC population", the multiple parents (founders) are intercrossed for n/2 generations (where "n" is the number of founders) until the founders are combined with equal proportions, followed by single seed descent (SSD) method to develop an 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). In a simulation study in rice, Yamamoto et al. (2014) illustrated that the number of subsequent intercrosses dramatically increases the power of QTL detection. Recently, 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 an 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*, a MAGIC population containing 19 founders has been 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 eight *japonica* parents and 16

parents (eight *indica* and eight *japonica*), respectively (Bandillo et al. 2013). Development of a peanut MAGIC population with eight founders and 14 funnels is currently in progress (Huang et al. 2015) under the ambit of the Peanut Mycotoxin Innovation Lab (PMIL) project at ICRISAT, India. Another peanut MAGIC is also under development at Tifton, Georgia, USA with eight founders, which includes Tifrunner, GT-C20, SunOleic 97R, NC94022 (reported in Qin et al. 2012), Florida 07 and SPT-0606 (used in a peanut CAPS population as reported by Holbrook et al. 2013), and Georgia 13 M and TifNV-High O/L (two newly released cultivars) (Guo, personal communication).

8.4.3 Nested Association Mapping (NAM) Population

The nested association mapping (NAM) scheme is a proven strategy to dissect the genetic basis of complex traits in crops such as maize (Yu et al. 2008). The aim of the NAM design is to capture genetic diversity by selecting diverse parents (founders) and developing a large set of interrelated RIL mapping populations. An NGS platform then is used for generating dense genotyping data which helps in achieving high level of resolution by taking advantage of ancestral recombination. Because of this, the NAM population has higher QTL detection power as compared to individual bi-parental mapping populations (Yu et al. 2008; McMullen et al. 2009). In maize, the process of developing NAM populations involved 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 an RIL population from each cross. The combined set of RILs arisen from each cross combination is called an NAM population (Yu et al. 2008). The 5000 lines developed from this effort in maize have 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 resistance (Kump et al. 2011), northern leaf blight resistance (Tian et al. 2011), and kernel composition traits (Cook et al. 2012).

At ICRISAT, India, efforts are underway toward the development of NAM populations in peanut. In the U.S., the development of 16 structured RIL populations has been accomplished by crossing two common parental lines to eight unique lines (2 × 8) to generate two 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. These parents represent a wide range of disease resistance, agronomic, and morphological traits. Half of these RIL populations have been completed, and are being used by different research groups either individually to study unique traits, or as a whole by phenotyping and genotyping the RILs together as two mini NAM populations (total 1150 RILs) using Tifrunner and Florida-07 as two common parents and N08082olJCT, C76-16, NC 3033, SPT 06-06 as unique parents (Wang et al. 2016). This demonstrates its usefulness in assessing phenotypic diversity such as for morphological and disease resistance traits such as leaf length and width, plant size, main stem height, and leaf spot resistance which segregated within the assembled population and exhibit normal distributions. We also calculated the variance and heritability of each trait, and found that plant size had the lowest narrow sense heritability (0.06), while disease resistance had the highest (0.67) in the Tifrunner NAM population. In the Florida-07 population, main stem height had the lowest (0.27) and leaf width had the highest (0.73). Phenotyping of pod and kernel traits was very interesting and further genotyping by peanut SNP array is in progress. The NAM concept will promote the evaluation of the genetic diversity present in peanut gene pool.

8.5 Conclusion

From lack of sufficient molecular markers to the release of the genome sequences of two of its diploid wild relatives, international peanut

community has come a long way in the last 10 years. The international peanut genome project has been deciphering the peanut genome in three major ways: developing useful molecular markers and producing genetic maps; mapping QTLs and markers associated with important traits; and sequencing the whole peanut diploid and tetraploid genomes. The IPGI and PGC released the two diploid sequences for public use in April 2014 and published the two genome sequences in February 2016 (Bertioli et al. 2016). There is a long way to go before genomics-assisted breeding will be a routine tool for peanut improvement. Nevertheless, the stage is now set to harvest the fruits of genomics research, and it is expected that with the increasing effort toward SNP-based markers there will augment the use of GAB in peanut. It has been already proven that GAB is useful in developing high oleic, resistance to root-knot nematode, and rust resistance in peanut.

Additionally, the collaborative and coordinated efforts of the international peanut community since 2004 have contributed to the development of large-scale genomic resources and tools to tap into the rich resource of germplasm collections for improvement of peanut breeding for sustainable production, quality, pest resistance, and water use efficiency. With the establishment of NGS technology platforms and cost reduction for DNA sequencing, whole-genome sequencing and resequencing will become a routine task for crop research and improvement. The most challenging task will be the development of multi-parental populations and the integration of the new sequencing technology and the sequencing data being generated for tetraploid peanut for fine mapping and accurate trait identification and characterization. The main issue will be in analyzing data and translating the information to peanut breeding and improvement through the discovery of genes governing and molecular markers associated with the important traits.

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