Chapter 9
Groundnut Entered Post-genome Sequencing Era: Opportunities and Challenges in Translating Genomic Information from Genome to Field

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Abstract Cultivated groundnut or peanut (*Arachis hypogaea*) is an allopolyploid crop with a large complex genome and genetic barrier for exchanging genetic diversity from its wild relatives due to ploidy differences. Optimum genetic and genomic resources are key for accelerating the process for trait mapping and gene discovery and deploying diagnostic markers in genomics-assisted breeding. The better utilization of different aspects of peanut biology such as genetics, genomics, transcriptomics, proteomics, epigenomics, metabolomics, and interactomics can be of great help to groundnut genetic improvement program across the globe. The availability of high-quality reference genome is core to all the "omics" approaches, and hence optimum genomic resources are a must for fully exploiting the potential of modern science into conventional breeding. In this context, groundnut is passing through a very critical and transformational phase by making available the required genetic and genomic resources such as reference genomes of progenitors, resequencing of diverse lines, transcriptome resources, germplasm diversity panel, and multi-parent genetic populations for conducting high-resolution trait mapping, identification of associated markers, and development of diagnostic markers for selected traits. Lastly, the available resources have been deployed in translating genomic information from genome to field by developing improved groundnut lines with enhanced resistance to root-knot nematode, rust, and late leaf spot and high oleic acid. In addition, the International Peanut Genome Initiative (IPGI) have made available the high-quality reference genome for cultivated tetraploid groundnut which will facilitate better utilization of genetic resources in groundnut improvement. In parallel, the development of high-density genotyping platforms, such as Axiom_Arachis array with 58 K SNPs, and

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S. S. Gosal, S. H. Wani (eds.), *Biotechnologies of Crop Improvement, Volume 3*,
https://doi.org/10.1007/978-3-319-94746-4_9

constitution of training population will initiate the deployment of the modern breeding approach, genomic selection, for achieving higher genetic gains in less time with more precision.

Keywords Genomic resources · Trait mapping · Gene discovery · Diagnostic markers · Genomics-assisted breeding · Molecular breeding products

9.1 Introduction

Groundnut, also popularly known as peanut, is a globally important legume crop grown in >100 countries of the tropic and subtropic regions of the world. This crop is classified as legume as well as oil seed crop and is known for its multiple usages for the society. Almost each plant part is useful such as seeds, which are used for making cooking oil, butter, and confectionary/table preparations, and shoots and oilcakes as cattle feed. Due to diversified use in industry for preparing several delicious preparations including chocolate industry, the importance of this crop has even increased further with reach to every household of the society. This crop also has several other industrial applications such as the use of groundnut oil in preparation for soaps, cosmetics, paint, varnish, furniture polish, lubricating oil, leather dressings, insecticides, and medicine while the use of groundnut shells for manufacturing abrasives, fuel, plastics, wallboard, artificial silk, paper, and glue. This crop also fits into different crop rotations as it increases soil fertility through nitrogen fixation and extend benefits to next crop grown in the same field. It is also an excellent source of nutrition for consumers across the globe and is often served similar to walnuts and almonds.

Groundnut is cultivated over 25.7 million hectares yielding a total 42.3 million tons of produce during the year 2014 with China (42%), India (18%), and Nigeria (7.7%) being the major contributors (http://www.fao.org/faostat/en/#data). Globally, the Asian and African regions together harvest 91% of produce from 95% growing area of groundnut. The last three to four decades could achieve 1.7% yield increase per annum, reaching to the maximum productivity (1823 kg/ha) during the year 2013 (Variath and Janila 2017). Development of improved varieties with high pod yield and resistance/tolerance to biotic and abiotic stresses has played a key role in increasing the productivity of groundnut over the decades. The changing climatic conditions and introduction of groundnut production to new areas have added further challenges to the existing problems of yield reduction due to biotic/abiotic stresses and other unfavorable factors. In addition to agronomic and biotic/abiotic stresses, oil content and oil quality (high oleic acid and low linoleic and palmitic acid) are the two most important traits for genetic improvement as these traits ultimately decide the price of the produce in the market.

The changing climatic conditions and ever-changing consumer preferences demand faster development of improved varieties possessing preferred traits of farmers, consumers, and industry. Genomics has demonstrated great potential in accelerating the process of trait dissection, gene discovery, and molecular breeding.

Therefore, genomics-assisted breeding (GAB) can play an important role in developing improved varieties with desired traits much faster than the conventional breeding (Varshney et al. 2018). In this context, this chapter provides updates on the current status of the germplasm, genetic and genomic resources, and their deployment in trait mapping and molecular breeding in groundnut.

9.2 Germplasm Resources and Priority Traits

India (15,445 accessions), USA (9310 accessions), and China (7837 accessions) have the largest collections of cultivated groundnut germplasm, while Brazil (1220 accessions), USA (1200 accessions), India (477 accessions), and Argentina (472 accessions) have the largest collections of wild groundnuts (see Pandey et al. 2012). These germplasm collections were characterized for various agronomic traits by each GenBank/institute based on the priority of traits required in their breeding program. Since a large number of germplasms cannot be maintained, ICRISAT, USA, and China have developed a core collection with 1704, 831, and 576 genotypes, respectively. Further to reduce the size to make it manageable for breeders, ICRISAT, USA, and China have developed a minicore collection of groundnuts with 184, 112, and 298 genotypes, respectively. Apart from these collections, ICRISAT has also developed two more collections, i.e., composite collection (based on phenotypic data, geographic origin, and taxonomy) and reference set (ICRISAT minicore + other diverse cultivated and wild accessions) (see Pandey et al. 2012). These different germplasm sets provide unlimited opportunities for trait discovery, and their deployment in breeding improved groundnut varieties. Breeders generally work with a limited set of germplasm and show high reluctance in introducing new germplasm to its breeding program due to fear of genetic linkage drag. A systematic evaluation of germplasm in multiple hotspot locations for desired traits and integration of genomics to get rid of linkage drag will provide more confidence to breeders in better utilization of these diverse germplasms in their breeding program.

Trait prioritization is a very dynamic process in groundnut breeding as it differs hugely across different regions, countries, societies, and cultures. In general, each breeding program is engaged in achieving high productivity, high shelling percentage, good pod/seed features, early maturity, resistance to diseases prevalent in target locations, drought tolerance, improved quality, and minimum aflatoxin contamination. The high oil content feature is a very important trait in Asian countries, such as India, where groundnut is used for oil extraction. The early leaf spot (ELS), late leaf spot (LLS), and rust diseases are the universal problem, while nematode and tomato spotted wilt virus (TSWV) are more prevalent in the Americas; bacterial wilt in China, Indonesia, Vietnam, and Uganda; groundnut rosette disease (GRD) and peanut clump virus disease (PCVD) in Africa; and peanut bud necrosis disease (PBND) and peanut stem necrosis disease (PSND) in India (see Variath and Janila 2017). Due to globalization and ease of doing busi-

ness, the industry and consumer-preferred traits, such as aflatoxin contamination, allergens and nutrition, deserve now more attention in the current breeding strategies to enhance research efforts in the coming years.

9.3 Genomic Resources: No More Issue for Genomics and Breeding Applications

There has been tremendous progress in the development of genomic resources for peanut over the last decade, and details of these resources have been reviewed time to time (see Pandey et al. 2012, 2014; Varshney et al. 2013; Ozias-Akins et al. 2017; Vishwakarma et al. 2017a). Six major resources are very useful for peanut research community including (i) reference genome of diploid progenitor species, i.e., *Arachis duranensis* (Bertioli et al. 2016; Chen et al. 2016) and *A. ipaensis* of cultivated groundnut (Bertioli et al. 2016), (ii) high-density genotyping array "Axiom_Arachis" with >58 K highly informative single nucleotide polymorphisms (SNPs) (Pandey et al. 2017a), (iii) gene expression atlas (Clevenger et al. 2016), (iv) genome-wide simple sequence repeat (SSR) and insertion/deletion markers (Zhao et al. 2017; Vishwakarma et al. 2017b), (v) next-generation genetic populations for high-resolution genetic mapping and breeding (see Pandey et al. 2016), and (vi) trait-linked diagnostic markers for use in GAB (see Vishwakarma et al. 2017a).

9.3.1 Reference Genome of Diploid Progenitors and Tetraploid Groundnut

Sequencing reference genome is one of the most important milestones for any crop species for accelerating the process of understanding genome architecture, gene discovery, and molecular breeding (see Varshney et al. 2014b). The International Peanut Genome Initiative (IPGI) initiated the genome sequencing project in 2010 through the Peanut Genome Consortium (PGC) (Wang et al. 2017). This consortium has already completed the sequencing of both the diploid progenitor species, namely, *A. duranensis*V14167 (A-genome) and *A. ipaensis*K30076 (B-genome) (Bertioli et al. 2016), and the finalization of genome assembly for cultivated tetraploid genotype has been completed recently. In addition to IPGI, another initiative, Diploid Progenitor Peanut A-Genome Sequencing Consortium (DPPAGSC), completed the sequencing of another A-genome genotype, PI475845, in the same duration (Chen et al. 2016). The quality of the genome assembly developed by IPGI is much better than the DPPAGSC as the later assembly could not reach up to the pseudomolecule level. The IPGI-led sequencing predicted 1.21 Gb genome size and 36,734 genes for A-genome while 1.51 Gb genome size and 41,840 genes in the B-genome. The DPPAGC-led sequencing predicted comparatively larger genome size (1.05 Gb) and higher

number of genes (50,324) for A-genome assembly as compared to IPGI. The reference genome of these two diploid progenitors are being used in different kinds of analysis such as genome comparisons, mining genome-wide structural variations, transcriptomics, trait mapping, and gene and marker discovery.

Most recently, genome sequencing for the cultivated tetraploid groundnut (cvTifrunner) has also been completed by the International Peanut Genome Initiative (IPGI, https://peanutbase.org/peanut_genome). This initiative has used several modern approaches and technologies for developing a very high-quality genome. This tetraploid genome assembly is 2556 Mbp in size and covers >99% of the actual genome. The scaffold N50, which provides information on assembly contiguity, was reported to be 135.2 MB (IPGI, https://peanutbase.org/peanut_genome). Different sequencing platforms, such as PacBio (48.25×, average read length 11,525 bp) and Illumina (~40×), were used for generating sequencing data. Realizing the allopolyploid genome with very high similarity, this genome was assembled using modern assembling tools including the integration of HiC data/technology. These genome sequences will accelerate the research on trait understanding, genomics, gene discovery, and molecular breeding in groundnut. Further, the availability of resequencing of hundreds of germplasm lines in addition to reference genome will further accelerate the pace of genomics and breeding research in groundnut in the coming years.

9.3.2 High-Density Genotyping "Axiom_Arachis" Array

Among all the structural variations in the plant genome, single nucleotide polymorphisms (SNPs) are the most abundant and hence can be detected very rapidly in large numbers at low cost using next-generation sequencing (NGS) technologies. Initially, genotyping-by-sequencing (GBS) was the most promising approach for generating SNP genotyping data, but high-density SNP array emerged promising too. The GBS platform gives large proportion of missing data which needs further imputation to complete the genetic analysis. The proportion of the missing data is very less or nil in case of SNP arrays, and data can be achieved for all the individuals/markers subjected for genotyping. A high-density SNP array "Axiom_*Arachis*" with 58,233 SNPs was recently developed using the sequencing data of 41 genotypes (30 tetraploids and 11 diploids) (Pandey et al. 2017a). Initially, a large number of genome-wide SNPs (163,782 SNPs) were identified, and then the number of high-quality SNPs were reduced to only 58,233 SNPs for the development of array. In addition to large proportion of SNPs (76.7%) from cultivated groundnut (*A. hypogaea*), this array also had fair representation from other important diploid species *A. duranensis, A. batizocoi*, *A. magna*, *A. stenosperma*, and *A. cardenasii* (Pandey et al. 2017a).

This SNP array has so far been deployed in two studies and has shown great promise in conducting high-resolution genetic studies. For example, Pandey et al. (2017a)

upon deployment of this array in ICRISAT, the "reference set" observed significant loss of genetic diversity in cultivated gene pool and provided greater insights on genetic relatedness and showed preferential selection of genomic regions in the different subspecies of *A. hypogaea*. In another study, Clevenger et al. (2017) genotyped US runner-type breeding material and identified genomic regions with positive selection during the course of the breeding program. This array has provided the groundnut research community for generating high-density genotyping data on genetic and breeding populations for conducting high-resolution trait mapping and more precise breeding.

9.3.3 Gene Expression Atlas

With the availability of reference genome sequence for tetraploid groundnut and its diploid progenitors, now it is a great challenge for the researchers to understand the functions of the entire sets of genes. The gene expression atlas provides detailed information on gene expression in different types of genotypes, organs, tissues, cell, and developmental stages. The information becomes more informative if such data is generated under different stress and treatment conditions. Keeping this in mind, the University of Georgia (UGA), USA, has developed a gene atlas using the RNA sequencing data generated from 22 tissues that represent the critical organs and growth stages. Most importantly, the emphasis was more on the specialized organs and stages such as formation, elongation, and penetration of peg in the soil and then up to seed formation (Clevenger et al. 2016). In addition to identifying 8816 putative homeologous genes, this gene atlas also detected >9000 alternative splicing events and > 6000 noncoding RNAs. Most recently, ICRISAT has also reported development of another gene expression atlas (AhGEA) using RNA-Seq data for 19 tissues from five different stages of an early maturing, high-yielding, drought tolerant groundnut variety, ICGV 91114. This study provided greater insights on understanding the developmental processes and their regulatory network in addition to shedding lights on key biological traits such as seed development, allergens and oil biosynthesis.

9.3.4 Genome-Wide Genetic Markers

The availability of optimum genetic markers is one of the most important milestones in any crop species for use in several genetics and breeding applications. This crop has lacked much-needed resources for genetic analysis and molecular breeding (see Pandey et al. 2012). Nevertheless, the last decade has been very fruitful as the groundnut research community developed a huge number of genetic markers such as simple sequence repeats (SSRs), insertion and deletion (InDel), and single nucleotide polymorphism (SNP) (see Pandey et al. 2016). In contrast to SNPs, the SSR markers are

very useful but are not amenable to high-throughput genotyping. Despite these limitations, SSRs have been well adopted and deployed in most of the crop species. In fact, still a majority of the research groups are using SSR markers especially for use in diversity, trait mapping, and molecular breeding applications in groundnut.

The availability of SSRs has been meager and insufficient in groundnut till the completion of genome sequences for diploid progenitors of cultivated groundnut in 2016 (Bertioli et al. 2016; Chen et al. 2016). Chen et al. (2016) used *A. duranensis* (PI475845) genome assembly and detected 105,003 SSRs and ~8 million SNPs in A-genome. The major problem with these SSRs was that these SSRs cannot be tracked to physical location as the assembly was not up to the pseudomolecule level, thereby restricting the use of these SSRs in genetic studies. Considering this limitation, the high-quality genome assembly developed by IPGI was mined for genome-wide SNPs leading to the detection of large-scale SSRs in both the genomes, i.e., 135,529 SSRs in A-genome (*A. duranensis*) and 199,957 SSRs in B-genome (*A. ipaensis*) (Zhao et al. 2017). For the above-detected SSRs, primers were successfully developed for 112,247 SSRs, i.e., 51,354 (49 SSRs per Mb density) in A subgenome and 60,893 (45 SSRs per Mb density) SSRs in B subgenome, respectively.

The comparative analysis of the draft genome assemblies of both the diploid progenitor species of cultivated tetraploid groundnut identified 515,223 InDels (Vishwakarma et al. 2017a). The sequence comparison of *A. ipaensis* with *A. duranensis* identified 269,973 insertions, while comparison of *A. duranensis* with *A. ipaensis* detected 245,250 deletions. Further, 163,782 SNPs (98,375 SNPs from A subgenome and 65,407 SNPs from B subgenome) were identified upon comparing the whole genome resequencing (WGRS) data of 41 diverse groundnut genotypes (30 tetraploids and 11 diploid accessions) (Pandey et al. 2017a; Clevenger et al. 2017). These genome-wide markers are very useful for conducting genetics and breeding studies in groundnut.

9.3.5 Trait Mapping and Linked Diagnostic Markers

Genomic resources play a key role in genetic dissection and understanding the trait mechanism in any crop species. Further, precise phenotyping data for traits of interest is equally important for genetic analysis and trait mapping. In simple words, the precision and efficiency of trait mapping and candidate gene discovery are directly proportional to the precise trait characterization in diverse genetic materials. The detailed trait mapping efforts and their outcomes have been reviewed time to time (Pandey et al. 2012, 2014, 2016; Varshney et al. 2013; Vishwakarma et al. 2017a; Ozias-Akins et al. 2017), and therefore, this chapter avoids to provide these details again here. Of the several efforts so far using different trait mapping approaches, linked and validated markers are available for only four traits which can be used as diagnostic markers in groundnut breeding. These traits include high oleic acid and resistance to root-knot nematode, rust, and late leaf spot.

Two homologous genes (*ahFAD2A and ahFAD2B*) located on A subgenome (substitution from G:C to A:T) and B subgenome (insertion from A:T) code for enzyme fatty acid desaturase (FAD) that facilitate the conversion of oleic acid to linoleic acid. These two genes have 99% homology, and different types of markers were developed for selecting mutant alleles in breeding program. These markers include allele-specific and cleaved amplified polymorphic sequences (CAPS) markers in addition to SNP-based genotyping (Chu et al. 2009; Chen et al. 2010). Among the diseases causing significant yield in groundnut, the linked markers become available for root-knot nematode caused by a soil-borne pest, *Meloidogyne arenaria*, rust caused by *Puccinia arachidis*, and late leaf spot (LLS) caused by another fungus *Phaeoisariopsis personata*. The DNA-based markers were developed for selecting resistance loci for nematode followed by their validation in US groundnut germplasm (Chu et al. 2007). The genomic regions for resistance to two foliar fungal diseases, rust and LLS, were mapped and linked to SSR markers validated in diverse germplasms (Sujay et al. 2012). Most recently, sequencing-based trait mapping approach, QTLseq, was deployed for developing allele-specific and SNP markers for both the foliar fungal diseases to deploy in breeding (Pandey et al. 2017b). The markers for these four traits have been well standardized in several genomics laboratories across the globe, and their deployment is now a routine in these breeding programs. Most recently, ICRISAT has developed a 10-SNP panel which contains associated SNPs for oil quality (high oleic acid and low palmitic and linoleic acid) and two foliar fungal diseases (rust and LLS). This 10-SNP panel contains associated SNPs for foliar diseases mapped on chromosomes, A02 (LLS) and A03 (rust and LLS) while SNP for high oleic on chromosome B09 (*AhFAD2B*). This panel is now deployed in ICRISAT breeding program for performing early-generation screening using a high-throughput genotyping project (HTPG). This platform, funded by Bill & Melinda Gates Foundation and led by ICRISAT, facilitates genotyping of breeding material at a very less cost, i.e., US$ 1.5 per sample for 10 SNP markers including DNA extraction. Further intensive research is required for developing more diagnostic markers for key traits so that early generation screening can be performed on each seed, before going for planting, to reduce the field and labour resources. Such SNP panels can also be made for ensuring the quality check in seed lots and also checking hybridity in conventional breeding programs.

9.4 Genomics-Based Groundnut Breeding for Achieving Higher Genetic Gains

NGS technologies have not only revolutionized the understanding of genomes and performing high-resolution trait mapping and accelerated gene discovery and marker development but also improved the ease and cost of genotyping with selected markers. The lack of genomic resources has greatly hampered the trait mapping efforts earlier, which got accelerated now with the availability of huge genomic resources. Nevertheless, the efforts with limited resources facilitated development

of linked/diagnostic markers for four important traits in groundnut, namely, high oleic acid and resistance to nematode, rust, and LLS.

US-based groundnut breeding program deployed linked markers for high oleic acid and nematode resistance and improved/developed multiple varieties (Chu et al. 2011). Similarly, ICRISAT deployed linked SSR markers for rust and LLS resistance for improving three popular groundnut varieties (ICGV 91114, JL 24, and TAG 24) in just 3 years' time (Varshney et al. 2014a). This effort not only provided improved lines with enhanced resistance but also showed increased yield and short maturity duration (Janila et al. 2016a, b). ICRISAT also deployed linked markers for achieving desirable proportion of the three key fatty acids (high oleic acid and low palmitic and linoleic acid) in the genetic background of three varieties (ICGV 06110, ICGV 06142, and ICGV 06420) (Janila et al. 2016a). Now the efforts are underway to deploy the linked markers for oil quality and FDR (rust and LLS) for pyramiding in the three popular cultivars (GJG 9, GG 20, and GJGHPS 1). Multiple promising lines developed for foliar disease resistance and oil quality by ICRISAT and its NARS partners in India are currently in national trials for yield assessment and further release. These potential releases (specially high oleic lines) in India will meet the increasing demand of high oleic raw material to domestic and international companies in India.

9.5 Conclusion and Future Prospects

Groundnut is a multipurpose crop with high nutritional value and gained global importance being an important component of the human food basket. Genetic enhancement of groundnut is key to sustain in competition to other crops in terms of key features that drive the demand in the market. NGS technologies coupled with modern genetic and genomic technologies have provided immense hope for achieving accelerated higher genetic gains in less time and resources with high precision and accuracy. Now this crop has ample genomic and genetic resources which were needed to accelerate the process of groundnut improvement. Currently few successful examples of molecular breeding products are available in groundnut; nevertheless, there will be more of such successful stories in the coming years. At the same time, it is also required to test some new breeding technologies and methods such as genomic selection, early-generation screening, and genome editing for getting more precise, faster, and accurate processes to develop next-generation groundnut varieties which can perform better under changing climate conditions.

Acknowledgments Financial support is acknowledged from the Peanut Foundation, MARS Inc., Bill & Melinda Gates Foundation (Tropical Legumes I, II, and III), National Agricultural Science Fund (NASF) of Indian Council of Agricultural Research (ICAR), Government of India, and World Bank Assisted Watershed Development Project II (KWDP-II) by Government of Karnataka, India. The work reported in this article was undertaken as a part of the CGIAR Research Program on Grain Legumes and Dryland Cereals (GLDC). ICRISAT is a member of the CGIAR.

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