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Genetics, Genomics and Breeding of Peanut: An Introduction

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ABSTRACT

Peanut stands second to soybean in both area and production in the world among legume oilseeds crops and is grown in >100 countries. Genetic barriers have not allowed sharing of useful alleles from wild relatives leaving the primary gene pool with a very narrow genetic base. Improving pod yield and oil content have been the main focus, along with providing resistance/tolerance against important biotic/abiotic stresses. Realizing the ever increasing demand among consumers, productivity needs to be increased significantly without compromising the oil quality and providing defense shield against biotic and abiotic stress. It is very difficult to achieve the above milestones without integrating the modern genomics tools with conventional breeding programs. The last decade witnessed significant progress in terms of genomic resources and molecular breeding activities. The objective of this book is to critically review the current updates on different aspects of peanut such as germplasm collections, genetics, genomics, transcriptomics, bioinformatics together with traditional and molecular breeding. The book also summarizes the success stories achieved through trait mapping and application of molecular markers

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in improving important traits. This chapter provides highlights of different chapters which are expected to be a good resource for young researchers, breeders and policy makers for employing better strategies towards food security.

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1.1 Introduction

Peanut (*Arachis hypogaea* L. Mill sp.) with a postfix of nut in the name is not a nut in the true sense, but is a leguminous crop, and because of a nutty cover, the pod wall, is called peanut. On the other hand, because of its growth and ripening of seed inside the ground, it is also known as groundnut. It has many characteristics of nuts such as high amount of fat (46g/100g) and other important constituents such as vitamins, protein, minerals and phytochemicals. During expeditions on foot to the South and North Poles by *Discovery* and *Terra Nova* expeditions in the early 19th century, consuming peanuts was the deciding factor between life and death. Peanut butter was the ideal foodstuff, freeing explorers from the transport and kindling of cooking fuel (a near-impossibility in the frigid polar winds), and high enough in protein and calories to fuel the party and keep them from freezing to death in the harsh weather and freezing night-time temperatures.

Peanuts are rich in nutrients, providing over 30 essential nutrients and phytonutrients such as niacin, folate, fiber, magnesium, vitamin E, manganese and phosphorus, etc. (Savage and Keenan 1994; Whitley et al. 2011). Plumpy'nut a ready-to-use therapeutic food made from peanut is a popular source of nutrient for malnutritioned children in Africa due to the presence of about 25% protein, a higher proportion than in any true nut. Peanuts are found to contain high concentration of antioxidant polyphenols than other nuts and other antioxidant sources such as blackberries, strawberries, carrots or beets (Craft et al. 2010). Furthermore, peanuts are a significant source of resveratrol equivalent to that present in red grapes (Sanders et al. 2000), a chemical associated with reduction in risk of cardiovascular disease (Fraser et al. 1992; Hu et al. 1998; Prineas et al. 1993), cancer (Awad et al. 2000) and anti-aging properties, hence would have a high impact in both health and cosmetic industry. In addition, peanuts are also a source of coenzyme Q10 (Pravst et al. 2010), as are oily fish, beef, soybeans and spinach.

Peanut is believed to have originated in South America and was first domesticated in the Brazilian-Paraguayan region (Vavilov 1951). The area of the valleys of Paraguay and Parana rivers is the most likely center of origin. Excavation in coastal Peru dating back to 800 BC evidenced the cultivation

of peanut. From South America, peanut spread to other parts of the world. It was commonly found in the West Indies but not in the United States in pre-Columbian times. Peanut was introduced to the Old World in the 16th century when the Portuguese took the seeds from America to Africa. The Spaniards introduced it into the Philippines. It then spread to China, India, Japan, Malaysia and other parts of the world. Human interaction through selection of most suited lines over the centuries resulted in loss of much of the genetic diversity/desirable alleles and genes whose importance is now been realized. Further, we are still unaware of future preferences for the so-called "lost" genetic diversity including genes for resistance/tolerance to biotic and abiotic stresses, as well as taste and nutritional composition along with yield. The domesticated peanut is an amphidiploid or allotetraploid, meaning that it has two sets of chromosomes from two different species, thought to be *A. duranensis* and *A. ipaensis* (Kochert et al. 1991, 1996; Seijo et al. 2007). These species combined in the wild to form the tetraploid species, which gave rise to the domesticated peanut. Cultivated peanut contains a fraction of the genetic diversity, which is not more than 13% (Varshney et al. 2009a), found in their closest wild relatives in section *Arachis* (Kochert et al. 1991), a legacy of the "domestication bottleneck".

The first domestication bottleneck was the combination of two species *A. duranensis* and *A. ipaensis* amongst 26 species from section *Arachis*. Crossing experiments between *A. duranensis* and *A. ipaensis* have shown that the diploid hybrid is highly sterile (Mallikarjuna et al. 2011a). Had the hybrid been fertile, there would not have been the need to double its chromosome number to form the fertile amphidiploid. It would probably have remained a diploid than a tetraploid as it is today. So the second bottleneck was in the formation of a diploid sterile hybrid. The third bottleneck was in the process of chromosome duplication to form the allotetraploid as it is known in literature that polyploidy causes genetic bottlenecks (Sanford 1983). Ancient farmers would have selected relatively few plants from the progenitors of modern crops, in a limited number of places and a similar situation would have existed for peanut in South America. This can be visualized as the fourth bottleneck. The early Portuguese and Spanish traders during their expeditions spread a few selected genotypes to the rest of the world thus giving rise to yet another, the fifth, bottleneck, superimposed by the sixth bottleneck which is the self-pollinating nature of the crop. To conclude peanut is the product of evolution after a series of six bottlenecks.

Traditionally wild relatives of peanut were directly used in a crossing program producing triploids as *Arachis* species in the compatible gene pool are diploid and cultivated peanut is a tetraploid. Triploids are cumbersome to use for peanut improvement, but such efforts have not gone without dividends (Mallikarjuna et al. 2004a,b). More recently, development of amphidiploid and autotetraploids utilizing *Arachis* species has been

encouraging. With the development of synthetic peanut by combining putative A and B genome donors as well as many other A and B genome *Arachis* species, a range of tetraploid peanut was synthesized at ICRISAT (Mallikarjuna et al. 2011a). Screening some of these has shown that they have not lost the traits present in the diploid species (Mallikarjuna et al. 2011b). Newly synthesized tetraploids possessing several good traits are fairly easy to use in the crossing program as minimum segregation distortion (Fonceka et al. 2009) and minimal disturbance in meiosis has been observed (Mallikarjuna et al. 2012) with high pollen fertility in the hybrids. Fonceka et al. (2012) used a synthetic amphidiploid (Favero et al. 2006) and applied conventional breeding technique to capture the genetic diversity in peanut wild relatives. In their study, a set of 122 Introgression Lines (ILs) that offered an extensive coverage of the cultivated peanut genome with generally a unique fragment per line and overlapping fragments between contiguous lines were developed and thus these newly developed synthetics have opened new avenues for peanut improvement using new sources of tetraploid/synthetic peanuts.

1.2 Pre-breeding Efforts

Although pre-breeding does not produce new varieties, but it does turn up intermediate lines that breeders find easier to use. It throws up enough variation to sustain breeding activities especially with the assistance of molecular markers. Many public agricultural research institutions, such as the International Rice Research Institute (IRRI), International Maize and Wheat Improvement Center (CIMMYT), International Institute for Tropical Agriculture (IITA) and International Crops Research Institute for Semi-Arid Tropics (ICRISAT) have active pre-breeding programs in their mandate crops. Pre-breeding is the link between conservation and use of wild crop relatives. Out of all the raw materials at the breeder's disposal, the diversity of wild crop relatives has been relatively neglected. The conserved germplasm in the gene banks is for present and future use. Urbanization, explosion in population growth, dwindling water resources and in a 2°C-warmer world, we may not have a choice but to bring in new sources of variation that the new sources of synthetic tetraploids are offering. Some of the recent success at ICRISAT in utilizing wild *Arachis* species for tackling those diseases/pests for which high levels of resistance is not present in cultivated peanut germplasm has been achieved. These are stable tetraploid introgression or aptly called the pre-breeding lines with trait(s) of interest.

i. *Aflatoxin* resistance: Inadequate levels of resistance in peanut germplasm are one of the important factors for not having resistance to *A. flavus*-

aflatoxin resistance in peanut. This means sources of resistances have to be scouted beyond the cultivated/primary gene pool. The report from Xue et al. (2005) showed that *Arachis* species *A. duranensis* (eight accessions) and *A. cardenasii* (two accessions) from section *Arachis* had high levels of resistance to aflatoxin production and interspecific derivatives derived from them continued to show the trait. ICRISAT screened advance generation lines derived from *A. cardenasii* in aflatoxin sick plot for three consecutive years and found many of the lines with low aflatoxin production. This opens up new avenues for aflatoxin resistance breeding in peanut (Mallikarjuna N and Sudini H, unpubl. data).

ii. *Late leaf spot*: Sources of resistance to Late Leaf Spot (LLS) caused by *Cercosporidium personatum* Berk. & M.A. Curtis is higher in wild *Arachis* species compared to moderate levels of resistance in cultivated germplasm (Subhramanyam et al. 1989). *Arachis cardenasii* derived lines showed resistance to LLS when screened under unprotected field conditions in different locations (Mallikarjuna N and Sudini H, unpubl. data).

iii. *Peanut bud necrosis disease*: Peanut Bud Necrosis Disease (PBND) is an economically important virus disease of peanut in many Asian countries where peanut is grown. The disease causes crop losses exceeding US$ 89 million in India alone (Anon 1992). Sources of resistance is absent in cultivated germplasm (Reddy 1998). Many of the *Arachis* species have been found to be resistant to the disease (Reddy et al. 2000). Stable lines derived from *Arachis* species were screened for PBND in disease hot spot location and a few resistant lines were identified (Sunkad and Mallikarjuna N, unpubl. data).

iv. *Root rot*: Among the soil-borne fungal diseases of peanut, stem rot caused by *S. rolfsii* is a potential threat to groundnut production throughout the world. The disease causes severe damage during any stage of crop growth, and yield losses over 25% have been reported by Mayee and Datar (1988). Sources of resistance to the constraint are not up to the desired level in cultivated germplasm. Stable lines derived from *Arachis* species were screened for *S. rolfsii* in the disease hot spot location at Dharwad, Karnataka state, India, and a few lines with resistance were obtained (Kenchanagowda R and Mallikarjuna N, unpubl. data).

v. *Spodoptera litura: Spodoptera litura* also called fall army worm, a polyphagous insect, is becoming an important insect pest of groundnut with sources of resistance to the pest absent in cultivated germplasm. Yield losses of groundnuts have been directly associated with higher density of larvae of *S. litura*, and the intensity of defoliation (Panchbhavi and Nethradani 1987).

Currently, no peanut cultivar is known to express resistance to *S. litura*, however, some wild relatives of peanut were found resistant to *S. litura*. Neonate larvae suffer high levels of mortality and the development of older larvae on resistant wild species is severely inhibited (Stevenson et al. 1993a). Flavonoids chlorogenic acid, quercetin and rutin present in *Arachis kempff mercadoi* responsible for resistance to *S. litura* were identified (Stevenson et al. 1993b). Mallikarjuna et al. (2004a) developed lines utilizing *A. kempff mercadoi* and screened the lines for *S. litura* resistance. Resistant derivatives were found to have high levels of flavonoids and antibiosis mechanism prevented larval growth. Susceptible derivatives and the female parent, *A. hypogaea* had low levels of flavonoids (Mallikarjuna et al. 2004b).

1.3 Germplasm Resources and Cytogenetics

Chapter 2 entitled "***Genetic Resources, Diversity and Association Mapping in Peanut***" deals with the conservation of a large collection of peanut germplasm including wild *Arachis* species, which is the key to the success in crop improvement. Much of the diversity of wild crop relatives that is available in gene banks is not actively used because most crop-breeding programs are generally not set up to best use it and wild relatives are viewed as too unwieldy to use with sufficient ease and speed. Further, all the closely related wild relatives in section *Arachis* are diploid whereas cultivated peanut is a tetraploid and, hence, crossing diploids with tetraploids or vice versa is a not a straight-forward process. Therefore, objective oriented manageable germplasm sets possessing agronomically important traits such as reference set, core collection, mini-core collection and mini-mini core collections were structured in order to use these sets judiciously and more efficiently. In addition to these sets, amphidiploids originating from distant wild *Arachis* species were also developed in order to overcome bottlenecks associated with peanut domestication and are being currently used in alien introgressions and for several other genetical and breeding applications which will enrich existing variability of primary gene pool.

Chapter 3 entitled "***Classical and Molecular Cytogenetics in Arachis***" deals with the recent progress made in understanding the chromosome complements of peanut and related wild species. In order to conduct genetical studies, proper understanding on chromosome number, size and structure play a significant role especially during integration of genomics tools with conventional breeding programs. Cytogenetics has played an important role through classical cytological studies in revealing important information about the complexity of the peanut genome. Comparative cytological mapping studies helped in defining chromosome numbers and their karyotype features to establish the relationships among species and

the taxonomic sections. Further, efforts made to understand chromosome structure and genome evolution within the genus by using chromosome specific markers developed by fluorescent *in situ* hybridization (FISH). These studies have also revealed variation in karyotype structure, which represents different genomes. This chapter also addresses the integration of genomic *in situ* hybridization (GISH) approaches with FISH analysis to differentiate chromosomes of the two progenitors of cultivated tetraploid peanut, i.e., *A. duranensis* and *A. ipaënsis* along with identification of center of origin.

1.4 Conventional and Molecular Breeding

Chapter 4 on *"Peanut Breeding"* reviews the recent progress in peanut breeding worldwide. Basically genetic enhancement through conventional approaches has been achieved for few qualitative traits such as resistance to *Sclerotinia* blight, root-knot nematode and Tomato Spotted Wilt Virus (TSWV), which is benefitting US peanut producers >$200 million annually. Similar trends have also been observed in China as efforts led to at least 30% yield increase during the past two decades. However, the conventional approaches are not able to address the further increased yield demand as well as existing and future breeding challenges. In such a scenario, integration of genomics with conventional breeding approaches has become mandatory for developing superior cultivars with higher yield, better quality and enhanced resilience.

Chapter 5 on *"Molecular Markers, Genetic Maps, and QTLs for Molecular Breeding in Peanut"* deals with development and use of genomic resources and their utilization in peanut improvement. The international research community neglected development of genomic resources in peanut, which left this crop in the group of "Orphan Crops". Nevertheless, recent efforts resulted in the development of limited genomic resources and it was mostly in the last decade, which witnessed a speedy development due to collaborative effort among several research partners. Large scale of molecular markers such as Simple Sequence Repeat (SSR) and Diversity Array Technology (DArT) markers have been developed recently, which paved the way for construction of genetic maps, initially for diploids and then for tetraploids (Pandey et al. 2012; Varshney et al. 2013). This chapter provides detailed development of genomics resources such as markers, genetic maps and Quantitative Trait Loci (QTL) analysis. SSR markers assembled from public domain or collaborators were screened on parental genotypes and several genetic maps were constructed based on cultivated × cultivated genotypes. These genetic maps were then used for marker-trait associations for drought tolerance and foliar diseases. The identified markers/gene specific markers were successfully deployed through Marker-

Assisted Backcrossing (MABC) for improving elite peanut varieties. With international collaborations, dense reference consensus genetic map was successfully improved from 897 (Gautami et al. 2012b) to 3,693 marker loci (Shirasawa et al. 2013) and these dense consensus maps will set the platform for several other genetic and molecular breeding activities in peanut. Efforts to sequencing the peanut genome have been initiated with the formation of a Peanut Genome Consortium (PGC) (http://www.peanutbioscience.com/peanutgenomeproject.html).

1.5 Genome Structure and Proteomics

Chapter 6 of this book entitled "***An Overview of Peanut Genome Structure***" is focused in defining peanut genome structure. The studies in this area have revealed that the A and B genomes are of similar size and are composed mostly of metacentric chromosomes. With the genome of about 2.8 Gb for tetraploid peanut seems to have high repetitive DNA content. *A. duranensis* and *A. ipaënsis* are considered as the most probable diploid ancestors and donors of the A and B genomes, respectively. The cytogenetical studies integrated with genomic approaches revealed the possible ancestors, period of origin of different subgenomes. The genetic similarity between A and B genomes at sequence level is very low. Most importantly, cultivated peanut genetically behaves as a diploid, the two subgenomes have a very high genetic synteny, and do not appear to have undergone major structural rearrangements after polyploidization. The structural genomics revealed significant genetic similarity of peanut subgenomes with other legumes that diverged during evolution.

This crop is witnessing a transition phase wherein the efforts are continued towards development of genomic resources along with a large amount of sequencing data, which need efficient data storage and retrieval system along with statistical analysis support. The transcriptome represents messenger RNA (mRNA) expressed in a particular cell/tissue/organ/organism, and their quantity at a particular growth stage. These resources are the primary source from where DNA markers are being developed to use in several genetical studies. Transcriptomics also improves understanding the genetic mechanism underlying important agronomic traits for peanut improvement. Transcriptomics or genomewide transcriptional profiling allows simultaneous examination of transcriptome that is the term designated to the specific subset or complete set of mRNA expressed in a particular cell, tissue, organ or organism, and their quantity for a given developmental stage or physiological condition. It has been increasingly used to understand transcriptomes of a range of peanut tissues at different developmental stages under various environmental stresses. Chapter 7 entitled "***Peanut Transcriptomics***" reviews commonly used transcriptomic

technologies, the definition of the transcriptomes for three principal tissues (pod/seed, root and leaf), the transcriptomics of stress response in peanut, as well as the use of transcriptome for marker development. Peanut transcriptomics will make great contributions to the understanding of genetic mechanism underlying important agronomic traits for peanut improvement.

Peanut improvement by conventional or molecular approach relies on an understanding of the biology of the plant, particularly interactions occurring across hierarchical scales of organization. In this regard, the application of metabolomics and proteomics is poised to deliver large volumes of data on protein and metabolite fluctuations associated with developmental and environmental cues. The challenge for the peanut research community will be to ensure that similar data is generated, interpreted and integrated towards crop improvement. Chapter 8 entitled *"Advances in Proteomics Research in Peanut Genetics and Breeding"* gives an insight into this field of research.

1.6 Transgenic Breeding

Chapter 9 entitled *"Transgenic Interventions in Peanut Crop Improvement: Progress and Prospects"* deals with the strength of transgenic technology specially when there is no source of variation for a trait in peanut genepool. Advances in tissue culture and genetic engineering comprising important areas of biotechnology have provided alternative pest control strategies. The development and standardization of protocols for genetic transformation in peanut for several genes are briefly discussed. Although this technology has not been received open heartedly in many countries, it has shown great potential in peanut improvement. Let us hope that once the regulatory issues are solved in certain countries of the world, the material will be available for peanut improvement across the world.

1.7 Bioinformatics Tools

Even though peanut lagged behind in generation of sequences still with the limited genomic resources studies on genetic diversity, genetic mapping and QTL analysis could be conducted. Expressed Sequence Tags (ESTs) generated provided raw material/sequence to apply some bioinformatics tools for extracting information to use them in genetic and breeding applications. Chapter 10 entitled *"Applications of Bioinformatics Tools to Genetic Mapping and Diversity Analysis in Peanut"* presents an overview of available resources on peanut bioinformatics and their role in elucidating biological and genomic information on peanut.

1.8 Summary

In summary, developments in last decade in several research areas promise to fill the research gaps required for handling the genetic bottlenecks in a better and precise way. Much needed diversification using genomic tools will facilitate the use of a diverse source for improving existing cultivars to equip them with genes for high resilience and new cultivars with desired traits. Although such concerns are raised at many of the scientific gatherings, however not many initiatives have been taken even for very important food crops. Hence, this is the prime time to retrieve desirable alleles not only to address existing problems but also for the future as well in order to sustain food production. Therefore, this is an effort to update the peanut research community on developments at different aspects in peanut by compiling all the developments made till date. It is also foreseen that compilation of updates will encourage more inter-displinary collaborations to tackle existing as well as advance initiatives to address future problems.

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