Series on
Genetics, Genomics and Breeding of Crop Plants

Series Editor
Chittaranjan Kole, Vice-Chancellor, BC Agricultural University, India

Genetics, Genomics and Breeding of Peanuts

Editors
Nalini Mallikarjuna • Rajeev K. Varshney

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GENETICS, GENOMICS AND BREEDING OF PEANUTS

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GENETICS, GENOMICS AND BREEDING OF PEANUTS

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Preface to the Series

Genetics, genomics and breeding has emerged as three overlapping and complimentary disciplines for comprehensive and fine-scale analysis of plant genomes and their precise and rapid improvement. While genetics and plant breeding have contributed enormously towards several new concepts and strategies for elucidation of plant genes and genomes as well as development of a huge number of crop varieties with desirable traits, genomics has depicted the chemical nature of genes, gene products and genomes and also provided additional resources for crop improvement.

In today's world, teaching, research, funding, regulation and utilization of plant genetics, genomics and breeding essentially require thorough understanding of their components including classical, biochemical, cytological and molecular genetics; and traditional, molecular, transgenic and genomics-assisted breeding. There are several book volumes and reviews available that cover individually or in combination of a few of these components for the major plants or plant groups; and also on the concepts and strategies for these individual components with examples drawn mainly from the major plants. Therefore, we planned to fill an existing gap with individual book volumes dedicated to the leading crop and model plants with comprehensive deliberations on all the classical, advanced and modern concepts of depiction and improvement of genomes. The success stories and limitations in the different plant species, crop or model, must vary; however, we have tried to include a more or less general outline of the contents of the chapters of the volumes to maintain uniformity as far as possible.

Often genetics, genomics and plant breeding and particularly their complimentary and supplementary disciplines are studied and practiced by people who do not have, and reasonably so, the basic understanding of biology of the plants for which they are contributing. A general description of the plants and their botany would surely instill more interest among them on the plant species they are working for and therefore we presented lucid details on the economic and/or academic importance of the plant(s); historical information on geographical origin and distribution; botanical origin and evolution; available germplasms and gene pools, and genetic and cytogenetic stocks as genetic, genomic and breeding resources; and

basic information on taxonomy, habit, habitat, morphology, karyotype, ploidy level and genome size, etc.

Classical genetics and traditional breeding have contributed enormously even by employing the phenotype-to-genotype approach. We included detailed descriptions on these classical efforts such as genetic mapping using morphological, cytological and isozyme markers; and achievements of conventional breeding for desirable and against undesirable traits. Employment of the *in vitro* culture techniques such as micro- and megaspore culture, and somatic mutation and hybridization, has also been enumerated. In addition, an assessment of the achievements and limitations of the basic genetics and conventional breeding efforts has been presented.

It is a hard truth that in many instances we depend too much on a few advanced technologies, we are trained in, for creating and using novel or alien genes but forget the infinite wealth of desirable genes in the indigenous cultivars and wild allied species besides the available germplasms in national and international institutes or centers. Exploring as broad as possible natural genetic diversity not only provides information on availability of target donor genes but also on genetically divergent genotypes, botanical varieties, subspecies, species and even genera to be used as potential parents in crosses to realize optimum genetic polymorphism required for mapping and breeding. Genetic divergence has been evaluated using the available tools at a particular point of time. We included discussions on phenotype-based strategies employing morphological markers, genotype-based strategies employing molecular markers; the statistical procedures utilized; their utilities for evaluation of genetic divergence among genotypes, local landraces, species and genera; and also on the effects of breeding pedigrees and geographical locations on the degree of genetic diversity.

Association mapping using molecular markers is a recent strategy to utilize the natural genetic variability to detect marker-trait association and to validate the genomic locations of genes, particularly those controlling the quantitative traits. Association mapping has been employed effectively in genetic studies in human and other animal models and those have inspired the plant scientists to take advantage of this tool. We included examples of its use and implication in some of the volumes that devote to the plants for which this technique has been successfully employed for assessment of the degree of linkage disequilibrium related to a particular gene or genome, and for germplasm enhancement.

Genetic linkage mapping using molecular markers have been discussed in many books, reviews and book series. However, in this series, genetic mapping has been discussed at length with more elaborations and examples on diverse markers including the anonymous type 2 markers such as RFLPs, RAPDs, AFLPs, etc. and the gene-specific type 1 markers such as EST-SSRs, SNPs, etc.; various mapping populations including F_2, backcross,

recombinant inbred, doubled haploid, near-isogenic and pseudotestcross; computer software including MapMaker, JoinMap, etc. used; and different types of genetic maps including preliminary, high-resolution, high-density, saturated, reference, consensus and integrated developed so far.

Mapping of simply inherited traits and quantitative traits controlled by oligogenes and polygenes, respectively has been deliberated in the earlier literature crop-wise or crop group-wise. However, more detailed information on mapping or tagging oligogenes by linkage mapping or bulked segregant analysis, mapping polygenes by QTL analysis, and different computer software employed such as MapMaker, JoinMap, QTL Cartographer, Map Manager, etc. for these purposes have been discussed at more depth in the present volumes.

The strategies and achievements of marker-assisted or molecular breeding have been discussed in a few books and reviews earlier. However, those mostly deliberated on the general aspects with examples drawn mainly from major plants. In this series, we included comprehensive descriptions on the use of molecular markers for germplasm characterization, detection and maintenance of distinctiveness, uniformity and stability of genotypes, introgression and pyramiding of genes. We have also included elucidations on the strategies and achievements of transgenic breeding for developing genotypes particularly with resistance to herbicide, biotic and abiotic stresses; for biofuel production, biopharming, phytoremediation; and also for producing resources for functional genomics.

A number of desirable genes and QTLs have been cloned in plants since 1992 and 2000, respectively using different strategies, mainly positional cloning and transposon tagging. We included enumeration of these and other strategies for isolation of genes and QTLs, testing of their expression and their effective utilization in the relevant volumes.

Physical maps and integrated physical-genetic maps are now available in most of the leading crop and model plants owing mainly to the BAC, YAC, EST and cDNA libraries. Similar libraries and other required genomic resources have also been developed for the remaining crops. We have devoted a section on the library development and sequencing of these resources; detection, validation and utilization of gene-based molecular markers; and impact of new generation sequencing technologies on structural genomics.

As mentioned earlier, whole genome sequencing has been completed in one model plant (Arabidopsis) and seven economic plants (rice, poplar, peach, papaya, grapes, soybean and sorghum) and is progressing in an array of model and economic plants. Advent of massively parallel DNA sequencing using 454-pyrosequencing, Solexa Genome Analyzer, SOLiD system, Heliscope and SMRT have facilitated whole genome sequencing in many other plants more rapidly, cheaply and precisely. We have included

extensive coverage on the level (national or international) of collaboration and the strategies and status of whole genome sequencing in plants for which sequencing efforts have been completed or are progressing currently. We have also included critical assessment of the impact of these genome initiatives in the respective volumes.

Comparative genome mapping based on molecular markers and map positions of genes and QTLs practiced during the last two decades of the last century provided answers to many basic questions related to evolution, origin and phylogenetic relationship of close plant taxa. Enrichment of genomic resources has reinforced the study of genome homology and synteny of genes among plants not only in the same family but also of taxonomically distant families. Comparative genomics is not only delivering answers to the questions of academic interest but also providing many candidate genes for plant genetic improvement.

The 'central dogma' enunciated in 1958 provided a simple picture of gene function—gene to mRNA to transcripts to proteins (enzymes) to metabolites. The enormous amount of information generated on characterization of transcripts, proteins and metabolites now have led to the emergence of individual disciplines including functional genomics, transcriptomics, proteomics and metabolomics. Although all of them ultimately strengthen the analysis and improvement of a genome, they deserve individual deliberations for each plant species. For example, microarrays, SAGE, MPSS for transcriptome analysis; and 2D gel electrophoresis, MALDI, NMR, MS for proteomics and metabolomics studies require elaboration. Besides transcriptome, proteome or metabolome QTL mapping and application of transcriptomics, proteomics and metabolomics in genomics-assisted breeding are frontier fields now. We included discussions on them in the relevant volumes.

The databases for storage, search and utilization on the genomes, genes, gene products and their sequences are growing enormously in each second and they require robust bioinformatics tools plant-wise and purpose-wise. We included a section on databases on the gene and genomes, gene expression, comparative genomes, molecular marker and genetic maps, protein and metabolomes, and their integration.

Notwithstanding the progress made so far, each crop or model plant species requires more pragmatic retrospect. For the model plants we need to answer how much they have been utilized to answer the basic questions of genetics and genomics as compared to other wild and domesticated species. For the economic plants we need to answer as to whether they have been genetically tailored perfectly for expanded geographical regions and current requirements for green fuel, plant-based bioproducts and for improvements of ecology and environment. These futuristic explanations have been addressed finally in the volumes.

We are aware of exclusions of some plants for which we have comprehensive compilations on genetics, genomics and breeding in hard copy or digital format and also some other plants which will have enough achievements to claim for individual book volume only in distant future. However, we feel satisfied that we could present comprehensive deliberations on genetics, genomics and breeding of 30 model and economic plants, and their groups in a few cases, in this series. I personally feel also happy that I could work with many internationally celebrated scientists who edited the book volumes on the leading plants and plant groups and included chapters authored by many scientists reputed globally for their contributions on the concerned plant or plant group.

We paid serious attention to reviewing, revising and updating of the manuscripts of all the chapters of this book series, but some technical and formatting mistakes will remain for sure. As the series editor, I take complete responsibility for all these mistakes and will look forward to the readers for corrections of these mistakes and also for their suggestions for further improvement of the volumes and the series so that future editions can serve better the purposes of the students, scientists, industries, and the society of this and future generations.

Science publishers, Inc. has been serving the requirements of science and society for a long time with publications of books devoted to advanced concepts, strategies, tools, methodologies and achievements of various science disciplines. Myself as the editor and also on behalf of the volume editors, chapter authors and the ultimate beneficiaries of the volumes take this opportunity to acknowledge the publisher for presenting these books that could be useful for teaching, research and extension of genetics, genomics and breeding.

Chittaranjan Kole

Preface

Peanut (*Arachis hypogaea* L. Millsp), a grain legume crop, which originated in South America, has become an important crop worldwide. Especially in the context of the developing world, where the crop is grown in a marginal environment by resource-poor farmers, peanut is either a crop for food security or for income generation. Due to exposure of the crop to a range of biotic and abiotic stresses, the crop productivity in developing countries is about 1 ton/ha. Therefore, it is imperative for peanut researchers across the world not only to understand peanut biology indepth but to use this information for crop improvement that can help in improving the livelihood of the poor in the developing countries.

Although peanut researchers have made great progress during the last 5–6 years, many of the latest findings are in the form of publications in various peer-reviewed journals. Much information has been generated on ways to get to the germplasm of interest and utilize it in breeding programs. The generation and utilization of a wide array of new sources of tetraploid peanut (also called synthetics) are expected to broaden the genetic base of peanut and to introduce useful traits. While transferring superior alleles from wild species and unadapted germplasm in elite varieties, there is an inherent issue of linkage drag. However, with the availability of large-scale molecular markers, dense genetic maps, and the information on the QTLs for traits of interest, issues like linkage drags can be overcome. Furthermore, recent advances in genomics, proteomics and bioinformatics are expected to enhance precision and efficiency in peanut breeding.

In view of above and with an objective of compiling information at one place, we planned to have a book dedicated to peanut. We, indeed, are privileged to have a panel of eminent scientists who are authorities in their fields, to write chapters for the book. The most important aspect of these chapters is that they don't just provide a compilation but also present a critical appraisal and future direction in the particular areas. In summary, the volume documents the latest advances in research on germplasm, molecular cytogenetics, genetic maps, trait mapping, transcriptomics, proteomics and bioinformatics.

We would like to avail this opportunity to extend our sincere thanks to all the authors (Annexure I) who accepted our invitation and wrote

excellent articles. Sincere thanks are also due to the reviewers (Annexure II) who spent their quality time, for the sake of high-quality science, for providing useful suggestions to further improve the quality of chapters. The editors are also thankful to Dr. William Dar, Director General, ICRISAT for his encouragement to do and share high quality science and Dr. C.L.L. Gowda, Deputy Director General-Research, ICRISAT for his support. We are also thankful to several colleagues from ICRISAT for useful discussions and support during the preparation of the book. The editors thank Prof. C. Kole, Series Editor for his invitation and help in editing this volume. The editors, also would like to thank Dr. Manish K Pandey, Dr. Manish Roorkiwal, Dr. Reyazul Rouf Mir and Ms. Anu Chitikineni for their help in editing this book.

The editors also recognize that the editorial work for this book volume took away precious time that they could have spent with their respective families. Nalini Mallikarjuna thanks her husband P Mallikarjuna for his unstinted support and encouragement. Rajeev K. Varshney also appreciates the help, support and understanding of his wife Monika and his children Prakhar and Preksha who allowed their time to be taken away to fulfill RKV's editorial responsibilities for this book volume in addition to research, managerial and other institutional duties at ICRISAT and Generation Challenge Program (GCP).

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Abbreviations

AFLP	:	Amplified fragment length polymorphism
BSA	:	Bulked segregant analysis
CAAS (China)	:	Chinese Academy of Agricultural Sciences
CAGE	:	Cap-analysis gene expression
CaMV	:	Cauliflower mosaic virus
CENARGEN	:	National Research Center for Genetic Resources and Biotechnology
CGIAR	:	Consultative Group on International Agricultural Research
CIMMYT	:	International Maize and Wheat Improvement Center
cM	:	CentiMorghan
CRI (China)	:	Crops Research Institute
DArT	:	Diversity array technology
DDRT-PCR	:	Differential display reverse transcription polymerase chain reaction
DGR (India)	:	Directorate of Groundnut Research
ELS	:	Early leaf spot
EMBRAPA	:	Brazilian Agricultural Research Corporation
EST	:	Express sequence tag
FAD	:	Fatty acid desaturase
FISH	:	Fluorescent *in situ* hybridization
GAAS (China)	:	Guangdong Academy of Agricultural Sciences
GAB	:	Genomics-assisted breeding
GISH	:	Genomic *in situ* hybridization
GRAV	:	Groundnut rosette assistor virus
GRV	:	Groundnut rosette virus
GS	:	Genomic selection
HiCEP	:	High coverage expression profiling
IBONE (Argentina)	:	Instituto de Botánica the Northeast
ICAR (India)	:	Indian Council of Agricultural Research
ICPV	:	Indian peanut clump virus

ICRISAT (India)	:	International Crops Research Institute for the Semi-Arid Tropics
IITA	:	International Institute for Tropical Agriculture
IL	:	Introgression line
INTA	:	InstitutoNacional de TechnologiaAgropecuaria
IRRI	:	International Rice Research Institute
ISSR	:	Inter-simple sequence repeats
LD	:	Linkage disequilibrium
LLS	:	Late leaf spot
LTR	:	Long terminal repeat
MABC	:	Marker-assisted backcrossing
MARS	:	Marker-assisted recurrent selection
MAS	:	Marker-assisted slection
MITEs	:	Miniature inverted-repeat transposable elements
MPSS	:	Massively parallel signature sequencing
NBPGR (India)	:	National Bureau of Plant Genetic Resources
NCSU (USA)	:	North Carolina State University
NGS	:	Next-generation sequencing
OCRI (China)	:	Oil Crops Research Institute
PAC	:	Preharvest aflatoxin contamination
PBND	:	Peanut bud necrosis disease
PDR	:	Pathogen-derived resistance
PGC	:	Peanut Genome Consortium
PGP	:	Peanut Genome Project
PMAGE	:	Polony multiplex analysis of gene expression
PMV	:	Peanut mottle virus
PStV	:	Peanut stripe virus
PTGS	:	Post-transcriptional gene silencing
PVE	:	Phenotypic variance explained
QTL	:	Quantitative trait locus
RAPD	:	Random apmplified polymorphic DNA
RFLP	:	Restriction fragment length polymorphism
RIL	:	Recombinant inbred line
RLD	:	Root length density
SAGE	:	Serial analysis of gene expression
SCAR	:	Sequence-characteized amplified region
SCMR	:	SPAD chlorophyll meter reading
SLA	:	Specific leaf area
SNP	:	Single nucleotide polymorphism
SSH	:	Suppressive subtractive hybridization
TAMU (USA)	:	Texas A & M University
TOG	:	Tentative orthologous gene

TSV	:	Tobacco streak virus
TSWV	:	Tomato spotted wilt virus
USDA (USA)	:	U.S. Department of Agriculture

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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.

Keywords: Peanut, Groundnut, *Arachis*, Allotetraploid, Amphidiploid, Synthetic, Genepool, Peanut improvement

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