Genome Mapping and Molecular Breeding in Plants
Volume 2

Series Editor: Chittaranjan Kole

Volumes of the Series
Genome Mapping and Molecular Breeding in Plants

Volume 1
Cereals and Millets

Volume 2
Oilseeds

Volume 3
Pulses, Sugar and Tuber Crops

Volume 4
Fruits and Nuts

Volume 5
Vegetables

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Technical Crops

Volume 7
Forest Trees

Chittaranjan Kole (Ed.)

Oilseeds

With 42 Illustrations, 7 in Color

Springer

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Library of Congress Control Number: 2006926550

ISBN-10 3-540-34387-3 Springer Berlin Heidelberg New York
ISBN-13 978-3-540-34387-5 Springer Berlin Heidelberg New York

Springer is a part of Springer Science+Business Media
springer.com

Editor: Dr. Sabine Schreck, Heidelberg, Germany
Desk Editor: Dr. Jutta Lindenborn, Heidelberg, Germany
Cover design: WMXDesign GmbH, Heidelberg, Germany
Typesetting and production: LE-TEX Jelonek, Schmidt & Vöckler GbR, Leipzig, Germany
39/3100/YL 5 4 3 2 1 0 – Printed on acid-free paper

Preface to the Series

Genome science has emerged unequivocally as the leading discipline of this new millennium. Progress in molecular biology during the last century has provided critical inputs for building a solid foundation for this discipline. However, it has gained fast momentum particularly in the last two decades with the advent of genetic linkage mapping with RFLP markers in humans in 1980. Since then it has been flourishing at a stupendous pace with the development of newly emerging tools and techniques. All these events are due to the concerted global efforts directed at the delineation of genomes and their improvement.

Genetic linkage maps based on molecular markers are now available for almost all plants of significant academic and economic interest, and the list of plants is growing regularly. A large number of economic genes have been mapped, tagged, cloned, sequenced, or characterized for expression and are being used for genetic tailoring of plants through molecular breeding. An array of markers in the arsenal from RFLP to SNP; tools such as BAC, YAC, ESTs, and microarrays; local physical maps of target genomic regions; and the employment of bioinformatics contributing to all the "-omics" disciplines are making the journey more and more enriching. Most naturally, the plants we commonly grow on our farms, forests, orchards, plantations, and labs have attracted emphatic attention, and deservedly so. The two-way shuttling from phenotype to genotype (or gene) and genotypte (gene) to phenotype has made the canvas much vaster. One could have easily compiled the vital information on genome mapping in economic plants within some 50 pages in the 1980s or within 500 pages in the 1990s. In the middle of the first decade of this century, even 5,000 pages would not suffice! Clearly genome mapping is no longer a mere "promising" branch of the life science; it has emerged as a full-fledged subject in its own right with promising branches of its own. Sequencing of the *Arabidopsis* genome was complete in 2000. The early 21st century witnessed the complete genome sequence of rice. Many more plant genomes are waiting in the wings of the national and international genome initiatives on individual plants or families.

The huge volume of information generated on genome analysis and improvement is dispersed mainly throughout the pages of periodicals in the form of review papers or scientific articles. There is a need for a ready reference for students and scientists alike that could provide more than just a glimpse of the present status of genome analysis and its use for genetic improvement. I personally felt the gap sorely when I failed to suggest any reference works to students and colleagues interested in the subject. This is the primary reason I conceived of a series on genome mapping and molecular breeding in plants.

There is not a single organism on earth that has no economic worth or concern for humanity. Information on genomes of lower organisms is abundant and highly useful from academic and applied points of view. Information on higher animals including humans is vast and useful. However, we first thought to concentrate only on the plants relevant to our daily lives, the agronomic, horticultural and technical crops, and forest trees, in the present series. We will come up soon with commentaries on food and fiber animals, wildlife and companion animals, laboratory animals, fishes and aquatic animals, beneficial and harmful insects, plant- and animal-associated microbes, and primates including humans in our next "genome series" dedicated to animals and microbes. In this series, 82 chapters devoted to plants or their groups have been included. We tried to include most of the plants in which significant progress has been made. We have also included preliminary works on some so-called minor and orphan crops in this series. We would be happy to include reviews on more such crops that deserve immediate national and international attention and support. The extent of coverage in terms of the number of pages, however, has nothing to do with the relative importance of a plant or plant group. Nor does the sequence of the chapters have any correlation to the importance of the plants discussed in the volumes. A simple rule of convenience has been followed.

I feel myself fortunate to have received highly positive responses from nearly 300 scientists of some 30-plus countries who contributed the chapters for this series. Scientists actively involved in analyzing and improving particular genomes contributed each and every chapter. I thank them all profoundly. I made a conscientious effort to assemble the best possible team of authors for certain chapters devoted to the important plants. In general, the lead authors of most chapters organized their teams. I extend my gratitude to them all.

The number of plants of economic relevance is enormous. They are classified from various angles. I have presented them using the most conventional approach. The volumes thus include cereals and millets (Volume I), oilseeds (Volume II), pulse, sugar and tuber crops (Volume III), fruits and nuts (Volume IV), vegetables (Volume V), technical crops including fiber and forage crops, ornamentals, plantation crops, and medicinal and aromatic plants (Volume VI), and forest trees (Volume VII).

A significant amount of information might be duplicated across the closely related species or genera, particularly where results of comparative mapping have been discussed. However, some readers would have liked to have had a chapter on a particular plant or plant group complete in itself. I ask all the readers to bear with me for such redundancy.

Obviously the contents and coverage of different chapters will vary depending on the effort expended and progress achieved. Some plants have received more attention for advanced works. We have included only introductory reviews on fundamental aspects on them since reviews in these areas are available elsewhere. On other plants, including the "orphan" crop plants, a substantial amount of information has been included on the basic aspects. This approach will be reflected in the illustrations as well.

It is mainly my research students and professional colleagues who sparked my interest in conceptualizing and pursuing this series. If this series serves its purpose, then the major credit goes to them. I would never have ventured to take up this huge task of editing without their constant support. Working and interacting with many people, particularly at the Laboratory of Molecular Biology and Biotechnology of the Orissa University of Agriculture and Technology, Bhubaneswar, India as its founder principal investigator; the Indo-Russian Center for Biotechnology, Allahabad, India as its first project coordinator; the then-USSR Academy of Sciences in Moscow; the University of Wisconsin at Madison; and The Pennsylvania State University, among institutions, and at EMBO, EUCARPIA, and Plant and Animal Genome meetings among the scientific gatherings have also inspired me and instilled confidence in my ability to accomplish this job.

I feel very fortunate for the inspiration and encouragement I have received from many dignified scientists from around the world, particularly Prof. Arthur

Kornberg, Prof. Franklin W. Stahl, Dr. Norman E. Borlaug, Dr. David V. Goeddel, Prof. Phillip A. Sharp, Prof. Gunter Blobel, and Prof. Lee Hartwell, who kindly opined on the utility of the series for students, academicians, and industry scientists of this and later generations. I express my deep regards and gratitude to them all for providing inspiration and extending generous comments.

I have been especially blessed by God with an affectionate student community and very cordial research students throughout my teaching career. I am thankful to all of them for their regards and feelings for me. I am grateful to all my teachers and colleagues for the blessings, assistance, and affection they showered on me throughout my career at various levels and places. I am equally indebted to the few critics who helped me to become professionally sounder and morally stronger.

My wife Phullara and our two children Sourav and Devleena have been of great help to me, as always, while I was engaged in editing this series. Phullara has taken pains ("pleasure" she would say) all along to assume most of my domestic responsibilities and to allow me to devote maximum possible time to my professional activities, including editing this series. Sourav and Devleena have always shown maturity and patience in allowing me to remain glued to my PC or "printed papers" ("P3" as they would say). For this series, they assisted me with Internet searches, maintenance of all hard and soft copies, and various timely inputs.

Some figures included by the authors in their chapters were published elsewhere previously. The authors have obtained permission from the concerned publishers or authors to use them again for their chapters and expressed due acknowledgement. However, as an editor I record my acknowledgements to all such publishers and authors for their generosity and good will.

I look forward to your valuable criticisms and feedback for further improvement of the series.

Publishing a book series like this requires diligence, patience, and understanding on the part of the publisher, and I am grateful to the people at Springer for having all these qualities in abundance and for their dedication to seeing this series through to completion. Their professionalism and attention to detail throughout the entire process of bringing this series to the reader made them a genuine pleasure to work with. Any enjoyment the reader may derive from this books is due in no small measure to their efforts.

Pennsylvania, Chittaranjan Kole
10 January 2006

Preface to the Volume

I believe some sort of explanation is due to readers regarding the contents of this volume. The conventional grouping of economic plants species, particularly crop plants, is conveniently based on the mode or purpose of their use. Some crop plants are unique in their use and find place in a particular group, say, rice under cereals, peanut under oilseeds, or apple under fruits. Certain crops have two or more important agricultural purposes and may belong to different groups. Such crops posed a problem for chapter allocation under the volumes in this series.

My initial intention was to have a volume for edible oil-yielding crops. This would have required grouping together oilseeds, oil palm, coconut, cottonseed, and olive, and then why not corn or rice! In that case, agricultural scientists would doubt on my minimum knowledge about plantation and cereal crops, and I had to retreat. I went for just the oilseed crops.

At least four oilseed crops have multifarious agronomic purposes. Soybean could with equal justification be categorized as an oilseed or as a pulse crop. But considering its dominating presence among oil-producing field crops, it should be included in the oilseed volume. The second problematic entrant was *Brassica rapa*. It could boast of being an oilseed as well as a vegetable. Moreover, it has several distinct subspecies under these two categories. Traditional breeding must have dealt with them separately with distinct objectives for genetic improvement. However, genetics, basic or modern, needed them together. Nucleotides do not distinguish between oil and vegetable! We placed it in this volume with detailed review on molecular aspects and also in the volume on vegetables with details on the basic aspects. Black mustard, which is a traditional condiment. But it has been of immense use in studies of comparative genomics in Brassicaceae and provided many clues to the evolution of genes and genomes. We placed it in this volume as well. A horticulturist would surely prefer to treat sunflower as an ornamental. However, it is among the four leading seed-oil- producing species, and so it is here in volume II on oilseed crops.

Some oilseed crops are grown in Asian countries, like sesame and safflower, which have recently attracted the attention of molecular biologists and been the object of considerable efforts at genome analysis. We had to omit them from the current volume with the hope of including chapters on them in future editions.

To our delight we were able to sign on highly eminent scientists to author the chapters in this volume. In addition, some of the chapters represent the results of the multilab and multinational efforts of their authors, who took pains for coordinated and concerted endeavors. I am thankful to all the authors for the high academic quality of their final output.

I worked on oilseed *Brassicas*, specifically *B. rapa* and *B. napus*, in the lab of Prof. Thomas C. Osborn at UW-Madison and later continued works in my own labs in India and have many close colleagues in that fraternity. It was a real pleasure and enriching to work on this volume with some of these friends, whom I used to meet annually in January at the Town & Country Hotel in San Diego during the Plant and Animal Genome conferences. I also wish to record my thanks to my wife, Phullara, who used to work with me at UW-Madison and India, and my colleagues and research students who worked with me on oilseed Brassicas for their continued interactions and inputs that made my life easier while editing this volume. The first volume produced by the publishers of this series has been well received by readers. The publishers have done an equally elegant job for this volume as well. I am thankful for their dedicated service to science.

Suggestions from any corner on how to improve this volume for future editions are welcome.

Pennsylvania, Chittaranjan Kole
26 February 2006

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Abbreviations

Δ9DES	Δ9-Steroyl-ACP-Desaturase
AAFC	Agriculture and Agri-Food Canada
AC	*Albugo candida*
ACP	Acetyl Carrier Protein
ACS	Acyl-CoA Synthase
AFLP	Amplified Fragment Length Polymorphism
AHAS	Acetohydroxyacid Syntheses
ANOVA	Analysis of Variance
ARS	Agricultural Research Service
AS-PCR	Allele-Specific Polymerase Chain Reaction
ASPE	Allele-Specific Primer Extension
AT	Acyltransferase
ATP	Adenosine Triphosphate
BAC	Bacterial Artificial Chromosome
BAGI	Brassica/Arabidopsis Genomic Institute
BC	Backcross
BSA	Bulked Segregant Analysis
BSR	Brown Stem Rot
CAPS	Cleaved Amplified Polymorphic Sequences
cDNA	Complementary DNA
CENARGEN	National Center of Genetic Resources
CID	Carbon Isotope Discrimination
CIM	Composite Interval Mapping
CLG	Classical Linkage Group
cM	centi-Morgan
CMS	Cytoplasmic Male Sterility
CO	Constans (gene)
CR	Clubroot Resistance
CSHL	Cold Spring Harbor Laboratory
DAF	DNA Amplification Fingerprint
DAG	DiAcylGlycerol
DAGAT	DiAcylGlyceral AcylTransferase
DAP	Days After Pollination
DAS	Days After Sowing
DD-RT-PCR	Differential Display Reverse Transcription PCR
DH	Direct Hybridization
DH	Doubled Haploid
DRE	Drought Responsive Elements
DTF	Days To Flowering
DUS	Distinctness, Uniformity and Stability
ECSs	Evolutionary Conserved Sequences
ELISA	Enzyme-Linked ImmunoSorbent Assay
ELS	Early Leaf Spot
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuaria
EMS	Ethyl Methane Sulphonate

EPSP	5-EnolPyruvyl 3-Shikimate Phosphate
EST	Expressed Sequenced Tag
FA	Fatty Acid
FAD	Fatty Acid Desaturase (gene)
FAEI	Fatty Acid Elongase (gene)
FAO	Food and Agricultural Organization
FAS	Fatty Acid Synthase
FISH	Fluorescence In Situ Hybridization
FLC	Flowering Locus C
G3P	Glycerol-3-Phosphate
G3PAT	Glycerol-3-Phosphate AcylTransferase
GFP	Green Florescence Protein
GISH	Genomic In Situ Hybridization
GMO	Genetically Modified Organism
GO	Gene Ontology
GPI	Glucose-6-Phosphate Isomerase
GRAS	Generally Recognized As Safe
GRAV	Groundnut Rosette Assistor Virus
GRV	Groundnut Rosette Virus
GS	Glutamine Synthetase
GST	Gene Sequence Tag
GUS	Glucuronidase
HDL	High Density Lipoprotein
HEAR	High Erucic Acid Rapeseed
HI	Harvest Index
HPLC	High Performance Liquid Chromatography
IC	Intercross
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IDC	Iron Deficiency Chlorosis
IFDB	International Flax Data Base
IMI	Imidazalinones
InDel	Insertion Deletion
IP	Interaction Phenotype
IPCV	Indian Peanut Clump Virus
ISSR	Inter-Simple Sequence Repeat
JSC	Jaccard's Similarity Coefficient
KAS	KetoAcyl-ACP Synthase
LDL	Low Density Lipoprotein
LEAR	Low Erucic Acid Rapeseed
LG	Linkage Group
LLS	Late Leaf Spot
LOD	Logarithm Of Odds
LPA	LysoPhosphatidic Acid-phosphate
LPAAT	LysoPhosphatidic Acid Transferase
MAS	Marker-Assisted Selection
MBGP	Multinational Brassica Genome project
MCFA	Medium-Chain Fatty Acid
MD	Microspore-Derived
MIPS	Munich Information Center for Protein
MMT	Million Metric tons
MTA	Material Transfer Agreement

MUFA	Monounsaturated Fatty Acid
NBS	Nucleotide-Binding Sites
NIAB	National Institute of Agricultural Biotechnology
NILs	Near Isogenic Lines
NIR	Near Infrared
NMR	Nuclear Magnetic Resonance
NOR	Nuclear Organizing Region
OL	Oligonucleotide Ligation
ORF	Open Reading Frame
PAP	Phosphatidic Acid Phosphates
PBC	Plant Biotechnology Center
PBNV	Peanut Bud Necrosis Virus
PBP	Plant by Plant
PC	PhosphatidylCholine
PCR	Polymerase Chain Reaction
PCV	Peanut Clump Virus
PD	Pod Dehiscence
PEP	PhosphoEnol Pyruvate
PFM	Physical Functional Markers
PGRC	Plant Gene Resource of Canada
PH	Plant Height
PMC	Peanut Mottle Potyvirus
PPR	PentatricoPeptide Repeat
PPT	PhosPhonoThricin
PSND	Peanut Stem Necrosis Disease
PT	Petiole Thickness
PTRD	Peanut Transcript Responsive to Drought
PUFA	PolyUnsaturated Fatty Acid
PW	Petiole Width
QTL	Quantitative Trait Loci
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
RGA	Resistant Gene Analogue
RGC	Recipient Genome content
RIL	Recombinant Inbred Line
RKN	Root-Knot Nematode
RNAi	RNA Interference
RT-PCR	Reverse Transcription PCR
RWC	Relative Water Content
Sat RNA	Satellite RiboNucleic Acid
SBE	Single-Base Extension
SCAR	Sequence Characterized Amplified Region
SCH	Seed Coat Hardiness
SCN	Soybean Cyst Nematode
SCR	S-locus Cysteine Rich (Protein)
SDS	Sudden Death Syndrome
SFA	Single Factor Analysis
SI	Self-Incompatibility
SLA	Specific Leaf Area
SLG	S-Locus Glycoprotein
SLN	Specific Leaf Nitrogen

SLW	Specific Leaf Weight
SMT	Selenocysteine Methyl Transferase
SMV	Soybean Mosaic Virus
SNP	Single Nucleotide Polymorphism
SP	S-locus Protein
SPD	Single-Pod-Descendent
SRAP	Sequence Related Amplified Polymorphism
SRK	S-locus Receptor Kinase
SSD	Single-Seed-Descent
SSR	Simple Sequence Repeat
STS	Sequence-Tagged Site
SUS	Sulphoneluries
SWP	Saskatchewan Wheat Pool
TAG	TriAcylGlycerols
TBA	Thio Barbiutric Acid
TE	ThioEsterases
TE	Transpiration Efficiency
TIGR	The Institute for Genomic Research
TLCSF	Total Long Chain Saturated Fatty Acid
TSF	Total Saturated Fat
TSM	Thousand Seed Mess
TSV	Tobacco Streak Virus
TSWV	Tomato Spotted Wilt Virus
TuMV	Turnip Mosaic Virus
TuYv	Turnip Yellow Virus
UCB	Catolica de Brasilia
UNESP	Universidade Estadual de Sao Paulo
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
USDA	United States Department of Agriculture
VFR	Vernalization-Responsive Flowering-Time in (*Brassica*) *Rapa*
WLL	Water Loss from (Excised) Leaves
WUE	Water-Use Efficiency
WUE	Water Use Efficiency
YAC	Yeast Artificial Chromosome