Nextgen Agriculture

ALLELE MINING FOR GENOMIC DESIGNING OF CEREAL CROPS

Edited by
Chittaranjan Kole, Sharat Kumar Pradhan,
and Vijay K. Tiwari

CRC Press
Taylor & Francis Group

Allele Mining for Genomic Designing of Cereal Crops

This book deliberates on the concept, strategies, tools, and techniques of allele mining in cereal crops and its application potential in genome elucidation and improvement, including studying allele evolution, discovery of superior alleles, discerning new haplotypes, assessment of intra- and interspecific similarity, and studies of gene expression and gene prediction. Available gene pools in global germplasm collections specifically consisting of wild allied species and local landraces for almost all major crops have facilitated allele mining. Development of advanced genomic techniques including PCR-based allele priming and Eco-TILLING-based allele mining are being widely used now for mining superior alleles. Allele's discovery has become more relevant now for employing molecular breeding to develop designed crop varieties matching consumer needs and with genome plasticity to adapt the climate change scenarios. All these concepts and strategies along with precise success stories are presented in the chapters dedicated to the major cereal crops.

The features of this book are as follows:

1. The first book on the novel strategy of allele mining in cereal crops for precise breeding.
2. Presents genomic strategies for mining superior alleles underlying agronomic traits from genomic resources.
3. Depicts case studies of PCR-based allele priming and Eco-TILLING-based allele mining.
4. Elaborates on gene discovery and gene prediction in major cereal crops.

This book will be useful to students and faculties in various plant science disciplines including genetics, genomics, molecular breeding, agronomy, and bioinformatics; the scientists in seed industries; and the policymakers and funding agencies interested in crop improvement.

NextGen Agriculture: Novel Concepts and Innovative Strategies
Chittaranjan Kole
Series Editor

Allele Mining for Genomic Designing of Fruit Crops
Chittaranjan Kole, Kenta Shirasawa, and Anil Kumar Singh

Allele Mining for Genomic Designing of Cereal Crops
Chittaranjan Kole, Sharat Kumar Pradhan, and Vijay K. Tiwari

For more information, please visit our website: Nextgen Agriculture: Novel Concepts and Innovative Strategies – Book Series – Routledge & CRC Press

Allele Mining for Genomic Designing of Cereal Crops

Edited by
Chittaranjan Kole, Sharat Kumar Pradhan, and
Vijay K. Tiwari

CRC Press
Taylor & Francis Group
Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

First edition published 2024
by CRC Press
2385 NW Executive Center Drive, Suite 320, Boca Raton FL 33431

and by CRC Press
4 Park Square, Milton Park, Abingdon, Oxon, OX14 4RN

CRC Press is an imprint of Taylor & Francis Group, LLC

ISBN: 9781032471907 (hbk)
ISBN: 9781032471938 (pbk)
ISBN: 9781003385004 (ebk)

DOI: 10.1201/9781003385004

Typeset in Times
by Newgen Publishing UK

Contents

Abbreviations

ABA	Abscisic acid
ABC	ATP-binding cassette
ABRE	Abscisic acid response element
AC	Amylose content
acdc1	*adult cyanide deficient 1* sorghum mutant
AFLP	Amplified fragment length polymorphism
AGPase	ADP glucose pyrophosphorylase
AM	Association mapping
AM	Axillary meristem
AP2	*Apetala2*
ARMS	Amplification refractory mutation system
asal	*Allium sativum*
ASI	Anthesis and silking interval
ASP	Allele-specific primers
AS-PCR	Allele-specific PCR
BAC	Bacterial artificial chromosome
BAP	Bioenergy Association Panel
BB	Bacterial blight
BC	Backcross population
BC3F1/ BC3F2	Backcross derived population
BETL	Basal endosperm transfer cell layer
bif2	*barren inflorescence 2*
BioDIG	Biological Database of Images and Genomes
BLB	Bacterial leaf blight
bmr	Sorghum *brown midrib* genes/mutants
BPH	Brown plant hopper
BS	Brown spot
bZIP	Basic region-leucine zipper protein
CAD	Cinnamyl alcohol dehydrogenase
CAP	Common Agricultural Policy
CAPS	Cleaved amplified polymorphic sequence
Cas	CRISPR associated protein
CDR	Ccarbon dioxide removal
CEP	C-terminal encoded peptide
CG	Candidate gene
CG	Comparative genomics
CGAM	Candidate gene-based association mapping
CIMMYT	International Maize and Wheat Improvement Center
CISP	Conserved intron specific primers
CK	Cytokinin
CLE	CLAVATA3/ESR-related
CLT	CACTA-like transposon element
CLV1/BAM	Clavata1/ barely any meristem
CLV-WUS	CLAVATA-WUSCHEL
CMS	Cytoplasmic male sterility
CNV	Copy number variant/variation
CORE	Collaborative Oat Research Enterprise

CRISPR	Clustered regularly interspaced short palindromic repeats
CRT	C-repeat element
CSL	Chromosome substitution line
CSSL	Chromosome segment substitution line
ct2	*compact plants 2*
CWR	Crop wild relatives
DAA	Days after anthesis
DArT	Diversity arrays Technology
DArTseq	DArT sequencing
DEGs	Differentially expressed genes
DH	Doubled haploid
Dhu1	Sorghum *Dhurrin 1* locus
DRE	DNA replication related element
DREB	Dehydration response element binding genes
DRO1	*Deeper Rooting 1* gene
DTY	*Yield under drought* gene
Dw1-4	Sorghum *Dwarfing 1-4* loci
EC	European Union
Eco-TILLING	Ecotype TILLING
ECQ	Eating and cooking quality
ED	Ear diameter
EFSA	European Food Safety Authority
EGW	Ear glume weight
EL	Ear length
EMS	Ethylmethane sulfonate
EREBP	Ethylene-responsive element binding protein
ERF	Ethylene responsive factor
EST	Expressed sequence tag
EW	Ear weight
FAO	Food and Agriculture Organization
FD	*FLOWERING LOCUS D*
fea2	*fascinated ear2*
fea3	*fascinated ear3*
fea4	*fascinated ear4*
FHB	Fusarium head blight
FIGS	Focused identification of germplasm strategy
FLO/LFY	*Floricaula and Leafy*
FLS2	*Flagellin-sensitive*
FMs	*Floral meristems*
FOAM	F-one association mapping
FRET	Fluorescence resonance energy transfer
FS	False smut
FT	*FLOWERING LOCUS T*
FTIR	Fourier-transform infrared spectroscopy
FWL	*Fw2.2-like*
GA	Gibberellic acid
GAB	Genomics-assisted breeding
GABA	Gamma-aminobutyric acid
GAB-ald	Gamma-aminobutyraldehyde
GBS	Genotyping-by-sequencing

GBSS	*granule bound starch synthase* gene
GBSSI	Granule-bound starch synthase I
GDD	Growing degree days.
GEBVs	Genome-assisted breeding values
GLW	Grain length and width
GM	Gall midge
GMO	Genetically modified organism
GMS	Gametic male sterile
GN	Grain number
gna	*Galanthus nivalis*
Gpc	Grain protein content
GRF	Growth-regulating factor
GRIN	Germplasm Resource Information Network
GS	Genomic selection
GS	Glutamine synthetase
GS	Grain shape
GSR	Green super rice
gSSRs	Genomic SSR
GT	Grain thickness/gelatinization temperature
GW	Grain weight
GWAS	Genome wide association study/studies
GxE	Genotype-by-environment
GxExM	Genotype-by-environment-by-management
GY	Grain yield
HCN	Hydrogen cyanide
HD-ZIP	Homeodomain-leucine zipper protein
HIF	Heterogeneous inbred family
HKW	Hundred kernel weight
HLT	Harbinger-like transposon
HMW	High molecular weight
HPC1	*PhosphatidylCholine 1*
HRW	Hard red winter
HTP	High-throughput phenotyping
HWW	Hard white winter
IAA	Indole acetic acid
IBD	Identity by descent
ICRISAT	International Crops Research Institute for Semi-Arid Tropics
id1	*indeterminate1 gene*
ids1	Indeterminate spikelet 1
IL	Introgression line
IM	Interval mapping
IM	Inflorescence meristem
InDel	Insertion-deletion
IPK	Institut für Pflanzengenetik und Kulturpflanzenforschung
Ipt	Isopentenyl transferase gene
IRD	Institut de Recherche Pour le Développement
JA	Jasmonic acid
KASP	Kompetitive allele specific PCR
KNPR	Kernel number per row
KRN	Kernel row number

KW	Kernel weight
LD	Linkage disequilibrium
LEA	Late embryogenesis abundant
LEA3	*LATE EMBRYOGENESIS ABUNDANT 3* locus
LMW	Low molecular weight
LOD	Logarithm of the odds
LRR	Leucine rich repeat
Ma1-6	Sorghum *Maturity 1-6* loci
MABB	Marker-assisted backcross breeding
MABC	Marker-assisted backcrossing
MAGIC	Multi-parent advanced generation intercross
MAI	Marker assisted introgression
maizezfl	Maize zeafloricaula
MALDI-TOF-MS	Matrix-assisted laser desorption ionization-time of flight mass spectrometry
MARS	Marker-assisted recurrent selection
MAS	Marker-assisted selection
MDH	Malondialdehyde
MEME	Multiple EM for Motif Elicitation
MFT-like	MOTHER OF FT-like
MIK	Myo-inositol kinase
MIPS	Myo-inositol-3-phosphate synthase
miRNA	MicroRNA
MPP	Multi-parental breeding population
MQTL	Meta-QTL
MTA	Marker-trait association
MYB	Myeloblastosis viral oncogene homolog
MYC	Myeloblastosis viral proto-oncogene homolog
NAC	Domain protein for NAM, ATAF1/2 and CUC2
NADH	Nicotinamide adenine dinucleotide (NAD) + hydrogen (H)
NAM	No apical meristem
NAM	Nested association mapping
NB-LRR	Nucleotide binding-LRR
NBPGR	National Bureau of Plant Genetic Resources
NBS	Nucleotide binding site
NCBI	National Center for Biotechnology Information
NDVI	Normalized difference vegetation index
NF-Y	Nuclear factor Y
NGS	Next-generation sequencing
NILs	Near isogenic lines
NPGS	National Plant Germplasm Systems
NSG	Non Stay-green
NSGC	National Society of Genetic Counselors
OFP	Ovate family protein
OPV	Open pollinated variety
OsSERK2	Rice Somatic Embryogenesis Receptor Kinase 2
P1	Maize *Pericarp color 1* gene
PAC	P1-derived artificial chromosome
PACE	PCR allele competitive extension
PAGE/RAGE	Promotion/removal of allele through genome editing
PAN	Parinthia

PASA	PCR-amplification of specific alleles
PBP	Pheromone-binding protein
PCR	Polymerase chain reaction
PGRC	Plant Gene Resources of Canada
PHYC	Phytochrome C
PID	PINOID protein kinase
PINII	Potato proteinase inhibitor
PLACE	Plant *cis*-acting regulatory DNA element
Pm3	Powdery mildew resistance
PMDTDb	Pearl Millet Drought Transcriptome Database
PMiGAP	Pearl millet inbred germplasm association panel
Ppd1	*Photoperiod 1*
PPR	P-type pentatricopeptide repeat
PSII	Photosystem II
pUBi	Maize ubiquitin promoter
QR-gene	Quantitative resistance gene
QTL	Quantitative trait locus
QTLs	Quantitative trait loci
QTN	Quantitative trait nucleotide
R allele	Resistant allele
ra	Ramose
RAD-seq	Restriction site-associated DNA sequencing
RAPD	Random amplified polymorphic DNA
rel2	*ramosa1 enhancer locus2*
RFLP	Restriction fragment length polymorphism
RFS	Renewable Fuel Standard
RGA	Rapid generation advancement
RGT	Rapid generation turn over
Rht	Reduced height
RIL	Recombinant inbred line
RLF	Rice leaf folder
RLK	Receptor-like kinase
RMES1	Sorghum Resistance to *Melanaphis sacchari 1* locus
ROS	Reactive oxygen species
RPG	Recurrent parent genome
RRL	Reduced representation library
RSA	Root system architecture
RSD	Rice stripe disease
RSV	Rice stripe virus
RTBV	Rice tungro bacilliform virus
RT-PCR	Reverse transcription-PCR
RTSV	Rice tungro spherical virus
RYMV	Rice yellow mottle virus
S allele	Susceptible allele
SAM	Shoot apical meristem
SAP	Stress associated protein
SAP	Sorghum association panel
SAVS	Senescence-associated vacuoles
SB	Stem borer
SBEIIb	*STARCH BRANCHING ENZYME IIb* gene

SBP	SQUAMOSA promoter-Binding protein
SCP	Sorghum Conversion Program
SES	Standard evaluation system
SG	Stay-green
ShB	Sheath Blight
SLAF-seq	Specific-locus amplified fragment sequencing
SM	Spikelet meristem
SNP	Single nucleotide polymorphism
Sor1	Sorghum *Sorgoleone 1* locus
SPDT	SULTR-like phosphorus distribution transporter
SPM	Spikelet-pair meristem
SRW	Soft red winter
SS	Starch synthase
SSCP	Single-stranded conformation polymorphism
SSIIa	*STARCH SYNTHASE IIa*
SSR	Simple sequence repeat
SSSII	Soluble starch synthase II
Stg1-5	Sorghum *Stay-green 1-5* loci
STS	Sequence-tagged site
SWDP	Sweet Sorghum Diversity Panel
SWEET	Sugars will eventually be exported transporters
SWW	Soft white winter
SYMD	SET and MYND
TALE	Transcription activation-like effector
TALEN	Transcription activator-like effector nuclease
TB1	*Teosinte branched 1*
tcd1	*totally cyanide deficient class 1* sorghum mutant
td1	*thick tassel dwarf1*
TF	Transcription factor
TFBS	Transcription factor binding site
TFIIA	Transcription Factor IIA
tga1	*teosinte glume architecture 1*
TGW	Thousand grain weight
TILLING	Targeting induced local lesions in genomes
ub2	*unbranched2*
UBN	Uniform blast nursery
UGT	UDP-glucosyltransferase
US FDA	United States Food and Drug Administration
USDA	United States Department of Agriculture
USDA-ARS	USDA-Agricultural Research Service
USDA-NPGS	USDA's National Plant Germplasm System
UTR	Untranslated region
UV	Ultraviolet
VI	Vegetation index
VIGS	Virus-induced gene silencing
Vip	Vegetative insecticidal protein
VIR	Vavilov All-Russian Institute of Plant Genetic Resources
VSP	Visual scale of plants
WAPO-A1	Wheat aberrant panicle organization-A1
WBPH	White backed plant hopper

WEW	Wild emmer wheat
WFZP	Wheat frizzy panicle
WGRS	Whole-genome resequence
WGS	Whole-genome sequencing
WUE	Water use efficiency
Wx	*Waxy* gene/locus
Wx-A1	Waxy gene and amylose biosynthesis
Xoo	*Xanthomonas oryzae* pv. *Oryzae*
XRD	X-ray diffraction
Y	Sorghum *YELLOW SEED* loci
YPP	Yield per plant
YSB	Yellow stem borer
ZEP	*Zeaxanthin epoxidase* gene
ZF-HD	Zinc finger homeodomain
Zfl	Zeafloricaula
ZFN	Zinc finger nuclease

Preface

The affordability, precision, and high-throughput nature of sequencing technologies in the last two decades have provided an unprecedented understanding of the genomes and target plant traits of economic importance. Further, the advances in the third-generation sequencing technologies including Hi-C especially in the last decade have made it possible for developing high-quality reference genomes, pangenomes, and gene annotations, including genome-wide structural variations. These developments have also increased the precision in gene and superior haplotype discovery followed by mining allelic diversity among breeding lines and gene bank collections. The high-throughput and cost-effective genotyping platforms have further boosted the adoption rate of genomic tools in the ongoing breeding programs across the world. Deployment of these advances in crops and making them well equipped to scale up the integration of genomic interventions in the breeding programs will facilitate development of future-ready crops.

The above advances have made gene/allele mining more precise and cost-effective for the target traits preferred by farmers, consumers, and industry as well as efforts towards mitigation of climate change impacts and achieving nutritional security prospective. It is important to accelerate the process of genomic designing to develop future-ready crops by bringing new allelic combination(s) at one or more loci underlying desired genes using modern breeding approaches, such as marker-assisted breeding, haplotype-based breeding, and gene/allele pyramiding; and also now through gene editing.

These new alleles originate through natural or induced mutations also at one or more genomic regions at a time. The traditional plant breeding methods practiced in the twentieth century depended solely on phenotypes for the development of new genotypes primarily through selection and hybridization. The advent of DNA-based molecular markers in the 1980s facilitated indirect identification of the alleles by using linked molecular markers using genetic linkage mapping. Molecular breeding as a supplement to traditional breeding has successfully been employed in almost all major crops for their genetic improvement in a short time. It is worthwhile to mention that transgenic breeding has also contributed significantly to crop improvement at least for some major input target traits, such as herbicide tolerance, insect resistance, etc., however, this technology is still facing challenges in societal adoption in different parts of the world, especially for food crops. Nevertheless, gene editing has been receiving positive vibes from the policymakers of different countries making a conducive environment for accelerating the use of this technology on large scale.

Despite the huge loss of diversity during domestication, several national and international gene banks have millions of diverse germplasms to explore variability for the traits that are needed to breed climate-resilient and future-ready crops. Genetic diversity played a pivotal role during the entire period of conventional plant breeding, traditional and molecular included. However, the plant breeders have been using mainly the primary gene pool constituting the indigenous germplasm lines and local landraces as a genetic resource of new alleles. In the meantime, a drastic dearth of new alleles in the primary gene pool happened due to genetic erosion caused naturally or due to domestication over time but aggravated because of the injudicious and irrational implementation of the so-called green revolution. Precisely, this highlighted the importance of allied wild crop relatives (WCRs) and thereby a mission of collection, conservation, characterization, and utilization of biodiversity. The emergence of advanced bioinformatics and the availability of cheaper and innovative genome sequencing technologies have empowered us to explore germplasm and identify a large number of donor alleles and allele mining has become a reality!

The strategy of association mapping, the most popular trait mapping approach in animal and human sciences, has received huge adoption in plant genomics studies. The availability of large sequenced diverse panels with multilocation phenotyping data has provided much-needed insights into trait genomics through genome-wide association studies (GWAS) leading to the discovery of

genes and superior haplotypes in many crops. This has led to the possibility of mining a large number of genes in the available accessions in crops. Mutations occur in the genome as single nucleotide polymorphisms (SNPs) or insertion/deletions (In/Dels) resulting in the generation of new alleles or changes in existing alleles and allele combinations. Using exactly this principle, the approach of Eco-TILLING has facilitated large-scale allele mining in several major crops. On the other hand, sequence-based allele mining has led to the discovery of allelic diversity both at the target gene and the whole genome. Recent advances in modern genomic tools and technologies, such as genome engineering, speed breeding, etc., facilitate the deployment of these new alleles in breeding programs in a relatively short time to accelerate the rate of genetic gains. Truly speaking, allele mining has revolutionized the strategy of utilizing genetic as well as genomic resources and become an important component of next-generation precision breeding and biotechnology!

Allele discovery has become more relevant now for employing molecular breeding to develop designed crop varieties matching consumer needs and with genome plasticity to adapt the climate change scenarios using targeted and precision breeding tools validated by both genomics and phenomics studies. All these concepts and strategies along with precise success stories are presented in over 50 chapters allocated under five volumes dedicated to the five crop groups including cereals, oilseeds, grain legumes, fruits, and vegetables under this book series.

This volume entitled, "Allele Mining for Genomic Designing of Cereal Crops" includes 12 chapters dedicated to rice, wheat, maize, barley, oat, sorghum, pearl millet and finger millet contributed by 73 scientists from six countries including India, Italy, the Netherlands, Philippines, Spain, and the USA. We express our thanks for their excellent contributions and timely cooperation.

This book will hopefully be useful to students, research scholars, and teaching faculties in the academia to learn about fundamentals and applications of allele mining; the scientists practicing plant breeding in public and private institutes in improvising their programs; and also, the policymakers and funding agencies in prioritizing research fields.

Chittaranjan Kole, Kolkata, India
Sarat Kumar Pradhan, New Delhi, India
Vijay K Tiwari
College Park, USA

Contributors

Jauhar Ali
International Rice Research Institute, Los Banos, Philippines

Supriya Ambawat
ICAR-AICRP on Pearl Millet, Jodhpur 342 304, Rajasthan, India

Lokeshkumar B.M.
Division of Crop Improvement, ICAR-Central Soil Salinity Research Institute, Karnal, Haryana, India-132001

Kalyana Babu
ICAR-Indian Institute of Oilpalm Research, Pedavegi 534475, AP, India

Franz W. Badeck
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Mary-Frances Behnke
Department of Plant & Environmental Sciences, Clemson University, Florence, SC, USA

Jayant S Bhat
ICAR-IARI-Regional Research Centre, Dharwad 580005, India

Zachary W. Brenton
Carolina Seed Systems, Inc., Darlington, SC, USA

Richard E. Boyles
Department of Plant & Environmental Sciences, Clemson University, Florence, SC, USA

Anilkumar C.
Division of Crop Improvement, ICAR-National Rice Research Institute, Cuttack, India-753006.

Ilaria Carrara
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Luigi Cattivelli
Council for Agricultural Research and Economics (CREA), Research Centre for Genomics and Bioinformatics, Via San Protaso 302, 29017, Fiorenzuola d'Arda, Italy

Kasarla Chaithanya
Plant Breeding, ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad-500030, India

Chandu singh
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

Hugo E. Cuevas
USDA-ARS, Tropical Agriculture Research Station, 2200 Pedro Albizu Campos Avenue, Mayagüez, Puerto Rico 00680, USA

Shivani D.
Plant Breeding, ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad-500030, India

Stefano Delbono
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Maroua Doghri
Department of Plant Biology, Faculty of Biology, Institute of Biotechnology and Biomedicine, University of Valencia, Valencia, Spain

Yves Emendack
Cropping Systems Research Laboratory, USDA-ARS, Lubbock, TX, USA

Franca Finocchiaro
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Abdul Fiyaz R
Plant Breeding, ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad-500030, India

RN Gadag
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

Vijay Gahlaut
Department of Biotechnology, Chandigarh University, Gharuan, Mohali, 140413, Punjab, India
University Center for Research and Development, Chandigarh University, Gharuan, Mohali, 140413, Punjab, India

Roberta Ghizzoni
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

R. Gobu
ICAR – Indian Institute of Spices Research, Kozhikode, Kerala, 673012, India

Davide Guerra
Council for Agricultural Research and Economics (CREA), Research Centre for Genomics and Bioinformatics, Via San Protaso 302, 29017, Fiorenzuola d'Arda, Italy

Chad M. Hayes
Cropping Systems Research Laboratory, USDA-ARS, Lubbock, TX, USA

Seyedali Hosseinirad
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

Vandana Jaiswal
Biotechnology Division, CSIR-Institute of Himalayan Bioresource Technology, Palampur, Himachal Pradesh 176061, India

Dinesh Chandra Joshi
ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora 263 601, UK, India

Anmol Kajla
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

Ashvinkumar Katral
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India-110012

Chandan Kapoor
ICAR – Indian Agricultural Research Institute, Pusa campus, New Delhi- 110012, India

Dileep Kumar G.D
Plant Breeding, ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad-500030, India.

Sachin Kumar
Department of Genetics and Plant Breeding, Ch. Charan Singh University, Meerut, India

Charu Lata
CSIR-National Institute of Science Communication and Policy Research, 14 Satsang Vihar Marg, New Delhi - 110067, India

Balram Marathi
Professor Jayashankar Telangana State Agricultural University, Hyderabad, India.

Kutubuddin A. Molla
Division of crop improvement, ICAR-National Rice Research Institute, Cuttack, India-753006

Caterina Morcia
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Ganapati Mukri
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

Varunseelan Murugaiyan
International Rice Research Institute, Los Banos, Philippines

Sunitha N.C.
Department of Genetics and Plant Breeding, University of Agricultural Sciences, Bangalore, India-560065.

Christian John Robiso
International Rice Research Institute, Los Banos, Philippines

Chandra Nayaka Siddaiah
Pearl Millet Pathology Laboratory, University of Mysore, Manasagangotri, Mysore, India

Bernardo Ordas
Misión Biológica de Galicia, Spanish National Research Council (CSIC), Pontevedra, Spain

Arunava Pattanyak
ICAR-Indian Institute of Agricultural Biotechnology, Ranchi 834003, Jharkhand, India

Chandra Prabha
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

Fulvia Rizza
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics,Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Davina H. Rhodes
Department Horticulture & Landscape Architecture, Colorado State University, Fort Collins, CO, USA

Krishnamurthy S.L.
Division of Crop Improvement, ICAR-Central Soil Salinity Research Institute, Karnal, Haryana, India-132001

Soumya SL
ICAR – Indian Agricultural Research Institute, Pusa campus, New Delhi- 110012, India

Rameswar Prasad Sah
Division of Crop Improvement, ICAR-National Rice Research Institute, Cuttack, India-753006

Jacobo Sanchez
Cropping Systems Research Laboratory, USDA-ARS, Lubbock, TX, USA

S. Mukesh Sankar
ICAR – Indian Agricultural Research Institute, Pusa campus, New Delhi- 110012, India

Gautam Saripalli
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

C Tara Satyavathi
ICAR-AICRP on Pearl Millet, Jodhpur 342 304, Rajasthan, India

Adam William Schoen
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

Hemant Sharma
Department of Genetics and Plant Breeding, Ch. Charan Singh University, Meerut, India

Samriti Sharma
University Institute of Biotechnology, Chandigarh University, Mohali, India, 140 103, India

Shilpa
Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

Radha Shivhare
CSIR-National Botanical Research Institute, Rana Pratap Marg, Lucknow-226001, India

Rakesh. K. Srivastava
International Crops Research Institute for Semi Arid Tropics, Patancheru-502 324, Telangana, India

Salej Sood
ICAR-Central Potato Research Institute, Shimla 171001, HP 171 001, India

R.M. Sundaram
Biotechnology, ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad-500030, India

Valeria Terzi
Council for Agricultural Research and Economics (CREA), Research centre for Genomics & Bioinformatics, Via S. Protaso, 302, I -29017 Fiorenzuola d'Arda PC, Italy

Vijay Kumar Tiwari
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

Alessandro Tondelli
Council for Agricultural Research and Economics (CREA), Research Centre for Genomics and Bioinformatics, Via San Protaso 302, 29017, Fiorenzuola d'Arda, Italy

Giorgio Tumino
Plant Breeding, Wageningen University and Research, Droevendaalsesteeg 1, 6708 PB Wageningen, the Netherlands

Wilfred Vermerris
Department of Microbiology & Cell Science, UF Genetics Institute, and Florida Center for Renewable Chemicals and Fuels, University of Florida, PO Box 103610, Gainesville, Florida 32610, USA

Zhanguo Xin
USDA-ARS, Plant Stress and Germplasm Development Unit, Crop Systems Research Laboratory, 3810, 4th Street, Lubbock, TX 79424, USA

Inderjit Singh Yadav
Department of Plant Science and Landscape Architecture, University of Maryland, College Park, MD-20783, USA

Venkata Rami Reddy Yannam
Sustainable Field Crops Program, Institute for Food and Agricultural Research and Technology (IRTA), 25198, Lleida, Spain

Melinda K. Yerka
Department of Agriculture, Veterinary & Rangeland Sciences, University of Nevada, Reno, NV, USA

Editor Biography

Chittaranjan Kole is an internationally reputed scientist with an illustrious professional career spanning over 40 years and globally recognized for his original contributions in the fields of plant genomics, biotechnology, and molecular breeding, leading to the publication of more than 150 quality research articles. He has edited over 180 books for the leading publishers of the world, including Springer, Wiley-Blackwell, and Taylor and Francis Group. His scientific contributions and editing acumen have been appreciated by seven Nobel Laureates including Profs. Norman Borlaug, Arthur Kornberg, Werner Arber, Phillip Sharp, Günter Blobel, Lee Hartwell, and Roger Kornberg. He has been honored with a number of fellowships, honorary fellowships, and national and international awards, including the 'Outstanding Crop Scientist Award' conferred by the International Crop Science Society. Prof. Kole has served in all prestigious positions in academia, including as Vice-Chancellor of the BC Agricultural university and Project Coordinator of Indo-Russian Center of Biotechnology in India, and Director of Research of the Institute of Nutraceutical Research of Clemson University in the USA. He worked also in the Pennsylvania State University and Clemson University as a Visiting Professor in the USA. He was awarded with the Raja Ramanna Fellow by the Department of Energy, Government of India. He is also heading the International Climate-Resilient Crop Genomics Consortium, International Phytomedomics and Nutriomics Consortium and Genome India International as their Founder President. Prof. Kole has recently established the Prof. Chittaranjan Kole Foundation for Science and Society and working as its Founding Chairman.

Sharat Kumar Pradhan, is Assistant Director General of the Indian Council of Agricultural Research (ICAR), New Delhi. At present, he is heading the Food and Fodder Crops (FFC) Section of the council. Before this assignment, he was Scientist at ICAR- NRRI, Cuttack for 25 years and 5 years under OUAT, Bhubaneswar. He has released 60 rice varieties for 18 states of the country. Dr. Pradhan is the lead developer of 35 and co-developer of 25 rice varieties. Many of his rice varieties namely CR Dhan409 (Pradhandhan), CR Dhan307 (Maudamani), CR Dhan800, CR Dhan801, CR Dhan802, CR Dhan507, CR Dhan508, etc., are very popular in the eastern region of the country. He has published about 200 peer reviewed research articles in various books and journals. He has reported more than 80 novel genes/QTL controlling various traits in rice through linkage and association mapping. He has guided 15 Ph.D and 12 M.Sc. students for their thesis research. Dr. Pradhan is a Fellow of National Academy of Agricultural Sciences (NAAS), New Delhi; Indian Society of Plant Breeding & Genetics (ISGPB), New Delhi, and Association of Rice Research Workers (ARRW), Cuttack. He is conferred with many prestigious Awards namely Dr. LK Sikka Endowment Award of NAAS; Professor Siddique Award & Hooker Award of IARI, New Delhi; Samanta Chandra Sekhar Award from DST, Govt. of Odisha; AB Joshi Award of ISGPB, New Delhi and many others. Dr. Pradhan is the former Editor-in-Chief, Oryza, and Vice President of the Indian Society of Genetics & Plant Breeding, New Delhi.

Vijay Kumar Tiwari is an assistant professor and small grain breeder at the University of Maryland College Park. His major research interest is focused on genetics and genomics of small grain crops with emphasis on wheat, barley, and triticale. His program integrates genomic tools and germplasm development to achieve the goals of sustainable agriculture. Identification of novel genes and alleles against abiotic and biotic stresses is a key step to perform genetic improvement of crop plants.

One of his research objectives involves genomics enabling gene discovery of important genes and alleles playing a vital role against abiotic and biotic stresses in small grain crops. His research is also focused on enhancing yield and yield contributing factors in bread wheat through the discovery and integration of some key genes playing an important role in spike morphology and grain number per spikelet. His program utilizes Speed Breeding and DH based approaches to deploy useful genes to develop high-yielding resilient MD wheat cultivars. He has published more than 60 peer reviewed research publications in high impact journals such as Nature, Science, Nature Biotechnology, Nature Genetics, Theoretical and Applied Genetics, Plant Journal, and Crop Science.

1 Allele Mining-Based Breeding Approaches to Enhance Tolerance to Various Biotic and Abiotic Stresses in Rice

Abdul Fiyaz R.[*$], *Jauhar Ali*[*$], *Balram Marathi*[*$], *Christian John Robiso, Varunseelan Murugaiyan, Kasarla Chaithanya, Shivani D., Dileep Kumar G.D., and R.M. Sundaram*

[$]Contributed equally.

*Corresponding authors: j.ali@irri.org; balumarathi@gmail.com; genefiyaz@gmail.com

1.1 INTRODUCTION

Rice is one of the most important staple crops in the world, providing food for billions of people globally. However, rice production is severely threatened by various abiotic and biotic factors, including drought, submergence, fungal, bacterial, and nematode-oriented biotic diseases, and pests such as brown plant hopper (BPH) and stem borer (SB). The principal biotic stresses, such as bacterial leaf blight (BLB), sheath blight (ShB), blast, brown spot (BS), false smut (FS), brown plant hopper (BPH), yellow stem borer (YSB), gall midge (GM), have a significant impact on the production and quality of rice grains. Among the different breeding techniques and control strategies available for reducing biotic stresses, the most effective, economical, and environmentally friendly is the host plant resistance, mainly acquired via conventional breeding methods. Traditional breeding approaches have successfully developed varieties with some level of resistance to these stresses. Still, the continuous evolution of new pathogen races and the emergence of new pests pose ongoing challenges to rice breeders. The progress made through these conventional breeding approaches has been slow due to the complexity of abiotic and biotic stress resistance. In addition, it is a polygenic trait influenced by multiple genes. Therefore, there is an urgent need to develop efficient and effective breeding approaches to enhance rice's tolerance to abiotic and biotic stresses. Agriculture's commercial significance depends on factors, such as crop yields, disease management techniques, and availability of disease-resistant plant sources. Disease resistance is vital in controlling various pathosystems, including viruses, nematodes, and fungal diseases, such as ergot in cereals (*Claviceps purpurea*), *Rhizoctonia solani* in maize, powdery scab in potato, or black leg in rapeseed. The genetic makeup of a plant determines its susceptibility to diseases, with homozygous and homogenous cultivars such as wheat, oats, barley, and peas being more prone to disease infections. Since most crops are homogenous, they are susceptible to disease outbreaks in different regions and countries.

Rice is a staple crop contributing to food and nutritional security (Fiyaz et al. 2022). Depending on the severity, rice disease incidences may lower yields by 20–100%. New minor diseases such as false smut, Bakanae, early seedling blight, sheath, and stem rot have developed as important issues. Disease losses vary on growth circumstances, susceptibility, etc. (Shivappa et al. 2021). Over 70 fungi, bacteria, viruses, and nematodes have infected rice (Zhang et al. 2009). Stem borer,

DOI: 10.1201/9781003385004-1

gall midge, plant hopper, Gundhi bug, and leaf folder are important rice pests (Jena et al. 2018). By 2030, rice demand will rise 40% to fulfill the needs of roughly 5.0 billion people (Khush 2005). Only increased production and productivity can meet this demand. Conventional plant breeding approaches were previously utilized for controlling abiotic and biotic stresses. Still, the current focus has shifted towards molecular breeding strategies due to environmental conditions, variability in phenotypic traits, and the labor-intensive nature of conventional approaches. Molecular breeding strategies help fill gaps in our understanding of abiotic and biotic stresses in different crops and aid in developing integrated management programs for controlling stresses. In recent decades, molecular markers, microarrays, and genetic alterations have been used to examine the genetic basis of stress tolerance and generate agricultural cultivars with better stress tolerance. DNA marker technology has helped create quantitative trait loci (QTLs) mapping, marker-assisted selection (MAS), genomic selection, and genetic transformation to generate stress-tolerant plants. Fine mapping may help breeders transfer resistance genes from donor cultivars into new, top rice cultivars via MAS. Connecting knowledge about genes and gene function is needed to generate highly productive, sustainable agricultural types (Ashkani et al. 2015).

This book chapter extensively covers the latest breakthroughs in enhancing rice's resistance to both biotic and abiotic stresses, specifically focusing on the use of allele mining-based breeding techniques. The chapter provides an inclusive overview of the successful implementation of these approaches, highlighting their potential impact in addressing food security concerns in the future. Alongside discussing the challenges, the chapter also identifies further research and development opportunities. This resourceful chapter will benefit policymakers, breeders, and researchers who aim to develop rice varieties with improved resistance to biotic and abiotic stresses. The innovative approaches highlighted in this chapter will undoubtedly play a crucial role in meeting future food security challenges.

1.2 MOLECULAR BREEDING FOR BACTERIAL BLIGHT RESISTANCE IN RICE

Over the last several decades, rice has developed a complex relationship with pathogens and pests. BLB is one of the most significant diseases (Vikal et al. 2017), substantially reducing rice productivity. Deployment of gene-conferred host plant resistance is an attractive technique that two critical approaches may enhance: marker-assisted breeding and genetic transformation for combating emerging diseases and deployment of resistance genes in plant breeding programs. However, the debate about food safety and restrictions in certain countries hindered the adoption of genetically modified crops, clearing the path for plant breeders to widely employ the marker-assisted breeding program (Jiang et al. 2020).

1.2.1 Disease Symptoms and Pathogenesis

BLB in rice is caused by the gram-negative bacterium *Xanthomonas oryzae pv. oryzae* (Xoo), depending on the development stage and climatic circumstances, may cause yield losses of up to 50 % (Liu et al. 2014). It is a vascular disease that may manifest throughout seedling, vegetative, and reproductive development. The symptoms are characterized by leaf dryness and yellowing that begins at the leaf tips and progresses downward. The disease generally prefers conducive temperatures between 25 to 34°C and relative humidity exceeding 70%. The presence of tiny droplets of bacterial ooze (pale amber in color) on the afflicted areas helps to visualize the disease. The most devastating phase of disease in the tropics is the "kresek" or wilt phase, which results from seed infection or early systemic infection in the nursery (Kumar and Rao 2014). In 1884, farmers first recognized the disease in the Fukuoka region of Kyushu prefecture, Japan (Mizukami and Wakimoto 1969). In India, the first report of bacterial blight disease on rice was made in Maharashtra (Srinivasan et al. 1959). Before its 1963 outbreak of the disease in the Shahabad area of Bihar, in India it was considered relatively mild (Srivastava 1967). However, damage caused by this disease was considerably exacerbated by the growth of semi-dwarf

and hybrid rice types and extensive fertilizer use. It was prevalent in Asia, including India, Philippines, Nepal, Indonesia, Sri Lanka, Australia, and West Africa. In recent years, it has been reported in almost all rice-growing nations worldwide (Naqvi 2019).

1.2.2 Bacterial Blight R-Genes and Quantitative Trait Loci

According to reports, several wild species of cultivated rice, including *O. longistaminata*, *O. rufipogon*, *O. minuta*, *O. barthii*, *O. brachyantha*, *O. granulate*, *O. ridleyi*, and *O. nivara*, are resistant to BLB (Brar et al. 1997). In the last two decades, much genetic research has been undertaken on BLB resistance. So far, 47 resistance (R) genes giving resistance to distinct Xoo strains have been mapped from diverse sources on 10 of the 12 chromosomes (Rao et al. 2017, Kim et al. 2018; 2019, Neelam et al. 2020, Xing et al. 2021). Among the resistant genes, 17 are recessive (*xa5, xa8, xa13, xa15, xa19, xa20, xa24, xa25, xa26, xa28, xa31, xa32, xa33, xa34, xa41, xa42,* and *xa44*), while remaining 30 are dominant (*Xa1, Xa2, Xa3, Xa4, Xa6, Xa7, Xa9, Xa10, Xa12, Xa14, Xa16, Xa17, Xa18, Xa21, Xa23, Xa24, Xa27, Xa29, Xa30, Xa35, Xa36, Xa37, Xa38, Xa39, Xa40, Xa43, Xa45, Xa46,* and *Xa47*) (Biswas et al. 2021, Xing et al. 2021, Chen et al. 2020). Out of the 47 resistance genes, nine (*Xa1*, *Xa3/xa26, xa5, Xa10, xa13, Xa21, Xa23, xa25*, and *Xa27*) have been cloned, and twelve (*Xa2, Xa4, Xa7, Xa22, Xa30, xa31, xa33, xa34, Xa38, Xa39, Xa40,* and *Xa42*) have been physically mapped (Kim et al. 2015, Bhasin et al. 2012, Kumar et al. 2012, Song et al. 1995, Sun et al. 2003, Gu et al. 2005, Niño et al. 2005, Cheema et al. 2008, Zhang et al. 2015).

Xa23, a dominant resistant gene effective at all growth stages, was identified in the wild rice species *O. rufipogon* (Zhang et al. 1998; 2001) and was discovered to be highly resistant to ten Philippine races (P1–P10), seven Chinese pathotypes (C1–C7), and three Japanese races (TI–T3) at maximum tillering stage (Zhou et al. 2011) Jin et al. (2007) isolated the BB resistance gene *Xa*30 from the wild rice species *O. rufipogon* and transferred it to cultivated rice to generate near-isogenic lines. Tan et al. (2004) identified the *Xa29* gene in *O. officinalis* and localized it inside a 1.3 cM area on Chromosome 1 bordered by RFLP (restriction fragment length polymorphism) markers. Similarly, the *O. australiensis Xa32*(t) gene is resistant to Xoo strains. *P1, P4, P5, P6, P7, P8, P9, KXO85*, but resistant to *P2* and *P3*; mapped using two SSR markers on the long arm of chromosome 11 (Zheng et al. 2009). Guo et al. (2010) introduced *Xa35*(t), a unique source of BB resistance gene from *O. minuta* (Acc. No. 101133), into the *O. sativa* L. cultivar IR24. The discovered genes for bacterial blight resistance are listed in (Table 1.1). Zhang et al. (2021) carried out an elaborate 1D/2D GWAS strategy to investigate the genetic systems underlying the reciprocal adaptation of rice (*Oryza sativa*) and its bacterial pathogen, *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) using the whole-genome sequencing and large-scale phenotyping data of 701 rice accessions and 23 diverse *Xoo* strains. Zhang et al. (2021) discovered 47 *Xoo* virulence-related genes and 318 rice quantitative resistance genes (QR-genes) located in 41 genomic regions. Genome-wide interactions between the detected virulence-related genes and QR genes were identified. This study helped understand the relationship between rice and *Xoo*, which was characterized by strong differentiation among *Xoo* races corresponding to the subspecific differentiation of rice. Further, genome-wide interactions between many rice QR genes and *Xoo* virulence genes, in a multiple-to-multiple manner, are likely to result from direct protein–protein interactions or genetic epistasis. Zhang et al. (2021) observed a complex genetic interaction system between rice and *Xoo* and in other crop–pathogen systems that would maintain high levels of diversity at their QR-loci/virulence-loci, resulting in dynamic coevolutionary consequences during their reciprocal adaptation.

1.2.3 BLB Genes Cloned

Categorizing nine cloned genes into four classes of resistance genes, including LRR-RLKs (leucine-rich repeat receptor-like kinases), NB-LRR, a wall-associated kinase, executor R proteins, SWEET

TABLE 1.1
List of Bacterial Blight Resistance Genes Identified, Origin, Source, and Linked Markers

R Gene	Chr	Position (bp)	Donor	Source	Inheritance	Cloned	Resistance to *Xoo* Race	Linked Markers	Marker Type	Reference
Xa1	4	31,638,099–31,644,795	Kogyoku, Java 14	Japan	Dominant	Yes	Japanese race-I	Npb235	RFLP	Sakaguchi, 1967; Yoshimura et al. 1998
Xa2	4	–	RantaiEmas II, Tetep	Vietnam	Dominant	No	Japanese race-II	HZR950-5	SSR	Sakaguchi, 1967; He et al. 2006; Kurata and Yamazaki (2006)
Xa3/Xa26	11	28,399,360–28,402,773	Wase Aikoku 3	Japan	Dominant	Yes	Chinese, Philippine, and Japanese races	C481S	RFLP	Ezuka et al. 1975; Yoshimura et al. 1992; Xiang et al. (2006); Gao et al. 2013
Xa4	11	–	TKM6, IR20, IR22, IR72	India	Dominant	Yes	Philippine race-I	Npb181 and RM224	RFLP and SSR	Petpisit et al. 1977; Wang et al. 2001
xa5	5	437,010–443,270	DZ192, IR1545-339	Bangladesh	Recessive	Yes	Philippine races I, II, and III	RG556 and RM122	CAPS and SSR	Petpisit et al. 1977; Blair et al. 2003
Xa6/xa3	11	–	MalagkitSungsong	Zenith USA	Dominant	No	Philippine race-I	Y68SSRA	RFLP	Sidhu et al. 1978
Xa7	6	–	DZ78, DV85	Bangladesh	Dominant	No	Philippine races	G1091, RM205S2	RFLP, SSR	Sidhu et al. 1978; Chen et al. 2008
xa8	7	–	PI231129	USA	Recessive	No	Philippine races	RM500, RM533	SSR	Singh et al. 2002; Vikal et al. 2014
Xa9	11	–	KhaolayNhay	Laos	Dominant	No	Philippine races	C4S1S	RFLP	Singh et al. 1983; Ogawa et al. 1988
Xa10	11	22,203,734–22,204,676	Cas 209	Philippines	Dominant	Yes	Philippine and Japanese races	M491/M419	RFLP, CAPS	Yoshimura et al. 1983; Kurata and Yamazaki (2006)
Xa11	3	–	RP9-3	Philippines	Dominant	No	Japanese races IB, II, IIIA, and V	–	–	Ogawa and Yamamoto, 1986; Goto et al. 2009; Kurata and Yamazaki (2006)
Xa12	4	–	Kogyoku, Java 14	Japan	Dominant	No	Indonesian race V	–	–	Ogawa et al. 1978
xa13	8	–	BJ1, ChinsurahEoro II	India	Recessive	Yes	Philippine race-6	RG136, xal3p	STS and SSR	Yoshimura et al. 1995; Zhang et al. 1996; Kurata and Yamazaki (2006)

Xa14	4	–	TN1	China	Dominant	No	Philippine race 5	VAZ190B/ RG163	RFLP	Taura et al. 1987; Kurata and Yamazaki (2006)
xa15	–	–	M41 Mutant	Japan	Recessive	No	Japanese races	–	-	Nakai et al. 1998; Ogawa 2008
Xa16	–	–	Tetep	Vietnam	Dominant	No	Japanese races	–	-	Sanchez et al. 1999; Kurata and Yamazaki (2006)
Xa17	–	–	Asominori	Japan	Dominant	No	Japanese races	–	–	Ogawa et al. 1989; Kurata and Yamazaki (2006)
Xa18	–	–	Toyonishiki, Miyang 23, IR24	Japan	Dominant	No	Burmese races	–	–	Ogawa et al. 1986; Kurata and Yamazaki (2006)
xa19	3	–	XM5 (Mutant of IR24)	Philippines	Recessive	No	Japanese races	–	–	Taura et al. 1992; Kurata and Yamazaki (2006)
xa20	–	–	XM6 (Mutant of IR24)	Philippines	Recessive	No	Japanese races	–	–	Taura et al. 1992; Kurata and Yamazaki (2006)
Xa21	11	20,802,924–20,806,518	*O. longistaminata, IRBB 21*	Africa, Mali	Dominant	Yes	Philippine and Japanese races	pTA248	STS	Khush et al. 1990; Song et al.1995
Xa22(t)	11	–	Zhachanglong	China	Dominant	No	Chinese races	L363B/P143	RFLP	Lin et al. 1996; Kurata and Yamazaki (2006)
Xa23	11	22,203,734–22,204,676	*O. rufipogon*(CBB 23)	China	Dominant	Yes	Indonesian races	–	–	Zhang et al. 1998; Zhang et al. 2001
xa24	2	–	DV86, DV85, Aus 295	Bangladesh	Recessive	No	Philippine and Chinese races	–	–	Mir and Khush, 1990; Khush and Angeles,1999
xa25(t)	12	17,302,073–17,305,326	HX-3, Minghui 63 (Somaclonal mutant of Minghui 63)	China	Recessive	Yes	Chinese and Philippine races	–	–	Lee et al. 2003; Liu et al. 2011
xa26(t)	11	–	Minghui 63, Nep Bha Bong	China	Recessive	No	Philippine races	C4S1S/ Y6855R	RFLP	Lee et al. 2003
Xa27(t)	6	–	*O. minuta* IRGC101141, IRBB27	Philippines	Dominant	Yes	Chinese strains and Philippine races 2–6	M10S1, M1095	RFLP	Amante-Bordeos et al. 1992; Lee et al. 2003; Gu et al. 2004
xa28(t)	11	–	Lota Sail	Bangladesh	Recessive	No	Philippine race 2	–	–	Lee et al. 2003

(*continued*)