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# Genomics of Crucifer's Host-Resistance

 Springer

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## Foreword

Cruciferous plants are challenged by large number of biotic and abiotic stresses at global level. Most of these result in deterioration of crop quality and yield. In agriculture cropping system, plant protection is being practiced using different approaches such as chemical and biological control, alterations and improvement of various agronomic practices, integrated pest management (IPM), and cultivation of biotic and abiotic stress resistant cultivars. Among these approaches, use of resistance cultivars is the most economical, effective, and environmentally sound means to control different biotic stresses. Use of available resistance sources for specific diseases is being practiced extensively. The interaction between a host species and a pathogenic species is such that a host species often loses the race-specific resistance due to evolution of new races of the pathogen, and thus a new gene for resistance has to be incorporated in the host variety against this new race. So, identification of new specific genes for resistance is one of the crucial factors for the development of resistant varieties. The genes for resistance can now be transferred, combined, or pyramided using molecular tools and new techniques such as gene cloning and gene editing using CRISPER–Cas9 system which also can enhance understanding of resistance mechanism. The mapped disease resistance genetic loci and closely linked molecular markers to these loci can be used for marker-assisted selection in cruciferous resistance breeding of *Brassica* species.

The book “*Genomics of Crucifer’s Host-Resistance*” authored by Prof. (Dr.) G. S. Saharan, Prof. (Dr.) Naresh K. Mehta, and Dr. Prabhu Dayal Meena is the seventh book in series on diseases of crucifers being published by Springer, Nature. Earlier books on *Albugo*, *Alternaria*, *Erysiphe*, *Hyaloperonospora*, *Plasmodiophora*, and *Sclerotinia* dealt with specific diseases in great details. The present book has been prepared after critical analysis of the world literature on all the major diseases of crucifers with detailed treatment of different aspects for better comprehension by the readers. The book contains the information on principles of host resistance, identification of sources of resistance, inheritance and transfer of disease resistance, host resistance signaling network system to multiple stresses, molecular mechanism of host resistance, management of disease resistance, and genomics of host resistance along with various techniques for the development of resistant cultivars through latest technology. The chapter on priorities areas of research on all major diseases of crucifers will motivate the researchers, teachers, and students to take further research

work on these areas. Appropriate subheadings, photographs, figures, tables, and graphs in each chapter greatly enhanced the clarity and comprehension of the subject matter. I am sure that this book will provide much needed background and current information on host pathogen system of cruciferous crops for developing disease-resistant varieties.

My heartiest congratulations to the authors for bringing out their lifelong professional interest, and expertise in the preparation of this book. I am sure the book will be quite useful for the researchers, teachers, students, and all those who are concerned with research and development of cruciferous crops.



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## Preface

Crucifers are challenged by large number of biotic and abiotic stresses but 16 pathogens are most important and widespread causing serious losses to these groups of crops. The variable losses in these crops have received attention of scientists to initiate the studies on genomics of crucifer's host resistance, host-pathogen interactions, and expression of molecular defense mechanisms actively operating in these crops. During the last three decades, substantial progress has been made on the investigations of mechanisms of host resistance using *Brassica* host-pathosystem as a model. The book "*Genomics of Crucifer's Host-Resistance*" has been attempted to present comprehensive information after scanning of large volume of available literature on fundamental and applied knowledge for developing varieties with resistance individually as well as to multiple major pathogens of crucifers like *Albugo*, *Alternaria*, *Erysiphe*, *Hyaloperonospora*, *Leptosphaeria*, *Plasmiodiophora*, *Sclerotinia*, *Turnip mosaic virus*, *Verticillium*, and *Xanthomonas* of crucifers through the use of conventional as well as latest biotechnological approaches including transgenics with agronomically superior background. It is well known that wild plant species represent a gene pool that can potentially provide a rich source of durable, broad-spectrum disease resistance for use in breeding program. Species that are interfertile with a particular crop have been used for transferring monogenic resistance which is often genotype or race specific. Disease resistance can potentially be improved by altering the expression of defense regulation, through broad-spectrum resistance by overexpression of *NPR1*, regulator of acquired disease resistance. In plant disease resistance (R) genes, the nucleotide-binding site (NBS) plays an important role in offering resistance to pathogens. The complete genome sequences provide an important opportunity for researchers to identify and characterize NBS-encoding R-genes based on a comparative genomics approach. The evolutionary analysis of CNL-type NBS-encoding orthologous gene pairs suggested that orthologous genes in crucifers especially in *B. rapa* have undergone stronger negative selection than those in other *Brassica* species. Tandem duplication and whole-genome triplication (WGT) analyses revealed that after WGT of the *Brassica* ancestor, NBS-encoding homologous gene pairs on triplicated regions in *Brassica* ancestor which were deleted or lost quickly, but NBS-encoding genes in *Brassica* species experienced species-specific gene amplification by tandem duplication after divergence of *B. rapa* and *B. oleracea*. Molecular

genetics investigations of disease resistance research of utilizing natural genetic variation (so-called *R*-genes) have revealed race-specific resistance to a wide assortment of pathogens now widely known by NB-LRR (nucleotide-binding site and leucine-rich repeat domains). The use of DNA sequence from NB-LRR genes and other known *R*-gene are being used to develop more effective genetic markers for breeding of resistant varieties. The advances in the plant sciences indicated that signaling mechanisms governing genotype-specific resistance govern species-level resistance through *EDSI* (enhanced disease susceptibility), restrictive host specialization, and molecular divergence. So, *EDSI* is an essential regulator of species-level resistance to some *Brassica* pathogens. The highly conserved protein, *SGTI* has also recently been reported as a key regulator for species-level resistance.

We have compiled the information generated so far on all the major and minor diseases of crucifers in the form of published reports, research articles, popular scientific articles, books, bulletins, reviews, etc. in this book, which have been arranged in ten chapters, with appropriate headings and subheadings with the sections of references to consult original publications. It is a seventh book on the diseases of cruciferous crops series after *Sclerotinia*, *Albugo*, *Alternaria*, *Hyaloperonospora*, *Erysiphe*, and *Plasmodiophora* published by Springer Nature. The chapter-wise sections include the information, viz. principles of host resistance, identification of *R*-genes sources, inheritance of disease resistance, molecular mechanisms of disease resistance, host resistance signaling network system to multiple stresses, transfer of disease resistance, and management of disease resistance. A chapter on standardized, reproducible techniques has been included for the researchers of cruciferous crops for developing resistant cultivars. The last section deals with the gaps in understanding, knowledge of genomics, and offers suggestions for future research priorities in order to initiate the advance research programs on disease resistance. The subject matter has been vividly illustrated with photographs, graphs, figures, histogram, tables, and colored plates, which makes it stimulating, effective, and easy to comprehend by the readers. The headings and subheadings of each chapter have been arranged in numbered series to make the subject matter contiguous.

We believe that this book will be immensely useful to the researchers especially *Brassica* breeders, molecular biologists, pathologists, teachers, extension specialists, students, industrialists, farmers, and all others who are interested to grow healthy and profitable cruciferous crops all over the world. Any shortcomings, lacunae, and flaws in the book are responsibility of ours. Any suggestions by the readers are always a source of inspiration for the authors and suggestions for its improvement are most welcome.

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Authors

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## Abbreviations

AAFC	Agriculture and Agri-Food Canada
AAP	Acquisition access period
AB	Alternaria blight
ABA	Abscisic acid
ADI	Average disease on inflorescence
ADK2	Adenosine kinase 2
ADL	Average disease on leaf
AFLP	Amplified fragment length polymorphism
AICORPO	All India Coordinated Research Project on oilseeds
AICRP-RM	All India Coordinated Research Project on Rapeseed-Mustard
AMP	Antimicrobial peptides
ANOVA	Analysis of variance
APX	Ascorbate peroxidase
AUDPC	Area under disease progress curves
AUWPC	Area under wilt progress curve
avr	Avirulence
AVRDC	Asian Vegetable Research and Development Centre
BABA	$\beta$ -amino butyric acid
BAP	Benzylaminopurine
BC	Backcross
BCN	Beet cyst nematode
bHLH	Basic helix-loop-helix
BLAST	Basic Local Alignment Search Tool
BLUPs	Best linear unbiased predictions
<i>BnMPK4</i>	<i>B. napus</i> mitogen-activated protein kinase
BSA	Bulked segregant analysis
BSMV	Barley stripe mosaic virus
BW	Burpee White
CAC	Clathrin adaptor complex
CaM	Calmodulin
CAMTA	Calmodulin-binding transcription activator
CaMV	Cauliflower mosaic virus

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CAPs	Cationic antimicrobial peptides
CAPS	Cleaved amplified polymorphic sequence
CAT	Catalase
CBF	C-repeat-binding factor
CBLs	Calcineurin-B-like proteins
CC	Coiled coil
CCaMK	Calcium and calmodulin-dependent protein kinase
CCC	Chlormequat chloride
CD	Critical difference
CDPKs	Calcium-dependent protein kinases
CF	Culture filtrate
cM	centiMorgans
CMLs	Calmodulin-like protein
CNL	CC-NBS-LRR
CNV	Copy number variation
COIP	Co-immune precipitation
CP	Coat protein
CPKs	Calcium-dependent protein kinases
CR	Clubroot
CR	Clubroot resistance
CrGC	Crucifer Genetics Cooperation
CRISPR	Clustered regulatory interspaced short palindromic repeats
CRR	Cysteine-rich repeat
CRW	China Rose Winter
CTAB	Cetyltrimethyl ammonium bromide
DAI	Days after inoculation
DAS	Days after sowing
DEGs	Differentially expressed genes
DH	Doubled haploid
DI	Disease indices
DM	Downey mildew
DNA	Deoxyribonucleic acid
DOS	Date of sowing
DR	Disease reaction
DRMR	Directorate of Rapeseed-Mustard Research
DSI	Disease severity index
dsRNA	Double-stranded ribonucleic acids
DSTI	Disease stress tolerance index
ECD	European clubroot differential
EDS1	Enhanced disease susceptibility 1
EDTA	Ethylene diamine tetra-acetic acid
EF-Tu	Elongation factor Tu
eIF	Eukaryotic initiation factor
ELISAs	Enzyme-linked immunosorbent assays
ELWL	Excised leaf water loss

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EMS	Ethyl methane-sulfonate
ENU	Ethyl nitrosourea
EPPO	European and Mediterranean Plant Protection Organization
ERK	Extracellular signal-regulated kinase
ESTs	Expressed sequence tags
ET	Ethylene
ETD	Ethylene thiuram disulfide
ETI	Effector-triggered immunity
FBA	Fructose biphosphatealdolase
FDR	False discovery rate
FIL	Final intensity of rust on leaf
FIP	Final intensity of rust on plant
FPKM	Fragments Per Kilobase of transcript per Million mapped
G × E	Genotype by environment
GBLUP	Genomic Best Linear Unbiased Prediction
GBS	Genotyping by sequencing
GCV	Genotypic coefficient of variance
GD	Geographical distribution
GG	Genetic gain
GISH	Genomic in situ hybridization
GLM	General linear model
GLM	Generalized linear models
GM	Genetically modified
GMP	Geometric mean productivity
GR	Genomics research
GRIN	Germplasm Resources Information Network
GSS	Genomic survey sequences
GWAS	Genome-wide association analysis
GWAS	Genome-Wide Association Study
HEs	Homeologous exchanges
HGP	Human Genome Project
HIB	High-efficiency integrated breeding
HIGS	Host-induced gene silencing
HMM	Hidden Markov Model
HNRT	Homeologous non-reciprocal transposition
<i>Hpa</i>	<i>Hyaloperonospora arabidopsidis</i>
HR	Horizontal resistance
HR	Host range
HR	Hypersensitive response
HS	Highly susceptible
HSPs	Heat shock proteins
HTGs	High-throughput genome sequences
IAA	Indole-3-acetic acid
IAP	Inoculation access period
IBA	Indole-butyric acid

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IBCN	International Blackleg of Crucifers Network
IBD	Isolation by distance
IC	Isochorismate
ICAR	Indian Council of Agricultural Research
ICIM	Inclusive composite interval mapping
iGS	Indole-glucosinolates
ILs	Introgression lines
INA	Isonicotinic acid
IP	Interaction phenotype
IP	Intron polymorphic
IPM	Integrated pest management
ISSRs	Inter-simple sequence repeats
ITS	Internal transcribed spacer regions
JA	Jasmonic acid
LB	Luria–Bertani
LC	Liquid chromatography
LCBs	Long chain bases
LD	Linkage disequilibrium
LDIA	Leaf disc inoculation assay
LGs	Linkage groups
<i>Lm</i>	<i>Leptosphaeria maculans</i>
LPs	Lipopeptides
LRR	Leucine-rich repeat
LRR-RLKs	Leucine-rich repeat receptor-like kinase
LRR-RLPs	Leucine-rich repeat receptors-like protein
LRRs	Leucine-rich repeats
LSD	Least significant difference
LZ	Leucine zipper
MAB	Marker-assisted backcross breeding
MAMPs	Microbe-associated molecular patterns
MAP	Mitogen-activated protein
MAPK	Mitogen-activated protein kinase
MAPKKK	MAP kinase kinase kinase
MAS	Marker-assisted selection
MDR	Multiple disease resistance
MET	Multi-environment trials
miRNAs	MicroRNAs
MKK	MAP kinase kinase
ML	Maximum likelihood
MP	Mean productivity
MPK	MAP kinase
MR	Moderately resistant
MS	Mass Spectrometry
MTAs	Marker trait associations
MTI	MAMPs-triggered immunity

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MYA	Million years ago
NAA	Naphthalene acetic acid
NaOCl	Sodium hypochlorite
NBPGR	National Bureau of Plant Genetic Resources
NBS	Nucleotide-binding site
NBS-LRR	Nucleotide-binding site leucine-rich repeat
NCBI	National Centre for Biotechnology Information
NGS	Next-generation sequencing
NHR	Non-host resistance
NIa-Pro	Nuclear inclusion a-protease domain
NIRS	Near-infrared reflectance spectroscopy
NLRs	Nucleotide-binding site leucine-rich repeats
NMR	Nuclear magnetic resonance
NOA	Nicotinic acid
NPR1	Nonexpressor of PR genes 1
NWCVT	National winter canola variety trials
ONT	Oxford Nanopore Technologies
OXO	Oxalate oxidase
PAD4	Phytoalexin-deficient 4
PAL	Phenylalanine ammonia lyase
PAMP	Pathogen-associated molecular pattern
PAMP/MAPM	Pathogen/microbe associated molecular patterns
PAMPs	Pathogen-associated molecular patterns
PAV	Presence/absence variation
PBS	Phosphate buffer saline
PCA	Principal component analysis
PCD	Programmed cell death
PCR	Polymerase chain reaction
PCV	Phenotypic coefficient of variance
PDA	Potato dextrose agar
PDI	Per cent disease index
PDI	Per cent disease intensity
PEG	Glycerine polyethylene glycol
PGA	Polygalacturonase
PIC	Polymorphic information content
PM	Powdery mildew
POX	Peroxidase
PPO	Polyphenol oxidase
PPT	Phosphinothricin
PPV	Percentage of polymorphic variants
PR	Pathogenesis related
ProCa	Prohexadione-calcium
PRRs	Pattern recognition receptors
PSbMV	Pea seed-borne mosaic virus
PTI	PAMPs-triggered immunity

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PTI	Pattern-triggered immunity
Pto	A Ser/Thr kinase protein
pv.	Pathovar
PVE	Phenotypic variation explained
QDR	Quantitative disease resistance
qPCR	Quantitative polymerase chain reaction
qRT-PCR	Quantitative reverse-transcription polymerase chain reaction
qRT-PCR	Real-time quantitative-PCR
QTL	Quantitative trait loci
R	Resistance
RAC	Recognition of <i>A. candida</i>
RAPD	Random Amplification of Polymorphic DNA
RBS	Round Black Spanish
RFLP	Restriction fragment length polymorphism
RGAs	Resistance gene analogs
RGL	Resistant gene like
RH	Relative humidity
RIP	Ribosome inactivating protein
RISC	RNA-induced silencing complex
RLCK	Receptor-like cytosolic kinase
RLKs	Receptor-like kinases
RLKs	Receptor-like protein kinases
RLPs	Receptor-like proteins
RNA	Ribonucleic acid
RNAi	RNA interference
ROS	Reactive oxygen species
RPP	Recognize <i>Peronospora parasitica</i>
RR-BLUP	Ridge Regression Best Linear Unbiased Prediction
RWC	Relative water content
SA	Salicylic acid
SAA	Systemic acquired acclimation
SAG	Salicylic acid glycoside
SAG101	Senescence-associated gene 101
SAR	Systemic acquired resistance
SCAR	Sequence characterized amplified region
SD	Standard deviation
SDW	Sterilized distilled water
Seq	Sequencing
SIGS	Spray-induced gene silencing
SMA	Single marker analysis
SNaP	Single Nucleotide Absence Polymorphism
SNP	Single nucleotide polymorphism
SOD	Superoxide dismutase
SRRs	Signal recognition receptors
SSH	Suppression Subtractive Hybridization