Chittaranjan Kole *Editor*

Genomic Designing for Abiotic Stress Resistant Cereal Crops

Springer

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Dedicated to

Dr. Gurdev S. Khush, FRS

Member, US National Academy of Sciences; Adjunct Professor Emeritus, University of California, Davis; and Former Head, Plant Breeding, Genetics and Biotechnology, International Rice Research Institute

With regards & gratitude for his generous appreciations of my scientific contributions and service to the global academic community, and his constant support and encouragement during my professional journey!

Preface

Crop production is drastically affected due to external or environmental stresses. The biotic stresses cause significant yield losses in the range of 31–42% together with 6–20% loss during the post-harvest stage. The abiotic stresses also aggravate the situation with crop damage in the range of 6–20%. Understanding the mechanisms of interaction of plants with the biotic stresses caused by insects, bacteria, fungi, viruses, oomycetes, etc., and abiotic stresses due to heat, cold, drought, flooding, submergence, salinity, acidity, etc., is critical to develop resilient crop varieties. Global warming and climate change are also causing emergence of new diseases and insects together with newer biotypes and physiological races of the causal agents on the one hand and aggravating the abiotic stress problems with additional extremes and unpredictability. Development of crop varieties resistant and/or adaptive to these stresses is highly important. The future mission of crop improvement should, therefore, lay emphasis on the development of crop varieties with optimum genome plasticity by possessing resistance or tolerance to multiple biotic and abiotic stresses simultaneously. A moderate estimation of world population by 2050 is about 9.3 billion that would necessitate an increase of crop production by about 70%. On the other hand, the additional losses due to climate change and global warming somewhere in the range of 10–15% should be minimized. Therefore, increase in the crop yield as well as minimization of its loss should be practiced simultaneously focusing on both ‘adaptation’ and ‘mitigation.’

Traditional plant breeding practiced in the last century contributed a lot to the science of crop genetic improvement. Classical plant breeding methods including selection, hybridization, polyploidy and mutation effectively catered to the basic F^5 needs—food, feed, fiber, fuel and furniture. The advent of molecular breeding and genetic engineering in the latter part of twentieth century complimented classical breeding that addressed the increasing needs of the world. The twenty-first century came with a gift to the geneticists and plant breeders with the strategy of genome sequencing in Arabidopsis and rice followed by the tools of genomics-aided breeding. More recently, another revolutionary technique, genome or gene editing, became available for genetic correction of crop genomes! The travel from ‘plant breeding’ based on visual or perceivable selection to ‘molecular breeding’ assisted by linked markers to 'transgenic breeding' using genetic transformation with alien genes to 'genomics-aided breeding' facilitated by known gene sequences has now arrived at the age of 'genetic rectification' employing genome or gene editing.

Knowledge on the advanced genetic and genomic crop improvement strategies including molecular breeding, transgenics, genomic-assisted breeding and the recently emerged genome editing for developing resistant, tolerant and/or adaptive crop varieties is useful to students, faculties and scientists in the public and private universities and organizations. Whole-genome sequencing of most of the major crop plants followed by genotyping-by-sequencing has facilitated identification of exactly the genes conferring resistance, tolerance or adaptability leading to gene discovery, allele mining and shuttle breeding which in turn opened up the scope for 'designing' or 'tailoring' crop genomes with resistance/tolerance to biotic and abiotic stresses.

To my mind, the mission of agriculture in this century is FHNEE security meaning food, health, nutrition, energy and environment security. Hence, genome designing of crops should focus on breeding of varieties with higher yields and improved qualities of the five basic F5 utilities; nutritional and neutraceutical compounds; and other industrially and aesthetically important products and possibility of multiple utilities. For this purpose of 'precise' breeding, employment of the genetic and genomic techniques individually or in combination as and when required will play a crucial role.

The chapters of the 12 volumes of this twin book series entitled *Genomic Designing for Biotic Stress Resistant Crops* and *Genomic Designing for Abiotic Stress Resistant Crops* will deliberate on different types of biotic and abiotic stresses and their effects on and interaction with crop plants; will enumerate the available genetic diversity with regard to biotic or abiotic stress resistance among cultivars; will illuminate on the potential gene pools for utilization in interspecific gene transfer; will brief on the classical genetics of stress resistance and traditional breeding for transferring them to their cultivated counterparts; will discuss on molecular mapping of genes and QTLs underlying stress resistance and their marker-assisted introgression into elite crop varieties; will enunciate different emerging genomics-aided techniques including genomic selection, allele mining, gene discovery and gene pyramiding for developing smart crop varieties with genetic potential to produce F^5 of higher quantity and quality; and also will elaborate the case studies on genome editing focusing on specific genes. Most of these chapters will discuss on the success stories of genetic engineering in the relevant crops specifically for generating crops with resistance and/or adaptability to diseases, insects and abiotic stresses.

There are obviously a number of reviews and books on the individual aspects of plant molecular breeding, genetic engineering and genomics-aided breeding on crops or on agro-economic traits which includes the 100-plus books edited by me. However, there is no comprehensive reviews or books available that has coverage on crop commodity groups including cereals and millets, oilseeds, pulses, fruits and nuts, vegetables and technical or industrial crops, and modern strategies in single volumes with precise focuses on biotic and abiotic stresses. The present volumes will fill this gap with deliberations on about 120 important crops or their groups.

This volume on "*Genomic Designing for Abiotic Stress Resistant Cereal Crops*" includes eight chapters on Rice, Wheat, Maize, Barley, Sorghum, Pearl Millet, Foxtail Millet and Finger Millet contributed by 61 scientists from six countries including Bangladesh, Egypt, India, Indonesia, Italy and Mexico. I remain immensely thankful for their highly useful contributions.

I am indebted to my wife Phullara who as always has assisted me directly in editing these books and indirectly through maintaining an academic ambience to pursue my efforts for science and society pleasantly and peacefully.

New Delhi, India Chittaranjan Kole

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Abbreviations

AAPK	Abscisic acid-activated protein kinase
ABA	Abscicic acid
ABF	ABA-binding factor
ABF3	ABF transcription factor
ABRE	ABA-responsive element
ADC	Arginine decarboxylase
AFLP	Amplified fragment length polymorphism
ALMT1	Al-activated malate transporter
ALS1	Aluminum sensitive 1
ALS3	Aluminum sensitive 3
Alt1	Al tolerance gene 1
AM	Association mapping
AMF	Arbuscular mycorrhizal fungi
AP2	*APETALA2/Apetala2* (gene)
APX	Ascorbate peroxidase
AREB	ABA-responsive cis-element binding protein
ART1	Al resistance transcription factor 1
ART2	Al resistance transcription factor 2
ASI	Anther silking interval
ASR1	Abscisic acid, stress and ripening 1
ASR5	Abscisic acid, stress and ripening 5
AtEPFL9	*Arabidopsis thaliana* epidermal patterning factor like-9
AtHAT1	*Arabidopsis thaliana* histone acetyltransferase 1
BAC	Bacterial artificial chromosome
bHLH	Basic helix–loop–helix
bHLHU8	bHLH transcription factor
BV	Breeding value
BWMRI	Bangladesh Wheat and Maize Research Institute

bZIP	Basic leucine zipper
CaM	Calmodulin
CaMK	CaM-dependent protein kinase
CaO-NP	Calcium oxide nanoparticle
CAPS	Cleaved amplified polymorphic sequence
Cas	CRISPR-associated protein
Cas9	CRISPR-associated protein 9
CAT	Catalase
CAX1	Ca2+/H+ antiporter
CBF	C-repeat binding factor
CBF4	AP2/ERF transcription factor CB4
CBL	Calcineurin B-like protein
CCaMK	Ca2+/CaM-dependent protein kinase
CDPK	Ca2+ dependent and CaM-independent protein kinase
CDPK1	Calcium-dependent protein kinase 1
CDPK12	Calcium-dependent protein kinase 12
CDPK7	Calcium-dependent protein kinase 7
CEC	Cation-exchange capacity
CG	Candidate gene
CGBS	Conventional GBS
CIM	Composite interval mapping
CIMMYT	International Maize and Wheat Improvement Center
CIPK	CBL interacting protein kinase
CNP	Chitosan nanoparticle
COR	Cold regulated
CP-ANN	Counter-propagation artificial neural network
cpGRs	Chloroplast glutathione reductases
CPK4	Calcium-dependent protein kinase 4
CRISPR	Clustered regularly interspaced short palindromic repeat
CRISPRa	CRISPR-activated
CRK	CDPK-related protein kinase
crRNA	CRISPR RNA
CT	Canopy temperature
CWR	Crop wild relative
DA	Drought avoidance
DArT	Diversity arrays technology
ddRAD-seq	Double digest restriction-site-associated DNA sequencing
DE	Differentially expressed
DEG	Differentially expressed gene
DERF1	AP2/ERF transcription factor 1
DGE	Differential gene expression
DHN	Dehydrin
DMA	2’-deoxymugineic acid

Dof	DNA binding with one finger only
DREB	Dehydration-responsive element binding
DREB1	AP2/ERF transcription factor DRE1
DREB2	AP2/ERF transcription factor DRE2
DRIP1	DREB2A-interacting protein1
DSB	Double-stranded break
DT	Drought tolerance
DTMA	Drought Tolerant Maize for Africa
DUS	Distinctness, uniformity and stability
EcGBF3	G-box binding factor 3
EcHNRT2	*E. coracana* high-affinity nitrate transporter 2
EcLNRT1	*E. coracana* low-affinity nitrate transporter 1
ELIP	Early light-inducible protein
ELWR	Excised leaf water retention
EMS	Ethyl methanesulfonate
ENM	Engineered nanomaterial
EPF	Epidermal patterning factor
epiHDMA	3-Epihydroxy-2'-deoxymugineic acid
epiHMA	3-3-Epihidroximugineic acid
epiRIL	Epigenetic recombinant inbred line
ERA	Enhanced response to ABA
ERE	Ethylene-responsive element
ERF	Ethylene response factor
ERF10a	AP2/ERF transcription factor 10a
ERF4a	AP2/ERF transcription factor 4a
EST	Expressed sequence tag
EW	Epicuticular wax
F_2	Second filial generation
FAO	Food and Agriculture Organization
FBP	Fructose-1,6-bisphosphate
FCR	Ferric-chelate reductase
Fd-GOGAT	Ferredoxin-dependent-glutamine oxoglutarate aminotransferase
Fm	Maximal chlorophyll fluorescence
FPS	Farnesyl pyrophosphate synthase
FR	Frost resistance
FRDL4	Ferric reductase defective3-like 4
FRO	Ferric chelate reductase
Fv	Variable chlorophyll fluorescence
G x E	Genotype x environment
GAB	Genomics-assisted breeding
GB	Glycinebetaine
GBLUP	Genomic best linear unbiased prediction
GBS	Genotyping-by-sequencing
GCA	General combining ability
GCP	Generation Challenge Program

GE	Genome editing
GEBV	Genomic estimated breeding value
GERLP	Gene encoding ribosomal L32-like protein
GO	Gene ontology
GPX	Guaiacol peroxidase
GR	Glutathione reductase
gRNA	Guide RNA
GS	Genomic selection/glutamine synthetase
GSH	Reduced glutathione reductase
GSNOR	S-nitrosoglutathione-reductase
GWAS	Genome-wide association study/studies
H^2	Heritability
HARDY	AP2/ERF transcription factor DY
HDR	Homology directed repair
HeDWIC	Heat and Drought Wheat Improvement Consortium
HKT	High-affinity K+ transporter
HRF1	Harpin protein
HSF	Heat shock factor
HSP	Heat shock protein
HTMA	Heat Tolerant Maize for Asia
HTP	High-throughput phenotyping
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IFPRI	International Food Policy Research Institute
IITA	International Institute of Tropical Agriculture
ILP	Intron length polymorphism
ILs	Introgression lines
INRA	National Institute for Agricultural Research
IPCC	Intergovernmental Panel on Climate Change
IRAP	Inter-retrotransposon amplified polymorphism
IRRI	International Rice Research Institute
IRT1	Iron-regulated transporter 1
ISBP	Insertion site-based polymorphism
ISSR	Inter-simple sequence repeat
IWYP	International Wheat Yield Partnership
JA	Jasmonic acid
JERF1	AP2/ERF transcription factor J1
JERF3	AP2/ERF transcription factor J3
JW	Juice weight
LD	Linkage disequilibrium
LMM	Linear mixed effects model
lncRNA	Long noncoding RNA
LOD	Logarithm of the odds
LRL	Lateral root length
MABB/MABCB	Marker-assisted backcross breeding

MABC	Marker-assisted backcrossing
MAGIC	Multi-parent advanced generation intercross populations
MARS	Marker-assisted recurrent selection
MAS	Marker-assisted selection
MDA	Malondialdehyde
MgO-NP	Magnesium oxide nanoparticle
miRNA	MicroRNA
ML	Machine learning
MQTL	Meta QTL
MT	Metallothionein
MTA	Marker–trait association
MT-GS	Multi-trait genomic selection
MYB2	MYB transcription factor 2
NA	Nicotinamide
NAC5	NAC transcription factor 5
NAC6	NAC transcription factor 6
NAC9	NAC transcription factor 9
NAC10	NAC transcription factor 10
NADH-NR	Nicotinamide adenine dinucleotide hydride-nitrate reductase
NAM	Nested association mapping
NBPGR	National Bureau of Plant Genetic Resources
NCED	9-cis-epoxycarotenoid dioxygenase
NCED2	9-cis-epoxycarotenoid dioxygenase 2
NDVI	Normalized difference vegetation index
NGS	Next-generation sequencing
NHEJ	Non-homologous end joining
NILs	Near-isogenic lines
NLR	Number of lateral root
Nramp	Natural resistance-associated macrophage protein
Nrat1	Nramp Al transporter 1
OECD	Organisation for Economic Co-operation and Development
OPVs	Open pollinated varieties
OsABH	Alpha/beta hydrolase family protein
OsALS1	*O. sativa*-ABC Al-sensitive 1
OsFer	Rice ferritin gene
OsIRO3	Iron transporter gene
OsMPPN	Mitotic phosphoprotein N' end family protein
OsSUI1	Translation initiation factor SUI1 domain containing protein
P5CS	Pyrroline-5-carboxylate synthase
P5CS1	Pyrroline-5-carboxylate synthase 1
PAM	Protospacer adjacent motif
PBF	Prolamin binding factor
PEG	Polyethylene glycol
PEP	Phosphoenolpyruvate
PEPRK	Phosphoenolpyruvate carboxylase kinase-related kinase

PH	Plant height
PHT1	Phosphate transporter 1
Pi	Inorganic phosphate
PKS	Phytochrome kinase substrate-like protein
PMiGAP	Pearl millet inbred germplasm association panel
PNHI	Panicle harvest index
POX	Peroxide dismutase
PP2A	Protein phosphatase 2A
PP2C	Protein phosphatase 2C
PPO	Protoporphyrinogen oxidase
PRL	Primary root length
PRO	Peroxidase
PS	Phytosiderophore
PSII	Photosystem II
PVE	Phenotypic variation explained
QTL	Quantitative trait locus
QTLs	Quantitative trait loci
RAPD	Random amplification of polymorphic DNA
RBIP	Retrotransposon-based insertion polymorphism
RCAR	Regulatory component of ABA response
RFLP	Restriction fragment length polymorphism
RILs	Recombinant inbred lines
RJJM	Repeat junction–junction marker
RJM	Repeat junction marker
RLI	Root length inhibition
RMAP	Retrotransposon microsatellite amplified polymorphism
RNAi	RNA interference
RNAseq	RNA-sequencing
RNP	Ribonucleoprotein
ROS	Reactive oxygen species
RRG	Root re-growth
RRL	Relative root length
RUBISCO	Ribulose-1,5-bisphosphate carboxylase–oxygenase
RWC	Relative water content
SAP	Sorghum association panel
SCA	Specific combining ability
SCP	Sorghum conversion program
SD	Stem diameter
SFW	Stem fresh weight
sgRNA	Single-guide RNA
SI	Salt tolerance index
SIPK	SOS3 interacting protein kinase
SKN	Supervised Kohonen network
SNP	Single-nucleotide polymorphism
SnRK	Sucrose non-fermenting-1-related kinase

SnRK2	Sucrose non-fermenting-1-related protein kinase 2
SOD	Superoxide dismutase
SOS	Salt overly sensitive
SPAR	Single primer amplification reaction
SQR	Shan qui red
SRL	Seminal root length
SRO1c	Reactive oxygen species scavenging
SSA	Sub-Saharan Africa
SSD	Single seed descent
SSH	Stress-responsive suppression subtractive hybridization
SSN	Site-specific nuclease
SSR	Simple sequence repeat
STAR1	Sensitive to Al rhizotoxicity1
STAR2	Sensitive to Al rhizotoxicity2
STI	Salinity tolerance index
STS	Sequence tagged site
TaDREB2	Dehydration-responsive element binding protein 2
TaERF3	Ethylene-responsive factor 3
TAF6	TATA-box binding protein associated factor 6
TALEN	Transcription activator-like effector nuclease
TB	Total biomass
TE	Transposable element
TF	Transcription factor
TGBS	Tunable GBS
TILLING	Targeted induced local lesions in genome
TP	Training population
TPC1	Two pore channel1
TR	Transcriptional regulator
TRL	Total root length
TSRF1	Transcription factor 1a
USDA	United States Department of Agriculture
UTLIEF	Ultrathin-layer isoelectric focusing
VP	Validation population
V-PPase	Vacuolar H+-inorganic pyrophosphatase
VRN	Vernalization
WEMA	Water efficient maize for Africa
WGRS	Whole-genome resequencing
WGS	Whole-genome sequence/sequencing
WRKY22	WRKY family transcription factor 22
WRKY30	WRKY family transcription factor 30
WSC	Water-soluble carbohydrate
WSI	Water stress-induced
WUE	Water use efficiency
XY-F	XY-fused networks
ZFN	Zinc-finger nuclease

ZFP10	Zinc-finger transcription factor 10
ZFP182	Zinc-finger transcription factor 182
ZFP245	Zinc-finger transcription factor 245
ZFP252	Zinc-finger transcription factor 252
ZnO-NP	Zinc oxide nanoparticle

Chapter 1
Genomic Improvement of Rice for Drought, Aluminum, and Iron Toxicity Stress Tolerance

Miftahudin, Miftahul Huda Fendiyanto, Rizky Dwi Satrio, Turhadi, and Tatik Chikmawati

Abstract The opportunity of plants to escape from unwanted environments is almost nonexistent due to their sessile characteristic. Drought, aluminum (Al), and iron (Fe) toxicity under acid soil conditions are the major constraints as abiotic stresses in rice cultivation, particularly in tropical areas. These abiotic stress tolerance mechanisms are contributed by morphological, physiological, biochemical, and anatomical alterations that affect yield. The level of tolerance to these abiotic stresses is inherited quantitatively and controlled by several genes as quantitative trait loci. The objectives of this review were to highlight the current progress in investigating genes responsible for the drought, Al, and Fe toxicity, and their utilization for genomic improvement in rice. The mechanisms at the levels of morphology, physiology, biochemistry, anatomy, and particularly at the molecular level were discussed in the review. Overall, this review presents a systemic brief of drought, Al, and Fe tolerance mechanisms, recent progress in exploring genes responsible for these traits to the latest innovation in the genomic improvement of high-yielding multi-tolerant rice variety. This review could assist as guidelines for researchers and rice breeders.

Keywords Aluminum toxicity · Drought stress · Genomic · Iron toxicity · Rice

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1.1 Introduction

Rice is the main staple food for about half of the world's population. After the success of the Green Revolution, global per capita consumption of rice grew from 50 to 65 kg per year. Particularly in Asia, per capita rice consumption raised from 85 to almost 103 kg in the 1960s to 1990s. Rice consumption globally grew from 150 to 350 million metric tons (MMT) during this time. This pattern is expected to have a balance and limit rice demand to 501 MMT compared to 502 MMT supply in 2021–2022 (Wailes and Chavez 2012).

Increasing consumption and demand for rice must be accompanied by increasing rice production and productivity. While rice productivity is still increasing, the growth rate of rice production has decreased. The rice growth production was 2.5% year-on-year between 1962 and 1979, then decreased to 1.4% between 1980 and 2011 (Adjao and Staatz 2015). The Food and Agriculture Organization (FAO) stated that cereal production in April–June 2015 was contributed by rice, wheat, and coarse grains of 500, 723, and 1,300 MMT, respectively. Globally, between 1961 and 2007, the share of rice particularly in total cereal production did not change substantially, beginning from 24.6% and eventually exceeding 28.1% (Timmer 2010), so about a quarter of the world's cereal supply was rice.

The rice-harvested area is likely to be 160 million hectares in 2015–2016, and it will not change much by 2021–2022. About 80% of the total global rice area is located in several Asian countries, i.e., China, Indonesia, India, Bangladesh, Philippines, Vietnam, Thailand, and Myanmar. Asia as a whole has 90% of the rice region of the world. In comparison, Africa has only 5% (IRRI 2006), along with about 5% in Latin America (Pulver et al. 2010). In Africa, the growth rate in the rice area was 3.1% per year during 1980–2011, compared to only 0.4% per year in Asia (Adjao and Staatz 2015). Asia's share of world rice production in 2010–2021 may drop slightly from 89.9 to 89.3% (Wailes and Chavez 2012).

Conversion of land use for housing and industry, along with the limited availability of arable land, is an obstacle in increasing the growth of rice production in Asia, particularly in Indonesia. Rice extensification on marginal land may be a solution, but the climatic and edaphic conditions limit the growth and productivity of rice. Drought, aluminum, and iron toxicity in acid soils are the major constraints in rice cultivation on suboptimum-marginal land.

Rice is classified as one of the most drought-susceptible plants, due to its narrow root architecture, thin cuticle, and dynamic stomatal closing. Almost 23 million hectares of rain-fed rice are reportedly faced with drought stress (Serraj et al. 2011). Globally, the rise in drought severity combined with the lack of drought-resistant high-yielding varieties suitable for water-limitation conditions are the most limiting factors responsible for rice production. Consequently, rice cultivation is seasonal. The decline in water availability due to the lack of groundwater supplies is impacting rice production. Extreme environmental fluctuations caused by global climate change will affect most agricultural lands (Myers et al. 2017) including land for rice cultivation.

For plants, due to their sessile characteristic, the opportunity to escape the drought crisis is almost non-existent. At all stages, drought stress can be deleterious to plant growth and development. The effects of a water deficit during the reproductive stage causes male sterility and embryo abortion, resulting in low yield (Ozga et al. 2016). Understanding how rice responds to water-limiting conditions is essential for the genetic improvement of drought-stress tolerant and high-yielding rice cultivars.

Acid soils are predominantly distributed throughout the world and are a problem especially in agriculture. Acid soils are mainly distributed in two belts, i.e., in North America, South Asia, and Russia with temperate climate to dry types, and rainy tropical routes covering Southeast Asia, Australia, South America, and South Africa (Von Uexkuell and Mutert 1995). Acid soils covering an area of up to 3,950 million ha (Von Uexkuell and Mutert 1995; Bian et al. 2013) affect agricultural land in varying percentages, i.e., 38, 20, 31, 56, and 50% in Southeast Asia, East Asia, South America, North Africa, and North America, respectively (Wood et al. 2000; Hoekenga et al. 2003). A total of 239 million ha of acid soils are found in Australia and New Zealand (Von Uexkuell and Mutert 1995). Additionally, 212 million ha of acid soils were found in China and India (Bian et al. 2013). In South America, 1616 million ha of acid soils were also reported (Bian et al. 2013). In tropical areas, e.g., Indonesia, Mulyani et al. (2004) reported the total area of dryland is around 148 million ha that can be classified into 102.8 million ha of acid dryland and 45.2 million ha non-acid dryland.

Acid soil can be classified into two types, i.e., acid dryland and acid wetland. Acid dryland is a land that has properties such as low pH, cation exchange capacity (CEC), alkaline saturation and low organic C; high aluminum content (Al-saturation), P fixation, iron, and manganese content; sensitive to erosion, and poor biotic elements (Adiningsih and Sudjadi 1993; Soepardi 2001). Climate variations and relatively high rainfall result in an intensive level of alkaline leaching in the soil so that the alkaline content is low and the soil becomes acidic (Subagyo et al. 2000). This is why most of the soils in dryland have high acidity (pH 4.6–5.5) and poor nutrient content. Another type of acid soil is an acid wetland, which is found as paddy fields originating from advanced weathered mineral materials and on swamps that are mainly as acid sulfate soils and organic soils (peat). Swamplands in tropical areas, i.e., in Indonesia, are quite extensive, around 33.4–39.4 million ha (Widjaja-Adhi et al. 2000), spreading predominantly in Sumatra, Kalimantan, Sulawesi, and Papua. The swamps consist of 23.1 million ha of tidal swamps and 13.3 million ha of lowland swamps (Subagyo and Widjaja-Adhi 1998).

Intropical areas, particularly in Indonesia, acid soils are also a major problem in rice cultivation, whether on dry or wetland. Acidy dryland is in the order Ultisols, Inceptisols, Oxisols, Entisols, and a few Spodosols. Of the total acid dryland of 102.8 million ha, the largest is in the Ultisols and Inceptisols orders, with the dominant distribution in Sumatra, Kalimantan, and Papua. For acid wetlands, especially swamps, around 34.7 million ha were found, which came from mineral soils covering 22.8 million ha and peatlands of around 11.9 million ha. Mineral soils are generally dominated by Inceptisols (Endoaquepts, Sulfaquepts) and Entisols (Hidraquents). While peat soils are dominated by Histosols (Haplohemists, Haplosafrists, and Sulfihemists). Swampy lands are spread across four major islands, namely Sumatra, Kalimantan, Sulawesi, and Papua with a total area of 33.4 million ha or 17% of Indonesia's total land area (188.2 million ha) (Nugroho et al. 1991).

According to Ritung et al. (2015) land is divided into three types, namely dry land, swampland, and non-swamp land. The increasing human population that needs settlements and other related infrastructures cause a reduction offertile agricultural land, therefore swampland can be an alternative solution to solve the decreasing agricultural land area. Swamplands are land types with stagnant continuously or seasonally submerged with water conditions. The problems faced in this type of land are acidic soil and high iron (Fe) content that triggers toxicity in plants, hence reduces the yield. Several areas in the world, especially in Asia and Africa, that have soil with high Fe content, are Vietnam (Mekong Delta), Thailand, Philippines, Indonesia, Sri Lanka, Liberia, Senegal, Burundi, Madagascar, Guinea, and Côte d'Ivoire (Becker and Asch 2005). The Fe content of the soil in those areas varies from 20 to 2,500 mg Fe^{2+}/L and could decrease rice yield ranges of 15–100%.

Since the 1980s, several studies on rice cultivation on tidal swamplands have been reported in Kalimantan, Indonesia (Noorsyamsi et al. 1984; Watson 1984), South Sumatera, Indonesia (Carew 1984; Koswara and Rumawas 1984), Bangladesh (Hamid and Islam 1984), Thailand (Arunin and Hillerislambers 1984), Samborondon, Ecuador (Johnson et al. 1984), Sri Lanka (Jayawardena 1984), West Bengal, India (Sinha and Bandyopadhyay 1984). Several rice varieties that have been cultivated by farmers in tidal swamp areas, South Sumatra, Indonesia, such as Nugu, Duku, Suwarambe, Kuatik, and Ampai were reported to have a productivity of 1.0–2.0 ton/ha (Koswara and Rumawas 1984). Apart from Indonesia, a variation of local (traditional) and modern rice productivity when cultivated on tidal swamp areas have been reported, such as the rice productivity of 2.1–3.6 ton/ha in Bangladesh (Hamid and Islam 1984), 1.2–3.5 ton/ha in Thailand (Arunin and Hillerislambers 1984), and 1.8–7.5 ton/ha in Samborondon, Ecuador (Johnson et al. 1984). Research conducted in the dry season of 2018 reported that several Indonesian swamp rice varieties cultivated in the tidal swamp of Barito Kuala Regency, South Kalimantan (tidal swamp type B overflow) had a productivity of 2.5–5.8 ton/ha with the highest productivity achieved by rice cv. Inpara 2 (Ningsih et al. 2020). The variation of rice productivity in tidal swampland mostly depends on the ability of rice cultivar to adapt to soil type with high Fe. Therefore, designing new rice genotypes that tolerant of the condition is an important task to provide new rice varieties that produce a high yield in such soil conditions.

Based on the study of soil categories, either acid dryland or acid wetland, both of which make plants experience abiotic stress and further reduce crop production. Plant growth in acid dry-soils causes plants to experience high drought and aluminum (Al) stress (Ma et al. 2014; Kochian et al. 2015). In rice, it was reported that Al stress resulted in shorter root length, increased reactive oxygen species

(ROS) content, and inhibited plant growth (Fendiyanto et al. 2019a). Drought stress can also inhibit the expression of several drought tolerance regulatory genes in rice (Satrio et al. 2019). In wetlands, plants will also encounter Fe (Turhadi et al. 2018) and Al toxicity stress and will further result in a bronzing response, disrupted rice growth and development, and will further reduce production. Thus, it is important to look for varieties, gene sources, mechanisms, regulatory genes of rice plants that are tolerant of various abiotic stresses (drought, Al, and Fe toxicity). Therefore, this chapter aimed to understand how the rice tolerance mechanism to drought, Al, and Fe stresses (multi-abiotic stress) is based on multi-studies of genetics, genomics, molecular physiology, plant breeding, and their use to design new rice cultivars that are tolerant and adaptive to abiotic stresses by manipulating the genome using CRISPR/C as genome editing approach and omics-technology.

1.2 Genetic Improvement of Rice for Drought Stress Tolerance

1.2.1 Water Availability and Drought Stress Tolerance in Rice

Water availability is the most significant abiotic factor that influenced plant evolution. Plant growth and productivity are highly dependent on water availability, particularly in paddy rice. The terminology of drought condition from an agricultural perspective is defined as a period of less than average precipitation, less regular rainfall, or above-normal evaporation, often decreasing crop production (Nelson et al. 2014). The severity of the drought relies on several variables, i.e., frequency and distribution of rainfall, level of evaporation, and storage capacity of soil moisture (Farooq et al. 2009; Hayes et al. 2010).

Drought stress affects morphology, physiology, biochemistry, anatomy, and agronomical traits (Fig. 1.1). Drought is observed by a decrease in water status, leaf rolling, stomatal closure, and a decrease in growth (Anjum et al. 2011; Takahashi et al. 2020). By influencing multiple morpho-physiological and biochemical processes like photosynthesis, respiration, ion absorption, plant height, and nutrient metabolism, as well as phytohormones, drought decreases plant growth (Praba et al. 2009). Extreme drought can lead to photosynthesis disturbance and severe metabolism disruption, contributing eventually to plant death (Osakabe et al. 2014).

Plant vulnerability to drought, however, depends on the degree and length of stress, types of plant, and stages of development. As phenotypic markers, various drought-related characteristics, including root and shoot characteristics, osmotic adjustment capacities, water status, abscisic acid (ABA) quantity, and cell membrane stability, have been used to determine drought resistance (Barik et al. 2020). Drought tolerance mechanisms at the genetic and molecular levels have been intensively investigated in an attempt to the genetic improvement in rice (Vinod

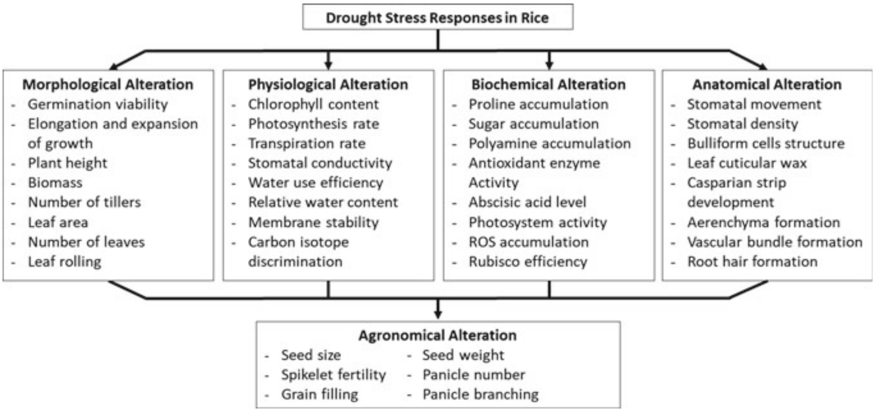

Fig. 1.1 Drought stress in rice induces various alteration that occurs at the morphological, physiological, biochemical, and anatomical levels, which in turn can affect the agronomicalalteration

et al. 2019). Drought stress responses are involved in various molecular networks (Todaka et al. 2015). Therefore, complete information of genes responsible for drought tolerance and dissection of their network is a key to understand drought stress tolerance and a way to conduct genomic designing for drought-stress resistance in rice.

1.2.2 Drought Tolerance Genes in Rice in Terms of Structural and Functional Genomics

Genes responsible for drought tolerance has been widely studied, either through structural and functional genomics approaches. Structural genomics refers to the localization and characterization of a set of genes responsible for a particular phenotype by physical or genetic mapping (Varshney et al. 2018). The structural genomics study on rice is growing rapidly along with the availability of the reference genome sequences for physical mapping (Kawahara et al. 2013). On the other hand, molecular markers for genetic mapping are also continuously developing. High-density genetic maps of 12 rice chromosomes on several genetic backgrounds are available (Harushima et al. 1998; Qu et al. 2020). The availability of these data that accompanied by the advanced phenotyping techniques and statistical methods causes genetic mapping is becoming increasingly easy to be performed. In contrast, functional genomics includes the use of both genomic and transcriptomic techniques to describe gene function that is specifically expressed for a particular phenotype (Li et al. 2018a, b). The study of expressed sequence tags is the earliest technique in the study of functional genomics (Satrio et al. 2019), followed by microarray which is more efficient in studying multiple gene expression simultaneously and has now been replaced by the RNA sequencing technique (Byrne et al. 2019).

Several structural genomics studies based on genetic mapping have been performed to investigate the genes responsible for drought stress tolerance, using both family-based mapping or the natural population. Drought stress tolerance in rice is quantitatively inherited and regulated by many genes, called quantitative trait loci (QTLs) (Sinclair 2011; Sahebi et al. 2018). In the bi-parental mapping population, the identification of QTLs controlling drought tolerance traits includes a chain of activities such as the genotyping of populations using molecular markers; genetic maps construction; and separately, analyze the phenotypes of the population according to the drought tolerance traits; then perform QTL mapping regarding the results of genotyping and phenotyping steps (Barik et al. 2019). The natural population can also be performed to discover genes responsible for drought tolerance in rice. Linkage disequilibrium based on association mapping using the natural population can be performed using the steps that are similar to QTL mapping, with the addition of consideration to population structure and kinship (Wang et al. 2020a, b).

Several QTLs linked to phenotypes related to drought stress tolerance have been well studied in rice. However, only a few studies have been reported on yield, which is important for agronomic value. According to a wide range of important traits correlated to drought tolerance, including root and shoot alterations, phytohormonal responses, osmotic adjustment, photosynthesis, transpiration, and globally plant response to drought tolerance, many QTLs for drought tolerance correlated traits in rice varieties have been identified (Table 1.1).

Transcriptome profiling greatly facilitated the development of the drought-tolerance-related functional genomics. Numerous genes that were induced by drought stress have been identified using transcriptomic analysis systems, e.g., microarray and RNA sequencing. Several transcriptome-wide expression studies for drought response in rice have been conducted. A dozen pathways along with their hundreds of genes were induced under drought stress treatment in two contrasting drought-tolerant rice genotypes (Lenka et al. 2011; Muthurajan et al. 2018; Ereful et al. 2020). Drought responsive genes can easily be identified using this approach, but their role in drought tolerance has not been proven. Functional analysis is needed to characterize the mode of action of the genes in the drought tolerance related traits. The most well-known and comprehensive models related to the drought-induced gene expression network as a part of functional genomics are the Abscisic acid (ABA)-dependent signaling pathway and the ABA-independent regulatory network mediated through dehydration responsive element-binding (DREB) (Yamaguchi-Shinozaki and Shinozaki 2006).

ABA phytohormone is a molecule that promotes signal transduction during the response to drought stress (Raghavendra et al. 2010). The 9-cis-epoxycarotenoid dioxygenase (NCED) is a critical enzyme for ABA biosynthesis (Iuchi et al. 2001). The *NCED3* expression level has been increased among genes encoding *NCED* in rice under water deficit conditions (Weiner et al. 2010). The ABA intercellular transport mechanisms have also emerged to be essential for ABA-dependent

Table 1.1 Quantitative trait loci (QTLs) for drought tolerance correlated traits in rice

Trait	Number of QTLs	Chromosome	References
Biomass	28	1, 2, 3, 4, 6, 7, 8, 10, and 12	Prince et al. (2015), Saikumar et al. (2014), Mishra et al. (2013), Sellamuthu et al. (2011), Srividya et al. (2011), Vikram et al. (2011), Gomez et al. (2010), Bernier et al. (2007), Kumar et al. (2007), Lanceras et al. (2004)
Canopy temperature	8	1, 2, 3, 4, and 7	Prince et al. (2015), Saikumar et al. (2014), Gomez et al. (2010), Yue et al. (2008)
Drought index	15	2, 4, 7, 10, and 12	Prince et al. (2015), Sellamuthu et al. (2011), Gomez et al. (2010), Yue et al. (2008), Zheng et al. (2008), Bernier et al. (2007), Li et al. (2005), Hemamalini et al. (2000)
Flowering time	8	2, 3, and 6	Prince et al. (2015), Palanog et al. (2014), Saikumar et al. (2014), Sandhu et al. (2017)
Grain weight	13	1, 2, 3, 5, 11, and 12	Prince et al. (2015), Zhou et al. (2013), Srividya et al. (2011), Zou et al. (2005), Thomson et al. (2003), Moncada et al. (2001)
Grain yield	74	All chromosomes	Prince et al. (2015), Palanog et al. (2014), Saikumar et al. (2014), Sandhu et al. (2017), Verma et al. (2014), Mishra et al. (2013), Zhou et al. (2013), Dixit et al. (2012), Ghimire et al. (2012), Sellamuthu et al. (2011), Srividya et al. (2011), Vikram et al. (2011), Bernier et al. (2007), Kumar et al. (2007), Xu et al. (2005), Lanceras et al. (2004)
Panicle length	7	1, 2, 3, 4, 8, and 11	Prince et al. (2015), Sellamuthu et al. (2011), Thomson et al. (2003), Lafitte et al. (2002)
Panicle number	9	1, 3, 4, 5, and 6	Mishra et al. (2013), Sellamuthu et al. (2011), Zou et al. (2005), Lafitte et al. (2004), Thomson et al. (2003), Lafitte et al. (2002), Moncada et al. (2001)
Seed setting rate	21	All chromosomes, except 11	Prince et al. (2015), Zhou et al. (2013), Sellamuthu et al. (2011), Srividya et al. (2011), Gomez et al. (2010), Thomson et al. (2003)
Tiller number	1	4	Hemamalini et al. (2000)
Plant height	27	1, 2, 3, 5, 7, 8, 9, 11, and 12	Prince et al. (2015), Saikumar et al. (2014), Sandhu et al. (2014), Mishra et al. (2013), Ghimire et al. (2012), Sellamuthu et al. (2011), Srividya et al. (2011), Vikram et al. (2011), Gomez et al. (2010), Lafitte et al. (2002), Venuprasad et al. (2002)
Root thickness	13	1, 2, 3, 4, 6, 7, 8, 9, and 12	Zhang et al. (2001), Ali et al. (2000)

(continued)