

Chittaranjan Kole *Editor*

Genomic Designing for Abiotic Stress Resistant Vegetable Crops

 Springer

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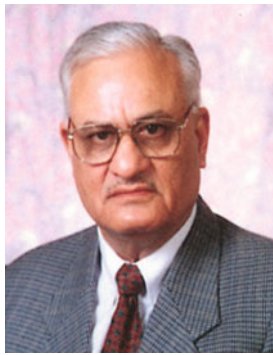
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Dedicated to



Dr. K. L. Chadha

*Padma Shri Awardee, former Deputy
Director General (Horticulture), Indian
Council of Agricultural Research and
Founder President of the Indian Academy of
Horticultural Sciences*

*With regards and 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, and 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 in 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 both on ‘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 F⁵ needs—food, feed, fiber, fuel and furniture. The advent of molecular breeding and genetic engineering in the latter part of that 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 nutraceutical 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; 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 F⁵ 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 Vegetable Crops” includes nine chapters focused on tomato, potato, Capsicums, eggplant, vegetable Brassicas, cucurbits, onion and garlic, amaranth and carrot contributed by 51 scientists from 6 countries including Greece, India, Italy, Israel, Malaysia and UK. 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

ABA	Abscisic acid
ABRE	ABA-responsive element
ACC	1-aminocyclopropane-1-carboxylic acid
ADC	Arginine decarboxylase
ADH	Alcohol dehydrogenase
AFLP	Amplified fragment length polymorphism
AFP	Antifreeze protein
Am	Association mapping
AMF	Arbuscular mycorrhizal fungi
AMOVA	Analysis of marker variance
Anx D1	Annexin D1
AOX	Alternative oxidase
APX	Ascorbate peroxidase
AQP	Aquaporin
AS	Alternate splicing
AtCBF3	<i>A. thaliana</i> C-repeat binding factor 3
AtCOR15A	<i>A. thaliana</i> cold-regulated 15A
AtRD29A	<i>A. thaliana</i> Responsive To Desiccation 29A
BAC	Bacterial artificial chromosome
BC1	First backcross generation
BC2	Second backcross generation
BIM	Bayesian interval mapping
BLAST	Basic local alignment search tool
BLUP	Best linear unbiased prediction
BR	<i>Brassica/Raphanus</i>
BSA	Bulked segregant analysis
BSR-Seq	BSA RNA-Seq
C4H	Cinnamate-4-hydroxylase
C5-MTases	Cytosine-5-methyltransferases
CAPS	Cleaved amplified polymorphic sequence
Cas9	CRISPR-associated protein 9

CAT	Catalase
CC	Core collection
CCC	Colombian central collections
CComT	Caffeoyl-CoA O-methyltransferase
cDNA	Complementary DNA
CDS	Coding sequence
CE-MS	Capillary electrophoresis-mass spectrometry
CFRB	Coordinated framework for regulation of biotechnology
CGIAR	Consultative Group on International Agricultural Research
CI	Chilling injury
CIM	Composite interval mapping
CIP	International Potato Center
CMS	Cytoplasmic male sterility
CNV	Copy number variation/variant
COMT	Caffeic acid-O-methyltransferase
COS	Conserved ortholog set
CPC	Commonwealth Potato Collection
CPR	Constitutive expression of pathogenesis-related gene
CR	Cold responsive
CRISPR	Clustered regularly interspaced short palindromic repeats
CRT	C-repeat
CS	Capsaicin synthase
CWR	Crop wild relative
DArT	Diversity array technology
DDBJ	DNA Data Bank in Japan
DEG	Differentially expressed gene
DH	Doubled haploid
DM	Doubled monoploid
DOF	DNA-binding with one finger gene family
DOT	Dihydroxyphenylalanine oxidation tyrosinase
DRE	Dehydration-responsive element
DREB	Dehydration-responsive element binding factor
DTE	Drought-tolerant efficiency
DUS	Distinctness, uniformity and stability
EBN	Endosperm balance number
EBVs	Estimated breeding values
ECPD	European Cultivated Potato Database
ECPGR	European Cooperative Programme for Plant Genetic Resources
<i>EDPG</i>	Extracellular dermal glycoprotein
EMBL	European Molecular Biology Laboratory
EMBO	European Molecular Biology Organization
EMS	Ethylmethane sulfanate
ERF	Ethylene response factor
EST	Expressed sequence tag
ET	Evapotranspiration

EUG	Eugenol
FAFLP	Fluorescent amplified fragment length polymorphism
FAO	Food and Agricultural Organizations
FAOSTAT	FAO Corporate Statistical Database
FBA	F-box associated
FBA	Fructose 1, 6 bisphosphate aldolase
FC	Field capacity
FISH	Fluorescence in situ hybridization
<i>FLC</i>	<i>Flowering locus C</i>
<i>FLD</i>	<i>Flowering locus D</i>
GA	Gibberellic acid
GABA	Gamma amino butyric acid
GB	Glycine betaine
GBS	Genotyping-by-sequencing
GC-MS	Gas chromatography-mass spectrometry
GE	Genome editing
GEBV	Genomic estimated breeding value
GFP	Green fluorescent protein
GM	Genetically modified
GMO	Genetically modified organism
GO	Gene ontology
GR	Glutathione reductase
GS	Genomic selection
GSH	Ascorbate–glutathione
GST	Glutathione S-transferase
GUS	β -Glucuronidase
GWAS	Genome-wide association study/studies
GxE	Genotype x environment interaction
HD-Zip	Homeodomain leucine zipper protein
HI-C	High chromosome conformation capture
HKT	High-affinity potassium transporter
HPLC	High-performance liquid chromatography
HRM	High-resolution melting
HSF	Heat shock factor
Hsp/HSP	Heat shock protein
HT	Heat tolerance
HTG	High-throughput genotyping
HTHH	High temperature and high humidity stress
HTP	High-throughput phenotyping
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IL	Introgression line
InDel	Insertion/deletion
IPCC	Intergovernmental Panel on Climate Change
IPT	Isopentyl transferase
ISSR	Inter-simple sequence repeat

ITAG	International Tomato Annotation Group
iTRAQ	Isobaric tag for relative and absolute quantification.
KAS	Keto acyl synthase
KEGG	Kyoto Encyclopedia of Genes and Genomes
LC-MS	Liquid chromatography-mass spectrometry
LD	Linkage disequilibrium
LEA	Late embryogenesis abundant
LOD	Logarithm of odds
LRR	Leucine-rich repeat
LTC	Low-temperature conditioning
MAGIC	Multiparental advanced generation intercross
MAPK	Mitogen-activated protein kinase
MAS	Marker-assisted selection
MBT	Mother and baby trial
MDA	Malondialdehyde
MeJA	Methyl jasmonate
MeSA	Methyl salicylate
MIM	Multiple interval mapping
MIP	Major intrinsic protein
miRNA	MicroRNA
<i>MLO</i>	<i>Mildew resistance locus</i>
MOD	Model Organism Database
MQTL	Meta-QTL
MSI	Membrane stability index
mtID	Mannitol-1-phosphodehydrogenase
NAD-ME	NAD-dependent malic enzyme
NADP	Nicotinamide adenine dinucleotide phosphate
NADP-ME	NADP-dependent malic enzyme
NAM	Nested association mapping
NBS	Nucleotide-binding site
NCBI	National Center for Biotechnology Information
NDPK	Nucleoside diphosphate kinase
NEU	<i>N</i> -nitroso- <i>N</i> -ethylurea
NGS	Next-generation sequencing
NIL	Near isogenic line
NMR	Nuclear magnetic resonance
NMU	<i>N</i> -Nitroso- <i>N</i> -methylurea
NPBT	New plant breeding techniques
NPTII	Neomycin phosphotransferase II
Nr	Never ripe
NUE	Nutrient-use efficiency
OA	Osmotic adjustment
OE	Overexpression lines
ORC5	Origin recognition complex subunit 5
ORF	Open reading frame

OSM	Osmotin protein
PAGE	Polyacrylamide gel electrophoresis
PAL	Phenyl ammonia lyase
pAMT	Putative aminotransferase
PAV	Presence/absence variants/variations
PCR	Polymerase chain reaction
PD	Protein disulfide isomerase
PEG	Poly ethylene glycol
PEPCK	PEP carboxykinase
PGD	Pepper Genome Database
PGDB	Pathway/Genome Databases
<i>PGIP</i>	Polygalacturonase inhibitor protein
PGSC	Potato Genome Sequencing Consortium
PLD	Phospholipase D
Pn	Photosynthesis
POD	Peroxidase
POLD1	DNA polymerase delta 1
PPO	Polyphenol oxidase
PPV&FR	Protection of Plant Varieties and Farmers' Rights
pQTL	Plasticity QTL
PR	Pathogenesis-related
PR1	Pathogenesis-related Protein 1
PS II	Photosystem II
Q	Ubiquinone
QTL	Quantitative trait locus
QTLs	Quantitative trait loci
RAD	Restriction site-associated DNA
Rad-Seq	Restriction site-associated DNA sequencing
RAPD	Random amplified polymorphic DNA
RBS	Ribosome-binding site
RDI	Regulated deficit irrigation
REL	Relative electrolyte leakage
REMAP	Retrotransposon-microsatellite amplified polymorphism
RFLP	Restriction fragment length polymorphism
RFO	Raffinose family oligosaccharide
RGA	Resistance gene analog
R-gene	Resistance gene
RIL	Recombinant inbred line
RLK	Receptor-like kinase
RLP	Receptor-like protein
RNAi	RNA interference
RNA-seq	RNA sequencing
ROS	Reactive oxygen species
RRS	Reduced representation sequencing
RSA	Root system architecture

Rubisco	Ribulose-1,5-bisphosphate carboxylase oxygenase
RWC	Relative water content
SA	Salicylic acid
SCoT	Start codon targeted
SDI	Subsurface drip irrigation
SHMT1	Serine hydroxymethyltransferase 1
SIM	Simple interval mapping
siRNA	Small interfering RNA
SLAF-seq	Specific locus amplified fragment sequencing
SMA	Single marker analysis
SNAT	Serotonin N acetyltransferase
SNP	Single-nucleotide polymorphism
SOC	Suppression of overexpression of constans
SOD	Superoxide dismutase
SOS	Salt overly sensitive
SR	Serine/arginine-rich
SRAP	Sequence-related amplification polymorphism
SSH	Suppression subtractive hybridization
SSLP	Simple sequence length polymorphism
SSN	Sequence-specific nuclease
SSR	Simple sequence repeat
STMS	Sequence-tagged microsatellite site
STS	Sequence-tagged site
SV	Structural variation
TALEN	Transcription activator like effector nuclease
TF	Transcription factor
TFC	Total flavonoid content
TILLING	Targeting induced local lesions in genomes
TIR	Temperature induction response
TLCV	<i>Tobacco leaf curl virus</i>
TLP	Thaumatococcus-like protein
TPC	Total polyphenol content
TRIA	Triacantanol
TRPV	Transient receptor potential cation channel
TSP	Trisodium phosphate
TuMV	Turnip mosaic potyvirus
UHD	Ultra-high-density
UPLC	Ultra-performance liquid chromatography tandem
UPOV	Union for the Protection of New Varieties of Plants
VIGS	Virus-induced gene silencing
WGS	Whole genome sequencing

WT	Wild type
WUE	Water-use efficiency
XET	Xyloglucan endotransglycosylase
ZEP	Zeaxanthin epoxidase
ZFN	Zinc finger nuclease

Chapter 1

Physiological, Molecular and Genetic Analysis of Abiotic Stress Tolerance in Tomato



R. H. Laxman, K. V. Ravishankar, H. C. Prasanna, K. V. Ramesh, K. Rashmi, S. Kannan, K. Hara Gopal, and S. S. Darshan

Abstract Tomato (*Solanum lycopersicum* L.) being most widely consumed vegetable is grown under diverse climatic conditions. It is exposed to episodes of abiotic stresses at critical stages and the potential yields are seldom realized. Abiotic stresses namely, high temperature, cold, drought, excess and low light, nutrient deficiency and toxicity and salinity limit production. Climate change is expected to further increase the incidence of various abiotic stresses. Under the circumstances it is rational to assess the adverse effects and devise means to overcome ill effects of diverse abiotic stresses on tomato. Tomato improvement efforts for desirable traits like yield and keeping quality have offered results. Evaluation of various tomato germplasm under different abiotic stresses has provided better insights into the existence of diversity in both cultivated and wild relatives. Though, substantial improvements have been made in understanding the abiotic stress tolerance mechanisms and gene discovery, the knowledge has not been exploited extent possible for development of tolerant commercial cultivars. Employing bioinformatics and molecular techniques there is remarkable opportunity for addressing complex breeding problems. Recent molecular tools have greatly helped the scientific community in assessing tomato germplasm for abiotic stress tolerance. Various physiological and biochemical analysis have been employed to understand the mechanisms operating during different abiotic stress tolerance. Using contrasting genotypes, many mapping and genetic studies have been conducted to identify genomic regions linked to abiotic stress tolerance. From these studies, various quantitative trait loci (QTLs) and genes have been identified. The markers could be valuable in improvement programs and for introgression of genes and QTLs from wild type species to *Solanum lycopersicum* using marker assisted selection (MAS). Many genetic engineering studies concerning transgenic and Crispr/CAS9 have demonstrated the association of various genes involved in imparting tolerance to abiotic stress in tomato. Sol Genomics, a database

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with genetic and genomic information on the plants belonging to Solanaceae family helps in providing sequence and marker related information which can be employed in MAS and genetic engineering. The opportunity for harnessing this information and devising strategies for tomato improvement for abiotic stress tolerance are discussed.

Keywords Abiotic stresses · Tolerance mechanisms · Quantitative Trait Loci · Transgenics · Breeding strategies · Marker assisted selection · Genomics

1.1 Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most widely consumed vegetables primarily due to its diverse consumption forms either as raw, cooked or various processed products. Its family Solanaceae also includes commercially important vegetables that are grown under diverse climatic conditions. Due to its demand for consumption in various forms, globally it is cultivated for both domestic needs and exports. Globally it is grown in an area of 5.03 million hectares with a total production of 180.76 million tons and productivity of 35.93 tons/ha (FAO 2019). Tomato crop is grown under diverse geographical regions either in open or under protected conditions. Two major tomato growing countries are China and India. Based on the extent of area and requirements it is harvested either manually or mechanically under intensive cultivation. The tomato fruit has diversity in color, shape and size. It is nutritionally important as it contains variety of phytochemicals. The fruit contains red color imparting pigment lycopene, which is a dominant antioxidant. Lycopene is important for maintaining eye health and reduces the incidence of cancer. The fruit also contains other carotenoids (β -carotene, phytoene, phytofluene) and phenolics (coumaric and chlorogenic acids, quercetin, rutin and naringenin). Vitamin C (ascorbic acid) in reasonable amounts is also present in tomato fruit. An alkaloid tomatine with fungicidal properties too is present. Hence, due its potential nutritional and health benefits, tomato is produced and consumed across the world.

1.2 Effect of Abiotic Stresses on Tomato Growth, Yield and Quality

Though tomato cultivation is widely adopted across the world in diverse agro-ecological regions, the potential yield is seldom realized due to episodes of many abiotic stresses. Abiotic stresses namely, high temperature, cold, drought, excess and low light, nutrient deficiency and toxicity and salinity limit crop production (Criddle et al. 1997; Cramer et al. 2011). Estimates of the effect of abiotic stress on global agriculture suggest that up to 70% of crop production is affected by ecological constraints (Boyer 1982; Cramer et al. 2011). Abiotic stresses are frequently interconnected, occurring either singly or in combination and cause morphological,

physiological, biochemical, and molecular changes in plants, reducing the development and production (Bulgari et al. 2019). Tomato requires accessibility of irrigation water throughout the crop growth cycle. It is sensitive to drought stress due to its succulent nature, and occurrence of deficit water stress during flowering and fruit set is very unfavorable. Deficit water stress caused reduction in yield to the extent of 11.69% and 30.60% under mild and severe water stresses, respectively. Conversely, fruit quality in terms of soluble sugars, total soluble solids, vitamin C contents, and fruit firmness was better under water stress (Hao et al. 2019b). The decline in plant height by 24%, stem diameter by 18% and chlorophyll concentration by 32% was observed in tomato under severe water stress condition. Consequently it resulted in 69% lower yield (Sibomana et al. 2013). The overall growth, flowering, yield and mineral nutrient uptake were significantly affected due to deficit irrigation (Ragab et al. 2019).

As a result of erratic rainfall the crops experience excess moisture stress and prolonged waterlogging situations. Such situations manifest into negative influence on crop growth and development. Waterlogging in tomato fields beyond two days leads to complete wilting and yield loss. Waterlogging induced anaerobic condition for 24 h resulted in 15% wilting and 40% yield loss (Hubbell et al. 1979). Flooding stress largely affected the physiology of tomato plants. Under stress tomato plants had lower photosynthesis rate, stomatal conductance, chlorophyll fluorescence, leaf water potential and chlorophyll content (Bhatt et al. 2015).

Maximum tomato rate of fruit growth and yield could be achieved at 25 °C (Adams and Valdes 2002). The critical nature of mean daily temperature on tomato was emphasized by Peet et al. (1997). The reduction in fruit number, per plant fruit weight and seed number was evident at mean daily temperature of 29 °C as compared to 25 °C. Thermal stress in tomato occurs at 35 °C. The exposure of plants to such high temperatures, results in physio-biochemical injury which adversely affect growth and yield (Rivero et al. 2004). High temperature stress during the growth of male reproductive part, leads to reduced fruit formation as a result of interruption in sugar and proline metabolism (Sato et al. 2006). Termination of flowers due to high temperature effect on bud formation and enlargement results in lower tomato yield (Peet et al. 1997; 1998; Sato et al. 2000). Increase in daily mean temperature adversely affects growth and productivity of tomato (Laxman et al. 2013, 2018).

Tomato is moderately sensitive to salinity. Salinity had its adverse influence on tomato root elongation, lateral root growth, reduced leaf, shoot height, stem diameter, photosynthesis and leaf chlorophyll content. At salinity equal and above 5 dS m⁻¹ the reduction in total yield was 7.2% per unit increase in salinity (Zhang et al. 2016). Since soil salinity influences seed germination and initial crop establishment, understating its influence is important for tomato production. Salinity level of 3.0‰ NaCl in Hoagland's solution affected germination of tomato seed. The germination process took longer and higher root/shoot dry weight ratio and Na⁺ content with reduction in K⁺ content were evident (Singh et al. 2012). At temperatures below 12 °C, the growth and development of tomato cultivars is adversely affected (Hu et al. 2006). Chilling stress damages tomato plants at prevailing temperatures between 0 and 12 °C depending on the duration of exposure (Adams et al. 2001). Thus, the

abiotic stresses have a greater bearing on overall physiology, growth, development and yield.

1.3 Growing Importance in the Face of Climate Change and Increasing Population

Tomato with desirable nutritional and health benefits is in great demand for domestic consumption and export. Increasing population driven demand poses a bigger challenge for sustainable tomato production. Further, there is a pressing need to manage the existing and future extreme weather events anticipated under climate change. The human induced increase in global surface temperature from 1850–1900 to 2010–2019 is likely in the range of 0.8 °C to 1.3 °C. Over the land surface the globally averaged precipitation has likely increased since 1950, with a quicker rate of increase since the 1980s. Currently observed variation in temperature events are projected to become more intense and last longer. The global temperature rise could be managed at 1.5 °C with determined efforts by cutting the emissions. These concerted efforts may prevent the most terrible climate impacts. However, as per the projections, under high emission scenario, the world may be warmer by 4.4 °C by 2100. Under such extreme scenarios the impacts would be devastating (IPCC 2021). Hence, there is an intense challenge of sustaining tomato production in the face of growing world's population on one hand and climate change on the other.

1.4 Limitations of Traditional Breeding and Rational of Genome Designing

Throughout the phenological development, tomato is subjected to a variety of abiotic stresses that adversely affect growth and yield. Among several approaches for sustaining and enhancing yields under adverse stress situations, identification of tolerant cultivars is of prime importance. Tomato breeding efforts for various desirable traits, especially yield and keeping quality, have been pursued in the past century employing pedigree method, hybridization, mass selection, and backcrossing. Such concerted efforts have led to improvements in tomato (Lucatti et al. 2013; Iqbal et al. 2019). Hybridization and pedigree selections have been the most important breeding techniques used in tomato improvement. The backcross method of breeding has been used to transfer desirable traits from wild species to cultivated varieties, among several other approaches (Sharma et al. 2019). Over the last seventy years, wild tomato species have been used in breeding programs to improve the cultivated tomato.

Development of tomato cultivars with enhanced abiotic stress tolerance is one of the most sustainable approaches to manage abiotic stresses. In this regard, considerable progress has been made to understand the stress tolerance mechanisms and gene discovery. Despite this there is no report of commercial cultivar tolerant to salt and/or drought stress. The literature on genetic variability, selection indices, important characteristics and genotypic responses to heat stress has been comprehensively reviewed by Hazra et al. (2007). The plant breeding programs need to translate the basic understanding gained from such studies into stress tolerant crop varieties using conventional and molecular tools. Tomato is a model plant for research in the Solanaceae family. The genomic sequence of tomato (*Solanum lycopersicum* L.) and its close wild relative (*Solanum pimpinellifolium* L.) are available (The Tomato Genome Consortium 2012; Aflitos et al. 2014). These advances encourage plant genomics and breeding studies for crop improvement.

Selection and breeding of tomato cultivars that can offer economic yield under abiotic stress situations signifies the lasting and balancing nature of this approach. An effective screening of the diverse genetic material is crucial for successful breeding strategy. The lack of a universal selection criterion for distinguishing tolerant and sensitive tomato accessions necessitates further research into identification of tolerance traits (Hirayama and Shinozaki 2010). The need for enhancing tolerance to abiotic stresses has necessitated the use of both traditional breeding techniques and marker-assisted selection. The evaluation of tomato germplasm under various abiotic stresses has provided better insights into the existence of diversity in both cultivated and wild relatives. However, utilization of diverse genetic resources in breeding tomatoes requires an efficient evaluation of germplasm using the phenotypic and genomic tools (Ayanan et al. 2019).

Following the breakthroughs in molecular biology and bioinformatics, breeding practices have improved (Caliman et al. 2008). These enhance the effectiveness of traditional plant breeding programs. The use of bioinformatics and molecular techniques can improve the screening of complex breeding problems (Ouyang et al. 2007). The narrow genetic basis in cultivated tomatoes for heat tolerance has triggered interest in exploiting tomato wild relatives, which have been sources for many abiotic and biotic stresses and yield related traits (Zhang et al. 2017a). Based on their ability to maintain photosynthetic rate and chlorophyll fluorescence under high temperature, Zhou et al. (2018) identified specific *S. pennellii* and *S. peruvianum* accessions as heat tolerant.

Current tomato breeding achievements are based on traditional breeding-genetic procedures, and limited improvements in introduction of useful traits into cultivars have been achieved. It's reasonable to believe that conventional breeding would not permit production to increase in the future (Fentik 2017). There has been significant development in molecular genetics and the application of molecular marker techniques. As a result, combining conventional breeding with modern plant biotechnology techniques such as marker-assisted selection and selection based on molecular markers could be useful tools for tomato breeding.

1.5 Response to Different Abiotic Stresses

Occurrence of abiotic stresses at critical growth stages not only severely limits productivity and yield but also quality of the produce. Under global climate change situations, abiotic stresses are of vital importance due to their widespread incidence. The occurrence of extreme high temperature and rainfall events are being reported across the world. Various abiotic stresses induce plant responses at different levels namely, morphological, physiological and biochemical/molecular alterations (Raza et al. 2019). At the morphological level, abiotic stress can cause altered shoot, root and leaf growth, as well as developmental changes that result in altered life cycle duration and fewer or smaller organs. Physiological activities such as photosynthetic rate, transpiration, respiration, assimilate partitioning to different organs within the plant, and mineral uptake is affected. At cellular level, membrane disruption, disorganized thylakoid structure, reduced cell size, stomatal guard cell function, alterations in cellular hydration and programmed cell death are manifested (Rao et al. 2016). At biochemical/molecular level, the effects include enzyme inactivation, production of reactive oxygen species (ROS), osmotic damage, changes in primary and secondary metabolite profiles, changed water and ion uptake or translocation and altered hormone concentrations (Etesami et al. 2021).

Maintenance of cell turgidity under stress is crucial for survival and to carry out metabolic activities. Plants have evolved various adaptive mechanisms to maintain positive turgor which mainly involves improving water relations and cellular level tolerance (Kapoor et al. 2020). Desired plant water status is sustained through mechanisms like alterations in phenology, maintaining positive turgor, and eventually sustaining cell metabolic activities despite decreased cell water potential. Cellular responses to stress include adjustments of the membrane system, modifications of the cell wall architecture, and alterations in cell cycle and cell division (Klutzn 2005). Therefore, two important relevant mechanisms are (a) improving water relations and (b) improving cellular level tolerance.

1.5.1 Roots Characters

Plants resort to several adaptive strategies through modifications in root characteristics. Such adaptations help to explore and access soil available water and maintain higher water use efficiency. Plants maintain positive turgor by taking up water from the deeper layers of soil (Robbins and Dinneny 2015). The roots act as crucial organ for meeting transpiration demand at a reasonably high leaf water status, given the condition that water is available in the rooting zone. Several root characters have relevance in stress adaptation. Studies have shown that genotypes with desirable root characteristics maintained cooler leaf temperature for longer period under water stress (White and Kierkegaard 2010). Nevertheless, these avoidance features help to maintain higher tissue water content under deficit moisture stress conditions. Such

adaptations facilitate plants to delay the immediate adverse effects of water stress. Hence, under severe deficit water stress conditions, the inherent tolerance characteristics are more important (Basu et al. 2016). Plants have exhibited many dehydration tolerance mechanisms under low tissue water potential by maintaining chloroplast integrity, membrane integrity and osmotic adjustment (Parkash and Singh 2020).

The importance of roots in accessing water from deeper layers of soil has also been the primary emphasis by the researchers. Roots, being below ground, respond to incidence of abiotic and biotic stresses in the soil and communicate with the aboveground plant parts via signaling pathways (Kim et al. 2020). The growth and development of plants is controlled by the root morphology and physiology through modifications in root to shoot transport of signaling molecules including hormones, proteins and RNAs and mineral nutrients (DoVale and Neto 2015). Roots being hidden in the soil are frequently exposed to multiple abiotic stresses occurring in the soil. Alterations in the shoot: root ratio is often detected when plants are subjected to various stresses (Fox and Fort 2019). Under drought, salt, or sub-optimal temperature stress, as well as some nutritional inadequacies or elevated levels of atmospheric CO₂, redistribution of metabolites from shoots to roots is frequently observed. Insufficient solar radiation or extra nutrients, on the other hand, usually result in a higher shoot-to-root ratio (Franco et al. 2011).

Roots have a greater ability to sense the physicochemical properties of the soil and change their development and performance, thus playing an important part in the plant's nutritional and development activities under abiotic stress (Kul et al. 2020). Roots are serving as the interface between the plant and the soil, hence more exposed to many abiotic stresses, especially drought, waterlogging and salt stresses than the aerial parts of the plant (He et al. 2018). Drought may cause a greater inhibition of shoot growth compared to root growth and in some cases; the absolute root biomass in drying soil may increase when compared to well-watered soils (Boudiar et al. 2020). Hence, the plants have developed various mechanisms to endure water or salt stress, including an altered shoot: root ratio.

Several studies have provided detailed insights into huge variations among tomato root traits (Table 1.1). The root characteristics like maximum root depth, total root length, root surface area, root volume, root diameter, root length density, root distribution pattern in the soil column, root to shoot ratio, root branching, root hydraulic conductance, root anatomy, root elongation rate, and hardpan penetrability. Intrinsic tolerance of roots plays a major role under stress condition (Sukeshini 2020). Hence, analysis of root phenotypes has revealed better understanding of root growth responses to a variety of environmental stimuli, as well as the extent of natural variation for root traits (Ristova and Busch 2014). Therefore, improving our understanding of the interactions between root functions and abiotic stress tolerance could have a significant impact on adaptation strategies.

Table 1.1 Root traits associated with different abiotic stresses in tomato species

Abiotic stresses	Root traits	References
Drought stress	Root length	Ron et al. (2013), Ghebremariam et al. (2013), Khan et al. (2014), Senthilkumar et al. (2017), Habib et al. (2019)
	Root biomass	Brdar-Jokanovic et al. (2014), Tron et al. (2015), Mahpara et al. (2018), Buhroy et al. (2017), Zhang et al. (2019), Zhang et al. (2020)
	Root/shoot ratio	Allerstorfer (2014), Niakan et al. (2014), Xiong et al. (2015), Zhang et al. (2020), Kamanga et al. (2020)
Salt stress	Root length	Almutairi, (2016), Tanveer et al. (2020), Habib et al. (2019), Altaf et al. (2020)
	Root biomass	Singh et al. (2012), Sajyan et al. (2018)
	Root/shoot ratio	Ebrahim et al. (2017), Parvin et al. (2019), Ladewig et al. (2021)
High temperature stress	Rootlength, Root biomass Root/shoot ratio	Keatinge et al. (2014), Haghighi et al. (2014), Shaheen et al. (2016), Ali et al. (2020)
Cold stress	Root length	Zhang et al. (2011), Subramanian et al. (2016), Wani et al. (2021)
	Root biomass	Ghorbanpour et al. (2018), Dezhabad et al. (2020)
	Root/shoot ratio	Klay et al. (2014), Altaf et al. (2021)

1.5.2 Heat Tolerance

As a result of global warming, coincidence of high temperature episodes with sensitive phenophases, leads to heat stress and is a major agricultural concern in many parts of the world. Heat stress is a vital limiting factor in agricultural output. There is a spike in air temperature over a threshold level for a period of time long enough to produce injury or irreversible damage to crop plants in general (Kumar et al. 2012; Lobell and Gourджи 2012; Gourджи et al. 2013; Teixeira et al. 2013). The extent of high temperature induced alterations in physiology, phenology, growth and yield depends on the duration, intensity and temperature increase over the threshold limits. The effects of heat stress on plants are very complex; resulting in denaturation of enzymes, disruption of metabolism activity, growth and development alterations, change in physiological functions and morphological structure (Mondal et al. 2013). Such alterations results in increased respiration, lower photosynthesis rate, closure of stomata, reduced chlorophyll fluorescence, lower chlorophyll content, membrane damage, ROS over production, and metabolic disruption upon exposure to heat stress (Hu and Zhu 2020). It could also alter the phenology, shorten the crop duration,

days to flowering and fruiting, hasten fruit maturity, ripening and senescence. These alterations result in reduced crop productivity and quality (Yu et al. 2019).

Tomato is cultivated in diverse agro-climatic regions across the world. It is very sensitive to high temperature (Camejo et al. 2005). Optimum mean daily temperature requirement is between 15–32 and 35 °C is considered as maximum threshold (Zhang et al. 2005). For growth, development and yield 40 °C is supra-optimum temperature (Morales et al. 2003). High temperature can undesirably impact seed germination, vegetative growth, pollination, flowering, fruit set, fruit weight and fruit quality (Foolad et al. 2005; Laxman et al. 2018). The gas exchange characteristics, photosynthesis, transpiration, stomatal conductance and photochemical efficiency of PSII were affected to a greater extent at peak flowering stage as compared to peak fruiting stage (Camejo et al. 2005, 2006; Laxman et al. 2013, 2014).

Previous studies have shown that the increase in daily mean temperatures adversely affect growth and productivity of tomato. The increase in temperature above the optimal, caused reduction in net photosynthetic rate, transpiration, stomatal conductance, and photochemical efficiency of PSII of five selected tomato genotypes during peak flowering and fruiting stages. The reductions were higher at peak flowering stage compared to peak fruiting stage (Laxman et al. 2013). The mild temperature also reduced in vitro pollen germination, fruit set percentage, fruit weight, number of leaves, number of branches, plant height, total dry matter accumulation, and harvest index in tomato plants. Concurrently, the number of trusses, flowers, and flower abortion also increased (Laxman et al. 2018). Antioxidant enzymes and the expression of HSPs/HSFs genes were found to be involved in the SIMAPK3-mediated heat stress response in tomato plants Yu et al. (2019). Mansy et al. (2021) studied six tomato lines, G1, G2, G3, G4, G5, and G6, under heat stress at the morphological, molecular, and cytological levels. The lines G2, G1, and G6 performed better in terms of morphological characters, vegetative development, fruiting, and yield.

In order to sustain productivity and quality under climate change situations, identification of tolerance source and development of suitable cultivars is the best adaptation strategy. For sustainable crop production under heat stress, two most imperative strategies could be followed: (a) introduction of tolerant cultivars, genetically modified or transgenic cultivars through molecular and biotechnological means along with conventional breeding approaches and (b) employing several agronomic management strategies for heat stress management under field conditions. As part of the strategy, coping up with high temperature stress under climate change conditions necessitates development of tolerant cultivars. This can be accomplished by breeding programs by exploiting the genetic capability of genotypes which are already temperature tolerant (Laxman et al. 2018). Bhattarai et al. (2016) examined a tomato cross to estimate combining ability and understand the genetic basis of tomato genotypes under heat stress. The genetic components and proportions studies showed that the heat tolerance was governed by non-additive gene action and is a dominant trait. The parental variance (V_r) and parent–offspring covariance (W_r) relationship (W_r-V_r) indicated that heat tolerance traits were governed by over dominance. Significant correlation occurred between yield and yield-attributing traits. Heterosis was high for yield and