Chittaranjan Kole *Editor*

Genomic Designing of Climate-Smart Vegetable Crops

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Chittaranjan Kole
Department of Atomic Energy
Government of India, ICAR-National
Institute for Plant Biotechnology
New Delhi, India

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Dedicated to

Late Prof. Subir Sen, D.Sc.

Head, Department of Genetics & Plant Breeding, Faculty of Agriculture, and Dean, Post-Graduate Studies, Bidhan Chandra Krishi Viswavidyalaya (Agricultural University), West Bengal, India

An exceptional scientist, outstanding academician and a visionary

who lived many decades ahead of his time

Preface

The last one hundred and twenty years have witnessed a remarkable evolution in the science and art of plant breeding culminating in quite a revolution in the second decade of the twenty-first century! A number of novel concepts, strategies, techniques and tools have emerged from time to time over this period and some of them deserve to be termed as milestones. Traditional plant breeding, immediately following the rediscovery of laws of inheritance, has been playing a spectacular role in the development of innumerable varieties in almost all crops during this entire period. Mention must be made on the corn hybrids, rust-resistant wheat, and obviously the high-yielding varieties in wheat and rice that ushered the so-called green revolution. However, the methods of selection, hybridization, mutation and polyploidy employed in traditional breeding during this period relied solely on the perceivable phenotypic characters. But most, if not all, of the economic characters in crops are governed by polygenes which are highly influenced by environment fluctuations, and hence phenotype-based breeding for these traits has hardly been effective.

Historical discovery of DNA structure and replication in 1953 was followed by a series of discoveries in the 1960s and 1970s that paved the way for recombinant DNA technology in 1973 facilitating the detection of a number of DNA markers in 1980 onwards and their utilization in construction of genetic linkage maps and mapping of genes governing the simply inherited traits and quantitative trait loci controlling the polygenic characters in a series of crop plants starting with tomato, maize and rice. Thus new crop improvement technique called as molecular breeding started in later part of the twentieth century. On the other hand, genetic engineering made modification of crops for target traits by transferring alien genes, for example, the *Bt* gene from the bacteria *Bacillus thuringiensis*. A large number of genetically modified crop varieties have thus been developed starting with the commercialization of 'flavr Savr' tomato in 1994.

Meantime, the manual DNA sequencing methodology of 1977 was being improved with regard to speed, cost-effectiveness and automation. The first-generation sequencing technology led to the whole genome sequencing of Arabidopsis in 2000 and followed by rice in 2002. The next-generation sequencing technologies were available over time and used for sequencing of genomes of many

other models and crop plants. Genomes, both nuclear and organellar, of more than 100 plants have already been sequenced by now and the information thus generated are available in public database for most of them. It must be mentioned here that bioinformatics played a remarkable role in handling the enormous data being produced in each and every minute. It can be safely told that the 'genomics' era started in the beginning of the twenty-first century itself accompanying also proteomics, metabolomics, transcriptomics and several other 'omics' technologies.

Structural genomics have thus facilitated annotation of genes, enumeration of gene families and repetitive elements, and comparative genomics studies across taxa. On the other hand, functional genomics paved the way for deciphering the precise biochemistry of gene function through transcription and translation pathways. Today, genotyping-by-sequencing of primary, secondary and even tertiary gene pools; genomewide association studies; and genomics-aided breeding are almost routine techniques for crop improvement. Genomic selection in crops is another reality today. Elucidation of the chemical nature of crop chromosomes has now opened up a new frontier for genome editing that is expected to lead the crop improvement approaches in near future.

At the same time, we will look forward to the replacement of genetically modified crops by cisgenic crops through transfer of useful plant genes and atomically modified crops by employing nanotechnology that will hopefully be universally accepted for commercialization owing to their human-friendly and environment-friendly nature.

I wish to emphatically mention here that none of the technologies and tools of plant breeding is too obsolete or too independent. They will always remain pertinent individually or as complimentary to each other, and will be employed depending on the evolutionary status of the crop genomes, the genetic resources and genomics resources available, and above all the cost-benefit ratios for adopting one or more technologies or tools. In brief, utilization of these crop improvement techniques would vary over time, space and economy scales! However, as we stand today, we have all the concepts, strategies, techniques and tools in our arsenal to practice genome designing, as I would prefer to term it, of crop plants not just genetic improvement to address simultaneously food, nutrition, energy and environment security, briefly the FNEE security, I have been talking about for the last 5 years at different platforms.

Addressing FNEE security has become more relevant today in the changing scenario of climate change and global warming. Climate change will lead to greenhouse gas emissions and extreme temperatures leading to different abiotic stresses including drought or waterlogging on one hand and severe winter and freezing on the other. It will also severely affect uptake and bioavailability of water and plant nutrients and will adversely cause damage to physical, chemical and biological properties of soil and water in cropping fields and around. It is also highly likely that there will be emergence of new insects and their biotypes and of new plant pathogens and their pathotypes. The most serious concerns are, however, the unpredictable crop growth conditions and the unexpected complex interactions among all the above stress factors leading to drastic reduction in crop yield and

quality in an adverse ecosystem and environment. Climate change is predicted to significantly reduce productivity in almost all crops. For example, in cereal crops the decline of yield is projected at 12–15%. On the other hand, crop production has to be increased at least by 70% to feed the alarmingly growing world population, projected at about 9.0 billion by 2050 by even a moderate estimate.

Hence, the unpredictability of crop growing conditions and thereby the complexity of biotic and abiotic stresses warrant completely different strategies of crop production from those practiced over a century aiming mostly at one or the few breeding objectives at a time such as yield, quality, resistance to biotic stresses due to disease-pests, tolerance to abiotic stresses due to drought, heat, cold, flood, salinity, acidity or improved water and nutrient use efficiency. In the changing scenario of climate change, for sustainable crop production, precise prediction of the above limiting factors by long-term survey and timely sensing through biotic agents and engineering devices and regular soil and water remediation will play a big role in agriculture. We have been discussing on 'mitigation' and 'adaptation' strategies for the last few years to reduce the chances of reduction of crop productivity and improve the genome plasticity of crop plants that could thrive and perform considerably well in a wide range of growing conditions over time and space. This is the precise reason of adopting genomic designing of crop plants to improve their adaptability by developing climate-smart or climate-resilient genotypes.

Keeping all these in mind, I planned to present deliberations on the problems, priorities, potentials and prospects of genome designing for development of climate-smart crops in about 50 chapters, each devoted to a major crop or a crop group, allocated under five volumes on cereal, oilseed, pulse, fruit and vegetable crops. These chapters have been authored by more than 250 of eminent scientists from over 30 countries including Argentina, Australia, Bangladesh, Belgium, Brazil, Canada, China, Egypt, Ethiopia, France, Germany, Greece, India, Ireland, Japan, Malaysia, Mexico, New Zealand, Kenya, Pakistan, Philippines, Portugal, Puerto Rico, Serbia, Spain, Sri Lanka, Sweden, Taiwan, Tanzania, Tunisia, Uganda, UK, USA and Zimbabwe.

There are a huge number of books and reviews on traditional breeding, molecular breeding, genetic engineering, nanotechnology, genomics-aided breeding and gene editing with crop-wise and trait-wise deliberations on crop genetic improvement including over 100 books edited by me since 2006. However, I believe the present five book volumes will hopefully provide a comprehensive enumeration on the requirement, achievements and future prospects of genome designing for climate-smart crops and will be useful to students, teaching faculties and scientists in the academia and also to the related industries. Besides, public and private funding agencies, policy making bodies and the social activists will also get a clear idea on the road travelled so far and the future roadmap of crop improvement.

I must confess that it has been quite a difficult task for me to study critically the different concepts, strategies, techniques and tools of plant breeding practiced over the last 12 decades that also on a diverse crop plants to gain confidence to edit the chapters authored by the scientists with expertise on the particular crops or crop groups and present them in a lucid manner with more or less uniform outline of

contents and formats. However, my experience gained over the last 7 years in the capacity of the Founding Principal Coordinator of the International Climate-Resilient Crop Genomics Consortium (ICRCGC) was highly useful while editing these books. I have the opportunity to interact with a number of leading scientists from all over the world almost on a regular basis. Organizing and chairing the annual workshops of ICRCGC since 2012 and representing ICRCGC in many other scientific meetings on climate change agriculture offered me a scope to learn from a large number of people from different backgrounds including academia, industries, policymaking and funding agencies and social workers. I must acknowledge here the assistance I received from all of them to keep me as a sincere student of agriculture specifically plant breeding.

This volume entitled Genomic Designing of Climate-Smart Vegetable Crops includes eight major crops including Potato, Tomato, Brassica Vegetables, Eggplant, Capsicum, Carrot, Alliums and Garlic. These chapters have been authored by 32 scientists from 9 countries including Argentina, Bangladesh, China, France, India, Japan, Poland, UK and USA. I place on record my thanks for these scientists for their contributions and cooperation.

I have always enjoyed working on horticultural crops during my entire academic career spanning over 40 years. I worked on molecular genetics and breeding in tomato while at the Pennsylvania State University, USA; molecular genetics, breeding and genomics in peach, apricot and bitter melon while at the Clemson University, USA; molecular genetics in country bean while at the Odisha University of Agriculture & Technology, India; molecular genetics in guava while at the Sam Higginbottom University of Agriculture, technology & Sciences, India; and molecular genetics and breeding in bitter melon while at the Bidhan Chandra Krishiviswavidyalaya (Agricultural University), and ICAR-National Institute for Plant Biotechnology, both in India.

However, I started working on horticultural crops in late seventies in the laboratory of (Late) Prof. Subir Sen Head of the Department of Genetics and Plant Breeding and later on Dean of Post-Graduate Studies in the Bidhan Chandra Krishiviswavidyalaya (Agricultural University), West Bengal, India as a Ph.D. student on genetics and breeding of a medicinal and aromatic plant, citronella. It is that time, we realized the potential of medicinal and aromatic plants as 'crops' in future and importance of exploration, collection, conservation, characterization and utilization of such crops the concepts that have become important in today's world. We are coming often across the terms 'biodiversity', 'health security' and 'crops of the future' only now! Prof. Sen was not only an outstanding scientist and an excellent teacher himself but also a visionary endowed with vast knowledge on arts, music and literature who lived many decades ahead of his time. Hence, I have dedicated this book to (Late) Prof. Sen as a token of my respect, appreciation and gratitude.

New Delhi, India Chittaranjan Kole

Contents

Abbreviations

$\bullet O_2^-$	Superoxide radical
•OH	Hydroxyl radical
5-azaC	5-Azacitidine
6-PF-2-K/Fru2,6-P_2ase	6-Phosphofructo-2-kinase/fructose2,6-bisphosphatase
ABA	Abscisic acid
ABF	ABA binding factor
ABRE	ABA-responsive element
ACC	1-Aminocyclopropane-1-carboxylic acid
ACS	*A. chinese* saponins
AFLP	Amplified fragment length polymorphism
AGO	Argonaute
AIR	Anthocyanin-impaired-response
AOX	Alternative oxidase
AP2	Apetala 2
AREB	ABA-responsive element binding protein
ASE	Allele-specific expression
ASH1	Absent, small or homeotic disks 1
ASHH2	ASH1 homolog 2
ATX	ARABIDOPSIS TRITHORAX
ATXR	ARABIDOPSIS TRITHORAX-RELATED
AVRDC	World Vegetable and Development Center (Tainan, Taiwan)
BAC	Bacterial artificial chromosome
BADH	Betaine aldehyde dehydrogenase
BC	Backcross
bHLH	Basic helix-loop-helix
BiFC	Bimolecular fluorescence complement
BPH	Best-parent heterosis
BR	Black rot
BSA	Bulked-segregant analysis

BSA-seq	Bulked-segregant analysis sequencing
BSR-seq	Bulked-segregant RNA sequencing
bZIP	Basic leucine zipper
CaM	Calmodulin
CaMV	Cauliflower mosaic virus
CAPS	Cleaved amplified polymorphic sequence
Cas9	CRISPR-associated 9 protein
CCA1	CIRCADIAN CLOCK ASSOCIATED 1
CC-NB-LRR	Coiled-coil NB LRR
CDF1	CYCLING DOF FACTOR1
cDNA	Complementary DNA
CDPK	Calcium-dependent protein kinase
CGMS	Cytoplasmic genic male sterility
ChIP	Chromatin immunoprecipitation
ChIP-seq	Chromatin immunoprecipitation sequencing
CI	Cytoplasmic inclusion
circRNA	Circular RNA
CK	Cytoplasmic kinase
cM	CentiMorgan
CMT	CHROMOMETHYLASE
CMV	Cucumber mosaic virus
CO	Constans
CoIP	Co-immunoprecipitation
Col	Columbia-0
COLDAIR	COLD ASSISTED INTRONIC NONCODING RNA
COLDWRAP	COLD OF WINTER-INDUCED NONCODING RNA FROM THE PROMOTER
COOLAIR	COLD INDUCED LONG ANTISENSE INTRAGENIC RNA
CP	Coat protein
CPB	Colorado potato beetle
CPGTH	Carboxypropyl glutathione
CR	Clubroot
CR	Cold responsive
CRISPR	Clustered regularly interspaced short palindromic repeats
CRTISO	Carotene cis-trans isomerase gene
CS	Chilling stress
CS	Climate smart
CWR	Crop-wild relative
CYP97A3	Carotene hydroxylase gene
DArT	Diversity arrays technology
DAS	Days after sowing
Dc	*Daucus carota* or carrot
DcAREB3	Carrot transcription factor to ABA-responsive elements
DcHSP	Carrot heat-shock protein

DCL	DICER-LIKE
DcPSY2	Carrot phytoene synthase2 protein (*gene*)
DDM1	Decrease in DNA methylation 1
DEG	Differentially expressed gene
DFR	Dihydroflavonol 4-reductase
DH	Doubled haploid
dpi	Days post inoculation
DREB	Dehydration responsive element binding protein
DRM	DOMAINS REARRANGED METHYLTRANSFERASE
E(z)	Enhancer of zeste
EBN	Endosperm balance number
ECD	European clubroot differential
eIF4E	Eukaryotic initiation factor 4E
EMS	Ethyl methanesulphonate
EpiRAD-seq	Epi-restriction site associated DNA sequencing
epiRILs	Epigenetic recombinant inbred lines
ER	Endoplasmic reticulum
ERF	Ethylene-responsive element binding factor
EST	Expressed sequence tag
ET	Ethylene
ET	Evapotranspiration
ETI	Effector triggered immunity
F_1	First filial generation
F3′,5′H	Flavonoid 3′,5′-hydroxylase
FAO	Food & Agriculture Organization (of the United Nation)
FAOSTAT	FAO statistics
FD	FLOWERING LOCUS D
FDA	Food and Drug Administration (USA)
FISH	Fluorescent *in situ* hybridization
FKF1	FLAVIN KELCH F BOX 1
FLC	FLOWERING LOCUS C
FLS	Flavonol synthase
Foc	*Fusarium oxysporum* f.sp. *conglutinans*
FOC	*Fusarium oxysporum* f.sp. *cepae*
FRI	FRIGIDA
Fru-2,6-P_2	Fructose 2,6-bisphosphate
FT	FLOWERING LOCUS T
FUL	FRUITFUL
FW	Fusarium wilt
G × E	Genotype × environment
GA	Gibberellin
gbM	Gene-body methylation
GBS	Genotyping-by-sequencing
GC-MS/MS	Gas chromatography-mass spectrometry

GD	Genetic distance
GEBV	Genome-estimated breeding value
GGT	γ-Glutamyl transpeptidases
GI	Gigantea
GIS	Geographic information system
Gly	Glycine
GMO	Genetically modified organism
GMS	Genic male sterility
GO	Gene ontology
GP	Genomic prediction
GPF	Green fluorescent protein
GRSV	Groundnut ringspot virus
GS	Genomic selection
GSPP	Good Seed and Plant Practices
GWAS	Genomewide association study
G×E×M	Genotype × environment × management
H_2O_2	Hydrogen peroxide
H3K27me3	Tri-methylation of the 27th lysine of histone H3
H3K36me3	Tri-methylation of the 36th lysine of histone H3
H3K4me3	Tri-methylation of the 4th lysine of histone H3
H3K9me2	Di-methylation of the 9th lysine of histone H3
HDR	Homologous recombination
HIB	High-efficiency integrated breeding
HIGS	Host-induced gene silencing
HP	High parent
HRM	High-resolution melting
HSF	Heat-stress transcription factor
HSP	Heat-shock protein
HT	High temperature
HVR	Hyper variable region
InDel	Insertion/deletion
IPCC	Intergovernmental Panel on Climate Change
IPT	Isopentytransperase
IRR	Interspersed repeat region
ISSR	Inter-simple sequence repeat
JA	Jasmonic acid
KASP	Kompetitive allele-specific polymerase chain reaction
KEGG	Kyoto Encyclopedia of Genes and Genomes
KYP	KRYPTONITE
LC-MS/MS	Liquid chromatography-mass spectrometry
LC-QqQ-MS	Liquid chromatography quadruple-mass spectrometer
LD	Long day
LD	Linkage disequilibrium
LEA	Late embryogenesis abundant
LF	Least fractionated

LG	Linkage group
LHP1	LIKE HETEROCHROMATIN PROTEIN 1
LHY	LATE ELONGATED HYPOCOTYL
lncRNAs	Long noncoding RNAs
LOD	Logarithm of odds
LP	Low parent
LRR	Leucine-rich repeat
MABC	Marker-assisted backcrossing
MAGIC	Multiparent advanced generation intercross
MAMP	Microbe-associated molecular pattern
MAPK	Mitogen-activated protein kinase
MAS	Marker-assisted selection
MBD-seq	Methyl-CpG-binding domain sequencing
mC	Methylated cytosine
MDB	Molecular design breeding
MeDIP-seq	Methylated DNA immunoprecipitation sequencing
MET1	METHYLTRANSFERASE I
MethylRAD	Methylation-dependent restriction site associated DNA
MF	More fractionated subgenomes
MIP	Major intrinsic protein
miRNA	Micro-RNA
MLMM	Multi-locus mixed model
MLPK	M-locus protein kinase
MPH	Mid-parent heterosis
MPV	Mid-parent value
mRNA	Messenger-RNA
MTMM	Multi-trait mixed model
MYB	Myeloblastosis oncogene
MYBR	Myeloblastosis oncogene responsive
MYC	Myelocytomatosis oncogene
MYCR	Myelocytomatosis oncogene responsive
NB	Nuclear-binding
NB-LRR	Nucleotide-binding leucine-rich repeat
NBS	Nucleotide-binding site
ncRNA	Noncoding RNA
NGS	Next-generation sequencing
NHEJ	Nonhomologous end joining
NILs	Near-isogenic lines
NIP	Nodulin-26 like intrinsic protein
NMR	Nuclear magnetic resonance
NRPD1	Nuclear RNA polymerase D1A
NRPE1	Nuclear RNA polymerase D1B
NUE	Nutrient use efficiency
OP	Open-pollinated
ORF	Open reading frame

OST2	OPEN STOMATA 2 gene
P5CS	Pyrroline-5-carboxylate synthetase
PAM	Protospacer adjacent motif
PAMP	Pathogen-associated molecular pattern
PAR	Photosynthetic active radiation
PAT	Phosphinothricin acetyltransferase
Pb	*Plasmodiophora brassicae*
PcG	Polycomb group
PCR	Polymerase chain reaction
PepMV	Pepino mosaic virus
PHD	Plant homeodomain
PIP	Plasma membrane intrinsic protein
Pol IV	Polymerase IV
Pol V	Polymerase V
PP2C-A	Protein phosphatase type 2C
PPR	Pentatricopeptide repeat
PR	Pathogenesis-related
PRC2	POLYCOMB REPRESSIVE COMPLEX 2
PRR	Pattern recognition receptor
PSII	Photosystem II
PTI	PAMPs/MAMPs triggered immunity
qPCR	quantitative PCR
QRL	Quantitative resistance loci
QTL	Quantitative trait locus
QTLs	Quantitative trait loci
R	Resistance
RAD-seq	Restriction site associated DNA sequencing
RAPD	Random amplified polymorphic DNA
RCA	Root cortical aerenchyma
RdDM	RNA-directed DNA methylation
RDR	RNA-DEPENDENT RNA POLYMERASE
retr	Recessive turnip mosaic virus resistance
Rf	Restorer-of-fertility gene
RFLP	Restriction fragment length polymorphism
RFO	RESISTANCE TO FUSARIUM OXYSPORUM
RGR	Relative growth rate
RILs	Recombinant inbred lines
RLCK	Receptor-like cytoplasmic kinase
RLK	Receptor-like kinase
RLP	Receptor-like protein
RNAi	RNA-interference
RNA-Seq	Ribonucleic acid sequencing
rnt1	Resistance and necrosis to tumv 1
ROS	Reactive oxygen species
rRF	Ribosomal RNA fragment

RSA	Root system architecture
RT	Reverse transcription
SA	Salicylic acid
SAM	Shoot apical meristem
SC	Self-compatibility
SCAR	Sequence-characterized amplified region
SCR	*S*-locus cysteine rich
SD	Short day
SE	Standard error
SET	SU(VAR)3-9, E(z), TRX
SI	Self-incompatibility
SIP	Small basic intrinsic protein
siRNAs	Small interfering RNAs
SIX1	Secreted-in-xylem 1
SLG	*S*-locus glycoprotein
Smi	*SP11*-methylation inducer
SMI	*SP11*-methylation-inducing region
SMRT	Single molecule real-time
snoRF	snoRNA fragment
SNP	Single nucleotide polymorphism
snRF	Small nuclear RNA fragment
SOC1	Suppressor of Overexpression of CO 1
SOD	Super oxidase dismutase
SP11	*S*-locus protein 11
SRAP	Sequence-related amplified polymorphism
SRK	*S* receptor kinase
SS	Salinity stress
SSH	Suppression subtractive hybridization
SSR	Simple sequence repeat
STF	*S*-locus retrotransposon family
STS	Sequence tagged site
SU(VAR)3-9	SUPRESSOR OF VARIEGATION 3-9
SUVH4	SU(VAR)3-9 HOMOLOG
SWI2/SNF2	Switch 2/sucrose non-fermentable 2
TALEN	Transcription activator like effector nuclease
TCSV	Tomato chlorotic spot virus
TDB	Transcriptome database
TE	Transposable element
TF	Transcription factor
TGRC	Tomato Genetic Resources Center (UC-Davis, USA)
TILLING	Targeting-induced local lesions in genomes
TIP	Tonoplast intrinsic protein
TIR-NB-LRR	Toll interleukin-1 receptor-NB-LRR
TLP	Thaumatin-like protein
TMV	Tobacco mosaic virus

ToBRFV	Tomato brown rugose fruit virus
ToMV	Tomato mosaic virus
tRF	tRNA fragment
tRNA	Transfer RNA
TRX	Trithorax
TSWV	Tomato spotted wild virus
TuMV	Turnip mosaic virus
TuRB01	*Turnip mosaic virus RESISTANCE IN BRASSICA 01*
TYLCV	Tomato yellow leaf curl virus
USDA	United States Department of Agriculture
VIN3	VERNALIZATION INSENSITIVE 3
VPg	Viral protein genome
VRE	Vernalization response element
WAKL22	WALL-ASSOCIATED KINASE-LIKE KINASE 22
WD	Water deficit
WGBS	Whole genome bisulfite sequencing
WGT	Whole genome triplication
WT	Wild type
WUE	Water-use efficiency
Xcc	*Xanthomonas campestris* pv.*campestris*
XIP	X intrinsic protein
Y2H	Yeast two hybrid
ZAT	Zinc finger of *Arabidopsis thaliana*
ZEP	Zeaxanthin epoxidase gene
ZF	Zinc finger
ZFN	Zinc finger nuclease
Zip	Zinc finger protein

Chapter 1
Climate-Smart Potato: An Integrated Breeding, Genomics, and Phenomics Approach

Jagesh Kumar Tiwari, Clarissa Challam, Swarup K. Chakrabarti and Sergio E. Feingold

Abstract Potato is an important source of food globally. Potatoes are among the most widely grown crop plants in the world, giving good yield under various soil and weather conditions. Yield losses of potato under current climate change keep increasing, despite the progressive increase in yield through breeding and management practices since the 1960s. Conventional breeding facilitated the development of high-quality potato with enhanced tolerance to severe environmental fluctuations such as drought, flooding, heat, and salinity. However, conventional approaches need to be complemented with advanced techniques in order to meet the increasing demands of the growing world population. The advances in marker-assisted and genomics-assisted breeding, sequencing technologies, and phenomics tools have enabled the potato improvement at a faster pace. The genomic resources have enabled the development of molecular markers associated with many important quantitative trait loci. It has also provided a clear picture of genomic variations in potato germplasm, and identified key genes for genetic engineering including genome editing. This knowledge is being utilized to facilitate the development of climate-smart potato. In this chapter, we discuss and summarize the advances in potato improvement through conventional and genomics-assisted breeding, genetic engineering, and phenomics approaches. This information could facilitate the incorporation of climate-smart traits (biotic and abiotic stresses) in modern breeding for more stable potato production with the changing climate.

Keywords Breeding · Climate change · Genomics · Phenomics · Potato

J. K. Tiwari (✉) · S. K. Chakrabarti
ICAR-Central Potato Research Institute, Shimla, Himachal Pradesh 171001, India
e-mail: jageshtiwari@gmail.com

C. Challam
ICAR-Central Potato Research Institute, Regional Station, Shillong, Meghalaya 793009, India

S. E. Feingold
Laboratorio de Agrobiotecnología EEA Balcarce, Instituto Nacional de Tecnología Agropecuaria (INTA), Balcarce, Argentina

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1.1 Introduction

In recent years, the rapidly changing climatic conditions are hitting agriculture hard and are likely to increase the problems of food insecurity, hunger, and malnutrition for millions of people, particularly in South Asia, Sub-Saharan Africa, and small islands (Intergovernmental Panel on Climate Change, IPCC 2007). Global warming is causing changes in temperature at a rate unmatched by any temperature change over the last 50 million years. As shown in the IPCC (2007) report, the main repercussions of climate change are a rise in temperature, an increase in CO_2 concentration in the air, and an altered precipitation pattern. Among the changes, the increasing temperature has the most likely negative impact on the yield of crops including potato.

Potato is a global food security crop and is the fourth most important food crop after rice, wheat, and maize (Chakrabarti et al. 2017). Recently, Raymundo et al. (2018) evaluated the SUBSTOR-Potato model in various potato growing regions and concluded that there could be a global reduction in tuber yield from −2 to −6% by 2055, with a potential higher decline by 2085 (−2 to −26%). Similarly, climate change scenario is supposed to adversely affect potato production and productivity in India. Potato cultivation in India has largely been uneven as nearly 85% of potato in the country is produced in north Indian plains. The potato season (September–February) in this region is likely to be a little warmer also slightly drier with an increase in temperature ranging from 0.78 to 1.18 °C and corresponding precipitation decrease of 1−3%, by 2020 (Singh et al. 2013). The 1 °C rise in temperature associated with 400 ppm of CO_2 in the year 2020 (IPCC 2007) will result in a decline in potato production by 3.16%, without adaptation (Dua et al. 2013). The situation is expected to further worsen by the year 2050, where the atmospheric CO_2 concentration will be 550 ppm with a likely increase in temperature of 3 °C (IPCC 2007). Under this scenario, potato production is expected to fall by 13.72%, in the absence of needed steps (Singh et al. 2013; Anonymous 2015).

The world's population is widely expected to increase to at least 9 billion by 2050 (FAO 2013). This represents an increase of 2 billion people over the next 40 years, which will require a 70% increase in food production (Anonymous 2015). Potato being the fourth most consumed food crop species, there is a significant demand for crop improvements (Chakrabarti et al. 2017). Although the progressive increase in yield through breeding and management practices has been achieved in potato crop, the yield losses under current climate change keep increasing. Furthermore, climate change has a potential impact on the spread and severity of diseases caused by viruses, bacteria, fungi, and oomycetes (Castillo and Plata 2016; Lehsten et al. 2017). Therefore, accelerating the rate of genetic gain to adapt to climate change effects to meet the target demands of food production requires the integration of multidisciplinary research platforms/disciplines (Tester and Langridge 2010). This means there is a need to focus on key adaptive traits in order to maintain and increase crop productivity in increasingly unpredictable climate change. Applications of potato improvement through conventional and genomics-assisted breeding,

genetic engineering approaches, and available bioinformatics tools for potato are being discussed.

1.2 Prioritizing Climate-Smart Traits

Potato, (*Solanum tuberosum* Group Tuberosum L.) ($2n = 4x = 48$), represents one such heterozygous, polyploid crop that is clonally propagated by tubers (Potato Genome Sequencing Consortium 2011). While conventional breeding and genetic analysis are challenging in cultivated potato due to the abovementioned features, the majority of diploid potatoes possess gametophytic self-incompatibility. Historically, conventional breeding has been used to create improved potato cultivars. Yet due to its unique challenges, breeding is inefficient when complex traits need to be combined or if novel traits are not present in the desired germplasm. The key will be the combination of classical plant breeding with the advances in genomics, crop physiology, and modeling in an integrated profile involving genotype, phenotype, and environment.

1.2.1 Flowering Time and Tuberization

Flowering time is a key adaptive trait, responding to environmental and endogenous signals that switch between the vegetative and reproductive, while tuberization is the process of tuber formation from an underground stem called a stolon. Flowering and tuberization are distinct reproductive strategies in potato, both of which involve the sensing of the photoperiod by expanded leaf and generation of a signal in the leaves (a process referred to as induction), the subsequent transport of the signal (known as florigen or tuberigen), and the response in a distinct organ, the vegetative meristem or stolon tips (called as evocation). The genetic control of flowering time has been extensively studied in model species, particularly in Arabidopsis as well as in a number of important fields and tree crop species. However, the controlling factors involved in the tuberization process are not precisely clear and are under considerable investigation in recent decades (review by Dutt et al. 2017).

1.2.1.1 Plant Hormone Controlling Tuberization

Numerous studies have implicated the growth regulators as both inhibitor and promoter working coordinatedly to control tuber induction. The relevant literature has been reviewed from time to time. Gibberellins (GAs) have been implicated in different aspects of potato tuber formation. Several workers have shown that the non-induced state in potato plants is correlated with high endogenous GA levels. GA levels in the leaf decrease under short-day photoperiods and increase under long-day

conditions. *StGA2ox1* was found to be upregulated during the early stages of potato tuber development prior to visible swelling and was predominantly expressed in the subapical region of the stolon and growing tuber. In addition to GAs, several other plant hormones such as auxin, cytokinin, and ABA have been studied for their effect on tuber initiation. The initiation and induction of tubers in potato appear to be regulated by a cross talk between GA and auxin. Microarray experiments revealed a large number of auxin-related genes differentially expressed during early events in tuber development (Kloosterman et al. 2005). Examples of such genes are two PIN-like genes, an *adr11-2* (auxin downregulated) and an *acrA*-like (auxin-regulated gene containing a GTP-binding site) genes.

1.2.1.2 Day-Length Control of Flowering Time

Photoperiod sensing by the function of photoreceptors and the circadian clock appears to regulate flowering time via Arabidopsis CONSTANS (*AtCO*), a putative transition factor that accelerates flowering in response to long days (LDs). Mutations in the GIGANTEA (*gi*), CONSTANS (CO), and flowering locus T (FT) genes cause late flowering in LDs but do not affect flowering in short days (SDs), indicating a role of these genes in the LD flowering pathway. CO expression is reduced in the *gi* mutants, and overexpression of *AtCO* overcomes the late-flowering phenotype of these mutants. This transcription factor functions as an output to the clock and directly activates expression of the downstream floral regulator genes FT and Suppressor of Overexpression of CO 1 (*SOC1*, also known as *AGL20*). When the plant is exposed to light at this particular phase, flowering is induced in LD plants or delayed in SD plants.

The genetic factors controlling plant photoperiodic responses other than flowering are little known. However, interspecific grafting experiments demonstrated that the flower-inducing (florigen) tuber-inducing (tuberigen) signals are functionally exchangeable. Constitutive overexpression in potato of the Arabidopsis flowering-time gene *AtCO* impairs tuberization under short-day inductive conditions; *AtCO* overexpressing lines require prolonged exposure to short days to form tubers. Grafting experiments using these lines indicated that *AtCO* exerts its inhibitory effect on tuber formation by acting in the leaves. This module would involve the action of CONSTANS in the production of the elusive and long-distance acting florigen–tuberigen signal(s).

1.2.1.3 CONSTANS-Tuberization Control

Evidence for a role of the CO protein in daylength control of tuberization was also obtained in transgenic andigena plants expressing the *CO* gene from Arabidopsis. Three *CO* homologs also have been identified in potato, and evidence for a role in tuberization control has been obtained for one of these genes, designated *StCOL3*. *StCOL3* is cyclically expressed with a biphasic peak of expression at the end of the

night. Under SDs, *StCOL3* expression rises during the second half of the night and is still high during the first day hours (Martınez-Garcia et al. 2002). In LDs, the peak is narrower and occurs only during the day. Hence, this transcript peaks at a different time of the day than observed for the CO/Hd1 transcripts in Arabidopsis or rice. Despite such a difference in the timing of expression, *StCOL3* accumulation seems to fit with a similar model as that described in rice, and tuberization is promoted when *StCOL3* is expressed during the night but delayed when the expression of this protein coincides with light. Therefore, it will be interesting to compare the orthologs from potato, rice, or the SD plant *Pharbitis nil* with the CO Arabidopsis protein, and to search for conserved domains that might explain the differential regulatory function of the SD proteins (Martınez-Garcia et al. 2002).

1.2.1.4 Transcription Factors

MADS-box genes are an example of a family of highly conserved transcription factors (TFs) that have diverse roles during plant development. In the early flowers, POTM1-1 transcripts were accumulated abundantly in the developing reproductive organs including the placentae of carpels and the pollen sacs of stamens. In contrast, the pattern of POTM1-1 distribution during late flower development was different from that of early flower development. The POTM1-1 transcripts were abundant in the sepals and petals of late flowers but were minimally expressed in the stamens and carpel. In the shoot apical meristem of the vegetative organs, transcripts were distributed throughout meristem domes, young leaves, and developing vascular cambium (Kloosterman et al. 2013). In the early tuberization, the transcripts were widely distributed in the swollen tips of the stolons. Taken together, the results suggested that POTM1–1 gene expression was temporally and spatially regulated in actively growing tissues of both vegetative and floral organs with specific distribution patterns dependent upon the developmental stages of the tissue. In another study, TFs family genes *ABF4* and *ABF2* transgenic potato exhibit ABA hypersensitivity during tuberization, accompanied by a GA deficient phenotype. *ABF4* expression triggered a significant rise in ABA levels in stolons under tuber-inducing conditions as compared with wild-type plants and transcriptional deregulation of GA metabolism genes. These results demonstrated that Arabidopsis *ABF4* functions in potato ABA–GA signaling cross talk during tuberization by regulating the expression of ABA and GA-metabolism genes. Hendriks et al. (1991) have reported that patatin and four serine proteinase inhibitor genes are differentially expressed during potato tuber development. The studies showed that the length of the day/light conditions differently influenced the expression level of these individual genes.

1.2.1.5 Molecular Targets for Tuberization

StSP6A (FT-like; Arabidopsis ortholog) is a mobile signal that has been shown to positively regulate tuberization transition in potato. Recently, it has been reported

that both photoperiod dependence on tuberization and the duration of the potato growing cycle are linked to a regulatory gene called *StCDF1* (Kloosterman et al. 2013). *StCDF1* acts as an intermediary in the way of signaling between the circadian clock mediated by the *Gi* (GIGANTEA) gene and the photoreceptors of blue light and *StSP6A* (Navarro et al. 2011; Abelenda et al. 2014). Natural allelic variants of the *StCDF1* gene could be responsible for the adaptation of potato at high latitudes, generating the Tuberosum group. Another FT member of potato, *StTFL1* has been suggested to increase the number of tubers produced when overexpressed. Two proteins, *StBEL5* and *POTH1* (transcription factors belonging to TALE superclass), have been proven to be positive regulators of the tuberization process in potato and can also be prominent candidates for improving tuberization through their simultaneous overexpression (Dutt et al. 2017). Other genes/proteins that are suggested for genetic engineering through overexpression include *POTM1*, *StPA2Ac, StTUB19, StTUB7, StABF2,* and *StABF4*. Whereas, *StCO TF*, *StSP5G,* and *StSUT4* sucrose transporters have been found to inhibit tuberization. Hence, their suppression may be utilized for promoting tuberization.

1.2.2 Cold Tolerance

Among the different abiotic stresses, cold is an essential factor that limits crop productivity worldwide. Low temperature affects the growth and development of agronomic species throughout the world. It is very important to study the frost damage mechanism and to breed cold-tolerant varieties since the average minimum temperature is below 0 °C in about 64% of the earth's land area and it is below −10 °C in about 48%. Potato crop adaptation is needed to increase production and stability under cold conditions that are getting worse with climatic change. Plants have adapted two mechanisms to protect themselves from damage due to below freezing temperatures. First, supercooling is a low-temperature tolerance mechanism that is usually associated with acclimated xylem parenchyma cells of moderately hardy woody plants. The second and most common low-temperature response mechanism is acclimation. Acclimation is a gradual process during which there are changes in just about every measurable morphological, physiological, and biochemical characterization of the plant (Takahashi et al. 2013). These changes are determined by genotype and environmental interactions that are quite complex.

1.2.2.1 Genetic Variation in Cold Tolerance

Many primitive cultivars and wild relatives of potato can tolerate environmental stress conditions in their habitats. Frost tolerance may be one of the oldest objectives of potato breeding. A very old study showed frost resistance or tolerance using hybrids between *S. demissum* and other susceptible species. Frost tolerance also occurred in certain accessions of *S. commersonii* and its hybrids. Bukasov (1933) evaluated

the frost resistance of several wild potato species and hybrids in the winters of the years 1930–31 and 1931–32. *S. demissum, S. acaule*, and *S. juzepczukii* were not affected by frost of −6 °C, *S. demissum* and *S. ajanhuiri* showed different reactions in different plants, and *S. andigenum* perished entirely under the same conditions, with the exception of one variety "Pacus," which proved to be resistant.

1.2.2.2 Gene Expression in Response to Cold Tolerance

Extensive researches have been conducted to improve the understanding of the biochemical and molecular basis of the cold acclimation response and the changes that take place throughout this process. However, the increase in cold tolerance obtained by acclimation is not static. Extensive physiological and biological changes occur during cold acclimation starting with a reduction in the growth rate and water content of various plant tissues. Through the cold acclimation process reprogramming of gene expression and various modifications in the metabolism take place (Chinnusamy et al. 2010). Acclimation also causes an increase in the production of antioxidants, abscisic acid (ABA), and compatible osmolytes such as soluble sugars and proline. A number of cold-responsive genes have been reported in various plant species: *COR* (cold-regulated) genes, *LEA* (late-embryogenesis abundant) genes, regulatory genes, antifreeze protein genes, and the genes encoding signal transduction proteins.

Proline has been shown to improve cold tolerance and aid cell structure protection in many crops, such as maize, potato, wheat, and barley, and in *L. perenne* had shown to improve osmotic adjustment during cold acclimation. Intracellular accumulation of endogenous polyamines (PA) occurs in response to cold stress as they contribute to plant response to low-temperature conditions. The increase in levels of diamine putrescine (Put) has been reported in cold-stressed Arabidopsis (Kaplan et al. 2004). The increased titers of Put on overexpression of S-adenosylmethionine decarboxylase (*StSAMDC)* were actually the result of high spermidine accumulation which was actively interconverted to Put by acetylation.

1.2.2.3 Role of CBF (C-Repeat Binding Factor) Gene

The *CBF* genes are the key regulatory elements in cold-responsive signaling pathways and hence serve as potential targets of genetic manipulation to engineer cold stress-tolerant plants. *CBFs* are discovered in all important field crops and some vegetable species like potato (Sanghera et al. 2011). Transgenic Arabidopsis plants overexpressing *CBF1* showed freezing tolerance while avoiding the negative impact of cold stress on development and growth characteristics. Constitutive overexpression of cold-inducible transcription factors like CBF1 has been shown to impart cold stress tolerance, through introduction of *CBF1* cDNA into chilling-sensitive tomato under the control of strong CaMV35S promoter (Hsieh et al. 2002). Another candidate target is the *CBF4*, a close *CBF/DREB1* homolog, whose overexpression alleviated both freezing and drought stress in Arabidopsis. Transgenic potato

and poplar plants expressing soybean cold-inducible C2H2-type zinc finger transcription factor (*SCOF-1*) increased cold and freezing stress tolerance in Arabidopsis. Overexpression of *bHLH* TFs with clone names such as *StMHJ91, StMEK79, StMDC31, StMDE79, StMDV67, StMER91, StMHZ85*, and *StMCU25* increase cold stress tolerant to potato.

1.2.2.4 Role of Ca^{2+} Signal Pathway

Ca^{2+} is considered to be the main signal transducer in signaling cascades motivated in response to plant abiotic stress types. Upon cold stress, cytosolic Ca^{2+} concentration immediately rises up to a level of designated Ca^{2+} signatures for cold. This designated cytoplasmic Ca^{2+} signature is decoded by Ca^{2+} sensors like Calmodulins (CaM), Calmodulin-like proteins (CMLs), Ca^{2+}-dependent protein kinases (CDPKs), Calcineurin B-like proteins (CBLs), and their interacting kinases (CIPKs) to transduce the signal intracellularly. Therefore, differentially expressed Ca-related genes in chilling-stressed potato could have major functions in intracellular signal transduction, thereby, in the development of cold acclimation. Moreover, reactive oxygen species (ROS) also play an important role as second messengers responding to various abiotic stresses. Some of the authors reported that abiotic stresses cause an oxidative burst and that a low level of ROS induces an increase in Ca^{2+} influx into the cytoplasm. The high level of Ca^{2+} activates NADPH oxidase in order to produce ROS through yielding O^{-2} which is then converted to H_2O_2 under the effect of super oxidase dismutase (SOD). Therefore, the production of ROS is Ca^{2+} dependent and the concentration of Ca^{2+} is also regulated by the concentration of ROS by the activation of Ca^{2+} channels in the plasma membrane. Therefore, a cross talk between Ca^{2+} and ROS modulates the activity of specific proteins that control the expression-specific definitive defense genes in the nucleus.

1.2.2.5 Role of Phytohormones

The existence of an ABRE cis-acting element (ABA-responsive element) is an essential requirement for the upregulation of ABA-induced gene expression (Shinozaki and Yamaguchi-Shinozaki 2000). Finkelstein et al. (2002) reported an important role of ABA in the induction of *LEA* gene expression. The role of ABA in the upregulation of *LEA* genes is considered to be one of the mechanisms that ABA has to increase plant drought and freezing tolerance. Moreover, the application of salicilic acid (SA) improved the cold tolerance of several plant species such as potato, rice, and maize. Gibberellin (GA) is the other plant hormone altered in plants under cold stress. It has been found that GA is involved in the expression of *CRT/DRE*-binding factor gene which in turn confers tolerance to drought, salt, and cold stress. Plant phytohormone jasmonic acid (JA) also plays an essential role as an important regulatory signal in plant cold tolerance. GA is associated with SA/JA balance in the CBF-mediated stress response. It has been proved that the external application of JA significantly

enhanced cold tolerance in plants with or without acclimation. Moreover, blocking of the endogenous JA increased the sensitivity to the cold stress. It has been proved that JA upregulated the *CBF/DREB1* signaling pathway (Hu et al. 2013).

1.2.3 Drought Tolerance

Most potato varieties have sparse and shallow root system and are vulnerable to a series of abiotic stresses, including drought and high salinity, thus resulting in a reduction in tuber yield and quality. Even short periods of drought stress can result in serious damage and cause a severe reduction in tuber production. Research on drought tolerance in potato only started during the period 60–80s as it was not considered as a major yield-limiting factor in potato for a long time. The situation drastically changed over the last few years due to the increasing importance of drought for potato production and the recognized interest in developing potato cultivars able to perform well in drought-prone areas. Moreover, in production areas under irrigation, drought tolerance and water use efficiency are of importance as there is a growing concern on carbon and water footprints. Similarly, a reduction of irrigation where water quality is poor will prevent salinity in soils enhancing sustainability. Knowledge of physiological mechanisms underlying drought tolerance in potato (e.g., the role of abscisic acid, osmotic adjustment, or rooting patterns) is however still poor compared with other crops.

1.2.3.1 Genetic Variation in Drought Tolerance

Screening for drought tolerance in potato landraces has been performed by many researchers. A high proportion of accessions combining drought tolerance with high irrigated yield was found in Andean landraces, particularly in the species *S. curtilobum* (Juz. and Bukasov) in the *S. tuberosum* L. cultivar groups Stenotomum, Andigenum, and Chaucha. Watanabe et al. (2011) identified *S. chillonanum, S. jamesii,* and S. *okadae* as potential drought-tolerant species by screening 44 accessions of wild species selected based on their drought habitats derived from geographic information system (GIS).

1.2.3.2 Root System Architectures (RSA)

Root systems are usually involved in both drought avoidance and tolerance during water deficits due to the constitutive and plastic characteristics of roots. RSA is also highly plastic to respond rapidly to environmental changes such as water deficit. Liu et al. (2005) found that the concentration of ABA in the xylem of potato plants increases significantly as the substrate contains less water. This suggests that the roots of potato plants are able to perceive the lack of water in the substrate and in response

to this situation produce ABA. When plants perceive water deficit stress, roots tend to keep growing and penetrate into deeper soil layers. The ability of plants to develop deeper rooting systems under drought stress depends on the tolerance levels of the roots to water deficit stress. In addition to deep rooting, drought stress also induces the plasticity responses of root systems by increasing the number of fibrous roots, decreasing lateral root diameter, and fluctuations in root biomass. Alterations in root anatomy, such as aerenchyma formation in maize, save the energy inputs to allow improved soil penetration and exploration to compensate water deficit (Wishart et al. 2013).

Breeding of new cultivars with excellent root characteristics to absorb water from deeper regions of the soil and under lower soil water potential will increase the usage of soil water and contribute to efficient utilization of water from precipitation or irrigation in potato production. Many studies found a positive relationship between the size of the root system and the amount of aboveground biomass. Quantitative trait locus (QTL) mapping has been conducted in potato and many QTLs associated with RSA and drought tolerance have been mapped. It can be concluded that the plants that have a more-developed root system at greater depths of the soil profile tend to have milder reactions to drought.

1.2.3.3 Water Use Efficiency (WUE)

Improving water use efficiency is another promising strategy to overcome drought stress. The essential factors to improve water use efficiency are to conserve water in plants and reduce the unnecessary transpiration losses. QTL analysis of near-isogenic lines of Arabidopsis has identified numerous QTLs involved with WUE, some co-localized with flowering-time QTLs involved with drought avoidance. However, some of these genes have been shown to be independent of QTL analyses, and it is possible to select for higher WUE while leaving out flowering-time QTLs. Molecular genetics represent an essential approach for identification and elucidation of the various traits that contribute to WUE. Some characterized genes have been identified that control water uptake and loss. To fully utilize knowledge of these genes to improve WUE, an integrated approach is required that implements functional characterization of promising QTLs, high-throughput phenotyping, field validation of traits, and stacking/pyramiding of these traits into WUE-efficient and drought-tolerant varieties for agriculture. This challenge represents one of the most complex tasks facing biotechnology today and will require both modern breeding and gene editing techniques to achieve. Regardless of the challenge, molecular genetics will be essential in the identification and characterization of genes that play an important role in increasing WUE and drought tolerance.

Molecular Strategies for improving WUE

Advances in genetics, "omics," precise phenotyping, and physiology coupled with new developments in bioinformatics and phenomics are or will be providing means for dissecting integrative traits that affect adaptation to stressful environments. In

this regard, it has been indicated that analyzing the effect of traits on crop yield with the aid of modeling and confirming through field experiment (and sound biometrics) will lead to identifying favorable alleles for enhancing adaptation to a stress-prone environment. Some traits used as proxy for selecting germplasm with enhanced adaptation to drought-prone environments (especially among grain crops) are anthesis–silk interval, early flowering (that could provide partial relief to water shortage during grain filling), floral fertility (by minimizing severe water deficit-induced damage at flowering), early vigorous growth (which improves crop establishment and reduces soil evaporation), root architecture and size (for optimizing water and nutrient harvest), and tiller inhibition (that increases tiller survival rates and carbohydrate storage in stems for ensuring further grain filling), among others (Tuberosa et al. 2007). Likewise, indirect selection has been used for improving WUE, e.g., through canopy temperature depression, carbon isotope discrimination (Δ13C) for C_3 crops (although both may differ across locations), and ear photosynthesis (Tambussi et al. 2007). Recent molecular approaches offer new alternatives to improve drought tolerance in several plant species, including potato, in terms of the identification of signaling pathways and master genes regulating drought tolerance. For example, hypersensitivity to ABA has been associated with a better behavior under water stress (Papp et al. 2004). Among the components involved in the transduction of the ABA signal, genes encoding phosphatases, protein kinases, and transcription factors have been identified (Xie et al. 2010; Christmann et al. 2006). Genomic tools for identifying genome regions and genes involved in the control of drought tolerance should be more extensively used in potato. More detailed information will become available in the future using the metabolomics and proteomics techniques together with integrated bioinformatics systems. These advances will facilitate the genetic engineering of single or multiple targets to create a cultivated phenotype with high-yielding potential under drought stress conditions. Changes in the gene expression profiles are induced in response to drought stress and several genes are regulated up or down with osmotic stress.

1.2.4 Heat Tolerance

Heat stress affects growth, quality, and yield traits by impacting the structure and metabolic functions of cells and several physiological processes, such as structural alterations of protein complexes, changes in protein synthesis and enzyme activities, cellular structure and membrane functions, production of detrimental reactive oxygen species, decoupling of metabolic pathways, and damage to the photosynthetic apparatus. The ideal temperature for potato aerial growth is 20–25 °C and the optimum temperature for tuber formation in 15–20 °C (Rykaczewska 2013). In fact, higher temperatures adversely affect tuber formation and tuber development in potato, and this inhibition of tuberization has been linked to the inhibition of tuberization signal StSP6A (an ortholog of Arabidopsis flowering *FT* locus) at elevated temperatures (Hancock et al. 2014) and reduced accumulation of carbon into starch in

the tuber at higher temperatures. Also, an adverse effect on photosynthesis resulting from chlorophyll loss and reduced CO_2 fixation has been reported for tuber-forming Solanum species.

A large number of differentially expressed genes involved in many biological processes and molecular functions as well as differential metabolite accumulation have been identified in response to mild to moderate heat stress in potato leaves and tubers. Tolerance to elevated temperatures in potato is likely a polygenic trait and, thus expected to be substantially influenced by genotype-environment interactions. As such, potato cultivars may show a wide variety of variations in their response to heat stress. However, so far most studies on heat stress response of potato have focused on some germplasm accessions (Reynolds and Ewing 1989) or only on a very few registered cultivars. In order to understand the biological basis of heat tolerance and select and develop potato varieties that are heat tolerant, it is critical to understand the variation in response of a large number of potato varieties/cultivars to heat stress. Indeed screening and breeding for heat-tolerant potato cultivars are urgently needed to stabilize potato productivity in the current and future warmer environment.

Maximum threshold temperatures at which high temperatures kill seedlings can depend on plant preconditioning. Seedlings subjected to high but sublethal temperatures for a few hours subsequently can survive higher temperatures than seedlings that have been maintained at moderate temperatures. This acclimation to heat can be induced by the gradual diurnal increases in temperature that occur in hot natural environments (Vierling 1991). The heat shock response involves repression of the synthesis of most normal proteins and mRNAs, and the initiation of transcription and translation of a small set of heat shock proteins (Vierling 1991). Studies of loss-of-function mutants of Arabidopsis thaliana demonstrated that the enhanced thermotolerance can be associated with at least three independent effects: the synthesis of a novel set of proteins (specifically Hsp101), protection of membrane integrity, and recovery of protein activity/synthesis (Queitsch et al. 2000). In order to combine multiple sources of heat tolerance, recurrent selection has been employed in diploid potato resulting in a 27% increase in yield in a single cycle of recurrent selection and is being employed to combine heat and drought tolerance in common bean.

Considered to be the most important environmental factor influencing the quality and yield of potato (Rykaczewska 2013), high temperature affects various biochemical and physiological processes in potato plants. High temperature negatively affects the tuber initiation and development by inhibiting the tuberization signal, StSP6A (Navarro et al. 2011). High temperature also causes nutrient source–sink problems by decreasing the carbon assimilation in tubers and inhibition of tuber filling (Krauss and Marschner 1984). Hence, high temperature, in turn, leads to reduced tuber quality and yield. Heat stress also causes a decrease in photosynthesis by decreasing the gas exchange and chlorophyll biosynthesis (Reynolds and Ewing 1989).

The heat stress causes osmotic and oxidative stresses in plants. Plants have evolved different defense mechanisms, such as avoidance and tolerance, activated under osmotic and oxidative stresses. Extended periods of drought or high temperatures lead to the production of reactive oxygen species, which are cytotoxic in high concentrations. Because reactive oxygen species are not only toxic but also participate