

Rajib Roychowdhury
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Sangeeta Srivastava *Editors*

Sustainable Agriculture in the Era of Climate Change



Springer

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Rajib Roychowdhury • Shuvasish Choudhury
Mirza Hasanuzzaman • Sangeeta Srivastava
Editors

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Preface

Since ancient times, human beings have been dependent on agricultural production, and previously the production systems were more natural and sustainable. Presently, climate change and global population increase jointly challenge sustainable agriculture and crop productivity. One of the imposing tasks for crop researchers globally is to diminish the negative effects of climate change on crop biology, especially in relation to yield and nutritive values of the harvested products of cereals, legumes, vegetables and fruits. This is of special significance in view of the impending climate change, with complex consequences for economically profitable and both ecologically and environmentally sound global agriculture. The challenge at the hands of the crop scientist in such a scenario is to promote competitive and multifunctional agriculture, leading to the overall crop improvement in a sustainable agricultural system. Hence, crop improvement is an urgent need for us to feed the ever-increasing world population. As a result of continuous climatic changes in the form of environmental hazards, abiotic stresses (water scarcity, salinity, high and low temperature, heavy metals and metalloids, oxidants, and others), high disease incidents, global warming, etc., natural and cultivated habitats of crop plants are continuously disturbed. Crop productivity and biology are seriously affected by such changing patterns. Beyond such kind of hazardous barriers, this book is aimed at crop improvement through sustainable agricultural processes.

In this book *Sustainable Agriculture in the Era of Climate Change*, Chap. 1 emphasizes the landraces of the crops which serve as the genetic stock having the many useful alleles/genes and can bridge between their genetic progenitors and modern cultivars and to utilize them in the modern breeding program. Chapter 2 is focusing on how to improve the grain damage of cereals due to pre-harvest sprouting and late maturity for gearing up production. Chapters 3 and 4 are dealing with the macro- and micronutrients for better crop development and physiological productivity. Chapter 5 describes the plant-mediated mitigation strategies of air pollution in the environment caused by the urbanization of lands. Chapters 6 and 7 are depicting the drought stress responses of crop plant and mitigation strategies with special aid from the involvement of silicon. Chapters 8, 9, and 10 are providing scientific background of crop plants that cope with salinity, high temperature, and

irradiation stress, respectively. As a part of abiotic and biotic stress response pathways, reactive oxygen species (ROS) are formed and needed to activate the crop's anti-oxidant mediated mitigation pathways, which are described in Chaps. 11 and 12. Chapter 13 is providing heavy metal-based tolerance of crops. More specifically, arsenic becomes a serious threat to contaminate the crops and human health. Chapters 14 and 15 are describing the arsenic stress response of plants and their signaling pathways to mitigate the serious issues caused by such metalloids. Chapter 16 is providing the idea of heme oxygenase enzyme activity for its role to mitigate the stress conditions. In organic agriculture, plant growth-promoting rhizobacteria (PGPR) are found to be very useful for crop's stress tolerance and it is described in Chaps. 17. 18 is focusing on different tissue cultural methods to propagate the crop *in vitro*. Chapter 19 is showing the involvement of different state-of-the-art omics technologies that can be utilized in crop stress response research. Chapter 20 is describing microbial influences for crop's abiotic stress response. Chapter 21 is briefing molecular mechanism of plant-pathogen interaction for disease resistance of crop plants. Chapter 22 is focusing on the role of small RNA or microRNA (miRNA) for crop's abiotic and biotic stress tolerance. Chapter 23 is dealing with the transgenic improvement of crops and Chap. 24 is describing the utilization of very new gene-editing tool CRISPR/CAS for crop improvement. Different bioinformatics tools and their utilization for crop improvement research have been detailed in Chap. 25. Chapter 26 is emphasizing on nano-biotechnological utility in crop's stress tolerance. Chapter 27 is describing how to improve crop's agrobiodiversity with special reference to the underutilized cereals "millets" which can be an alternative source of carbohydrate and nutrition for the global population. Thus, *Sustainable Agriculture in the Era of Climate Change* covers a wide range of topics under present-day environmental challenges, agronomy and agriculture processes, and biotechnological approaches.

We are grateful to all the authors/contributors who gave their valuable time to write the scientific chapters within the deadline for the possible success of this book. We shall be highly thankful to the readers for pointing out the errors and omissions which, in spite of all care, might have crept in. All suggestions for further improvement of this edited volume will be highly appreciated and accepted. We, along with all the contributors, apologize to those researchers for the parts of their work that could not be cited in this edited volume/chapters due to the space limitation.

We are highly thankful to Kenneth Teng (Publishing Editor, Springer Nature, New York), Jacco Flipsen (Vice President, Springer, New York), Eric Schmitt (Managing Director, Springer International Publishing AG, New York), Nicholas DiBenedetto (Editorial Assistant, Springer Nature, New York), Saveetha Balasundaram (Production Editor for Springer Nature, SPi Global, Chennai, India), Mario Gabriele (Senior Project Manager, SPi Global, Chennai, India), Anthony L Dunlap (Project coordinator, Springer Nature, New York), and other members of the editorial staff for their approval of this book project, prompt and timely responses during the acquisition, production coordination and support, formatting, proof checking, and editorial corrections in the manuscripts to make this volume complete and publishable.

In this book *Sustainable Agriculture in the Era of Climate Change*, the diverse chapters are contributed by experienced, highly dignified, and internationally reputed scientists, researchers, and academicians from around the world who have worked on the challenging problems of achieving crop improvement in the variable environments. Every chapter has been written in such a way that it deals with the theoretical as well as applied aspects of its specific theme. Hope such hot topics will be helpful to formulate the future keys toward the crop improvement in the present challenging and changing climate. This book has been written for a wide range of readers with easy-to-understand tables and simplified diagrams.

We believe this book will be very useful for scientists, researchers, and students working in the fields of agriculture, plant science, environmental biology, and biotechnology.

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About the Editors



Rajib Roychowdhury is presently working as Postdoctoral Visiting Scientist at the Institute of Plant Sciences of Agricultural Research Organization (ARO) – Volcani Center, Ministry of Agriculture and Rural Development, Israel. His current research is focusing on Genetics and Breeding of Berry fruits (strawberry, blueberry, raspberry) to improve yield and quality under Mediterranean climate. In the postdoctoral tenure, Dr. Roychowdhury extensively worked on Winter Cereal Genetics and Breeding, especially to improve wheat in Israeli semi-arid environments (a part of fertile crescent of wheat domestication) using diverse genetic stocks like modern cultivars, landraces, durum, spelt, dicoccum, emmer, etc. Dr. Roychowdhury received his Ph.D. in Plant Biotechnology from Visva-Bharati Central University (India) for research on previously unreported rice landraces for their agromorphology, grain quality, and abiotic stress tolerance. Later, he also did short-term postdoctoral research on “Metalloid stress tolerance in rice” under a CSIR project (Government of India) from Assam Central University, Silchar, India. During master’s and post-master’s tenure, he worked a lot on mutation breeding in Carnation, which was a pioneering work on this floricultural crop in South-East Asia. Dr. Roychowdhury was elected as a Fellow Member of the Linnaean Society of London, UK. His biography was published in the Pearl Edition of Marquis Who’sWho of the World, USA. In 2019, he got the travel award by International Wheat Initiative (Germany) for presenting his research in the 1st International Wheat Congress

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Chapter 1

Stress Management in Crops by Utilizing Landraces: Genetics and Plant Breeding Perspective



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Abstract Native germplasm is often the untapped resource that is supposed to hold the key to unlocking nature's repository of stress overcoming genes of crop plants. With an increasing global population, crop plants are expected to yield more under a variety of environmental conditions, hence exposing them to severe stress conditions. Locally available landraces of various crop plants that are often ignored in the presence of high-yielding developed varieties, however, have survived environmental turmoil over the ages and thus are the urgent need of the hour in order to couple yield or another desirable trait with stress tolerance. To bring these landraces to use, various mechanisms by which they tolerate environmental stress need to be understood. The use of conventional breeding techniques such as hybridization, selective backcrossing, gene pyramiding, etc. along with modern techniques such as mutagenesis, use of genetic markers, development of transgenic crops, etc. enables the use of trait diversity of landraces to counter environmental stresses while maintaining crop productivity. This chapter deals with various methods for identification of causal genetic factors responsible for stress tolerance in crop landraces and the possible techniques for developing tolerant varieties in the face of increasing frequency and severity of biotic and abiotic stresses.

Keywords Stress management · Landraces · Genetics · Plant breeding · Domestication

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1 Introduction

The process of crop domestication is closely associated with the various agricultural practices, human preferences, and the changing environment (Meyer et al. 2012; Smýkal et al. 2018). With the change in climate or environment and changing patterns in the use of natural resources, plants have been subjected to a variety of stresses. This led to the process of development and evolution of different adaptive strategies that permit plant cells to sense environmental stimuli and to activate responses that allow avoidance or survival of the environmental stresses encountered. The interaction of genotype and environment, which affects both agricultural practices and crop yield, is a critical point of research during the development of stress-tolerant plants under different field regimes (Mohammed 2009; Yumurtaci 2015). In the process of domestication, plants emerged in variable types, some as wild types, landraces, or the traditional domesticated genotypes. The crops plants have been globally dispersed with the spread of humans or evolution and due to various other environmental factors such as wind, water, or different natural disaster creating a geographical barrier. The crop plants thereby varied across the world based on the different process of cultivation and in accordance served to be the landrace to a particular area. The residues of the ancient crops undergo a very slow process of domestication like that of an evolutionary process, making the crop tolerant or highly diverse (Tanno and Willcox 2006; Smýkal et al. 2018).

Stress can be defined, in the widest biological sense, as any factor that may produce an adverse effect in individual organisms, populations, or communities. It is also defined as the overpowering pressure that affects the normal functions of individual life or the circumstances in which plants are interrupted from fully expressing their genetic potential for overall growth, development, and reproduction (Rhodes and Nadolska-Orczyk 2001). As per the agricultural viewpoint, stress includes the external factors that limit crop productivity or destroys biomass (Grime 1979). Stress can be biotic or abiotic in nature. Biotic stresses emerge through interactions between organisms, whereas abiotic stresses are those that depend on the interaction between organisms and the physical environment. Abiotic stresses, which include the various external factors of disturbance, are often interrelated, and either individually or in combination, they hamper the physiological, biochemical, and molecular processes that adversely affect plant growth and productivity. The combined effect of the stress factors is based on its nature of interactions with its effect on the crop plants ranging from germination stage to grain filling. Crop plants in response to stress undergo a series of modifications and process of adaptations that includes both morphological and genetic changes such as genome rearrangement, induction of various tolerance genes, etc., as per its ability to tolerate the adverse effect (Tester and Bacic 2005; Pandey et al. 2017). Plants to withstand against the stress effect induce a series of regulatory mechanisms which are either constitutively expressed or induced (Roy et al. 2014; Pradhan et al. 2019). Thereby, understanding the genetic regulatory mechanism of the landraces against the stress effect and its ability to adapt to such adverse conditions serves as a source to identify or understand the process of tolerance against stress.

Breeding approach to enhance the crops' ability to adapt adverse stress conditions though due to various effects of cultivation bottleneck that has a negative impact on crop production must be a continuous process with an added focus on the different stress factors in addition to its yield (Bertoldo et al. 2014). Application of constant monitoring of the individuals using the modern noninvasive method as well as sequencing of the genotype helps in the proper screening of the crops for its application in breeding and development of cultivar with high adaptability. In the majority of the cases toward the increase of the agronomic value of cultivated crops, its genome structure, the type of stress factors exposed, and the variable environmental conditions help in the proper selection of the suitable strategies (Yumurtaci 2015). So there is a need to build effective crop screening methods and use the prevalent crop biodiversity on the basis of present technical advancements for the detailed evaluations of the different type of landraces which will enhance and improve the efficiency of breeding and crop improvement.

With advances in fields like physiology, molecular biology, and genetics, our understanding of crops' response to stress and the basis of varietal differences in tolerance have greatly improved. In this chapter, the biotic and abiotic stress management of crops by utilizing landraces and their wild relatives through plant breeding and genetic approaches are addressed.

2 Crop Landraces and Their Significance

Landraces include a group of progressive cultivated plant populations with a distinct location of origin and specific distinguishing characters, with high genetic diversity and ability to adapt variable local weather conditions. The process of landrace origin includes the set of seed selection practices or the crop domestication by farmers and the process of field management as per the different agricultural practices by farmers which vary with the area (Fuller 2007; Casañas et al. 2017). As reported by Dwivedi et al. (2016), plant landraces encompass mainly the domesticated plant species with heterogeneous local adaptations which provide the genetic elements required to meet the growing challenges of farming crops in stressful environments. These local heterogeneous genotypes with wide genetic diversity show changing phenotype with its yield ranging from low to moderate level but with high nutritional quality. Thereby, landraces with high ability to cope with stress factors include the traditional cultivars with high nutritional content and yield ability under low input system of agriculture (Zeven 1998; Azeez et al. 2018). A landrace which serves as the repository of various mechanisms of tolerance completely varies from that of the new selectively improved cultivar or variety developed by breeder taking into account a specific trait. Landraces with high genetic diversity and different traits responsible for adaptation to adverse conditions thereby serve as the source of efficient crop development using plant breeding techniques contributing mainly toward the efficient traits of nutrient uptake, utilization, and genes of tolerance against stress conditions. An unambiguous evaluation of the landrace with the

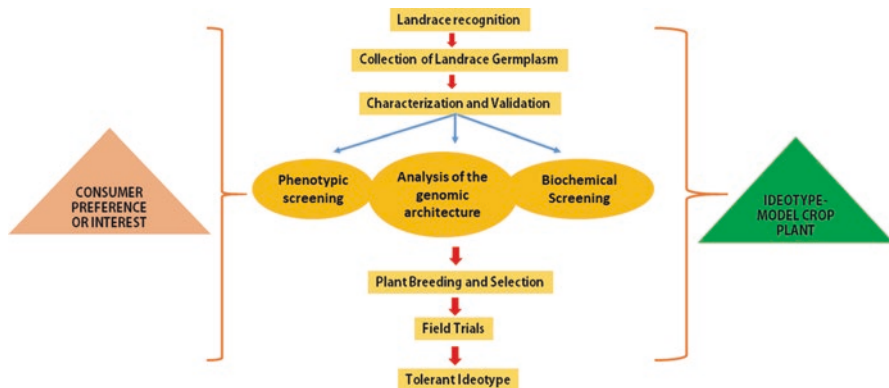


Fig. 1.1 Schematic representation of the process of landrace utilization in crop breeding programs

improved techniques of identification (Fig. 1.1) may uncover the different patterns of diversity present, which will expedite in identifying alleles/gene loci for increasing growth, yield, and adaptation to stress, thus increasing the productivity and stability of staple crops in vulnerable environments.

Landraces are normally low yielding and less productive in comparison to the developed commercial varieties, but with the advancement in modern research in the recent years, they now serve as the repository source of genetic variability in the search for genes or traits responsible for tolerance or resistance to biotic and abiotic factors for the proper establishment of agriculture in that specific locality (Casañas et al. 2017). However, the intense use of developed varieties or transgenic plants led to decrease in use, management, and conservation of local landraces, thereby causing less presence of the agronomic or genetic data of the landraces which appear to be of great importance with changing the environment. Zeven (1998) proposed the importance and role that landraces played in the development of the crop worldwide and also its role in the improvement of crops and agricultural production which served to have been in existence since the origin of agriculture itself. Since the time of origin of agriculture, landraces have been subjected to various natural genetic modifications which include both the abiotic and biotic interventions, leading to the development of a mechanism of adaptation and tolerance (Bansal et al. 2014). Crop landraces are thereby the principal focus for the development of the agricultural system from century's immemorial (Umakanth et al. 2017). The traditional process of farmers sowing, harvesting, and storage of some proportion of seeds for sowing in the subsequent season highly enriched the genetic pools promoting intraspecific diversity (Frankel et al. 1998). This traditional concept of crop cycle for conservation and maintenance of crop landrace with the beginning of plant breeding leading to generation of generally higher-yielding cultivar resistant to specific stress subsequently replaced the traditional process leading to decrease in diversity and gene pool, thereby causing downfall to agricultural production in the present condition (Frankel and Hawkes 1975; Casañas et al. 2017).

Hawkes (1983) remarked landraces as crops associated to one specific geographical area in contrast to that of cultivars, which are bred and trialed in diverse locations seeking its ability of tolerance to that of the trait opted for. Thus, landraces of a particular location are highly specific to that particular location and with most of the landrace nomenclature taken as per the name of the location likewise the Kent Wild White Clover from Kent, UK. However, various ecological factors often led to the introduction of informal landrace varieties and migration of traditional landraces from native region to new regions.

The occurrence and maintenance of landrace germplasm include various processes like that of seed exchange or replacement among farmers in a geographical area (Louette and Smale 1996). The process of continuous cultivation by an individual farmer or discontinuous but collective cultivation of landraces also forms a significant process of maintenance. Therefore, open cultivation system with routine local or the remote introduction of landrace germplasm serves as the major process for the maintenance and occurrence of genetic diversity among landraces belonging to a particular location.

3 Genetic Mechanisms of Plant Against Different Stresses

Plants respond to various stresses with alterations in different gene expressions. Genes that are induced by the effect of biotic or abiotic stresses often impart stress tolerance to the plants. Genes induced by stress include functional genes or regulatory genes. Stress response genes also induce the activation of antioxidant response pathways and protection against damage from oxidative injury. Salinity, drought, heat, cold, heavy metals, radiation, and submergence are various abiotic factors responsible for stress in plants, whereas pathogens also induce biotic stress in plants. Genes responsible for stress tolerance have been identified in many plants for a variety of stresses, and overexpression of such genes in transformed plants has been shown to result in increased tolerance.

3.1 Salinity

Salinity induces both osmotic and ionic stress in plants. The salt overly sensitive (SOS) pathway is an important mechanism maintaining ion homeostasis during salt stress. The SOS signaling pathway comprises of three important genes, *SOS1*, *SOS2*, and *SOS3* (Ji et al. 2013). Maintenance of ion homeostasis is a key response to salt stress, where Na^+ extrusion is the primary process, providing tolerance to the plant against salt. Elevation in Na^+ levels disrupts enzymatic functions and is toxic to plant cells. During salt stress, a Ca^+ spike activates the cascade of SOS signal transduction in the root cell cytoplasm. *SOS3* is responsible for activation of a primary Ca^+ sensor, and with the binding of Ca^+ and *SOS3*, the *SOS2* gets activated.

In shoots, however, S_{Ca}BP8 (SOS3-like calcium-binding protein 8) is the dominant activator of SOS2. Activation of SOS2 recruits it to the plasma membrane, thereby activating the downstream target SOS1. SOS1 is a Na⁺/H⁺ antiporter, and its activation leads to the extrusion of Na⁺. *SOS1* mutants are found to be highly sensitive to salt (Ji et al. 2013). High-affinity potassium transporter (*HKT*) genes are also involved in ion exclusion. *HKT2* has been found to increase salt tolerance through Na⁺ exclusion (Roy et al. 2014). Tolerance to salinity is also achieved by sequestration of Na⁺ to vacuoles by vacuolar Na⁺/H⁺ antiporters such as OsNHX1, OsNHX2, OsNHX3, and OsNHX4 in rice. Activities of Na⁺/H⁺ antiporters increase during salinity, and the increase is found to be more in case of tolerant plants. Increased expression of *OsNHX1* leads to increased tolerance due to Na⁺ compartmentalization in vacuoles and also increases tolerance in transgenic rice plants. Upregulation of *OsHKT1;1*, *OsHAK10*, and *OsHAK16* leads to increased Na⁺ accumulation in old leaves and is an important stress adaptive feature in rice (Reddy et al. 2017).

High salinity induces the biosynthesis of abscisic acid (ABA) hormone that leads to the closure of guard cells and helps plants to overcome osmotic stress occurring due to salinity. Jasmonic acid (JA) is important in the ABA-dependent regulation of salinity response genes. Homologues of the JASMONATE ZIM DOMAIN (JAZ), *OsTIFY1*, *OsTIFY6*, *OsTIFY9*, *OsTIFY10*, and *OsTIFY11* have been identified in rice. Several protein kinases (MAPK, RLK, etc.) are also parts of the ABA-dependent pathways of regulation of gene expression besides transcription factors such as *ONAC022* and microRNAs. Transcription factors such as DREB (dehydration-responsive element-binding protein) are important in ABA-independent pathways. Overexpression of *OsDREB1A*, *OsDREB1F*, and *OsDREB2A* has improved salt tolerance in transgenic rice. Genes such as *PDH45*, *OsCPK12*, etc. regulate the accumulation of ROS during salt stress and improve tolerance to salinity (Reddy et al. 2017).

3.2 Drought

Drought induces osmotic stress in plants. Expressions of late embryogenesis abundant (LEA) proteins involved in protection against desiccation are upregulated during drought. Overexpression of some LEA class genes has led to increased tolerance to dehydration. A gene coding for galactinol synthase (*Gols*), which is involved in the biosynthesis of raffinose family oligosaccharide, has enhanced drought tolerance in transgenic *Arabidopsis*. Gene expressing raffinose synthase is also upregulated during drought. Raffinose functions as an osmoprotectant and alleviates cellular damage during drought stress (Shinozaki and Yamaguchi-Shinozaki 2007). Methionine sulfoxide reductase (MSR) proteins encoding gene *MsrB2* induces tolerance to drought in terms of reduction of oxidative injury by ROS. *CaMsrB2* from *Capsicum annuum* overexpressed in transgenic rice has improved rice tolerance to drought (Nahar et al. 2016).

DRE/CRT (dehydration responsive element/C-repeat) regulons cooperatively with ABRE (ABA-responsive element) regulate the expression of *RD29A* gene encoding LEA-like proteins. *RD29B*, also encoding for LEA-like proteins, is regulated by ABRE elements. Drought induced *DREB* genes to regulate the expression of several drought tolerance genes. Overexpression of *DREB1A* in transgenic rice increases drought tolerance. *DREB2* genes are also induced by drought stress. However, overexpression of *DREB2* does not result in increased drought tolerance in transgenic plants, which suggests that DREB2 protein requires posttranslational activation (Nakashima and Yamaguchi-Shinozaki 2006). Two basic leucine zipper (*bZIP*) transcription factors AREB/ABF activate ABA-dependent gene expression by binding to ABRE. Overexpression of *ABF3* or *AREB2/ABF4* leads to ABA hypersensitivity and reduces transpiration, enhancing drought tolerability of transgenic *Arabidopsis* plants. Transcription factors *AtMYC2* and *AtMYB2* cooperatively activate the *RD22*, a drought-inducible gene, following the accumulation of endogenous ABA. Overexpression of both *AtMYC2* and *AtMYB2* enhanced osmotic stress tolerance in transgenic plants (Shinozaki and Yamaguchi-Shinozaki 2007).

3.3 Heat

Thermo-tolerance in plants is measured in terms of cell membrane thermostability (CMS). QTL and co-segregation analyses revealed several heat shock proteins to be the genetic cause of thermo-tolerance in many cereals. Thermo-tolerance is not controlled by a single gene in cereals (Maestri et al. 2002). Heat stress results in the expression of heat shock genes (*HSG*) that encode heat shock proteins (HSP). Heat shock factors (HSF) bind to the specific binding sites of Heat Shock Elements (HSE) in the promoters of HSGs, inducing the expression of HSPs on heat treatment. HSPs act as chaperones and protect intracellular proteins against denaturation, maintaining their structural stability through protein folding and keeping their functions intact. HSPs are categorized on the basis of their molecular mass, viz., HSP100, HSP90, HSP70, HSP60, and HSP20 (sHSP). Small heat shock proteins (sHSPs) show the highest diversity among all the HSPs (Hasanuzzaman et al. 2013). All sHSPs have a conserved 90-amino acid carboxyl-terminal domain, the α -crystallin domain (ACD). ACD distinguishes sHSPs from other heat-induced proteins. Tolerance to heat stress is induced in sHSP-overexpressing plants (Sun et al. 2002). *HSP70* and *HSP101* are involved in heat stress tolerance in *Arabidopsis*. Three *HSP101* members, *Tahsp101a*, *Tahsp101b*, and *Tahsp101c*, have also been cloned in wheat (Maestri et al. 2002). *Hsp17.7* and *Hsp100* have been found to confer thermo-tolerance in transgenic plants overexpressing these genes. *NPK1*-related transcripts are significantly elevated by heat. Constitutive overexpression of H_2O_2 -responsive *ANP1/NPK1* was found to increase protection against heat stress in tobacco. Overexpression of *APX1*, coding for antioxidant ascorbate peroxidase, was also found to confer moderate heat tolerance in barley (Hasanuzzaman et al. 2013).

DREB2A in its active form during high-temperature stress regulates the expression of heat shock-related genes (Sakuma et al. 2006). Heat induces the expression of many HSFs. Plants have multiple copies of HSF genes. Heat stress regulatory proteins have conferred thermo-tolerance in transformed plants. *Arabidopsis HSF1a* and *HSF1b* control early response of many genes to heat. *HSF1* has been proposed to be the master regulator of heat shock response in tomato (Hasanuzzaman et al. 2013).

3.4 Cold

A number of functional and regulatory genes in plants respond to cold stress. Desaturation of fatty acids is important for membrane functioning during cold stress. Glycerol-3-phosphate acyltransferase (*GPAT*) gene from *Cucurbita maxima* and *Arabidopsis thaliana*, which induces desaturation of phosphatidyl glycerol fatty acid, results in an increase in unsaturated fatty acids in transgenic tobacco plants and reduces cold sensitivity. Mutants of *FAB1* (involved in fatty acid biosynthesis), *fad5*, and *fad6* or triple mutants of genes *fad3-2*, *fad7-2*, and *fad8* (genes involved in fatty acid desaturation) lead to increase in saturated membranes and show decrease in chlorophyll content and photosynthetic efficiency and growth retardation during cold stress, suggesting their significance in low-temperature tolerance. LEA proteins functioning against cellular damage and anti-aggregation of enzymes under freezing stress increase plant cold tolerance. *Arabidopsis* genes *LOS4* and *AtNUP160* responsible for the export of RNA from the nucleus to the cytoplasm are also crucial for chilling and freezing tolerance in plants (Sanghera et al. 2011).

Transcriptional regulation during cold stress is mediated by *ICE1* [inducer of C-repeat binding factor (*CBF*) expression 1]. *ICE1* induces expression of *CBF3*, which in turn regulates transcription during cold stress. *CBFs* regulate genes involved in membrane transport and hormone metabolism, phosphoinositide metabolism, osmolyte biosynthesis, ROS detoxification, and signaling (Chinnusamy et al. 2007). *DREB1A/CBF3*, *DREB1B/CBF1*, and *DREB1C/CBF2* regulons are found to be involved in cold stress-responsive gene expression. The products of cold-induced *DREB1/CBF* genes regulate the expression of many stress-inducible genes. Overexpression of these genes in transgenic *Arabidopsis* led to increased tolerance to freezing. *ICE1* gene was found to regulate the expression of *DREB1A* promoter without affecting the other *DREB1/CBF* genes. A homologue of *DREB1/CBF*, *LeCBF1* from tomato was found to induce freezing tolerance in transgenic *Arabidopsis*. Novel *DREB1/CBF* transcription factor, *ZmDREB1A*, from maize was found to regulate cold-responsive gene expression (Nakashima and Yamaguchi-Shinozaki 2006).

3.5 Heavy Metal

Heavy metals lead to the onset of oxidative injury in plants (Roychowdhury and Tah 2011h; Basu et al. 2012; Roychowdhury et al. 2018, 2019). In *Arabidopsis thaliana*, cadmium uptake induces expression of *Atcys-3A*, which is involved in cysteine biosynthesis under heavy metal stress. Cysteine is the precursor in glutathione biosynthesis, which in turn is required for phytochelatin production. Phytochelatin binds to heavy metals and increases plant tolerance against heavy metal stress. Transformed *Arabidopsis* plants overexpressing *Atcys-3A* have shown increased tolerance to cadmium (Domínguez-Sofis et al. 2001). *CABPRI* overexpression in tobacco also showed increased tolerance to heavy metal stress (Sarowar et al. 2005). In rice, *OsPIP2;6* has been demonstrated to play a role in As^{3+} efflux, thereby increasing plant tolerance against arsenic. Transgenic *Arabidopsis thaliana* overexpressing *PvACR3* from *Pteris vittata*, involved in vacuole sequestration of arsenic, have been shown to have increased tolerance to arsenic (Kalita et al. 2018).

3.6 Radiation

Transcript levels of *PyroA*, *Ubp3*, and *MEB5.2* were found to be increased by a low dose of UV-B radiation. *PyroA*, involved in the biosynthesis of pyridoxine, is important in protection of cellular structures against singlet oxygen. *Ubp3* encodes ubiquitin, associated with protein degradation. *MEB5.2* is a novel gene with unknown function (Brosche et al. 2002). Plant flavonoids are important secondary metabolites that protect against UV-B exposure, due to its absorbance in this wavelength region and elevation of its levels in epidermal cell layers. Flavonoids are also found to inhibit oxidative stress. Flavanone 3-hydroxylase (F3H) is a key enzyme in the flavonoid biosynthetic pathway, which is encoded by *RsF3H* in *Reamuria soongorica*. *RsF3H* gene expression and enzyme activity increase rapidly under stress (Liu et al. 2013).

3.7 Submergence

A QTL for submergence response in rice, *Sub1*, has been identified near the centromere of chromosome 9 of rice. *Sub1A*, *Sub1B*, and *Sub1C* are three genes identified in the *Sub1* locus, of which *Sub1B* and *Sub1C* are present in all genotypes. *Sub1A* which is the variant gene has two alleles, of which *Sub1A-1* is specific for submergence tolerance and *Sub1A-2* is specific for intolerance. *Sub1A-1* overexpression has been found to confer submergence tolerance in transgenic rice (Xu et al. 2006).

3.8 Biotic Stress

Expressions of various regulatory genes determine tolerance or susceptibility to biotic stress caused by pathogen attack (Mamgain et al. 2013). ABA-independent dehydration-responsive *DREB2A* signaling pathways were found to crosstalk with *adr* signaling pathways, associated with disease resistance (Agarwal et al. 2006). Transgenic tobacco plants constitutively expressing *OsDREB1B* were found to induce pathogenesis-related (PR) gene expression. The promoter of *OsDREB1B* contains several disease-responsive cis-elements, and transgenic tobacco overexpressing *OsDREB1B* has shown reduced disease manifestations and delayed systemic infections with induced expression of PR genes such as *PR1b*, *PR2*, *PR-3*, *PR5*, and *CHIN50* (Gutha and Reddy 2008). Plants overexpressing *OsEREBP1* showed the reduced impact of the fungus *Magnaporthe grisea* where transcriptome analysis revealed high expression of transcription regulators belonging to the NAC and WRKY families (Jisha et al. 2015). Overexpression of *MBF1a* transcriptional coactivator gene has been found to induce resistance to fungal disease in *Arabidopsis* (Kim et al. 2007). Rice 14-3-3 family genes *GF14b*, *GF14c*, *GF14e*, and *GF14f* are differentially regulated in the interactions of rice with fungal pathogen *Magnaporthe grisea* and bacterial pathogen *Xanthomonas oryzae* pv. *oryzae*. 14-3-3 proteins act as scaffoldings for the assemblage of large signaling complexes and are potential factors in disease resistance and tolerance of stress. Response of 14-3-3s in defense against pathogens has also been reported in many other plants such as soybean, cotton, and tomato (Chen et al. 2006). Rice gene *Osmyb4* which encodes an Myb transcription factor leads to the upregulation of several genes with known functions in resistance against pathogens. Myb is effective in induction of systemic acquired resistance (SAR) (Vannini et al. 2006). Overexpression of *SIAREB1*, a member of the AREB/ABF subfamily of bZIP transcriptional factors, from *Solanum lycopersicum* has been found to enhance the expression of PR proteins (Orellana et al. 2010). NAC transcriptional factors are important in plant pathogen interactions. NAC proteins activate PR genes, induce hypersensitive response (HR), and result in cell death at the infection site. Some NAC proteins, however, also increase the susceptibility of plants against pathogens. *ATAF2* overexpression was found to increase susceptibility toward *Fusarium oxysporum* by repressing PR genes. *ATAF1* increases resistance against *Blumeria graminis* f. sp. *graminis* (Bgh) but reduces resistance against *Pseudomonas syringae*, *Botrytis cinerea*, and *Alternaria brassicicola* (Puranik et al. 2012). Overexpression of *OsNAC6* in transgenic rice has led to increased tolerance against blast disease (Nakashima et al. 2007).