

Shabir Hussain Wani *Editor*

Recent Approaches in Omics for Plant Resilience to Climate Change

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Mountain Research Centre for Field Crops
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Prof. Sudhir Kumar Sopory is an Indian academician and eminent plant molecular biologist. He is a stalwart of Indian Scientific Research with prominence in the areas of Molecular Plant Physiology, Stress Biology and Plant Biotechnology.

Prof. Sopory had his education first in the University of Kashmir for his graduate and postgraduate degree and then completed his doctorate at the University of Delhi in the field of Plant Molecular Biology. He began his academic career in the year 1973 as a faculty at the School of Life Sciences, Jawaharlal Nehru University, and worked there till 1996. His teaching and research career spans over 45 years inclusive of that as visiting scientist at Max Planck Institute

for Plant Breeding Research, Germany; visiting Fulbright fellow at the Department of Botany, University of Texas, USA, and Plant Molecular Biology Lab of the US Department of Agriculture, USA; and visiting Humboldt professor at the University of Munich, Germany.

He has broadly worked in the area of light signal transduction and plant stress biology. His group identified the involvement of a number of novel genes in abiotic stress responses and was the first to work out in details the role of glyoxalase pathway in plant stress biology. Many groups across the globe are now working on this pathway. His researches have been documented in over 250 articles published in peer-reviewed journals. He has been the editor of 13 books and has contributed more than 50 chapters to books written by others. He has also been the president of the Indian Society of Plant Physiology; the vice president of the National Academy of Sciences, Allahabad, India; Indian Society for Plant Physiology and Biochemistry; Indian National Science Academy, New Delhi; and Society for Plant Biochemistry and Biotechnology, New Delhi, and is a former secretary of the Plant Tissue Culture Association of India.

Prof. Sopory has been recipient of many national and international honours for his pioneering contributions to scientific research and teaching, including the 1987 Shanti Swarup Bhatnagar Prize by CSIR, the highest Indian award in the Science and Technology categories. Some of the other notable awards include the Chakravorty Award, Birbal Sahni Medal of the Botanical

Society, Birbal Sahni Birth Centenary Award of Indian Science Congress, Godnev Award Lecture of Belarus Academy of Sciences, T. N. Khoshoo Memorial Award, B. M. Johri Memorial Award, NASI Prof. R. N. Tandon Memorial Award, and Padma Shri, the fourth highest civilian honour by the Government of India. He is an elected fellow of several major Indian science academies, namely, the Indian National Science Academy (New Delhi), Indian Academy of Sciences (Bangalore), National Academy of Sciences (Allahabad), National Academy of Agricultural Sciences (New Delhi), as well as The World Academy of Sciences (Trieste, Italy). He is the first Indian to receive Corresponding Membership Award of the American Society for Plant Biologists in 2010.

After he left JNU in 1996, he joined the International Centre for Genetic Engineering and Biotechnology, New Delhi, as a group leader of research in plant molecular biology and also became the interim director of the institution. He was the eleventh vice chancellor of the Jawaharlal Nehru University from Jan. 2011 to Jan. 2016. He was appointed as Arturo Falaschi emeritus scientist at ICGEB, New Delhi, since 2016, and currently, he is working as SERB distinguished fellow of the Dept. of Science and Technology, Government of India, at ICGEB, New Delhi.

Foreword

I am pleased to hear that Dr. Shabir Hussain Wani has edited this volume entitled *Recent Approaches in Omics for Plant Resilience to Climate Change* for the well-renowned publisher, Springer Nature. I personally know him since the year 2009 when he was working as research associate in the Biotechnology Laboratory at the ICAR-Central Institute for Temperate Horticulture, Srinagar, Jammu and Kashmir, India. He had a good experience to work in the area of plant biotechnology particularly the *omics* techniques for abiotic stress tolerance in plants. I was overwhelmed with his passion and dedication for science, including research, teaching, and dissemination of scientific knowledge. Hence, this is the book edited by him in the area of *omics* approaches. Therefore, a book coming from him in the said area for plant resilience to climate change is a commendable task.

Climate change has led to many aberrations in extreme temperatures and increases in other abiotic stresses which hinder plant growth and productivity. Recent *omics* approaches are the key to overcome such limitations and can help in opening vistas for novel approaches of improving plant resilience to major stresses which are otherwise very slow or impossible with the conventional plant improvement approaches like plant breeding. Climate change has resulted in the widespread occurrence of abiotic stresses, such as drought, extreme temperatures, salinity, etc. These stresses are responsible for the reduction in yields in many crop plants worldwide. While noteworthy developments have been made in unravelling the plant resilience to abiotic stresses, due to the complex and quantitative nature of these resilience traits, very less success has been achieved through the conventional plant breeding approaches. Many novel omics technologies, including genomics, proteomics, metabolomics, and ionomics, have progressed during the last few decades to scientifically investigate the changes in the genome, transcriptome, proteome, and metabolome, which are occurring as a result of various changes in plants' response to changing stress conditions. This book by Dr. Wani is an emerging area of plant science and is more demanding in both the developing and developed nations as efforts are being made to elucidate the molecular mechanisms underlying the complex traits of stress tolerance in plants.

Dr. Wani has done an excellent effort by bringing up this volume comprising of high-quality chapters from the international- and national-level experts in various research fields. The 13 chapters included in this book are well written by experts including from various developed nations, such as the USA. Diverse chapters include the overview on *omics* approaches under changing climate and application of various *omics* approaches, including genomics, proteomics, and metabolomics, in important commercial crops, like rice, maize, cotton, chickpeas, etc. This book is a suitable reference source for academicians, researchers, and graduate students working in the area of climate resilience in plants using *omics* approaches. I congratulate Dr. Wani for editing this wonderful book volume.



Nazeer Ahmed
Sher-e-Kashmir University of Agricultural
Sciences and Technology of Kashmir
Kashmir, India

Preface

Human population is growing at a startling pace and assumed to exceed 9.7 billion by 2050, whereas, at the same time, the agricultural productivity is dwindling due to the growing environmental constraints as a result of global climate change. Climate change has resulted in pervasive episodes of abiotic stresses, such as drought, extreme temperatures, salinity, flooding, etc. These stresses are liable for the decrease in yields in many crop plants at global level. While significant accomplishments have been made in extricating the plant resilience to abiotic stresses, due to the multifaceted and quantitative nature of these resilience traits, very less success has been achieved through the conventional plant breeding approaches. Many novel omics technologies, including genomics, proteomics, metabolomics, and ionomics, have progressed during the last few decades to scientifically investigate the changes in the genome, transcriptome, proteome, and metabolome which are occurring as a result of various changes in plants' response to changing stress conditions. Through this book *Recent Omics Approaches for Plant Resilience to Climate Change*, an effort has been made to include chapters describing the implication of climate change on global food security and its management using the recent novel omics tools. This book is an incredible and a comprehensive reference material for researchers, teachers, and graduate students involved in climate change-related abiotic stress tolerance studies in plants using omics tools by unraveling principles of lately developed technologies and their application in the development of abiotic stress resilience in plants. The chapters are written by reputed researchers and academicians in the field of plant stress biology. I express sincere thanks and gratefulness to my venerated authors; without their untiring efforts, this book project would not have been possible. I am also thankful to Springer Nature for providing such an opportunity to complete this book project. I am thankful to all my family members, especially my wife, for their support during the language editing process.

Finally, I bow in reverence to Almighty Allah who gave me the intellect and strength to complete this book project.

Kashmir, India

Shabir Hussain Wani

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About the Editor



Shabir Hussain Wani is Assistant Professor (Senior Scale) at Mountain Research Centre for Field Crops, Khudwani—192101, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, J&K, India. He received his Ph.D. degree in plant breeding and genetics on “transgenic rice for abiotic stress tolerance” from the Punjab Agricultural University, Ludhiana, India. After obtaining his Ph.D., he worked as a research associate in the Biotechnology Laboratory, Central Institute of Temperate Horticulture (ICAR), Srinagar, India. He then joined the Krishi Vigyan Kendra (Farm Science Centre) as programme coordinator at Senapati, Manipur, India. He teaches courses related to plant breeding, seed science and technology, and stress breeding and has published more than 100 papers/chapters in journals and books of international and national repute. He served as guest editor and reviews editor for the journal *Frontiers in Plant Science* (2015–2018). He has also edited several books on current topics in crop improvement for abiotic stress tolerance published by Springer Nature and CRC Press USA. His Ph.D. research fetched first prize in the North Zone Competition, at national level, in India. He was awarded a Young Scientist Award from the Society for Promotion of Plant Sciences, Jaipur, India, in 2009. He is a fellow of the Society for Plant Research, India. Recently he also received the Young Scientist Award (Agriculture) 2015 from the Society for Plant Research, Meerut, India. He also served as visiting scientist in the Department

of Plant Soil and Microbial Sciences, Michigan State University, USA, under the UGC Raman Post-Doctoral Fellowship programme. Currently, he is leading the wheat improvement programme at MRCFC Khudwani SKUAST Kashmir.

Omics Technologies for Abiotic Stress Tolerance in Plants: Current Status and Prospects



Sahil Mehta, Donald James, and M. K. Reddy

1 Introduction

In nature, plants are complex, sessile organisms and are hence continuously exposed to a number of environmental stresses from vegetative to the post-reproductive stage (Jakab et al. 2005; Zhao et al. 2007; Mosa et al. 2017; Parida et al. 2018). These environmental factors have a detrimental effect on the growth, development, and productivity of the plant. Due to these stresses, there is a severe decline in plant yield and productivity due to the imbalance at cellular, molecular, physiological, and developmental levels (Xiong and Zhu 2002; Singh et al. 2018). These environmental factors are generally divided into two categories, abiotic and biotic stress. The abiotic stress factors include high and low temperatures, drought, salinity, freezing, heavy metals, high irradiance and ultraviolet (UV) light, and low oxygen conditions (Reyes and Cisneros-Zevallos 2007; Singh et al. 2018). The term biotic stress encompasses mainly pathogens and pests such as bacteria, fungi, viruses, insects, nematodes, rodents, etc. In the current scenario, abiotic stresses are poised to be most detrimental as they severely reduce crop yield and productivity. This is evident from the reports of the Intergovernmental Panel on Climate Change (IPCC) (<http://www.ipcc.ch>). The report concludes that in the near future abiotic stresses will delimit the productivity of standing crops more adversely because of global warming, depletion of water resources, deforestation, and anthropogenic activities (Singh et al. 2018).

S. Mehta (✉)

Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology,
New Delhi, India

D. James · M. K. Reddy

Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology,
New Delhi, India

Centre for Plant Biotechnology and Molecular Biology, Kerala Agricultural University,
Thrissur, India

In order to enhance stress tolerance and increase the plant productivity, the focus of research has already shifted toward understanding the key molecular targets, regulators, and their signaling involved in plant interactions with the environment (Mosa et al. 2017; Singh et al. 2018; Parida et al. 2018). In the past two decades, a new integrative “omics” approach has gained momentum in the plant biology research field, fueled by advancements in nucleic-acid sequencing platforms, peptide-sequencing platforms, mass spectrometry (MS) technology, advanced computational capabilities, and statistical methodologies. This is evident from the fact that the keyword “Plant omics” fetched 75,700 publications in Google Scholar website (<https://scholar.google.co.in>) in 2018. This integrative “omics” method gives a snapshot of the development, functioning, and interactions of a cell, tissue, or organism by characterizing and quantifying all its biomolecules in a high-throughput approach (Soda et al. 2015; Mosa et al. 2017; Parida et al. 2018).

2 Insights into Omics in Plant Abiotic Stress

In the past 20 years, research has shown that the plant’s response to stress is controlled by a set of genes being upregulated and downregulated dynamically. As a result, many researchers have applied various “omics” approaches to get an integrated view of the response of plants to various abiotic stresses (Govind et al. 2009; Mochida and Shinozaki 2010, 2011; Burgos et al. 2011; Witt et al. 2012; Bowne et al. 2012; Collino et al. 2013; Chen and Thelen 2013; Dubery et al. 2013; Duque et al. 2013; Cusido et al. 2014; Kumar et al. 2016; Freund and Hegeman 2017; Zhu et al. 2017; Parida et al. 2018; Gupta et al. 2018; Zhang et al. 2018a, b). Omics approaches have emerged as essential tools to address and understand the plant molecular systems and their functions; to gain insights into biological networks; and promote the translational research (Burgos et al. 2011; Kumar et al. 2016; Parida et al. 2018). Omics approaches are aimed at characterizing the plant’s biomolecule pool because these molecules play roles in maintaining homeostasis as well as signalling responses to altering environments. Although initially much work progressed in genomics, it became clear that an integrative approach involving the study of other omics levels, including transcriptional, proteomic, and metabolic profiles, and their flux distributions is essential for a more comprehensive understanding (Vidal 2009; Shen et al. 2018). Due to technical advances in the experimental protocols, data analysis, and visualization techniques, the expression, and activity of any gene, its interacting partners and regulators in the whole system can be studied at any time (Sussman et al. 2009). The advent of omics-based approaches has thus led to investigations on biologically relevant patterns shifting largely to “data and knowledge-driven” from being purely “hypothesis-driven” (Mousavi et al. 2016; Zhang et al. 2017). Furthermore, progress in computational biology has led to the application of data mining methods to reconstruct the biomolecular networks for each omic level.

Various omics-based approaches have been utilized for understanding plant abiotic stress biology (Li et al. 2006; Skiryycz et al. 2010; Bowne et al. 2012; Pant et al. 2015;

Narayanan et al. 2016a; Zhu et al. 2017; Bajwa et al. 2018). The various omics-based approaches include genomics (Agarwal et al. 2014; Shen et al. 2018), transcriptomics (Iyer et al. 2013; Shen et al. 2018), proteomics (Liu et al. 2015; Kosová et al. 2018), metabolomics (Colmsee et al. 2012; Khan et al. 2018), miRNAomics (Song et al. 2017), lipidomics (Pant et al. 2015; Zhang et al. 2018a, b), ionomics (Huang and Salt 2016), interactomics (Vandereyken et al. 2017), secretomics (Krause et al. 2013), phenomics (Yang et al. 2013b), microbiomics (Lakshmanan et al. 2017), proteogenomics (Zhu et al. 2017), primeomics (Yang et al. 2018), etc (Fig. 1). All these approaches focus on the elucidation of key genes, their regulators and interactors, and the characterization of changes at various levels in plants exposed to abiotic stress. The derived knowledge is used in targeting the key regulators and/or signaling pathways prevailing under abiotic stress and enhancing the tolerance against different abiotic stresses in plants. Thus, various omics-based approaches seek to provide novel insights into the integrated mechanisms and regulation involved in plant abiotic stress response and to translate this knowledge for better utilization in crop improvement programmes.

3 Genomics: Elucidating Stress-Responsive Genes

Genomics is a branch of “omics” which deals with the study of a given genome and reveals valuable data about the biology of the organism (Gilliham et al. 2017). The researchers identify intragenic and gene sequences, structures of genes, and provide annotation (Duque et al. 2013). The advance of genomics has been exponentially boosted by rapid developments in genome sequencing technology which began in the 1970s (first generation), continued into the mid-1990s (next-generation sequencing-NGS), and currently utilizes third-generation sequencing technologies (El-Metwally et al. 2013, 2014a). The study of genomics involves a series of steps including DNA extraction, amplification, sequencing, assembly, quality assessment, and most importantly, structural and functional annotation of the genome. This whole procedure provides valuable data about the genomics structure of the organism.

Functional genomics has been successfully utilized in identifying various genes involved in abiotic stress responses in plants (Govind et al. 2009; Ramegowda et al. 2013, 2014; Zhang et al. 2017; Wang et al. 2018). Many of these genes have also been successfully utilized in developing abiotic stresses tolerant crop plants (Yao et al. 2011; Le et al. 2012; Chen et al. 2012; Shankar et al. 2013; Agarwal et al. 2014; Thiry et al. 2016; Wang et al. 2016a, b, c; Gilliham et al. 2017). Additionally, the huge online genomic data—repositories developed in the genomics—era serve as a foundation for transcriptomics, proteomics, and genome engineering studies (Mochida and Shinozaki 2010, 2011; Jung and Main 2014; Alter et al. 2015; Mousavi et al. 2016; Shen et al. 2018; Zhang et al. 2018a, b). The advances in genomics of wild germplasm and weedy relatives of crop plants have led to the identification of several novel gene candidates and/alleles for abiotic stress tolerance. For example, Zhang et al. reported a high-quality, assembled genome sequence

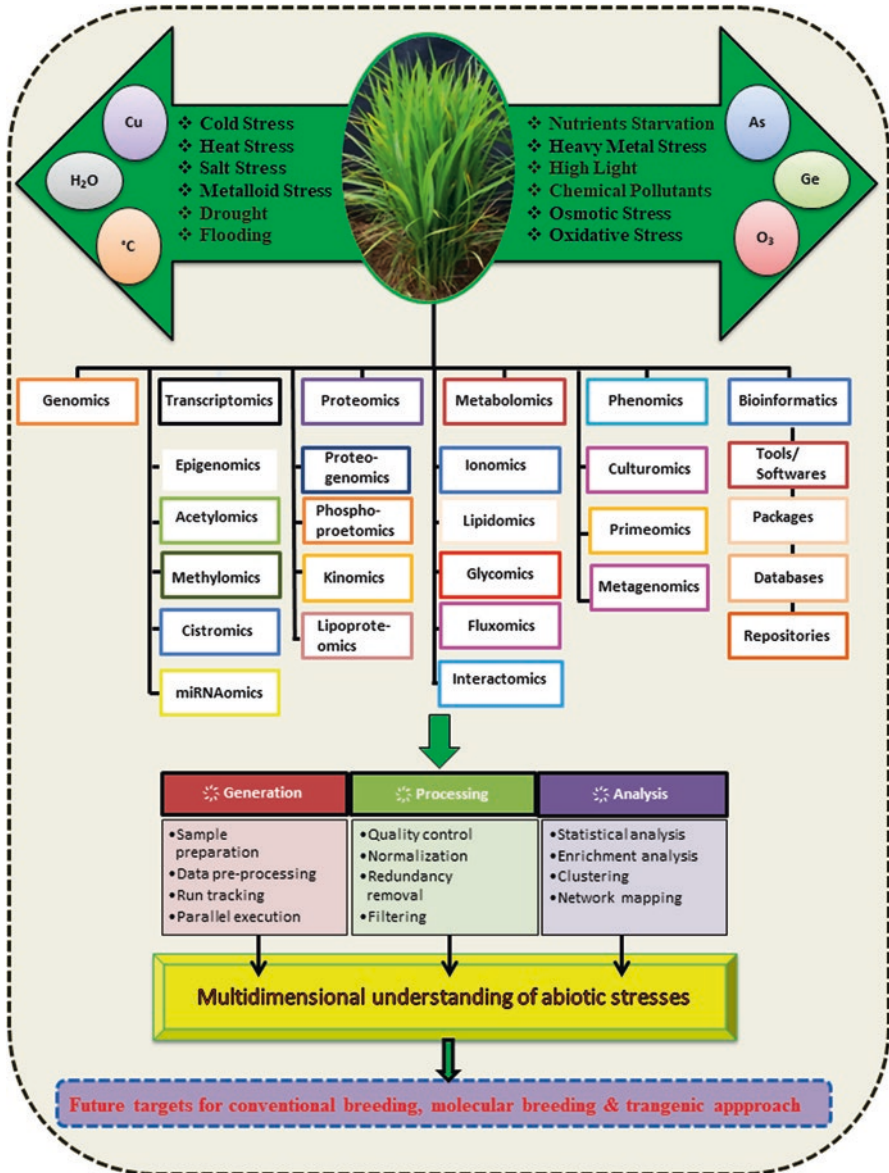


Fig. 1 Omics technologies for abiotic stress tolerance in plant

of Tartary buckwheat using whole-genome shotgun sequencing, genome maps, online available Hi-C sequencing data, and fosmid libraries. They annotated about 33,500 protein-coding genes, revealed whole-genome duplication, and identified the many putative genes related to cold stress, heavy metal stress, and drought resistance (Zhang et al. 2017).

4 Transcriptomics: A Closer Look at Transcripts

The transcriptomics is the branch of “omics technologies” which deals with organism’s RNA expression profile in spatial and temporal bases (Duque et al. 2013; El-Metwally et al. 2014a; Shen et al. 2018). Unlike genome, the transcriptome is highly dynamic and changes with age, development stage, nutrient availability, or environment (El-Metwally et al. 2014a). Currently, the RNA profiling is accomplished using RNA sequencing, microarray platforms, digital gene expression profiling, and serial analysis of gene expression (SAGE) (Molina et al. 2011; Duque et al. 2013; Xu et al. 2013; Raney et al. 2014; Li et al. 2017; Leisner et al. 2017; Kreszies et al. 2018). This approach helps in finding the candidate genes which are responsible for phenotypic alterations, stress tolerance by comparing plant under control and stress conditions (Le et al. 2012; Zhang et al. 2014a); prediction of tentative gene functions and providing a better crop productivity (Jogaiah et al. 2013; Agarwal et al. 2014). Similarly, the availability of online databases and archives enables users to perform genome-wide and transcriptome-wide analysis of plant’s stress response (Mochida and Shinozaki 2011; Le et al. 2012; Jogaiah et al. 2013; Agarwal et al. 2014; Raney et al. 2014; Alter et al. 2015; Mousavi et al. 2016; Zhang et al. 2018a, b). Rizhsky et al. (2004) used the transcriptomic analysis of *Arabidopsis* plants under a combination of heat and drought and reported around 770 transcripts level were unaltered. Similarly, they reported an accumulation of at least 53 different unique proteins during the stress combination (Rizhsky et al. 2004). Their results were confirmed in the *Arabidopsis* (Koussevitzky et al. 2008), sunflower (Hewezi et al. 2008). Additionally, the cytosolic Ascorbate peroxidase1 (APX1) was found to be upregulated during the stress combination (Koussevitzky et al. 2008). Molina et al. (2008, 2011) used NGS and SAGE techniques together to characterize the whole salt and drought-stressed transcriptome in chickpea. The subtractive cDNA suppression hybridization approach was also implied to study transcriptomic profile in plants under stress conditions (Jain and Chattopadhyay 2010).

Similarly, Rasmussen et al. (2013) used large-scale microarray analysis to study the *Arabidopsis thaliana* responses to stresses including high light, salt, heat, and cold. They reported different patterns of transcripts in both individual and combination of stresses. Approximately 7% and 25% of transcripts had a different response to the individual and combination of stresses, respectively. These differentially expressed transcripts were associated with a plant’s defense. Around 28% of the total transcripts were involved in the maintenance of photosynthetic machinery. Li et al. (2013) subjected the switchgrass under heat stress conditions and identified around 5350 differentially expressed transcripts using Affymetrix gene chips based transcriptome analysis. Furthermore, they mostly identified probes were related to protein refolding. Under dehydration stress, the RNAseq approach was used for chrysanthemum (Xu et al. 2013). Furthermore, Zhu et al. (2013) studied the changes in the cotton seedlings transcriptome under multiple stress conditions using a comparative microarray analysis technology. Additionally, their work revealed the information about crosstalk of pathways and functional genes under stress.

Prasch and Sonnewald (2013) used transcriptome analysis to understand the effect of heat stress, drought, virus infection, or double or triple combinations on *Arabidopsis* plants. They observed the effect of the stress response is reflected in the transcriptome profile of a plant. Only 11 transcripts expression were found to be altered under all the conditions, namely G-Box binding factor3, Rap2.9 and DEAR1, DREB2A, and two zinc finger proteins. Interestingly, their results confirmed that abiotic stress factors could significantly alter pathogen-related signaling networks, which lead to higher susceptibility of plants. Similarly, Iyer et al. (2013) subjected *Medicago* plants to single or combination of drought, O₃, and evaluated the effect on the transcriptomic level. The transcripts related to ABA signaling, proline biosynthesis were upregulated in drought subjected plants. However, ozone-stressed plants showed upregulation in the transcripts related to sugars metabolism and phenylalanine ammonia-lyase (PAL) biosynthesis. Under a combination, the jasmonic acid (JA) signaling transcripts were up-regulated. Interestingly, even transcription factors including MYC3 and WRKY were up-regulated. Using RNA-sequencing method, the transcriptomic profile was studied in *Chenopodium quinoa* under drought conditions (Raney et al. 2014). Li et al. used RNA sequencing approach for understanding the effects of heat stress, salt stress, drought, and cold stress on changes in maize leaf transcriptome profile. They reported about 2346, 2019, 1661, and 1841 genes were differentially expressed in each treatment, respectively. These genes were related to transcription, metabolism, signaling using functional annotation approach (Li et al. 2017). Leisner et al. (2017) subjected the soybean plants to low rainfall, ozone stress, and heat stress and reported a significant decline in the stomatal conductance and photosynthesis. Additionally, they studied the effect of these stresses on the seed coat transcriptome using RNAseq analysis. They reported approximately 1576, 148, and 48 genes were differentially expressed under heat stress, ozone stress, and drought, respectively. Muthuramalingam et al. (2017) analyzed the rice response to salt stress, heavy metal stress, and drought by meta-analysis. They reported about 1175 and 12,821 genes are expressed meta-differentially and individually, respectively. They further selected 100 differentially expressed genes and studied their physiochemical properties, transcription factors, and protein–protein interactions. More recently, Shen et al. (2018) assessed the expression levels of HD-Zip genes in tea plant in response to five abiotic stress conditions (heat stress, cold stress, salt stress, ABA, and drought). They reported approximately five, six, nine, six, and three HD-Zip genes were differentially upregulated, respectively. Furthermore, Kreszies et al. (2018) studied the effect of osmotic stress on the transcriptome level in barley roots using RNASeq approach. They observed the upregulation of genes related to suberin biosynthetic pathway (Kreszies et al. 2018). All these data about the differentially expressed genes and their role in signaling pathway can be used to enhance the abiotic stress tolerance.

Muthusamy et al. (2017) analyzed the transcriptional regulation and differential expression levels of heat shock protein 20 (HSP20) family members of wheat under drought, salt, and heat stress. Ruan et al. (2017) performed a genome-wide transcriptome analysis in cassava and predicted about 299 putative members of myeloblastosis (*MYB*) gene family. Additionally, they reported the differential expression

of many MYB genes in cassava leaves subjected to cold and drought conditions. They found that four members of the superfamily respond to ABA treatment. Adding to this, they found that MeMYB2 acts as a negative regulator for drought and cold tolerance using RNAi technology (Ruan et al. 2017). He et al. (2017) identified and evaluated the differential expression pattern of about 17 members of PIN efflux family in stressed cotton plants. Furthermore, they reported these genes to contain salicylic acid and auxin responsive elements in their promoter region. In another instance, Shen et al. (2018) used genomic technology to assess the expression levels of HD-Zip genes in tea plant in response to five different treatments. Recently, Wang et al. identified about 95 grape basic helix-loop-helix (bHLH) genes using a genome-wide analysis and studied the divergence of bHLH family. Additionally, they found around 22 and 17 bHLH genes were induced under osmotic stress and cold stress, respectively. Three other genes were related to secondary metabolite synthesis using GO function annotations. These gene promoters may contain G-box elements which play a role in recognition (Wang et al. 2018).

5 Proteomics: A Key for Understanding Protein Structure, Function, and Regulation

In a wide-ranging term, the proteomics is the quantitative and/or qualitative study of total expressed set of proteins in a given cell, tissue, organ, or organism in spatial and temporal bases (Tyers and Mann 2003; Luan et al. 2018). In the same manner to the transcriptome, the proteome profile is also highly dynamic and changes with age, organ, development stage, nutrient availability, or environmental conditions. The proteomics studies reveal huge information about the set of expressed proteins. Earlier, only the whole proteome were measured in plant stress tolerance; however, later many proteome-related studies including the phosphoproteome, proteogenome, organellar proteome, nuclear proteome, cell wall proteome, also started (Pandey et al. 2010; Helmy et al. 2011, 2012; Nakagami et al. 2012; Duque et al. 2013; Castellana et al. 2014; Cook et al. 2004; Jaiswal et al. 2014; Yin and Komatsu 2016; Wu et al. 2016; Tamburino et al. 2017). Currently, the proteome profiling is accomplished using different types of mass spectrometry (Komatsu et al. 2014; Shao et al. 2014; Luan et al. 2018). In these technologies, the mass and charge of small protein fragments are measured which results from proteases digestion (Nakagami et al. 2012). This generates a standard MS-spectra that is later interpreted to reveal the sequences of peptides and the occurred modification in protein samples (Helmy et al. 2012; Nakagami et al. 2012; Luan et al. 2018). Additionally, many researchers use two-dimensional gel electrophoresis (2-DGE) in plant proteomics (Komatsu et al. 2014; Arentz et al. 2014; Luan et al. 2018).

This approach generates a huge amount of information when used in both genome-wide or sample scale plant stress response studies. Furthermore, it is used to compare the proteome profiles under all optimal, stress and prolonged stress conditions, pinpoint to all the differentially expressed stress tolerant proteins and understand the role of specific proteins in abiotic stress-induced signalling (Hopff et al. 2013;

Yan et al. 2014; Lassowskat et al. 2014; Zhang et al. 2014b; Liu et al. 2015; Kosová et al. 2018). Additionally, the phosphoproteome has received the attention by researchers because the phosphorylated proteins play a major role during abiotic stress conditions (Nakagami et al. 2012; Cheng et al. 2014; Lassowskat et al. 2014; Zhang et al. 2014b; Yin and Komatsu 2015; Tamburino et al. 2017; Luan et al. 2018).

The effect of salt stress on phosphoproteins relative abundance has been studied by Kwon et al. (2006). Tanou et al. (2009) reported the role of post-translational modification in the enhanced tolerance of citrus to salt stress. These data were also supported by Wu et al. (2016). Pandey et al. (2010) studied the extracellular matrix proteome of dehydration stressed rice plants. They revealed alterations in proteins related to signaling, carbohydrate metabolism, ROS scavenging, wall modifiers (Pandey et al. 2010). Many reports in the literature cite about the application of proteomics techniques for understanding the effect of Cd stress in *Brassica juncea* (Alvarez et al. 2009), *A. thaliana* (Semane et al. 2010), *Linum usitatissimum* (Hradilova et al. 2010), *Glycine max* L. (Hossain et al. 2012; Ahsan et al. 2012). Other researchers also evaluated the effect of B (Alves et al. 2011), Al (Duressa et al. 2011) and Cr (Sharmin et al. 2012; Wang et al. 2013). Similarly, Yanguéz et al. (2013) studied mRNAs translation efficiency in *A. thaliana* under temperature stress seedlings using genome-wide analysis. Additionally, the proteomic profile of chickpea subjected to cold stress conditions have been evaluated comprehensively by Heidary and Amiri (2013). Subba et al. (2013) studied the nuclear proteins profile in chickpea subjected to drought conditions. Similarly, other researchers also studied nuclear proteome (Jaiswal et al. 2014). The effect of sublethal hypoxia stress on mRNAs was studied in *A. thaliana* using ribosome footprints mapping (Juntawong et al. 2014). Zhang et al. (2014) studied the leaves phosphoproteome of wheat under drought conditions and reported upregulation of several phosphorylated proteins, transcription factors, transporters, and chaperones. Yin and Komatsu (2015) analyzed the root tips for nuclear phosphoproteome in soybean during flooding and reported around 27 phosphoproteins. Additionally, Yin and Komatsu reported the change in the nuclear proteome of soybean after flooding. They reported the H2, H3, and H4 proteins were differentially regulated indicating profound chromatin remodeling (Yin and Komatsu 2016). Wang et al. (Wang et al. 2016a, b, c) induction of different isoforms of *S*-adenosylmethionine synthetase in soybean under drought and flooding, respectively. The fibrillins proteins are differentially expressed under drought stress (Kosmala et al. 2012; Urban et al. 2017). Santisree et al. (2017) studied the leaf proteome of chickpea. Additionally, they evaluated the effect of different stresses such as heat stress, drought stress, and salt stress on the leaf proteome. They reported about 248, 590, and 797 proteins were differentially regulated, respectively, through comparative label-free quantitative proteomics approach. Tamburino et al. (2017) studied the chloroplast proteome of drought-stressed tomato plants and reported the chloroplast proteins to crosstalk with nuclear signaling proteins.

More recently, Luan exposed two contrasting genotypes of barley to waterlogging conditions and studied the proteome profile of different vegetative organs using 2-DE and tandem MS approaches. They reported a decline in the total biomass, photosynthetic performance in the barley sensitive genotype. Furthermore, they found around 30 and 70 proteins were upregulated in the leaves and roots, respectively.

These differentially expressed proteins were related to energy metabolism and antioxidants in leaves and roots, respectively. Their results highlighted our knowledge about the key players of waterlogging tolerance. This information can be used to enhance the tolerance of crops in future (Luan et al. 2018).

6 Metabolomics in Plant Abiotic Stress

In a wide-ranging term, metabolomics is the fast-growing, advanced branch of omics approach used to study, characterize, identify, detect, and quantify the metabolic profile of cells, tissues, and living organisms under certain environmental circumstances (Collino et al. 2013; Dubery et al. 2013; Kumar et al. 2016; Freund and Hegeman 2017; Parida et al. 2018). The metabolome consists of a broad array of small-sized molecules (molecular mass less than 2000 Da) which exhibits huge diversity in chemical structure and composition. The researchers employ either non-targeted and targeted approaches in their studies for the endogenous metabolites as well as metabolites from exogenous sources (Kosmides et al. 2013; Li et al. 2014). These metabolites include amino acids, peptides, lipids, organic acids, aldehydes, ketones, steroids, vitamins, hormones, and even secondary metabolites. This approach reproduces more thorough data compared to proteomics and transcriptomics (Dos Santos et al. 2017). The advancements in mass spectrometry with liquid chromatography or gas chromatography (LC-MS and GC-MS), high-performance liquid chromatography (HPLC), nuclear magnetic resonance spectroscopy (NMR), direct injection mass spectrometry (DIMS), and other metabolomic techniques have boosted the elucidation of stress tolerance mechanisms as well as metabolite profiling in plants (Wolfender et al. 2013; Parida et al. 2018). This is evident from the fact that in the past decade, various aspects of metabolomics have been used to study plants and their interacting environment. Due to the accuracy, sensitivity, and precision, the metabolomics studies have gain importance in plant sciences research due to mitigating the agricultural losses (Genga et al. 2011) as well as providing knowledge about plant signalling and various regulatory pathways (Carreno-Quintero et al. 2013; Cusido et al. 2014; Shen et al. 2016; Dos Santos et al. 2017; Parida et al. 2018).

In plants, the total metabolite contents are found to be around 250,000 (Kim et al. 2010). Under stress conditions in plants, the total number, concentration, and types of metabolites are significantly enhanced. This alteration in gene expression is directly reflected in the metabolite profiles of plants. Gaining knowledge about the important metabolites which play an essential role in the growth, development, survival, and their modulation upon the onset of various abiotic stresses is highly important. This opened up the scope for the identification of viable metabolomics markers which are important for abiotic stress tolerance of plants (Lafitte et al. 2007; Obata and Fernie 2012; Kumar et al. 2016; Freund and Hegeman 2017; Parida et al. 2018). Various researchers have used the metabolomics approach to study the metabolic profiles in plants under stressed conditions (Urano et al. 2009; Skirycz et al. 2010; Witt et al. 2012; Bowne et al. 2012; Srivastava et al. 2013; Yang et al.

2014; Shen et al. 2016; Muthuramalingam et al. 2018). As a result, it became an indispensable tool in understanding the molecular mechanisms underlying stress responses. Urano et al. (2009) subjected *Arabidopsis thaliana* plants to drought stress and revealed the accumulation of several metabolites, including proline, raffinose family oligosaccharides, gamma-aminobutyrate (GABA), and several tricarboxylic acid (TCA) cycle metabolites. Additionally, they demonstrated that the ABA-dependent transcriptional regulation was responsible for the activation of stress-related metabolic pathways. Skirycz et al. (2010) studied the temporal changes in the profile of proline, erythritol, and putrescine by subjecting *A. thaliana* to mild osmotic stress. They also reported a typical correlation between metabolites and the transcriptional response. Similarly, Verslues and Juenger (2011) revealed osmolytes accumulation during a drought stress response. Caldana et al. subjected *A. thaliana* plants to eight environmental conditions and used metabolome profiling to understand the changes in plant metabolome in response to the environment. They reported accumulation of the photorespiratory intermediates such as glycolate and glycine in the early phase as well as the mid-phase of light stress. In cold stress, they observed an enhancement in the fructose and phenylalanine levels, and a decline in the succinate accumulation. However, they did not give the reason for these overlapped responses (Caldana et al. 2011). Kusano et al. (2011) documented the UV light effect on *A. thaliana* metabolism. They reported major changes in the primary metabolites level in the early phase. Contrastly, they observed an enhancement in the levels of UV-B protectants including phenolics, ascorbate, and flavonoids in the mid and late phases. They concluded reprogramming of the metabolism of carbon toward the production of UV-B protectants. Under dark stress, the function of the different subunits of mitochondrial alternative electron transport pathway was altered (Araujo et al. 2011). Additionally, the levels of branched-chain amino acids (BCAAs) were also elevated under abiotic stress such as salinity, drought, etc. Their findings confirmed the results of the study from the Joshi et al. (2010). These researchers affirmed the function of BCAAs as compatible osmolytes in various plant tissues under stress conditions. The accumulation of amino acids depends upon the desiccation severity. This was confirmed by the amino acid profiling of maize and wheat under water desiccation (Witt et al. 2012; Bowne et al. 2012). In another instance, Colmsee et al. (2012) established a data resource platform namely OPTIMAS-DW to answer different questions of *Zea mays* biology. It can be used to handle different data domains as well as for the integration of metabolomics, transcriptomics, proteomics, ionomics data. Amiour et al. (2012) used the integration of metabolomics, proteomics, and transcriptomics studies to identify key regulating steps in the nitrogen metabolism control. Similarly, Srivastava et al. (2013) documented a study in transgenic *Populus* plant containing superoxide dismutase gene. They applied data processing platform which generated system-level information on ROS metabolism. Yang et al. (2014) focussed on the applications of omics approaches in understanding secondary metabolism. AbdElgawad et al. (2015) reported the enhancement of tocopherol in the maize shoots and a steep decline in the levels of ascorbic acid after subjecting plants to salt stress. Furthermore, Wang et al. (2015) confirmed the enhancement in the proline levels in *Kosteletzkya virginica*

seedlings when exposed to salinity conditions. Shen et al. (2016) reported a rapid decline in the levels of glycolysis pathway related sugars in barley under salt stress. Furthermore, Shin et al. (2016) observed the accumulation of proline in the peach plant when exposed to higher temperatures.

Recently, Sun et al. (2016a, b) assessed the differences in the metabolome of maize after subjecting to different such as heat stress, salinity, and drought. They concluded the effect of individual stresses is different from the combination of stresses based on the metabolomics data. More recently, Khan et al. (2018) assessed the effect of drought on metabolome of sensitive and tolerant chickpea varieties using untargeted metabolic profiling technology. They reported a significant reduction in growth, dry weight, relative water, and chlorophyll content. They reported the most significant enhancement in allantoin and branched chain amino acids; decrease in levels of aromatic amino acids, aspartic acid, and glucosamine (Table 1).

Table 1 List of changes in different metabolites associated with major abiotic stresses

S. No.	Abiotic stress type	Metabolites change(s)	Function(s)	References
1	Heat stress	Amino acids	Antioxidant activity, protein stabilization, signaling	Luengwilai et al. (2012), Chebrolu et al. (2016), Shin et al. (2016)
		Organic acids	Nitrogen cycle	Luengwilai et al. (2012)
		Fatty acid	Cell ultrastructure reconstruction, isoprenoid synthesis	Luengwilai et al. (2012), Mueller et al. (2015)
		Polyamines	Antioxidant activity	Cvikrová et al. (2012)
		Sugars	ROS scavenging, osmoprotectant	Rivero et al. (2014), Chebrolu et al. (2016)
		Flavonoids	Signaling, ROS scavenging, structural integrity	Gill and Tuteja (2010), Chebrolu et al. (2016)
2	Salt stress	Amino acids	Osmoprotectant, nitrogen cycle, carbohydrate metabolism, amino acids synthesis	Joshi et al. (2010), Skirycz et al. (2010), Akçay et al. (2012), Wu et al. (2013), Ni et al. (2015), Chen and Hoehenwarter (2015), Wang et al. (2015)
		Glycolysis metabolites	Osmoprotectant, energy metabolism	Sobhanian et al. (2010), Wu et al. (2013), Chen and Hoehenwarter (2015), Shen et al. (2015)
		Organic acids	Nitrogen cycle	Ni et al. (2015)
		Cyclic acids	Phosphate storage	Zhang et al. (2011), Sung et al. (2015)
		TCA cycle metabolites	Energy metabolism, nitrogen cycle, phosphorus acquisition	Ni et al. (2015), Chen and Hoehenwarter (2015), Pang et al. (2016)

(continued)

Table 1 (continued)

S. No.	Abiotic stress type	Metabolites change(s)	Function(s)	References
3	Drought	Polyols	Osmoprotectant, antioxidant activity	Verslues and Juenger (2011), Warren et al. (2012), Wenzel et al. (2015); de Miguel et al. (2016)
		Organic acids	Membrane integrity, signaling	Wenzel et al. (2015), Alcázar et al. (2014), Lanzinger et al. (2015)
		Sugar alcohols	Osmoprotectant	Sun et al. (2016a, b), de Miguel et al. (2016)
		Sugars	Osmoprotectant	Urano et al. (2009), Shi et al. (2015), Pires et al. (2016), Nakabayashi et al. (2014), Lanzinger et al. (2015)
		Amino acids	Protein stabilization, antioxidant activity, osmoprotectant, signaling	Urano et al. (2009), Joshi et al. (2010), Witt et al. (2012), Bowne et al. (2012), Mao et al. (2013), Shi et al. (2015), Muscolo et al. (2015), Sun et al. (2016a, b), de Miguel et al. (2016), Khan et al. (2018)
		TCA cycle metabolites	Energy metabolism, nitrogen cycle, phosphorus acquisition, secondary metabolism	Urano et al. (2009), Griesser et al. (2015), Sun et al. (2016a, b), de Miguel et al. (2016)
		Phenols	Antioxidant activity	Griesser et al. (2015)
4	Heavy metals	Peptides	Antioxidant activity, metal chelators, photoprotection	Manivasagaperumal et al. (2011), Sytar et al. (2013)
		Amino acids	Osmoprotectant, phytochelatins synthesis, polyamines synthesis	Okem et al. (2015), Begum et al. (2016)
		Phenolics, flavonoids, phytochelatins	Antioxidant, ROS scavenging, structural integrity	Pal and Rai (2010), Okem et al. (2015)
5	Cold stress	Carbohydrate	Cryoprotectant	Caldana et al. (2011), Maruyama et al. (2014)
		Lipids	Membrane stabilization	Degenkolbe et al. (2012)
		Carotenoids and Flavonoids	Energy dissipation, antioxidant activity, UV absorbent	Latowski et al. (2011), Neugart et al. (2016)

Muthuramalingam et al. (2018) used genome-wide based computational metabolomics to study threonine profiling. They identified around 16 genes which modulate threonine levels in abiotic stressed rice plant using in silico expression studies.

7 Lipidomics

Compared to other approaches like metabolomics and genomics, there are fewer studies in the literature which confirm changes in lipid profile and remodeling on exposure to stress (Li et al. 2006; Chen and Thelen 2013; Xie et al. 2015; Pant et al. 2015; Moradi et al. 2017; Zhang et al. 2018a, b). Cold stress brings about many changes in membrane lipids. Burgos et al. (2011) exposed *Arabidopsis* plants to eight different type of stresses and studied the glycerolipid remodeling and saturation profile of fatty acids. Using the lipidomic data from Burgos et al., Szymanski et al. correlated the changes in glycerolipid levels with gene expression (Szymanski et al. 2014). Vu et al. (2014) studied the effect of wounding on changes in lipidomic profile in *Arabidopsis* plants. They also performed a co-occurrence analysis to understand the sorting of different lipids based on pathways. Similarly, Higashi et al. (2015) used *Arabidopsis* plants under heat stress correlated the changes in the lipidome with transcriptomic data. Xie et al. (2015) reported the ceramides accumulation as well as enhancement in fatty-acid unsaturation of lipid bilayer of *Arabidopsis* plants subjected to hypoxic conditions. Narayanan et al. (2016a, b) studied the effect of heat stress, day, and night temperatures on leaf lipid composition of the wheat plant. Tarazona et al. (2015) developed a multiplexed LC-MS lipidomics platform for the better coverage of plant lipidomes. Additionally, they used their own platform to study leaf lipidome of cold or drought treated plants. Their analysis yielded around 23 different classes of lipids. They also reported the accumulation of steryl glycosides, acylated steryl glycosides, and glycosylinositolphosphoceramides in drought-stressed plants.

Natera et al. (2016) studied the effect of salinity on changes in lipid metabolism and composition in the roots of two different *Hordeum vulgare* L. cultivars. They compared both of different genotypes on parameters like fatty acid composition, untargeted, and targeted lipid profiles. Wang et al. (2016a, b, c) used high-resolution EIT-MS to identify about 126 phospholipid molecules in the seedling of *Arabidopsis* under mild light conditions. Spicher et al. (2016) assessed the effect of higher temperature on *Solanum lycopersicum* lipidome. They identified about 791 lipid molecules including membrane lipids, prenylquinones, carotenoids, etc., using the advanced MS technique. The levels of galactolipids, phosphatidyl ethanolamine, prenylquinones, α -tocopherol, and plastoquinone drastically changed under high-temperature stress. They concluded the thylakoid membrane is remodeled with respect to the galactolipids saturation profile and concentrations. Recently, Moradi et al. evaluated the differences in the lipid profile of sensitive and tolerant thyme plants by subjecting under drought conditions (Moradi et al. 2017). More recently, Zhang et al. (2018a, b) evaluated the effect of heat stress on drought primed *Festuca arundinacea* lipidomic profile. They observed primed plants performed better in heat stress conditions compared to non-primed plants.

8 Proteogenomics: A Comprehensive Approach for Elucidating Regulatory Mechanisms

This integrative approach combines the large-scale genomics and transcriptomics data with proteomic data to elucidate the novel regulatory mechanisms (Helmy et al. 2012; Mosa et al. 2017). In proteogenomics studies, the proteomic techniques generate well defined, accurate, and high throughput translation-level data. Therefore, these generated data are mapped back to the genomic and/or transcriptomic data. These mapped back data act as a source for making several predictions for performing large-scale experiments in future (Armengaud 2010; Helmy et al. 2012; Chapman and Bellgard 2017).

In the past years, this approach has been used in elevating our understanding about plant sciences research (Baerenfaller et al. 2008; Castellana et al. 2008, 2014; Helmy et al. 2011; Zhu et al. 2017). Baerenfaller et al. (2008) performed a proteogenomics study in *Arabidopsis thaliana*. They identified around 57 new genes. Furthermore, they annotated hundreds of genes using intensive sampling from *Arabidopsis* under various conditions. Helmy et al. (2011, 2012) developed and expanded a rice proteome database namely OryzaPG-DB. Similarly, Risk et al. (2013) developed another database namely Peppy. Recently, D'Agostino et al. (2016) extended the use of proteogenomics to the plant symbiotic partner *Anabaena*. They analyzed the effect of nutrient depletion and NaCl stress on two different genotypes using the proteogenomic approach. They reported a huge change in protein profile related to transcription, translation, photosynthesis, and metabolism in both conditions (D'Agostino et al. 2016). Recently, Zhu et al. annotated a number of the alternative isoforms of a number of proteins in response to abscisic acid (ABA) treatment using a combination of RNA sequencing (long-read and short-read) and mass spectrometry methodology. Furthermore, they reported about 83.4% of total intron-containing genes undergo alternatively splicing (Zhu et al. 2017). By understanding the proteogenome of plants, the focus of research can be shifted toward increasing the nutritional improvement, total yield, and performance under stress conditions.

9 miRNAomics: For the Better Understanding of the Small RNA Networks

The microRNAs (miRNAs) are a class of small, noncoding RNAs, which act as endogenous posttranscriptional regulators. They play a role in every aspect of signaling (Sharma et al. 2017), development (Hernandez and Sanan-Mishra 2017), and environmental responses (Hernandez and Sanan-Mishra 2017).

The first report about the miRNAs involvement in abiotic stress response came from Jones-Rhoades and Bartel. In *Arabidopsis*, they reported the upregulation of

miR395 in particular during sulfate starvation. This specific miRNA was found to be targeting a transporter and enzymes of sulfate assimilation (Jones-Rhoades and Bartel 2004). Afterward, many researchers also reported the role of other classes of miRNAs in abiotic stress tolerance (Jones-Rhoades and Bartel 2004; Yang et al. 2013a, b; Stief et al. 2014; Cui et al. 2015; Sun et al. 2015; Khaksefidi et al. 2015; Roy 2016; Hivrale et al. 2016; Chauhan and Kumar 2016; Song et al. 2017). Till date, more than 400 miRNAs have been reported in abiotic stresses in plant species from different families including Brassicaceae, Solanaceae, Papaveraceae, Poaceae, Euphorbiaceae, Rosaceae, Amaranthaceae, and Apocynaceae. These *miRNAs respond in a tissue-, stress-, genotype-, and miRNA-dependent manner* (Zhang 2015) *to abiotic stress*. All the major miRNA involved in the abiotic stress response and tolerance are listed in Table 2.

Table 2 List of miRNA families associated to different abiotic stresses

S.No.	miRNA Family name	Abiotic stresses	Reference(s)
1	miR156	Salt stress, drought, heat stress, cold stress, heavy metal stress, UV-B	Stief et al. (2014), Cui et al. (2015), Sun et al. (2015)
2	miR159	Salt stress, heat stress, osmotic stress, ABA hypersensitivity, UV-B	Roy (2016), Hivrale et al. (2016)
3	miR160	Salt stress, heat stress, drought, heavy metal stress, UV-B	Khaksefidi et al. (2015), Hivrale et al. (2016)
4	miR164	Salt stress, heat stress, drought, heavy metal stress, UV-B	Qiu et al. (2016), Hivrale et al. (2016)
5	miR166	Salt stress, heat stress, cold stress, drought, heavy metal stress, UV-B	Hivrale et al. (2016)
6	miR167	Hypoxia, heat stress, cold stress, UV-B, ABA hypersensitivity	Khaksefidi et al. (2015), Hivrale et al. (2016)
7	miR169	Salt stress, drought, heat stress, cold stress, heavy metal stress, ABA hypersensitivity, nitrogen starvation, UV-B	Cheng et al. (2016)
8	miR170	Drought, UV-B	Chauhan and Kumar (2016)
9	miR171	Salt stress, drought, heat stress, heavy metal stress, UV-B	Hivrale et al. (2016), Esmaeili et al. (2017)
10	miR172	Salt stress, drought, heat stress, UV-B, heavy metal stress, cold stress	Khaksefidi et al. (2015), Li et al. (2016)
11	miR319	Salt stress, drought, heat stress, heavy metal stress, cold stress	Zhou et al. (2013), Yang et al. (2013a, b)
12	miR393	Salt stress, drought, heat stress, UV-B, heavy metal stress, cold stress	Hivrale et al. (2016)
13	miR396	Salt stress, drought, heat stress, heavy metal stress, cold stress, alkalinity stress	Hivrale et al. (2016), Song et al. (2017)

Table 2 (continued)

S.No.	miRNA Family name	Abiotic stresses	Reference(s)
14	miR408	Salt stress, drought, heat stress, heavy metal stress	Hajyzadeh et al. (2015)
15	miR444	Nitrogen starvation, phosphate accumulation, salt stress, dehydration, drought, cold stress, heavy metal stress	Song et al. (2017)
16	miR528	Salt stress, heavy metal stress	Bottino et al. (2013), Gentile et al. (2015)
17	miR529	Drought, cold stress, heavy metal stress	Wang et al. (2016a, b, c)
18	miR809	Salt stress, drought	Yang et al. (2013a, b)
19	miR828	Oxidative stress, heat stress	Wang et al. (2016a, b, c)
20	miR2871	Salt stress, cold stress, drought	Hivrale et al. (2016)

These data are based on the currently available literature of *Arabidopsis*, rice, cotton, wheat, rapeseed, barley, bentgrass, sugarcane, and switchgrass

10 Prime-Omics: A Comprehensive Approach to Priming

Plant priming has emerged as a technology over the past decade (Balmer et al. 2015; Hussain et al. 2016; Lal et al. 2018). It is defined as an induced state by which a plant reacts more efficiently, rapidly, and vigorously to the stress conditions (Hussain et al. 2016; Lal et al. 2018). As a result, the germination rate is enhanced adding to better yield, high vigor in crops, forage, and medicinal plants (Lal et al. 2018). There are multiple priming techniques used by researchers all over the world including chemical priming, hydropriming, hormone priming, and nutrient priming (Lal et al. 2018).

Due to the phenomena of priming, many changes occur in the genetic, transcriptome, proteome, and metabolome levels. As a result, the techniques for accomplishing genomics, transcriptomics, proteomics, and metabolomic approaches can be used in priming. There are many reports in the literature citing about the effect of priming on enhanced abiotic stress tolerance (Guan et al. 2009; Srivastava et al. 2010a; Afzal et al. 2012; Sali et al. 2015; Bajwa et al. 2018) (Table 3). Peroxide primed wheat seeds show a higher salt tolerance (Wahid et al. 2007). Akbari et al. (2007) treated wheat seeds with a higher dose of NaCl and observed a reduction in the seed germination. The priming of maize seed with chitosan improved the tolerance at low temperature (Guan et al. 2009). The halopriming also alleviate the harmful effects of drought and salt stress in sugarcane (Patade et al. 2009) and mung bean (Saha et al. 2010). Srivastava et al. (2010a) reported hydro-primed and chemical-primed mustard seeds to exhibit an enhancement in germination rate, total dry weight, and chlorophyll content under salt conditions. Furthermore, they observed the same results in osmotic stress. The supplementation of thiourea in *Brassica juncea* roots enhances salt tolerance (Srivastava et al. 2010b). Anosheh et al. (2011) reported the chemical priming enhanced the tolerance in drought and salt stress in maize. The CaCl₂ and KCl seed priming induced salt tolerance in rice cultivar (Afzal et al. 2012). CaCl₂ primed wheat seeds showed the enhancement in seedling