Muhammad Shahid
Rajarshi Gaur *Editors*

Molecular Dynamics of Plant Stress and its Management

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Editors
Muhammad Shahid
Department of Plant Sciences
College of Agricultural and Marine Sciences, Sultan Qaboos University
Muscat, Oman

Rajarshi Gaur
Department of Biotechnology
Deen Dayal Upadhyaya Gorakhpur University
Gorakhpur, India

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Preface

Molecular Dynamics of Plant Stress and its Management is a book that focuses on the study of stress in plants and how it can be effectively managed. With the growing global population, the importance of crop yield and stress management has become a critical issue, and this book offers solutions to these challenges. The book looks at how plants respond to stressors, how plants can cope with stress, and how stress can be managed. The book is not only written in a way that is accessible to anyone interested in the topic, but it also provides a more in-depth look at the molecular dynamics of plant stress and its management. The book explores the impact of abiotic and biotic stressors on plant growth and development, including drought, salinity, temperature stress, pests, and diseases. It also examines the role of genetic engineering and biotechnology in developing stress-tolerant plants. It offers insights on the latest research and advancements in plant breeding, genomics, and proteomics, which are essential in developing crops that can withstand harsh environmental conditions. It offers solutions for managing these challenges, including genetic engineering, proteomics, and genomics. The book provides a detailed overview of the latest research and advancements in plant stress management and offers practical advice on how to apply these findings in real-world scenarios. The book explores the impact of climate change on agricultural production and provides insights on how to develop stress-tolerant crops that can withstand changing environmental conditions. In conclusion, *Molecular Dynamics of Plant Stress and its Management* is an essential resource for anyone interested in plant biology, biotechnology, and agricultural science. With its comprehensive coverage of the latest research and practical insights, the book is an invaluable guide for students, researchers, and professionals looking to develop sustainable agricultural practices and ensure food security for future generations.

Muscat, Oman — Muhammad Shahid
Gorakhpur, India — Rajarshi Gaur

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Editors and Contributors

About the Editors

Muhammad Shahid has been Associate Professor at the Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Al-Khoud 123, Muscat, Oman, since 2015. His research interests include epidemiology and population structure of plant viruses, pathogen–host interaction, and application of nanotechnology in plant pathogen management. He has been a member of several scientific societies, reviewers for several scientific journals, and Guest Associate Editor of one of the major reputed Journal.

Rajarshi Gaur has been Professor at the Department of Biotechnology, Deen Dayal Upadhyaya Gorakhpur University, Gorakhpur, India, since 2019. His research interests include Plant Virology, Molecular Biology, and Bioinformatics. He is fellow of the Indian Virological Society and member of the editorial board of various international Journals. Currently, he is working on Plant–Virus Interaction project funded by the Government of India.

Contributors

Aown Abbas Department of Geography and Resource Management, The Chinese University of Hong Kong, Shatin, Hong Kong, China

Abdulla A. R. Abdulla Department of Biology, College of Science, University of Bahrain, Sakhir, Kingdom of Bahrain

Muhammad Afzal Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Temoor Ahmed Institute of Biotechnology, Zhejiang University, Hangzhou, China

State Key Laboratory of Rice Biology and Breeding, Ministry of Agriculture Key Laboratory of Molecular Biology of Crop Pathogens and Insects, Key Laboratory of Biology of Crop Pathogens and Insects of Zhejiang Province, Institute of Biotechnology, Zhejiang University, Hangzhou, China

Xianghu Laboratory, Hangzhou, China
MEU Research Unit, Middle East University, Amman, Jordan

Jannat Akram Lahore College for Women University, Lahore, Pakistan

Husam Al-Hinai Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman

Hayssam M. Ali Department of Botany and Microbiology, College of Science, King Saud University, Riyadh, Saudi Arabia

Liaqat Ali University of Agriculture Faisalabad, Sub-Campus Burewala, Pakistan

Sajid Ali Department of Agronomy, University of the Punjab, Lahore, Pakistan

Ali Al-Subhi Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman

Nazia Aslam Government College University, Faisalabad, Pakistan

Maysoon Awadh Department of Biology, College of Science, University of Bahrain, Sakhir, Kingdom of Bahrain

Muhammad Jawad Akbar Awan Agricultural Biotechnology Division, National Institute for Biotechnology and Genetic Engineering (NIBGE), Constituent College of Pakistan Institute of Engineering and Applied Sciences, Faisalabad, Pakistan

P. Ayyadurai Agronomy, Agricultural College and Research Institute (AC&RI), TNAU, Vazhavachanur, Tiruvannamalai, India

Farrukh Azeem Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Leila Bendifallah M'hamed Bougara University, Boumerdes, Algeria

Rakesh Bhardwaj Division of Germplasm Evaluation, ICAR-National Bureau of Plant Genetic Resources, New Delhi, India

A. Chandrasekar Biotechnology, Department of Crop Improvement, SRM College of Agricultural Sciences, Baburayanpettai, Tamil Nadu, India

Ankita V. Chinche Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Akola, Maharashtra, India

Kartik D. Chopkar Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Akola, Maharashtra, India

M. Deivamani Plant Pathology, Krishi Vigyan Kendra (KVK), TNAU, Papparapatti, India

Ajeet Singh Dhaka Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

Minakshi Dutta Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

ICAR-Indian Agricultural Research Institute, New Delhi, India

Mifahul Huda Fendiyanto Department of Biology, Faculty of Military Mathematics and Natural Sciences, The Republic of Indonesia Defense University, Komplek Indonesia Peace and Security Center (IPSC) Sentul, Bogor, Indonesia

Rajarshi Gaur Department of Biotechnology, Deen Dayal Upadhyay Gorakhpur University, Gorakhpur, Uttar Pradesh, India

Saira Ghafoor Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Pablo L. Godínez-Mendoza Center of Applied Research in Biosystems (CARB-CIAB), School of Engineering, Autonomous University of Querétaro, El Marqués, Querétaro, Mexico

Nagesh R. Gowda ICAR-Indian Agricultural Research Institute, New Delhi, India

Ramon G. Guevara-González Center of Applied Research in Biosystems (CARB-CIAB), School of Engineering, Autonomous University of Querétaro, El Marqués, Querétaro, Mexico

Rosario Guzman-Cruz Center of Applied Research in Biosystems (CARB-CIAB), School of Engineering, Autonomous University of Querétaro, El Marqués, Querétaro, Mexico

Muhammad Zeshan Haider Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan

Muhammad Saleem Haider Department of Plant Pathology, University of the Punjab, Lahore, Pakistan

Soumaya Haouel-Hamdi Laboratory of Biotechnology Applied to Agriculture, National Agricultural Research Institute of Tunisia (INRAT), University of Carthage, Tunis, Tunisia

Muzaffar Hasan ICAR-Central Institute of Agricultural Engineering, Bhopal, India

Zuhair Hasnain PMAS, Arid Agriculture University, Rawalpindi, Pakistan

Somnath K. Holkar ICAR-National Research Centre for Grapes, Pune, India

Andrea Hurtado-Zuñiga Center of Applied Research in Biosystems (CARB-CIAB), School of Engineering, Autonomous University of Querétaro, El Marqués, Querétaro, Mexico

Munazza Ijaz State Key Laboratory of Rice Biology and Breeding, Ministry of Agriculture Key Laboratory of Molecular Biology of Crop Pathogens and Insects, Key Laboratory of Biology of Crop Pathogens and Insects of Zhejiang Province, , Institute of Biotechnology, Zhejiang University, Hangzhou, China

Rafia Ijaz Department of Bioinformatics and Biotechnology, Government College University Faisalabad, Faisalabad, Pakistan

Khushboo Jain Department of Biotechnology, Vigyan Bhawan—Block B, New Campus, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Jouda Mediouni Ben Jemâa Laboratory of Biotechnology Applied to Agriculture, National Agricultural Research Institute of Tunisia (INRAT), University of Carthage, Tunis, Tunisia

Guo Junning State Key Laboratory of Rice Biology and Ministry of Agriculture Key Laboratory of Molecular Biology of Crop Pathogens and Insects, Institute of Biotechnology, Zhejiang University, Hangzhou, China

Hira Kamal Department of Plant Pathology, College of Agricultural, Human, and Natural Resource Sciences, Washington State University, Pullman, WA, USA

Azmi Khan Department of Life Science, School of Earth, Biological and Environmental Sciences, Central University of South Bihar, Gaya, Bihar, India

Fahad Khan Tasmanian Institute of Agriculture, University of Tasmania, Hobart, Australia

Muhammad Kamran Khan Government College University, Faisalabad, Pakistan

Ravinsh Kumar Department of Life Science, School of Earth, Biological and Environmental Sciences, Central University of South Bihar, Gaya, Bihar, India

Arti Kumari Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

Rosalin Laishram Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

ICAR-Indian Agricultural Research Institute, New Delhi, India

Bin Li State Key Laboratory of Rice Biology and Breeding, Ministry of Agriculture Key Laboratory of Molecular Biology of Crop Pathogens and Insects, Key Laboratory of Biology of Crop Pathogens and Insects of Zhejiang Province, Institute of Biotechnology, Zhejiang University, Hangzhou, China

Chirag Maheshwari Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

Pawan Mainkar ICAR-Directorate of Onion and Garlic Research, Pune, India

Ayushi Malik Department of Biotechnology, Vigyan Bhawan—Block B, New Campus, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Smriti Mall Molecular Plant Pathology Lab, Department of Botany, Deen Dayal Upadhyaya Gorakhpur University, Gorakhpur, Uttar Pradesh, India

Muhammad Tariq Manzoor Department of Plant Pathology, University of the Punjab, Lahore, Pakistan

Natasha Manzoor Department of Soil and Water Sciences, China Agricultural University, Beijing, China

Avinash Marwal Department of Biotechnology, Vigyan Bhawan—Block B, New Campus, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Hafiza Ayesha Masood Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Faisalabad, Pakistan

MEU Research Unit, Middle East University, Amman, Jordan

Mukesh Meena Laboratory of Phytopathology & Microbial Biotechnology, Department of Botany, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Botany, Laboratory of Phytopathology and Microbial Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Nand Lal Meena Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

Division of Germplasm Evaluation, ICAR-National Bureau of Plant Genetic Resources, New Delhi, India

Miftahudin Miftahudin Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, Bogor, Indonesia

Anita Mishra Department of Science (Biotechnology), Biyani Girls College, Vidhyadhar Nagar, Jaipur, India

Department of Science (Biotechnology), Biyani Girls College, University of Rajasthan, Jaipur, Rajasthan, India

Saima Muzammil Institute of Microbiology, Government College University, Faisalabad, Pakistan

Habibullah Nadeem Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

C. R. Nagesh Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

Chitra Nehra Gujarat Biotechnology Research Centre, Department of Science and Technology, Government of Gujarat, Gandhinagar, Gujarat, India

Muhammad Noman State Key Laboratory for Managing Biotic and Chemical Treats to the Quality and Safety of Agro-Products, Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, Hangzhou, China

Shagufta Perveen Department of Botany, Government College University, Faisalabad, Pakistan

Nikolay M. Petrov Laboratory of Virology, Department of Natural Sciences, New Bulgarian University, Sofia, Bulgaria

Arash Rasekh Department of Plant Protection, College of Agriculture, Shahid Chamran University of Ahvaz, Ahvaz, Iran

Ijaz Rasul Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Aiman Raza Agricultural Biotechnology Division, National Institute for Biotechnology and Genetic Engineering (NIBGE), Constituent College of Pakistan Institute of Engineering and Applied Sciences, Faisalabad, Pakistan

Amir Raza School of Plant Sciences, College of Agriculture, Life and Environmental Sciences, University of Arizona, Tucson, AZ, USA

Atiq Ur Rehman Agricultural Biotechnology Division, National Institute for Biotechnology and Genetic Engineering (NIBGE), Constituent College of Pakistan Institute of Engineering and Applied Sciences, Faisalabad, Pakistan

Shahira Al-Risi Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman

Adnan Sami Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan

Rizky Dwi Satrio Department of Biology, Faculty of Military Mathematics and Natural Sciences, The Republic of Indonesia Defense University, Komplek Indonesia Peace and Security Center (IPSC) Sentul, Bogor, Indonesia

Muhammad Shafiq Department of Horticulture, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan

Muhammad Shahid Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman

Muhammad Adnan Shahid Department of Horticultural Science, North Florida Research and Education Center, University of Florida/IFAS, Quincy, FL, USA

S. Shakespear ICAR-National Institute of Biotic Stress Management, Baronda, Raipur (CG), India

Prashant R. Shingote Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Akola, Maharashtra, India

Valeria Siboney-Montante Center of Applied Research in Biosystems (CARB-CIAB), School of Engineering, Autonomous University of Querétaro, El Marqués, Querétaro, Mexico

Abu Bakar Siddique Tasmanian Institute of Agriculture, University of Tasmania, Launceston, Australia

Muhammad Hussnain Siddique Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Riffat Siddique Department of Botany, Lahore College for Women University, Lahore, Pakistan

Ashutosh Singh Department of Life Science, School of Earth, Biological and Environmental Sciences, Central University of South Bihar, Gaya, Bihar, India

Pratika Singh Department of Life Science, School of Earth, Biological and Environmental Sciences, Central University of South Bihar, Gaya, Bihar, India

M. Sivaji Agricultural Biotechnology, Agricultural College and Research Institute (AC&RI), TNAU, Vazhavachanur, Tiruvannamalai, India

Amrita Srivastava Department of Life Science, School of Earth, Biological and Environmental Sciences, Central University of South Bihar, Gaya, Bihar, India

Apoorva Srivastava Molecular Plant Pathology Lab, Department of Botany, Deen Dayal Upadhyaya Gorakhpur University, Gorakhpur, Uttar Pradesh, India

Mariya I. Stoyanova Department of Plant Protection, Institute of Soil Science, Agrotechnologies and Plant Protection "N. Pushkarov", Agricultural Academy, Sofia, Bulgaria

Khalid Sultan Department of Botany, Government College University, Faisalabad, Pakistan

J. Sushmitha Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi, India

ICAR-Indian Agricultural Research Institute, New Delhi, India

Mayank Suthar Department of Biotechnology, Vigyan Bhawan—Block B, New Campus, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Shalini Tailor Department of Biotechnology, Vigyan Bhawan—Block B, New Campus, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Department of Biotechnology, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Dhiraj L. Wasule Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Akola, Maharashtra, India

M. Yuvaraj Soil Science and Agricultural Chemistry, Agricultural College and Research Institute (AC&RI), TNAU, Vazhavachanur, Tiruvannamalai, India

Sara Zafar Government College University, Faisalabad, Pakistan

Haitham E. M. Zaki Applied Biotechnology Department, University of Technology and Applied Sciences-Sur, Sur, Oman

Muhammad Zubair Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Part I

Plant Abiotic Stress

Molecular Mechanisms Underpinning Plant Stress Responses: Insights into the Cellular and Systemic Regulation

1

Amir Raza

Abstract

Plants are under constant environmental stress including extreme temperature, salinity, drought as well as insect and pathogen problems, which affect the development and productivity of plants. To deal with these challenges, plants have developed complex underlying molecular mechanisms to pre-empt the stress signals and initiate appropriate molecular responses. This chapter explores the molecular mechanisms underlying plant stress responses, focusing on the cellular and systemic regulation of these processes. Plant stress responses are complex and dynamic, involving a range of molecular signaling pathways that allow plants to sense and respond to adverse environmental conditions. Key topics covered include the role of reactive oxygen species (ROS) and antioxidant defense mechanisms, hormonal regulation, transcriptional regulation of stress-responsive genes, protein modifications, and post-translational regulation. Additionally, the chapter delves into the cellular responses to stress, including metabolic adaptations, and the systemic signaling that coordinates plant stress responses across different tissues and organs. The chapter concludes with a discussion on the crosstalk and integration of stress signaling pathways and highlights future directions and challenges in this field.

Keywords

Plant stress responses · Molecular mechanisms · Reactive oxygen species · Antioxidant defense · Hormonal regulation · Protein modifications

A. Raza (✉)
School of Plant Sciences, College of Agriculture, Life and Environmental Sciences, University of Arizona, Tucson, AZ, USA
e-mail: razaa@arizona.edu

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Abbreviations

ABA	Abscisic Acid
BRs	Brassinosteroids
CAM	Crassulacean acid metabolism
CDPKs	Calcium dependent protein kinases
DREB	Dehydration responsive element binding
HR	Hypersensitivity response
HSP	Heat shock protein
JA	Jasmonic acid
NO	Nitric oxide
PR	Pathogenesis related
PTMs	Post-translational modifications
RLKs	Receptor-like kinases
ROS	Reactive oxygen species
SA	Salicylic acid
SAR	Systemic acquired resistance
SnRKs	SNF1 related protein kinases

1.1 Introduction

Like all other living organisms, plants are also susceptible to environmental stresses. The term "plant stress" describes the unfavorable circumstances that interfere with the normal functioning of the plant and can impede growth and development (Chaves et al. 2009). We could take steps to diminish the effect of stress and encourage healthier plant growth by being aware of its sources and effects. Stress on plants can have severe effects where lower yields are often the result of stunted growth leading to decreased productivity (Chaves et al. 2009).

Plants also exhibit physical and physiological indicators such as leaf chlorosis, which causes leaves to turn yellow, and necrosis, which causes tissues to die and wilt (Mittler 2006). Stressed plants are more prone to disease and pest infestations because of their weaker defense mechanisms (Saha et al. 2022). Additionally, stress can impair the fundamental metabolic processes of plants, impacting hormone balance, respiration, and photosynthesis (Foyer and Noctor 2005). Stress that lasts for a longer period of time can damage the plant permanently thereby limiting their ability to reproduce (Chaves et al. 2009).

There are various strategies that could be adopted to lessen the effects of stress for example watering at appropriate times and dispensing only the required amount of water based on their physiological requirements can prevent both drought and waterlogging problems (Chaves et al. 2009). Plant health and resilience can also be supported by maintaining a balanced supply of nitrogen and other appropriate fertilizers based on soil analysis (Mittler 2006). To reduce the effect of pests and diseases on plants, integrated pest management techniques can be used (Saha et al. 2022). A variety of other factors including mulching, windbreaks, shading, and greenhouse cultivation can also improve the environment for plant growth (Mittler 2006). It can also be advantageous to take into account cultivars that have been bred or designed to withstand particular stresses (Saha et al. 2022). Regular observation, early recognition of stress signs, and swift response are also crucial in reducing stress escalation (Chaves et al. 2009). We can support sustainable agriculture and improve crop yields in the face of difficult environmental conditions by managing plant stress (Hussain et al. 2018).

Throughout their life cycle, plants are also constantly exposed to pathogens, extreme temperatures, and high saline environments (Leslie et al. 2013). In order to maintain cellular homeostasis under these harsh conditions, plants should be able to survive and thrive by employing their highly developed stress response mechanisms. As a prerequisite, the plant must be able to recognize the stress signals and have the ability to respond accordingly. The stress sensors in plants, which include cytoplasmic sensors, membrane receptors, and ion channels (Kilian et al. 2007; Beilby and Al Khazaaly 2009; Amtmann and Beilby 2010), enable the plants to identify various stress signals and trigger the relevant signal transduction pathways which, in turn, initiate stress-specific response by sending signals to the nucleus and other cellular compartments.

There are certain signaling molecules such as abscisic acid (ABA), a well-known signaling molecule produced as a result of a plant's response toward a particular stress, which regulates the expression of stress-responsive genes (Zhao et al. 2020; Holsteens et al. 2022). ABA-dependent and ABA-independent signaling mechanisms influence gene expression and protein synthesis in different ways (Wang et al. 2021). A number of components play a critical role in controlling both protein function and gene expression which includes protein kinases, protein phosphatases, and transcription factors to name some of these elements. Plant stress responses could also be dependent on calcium-mediated signaling where cytosolic calcium operates as a secondary messenger that transmits stress signals to destinations and activates genes and proteins that respond to stress (Seifikalhor et al. 2019). Also, there are some other molecular species that mediate the plant's stress response such as signaling via reactive oxygen species (ROS) which are produced as a result of oxidative stress. However, plants have evolved antioxidant defense mechanisms that include enzymes such as superoxide dismutase, catalase, and peroxidases to scavenge ROS and maintain cellular redox equilibrium (Mittler et al. 2011). By participating in the transduction of stress signals and activating specific stress-responsive genes, ROS also plays a signaling role in plants.

Genes and proteins that respond to stress have a significant impact on a plant's ability to withstand stress. Various transcription factors such as DREB (dehydration-responsive element-binding) and WRKY (involved in a number of stress responses) regulate the expression of genes that respond to stress (Phukan et al. 2016). Heat shock proteins (HSPs) serve as molecular chaperones by preventing protein denaturation and maintaining proper folding under demanding conditions (Mhamdi and Van Breusegem 2018; Huang et al. 2019). Proteins that are abundant in late embryogenesis help stop the loss of hydration-induced damage to proteins and cellular structure. Proline and soluble sugars are examples of osmoprotectants that function as complementary solutes to maintain cellular osmotic balance and protect against stress-related protein and membrane damage (Singh et al. 2015). These compounds help plants withstand the osmotic stress caused by salinity and drought. In addition to individual stress reactions, plants frequently experience multiple stresses sequentially or concurrently. Cross-talk and integration of stress responses occur at the molecular and cellular levels, allowing plants to efficiently prioritize responses and allocate resources (Foyer et al. 2016). Hormonal crosstalk, such as interactions between ABA, jasmonic acid (JA), and salicylic acid (SA), is crucial for coordinating responses to various stresses.

1.2 Signaling Components and Their Molecular Pathways

Plants' response to stress involves a number of signaling molecules that are crucial (Corina Vlot et al. 2009; Fu and Dong 2013) for the respective signaling pathways. These important signaling chemicals include abscisic acid (ABA), salicylic acid (SA), ethylene, and nitric oxide (NO) as discussed below.

1.2.1 Abscisic Acid (ABA) Signaling

A phytohormone known as ABA plays a critical role in drought and osmotic stress responses (Corina Vlot et al. 2009). ABA levels increase in response to drought, which causes stomatal closure and lowers transpirational water loss. Additionally, ABA stimulates the production of defense-related proteins and osmolytes, improving plant stress resistance. A signaling cascade encompassing transcription factors, protein kinases, and phosphatases starts when ABA receptors detect an increase in ABA levels (Corina Vlot et al. 2009). Activation of such signaling cascades leads to the expression of genes that regulate the opening and closure of stomata and produce osmolytes that protect against reactive oxygen species (ROS).

1.2.2 Salicylic Acid (SA) Signaling

Salicylic acid is essential for systemic acquired resistance (SAR) activation and defense against biotrophic problems (Corina Vlot et al. 2009; Dempsey and Klessig 2012). SAR is a persistent immune response that offers improved resistance against a variety of pathogens. The recognition of pathogen infection or stress signal triggers the SA pathway, which results in the production of SA and the subsequent activation of defense mechanisms.

SA levels rise in plant cells in response to pathogen infection or stress perception (Corina Vlot et al. 2009; Dempsey and Klessig 2012). A protein called NPR1 identifies SA, which causes the activation of defense mechanisms where NPR1 interacts with the TGA family of transcription factors to control the expression of genes linked to SA-associated defense response (Fu and Dong 2013). Pathogenesis-related (PR) proteins, antimicrobial substances, and other defense-related molecules are produced as a result of SA pathway activation.

1.2.3 Ethylene Signaling

Ethylene regulates various factors of plant response to certain external stimuli, including physiological damage to plants and pathogen attacks (Bleecker and Kende 2000). It also modulates a wide range of physiological processes, including fruit ripening, seed germination, and senescence. To enhance the stress tolerance response, ethylene also controls the growth and development of plants in challenging environmental conditions. Downstream signaling is triggered by ethylene receptors when they undergo conformational changes in the presence of ethylene leading to the activation of associated signaling elements (Bleecker and Kende 2000). EIN3, a transcription factor that controls the expression of ethylene-responsive genes, is activated as part of the downstream cascade (Xin et al. 2019).

1.2.4 Nitric Oxide (NO) Signaling

Nitric acid is an important signaling molecule that determines the mechanism of a plant's response to various stresses (Shi et al. 2012). It contributes to a number of physiological functions, including the ability to withstand abiotic stress and combat certain pathogens. NO modulates the activity of antioxidant enzymes, promotes the synthesis of defense-related chemicals, and regulates gene expression.

Each signaling molecule mentioned above follows a specific signal transduction pathway to elicit the desired stress response. NO is generated in response to stress and controls the expression of genes involved in defense (Shi et al. 2012) and the activation of downstream signaling components resulting from its interactions with a number of molecules and proteins. NO controls the activity of antioxidant enzymes and stimulates the production of defense-related genes (Gupta et al. 2022). Researchers can acquire insight into the complex mechanics of plant stress response by comprehending the distinctive signaling routes, such as the salicylic acid pathway, ethylene pathway, and nitric oxide pathway. These pathways provide prospective targets for genetic engineering and breeding techniques to improve crops' ability to withstand stress, thereby improving global food security. To create more potent methods to lessen the effects of stress on plant growth and productivity, additional investigation is required to elucidate the precise molecular components and interactions within these pathways (Fig. 1.1).

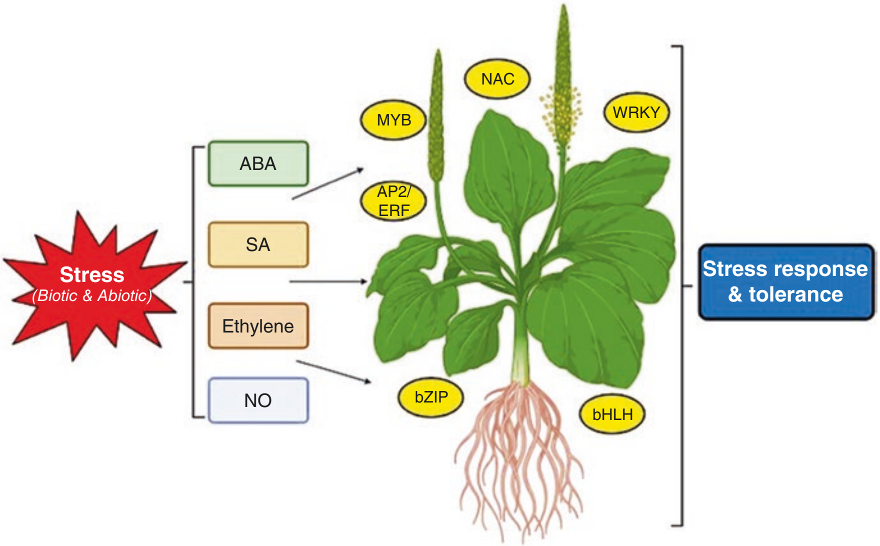

Fig. 1.1 Illustration of the role of different signaling elements and gene expression activation in response to various stresses

1.3 Role of Reactive Oxygen Species and Antioxidant Defense in Plant Stress

Higher plants use the production of ROS, a fundamental process, to transmit cellular signals in response to shifting environmental conditions. The disruption of the balance between the production of ROS and antioxidant defense mechanisms, which leads to an excessive buildup of ROS and causes oxidative stress in plants, is one of the most significant effects of abiotic stress (Hasanuzzaman et al. 2020). Such factors severely damage a plant's ability to grow and develop but also cause a reduction in overall crop productivity. A number of environmental factors such as salt, drought, and temperature stress in addition to the pathogen attacks trigger the production of reaction oxygen species (ROS) (Pereira 2016; Huang et al. 2019; Raza et al. 2019). These ROS play an essential role as signaling components in plants.

On the other hand, plants also possess a potent antioxidant defense system that has developed over time which maintains equilibrium and prevents oxidative damage (Gill and Tuteja 2010). By scavenging ROS, enzymatic and nonenzymatic antioxidants collaborate to maintain the redox balance in plant cells (Akram et al. 2017). Enzymes that function as antioxidants such as superoxide dismutase, glutathione peroxidase, glutathione reductase, and ascorbate peroxidase are necessary for ROS detoxification. At ROS generation sites, these enzymes continue to degrade hydrogen peroxide, producing safe compounds and water (Mhamdi et al. 2010) (Fig. 1.2).

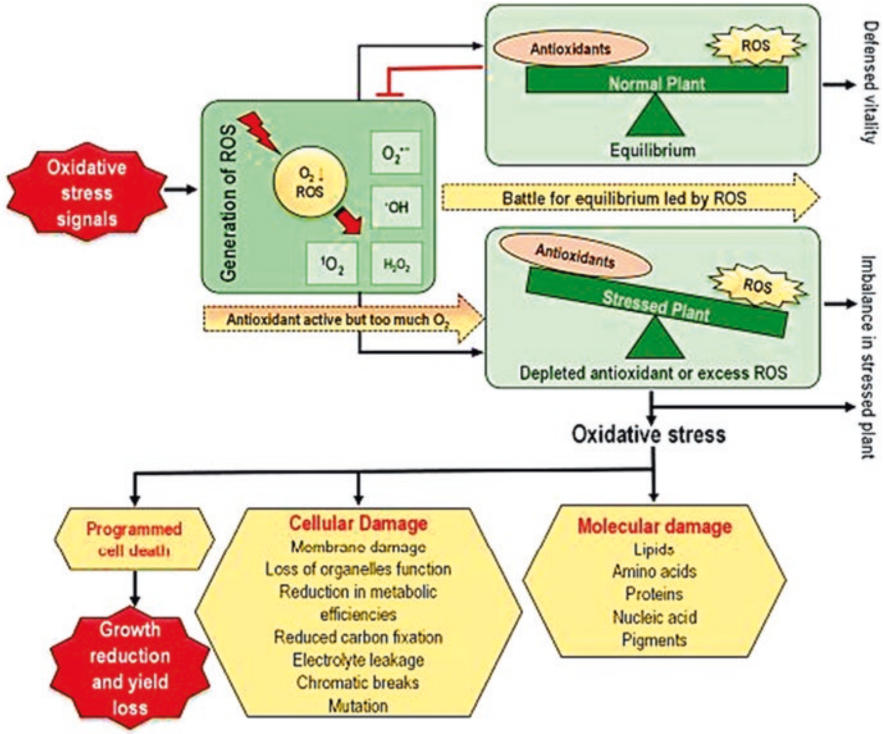

Fig. 1.2 Illustration of the importance of equilibrium between the ROS and antioxidant concentrations in plants in response to certain stresses. [The figure is adapted from Hasanuzzaman et al. (2020) regarding the role of ROS and antioxidants in defense against abiotic stress]

Since it postpones programmed cell death, plants in stressful environments benefit greatly from having a well-in-place antioxidant defense system. The damage to nucleic acid, lipid peroxidation, oxidative protein damage, production of several enzyme inhibitions, and excessive ROS production are all consequences of insufficient antioxidant enzymes in plants to scavenge excessive ROS (Dumanović et al. 2021). The antioxidant defense system delays oxidation and regulates DNA and nucleic acid damages under stress to ensure effective ROS detoxification, decreased lipid peroxidation in membranes, and the prevention of protein damage (Fig. 1.2). The ability of the plants to withstand stress is thus a consequence of the overall cellular protection provided by this system (Fujita and Hasanuzzaman 2022).

The precise equilibrium between the generation of ROS and antioxidant defense mechanisms will be disturbed under stressful situations. Under these circumstances, upregulated stress-responsive genes could result in increased antioxidant enzyme production and activity leading to alleviating the overall damaging effects of ROS (Huang et al. 2019). Plants also stimulate the production of nonenzymatic antioxidants such as tocopherols, ascorbate, and carotenoids, which helps in fending off oxidative stress. Plant stress tolerance and survival depend heavily on the regulation of ROS and antioxidant defense systems (Hasanuzzaman et al. 2021) as stronger antioxidant defense systems impart the ability to plants to withstand stress thereby making them resistant to a variety of environmental challenges (Nadarajah 2020). In contrast, plants with weak antioxidant defense are more vulnerable to stress-related deterioration. Figure 1.2 demonstrates the significance of balance and imbalance between the respective concentrations of reactive oxygen species and antioxidants in plants in response to stress.

An in-depth understanding of the interactions between the production of ROS and antioxidant defense system during plant stress response could lead to the development of better strategies and approaches in agriculture and environmental management. Researchers can design methods based on the interplay of ROS-antioxidant defense systems for the improvement of crops' ability to withstand stress, which will increase productivity and yield stability (Li et al. 2022). Numerous plant species' ability to withstand stress has been improved by genetic engineering techniques that increase the production of antioxidant enzymes or alter ROS scavenging pathways (Hasanuzzaman et al. 2021). In a nutshell, plant stress responses depend on an intricate equilibrium between ROS production and antioxidant defense mechanisms (Hasanuzzaman et al. 2020). Initiating stress reactions is significantly aided by ROS, which function as signaling molecules. Antioxidant defense mechanisms attempt to preserve the homeostasis of ROS and avert oxidative damage.

1.4 Hormonal Regulation of Plant Stress Responses

Plants are susceptible to various environmental challenges in terms of their growth and development. These stresses encompass salinity, drought, extremely high temperatures, and pathogenic infections, and plants have specialized mechanisms to combat such challenges. One of the mechanisms is the hormonal regulation in plants. These processes play a key role in plants' response toward stress which assists them in adapting and surviving under harsh climatic conditions. Brassinosteroids, cytokinins, melatonin, ethylene, and abscisic acid are some of the key hormones involved in mediating these responses. These hormones modulate gene expression, regulate physiological responses, and activate defense mechanisms, ultimately enabling plants to withstand adverse conditions and ensure their survival (Fig. 1.3). Understanding the intricate hormonal networks governing stress responses in plants can provide valuable insights for developing strategies to enhance crop resilience and productivity in the face of changing environmental conditions.

1.4.1 Brassinosteroids (BRs)

Brassinosteroids are one of the plant hormones that function in a variety of processes including the ones that are quite crucial in maintaining the plant's physiology. Recent studies have determined the significance of brassinosteroids in

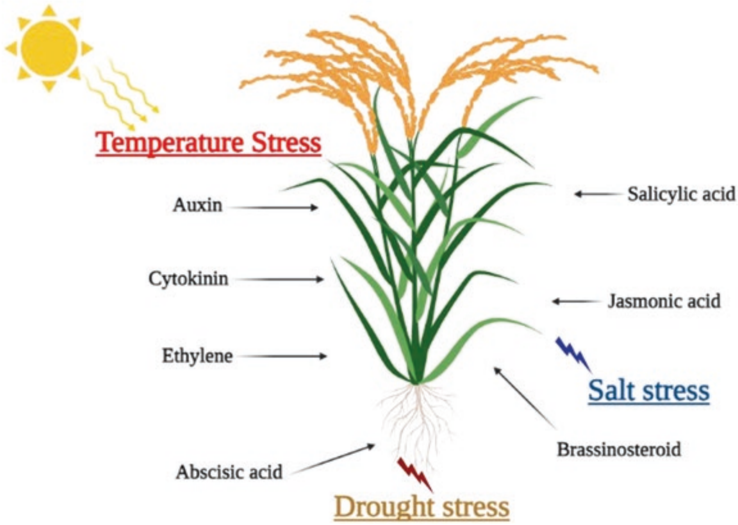

Fig. 1.3 Demonstration of different plant hormones involved in regulating the stress response against various environmental conditions including high temperature, salt, and drought stress

enhancing the capability of plants to withstand different abiotic stresses such as salinity and drought. BRs regulate stomatal behavior, enabling plants to maintain optimal water balance during water-deficit conditions and also promote antioxidant defense mechanisms thereby reducing oxidative damage (Fig. 1.3). Additionally, BRs modulate gene expression to enhance stress tolerance, activating stress-responsive genes involved in osmoprotection and detoxification pathways (Chaudhuri et al. 2022).

1.4.2 Cytokinins

Cytokinins are plant hormones involved in regulating cell division, shoot development, and nutrient allocation. Emerging evidence suggests their role in plant stress response where they are found to be involved in increasing the plant's ability to tolerate various abiotic stresses such as nutritional deficiency, drought, high temperature, and salinity. Cytokinins promote root growth and development, enabling plants to explore a larger soil volume to access water and nutrients. Cytokinins also regulate stomatal conductance, influencing the rate of transpiration and water loss. Moreover, they also help in the regulation of gene expression which contributes to activating the defense pathways in plants (Akhtar et al. 2020).

1.4.3 Melatonin

Another important hormone that is present in living organisms including plants is melatonin, which plays a significant role as a signaling molecule in response to different types of stresses. Many of the recent studies provided insights into the importance of melatonins in assisting plants to tolerate drought, extreme temperatures, heavy metals, and saline conditions. It also targets the reactive oxygen species (ROS) leading to the reduction in oxidative stress triggered damage in plants. Moreover, melatonin also modulates the functioning of antioxidant enzymes ultimately increasing their activity and production. Additionally, it regulates the key pathways that are related to stress defense and promotes the plant's capability to tolerate stress (Tan et al. 2015).

1.4.4 Ethylene

Ethylene is a gaseous plant hormone involved in stress responses. Ethylene promotes fruit ripening but also plays an important role in plant defense against pathogens, particularly necrotrophic fungi. Ethylene signaling triggers various defense mechanisms, including the production of pathogenesis-related proteins, phytoalexins, and reactive oxygen species (ROS) (Zhou et al. 2019) (Fig. 1.3).

1.4.5 Abscisic Acid (ABA)

Abscisic acid (ABA) is a critical stress hormone in plants that helps plants respond to drought, salinity, and other abiotic stresses. It regulates stomatal closure, reducing water loss through transpiration and helping plants to conserve water during water-deficit conditions. ABA also influences the expression of stress-responsive genes, leading to the synthesis of protective proteins and enzymes (Cutler et al. 2010).

1.5 Transcriptional Regulation of Stress-Responsive Genes

There are a number of strategies that living organisms have adapted in order to survive under stressful environments. One such adaptation is the modulation of key stress-responsive genes by a variety of transcription factors. This regulation is associated with the mechanism that controls the synthesis of RNA from DNA; hence, affecting the levels of gene expression. There are genes that respond to stress conditions and are activated or deactivated in response to various stimuli which help the organism to initiate a protective response. An in-depth understanding of this phenomenon can provide us with insights into the mechanics of how a living organism responds to environmental challenges. Further research in this area of study can contribute to exploring the mechanisms of stress tolerance enhancement in different agricultural crops to improve their physiology and ultimately increase productivity. Following are some of the ways of transcriptional regulation of such stress-responsive genes in plants.

1.5.1 Transcription Factors

Transcription factors are important modulators of gene expression levels. There are specific sites at the promoter region of the targeted genes where these transcription factors bind, known as transcription factor binding sites. Certain transcription factors are either directly or indirectly activated by various stress signals including cold, heat, pathogen attack, or oxidative stress. The transcriptions can then elevate or suppress the transcription of certain stress response genes by binding to their respective transcription binding sites and, hence, trigger a series of events that modulate the gene expression in response to different plant stresses (Nover et al. 2001; Ohama et al. 2016).

1.5.2 Stress-Responsive Promoters

Promoters are the sites in DNA that assist in the binding of transcription factors and other modulating proteins at their respective regions. The stress response genes have specified promoters that possess certain regulatory components such as *cis*-acting motifs, which are one of these components that function as the binding regions for stress-responsive transcription factors. Transcription factors regulate the selection of transcriptional components including RNA polymerase by interacting with these promoters, ultimately regulating the transcription initiation rate (Miller et al. 2012; Cussat-blanc and Harrington 2019).

1.5.3 Chromatin Remodeling

Chromatin is the combination of DNA and histone proteins that influence the level of gene expression by structural alterations. Under stressful conditions, the remodeling of chromatin occurs which enables the relevant stress-responsive genes to be either activated or suppressed. This remodeling involves the repositioning of the nucleosomes, the selection of respective chromatin complexes, and the post-translational modifications of the histones. These vital alterations ultimately regulate the binding of transcription factors to the DNA on respective sites, therefore, affecting the functioning of stress-responsive genes (Yamaguchi-Shinozaki and Shinozaki 2006).

1.5.4 Epigenetic Modifications

The regulation of epigenetic factors can result in dynamic alterations, such as the plant hypersensitivity response (HR), alterations in the chromatin's structural organization, and effects on the phenotype of the plant, which aid native plants to adapt to stress (Thiebaut et al. 2019). Additionally, epigenetic markers also offer a stress-related systematic memory, which enables plants to respond to repeated exposures to the stress more efficiently and effectively. The plants also pass this information on to the next generations to help them cope with potential future stresses. To better comprehend the molecular mechanisms underlying plant stress responses, epigenetic changes in addition to genetic factors must be studied (Matin 2021).

1.5.5 Post-transcriptional Regulation

While transcriptional regulation primarily governs the synthesis of RNA molecules, post-transcriptional mechanisms fine-tune the gene expression. Stress-responsive genes can be subject to post-transcriptional regulation through processes like alternative splicing, RNA stability, and translation efficiency. These processes assist the proteins encoded by the stress-responsive genes to adapt more appropriately, in compliance to respond to the stress conditions (Mizoi et al. 2012; Oa et al. 2013).

1.6 Protein Modifications and Post-translational Modifications (PTMs)

Under biotic and abiotic stresses some post-translational modifications (PTMs) are essential for plant adaptability and persistence. Phosphorylation, ubiquitination, acetylation, and methylation are the PTMs significantly carried out under plant stress-responsive conditions. The most well-studied PTM is phosphorylation, which is an important component of stress signaling and response. Activity, stability, and subcellular localization of target proteins are altered by their phosphorylation under stress-activated protein kinases (Wu et al. 2016).

Protein phosphorylation and dephosphorylation statuses modify plant development and stress responses by affecting the structure, function, subcellular distribution, and interactions of proteins. A recent study reported a total of 753 phosphorylated peptides that were brought on by heat stress alone, by drought priming, or by both in a cool-season grass species. Particular drought-related proteins (DRPs) that were upregulated by drought priming and maintained during the subsequent heat stress were especially intriguing and may be connected to priming-enhanced stress tolerance. The majority of those DRPs were categorized into four functional groups: RNA splicing, transcription regulation, stress protection, and stress perception/signaling (Zhang et al. 2020).

Previously, *A. thaliana* has been used as a model system to best describe the role of mitogen-activated protein kinases (MAPKs) in ABA signaling. However, a recent study has demonstrated that MAPKs are also known to be involved in the ABA signaling pathway in other species as well, e.g., MnMPK1 expression is induced by ABA signaling in mulberry and can also activate PsMPK2 in pea plants. Additionally, the PsMPK2 activation profile resembles that of previously reported AtMPK1 and AtMPK2 in *A. thaliana*. Similarly, the kinase activity is increased by JA and H_2O_2, which shows that MAPKs may serve similar roles in different species under stressful circumstances. Another kinase, NaMPK4 plays an important role in ABA-induced stomatal closure in *Nicotiana attenuata*. MPK4 is also implicated in the defense against *Alternaria alternata*, a tobacco pathotype as well as against invasive pathogenic bacteria and aphids.

Phosphorylation-induced stress signaling is also mediated by other protein kinase families besides MAPKs, including receptor-like kinases (RLKs), calcium-dependent protein kinases (CDPKs), and SNF1-related protein kinases (SnRKs). RLKs play a critical role in detecting extracellular signals and starting subsequent stress-associated responses. For instance, the receptor-like kinase FERONIA controls the stomatal closure and root development in response to drought stress (Lin et al. 2021). In stress signaling pathways, calcium-dependent protein kinases, or CDPKs, act as molecular switches. They control a range of stress-related reactions, including hormone signaling, pathogen defense, and abiotic stress tolerance (De Recherche et al. 2014).

Another important PTM that controls protein turnover and breakdown is ubiquitination. Target proteins are tagged for ubiquitination by E3 ubiquitin ligases, which triggers the 26S proteasome to degrade the labeled proteins. The control of stress-responsive transcription factors and the elimination of damaged proteins are both crucially influenced by ubiquitination-mediated protein degradation. For example, the E3 ligase OsRING1a degrades the transcription factor OsMYB30 to enhance the ability to withstand drought stress in *Oryza sativa* (Chen et al. 2022). Furthermore, it has been demonstrated that the Arabidopsis RING-type E3 ligase PUB13 controls the response to drought stress by selecting particular proteins for ubiquitination and subsequent destruction.

Another example of PTM-mediated stress management is the stability and functionality of the ABA receptor PYL8 in the response to drought stress depending on N-glycosylation in Arabidopsis (Lim et al. 2013). On the other hand, O-glycosylation, the process of attaching sugar moieties to serine or threonine residues, has been connected to the control of defense-related protein activity and the improvement in stress tolerance (Strasser and Strasser 2022). Additionally, PTMs like acetylation and methylation also aid in plant's response to stress, for example, the acetylation of proteins is involved in protein constancy, which is facilitated by lysine acetyltransferases (KATs) and de-acetylases (KDACs). Under stressful conditions, the acetylation process has the ability to fine-tune transcriptional regulation and DNA binding activity of stress-related transcription factors (Xu et al. 2023). Another post-translational modification known as protein methylation affects transcriptional control, stress response, and protein–protein interactions via methyl transferases. Methylation of histones and nonhistone proteins helps to regulate gene expression and modification under stress conditions (Van Antro et al. 2023).

1.7 Cellular Response to Stress

Complex cellular systems are triggered by plant stressors, allowing plants to respond and adapt to challenging circumstances. These mechanisms, which collectively aid in stress tolerance, involve numerous cellular processes, signaling networks, and chemical reactions. Here, we will discuss some of the details of the cellular systems