

Mirza Hasanuzzaman
Khalid Rehman Hakeem · Kamrun Nahar
Hesham F. Alharby *Editors*

Plant Abiotic Stress Tolerance

Agronomic, Molecular and
Biotechnological Approaches

 Springer

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Editors

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Editors

Mirza Hasanuzzaman
Department of Agronomy
Faculty of Agriculture
Sher-e-Bangla Agricultural University
Dhaka, Bangladesh

Khalid Rehman Hakeem
Department of Biological Sciences
King Abdulaziz University
Jeddah, Saudi Arabia

Kamrun Nahar
Department of Agricultural Botany
Faculty of Agriculture
Sher-e-Bangla Agricultural University
Dhaka, Bangladesh

Hesham F. Alharby
Department of Biological Sciences
King Abdulaziz University
Jeddah, Saudi Arabia

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Foreword



The plant stresses are defined as responses describing a suite of molecular and cellular processes triggered by the detection by a plant of some form of stress. These can be abiotic such as water deficit, water-logging or flooding, extreme cold, frost, heat, salinity, sodicity, and metal and metalloid toxicity or biotic which are responsible for the damage done to an organism by other living organisms like herbivores or pathogens, bacteria, viruses, fungi, parasites, beneficial and harmful insects, weeds, and cultivated or native plants. It has been estimated that salinity and drought are expected to cause serious salinization of more than 50% of all available productive, arable lands by the year 2050. Extreme environmental events in the era of global climatic change further aggravate the problem and remarkably restrict the plant growth and development. We now have very high yielding crops, but these too are susceptible to abiotic stresses. Potential yield of economically important crops is drastically coming down every year just because of abiotic stresses. In view of this, improvement in crop stress responses is a big challenge. Understanding the mechanisms by which plants perceive and transduce the stress signals to initiate adaptive responses is essential for engineering stress-tolerant crop plants. Systems biology approaches facilitate a multi-targeted approach, which involves the molecular parts of an organism and attempts to fit them into functional networks or models designed to describe and predict the dynamic activities of that organism in different

environments. Recent advances in biotechnology have changed our capabilities for gene discovery and functional genomics. While many of the functions of individual parts are unknown, their function can sometimes be inferred through association with other known parts, providing a better understanding of the biological system as a whole. High-throughput omics technologies facilitate the identification of new genes and gene function. The mechanisms underlying stress factors have long been the focus of research. Plants overcome environmental stresses by the development of tolerance, resistance, or avoidance mechanisms.

This book titled *Plant Abiotic Stress Tolerance: Agronomic, Molecular and Biotechnological Approaches*, edited by Dr. Mirza Hasanuzzaman, Professor of Agronomy in Bangladesh with a Ph.D. in Plant Stress Physiology and Antioxidant Metabolism from Japan; Dr. Khalid Rehman Hakeem, Associate Professor at King Abdulaziz University, Saudi Arabia, with specialization in Plant Ecophysiology, Biotechnology, and Molecular Biology; Dr. Kamrun Nahar, Associate Professor at Sher-e-Bangla Agricultural University, Bangladesh, with Ph.D. in Plant Abiotic Stress Physiology from Japan; and Dr. Hesham F. Alharby, Head of Plant Section, King Abdulaziz University, Saudi Arabia, presents a collection of 18 chapters. It presents the trends in plant abiotic stress tolerance: agronomic, molecular, and biotechnological approaches. The chapters included here provide detailed latest information. It will be a good guide for researchers working in the field of crop improvement, genetic engineering, and abiotic stress tolerance.

Chapter 1 deals with the maize production under salinity and drought condition: oxidative stress regulation by the antioxidant defense and glyoxalase systems. Authors have reviewed and discussed the present circumstances of maize production and recent progress of varietal improvement for drought and salt tolerance emphasizing how ROS and MG are being regulated in a plant cell by the antioxidant defense and glyoxalase pathways. This chapter also focused on the recent approaches in attenuating oxidative stress in maize plants grown under salinity and drought. Chapter 2 focuses on plants' behavior under soil acidity stress: insight into morphophysiological, biochemical, and molecular responses. This chapter reviews the mechanism of damage under acidity (H^+ rhizotoxicity) stress on plants and also the recent approaches to improve growth and productivity under acidic condition, from the available literature. Chapter 3, titled as salinity: a major agricultural problem—causes, impacts on crop productivity, and management strategies, uncovers decreased crop productivity due to salinity which is expected to elevate in the coming decades. It is expected to pose severe threats to global food security in the future if the challenge is not properly directed. Authors present sustainable agronomic practices, deployment of molecular and functional genomic approaches here which can boost our understanding of salinity stress and create salt-tolerant traits in major field crops. These will potentially contribute to production and yield enhancement under elevated saline conditions. In Chapter 4, plant salinity stress tolerance in plants—physiological, molecular, and biotechnological approaches—has been dealt with considering the advances made in recent decades. The breeding for increased tolerance through gene transfer and the production of transgenic plants is considered an excellent and low-cost method. Perhaps the most valuable outcome of

the biotechnology program is to use molecular tools for the breeding programs. Identifying tightly linked molecular markers with the target gene and mapping on the chromosome is an important goal for cloning the genes and marker-assisted selection. Chapter 5 talks about water-deficit stress effects and responses in maize. This chapter describes the mechanism of drought resistance in plants on a morphological, physiological, and molecular basis. The development of crop varieties with increased tolerance to drought, both by conventional breeding methods and by genetic engineering, is given as an important approach to meet up global food demands with less water. Chapter 6 sheds light on the temperature extremes: impact on rice growth and development. In this chapter, authors have summarized the studies regarding the effect of temperature extremes on different growth stages of rice and discussed the possible strategies and opportunities for improving the rice tolerance to heat and cold stresses. Chapter 7 discusses submergence stress in rice: physiological disorders, tolerance mechanisms, and management. Authors mention that several transcription factors are involved in the negative regulation of genes to reduce the elongation. In escape strategy, ethylene-mediated factors are involved in elongation of internodal distance; they have also proposed the physiological and molecular approaches for enhancing the rice tolerance to flood-prone and rainfed lowland conditions. Chapter 8 deals with the oxidative stress and antioxidant defense mechanism in plants under salt stress. It presents studies emphasizing on the plant response to salinity stress through physical, biological, and DNA changes and its alterations to saline places by osmoregulation, ion homeostasis, apoplasmic acidification, production of various antioxidants, several genes, hormonal conventions, and production of stress-responsive proteins. According to the authors, intensive exploration work on a combination of several control practices may lead to excellent crop yield in saline soils that might contribute significantly and efficiently to global food security. Chapter 9 titled as oxidative stress and antioxidant defense in plants under drought discusses the oxidative damage caused by the water deficit condition in plant and focuses on the production and scavenging system of ROS in plants. It also provides the details of production site of reactive oxygen species and their reaction with different cellular organelles. A comprehensive scavenging enzymatic and nonenzymatic types and their mode of action to neutralize the harmful effects imposed by drought stress are presented. Chapter 10 discusses the potential of reactive oxygen species metabolism and antioxidant defense in plants under metal/metalloid stress. It is gaining enormous research interest as it limits crop production by harshly altering the physiology and biochemistry of plants. Authors have reviewed the recent reports on different molecular approaches of metal-/metalloid-induced stress tolerance strategies. Chapter 11 covers reactive oxygen species signaling in plants. Various aspects of reactive oxygen species and enzymes in plant response to stress regulation and metabolism are discussed here. Chapter 12 deals with the role of selective exogenous elicitors in plant responses to abiotic stress tolerance. This chapter summarizes the role of elicitors during stressful environments. Some of the signaling aspects through which the cell metabolism is modulated by these elicitors have also been discussed. A brief crosstalk mechanism of some of these exogenous elicitors during these environmental perturbations has also been covered.

Chapter 13 uncovers calcium-mediated growth regulation and abiotic stress tolerance in plants. Authors have focused on the role of calcium against devastating effect of abiotic stresses in plant growth, development, physiology, and yield. Recent information focused on the calcium-induced stimulation of plant growth and physiology as well as abiotic stress tolerance in plants has been presented at length. Chapter 14 deals with silicon—a sustainable tool in abiotic stress tolerance in plants. Silicon fertilizer provides economic as well as ecological benefits to plant growers. Authors enlighten the fact that concerted efforts in the area of silicon research can lead to its accelerated and improved application in the form of fertilizer for sustainable agriculture. Chapter 15 deals with the response of gerbera plants to different salinity levels and leaching ratios on soilless culture. This study has been carried out in order to determine the effects of different salinity levels and leaching ratios on plant growth, yield and quality, and water consumption of gerbera grown by soilless culture. In Chapter 16, crosstalk of nitric oxide and reactive oxygen species in various processes of plant development: past and present, nitric oxide is discussed as a regulator of many physiological processes including cell wall biosynthesis, reactive oxygen species metabolism, stress-induced or constitutive gene expression, programmed cell death, ripening, and senescence. Chapter 17 evaluates the ameliorative capability of plant growth promoting rhizobacteria and arbuscular mycorrhizal fungi against salt stress in plants. Authors describe the causes of soil salinization and discuss potential impacts of salinity stress on plants as well as the action mechanisms of plant growth promotion and/or regulation. They are also highlighting their intrinsic traits that can be upscaled to increase their usefulness as a value-added product for stress agriculture. In Chapter 18, plant miRnome, miRNA biogenesis and abiotic stress response, has been discussed with current knowledge on miRNA biogenesis, mode of action, and the role of miRNA in abiotic stress response in plants.

This book includes a practical update on our knowledge on plant abiotic stress tolerance with special reference to agronomic, molecular, and biotechnological approaches. It will lead to new discussions and efforts to the use of various tools for the improvement of crops for abiotic stress tolerance.

Izmir, Turkey

Münir Öztürk

Preface

Plants have to experience a series of environmental stresses throughout the entire life-span in terms of biotic and abiotic stress. Among these, abiotic stress is the most detrimental one that is responsible for nearly 50% of crop yield reduction, and it appears to be a potential threat to global food security in coming decades. Plant growth and development reduces drastically due to adverse effects of abiotic stresses. It has been estimated that crop can exhibit only 30% of their genetic potentiality under abiotic stress condition. Therefore, this is a fundamental need to understand the stress responses, thus facilitating breeders to develop stress-resistant and stress-tolerant cultivars along with good management practices to withstand abiotic stresses. Also a holistic approach to understand molecular and biochemical interactions of plants is important to implement the knowledge of plant resistance mechanisms under abiotic stresses. Agronomic practices like selecting cultivars that are tolerant to a wide range of climatic condition, planting date, irrigation scheduling, and fertilizer management could be some of the effective short-term adaptive tools to fight against the abiotic stresses. In addition, for long-term adaptation changes and alternations in plant molecular level, “system biology” and “omics approaches” in recent studies could bring some tremendous revolutionary modification in realizing abiotic stresses. The genetic approach, for example, selection and identification of major conditioning genes by linkage mapping and quantitative trait loci (QTL), production of mutant genes, and transgenic introduction of novel genes, has imparted some tolerant characteristics in crop varieties from their wild ancestors. Recently, research has revealed the interactions between micro-RNAs (miRNAs) and plant stress responses exposed to salinity, freezing stress, and dehydration. Transgenic approaches to generate stress-tolerant plant are one of the most interesting researches until now.

The current book is presenting the recent development of agronomic and molecular approaches in conferring plant abiotic stress tolerance in an organized way. The abiotic stresses covered in this book include salinity, water deficiency, water submergence, and extreme temperatures. We have mentioned the strategies in use to mitigate these stresses by incorporating various approaches. These strategies include the application of silicon, AMF, and various exogenous elicitors. The book

is also highlighting the mechanism of action of these stress busters in order to increase their usefulness as a value-added product for stressed agriculture. The role of antioxidant enzyme machinery as a defensive feature has been broadly explained in this book. Besides, the current knowledge on miRNA biogenesis, mode of action and the role of miRNA in abiotic stress response in plants.

This is our opportunity to thank the authors who have given their time unselfishly to meet the deadlines for each chapter. We greatly appreciate their commitment. Our profound thanks also to Mr. Abdul Awal Chowdhury Masud, Ms. Khursheda Parvin, Mr. Sayed Mohammad Mohsin, and Mr. MHM Borhannuddin Bhuyan for their critical review and valuable support in formatting and incorporating all editorial changes in the manuscripts. We are also thankful to Prof. Münir Öztürk for his suggestions and writing the foreword for this volume.

We also thank Springer International team for their generous cooperation at every stage of the book production.

Dhaka, Bangladesh
Jeddah, Saudi Arabia
Dhaka, Bangladesh
Jeddah, Saudi Arabia

Mirza Hasanuzzaman
Khalid Rehman Hakeem
Kamrun Nahar
Hesham F. Alharby

About the Book

Abiotic stress is one of the major constraints for crop production in the era of climate change. Therefore, this is a fundamental need to understand the stress responses, thus facilitating breeders to develop stress-resistant and stress-tolerant cultivars along with good management practices to withstand abiotic stresses. Also, a holistic approach to understand molecular and biochemical interactions of plants is important to implement the knowledge of plant resistance mechanisms under abiotic stresses. Agronomic practices like nutrient management could be some of the effective short-term adaptive tools to fight against the abiotic stresses. In addition, for long-term adaptation changes and alternations in plant molecular level, “system biology” and “omics approaches” in recent studies could bring some tremendous revolutionary modification in realizing abiotic stresses.

In the recent years, considerable progress has been made in improving crops for changing environments, and many reports have been published. This book contains 18 informative chapters about the up-to-date knowledge on wheat responses and tolerance to various abiotic stresses written by 74 experts aiming to become a useful information tool for agronomists, plant breeders, and plant physiologists as well as a guide for students in the field of plant science and agriculture. Importantly, this book will lead to new discussion and efforts toward plant abiotic stress tolerance using agronomic and molecular approaches.

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Editors

Mirza Hasanuzzaman Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Khalid Rehman Hakeem Department of Biological Sciences, King Abdulaziz University, Jeddah, Saudi Arabia

Kamrun Nahar Department of Agricultural Botany, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Hesham F. Alharby Department of Biological Sciences, King Abdulaziz University, Jeddah, Saudi Arabia

Contributors

Sandeep B. Adavi Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi, Delhi, India

Bilal Ahmad Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, India

Niaz Ahmad Department of Soil Science, Bahauddin Zakariya University, Multan, Pakistan

Riaz Ahmad Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Shakeel Ahmad Department of Agronomy, Faculty of Agricultural Sciences and Technology, Bahauddin Zakariya University, Multan, Punjab, Pakistan

Ishtiaq Ahmed Department of Horticultural Sciences, University College of Agriculture and Environmental Sciences, The Islamia University of Bahawalpur, Bahawalpur, Punjab, Pakistan

Sadia Sabrina Alam Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Basharat Ali Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

Muhammad Arif Ali Department of Soil Science, Bahauddin Zakariya University, Multan, Pakistan

Shafaqat Ali Department of Environmental Sciences and Engineering, Government College University, Faisalabad, Pakistan

Jubayer Al Mahmud Department of Agroforestry and Environmental Science, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Mohammad Amiruzzaman Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Taufika Islam Anee Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Muhammad Akbar Anjum Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Muhammad Saleem Arif Department of Environmental Sciences and Engineering, Government College University, Faisalabad, Pakistan

Umair Ashraf Department of Botany, University of Education (Lahore), Faisalabad, Punjab, Pakistan

Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

Shafia Bashir Department of Botany, Punjab Agricultural University, Ludhiana, Punjab, India

Shahnewaz Begum Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Tasnim Farha Bhuiyan Department of Agricultural Botany, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

M. H. M. Borhannuddin Bhuyan Laboratory of Plant Stress Responses, Department of Applied Biological, Sciences, Faculty of Agriculture, Kagawa University, Takamatsu, Kagawa, Japan

Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Citrus Research Station, Bangladesh Agricultural Research Institute (BARI), Jaintiapur, Sylhet, Bangladesh

Muhammad Adnan Bukhari Department of Agronomy, University College of Agriculture and Environmental Sciences, The Islamia University of Bahawalpur, Bahawalpur, Punjab, Pakistan

Shaghef Ejaz Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Shah Fahad Department of Agriculture, The University of Swabi, Swabi, Khyber Pakhtunkhwa, Pakistan

Masayuki Fujita Laboratory of Plant Stress Responses, Department of Applied Biological, Sciences, Faculty of Agriculture, Kagawa University, Takamatsu, Kagawa, Japan

Mirza Hasanuzzaman Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Ahmad Hassan Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Mamta Hirve School of Biochemistry, Devi Ahilya University, Indore, Madhya Pradesh, India

Hafiz Athar Hussain College of Agronomy and Biotechnology, Southwest University, Chongqing, China

Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China

Sadam Hussain Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

Sajjad Hussain Department of Horticulture, Faculty of Agricultural Sciences and Technology, Bahauddin Zakariya University, Multan, Punjab, Pakistan

Shahid Iqbal College of Plant Protection, Yunnan Agricultural University, Kunming, China

Md. Robyul Islam Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Meeta Jain School of Biochemistry, Devi Ahilya University, Indore, Madhya Pradesh, India

Shailendra K. Jha Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, Delhi, India

Riti Thapar Kapoor Plant Physiology Laboratory, Amity Institute of Biotechnology, Amity University, Noida, Uttar Pradesh, India

Sunita Kataria School of Biochemistry, Devi Ahilya University, Indore, Madhya Pradesh, India

Muhammad Fasih Khalid Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Abdul Khaliq Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

Mojtaba Kordrostami Department of Plant Biotechnology, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran

Yasemin S. Kukul Kurttaş Department of Agricultural Structures and Irrigation, E.U. Faculty of Agriculture, Ege University, Bornova-Izmir, Turkey

Tang Li College of Plant Protection, Yunnan Agricultural University, Kunming, China

Umer Mahmood Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

College of Agronomy and Biotechnology, Southwest University, Chongqing, China

Abdul Majeed Department of Botany, Government Degree College Naguman, Peshawar, Khyber Pakhtunkhwa, Pakistan

Chanchal Malhotra Plant Physiology Laboratory, Amity Institute of Biotechnology, Amity University, Noida, Uttar Pradesh, India

Maryam Department of Botany, Government Sadiq College Women University, Bahawalpur, Punjab, Pakistan

Hari Singh Meena Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi, Delhi, India

M. Kamil Meriç E.U. Bergama Vocational School, Ege University, Bergama-Izmir, Turkey

Zahir Muhammad Department of Botany, University of Peshawar, Peshawar, Khyber Pakhtunkhwa, Pakistan

Muhammad Nafees Department of Horticultural Sciences, University College of Agriculture and Environmental Sciences, The Islamia University of Bahawalpur, Bahawalpur, Punjab, Pakistan

Kamrun Nahar Department of Agricultural Botany, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Tahia Naznin Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

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

Sumaiya Haque Omy Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Deepu Pandita Government Department of School Education, Jammu, Jammu and Kashmir, India

Khursheda Parvin Laboratory of Plant Stress Responses, Department of Applied Biological, Sciences, Faculty of Agriculture, Kagawa University, Takamatsu, Kagawa, Japan

Department of Horticulture, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Rajkumar Prajapati School of Biochemistry, Devi Ahilya University, Indore, Madhya Pradesh, India

Tauqeer Qadir Department of Agronomy, University of Agriculture, Faisalabad, Punjab, Pakistan

Babak Rabiei Department of Agronomy and Plant Breeding, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran

Muhammad Junaid Rao Key Laboratory of Horticultural Plant Biology (Ministry of Education), Huazhong Agricultural University, Wuhan, People's Republic of China

College of Horticulture and Forestry Sciences, Huazhong Agricultural University, Wuhan, People's Republic of China

Muhammad Riaz Department of Environmental Sciences and Engineering, Government College University, Faisalabad, Pakistan

Md. Motiar Rohman Plant Breeding Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh

Yawar Sadiq Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, India

Muhammad Saqib Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

Özlem Akat Saraçoğlu E.U. Bayindir Vocational School, Ege University, Bayindir-Izmir, Turkey

Lekshmy Sathee Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi, Delhi, India

Adnan Noor Shah Department of Agronomy, Faculty of Agriculture, Gomal University, Dera Ismail Khan, Khyber Pakhtunkhwa, Pakistan

Sher Muhammad Shahzad Department of Soil and Environmental Sciences, University College of Agriculture, University of Sargodha, Sargodha, Pakistan

Mohsin Tariq Department of Bioinformatics and Biotechnology, Government College University, Faisalabad, Pakistan

Department of Integrative Biology, University of California, Berkeley, CA, USA

İ. Hakkı Tüzel Department of Agricultural Structures and Irrigation, E.U. Faculty of Agriculture, Ege University, Bornova-Izmir, Turkey

Shabir H. Wani Mountain Research Centre for Field Crops, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Anantnag, Jammu and Kashmir, India

Tahira Yasmeen Department of Environmental Sciences and Engineering, Government College University, Faisalabad, Pakistan

Key Laboratory of Economic Plants and Biotechnology, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China

Abbu Zaid Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, India

Iqra Zakir Department of Agronomy, Bahauddin Zakariya University, Multan, Pakistan

Department of Agriculture, The University of Swabi, Swabi, Khyber Pakhtunkhwa, Pakistan

About the Editors



Mirza Hasanuzzaman is Professor of Agronomy at Sher-e-Bangla Agricultural University in Dhaka. He received his Ph.D. on “Plant Stress Physiology and Antioxidant Metabolism” from Ehime University, Japan, with a scholarship from the Japanese government (MEXT). Later, he completed his postdoctoral research at the Center of Molecular Biosciences, University of the Ryukyus, Japan, as a Recipient of the Japan Society for the Promotion of Science (JSPS) postdoctoral fellowship. He was also the Recipient of the Australian Government’s Endeavour Research Fellowship for postdoctoral research as an Adjunct Senior Researcher at the University of Tasmania, Australia. Dr. Hasanuzzaman’s current work is focused on the physiological and molecular mechanisms of environmental stress tolerance. Dr. Hasanuzzaman has published over 80 articles in peer-reviewed journals. He has edited 6 books and written 30 book chapters on important aspects of plant physiology, plant stress tolerance, and crop production. According to Scopus®, Dr. Hasanuzzaman’s publications have received about 3300 citations with an *h*-index of 30. He is an Editor and Reviewer for more than 50 peer-reviewed international journals and was a Recipient of the “Publons Peer Review Award 2017 and 2018.” He has been honored by different authorities for his outstanding performance in different fields like research and education, and he has received the World Academy of Science Young Scientist Award (2014).



Khalid Rehman Hakeem (Ph.D.) is Associate Professor at King Abdulaziz University, Jeddah, Saudi Arabia. After completing his doctorate (Botany; specialization in Plant Eco-physiology and Molecular Biology) from Jamia Hamdard, New Delhi, India, in 2011, he worked as a lecturer at the University of Kashmir, Srinagar, for a short period. Later, he joined Universiti Putra Malaysia, Selangor, Malaysia, and worked there as Postdoctorate Fellow in 2012 and Fellow Researcher (Associate Professor) from 2013 to 2016. Dr. Hakeem has more than 10 years of teaching and research experience in plant eco-physiology, biotechnology and molecular biology, medicinal plant research, plant-microbe-soil interactions as well as in environmental studies. He is the recipient of several fellowships at both national and international levels; also, he has served as the visiting scientist at Jinan University, Guangzhou, China. Currently, he is involved with a number of international research projects with different government organizations.

So far, Dr. Hakeem has authored and edited more than 35 books with international publishers, including Springer Nature, Academic Press (Elsevier), and CRC Press. He also has to his credit more than 80 research publications in peer-reviewed international journals and 55 book chapters in edited volumes with international publishers.

At present, Dr. Hakeem serves as an editorial board member and reviewer of several high-impact international scientific journals from Elsevier, Springer Nature, Taylor and Francis, Cambridge, and John Wiley Publishers. He is included in the advisory board of Cambridge Scholars Publishing, UK. He is also a fellow of Plantae group of the American Society of Plant Biologists, member of the World Academy of Sciences, member of the International Society for Development and Sustainability, Japan, and member of Asian Federation of Biotechnology, Korea. Dr. Hakeem has been listed in Marquis Who's Who in the World, since 2014–2019. Currently, Dr. Hakeem is engaged in studying the plant processes at eco-physiological as well as molecular levels.



Kamrun Nahar is Associate Professor in the Department of Agricultural Botany at Sher-e-Bangla Agricultural University, Dhaka, Bangladesh. She received her Ph.D. Degree on “Environmental Stress Physiology of Plants” in 2016 from the United Graduate School of Agricultural Sciences, Ehime University, Japan, with Japanese Government (MEXT) Scholarship. Dr. Nahar has been involved in research with field crops emphasizing stress physiology since 2006. She has completed several research work and also continuing research project funded by Sher-e-Bangla Agricultural University Research System and Ministry of Science and Technology (Bangladesh). She is supervising M.S. students. Dr. Nahar published 50 articles and chapters related to plant physiology and environmental stresses with Springer, Elsevier, CRC Press, Wiley, etc. Her publications reached about 2000 citations with h-index of 22 (according to Scopus®). She is involved in editorial activities and Reviewer of international journals. She is Active Member of about 20 professional societies. Dr. Nahar attended different international conferences and presented 10 papers and posters in national and international conferences in different countries (the USA, Australia, Japan, Austria, Russia, China, etc.).



Hesham F. Alharby (Ph.D.) is Associate Professor in the Department of Biological Sciences at King Abdulaziz University (KAU), Jeddah, Saudi Arabia. He received his Ph.D. from the School of Plant Biology at the University of Western Australia, Perth, Australia, in 2014. Dr. Alharby’s current research works are related to various aspects of plant biology, particularly in eco-physiology and molecular biology. So far, Dr. Alharby has published more than 40 papers in peer-reviewed international journals and attended several international conferences. He was a Head of the Laboratories at Teachers College, Jeddah, Saudi Arabia, in 2005. At the moment, he is the Head of Plant Section in the Department of Biological Sciences at KAU.

Maize Production Under Salinity and Drought Conditions: Oxidative Stress Regulation by Antioxidant Defense and Glyoxalase Systems



Md. Motiar Rohman, Md. Robyul Islam, Tahia Naznin, Sumaiya Haque Omy, Shahnewaz Begum, Sadia Sabrina Alam, Mohammad Amiruzzaman, and Mirza Hasanuzzaman

Introduction

Abiotic stress factors, particularly drought and soil salinity, are the major stresses limiting crop yields worldwide. The forthcoming global climate changes have been increasing the possibilities of higher mean temperatures, extreme seasonal weather patterns, and the frequency, intensity and duration of drought, as well as heat waves. At the same time, increasing soil salinity in coastal regions has focused attention on the possibility of crop damage in fields located in sea regions worldwide. These problems due to salinity and drought will affect the production of agricultural crops in the upcoming years, particularly in arid and semiarid regions (IPCC 2014). This situation is a great threat to ensuring food security for densely populated countries, because crops that have a higher yield but have lower adaptability to salinity and drought will need to be replaced by crops that have higher adaptive potential but are likely to have a lower yield. As a result, there is an urgent need to develop highly adaptive crops that also have a higher yield, in order to address both salinity and drought.

The primary effects of drought stress are changes in key biochemical and physiological processes as a consequence of drought-induced osmotic stress, which may cause oxidative damage in most plants (Ashraf 2010). Salinity affects plant growth and development in two ways. First, it imposes osmotic stress by reducing the soil water potential, leading to limited water uptake. Second, it causes excessive uptake of ions, particularly Na^+ and Cl^- , that ultimately interfere with various metabolic

M. M. Rohman (✉) · M. R. Islam · T. Naznin · S. H. Omy · S. Begum
S. S. Alam · M. Amiruzzaman
Plant Breeding Division, Bangladesh Agricultural Research Institute,
Joydebpur, Gazipur, Bangladesh
e-mail: mrahman@bari.gov.bd

M. Hasanuzzaman
Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University,
Dhaka, Bangladesh

processes. Plant responses to the osmotic and ionic components of salt stress are complicated and involve many gene networks and metabolic processes (Hasegawa et al. 2000; Munns and Tester 2008). Such responses depend mainly on the inherent salt tolerance of the plant, the severity of salt stress (the concentration of salt in the soil solution), and the duration of the plant roots' exposure to the salt. Both salinity and drought tolerance are complex traits, and plant breeders' efforts to produce crops with higher yields have largely been unsuccessful because of mutagenic adaptive responses to these traits.

Both salinity and drought stresses have negative consequences for gas exchange, resulting in low CO₂ assimilation for photosynthesis and consequently a significant reduction in electron transportation. As a result, reactive oxygen species (ROS) are generated, such as singlet oxygen (¹O₂), superoxide anions (O₂⁻), hydrogen peroxide (H₂O₂), perhydroxy radicals (HO₂^{*}), and alkoxy radicals (RO^{*}) (Gill and Tuteja 2010; Moller et al. 2007). Normally, generation of ROS is balanced with scavenging by various antioxidants (Foyer and Noctor 2005). This balance between the generation and scavenging of ROS is broken down by various biotic and abiotic stresses, including salinity and drought. At higher concentrations, ROS are highly reactive and cause damage to proteins, DNA, lipids, and carbohydrates, resulting in cell death (Fig. 1). As a result, accumulation of ROS under environmental stresses is the foremost reason for reduced productivity of crops (Mittler 2002; Apel and Hirt 2004; Mahajan and Tuteja 2005). Methylglyoxal (MG) is a potentially cytotoxic compound, which can react with and modify other molecules, including DNA and proteins (Yadav et al. 2005a). It is an α-oxoaldehyde compound and is produced copiously under different abiotic stress via different enzymatic and nonenzymatic reactions (Singla-Pareek et al. 2008; Yadav et al. 2005a, b). Therefore, both ROS and MG must be detoxified, or dangerous increases of them must be prevented, to keep them below toxic levels for cellular survival under stressful conditions.

Plants possess efficient means for scavenging of ROS produced during various environmental stresses, including salinity and drought. This requires the defense mechanisms of both enzymatic and nonenzymatic antioxidants for cellular protec-

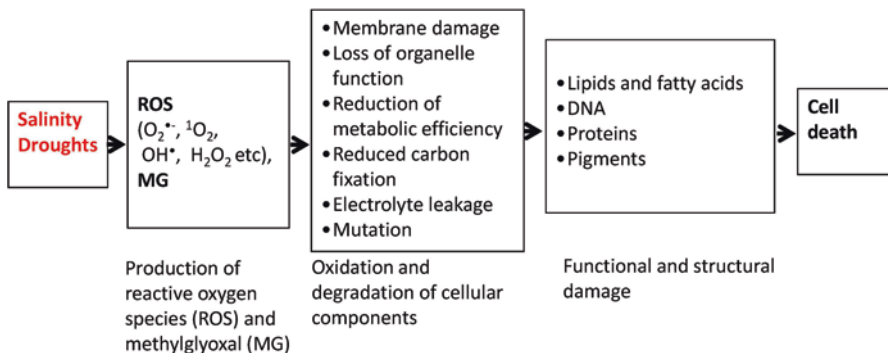


Fig. 1 General effects of reactive oxygen species (ROS) and methylglyoxal (MG) in plant cells under salinity and drought. ¹O₂, singlet oxygen; O₂⁻, superoxide anions and H₂O₂, hydrogen peroxide

tion (Choudhury et al. 2013). The enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), and glutathione *S*-transferase (GST). The non-enzymatic antioxidants include ascorbic acid (AsA), glutathione (GSH), phenolic compounds, alkaloids, nonprotein amino acids, and α -tocopherols (Apel and Hirt 2004; Gill and Tuteja 2010). Cytotoxic MG is detoxified and GSH homeostasis is maintained via the glyoxalase (Gly) system (Yadav et al. 2005a, b), which consists of two enzymes: Gly I and Gly II. It has been reported that coordinated induction or regulation of both antioxidant and glyoxalase pathway enzymes are necessary for the plant to achieve substantial tolerance of oxidative stress (Singla-Pareek et al. 2008; Saxena et al. 2011).

Maize (*Zea mays* L.) is a C₄ plant belonging to the Poaceae family. Naturally, it is a cross-pollinated crop, and it is assumed to have adaptability due to improved photosynthesis, in comparison with C₃ plants, but at the expense of reduced photorespiration (Kanai et al. 1999). As a result, maize has been thought to suffer the least oxidative stress. However, several studies have recently proved that maize suffers substantially from oxidative damage under abiotic stress, particularly under salinity and drought. At the same, efficient antioxidant defense, with an important role in ROS scavenging, has been reported in maize (Stepien and Klobus 2005). In 2015, Farooq et al. (2015) published a review highlighting osmoregulation and osmoprotection, ion homeostasis, apoplastic acidification, an antioxidant defense system, hormonal regulation, and molecular mechanisms in maize. They also recommended some management practices to reduce salinity-mediated damage. Since then, a good number of studies have demonstrated regulation of oxidative stress under salinity in maize, but they have been very scattered. At the same time, studies on antioxidant-mediated mitigation of oxidative damage under drought stress have yielded information that has improved our understanding of oxidative damage. Therefore, this chapter focuses on recent approaches to attenuation of oxidative stress in maize plants grown under salinity and drought.

General Situation of Maize Production Under Salinity and Drought

Globally, maize is the third most important crop. It is a versatile crop grown in a wide range of agroclimatic zones. In fact, the suitability of maize for diverse environments is unmatched by that of any other crop. It is grown from below sea level to altitudes higher than 3000 m, in areas with 250 mm to more than 5000 mm of rainfall per year, and with a growing cycle ranging from 3 to 10 months (Sheikh et al. 2017). According to the Food and Agriculture Organization of the United Nations (FAO 2016), in 2016 the total area of maize cultivation was 195.4 million hectares, with production of 1100.2 million tonnes and an average yield of 5.63 tonnes per hectare (Fig. 2).

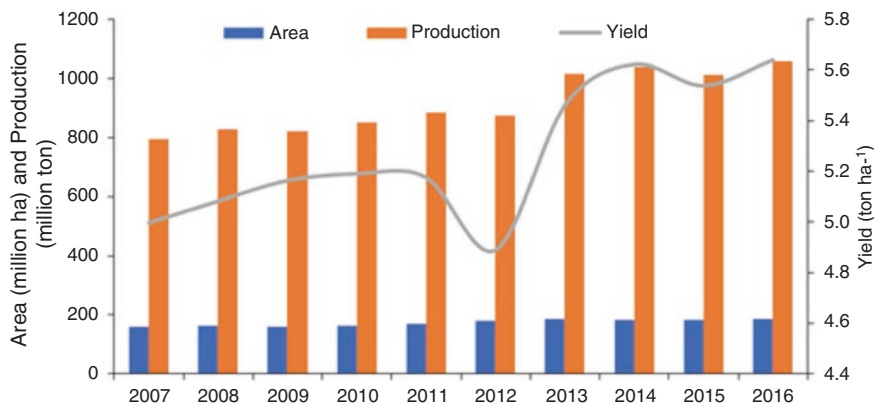


Fig. 2 Total area of production and yield of maize in the world

Abiotic stresses such as salinity, drought, and extreme temperatures are responsible for up to a 50–70% decline in major crop production (Mittler 2006). In the world, more than 800 million hectares of land is affected by either salinity (397 million hectares) or sodicity (434 million hectares) (Munns 2005). Drought affects agricultural crops more than any other stress and is becoming even more severe in the world as a result of global climate change. Statistically, drought stress doubled globally from 1970 to 2000 (Isendahl and Schmidt 2006). Therefore, it has become essential to develop crop varieties for those problematic soils. With this view, understanding of the mechanisms of salinity and drought tolerance has allowed significant achievements in the development of saline-tolerant and drought-tolerant maize globally. Drought-tolerant maize hybrids and open-pollinated varieties (OPVs), developed by the International Maize and Wheat Improvement Center (CIMMYT) in collaboration with other partner organizations, have been reported by Aslam et al. (2015). Recently, the Bangladesh Agricultural Research Institute (BARI) released two maize hybrids for cultivation in drought-prone areas of Bangladesh.¹ However, development of maize varieties for saline soil has not yet been successful, although numerous attempts have been undertaken.

Oxidative Stress in Maize

Both salinity and drought-mediated osmotic stress impel stomatal closure, resulting in low CO₂ assimilation. The osmotic effect of salt outside the roots induces stomatal responses (Munns and Tester 2008). As stress becomes prolonged, photosynthetic inhibition occurs because of severe water shortage, complete stomatal closure, ion toxicity, nutritional imbalance, and membrane disruption, affecting a range of physiological processes involved in cell metabolism (Munns 2002). The O₂ molecule has two impaired electrons. This spin restriction makes O₂ preferentially accept its

¹Information collected from the Plant Breeding Division, BARI, Gazipur, Bangladesh.

electrons one at a time, leading to generation of ROS, which can damage cells (Gill and Tuteja 2010). ROS are also produced continuously as by-products of various metabolic pathways that are localized in different cellular compartments such as the chloroplast, mitochondria, and peroxisomes (del Rio et al. 2006; Navrot et al. 2007). Molecular oxygen is essentially a relatively stable molecule and nonreactive to living cells. However, when triplet oxygen receives extra energy or electrons under environmentally stressful conditions, it generates a variety of ROS, causing oxidative damage to cellular organs, including lipids, proteins, and nucleic acids. The most common ROS are $^1\text{O}_2$, H_2O_2 , $\text{O}_2^{\cdot-}$, and OH^{\cdot} . Triplet oxygen has two unpaired electrons with parallel spins located in different orbitals. Upon receiving extra energy from a photosensitizer such as chlorophyll (chl), these two electrons show antiparallel spin, increasing the oxidizing power of oxygen (singlet oxygen) [reviewed by Krieger-Liszka (2004)]. When triplet oxygen receives an electron, it produces $\text{O}_2^{\cdot-}$, which generates H_2O_2 and OH^{\cdot} through a series of chemical conversions [reviewed by Apel and Hirt (2004)]. In photosynthesis, light energy is captured by photosystems I and II (PSI and PSII) and used to excite electrons, which go through a series of electron transport reactions. It is estimated that about 10% of the photosynthetic electrons leak from the photosynthetic electron transport chain (ETC) to oxygen as a final electron acceptor (the Mehler reaction), resulting in formation of $\text{O}_2^{\cdot-}$ (Foyer and Noctor 2000). When the terminal oxidases—cytochrome c oxidase and the alternative oxidase—react with O_2 , four electrons are transferred and H_2O is released (Gill and Tuteja 2010). However, occasionally O_2 reacts with other ETC components and only one electron is transferred, resulting in formation of $\text{O}_2^{\cdot-}$. It has been noted that $\text{O}_2^{\cdot-}$ is the first ROS to be generated in plant tissues, accounting for 1–2% of O_2 consumption (Puntarulo et al. 1988). Usually, $\text{O}_2^{\cdot-}$ is produced during electron transport upon reduction of O_2 and also via the noncyclic pathway in the ETC of chloroplasts and other compartments of the plant cell. Reduction of O_2 to $\text{O}_2^{\cdot-}$ can occur in the ETC at the level of PSI. The $\text{O}_2^{\cdot-}$ may produce more reactive ROS such as OH^{\cdot} and $^1\text{O}_2$ (Elstner 1987). These ROS are responsible for peroxidation of membrane lipids and cellular leakage. The protonation of the generated $\text{O}_2^{\cdot-}$ can produce a powerful oxidizing agent, perhydroxy radical (HO_2^{\cdot}), on negatively charged membrane surfaces, and the HO_2^{\cdot} then directly attacks polyunsaturated fatty acid (PUFA) (Bielski et al. 1983). Furthermore, $\text{O}_2^{\cdot-}$ can produce H_2O_2 and OH^{\cdot} through the Haber–Weiss reaction and the Fenton reaction (Apel and Hirt 2004).

Under normal conditions, the most common ROS ($\text{O}_2^{\cdot-}$ and H_2O_2) result from electron leakage from the photosynthetic and respiratory ETCs to oxygen. H_2O_2 is also produced through photorespiration resulting from the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Rates of photorespiration are controlled by the ratio of $[\text{CO}_2]$ to $[\text{O}_2]$ and temperature. The key feature of C_4 photosynthesis is the operation of a CO_2 -concentrating mechanism in the leaves (Hatch 1987). C_4 plants such as maize use nicotinamide adenine dinucleotide phosphate (NADP)–malic enzyme–type photosynthesis (Omoto et al. 2012) and fix atmospheric CO_2 principally into oxaloacetate through phosphoenolpyruvate carboxylase in mesophyll cells. Oxaloacetate is then transported to mesophyll cell chloroplasts and reduced to malate by the NADP-dependent malate dehydrogenase enzyme. Malate is then shifted to bundle sheath cells of chloroplasts and decarbox-