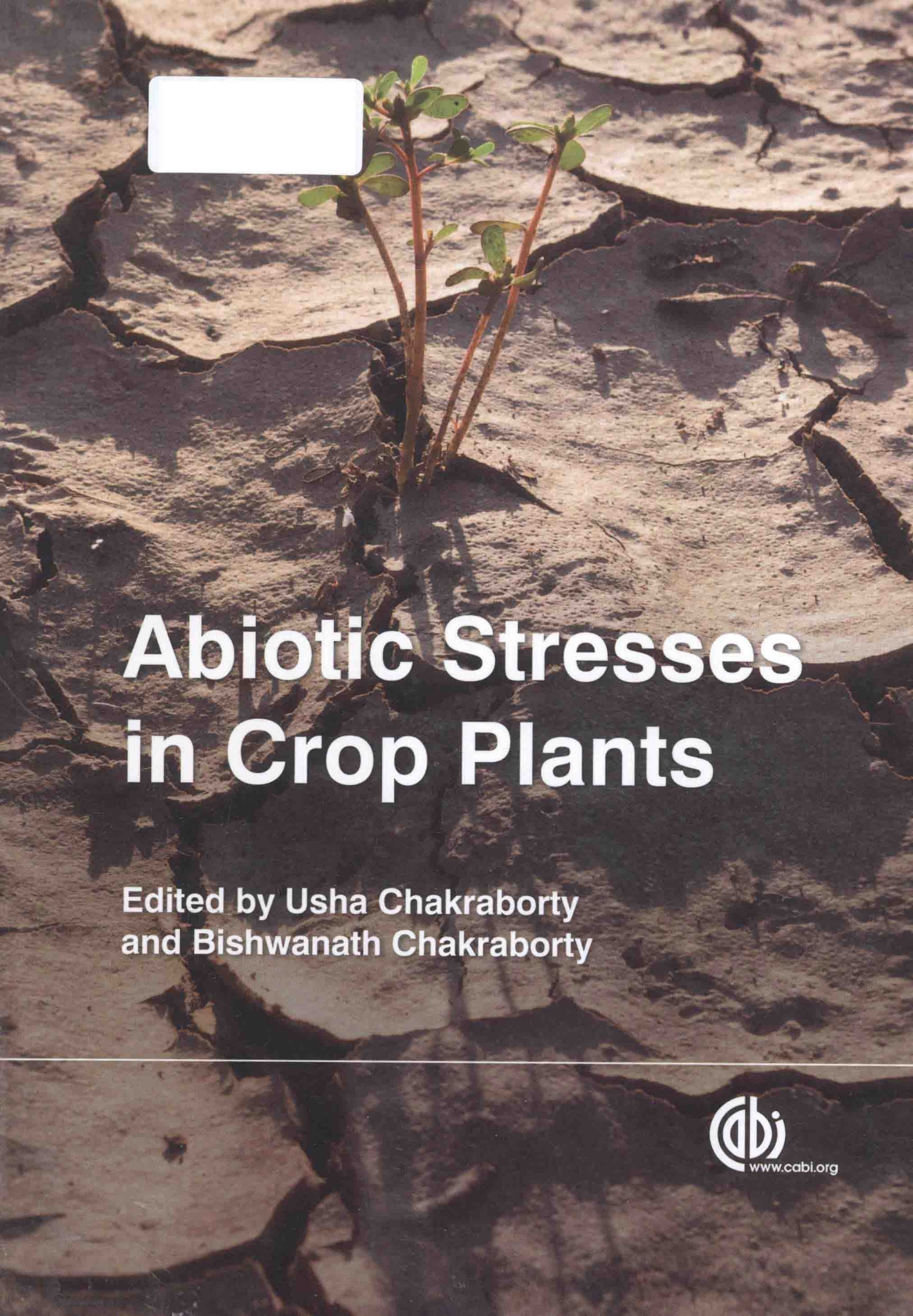

Abiotic Stresses in Crop Plants

Edited by Usha Chakraborty
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Usha Chakraborty

*Plant Biochemistry Laboratory, Department of Botany,
University of North Bengal, India*

and

Bishwanath Chakraborty

*Immuno-Phytopathology Laboratory, Department of Botany,
University of North Bengal, India*

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CABI
Nosworthy Way
Wallingford
Oxfordshire OX10 8DE
UK

Tel: +44 (0)1491 832111
Fax: +44 (0)1491 833508
E-mail: info@cabi.org
Website: www.cabi.org

CABI
38 Chauncy Street
Suite 1002
Boston, MA 02111
USA

Tel: +1 800 552 3083 (toll free)
Tel: +1 (0)617 395 4051
E-mail: cabi-nao@cabi.org

A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Abiotic stresses in crop plants / edited by Usha Chakraborty and Bishwanath Chakraborty.
pages cm
ISBN 978-1-78064-373-1 (hbk : alk. paper) 1. Crops--Effect of stress on. 2. Crops--Physiology. I. Chakraborty, Usha. II. Chakraborty, Bishwanath. III. C.A.B. International.

SB112.5.A24 2014
631.5'82--dc23

2014011777

ISBN-13: 978 1 78064 373 1

Commissioning editor: Sreepat Jain
Editorial assistant: Emma McCann
Production editor: Shankari Wilford

Typeset by SPi, Pondicherry, India.
Printed and bound in the UK by CPI Group (UK) Ltd, Croydon, CR0 4YY.

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Contributors

J. Amudha, Central Institute for Cotton Research, Post Box 2, Shankar Nagar (PO), Nagpur, 440 010 Maharashtra, India.

Mohd Asgher, Department of Botany, Aligarh Muslim University, Aligarh 202 002, India.

André Dias de Azevedo Neto, Laboratory of Biochemistry, Centre of Exact and Technological Sciences, Federal University of Recôncavo of Bahia, Cruz das Almas, 44380-000, BA, Brazil.

G. Balasubramani, Central Institute for Cotton Research, Post Box 2, Shankar Nagar (PO), Nagpur 440 010 Maharashtra, India.

Asok K. Biswas, Plant Physiology and Biochemistry Laboratory, Centre for Advanced Study, Department of Botany, University of Calcutta, 35 Ballygunge Circular Road, Kolkata 700 019, India.

Stefania Bonsegna, CNR-ISPA, Institute of Sciences of Food Productions, via Monteroni, 73100 Lecce, Italy.

Rafael Calixto Bortolin, Department of Biochemistry, Center for Oxidative Stress Research, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil.

Fernanda Freitas Caregnato, Department of Biochemistry, Center for Oxidative Stress Research, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil.

Arka Pratim Chakraborty, Immuno-Phytopathology Laboratory, Department of Botany, University of North Bengal, Siliguri 734013, West Bengal, India.

Bishwanath Chakraborty, Immuno-Phytopathology Laboratory, Department of Botany, University of North Bengal, Siliguri 734013, West Bengal, India.

Usha Chakraborty, Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Siliguri 734013, West Bengal, India.

Elizamar Ciríaco da Silva, Laboratory of Applied Botany, Department of Biology, Federal University of Sergipe, Aracaju, 49100-000, SE, Brazil.

Stefania De Domenico, CNR-ISPA, Institute of Sciences of Food Productions, via Monteroni, 73100 Lecce, Italy.

Pannalal Dey, Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Siliguri 734013, West Bengal, India.

Armando Molina Divan Junior, Laboratory of Plant Bioindication, Center of Ecology, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil.

Mehar Fatma, Department of Botany, Aligarh Muslim University, Aligarh 202 002, India.

Ch.B. Gandonou, Laboratoire de Biologie et Santé, Faculté des Sciences de Tétouan, Université Abdelmalek Essaâdi, BP 2121 Tétouan, Morocco.

Kapuganti J. Gupta, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK.

Kim H. Hebelstrup, Department of Molecular Biology and Genetics, Aarhus University, Forsøgsvej 1, DK-4200 Slagelse, Denmark.

M. Kapoor, Department of Biological Sciences, The University of Calgary, Calgary, Alberta, Canada T2N 1N4.

Rup Kumar Kar, Plant Physiology & Biochemistry Laboratory, Department of Botany, Visva-Bharati University, Santiniketan 731 235, West Bengal, India.

M. Iqbal R. Khan, Department of Botany, Aligarh Muslim University, Aligarh 202 002, India.

Nafees A. Khan, Department of Botany, Aligarh Muslim University, Aligarh 202 002, India.

Renu Khanna-Chopra, Stress Physiology Lab, Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012, India.

José Cláudio Fonseca Moreira, Department of Biochemistry, Center for Oxidative Stress Research, Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil.

Luis A.J. Mur, Institute of Environmental and Rural Science, Aberystwyth University, Edward Llwyd Building, Aberystwyth SY23 3DA, UK.

Maria Nuzzaci, School of Agricultural, Forestry, Food and Environmental Sciences, University of Basilicata, Viale dell'Ateneo Lucano, 10-85100 Potenza, Italy.

Piyalee Panda, Plant Molecular Biotechnology Laboratory, Department of Life Science and Bioinformatics, Assam University, Silchar 788 011, India.

Sanjib Kumar Panda, Plant Molecular Biotechnology Laboratory, Department of Life Science and Bioinformatics, Assam University, Silchar 788 011, India.

Palmiro Poltronieri, CNR-ISPA, Institute of Sciences of Food Productions, via Monteroni, 73100 Lecce, Italy.

S.S. Roy, Department of Biological Sciences, The University of Calgary, Calgary, Alberta, Canada T2N 1N4.

Lingaraj Sahoo, Department of Biotechnology, Indian Institute of Technology, Guwahati, India.

Angelo Santino, CNR-ISPA, Institute of Sciences of Food Productions, via Monteroni, 73100 Lecce, Italy.

Antonio Scopa, School of Agricultural, Forestry, Food and Environmental Sciences, University of Basilicata, Viale dell'Ateneo Lucano, 10-85100 Potenza, Italy.

Vimal Kumar Semwal, Stress Physiology Lab, Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012, India.

N. Skali-Senhaji, Laboratoire de Physiologie Végétale et d'Etude des Stress Environnementaux, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, République du Bénin.

Adriano Sofo, School of Agricultural, Forestry, Food and Environmental Sciences, University of Basilicata, Viale dell'Ateneo Lucano, 10-85100 Potenza, Italy.

Marco Taurino, CNR-ISPA, Institute of Sciences of Food Productions, via Monteroni, 73100 Lecce, Italy.

Antonella Vitti, School of Agricultural, Forestry, Food and Environmental Sciences, University of Basilicata, Viale dell'Ateneo Lucano, 10-85100 Potenza, Italy.

Zlatko Stoyanov Zlatev, Department of Plant Physiology and Biochemistry, Agricultural University-Plovdiv, 4000 Plovdiv, Bulgaria.

Introduction

The existence of life on earth depends on the interaction of environment and living organisms and unless this is maintained at a steady balance this whole existence is at risk. Fast changing environment, increasing population, urbanization and a multitude of related factors affect food productivity by plants – the main food factory of the earth. What is of major concern is the ever-increasing population, projected to be around 9.2 billion by 2050, making demands on food production on the one hand, coupled with decreasing crop productivity on the other. In this scenario, looking for ways and means of maintaining sustainable food production seems a daunting task. Abiotic stresses, mainly due to changing climatic conditions, provide the main challenge to sustainable agriculture. Plant abiotic stressors include: fluctuating temperatures, from very low to extremely high; water level shifts, ranging from water scarcity to flooding; excessive soil salinity, caused in part by prolonged use of irrigation water and low quantities of rainfall, combined with rising saline groundwater levels; heavy metals and other pollutants in soil and air etc. Fortunately for life on earth, many plants are resilient and have developed degrees of tolerance to such stresses. The major thrust for increasing food productivity would be to accelerate such tolerance or resistance mechanisms in the plant at physiological, cellular or molecular levels, leading to improved crop health. However, sufficient caution has to be exercised while dealing with the intricate molecular mechanisms in the plant, as interference in nature's mechanisms may sometimes be counter-productive. To this end, scientists across the globe are working on developing tools for engineering enhanced resistance of plants against abiotic stresses with subsequent increase in productivity.

This book is a compilation of articles that focus on the above problem and will give an overall perspective on the current progress being made in the area of abiotic stresses and their management for sustainable agriculture. The 15 chapters in the book are divided into three sections: Temperature, water and salinity stress; Heavy metals and ozone; and General abiotic stresses and their alleviation by microbes.

The section on temperature, water and salinity stress covers seven chapters and occupies the bulk of the book. All the three major abiotic stresses have been clubbed together as there is a definite interrelationship among all three. Elevated temperatures can lead to rapid water loss, which in turn leads to drought conditions. Similarly, excess salinity also reduces available water to the plant, leading to symptoms related to water deficiency. The first chapter in this section deals with heat-shock proteins (Hsps), which show accelerated synthesis and accumulation in eukaryotes immediately following hyperthermia and confers thermotolerance as well as the capacity to withstand subsequent exposure to lethal temperature and other metabolic insults.

Many of the Hsps on the other hand, are molecular chaperones with vital functions in metabolic pathways, signal transduction, cell proliferation, differentiation and apoptosis under permissive growth conditions. Understanding the role of Hsps in thermotolerance can lead to development of strategies for induction of heat tolerance in plants. The reproductive phase in crops is particularly vulnerable to heat and drought stress and their combination, and in the second chapter the authors discuss how the interplay between leaf senescence, oxidative stress and sugar signalling in reproductive tissues contributes towards reduction in growth and yield in heat-stressed plants.

Both an excess and a deficit of water are abiotic stressors. Three chapters are devoted to this specifically. Chapter 3 will detail our understanding of the roles of nitric oxide, ethylene and haemoglobin in flooding stress and consider how this can be exploited in breeding programmes and sustainable agricultural practice. Nitric oxide (NO) has been shown to trigger the biosynthesis of ethylene during stress and also play key roles in programmed cell death and the hyponastic response. It is discussed as to how the expression of non-symbiotic haemoglobins which oxidize NO to NO_3 play an important role in controlling NO production and thus ethylene-mediated responses to submergence. In Chapter 4, the authors focus on the defence mechanisms against stresses at the molecular level, with special reference to oxylipin metabolism, which according to the authors, represents one of the main defence mechanisms employed by plants. One of the members of this family, jasmonic acid, is well known to be involved in resistance to both abiotic and biotic stresses. Authors have taken the specific example of chickpea hybrids to illustrate the roles. In Chapter 5, the authors discuss how, in contrast to conventional breeding techniques, genetic engineering offers a fast and efficient tool to produce drought-resistant and drought-tolerant plants and thus improved water uptake, use and retention by plants. In order to genetically manipulate plants to be drought tolerant or resistant, genes from the plants that are tolerant or even from other organisms can be selected, which can be grouped into three drought-tolerance engineering strategies: the engineering of functional proteins, manipulating the expression of transcription factors and the regulation of signalling pathways involved in drought tolerance. Chapters 6 and 7 deal with salinity. In Chapter 6, the authors provide an overview of the physiological, biochemical and molecular mechanisms underlying salt tolerance, combining knowledge from classic physiology with information from recent findings. Special emphasis has been given on salt signal perception and transduction and mechanisms related to maintenance of osmotic, ionic, biochemical and redox homoeostasis in salt-stressed plants. A fundamental biological knowledge in conjunction with the understanding of the salt-stress effects on plants is necessary to provide additional information for the dissection of the plant response to salinity and in trying to find future applications for reducing the deleterious effects of salinity on plants, improving the productivity of species important to agricultural sustainability. In Chapter 7, based on results from sugarcane, the authors discuss the results that indicate that the salt tolerance of a variety depends on the stage of development and the level considered. Consequently, salt tolerance of a given cultivar at whole-plant level does not guarantee salt tolerance of tissue or cell cultures issued from this cultivar.

The section on heavy metals, ethylene and ozone consists of four chapters, which deal with the negative effects of heavy metals and air pollutants. Chapter 8 deals with ozone phytotoxicity caused mainly because of its high oxidation potential to generate reactive oxygen species in exposed plant tissue. The balance between the production and the scavenging of activated oxygen is crucial to plant growth maintenance and overall environmental stress tolerance. While increased accumulation of plant secondary metabolites in leaves in response to ozone exposure has been reported, the changes on crop plants' composition and nutritional quality needs to be further studied and discussed to guide our efforts to select ozone-tolerant crops in an attempt to provide a secure food supply for a developing world. Chapters 9 and 10 deal with heavy metal toxicity including cadmium and arsenic among others. In Chapter 9, the authors have mainly focused on the interactive role of ethylene, sulfur, antioxidant system and tolerance of cadmium in plants. Ethylene is the gaseous plant hormone and is now considered to regulate many plant developmental processes throughout the plant's life from germination to senescence and also mediate the plant's responses to abiotic and biotic stress. The basic mechanisms and functional genomics perspective underlying heavy metal toxicity in plants, knowledge of which is essential for development of sustainable agriculture, are dealt with in Chapter 10. Several genetic studies have revealed major signalling pathways that are interconnected and lead to multiple responses in plants under heavy-metal stress. Functional genomics is now considered as an important dissecting tool to understand heavy-metal toxicity as well as tolerance in plants. In Chapter 11, the author has dealt with the negative effects of arsenic, which is a naturally occurring highly toxic metalloid to all forms of life, taking the example of the growth and metabolism of cereals and pulses. Combined application of phosphate with arsenate can ameliorate the damaging effects caused by arsenate treatment alone in cereal and legume seedlings. Hence, the use of phosphate-enriched fertilizers in arsenic-contaminated soil may help normal growth of cereals and legumes.

In the final section, which deals with abiotic stresses in general and their alleviation by microbes, four chapters have been included. In Chapter 12, the authors have focused mainly on recent information about the effects of abiotic stress on plant growth, water relations and photosynthesis, as well as mechanisms of adaptation. The higher acclimation capacity, and hence greater resistance to a given stress factor, is determined by the plant's capacity to maintain its physiological processes within the reaction norm, at a greater variation of this factor. Chapter 13 deals with small molecules such as polyamines, which may play a definitive role in protective or adaptive mechanisms that combat the potential stress-induced injuries in plants encountering abiotic stresses regularly under natural conditions apart from abrupt natural calamities for which the plant may not be prepared. Moreover, it is apprehended that PA-ROS-mediated signalling under stress may have a cross-talk with the phytohormones, figuring a further complex network of signalling for stress tolerance, analysis of which will be a challenging task in near future. The last two chapters deal with a recent, ecofriendly, cost-effective mechanism for stress alleviation through the use of beneficial soil microbes. Chapter 14 deals with the potential of *Trichoderma harzianum* to directly increase plant tolerance against abiotic stresses, such as drought, salinity and soils with low fertility, though traditionally it has been successfully used for the biological control of many plant pathogens through chemiotropic mycoparasitic interactions with the target fungal or bacterial organism. This could promote a rational and non-empirical inclusion of this important fungal species in modern agricultural sustainable practices. The possibility that soil microorganisms could play a significant role in evolving efficient low-cost technologies for abiotic stress management has been dealt with in Chapter 15. Their unique properties of tolerance to extremities, their ubiquity, genetic diversity and their interaction with crop plants can be exploited in order to develop methods for their successful deployment in agricultural production. Soil microorganisms can help crops withstand abiotic stresses, such as drought, chilling injury, salinity, metal toxicity and high temperature, through different mechanisms such as the induction of osmo-protectants and Hsps etc. in plant cells more efficiently. This ability in alleviating abiotic stress conditions in different crop systems can be used for cost-effective sustainable agriculture.

We have endeavoured to compile this book taking a holistic approach from basics to advanced technologies, with the main objective being to put together sufficient information on how to take forward sustainable agriculture in the face of mild to extreme environmental changes occurring in nature. The whole book is well focused and offers insights into the various factors reducing crop productivity and highlights different mechanisms of resistance and approaches that could be used in sustainable agriculture. The editors and authors hope that this book will be of use to agricultural scientists, the agro-industry, academicians and researchers working in the area of abiotic stress and its management.

We would like to thank all the authors who responded in time, which made it possible to bring out this book within the prescribed time. Finally, it is our pleasure to thank CABI for making this possible. Special thanks are also due to Dr Sreepat Jain, Commissioning Editor, CABI and Emma McCann, Editorial Assistant, CABI for their involvement at various stages of publication.

Usha Chakraborty
Bishwanath Chakraborty

About the Editors

U. Chakraborty

Dr Usha Chakraborty, an MSc Gold Medallist of Calcutta University, is Professor of Plant Biochemistry in the Department of Botany, University of North Bengal, Siliguri. She joined the department as a lecturer in 1986 and has since been Head of the Department of Botany twice, been member of University Court, Executive Council and has generally been involved in university administration at various levels. Currently, she is the Programme Co-ordinator of UGC SAP DRS-III level. Her main research focus is on the elucidation of mechanisms of abiotic and biotic stress responses in plants and development of markers for tolerance. She is also engaged in research on crop improvement through biological means and determination of mechanisms of action of such plant growth promoting rhizobacteria. To date, 22 students have received PhD under her guidance and many more are registered. She has published more than 120 research papers in national and international journals, 14 chapters in books and three edited books. She has travelled widely in Canada, USA, Malaysia, UK, Japan, Russia, Italy, China and made representation in International forums. Dr Chakraborty has been elected as Fellow of IPS, ISMPP and Royal Society of Chemistry, London.

B. Chakraborty

Dr Bishwanath Chakraborty is Professor of Plant Pathology in the Department of Botany, University of North Bengal, Siliguri. He has served the institution in various capacities, namely Dean, Faculty of Science; Director, Centre for Development Studies, Programme Coordinator, SAP of the UGC on the subject of Microbiology including mycology and plant pathology and plant diversity. He has to his credit over 140 research papers published in national and international journals, ten review articles, 15 chapters in books, four edited books which have opened up a new line of research on molecular plant pathology and fungal biotechnology. Twenty six students obtained PhD under his guidance. He has travelled widely in Japan, Canada, USA, UK, Germany, Australia, Italy, Russia, New Zealand and made representation in International forums and established International Collaboration in UK and Canada. Dr Chakraborty has been elected as Fellow of IPS, ISMPP, West Bengal Academy of Science and Royal Society of Chemistry, London.

Contents

1 Heat-Shock Proteins and Molecular Chaperones: Role in Regulation of Cellular Proteostasis and Stress Management

M. Kapoor* and S.S. Roy
Department of Biological Sciences, The University of Calgary, Alberta, Canada

Abstract
The multiplicity of environmental and physiological stresses experienced by all organisms presents a formidable challenge to survival. Encounters with near-lethal temperature, extreme cold, pathogens and parasites, metabolic toxins, heavy metals, nutrient deficit, hypoxia and desiccation comprise some of the more common forms of stress that negatively impact all three domains of life. Many of these agents lead to protein unfolding and structural damage to intracellular organelles and cell membranes, and genome replication, transcriptional and translational machinery. The prime strategy to ameliorate the effect of adverse conditions relies upon the evolutionarily conserved stress response: the rapid and transient production of numerous defence-capable proteins, the molecular chaperones. The most prominent and extensively investigated amongst this group are the heat shock proteins (Hsps). Their accelerated synthesis and accumulation, immediately following hyperthermia, confers thermotolerance: the capacity to withstand subsequent exposure to lethal temperature and other metabolic insults. The appearance of aberrant, unfolded or mis-folded aggregation-prone proteins is a signal for mounting the heat shock-stress response. Many of the Hsps are molecular chaperones with vital functions in metabolic pathways, signal transduction, cell proliferation, differentiation and apoptosis even under permissive growth conditions. The accumulation of molecular chaperones under adverse conditions provides the basic strategy for stress management. Molecular chaperone families are classified into two general categories. The first comprises the 'foldases', including the ATP-dependent chaperonins, Hsp70, Hsp90 and Hsp110 families, involved in folding nascent polypeptides and refolding proteins unfolded as a result of stress. The second group, the 'holdases', sequester unfolded or partially folded proteins, which are subsequently processed by the foldases. The ubiquitous set of small Hsps (sHsps) represents the ATP-independent holdases that play a major role in protection against hyperthermia, oxidative stress and a variety of other abiotic stresses. In plants, sHsps have an important role in development of thermotolerance and adaptation to osmotic and high salinity stress. In addition, some subfamilies of plant sHsps are not heat shock-inducible but are expressed constitutively during specific developmental stages.

1.1 Introduction

Numerous factors in the life of an organism elicit moderate to severe physiological/environmental stress. The most prevalent forms of stress experienced on a regular basis include hyperthermia, exposure to ultraviolet light, nutrient deficit, dehydration/drought and metabolic

*E-mail: mkapoor@ucalgary.ca

poisons, heavy metals, microbial pathogens and other toxic substances in the milieu. Consequently, during the course of evolution, a wide variety of strategies for managing potentially lethal effects of stress have been perfected in different organisms to counteract specific threats to survival. The best understood and the most extensively investigated strategy for protection against hyperthermal conditions, in prokaryotes and eukaryotes alike, is the evolutionarily conserved phenomenon referred to as the heat shock (stress) response. In addition to high temperature, a surfeit of reactive oxygen species (ROS) is a universal elicitor of stress response, while persistence of herbicides and toxins in the soil, salinity and bacterial and fungal infections also induce a powerful stress response in plants.

Hyperthermia and other stresses present a serious threat to survival by causing unfolding and mis-folding of proteins, resulting in disturbance of intracellular protein homoeostasis. As partially or completely unfolded/mis-folded proteins are intrinsically aggregation-prone, reversal of the process by refolding or removal of the offending proteins constitutes the prime strategy for stress management. Appearance of unfolded proteins in the cytosol acts as the principal signal for immediate deployment of the heat shock-stress response: elevated expression of a plethora of stress-inducible genes and the rapid synthesis of defence-capable proteins (Hsps) fortifies the target organism against adverse environmental conditions. Such a defence mechanism can react swiftly to a wide range of physiological and chemical challenges leading to protein unfolding and is encountered universally in all three biological kingdoms: the Eubacteria, Archaea and Eukarya. The Hsps, also known as molecular chaperones, are exquisitely designed for shielding the cellular machinery from damaged macromolecules. Although most Hsps are required at low levels during normal growth and metabolism, a dramatic up-regulation of their synthesis is necessitated under stress conditions, as molecular chaperones are required in stoichiometric amounts relative to the population of unfolded/mis-folded or aggregated polypeptides.

In the eukaryotes, pathogen attack and several genetic/physiological factors also cause a substantial build-up of unfolded proteins in the endoplasmic reticulum (ER), the lumen of ER being the locale of synthesis of secretory and membrane-specific proteins. Perturbations in the redox status, calcium homoeostasis or post-translational modifications of secretory proteins, can result in substandard local folding capacity culminating in the accumulation of unfolded or mis-folded ER macromolecules. To counter this cytotoxic hazard, a robust surveillance system – designated the unfolded protein response (UPR) – conserved in plant, fungal and mammalian species, is launched. UPR is critical for adjustment of ER homoeostasis under stress elicited by mis-folded proteins (Walter and Ron, 2011). This system implements an immediate cessation of normal protein synthesis and activation of a preferred set of genes encoding chaperone and co-chaperone proteins, affording protection by induction of the ER-specific degradation system, or apoptosis as a last resort. Fortuitously these chaperones also promote resumption of proper folding (Lai *et al.*, 2006). Irreversibly damaged ER proteins are moved to the cytoplasm and subjected to degradation by the ERAD system (ER-associated degradation).

Persisting ER stress is linked to several metabolic disorders, such as obesity, diabetes, diseases of the liver and atherosclerosis. Avenues are being explored to develop therapeutic approaches targeting specific components of the UPR for treatment of human diseases (reviewed in Lee and Ozcan, 2014). Insightful analyses of the heat shock response, protein folding, aggregation, macromolecular assemblies, and structure and function of molecular chaperones are available in recent reviews (Pearl and Prodromou, 2006; Hartl and Hayer-Hartl, 2009; Richter *et al.*, 2010; Tyedmers *et al.*, 2010; Waters, 2013). The following is a brief overview of commonly encountered environmental stresses and properties and structural features of selected, typical molecular chaperones that respond to them.

1.2 Molecular Chaperones: Functions and Properties

During the last two decades a large number of molecular chaperone families (exceeding 100)