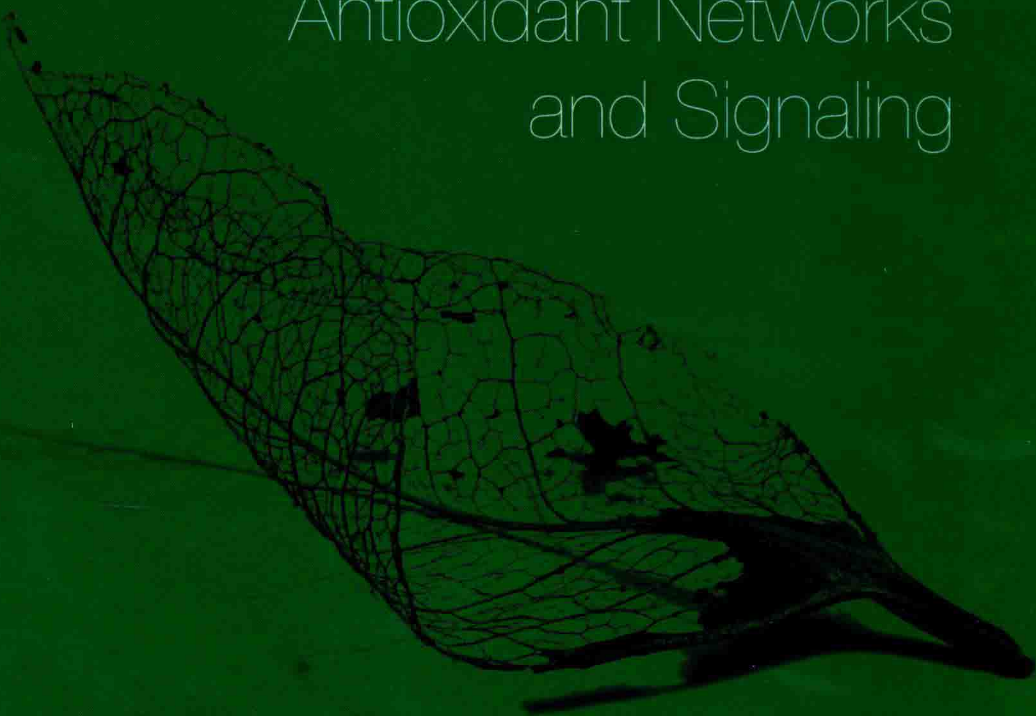
Oxidative Damage to Plants

Antioxidant Networks and Signaling



Edited by
Parvaiz Ahmad

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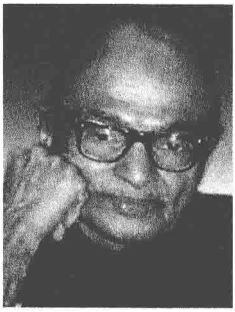
Dedication

This book is dedicated to



Hakim Abdul Hameed
(1908–1999)
Founder of Jamia Hamdard (Hamdard University)
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Foreword

Nearly 2.7 billion years ago, the introduction of molecular oxygen (O_2) into our atmosphere, resulted in the reactive oxygen species (ROS) as unwelcome companions in the ecosystem. Although they control many different processes in plants, their toxic nature is also capable of injuring cells. How plants solve this problem is still unknown. However, we do know that the steady-state level of ROS in cells needs to be tightly regulated. Recent studies have suggested some key players in this connection, but many questions regarding its mode of regulation, protective role and modulation of signaling networks controlling growth, development and stress responses still need an answer. The studies suggest a dual role for ROS in plant biology as both toxic byproducts and key regulators.

Plants live in continuously changing environment. As a result they have been driven to evolve a very flexible growth and development cycle within the environment surrounding them. This is led by the cell regulation process involving an important indicator such as the redox state. The antioxidants present within the plant cells give a response to the changing environment continuously as they are affiliated to their metabolic state. As plants do not show mobility they develop phtorespiratory, enzymatic and non-enzymatic pathways at different stages in order to face different stresses like drought, salinity, low temperature, and UV-B, thereby producing more ROS. The responses also include gene regulation as well as anatomical aspects. At present, responses to both abiotic as well as biotic stresses have been investigated under controlled conditions following the challenges singly, not the way it happens in the natural world of plants. The metabolic activities in a plant cell are perfectly regulated to follow different biosynthetic pathways with photodynamic or reductive activation of molecular oxygen to produce ROS. Later changes are programmed genetically, in many cases following developmental and environmental changes which in turn have an impact on primary, as well as secondary, metabolism. The transmission of information in plants following the environmental changes is also expressed in the form of production of bursts of superoxide at the plasma membrane. The levels of ROS determine the type of response, and enhanced ROS production has been related to oxidative stress – a negative term depicting a harmful process however, in several cases it helps in sending signals for proper adjustment of gene expression. In fact, the antioxidants and ROS interact with each other, leading towards different functions in higher plants, giving them a high flexibility.

The steps in the biosynthetic pathways leading to antioxidant accumulation in plants have basically been characterized both at a physiological and molecular level. However, all participants involved are still not yet identified. A better understanding of antioxidant degradation and transport in plants is needed, together with an elucidation of the molecular events involved. The future will determine the involvement of ascorbate, glutathione, and tocopherol, as well as how they initiate and control redox signal transduction and trigger the gene expression for optimization of different survival strategies. Other questions are related to the coordination of antioxidants in plant growth and development in the changing environment, linkage of redox signaling with hormonal regulation, nutrient status and redox potential in plants, as metabolism in plants must be highly regulated for an effective integration of biosynthetic pathways.

This first chapter of this book covers reactive oxygen species and photosynthesis, presenting an overview of the general characteristics of various stress factors and their capability to increase the generation of ROS in the cells, as its generation in photosynthesizing tissues is significantly exacerbated under environmental stress conditions. It discusses the complex set of mechanisms for avoidance of ROS production or scavenging the ROS. The main concept is presented as the signaling role of ROS as well as electron transport components as redox molecules, which may precisely regulate the expression of nucleus-encoded genes through the redox status of plastids. Accordingly, chloroplasts have been regarded as sensors for environmental signals that link the effect of stress factors to the plant metabolism in general and carbon reactions in particular.

The first chapter of the book, on reactive oxygen species and plant hormones, discusses the evidence related to ROS and plant hormone signaling pathways regulating plant growth and development, in relation to the responses to environmental factors. Plant hormones and ROS are intrinsically interlinked in plant biology and development, as well as in stress responses. The discussion includes interactions between ROS and plant hormones during the physiological events of seed germination, under environmental stress and during plant development. It is mentioned that the identification of new plant hormones and their functions, as well as identification of ROS receptors, will help in clarifying the roles and signal interactions between ROS and hormones in plant physiology.

In Chapter 3, *Superoxide Dismutase and Abiotic Stress Tolerance in Plants: An Overview*, an attempt has been made to highlight the facts about the influence of abiotic stress factors on plants, because their direct or indirect presence may affect the development, growth, and basic metabolism in plants. The factors considered are heavy metals, salt stress, chilling, drought, and UV-B radiation. These may induce the formation or the overproduction of ROS. The restoration of redox homestasis through cells' evolution of large scale enzymatic and non-enzymatic antioxidants to scavenge ROS in plants is discussed. An attempt has been made to summarize the characteristics of SOD enzymes and show the differences and similarities in the effects of different abiotic stress factors on SOD activity.

Chapter 4 presents a discussion on catalase, an antioxidant enzyme present in all aerobic organisms, catalysing H_2O_2 in an energy-efficient manner in the cells exposed to environmental stress. Its deficiency in plants develops anomalies. Multiple molecular forms of catalase isozymes indicate its versatile role within plants. The expression of *cat* gene shows time, species and stress specificity. The chapter compiles the up-to-date information on catalase structure, localization, biochemistry, genes and function in plants.

In Chapter 5, the role of glutathione (GSH) in abiotic stress tolerance is discussed at length. GSH is a non-protein low molecular weight tripeptide found in most plant tissues, that plays a role in biosynthetic pathways, detoxification of xenobiotics, antioxidant chemistry, whilst at the same time protects plants against oxidative stress, acting as a storage and transport form for reduced sulfur.

Chapter 6 on glutathione metabolism in plants under environmental stress looks at the essential role of glutathione as a part of defense system in plants and human beings exposed to various environmental stresses, mechanisms involving metal sequestration and scavenging of ROS. The chapter contains information regarding the mechanism of a glutathione mediated protection system, metabolism, transport and biosynthesis of glutathione in plants.

Non-enzymatic Antioxidants in Plants, Chapter 7, relays information about the oxidative stress caused by abiotic and biotic factors that include salinity, pathogen colonization, UV stress, herbicide activity and oxygen deficiency, which affect biochemical, physiological, developmental and structural processes within individual plant and plant communities. The defence mechanisms for protection from the spectrum of harmful effects are given.

Chapter 8 is a discussion of ascorbic acid, a reduced form of vitamin C synthesized from hexose sugar. The text provides insight on various aspects of ascorbic acid such as biosynthesis, diverse functions with a particular reference to environmental stresses, an update on new roles and manipulation of ascorbic acid levels in the stresses of plants through transgenic approaches.

A discussion of carotenoids involved in chloroplasts is presented in Chapter 9. The properties of carotenoids as effective non-enzymatic plant antioxidants have been described. The chemical structure of carotenoids in relation to their antioxidant properties is explained, followed by photoprotective role of two all-*trans*β-carotene molecules existing in PSII reaction center. The role of ascorbate as an antioxidant and as a reductant required to carry out de-epoxidation has been considered. In the last part of the chapter, the significance of xanthophylls in photoprotection is discussed. Special attention has been paid on the role of carotenoids involved in several types of the xanthophyll cycle.

In Chapter 10, lipophilic molecules occurring in plant cell with strong antioxidant properties have been given, with the prenyllipids being the most efficient. In the first section, characterization of the mechanisms leading to production of ROS at different sites of chloroplasts during exposure to abiotic stress factors are given together with their negative effects. The second section of the chapter outlines the current knowledge about antioxidant properties of prenyllipids, followed by a discussion on the function of ROS and prenyllipids (vitamin E) as signaling molecules.

In Chapter 11, the discussion revolves around the effects of abiotic factors on the metabolic activities of plants, in order to understand how water deficit can significantly enhance the production of crop plants and quality of the environment. An attempt has been made to describe the mechanism of drought resistance in plants on the basis of antioxidants, physiology, enzymatics, and proteomics.

Chapter 12 considers thermotolerance mechanisms in plants to minimize damage and ensure protection of cellular homeostasis. ROS detoxification mediated by antioxidant compounds and antioxidant enzyme systems is one of the mechanisms for high temperature stress (HTS) tolerance. Very little information is available on the cellular factors essential for this response. Previous efforts to improve HTS tolerance through breeding and genetic engineering has had limited success. Comparative genomics, high-throughput sequencing, gene expression analysis, and gene function validation may provide necessary insights in the mechanisms of stress tolerance and critical genes for enhancement of genetic improvement in crops.

Chapter 13, entitled *Reactive Oxygen Species and Antioxidants in Response to Pathogens and Wounding*, discusses the development of mechanisms in plants to help cope with biotic and abiotic stresses. In the case of an injury, wound healing cascades activate that help secure the wound and keep the pathogens at bay, to speed up the healing process. The accumulation of ROS is highest around the wounds. Due to ROS's high toxicity, pathogens trying to access the wounds are killed. Attempts have been made to discuss in detail the role of different types of ROS in evading stress and injury, the independent roles of each antioxidant in wound healing, the genes involved in their synthesis and the pathways of wound healing.

The role of ascorbate peroxidase on postharvest treatments in horticultural crops is covered in Chapter 14. Proper postharvest handling is of utmost importance for increasing food availability. Plants have evolved an efficient antioxidant defense system which prevents the accumulation of ROS. Ascorbate peroxidase (APX) is involved in ascorbate-glutathione cycle and utilizes ascorbate as the electron donor and plays the most essential role in scavenging ROS. APX plays an important role in controlling the concentration of ROS that participates in the signal transduction in many physiological processes, and the management of ROS during stress in horticultural crops. There are some connections between APX induction and regulation of metabolism. Postharvest treatments can therefore be very important for improving shelf life and quality retention during postharvest handling of horticultural crops.

Chapter 15, entitled *Mycorrhizal Association and ROS in Plants* reviews beneficial microorganisms distributed in the soil ecosystem, such as the arbuscular mycorrhizal fungi. In view of the fact that relations between the mycorrhizal associations and ROS are widely concerned with plants, mycorrhizal symbiosis is generally restricting the oxidative burst under environmental stresses. Therefore, arbuscule is associated with accumulation of H_2O_2, whose overaccumulation in arbuscules may predicate the collapse or degradation of arbuscules during mycorrhizal development. The mycorrhizal associations can enhance antioxidant enzyme activities and increase antioxidant contents of the host plant, partly alleviating oxidative stress. The mycorrhizal symbiosis, ROS occurrence under mycorrhizal symbiosis, and role of mycorrhizal association in antioxidant enzymes and antioxidants of the host plant have been discussed, together with some future prospects.

Chapter 16 sees authors presenting their views on proline protecting against abiotic oxidative stress. They have summarized and discussed the current understanding of ROS formation, proline biosynthesis and its accumulation in plants under various abiotic stresses. New insights gained about the molecular mechanisms of proline mediated oxidative stress tolerance have also been discussed.

Trace elements tolerance modulated by the plant antioxidant system is detailed in Chapter 17. The authors have analyzed the information available regarding trace element induction of oxidative stress and trace element tolerance modulation in seeds and seedlings through antioxidant activities.

Chapter 18 deals with plant signaling under environmental stress. The role of small RNAs is of significance in plants under stress. The review highlights the fact that the use of the proteomic technique can be useful for evaluating plant responses under stress. Plants, with the higher ability to manage their signaling pathways under stress, are more likely to survive. Recognition of the signaling pathways under stress can be important for the production of tolerant plants.

In Chapter 19, entitled *Hydrogen Peroxide Generation, Scavenging, and Signaling in Plants,* authors present the biochemistry of H_2O_2 and their production sites, H_2O_2 scavenging antioxidant defense machinery, the mechanisms of H_2O_2 perception and signal transduction, the factors that act downstream and H_2O_2 interference with other signaling pathways such as calcium and protein phosphorylation networks. Reviewing this biochemistry will provide new insights into how plants balance H_2O_2.

Finally, Chapter 20 looks at the role of ROS as signaling molecules in plants. An attempt has been made to discuss two of the main roles of ROS: signaling molecules regulating many processes in plants under normal and adverse conditions, and the production of toxic byproducts from aerobic metabolisms. The authors have also tried to bring some insights of ROS generation, and its role in plant development together with the signaling roles of ROS and their interactions with other molecules.

I hope that the chapters presented in this book will be useful for scientists and graduate students in the area towards encouraging further discussion, research and development on Oxidative Damage to Plants: Antioxidant Networks and Signaling.

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Preface

Industrialization and urbanization in the name of growth and development is rapidly proceeding on a global level. This growth and development has deteriorated our environment to a great extent. Pollution of soil, water, air is creating havoc in our living environment. Environmental stresses, such as high levels of salinity, drought, floods, temperatures, and UV damage is increasing at an alarming rate, resulting conversion of agricultural land to non-agricultural. Increases in population and decreases in agricultural and horticultural production are leading towards starvation and malnutrition for nearly one billion stomachs around the world. It will definitely prove more dangerous for our future generations if steps are not taken.

Environmental stress has led to oxidative stress, caused by the generation of reactive oxygen species (ROS) in plants and animals. ROSs react with cell biomolecules, leading to organelle dysfunction. However, Nature has equipped plants with defense mechanisms, including enzymatic and non-enzymatic antioxidants. Upregulation and downregulation of these antioxidants helps plants tolerate stress. ROSs also have a significant role as signaling molecules under stress.

Oxidative Damage to Plants: Antioxidant Networks and Signaling is an attempt to gain more insight of the devastating role of oxidative stress in plants and the defense mechanisms required. Chapter 1 describes the protection of photosynthetic plants against ROS and role of ROS in signaling. Chapter 2 discusses reactive oxygen species and plant hormones, highlighting the role of ROS in plant signaling and seed germination. Chapters 3 and 4 discuss superoxide dismutase and catalase in detail and their role under stress. Chapters 5 and 6 deal with glutathione metabolism and its role under stress. Chapters 7–10 deal with the role of different non-enzymatic antioxidants, such as ascorbic acid, carotenoids, and lipophylic molecules under different stresses.

Chapters 11–13 deal with drought, temperature stress and pathogens and wounding. The generation of ROS, ROS sites, antioxidants, proteomics and transcriptional regulation are also discussed in these chapters. In Chapter 14 the role of ascorbate peroxidase under environmental stress and postharvest produce is reviewed. Mycorrhizal association and ROS in plants is explained in Chapter 15. Chapters 16 and 17 discuss the role of proline and trace elements in helping plants to withstand stress. Chapters 18–20 review the different roles of ROS and signaling under stress.

This book is the compilation of different chapters on oxidative stress and signaling in plants. Each topic has been discussed to its full potential to ensure that readers receive the maximum information for each topic. There may be some errors in the book even after my best efforts. I need your feedback and suggestions for this.

I would like to thank all the contributors of this volume for their timely submission. Their collaboration and patience during the preparation of this book is unforgettable. I would also like to thank Kristi S. Gomez (Acquisition Editor, Elsevier), Patricia Gonzalez (Editorial Project Manager, Elsevier) and other team members of Elsevier for their help, suggestions and timely publication of this volume.

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