ETHYLENE IN PLANT BIOLOGY

EDITED BY

SAMIKSHA SINGH ▪ TAJAMMUL HUSAIN
VIJAY PRATAP SINGH ▪ DURGESH KUMAR TRIPATHI
SHEO MOHAN PRASAD ▪ NAWAL KISHORE DUBEY

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Ethylene in Plant Biology

Edited by

Samiksha Singh
Banaras Hindu University
Varanasi, India

Tajammul Husain
University of Allahabad
Prayagraj, India

Vijay Pratap Singh
C.M.P. Degree College
Prayagraj, India

Durgesh Kumar Tripathi
Amity University Uttar Pradesh
Noida, India

Sheo Mohan Prasad
University of Allahabad
Prayagraj, India

Nawal Kishore Dubey
Banaras Hindu University
Varanasi, India

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List of Contributors

Nisha Agrawal
School of Biochemistry, Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India

Juan D. Alché
Department of Stress, Development and Signaling, Estación Experimental del Zaidín, Spanish National Research Council (CSIC), Granada, Spain

Nimisha Amist
Plant Physiology Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Renu Bhardwaj
Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Savita Bhardwaj
Department of Botany, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Sebastian Burchardt
Department of Plant Physiology and Biotechnology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University, Toruń, Poland

Kumar Chandra-kuntal
School of Life Sciences, Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India

Anita Dubey
MB Khalsa College, Indore, Madhya Pradesh, India

Neeraj Kumar Dubey
Botany Department, Rashtriya Snatkottar Mahavidyalaya,

Jamuhai, Jaunpur, Uttar Pradesh, India

Mehar Fatma
Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Víctor García-Gaytán
El Colegio de Michoacán, A.C. LADIPA, La Piedad, Jardines del Cerro Grande, México

Alicia García
Departamento de Biología y Geología, Research Center CIAIMBITAL and Agrifood Campus of International Excellence CeiA3, University of Almería, Almería, Spain

Harsha Gautam
Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Parishmita Gogoi
Biological Science & Technology Division, CSIR-North East Institute of Science and Technology, Jorhat, Assam, India

Priyanka Gogoi
Biological Science & Technology Division, CSIR-North East Institute of Science and Technology, Jorhat, Assam, India

Aditi Gupta
CSIR-National Botanical Research Institute (NBRI), Lucknow, India

Arvind Gupta
Department of Biotechnology, Hemvati Nandan Bahuguna Garhwal (Central) University, Srinagar Garhwal, Uttarakhand, India

Kapil Gupta
Department of Plant Biotechnology, CSIR-Central Institute of Medicinal and Aromatic Plants, Lucknow, Uttar

PradeshandDepartment of Biotechnology, Siddharth University, Kapilvastu, Uttar Pradesh, India

Shubhra Gupta
Department of Biotechnology, Central University of Rajasthan, Ajmer, Rajasthan, India

Noushina Iqbal
Department of Botany, Jamia Hamdard University, New Delhi, India

Badar Jahan
Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

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

Manuel Jamilena
Departamento de Biología y Geología, Research Center CIAIMBITAL and Agrifood Campus of International Excellence CeiA3, University of Almería, Almería, Spain

Sadaf Jan
Department of Biotechnology, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Raman Jasrotia
Department of Zoology, University of Jammu, Jammu and Kashmir, India

Shivam Jasrotia
Department of Zoology, GovtDegree College Basohli, Jammu and Kashmir, India

Kanchan Jumrani
Division of Plant Physiology, Indian Institute of Soybean Research, Indore, Madhya Pradesh, India

Dhriti Kapoor
Department of Botany, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Jacek Karwaszewski
Department of Plant Physiology and Biotechnology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University, Toruń, Poland

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

Ekhlaque A. Khan
Department of Biotechnology, Chaudhary Bansi Lal University, Bhiwani, Haryana, India

Nafees A. Khan
Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Shubhra Khare
Plant Physiology Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Jasminkumar Kheni
Department of Biotechnology, Junagadh Agricultural University, Junagadh, Gujarat, India

Agata Kućko
Department of Plant Physiology, Institute of Biology, Warsaw University of Life Sciences-SGGW, Warsaw, Poland

Pragati Kumari
Department of Botany and Microbiology, Hemvati Nandan Bahuguna Garhwal (Central) University, Srinagar Garhwal, Uttarakhand, India

Cecilia Martínez
Departamento de Biología y Geología, Research Center CIAIMBITAL and Agrifood Campus of International Excellence CeiA3, University of Almería, Almería, Spain

Asim Masood
Plant Physiology and Biochemistry Division, Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Niharika
Plant Physiology Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Satendra Pal Singh
Department of Botany, Y.D. (P.G.) College, Lakhimpur Kheri, Uttar Pradesh, India

Juhie Joshi-Paneri
Plant Science Department, McGill University, Montreal, Canada

Jogeswar Panigrahi
Department of Biosciences and Bioinformatics, Khallikote University, Berhampur, Odisha, India

Surendra Pratap Singh
Department of Botany, D.A.V. College, C.S.J.M. University, Kanpur, Uttar Pradesh, India

Anshu Rastogi
Laboratory of Bioclimatology, Department of Ecology and Environmental Protection, Poznan University of Life Sciences, Poznan, Poland

Peer Saffeullah
Department of Botany, Jamia Hamdard, New Delhi, India

Zebus Sehar
Plant Physiology and Biochemistry Division, Department of

Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Dhriti Sharma
Department of Botany, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Ratul Saikia
Biological Science & Technology Division, CSIR-North East Institute of Science and Technology, Jorhat, Assam, India

Ajey Singh
Nehru Gram Bharti (Deemed toBe University), Prayagraj, Uttar Pradesh, India

Manjul Singh
Centre for Research in Agricultural Genomics (CRAG), CSIC-IRTA-UAB-UB, Barcelona, Spain

N.B. Singh
Plant Physiology Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Rattandeep Singh
Department of Biotechnology, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Zahra Souri
Laboratory of Plant Physiology, Department of Biology, Faculty of Science, Razi University, Kermanshah, Iran

Archana Thakur
University Grants Commission, New Delhi, India

Rahul Thakur
Department of Biotechnology, Hemvati Nandan Bahuguna Garhwal (Central) University, Srinagar Garhwal, Uttarakhand, India

Timothy J. Tranbarger
UMR DIADE, IRD Centre de Montpellier, Université de Montpellier, Institut de Recherche pour le Développement, Montpellier, France

Rachana Tripathi
School of Life Science, Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India

Shahid Umar
Department of Botany, Jamia Hamdard, New Delhi, India

Tunisha Verma
Department of Botany, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab, India

Emilia Wilmowicz
Department of Plant Physiology and Biotechnology, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University, Toruń, Poland

Archana Yadav
Biological Science & Technology Division, CSIR-North East Institute of Science and Technology, Jorhat, Assam, India

Saurabh Yadav
Department of Biotechnology, Hemvati Nandan Bahuguna Garhwal (Central) University, Srinagar Garhwal, Uttarakhand, India

Preface

Ethylene, a gaseous plant hormone, has emerged as an important signaling molecule that regulates several steps of the plant life cycle. The development of plants requires complex signaling of various molecules like ethylene. Further, to restore and reestablish cellular homeostasis under stress conditions, regulation at the gene expression level takes place, which helps in achieving a proper phenological response.

In the recent past, various studies have demonstrated the role of ethylene in regulating seed germination, nodule formation, and nitrogen fixation, reactive oxygen species, and other plant hormonal signaling, and their subsequent impact on plant development under stress-challenged and non-stress-challenged conditions. In recent years, various implications of ethylene have been reported on the growth and development of plants. Further, the roles of ethylene are emerging in plant developmental processes, and thus, research on the roles of ethylene in plant biology continues to increase. Moreover, research on the new roles of ethylene in plant biology is ongoing.

This edited book combines ethylene research from leading laboratories around the globe in one place to make it easily accessible to researchers, students, academics, etc. Twenty chapters have been compiled, and the topics covered range from the discovery of ethylene to its wide roles in plant growth and development and stress acclimation. Chapter 1 deals with the role of ethylene in root development. Chapter 2 presents the role of ethylene in plant development. Chapter 3 deals with the regulation of metabolites by ethylene. Chapter 4 deals with the regulatory role of ethylene in abscission processes. Chapter

5 presents the regulation of drought stress by ethylene. Chapter 6 discusses ethylene and fruit ripening. Chapter 7 deals with ethylene and reactive oxygen species crosstalk in plant development. Chapter 8 examines the role of ethylene in flower and fruit development. Chapter 9 deals with the role of ethylene in nutrient regulation in plants. Chapter 10 presents plant metabolism adjustments by ethylene under stress. Chapter 11 deals with the role of ethylene and reactive oxygen species in salinity stress tolerance and transgenic approaches to making salt-tolerant crops. Chapter 12 presents ethylene and phytohormonal crosstalk in plant defense against abiotic stress. Chapter 13 describes the mechanism of ethylene synthesis and homeostasis in plants. Chapter 14 deals with ethylene and nitric oxide crosstalk under salt stress. Chapter 15 presents ethylene and metabolic reprogramming under abiotic stresses. Chapter 16 deals with the regulation of thermal stress in crops by plant growth-promoting rhizobacteria through ethylene homeostasis. Chapter 17 discusses ethylene signaling, transgenics, and their applications in crop improvement. Chapter 18 presents the role of ethylene in combating biotic stress in plants. Chapter 19 deals with ethylene and nitric oxide crosstalk in plants under abiotic stress. Chapter 20 discusses polyamine metabolism and ethylene signaling in plants.

We believe that this book will serve as an important repository for students, academics, and researchers to understand various implications of ethylene in plants ranging from plant development to stress acclimation.

Samiksha Singh
Tajammul Husain
Vijay Pratap Singh
Durgesh Kumar Tripathi

Sheo Mohan Prasad
Nawal Kishore Dubey

1
Ethylene Implication in Root Development

Aditi Gupta[1], Anshu Rastogi[2], and Manjul Singh[3]
[1] CSIR-National Botanical Research Institute (NBRI), Lucknow, India
[2] Laboratory of Bioclimatology, Department of Ecology and Environmental Protection, Poznan University of Life Sciences, Poznan, Poland
[3] Centre for Research in Agricultural Genomics (CRAG), CSIC-IRTA-UAB-UB, Barcelona, Spain

1.1 Ethylene and Its Role in Overall Plant Development

Ethylene (or ethene, according to International Union of Pure and Applied Chemistry [IUPAC] nomenclature) is the simplest olefin gas biosynthesized by plants. Ethylene (ET) is the smallest phytohormone and one of the first gaseous hormones discovered around 100 years ago. It is widely known to regulate fruit ripening; however, the roles of the ET signaling pathway in regulating different aspects of plant development, growth, and stress responses have also been well-studied in the last three decades (Dubois et al. 2018). ET functions as a hormone by performing cell-to-cell communication of signals in plants and can also act as a pheromone by diffusing to surrounding plants and inducing ET responses in them. As a signaling molecule, ET is able to regulate various developmental processes of plants such as seed germination, seedling development, root and shoot growth, fruit ripening, senescence, and abscission (Iqbal et al. 2017). It regulates root growth through a seemingly conserved pathway across monocot and dicot species. ET signals balance cell division and differentiation processes and can negatively affect tissue extension by interfering with cell elongation and proliferation. This balance between cell division, elongation, and differentiation events caused by ET and its interaction with other phytohormones, predominantly auxin, controls root system architecture (RSA) development. Besides the general growth and developmental regulatory functions, ET has a prominent role in plant responses to different stresses, such as salinity, flooding, cold, heavy metals, drought, etc. (Tao et al. 2015; Iqbal et al. 2017; Pan et al. 2019; Sytar et al. 2019; Wang and Huang 2019; Wang et al. 2020). This chapter summarizes the current knowledge about mechanisms of root development and root growth response via ET actions both independently and via signal crosstalk with other pathways.

1.2 Ethylene Response Pathway in Plants

ET is a small gaseous hormone that can freely diffuse across membranes and permits plant-to-plant communication. It is synthesized from methionine in three simple steps. The direct precursor of ET is 1-aminocyclopropane-1-carboxylic acid (ACC). The rate-limiting enzyme ACC-synthases (ACS) catalyzes ACC to ET (Dubois et al. 2018) (Figure 1.1). ET homeostasis is maintained by transcriptional and post-translational regulation of the ACS enzymes, as the ACS transcripts are responsive to different environmental factors such as water and light availability, and the enzyme can be phosphorylated and undergo protein degradation via mitogen-activated protein kinase (MAPK) and ubiquitin-mediated pathways, respectively (Dubois et al. 2018).

The ET signal transduction pathway has been extensively studied, and the components of the pathway were discovered mainly by studies performed with the model plant system *Arabidopsis thaliana*. The ET-induced triple response in young seedlings was utilized to identify the components of the ET response pathway in plants through genetic screens. ETHYLENE RESISTANCE1 (ETR1) was the first ET receptor discovered through this approach (Bleecker et al. 1988). Further, a family of ET receptors was identified in the membrane of the endoplasmic reticulum, and Golgi bodies that include ETR2, ETHYLENE RESPONSE SENSOR1 (ERS1), ERS2, and ETHYLENE INSENSITIVE4 (EIN4) (Guo and Ecker 2004). ET signaling is essentially linear and includes a protein kinase CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1), an ER-localized transmembrane protein ETHYLENE-INSENSITIVE 2 (EIN2), and downstream nuclear components such as EIN3, EIN3-LIKE (EIL), and ETHYLENE RESPONSE FACTOR (ERF) transcription factors (Guo and Ecker 2004; Dubois et al. 2018) (Figure 1.1). The phytohormone receptors are primarily positive regulators, but in the case of ET, they act as negative regulators (Dubois et al. 2018). In the absence of ET, the receptors interact with and activate CTR1 (Lacey and Binder 2014). CTR1 then phosphorylates and represses EIN2. Two F-box proteins, ETHYLENE INSENSITIVE2 TARGETING PROTEIN1 (ETP1) and ETP2, target phosphorylated EIN2 for 26S proteasomal degradation (Ju and Chang 2015). Upon ET perception, the receptor/CTR1 is targeted for 26S proteasome degradation (Shakeel et al. 2015) (Figure 1.1). In the presence of ET, when the repression of EIN2 is released, EIN2 is dephosphorylated; this dephosphorylation leads to its cleavage, thus releasing a C-terminal fragment (EIN2-C) that forms processing bodies or moves to the nucleus (Li et al. 2015; Merchante et al. 2015). The cleaved EIN2-C binds to the 3′-

untranslated regions (3′-UTRs) of *ETHYLENE INSENSITIVE3 BINDING F-BOX1* (*EBF1*) and *EBF2*, thereby repressing their turnover. EBF1 and EBF2 belong to F-box proteins, which target the ET-responsive TFs EIN3 and EIN3-LIKE 1 (EIL1) for degradation (Guo and Ecker 2003; Potuschak et al. 2003). ET-responsive TFs bind to ethylene-responsive element (ERE) on the promoter of target genes to regulate transcription of many ET-responsive genes and secondary TFs (Chang et al. 2013) (Figure 1.1). ET, through hierarchical events, regulates several developmental processes in plants by regulating gene expression differentially.

Although this canonical pathway is the predominant signaling cascade, alternative pathways also affect ET responses. Noncanonical pathway components such as RTE1 (REVERSION TO ETHYLENE SENSITIVITY1) and Auxin-Regulated Gene involved in Organ Size (ARGOS) can negatively regulate the ET receptor and promote ET sensitivity (Resnick et al. 2006; Rai et al. 2015). There are multiple evidences of the interplay between specific ET receptor isoforms with the components of other phytohormone cascades such as Abscisic acid (ABA) and cytokinin. For instance, ETR1 and ETR2 are shown to be involved in ABA-mediated control of seed germination in *Arabidopsis* (Yasumura et al. 2015; Bakshi et al. 2018). It was also demonstrated that ETR1 could physically interact with cytokinin receptor protein AHPs (*Arabidopsis thaliana* HISTIDINE PHOSPHOTRANSFER PROTEINS) and the ARRs (RESPONSE REGULATOR protein family in *Arabidopsis*) by its C-terminal portion (Scharein et al. 2008; Scharein and Groth 2011; Zdarska et al. 2019). Both AHPs and ARRs can also control ET responses such as ET sensitivity, recovery upon ET removal, stomatal opening, and root apical meristem (RAM) development (Street et al. 2015; Binder et al. 2018; Zdarska et al. 2019). Finally, the