

Azamal Husen *Editor*

# Plant Performance Under Environmental Stress

Hormones, Biostimulants and  
Sustainable Plant Growth Management

 Springer

# Plant Performance Under Environmental Stress

Azamal Husen  
Editor

# Plant Performance Under Environmental Stress

Hormones, Biostimulants and Sustainable  
Plant Growth Management

 Springer

*Editor*

Azamal Husen 

Wolaita Sodo University

Wolaita, Ethiopia

ISBN 978-3-030-78520-8

ISBN 978-3-030-78521-5 (eBook)

<https://doi.org/10.1007/978-3-030-78521-5>

© The Editor(s) (if applicable) and The Author(s), under exclusive license to Springer Nature Switzerland AG 2021

This work is subject to copyright. All rights are solely and exclusively licensed by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG  
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

*To my wife, Shagufta Yasmeen and children  
Zaara, Mehwish, and Huzaiifa, for their  
inspiration, encouragement, and support.*

# Preface

Global climate change is bound to create a number of abiotic and biotic stresses in the environment, which would affect the overall growth and productivity of plants. Like other living beings, plants have the ability to protect themselves by evolving various mechanisms against stresses, despite being sessile in nature. They manage to withstand extremes of temperature (hot and cold), extremes of water availability (drought and flooding), salinity, heavy metals, atmospheric pollution, toxic chemicals (fertilizers, pesticides, herbicides), and a variety of living organisms, especially viruses, bacteria, fungi, nematodes, insects, arachnids, weeds, etc. Incidence of abiotic stresses may alter the plant–pest interactions by enhancing susceptibility of plants to pathogenic organisms. These interactions often change plant response to abiotic stresses.

Food security for the rapidly growing human population in a sustainable ecosystem is a major concern of the present-day world. Understanding the core developmental, physiological, and molecular aspects that regulate plant performance in terms of growth and productivity under stresses is a pivotal issue to be tackled skillfully by the scientific community dealing with sustainable agricultural and horticultural practices. Plant growth regulators modulate plant responses to biotic and abiotic stresses and regulate their growth and developmental cascades. Also, interaction between biotic and abiotic stresses is controlled by hormone signaling. A number of physiological and molecular processes that act together in a complex regulatory network, further manage these responses. Crosstalk between autophagy and hormones also occurs to develop tolerance in plants towards multiple abiotic stresses. Similarly, biostimulants, in combination with correct agronomic practices, have shown beneficial effects on plant metabolism due to the hormonal activity that stimulates different metabolic pathways. At the same time, they reduce the use of agrochemicals and impart tolerance to biotic and abiotic stress. Further, the use of bio- and nano-fertilizers seem to hold promise to improve the nutrient use efficiency and hence the plant yield under stressful environment. Overall, plant exposure to bio-stimulants or hormones reduces damage caused by stress, improves the defense mechanisms involved, and also helps in disease management and nutrient-use efficiency. It has also been shown that under a stressful environment, use of bio- and

nano-fertilizers determines plant yield and quality, while seed priming agents impart stress tolerance. Additionally, tolerance or resistance to stress may also be induced by using specific chemical compounds such as polyamines, proline, glycine betaine, hydrogen sulfide, silicon,  $\beta$ -aminobutyric acid, and  $\gamma$ -aminobutyric acid.

This book comprises of 22 chapters that cover a wide range of topics, as mentioned above, and discusses the trends and advances in plant performance under stressful conditions. The vast coverage of diverse aspects of the subject reflects well from the table of contents. It must be equally useful for graduate students, teachers, researchers, and scientists related to botanical science, crop science, agriculture, horticulture, and environmental science.

I express my sincere thanks to the distinguished authors who have shared their knowledge and contributed chapters for this book. I feel indebted to Mr. Eric Stannard, Senior Editor (Botany) at Springer, and all his associates, for their sustained cooperation. I am also grateful to Professor Muhammad Iqbal (Jamia Hamdard, New Delhi, India); Dr. Mansur Osman (University of Gondar, Gondar, Ethiopia); Dr. Mohammad Babar Ali (University of Kentucky, Lexington, USA); Dr. Sophie Mavrikou (Agricultural University of Athens, Athens, Greece); Dr. Adalberto Benavides-Mendoza (Autonomous Agricultural University Antonio Narro, Saltillo, Mexico), and Dr. Rakesh Kumar Bachheti (Addis Ababa Science and Technology University, Addis Ababa, Ethiopia) for their generous help in reviewing various chapters. I shall be happy receiving comments and criticism, if any, from subject experts and general readers of this book.

Wolaita, Ethiopia  
May, 2021

Azamal Husen

# Contents

<b>Cross Talk Between Autophagy and Hormones for Abiotic Stress Tolerance in Plants</b> .....	1
Azamal Husen	
<b>Abscisic Acid and Plant Response Under Adverse Environmental Conditions</b> .....	17
Jorge Gonzalez-Villagra, Carla Figueroa, Ana Luengo-Escobar, Melanie Morales, Claudio Inostroza-Blancheteau, and Marjorie Reyes-Díaz	
<b>Auxins and Plant Response to Adverse Environmental Conditions</b> .....	49
Swati T. Gurme, Pankaj S. Mundada, Mahendra L. Ahire, and Supriya S. Salunkhe	
<b>Jasmonic Acid for Sustainable Plant Growth and Production Under Adverse Environmental Conditions</b> .....	71
Sahil, Adhip Das, Sahil Mehta, K. F. Abdelmotelb, Shivaji Ajinath Lavale, S. K. Aggarwal, Bahadur Singh Jat, Anurag Tripathi, and Surbhi Garg	
<b>Salicylic Acid for Vigorous Plant Growth and Enhanced Yield Under Harsh Environment</b> .....	99
Sahil, Radhika Keshan, Sahil Mehta, K. F. Abdelmotelb, S. K. Aggarwal, Shivaji Ajinath Lavale, Bahadur Singh Jat, Anurag Tripathi, and Laxman Singh Rajput	
<b>Strigolactones for Sustainable Plant Growth and Production Under Adverse Environmental Conditions</b> .....	129
Ali Raza, Rida Javed, Zainab Zahid, Rahat Sharif, Muhammad Bilal Hafeez, Muhammad Zubair Ghouri, Muhammad Umar Nawaz, and Manzer H. Siddiqui	



<b>Polyamines for Sustainable Plant Growth and Production Under Adverse Environmental Conditions</b> . . . . .	167
Brij Bihari Pandey, Ratnakumar Pasala, Kulasekaran Ramesh, Sumit Kumar Mishra, Nidhi Tyagi, Akankhya Guru, Pappu Lal Bairwa, C. L. N. Manikanta, and Arti Guhey	
<b>Plant Performance and Defensive Role of Proline Under Environmental Stress</b> . . . . .	201
Pankaj S. Mundada, Suchita V. Jadhav, Supriya S. Salunkhe, Swati T. Gurme, Suraj D. Umdale, Tukaram D. Nikam, and Mahendra L. Ahire	
<b>Plant Performance and Defensive Role of Glycine Betaine Under Environmental Stress</b> . . . . .	225
Praveen Jain, Brijesh Pandey, Pratibha Singh, Ranjana Singh, Satarudra Prakash Singh, Sashi Sonkar, Rahul Gupta, Saurabh Singh Rathore, and Akhilesh Kumar Singh	
<b>Plant Performance and Defensive Role of <math>\beta</math>-Amino Butyric Acid Under Environmental Stress</b> . . . . .	249
Anuj Choudhary, Antul Kumar, Harmanjot Kaur, A. Balamurugan, Asish Kumar Padhy, and Sahil Mehta	
<b>Plant Performance and Defensive Role of <math>\gamma</math>-Gamma Amino Butyric Acid Under Environmental Stress</b> . . . . .	277
Antul Kumar, Anuj Choudhary, Harmanjot Kaur, Mohammed Javed, and Sahil Mehta	
<b>Nitric Oxide: A Key Modulator of Plant Responses Under Environmental Stress</b> . . . . .	301
Pankaj Pandey, Asha Devi Pallujam, S. Leelavathi, Sahil Mehta, Manesh Chander Dagla, Bharat Bhushan, and S. K. Aggarwal	
<b>Functions of Hydrogen Sulfide in Plant Regulation and Response to Abiotic Stress</b> . . . . .	329
Sashi Sonkar, Akhilesh Kumar Singh, and Azamal Husen	
<b>Silicon and Plant Responses Under Adverse Environmental Conditions</b> . . . . .	357
Pankaj S. Mundada, Suchita V. Jadhav, Supriya S. Salunkhe, Swati T. Gurme, Suraj D. Umdale, Rajkumar B. Barmukh, Tukaram D. Nikam, and Mahendra L. Ahire	
<b>Nanofertilizers as Tools for Plant Nutrition and Plant Biostimulation Under Adverse Environment</b> . . . . .	387
Misbah Naz and Adalberto Benavides-Mendoza	
<b>Biostimulants and Plant Response Under Adverse Environmental Conditions: A Functional Interplay</b> . . . . .	417
Giacomo Cocetta, Andrea Ertani, Roberta Bulgari, Giulia Franzoni, Silvana Nicola, and Antonio Ferrante	

**Biofertilizers-Mediated Sustainable Plant Growth and Production Under Adverse Environmental Conditions** . . . . . 437  
 Swetika Porwal, Akhilesh Kumar Singh, Ashok Kumar Yadav, Sudhir Kumar, and Paras Porwal

**Seed Priming: A Cost-effective Strategy to Impart Abiotic Stress Tolerance** . . . . . 459  
 Akhila Sen, Riya Johnson, and Jos T. Puthur

**Significance of Cyanobacteria in Soil-Plant System and for Ecological Resilience** . . . . . 481  
 Subhra Chakraborti, Abhishek Sen, Kuntal Bera, Puspendu Dutta, Shovik Deb, Satyajit Hembram, and Ashok Choudhury

**Phytomicrobiome Community: An Agrarian Perspective Towards Resilient Agriculture** . . . . . 493  
 Mayur Mukut Murlidhar Sharma, Pankaj Sharma, Divya Kapoor, Puneet Beniwal, and Sahil Mehta

**Adverse Environment and Pest Management for Sustainable Plant Production** . . . . . 535  
 Priyanka Saxena, Akhilesh Kumar Singh, and Rahul Gupta

**Eco-friendly Approaches of Using Weeds for Sustainable Plant Growth and Production** . . . . . 559  
 Satish Kumar Ameta and Suresh C. Ameta

**Index** . . . . . 593

## About the Editor



**Azamal Husen** (BSc from Shri Murli Manohar Town Post Graduate College, Ballia, UP; MSc from Hamdard University, New Delhi; and PhD from Forest Research Institute, Dehra Dun, India) is a Foreign Delegate at Wolaita Sodo University, Wolaita, Ethiopia. He has served the University of Gondar, Ethiopia, as a Full Professor of Biology, and also worked as the Coordinator of MSc Program and the Head, Department of Biology. He was a Visiting Faculty of the Forest Research Institute, and the Doon College of Agriculture and Forest at Dehra Dun, India. He has a more than 20 years' experience of teaching, research and administration. Dr.

Husen specializes in biogenic nanomaterials fabrication and their application, plant response to nanomaterials, plant production and adaptation to harsh environments at physiological, biochemical and molecular levels, herbal medicine, and clonal propagation and improvement of tree species. He has conducted several research projects sponsored by various funding agencies, including the World Bank, the Indian Council of Agriculture Research (ICAR), the Indian Council of Forest Research Education (ICFRE); and the Japan Bank for International Cooperation (JBIC), etc. He has published over 100 research papers, review articles and book chapters, edited books of international repute, presented papers in several conferences, and produced over a dozen of manuals and monographs. Husen received four fellowships from India and a recognition award from University of Gondar, Ethiopia, for excellent teaching, research and community service. An active organizer of seminars, and conferences, and an efficient evaluator of research projects and book proposals as he is, Dr. Husen has been on the Editorial board and the panel of reviewers of several reputed journals of Elsevier, Frontiers Media SA, Taylor & Francis, Springer Nature, RSC, Oxford University Press, Sciendo, The Royal Society, CSIRO, PLOS and John Wiley & Sons. He is included in the advisory board of Cambridge Scholars Publishing, UK. He is a Fellow of the Plantae group of

American Society of Plant Biologists, and a Member of International Society of Root Research, Asian Council of Science Editors, and INPST, etc. Also, he is Editor-in-Chief of American Journal of Plant Physiology; and a Series Editor of 'Exploring Medicinal Plants' published by Taylor & Francis Group, USA.

# Cross Talk Between Autophagy and Hormones for Abiotic Stress Tolerance in Plants



Azamal Husen 

## Abbreviations

ABA	Abscisic acid
ACC	1-(Aminocarbonyl)-1cyclopropanecarboxylic acid
AOX	Alternative oxidase
ATGs	Autophagy-related genes
ATI1	Autophagy interacting protein 1
DRE	Drought-responsive elements
DSK2	DOMINANT SUPPRESSOR OF KAR 2
ERF5	Ethylene response factor 5
ERF5	Ethylene response factor 5
ET	Ethylene
HSE	Heat-shock elements
HsfA1a	Heat-shock transcription factor A1a
HSPs	Heat-shock proteins
IAA	Indole acetic acid
PBR	Peripheral-type benzodiazepine receptor
PDC	Programmed cell death
PIP2;7	PLASMA-MEMBRANE INTRINSIC PROTEIN 2;7
RNAi	RNA interference
SA	Salicylic acid
TOR	Target of rapamycin
TSPO	Tryptophan-rich sensory protein

---

A. Husen (✉)  
Wolaita Sodo University, Wolaita, Ethiopia

# 1 Introduction

Plants, like other living beings, have the ability to protect themselves by evolving numerous mechanisms against abiotic stresses despite being sessile in nature (Anjum et al. 2012, 2014; Bechtold and Field 2018; He et al. 2018). They manage to withstand harsh environmental conditions such as extreme temperatures (Bita and Gerats 2013; Nahar et al. 2015), water scarcity (Husen et al. 2014; Getnet et al. 2015; Embiale et al. 2016), flooding (Loreti et al. 2016; Zhou et al. 2020), salinity (Yousuf et al. 2016a, b; Hussein et al. 2017), heavy metals (Moinuddin et al. 2004; Ghori et al. 2019; Ding et al. 2020), ionizing radiation (Esnault et al. 2010; Aref et al. 2016; Caplin and Willey 2018), nutrient deficiency (Ahmad et al. 2005; Ganie et al. 2016, 2017; Bagheri et al. 2017), atmospheric pollution (Husen 1997; Husen et al. 1999; Husen and Iqbal 2004; Iqbal et al. 2000, 2010), chemicals (Bashir et al. 2007, 2014; Majid et al. 2013; Bashir and Iqbal 2014), and so on as mentioned in Fig. 1.

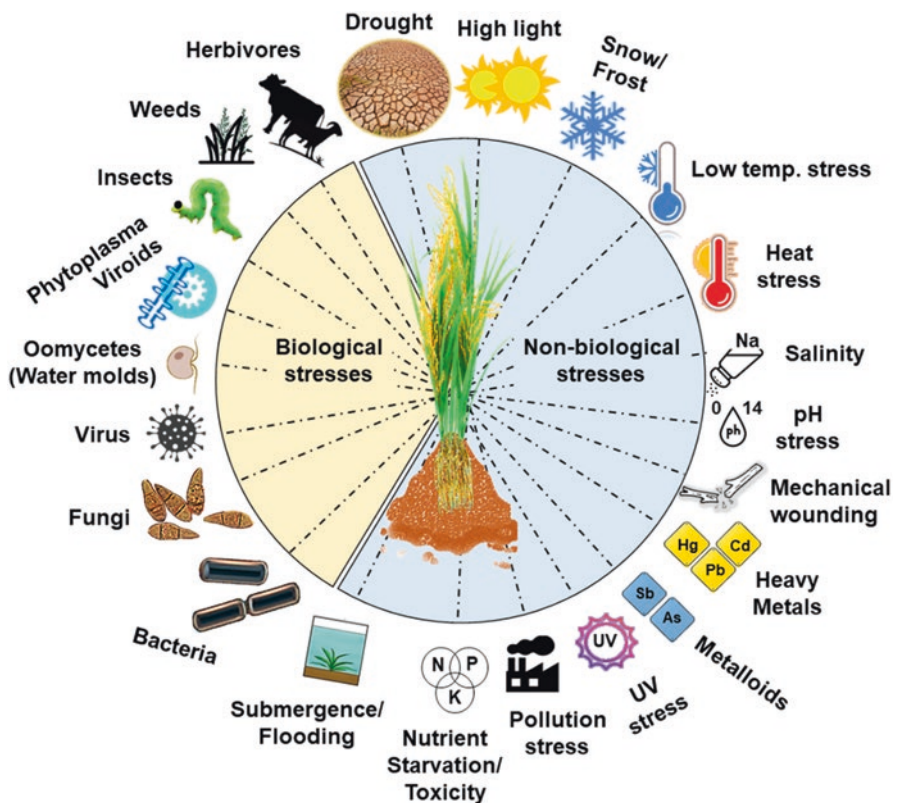


Fig. 1 Biological and nonbiological stress factors

Of late, environmental adversities have grown more prominent due to rapidly increasing atmospheric pollution and the drastic fluctuations in the global climate conditions. For instance, worldwide drought stress may increase due to prolonged exposure to high temperature in rainfed areas. This may also induce osmotic stress, if water evaporates from soils, leading to elevated salt concentrations. Rafferty et al. (2017) have suggested an increase of global average temperature from 2.0 to 4.9 °C by 2100. Thus, in the near future, combination of high temperature, drought, and salt stress may possibly lead to a drastic reduction in plant fitness and their overall productivity at the global level. It has also been projected that about 90% of arable lands are now prone to single or multiple stress conditions (dos Reis et al. 2012).

Phytohormones such as auxins, gibberellins, cytokinins, ethylene, abscisic acid, jasmonates, brassinosteroids, and strigolactones play a significant role in saving plants from single or multiple stress conditions, by mediating plant growth and development, nutrient allocation and the source and or sink transitions (Peleg and Blumwald 2011; Colebrook et al. 2014; Kazan 2015; Husen et al. 2016, 2017, 2018, 2019; Siddiqi and Husen 2017a, 2019; Podlešáková et al. 2019). In general, they are responsible for stress signaling in plants. Further, during the process of plant adaptation to stress, cells require to recycle the damaged/unwanted proteins and organelles. In this connection, the term autophagy (i.e., self-eating) evolved. In plant, three kinds of autophagy, namely micro-autophagy, macro-autophagy, and mega-autophagy, have been reported. In the first case, the cytoplasmic constituents are sequestered by the tonoplast invagination, which is then released into the vacuolar lumen, producing single-membrane autophagic bodies (Todde et al. 2009; May et al. 2012; Marshall and Vierstra 2018). In macro-autophagy, on the other hand, the double-membrane-bound organelles, called phagophores, develop in the cytoplasm to engulf cytoplasmic material (Thompson and Vierstra 2005; Bassham et al. 2006), and the resulting double-membrane vesicles, autophagosomes, reach the vacuole. The outer membrane of autophagosome combines with the tonoplast to release an autophagic body into the vacuolar lumen; this autophagic body is degenerated in the vacuole to release its content for recycling (Li and Vierstra 2012). Mega-autophagy (massive autophagy) is an utmost form of autophagy, the final phase of the developmental programmed cell death (PCD). In plant cells, two main types of PCD are noticed. The first one is observed during the normal development and after the abiotic stress (developmental PCD), whereas the second one occurs after pathogen attack (pathogen-related PCD). The mega-autophagy process begins with the permeabilization or rupture of vacuolar membrane, which permits vacuolar hydrolases to release into the cytoplasm. These vacuolar hydrolases totally damage the cytoplasm, and in several cases also the cell walls, finally leading to cell death (Fukuda 1996; Marshall and Vierstra 2018; Locato and De Gara 2018; Papini 2018).

Salinity, drought and heat stress, nutrient deficiency, oxidative stress, hypoxia, and pathogen attack has been shown to induce autophagy in different cellular settings (Doelling et al. 2002; Xiong et al. 2007; Liu et al. 2009; Zhou et al. 2014; Chen et al. 2015; Lai et al. 2011; Luo et al. 2017; Hofius et al. 2017). Autophagy has also been noticed to control the growth and development processes in plants (Yang et al. 2019). Autophagy-related genes (ATGs) have been shown to be involved in

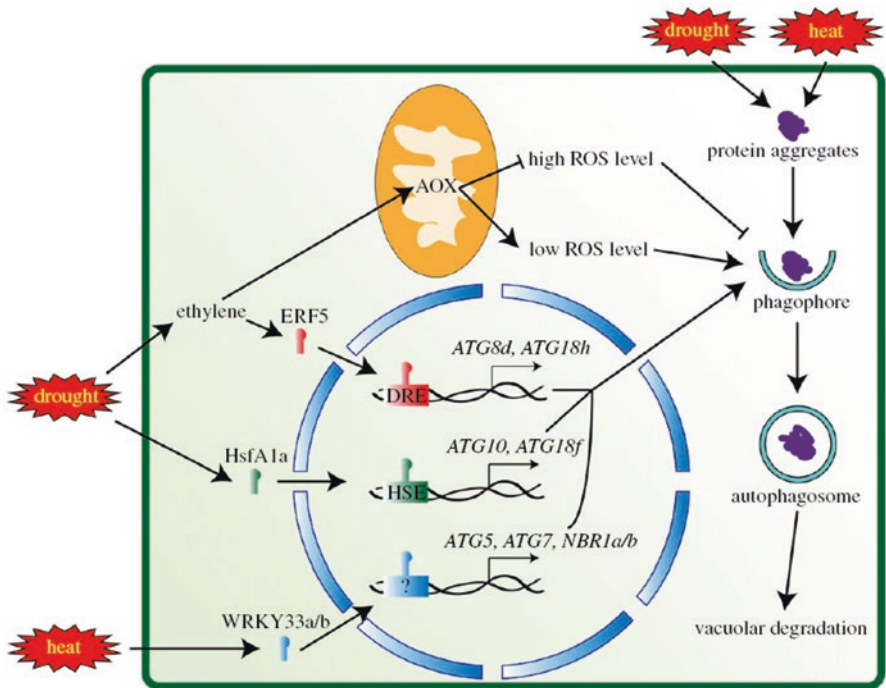
pollen growth, *seed* development and *germination*, leaf senescence, and nitrogen use efficiency (Wang et al. 2016; Yu et al. 2019; Zhen et al. 2019; Han et al. 2020; Hanamata et al. 2020). Further, the autophagy regulates hormone synthesis and signaling pathways, whereas hormone signaling regulates autophagy gene expression also (Liao and Bassham 2020). The significance of autophagy has increased after the report of mutagenesis in yeast (Tsukada and Ohsumi 1993; Thumm et al. 1994; Harding et al. 1995), and to date, more than 30 ATGs associated with the autophagy pathway have been recognized (Yoshimoto 2012; Marshall and Vierstra 2018). Recently, Signorelli et al. (2019) have suggested that the accumulation of  $\gamma$ -aminobutyric acid, proline, and polyamines in a stressful environment may indirectly promote autophagy through different pathways and also facilitate the osmotic adjustment that coordinates the autophagic process to avoid mega-autophagy. On the whole, cross talk between autophagy and hormones under abiotic stress conditions are poorly understood in the plant system. Based on the available information, this article discusses the current understanding of autophagy under abiotic stress, and hormones coordination/modulation in plant growth and development.

## 2 Autophagy and Abiotic Stresses

In general, most of the abiotic stresses exhibit some common responses, though they are controlled in different ways. For instance, salinity differs from drought stress in generating ionic stress in addition to osmotic stress, which leads to membrane disruption and enzyme dysfunction. Salinity, drought, and other stresses including nanoparticles exposure lead to an enhanced production of reactive oxygen species (ROS) which damage cellular membranes, proteins, and nucleic acids (Miller et al. 2008; Jaspers and Kangasjärvi 2010; Gill and Tuteja 2010; Husen 2010; Siddiqi and Husen 2016, 2017b; Singh and Husen 2019, 2020). Plant system has shown numerous mechanisms to tolerate abiotic stress, for example, regulating the growth rate by altering cell wall biosynthesis, protein synthesis, as well as cell division (BursSENS et al. 2000; Le Gall et al. 2015; Kosová et al. 2018). At the cellular level, overproduction of ROS may harm organelles and biomolecules, affecting their functionality (Umar et al. 2018). An interplay between ROS and autophagy is noticed; ROS induce autophagy and autophagy reduces ROS production (Signorelli et al. 2019). Further, several genes have been shown to respond under abiotic stress condition and get involved in mechanisms of stress tolerance (Zhu 2001; Haak et al. 2017; Baillo et al. 2019). In this connection, several potential roles of autophagy in response to abiotic stress have been unraveled in terms of plant resistance. For instance, autophagosome induction was noted under mannitol and salinity effects, and *Arabidopsis* RNAi-ATG18a plants growing under drought, salt, or osmotic stress displayed enhanced sensitivity to the stress (Liu et al. 2009). Similarly, Luo et al. (2017) have reported various ATG mutants under salt stress, which had higher oxidized proteins in comparison to wild-type plants. Wang et al. (2017) have suggested that the overexpression of ATG3 homologs from *Malus*



*domestica* in *Arabidopsis* augmented their resistance to salt and osmotic stress. This study suggested an anticipated autophagy function under drought stress to control quality of protein. In *Solanum lycopersicum*, silencing heat-shock transcription factor A1a (HsfA1a) led to a higher insoluble protein accumulation, whereas overexpression of HsfA1a decreased the insoluble protein content under drought stress (Wang et al. 2015). This was supported by the observation of reduced insoluble protein and less oxidation of soluble proteins in ATG18a overexpressing *M. domestica* (Sun et al. 2018a) (Fig. 2). In this experiment, Sun et al. (2018a) observed that the overexpression of ATG18a from *M. domestica* in *S. lycopersicum* as well as in *M. domestica* enhanced their resistance to drought stress in comparison to wild-type plants. In another study, Zhu et al. (2018) found that mitochondrial alternative oxidase (AOX) regulates autophagy via mitochondrial ROS under drought stress



**Fig. 2** Identified regulators of autophagy during drought and heat stress in *Solanum lycopersicum*. AOX within mitochondria and the transcription factor ERF5 are induced by drought stress, in a process mediated by ethylene. AOX can positively regulate autophagy by balancing the level of ROS; lower ROS levels are thought to activate autophagy, whereas higher ROS levels inhibit autophagy. ERF5 induces the expression of ATG8d and ATG18h by binding to DRE in their promoters. HsfA1a is also induced by drought stress and activates the expression of ATG10 and ATG18f by binding to HSE in their promoters. Under heat stress, the transcription factors WRKY33a and WRKY33b activate the expression of ATG5, ATG7, NBR1a, and NBR1b *S. lycopersicum*. Autophagy in turn functions to degrade the protein aggregates induced by drought or heat (adopted from Tang and Bassham 2018)

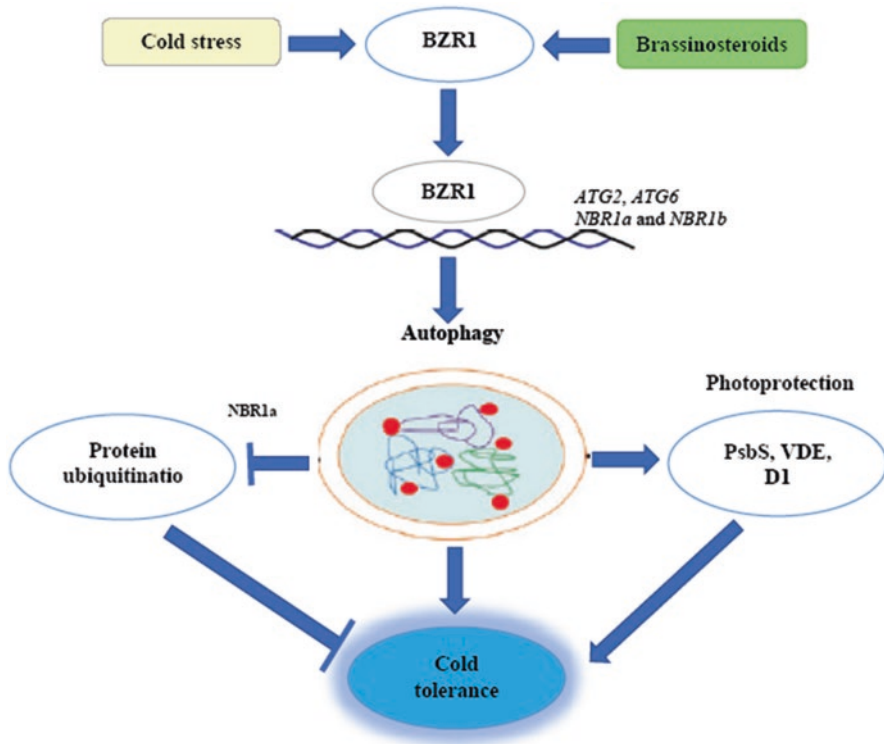
conditions in *S. lycopersicum* plants. AOX limits the ROS formation by preventing the over-reduction of the electron transport chain (Selinski et al. 2018). In *S. lycopersicum*, AOX-overexpressing plants exhibited augmented drought stress tolerance, whereas AOX-silenced *S. lycopersicum* revealed hypersensitivity in comparison to wild-type plants, signifying the functions of AOX in terms of drought responses (Zhu et al. 2018) (Fig. 2). Also, the AOX transcript and protein were induced by application of ethylene (ET) precursor 1-(aminocarbonyl)-1-cyclopropanecarboxylic acid (ACC). ACC application conferred higher autophagy activity and better drought tolerance to *S. lycopersicum* plants by either overexpressing or silencing the AOX (Zhu et al. 2018) (Fig. 2). ATGs were transcriptionally controlled by drought stress in *S. lycopersicum*. The transcription factor ethylene response factor 5 (ERF5), induced by both drought and ACC application, binds to the promoters of ATG8d and ATG18h, and inducing their expression (Zhu et al. 2018).

In heat stress also, autophagy plays a significant role in stress alleviation. Accumulation of autophagosomes in *Arabidopsis* and *L. esculentum* plants growing under heat stress has been reported (Zhou et al. 2013, 2014; Yang et al. 2016). In the case of *Arabidopsis*, ATG5 and ATG7 mutants have shown more sensitivity under heat stress condition in comparison to wild-type plants, as demonstrated by more wilting, higher electrolyte leakage, and decreased rate of photosynthesis. Moreover, ATG7 mutant plants exhibited insoluble protein aggregates accumulation, labeled by ubiquitin (Zhou et al. 2013). In accordance with this observation, Zhou et al. (2014) reported a virus-induced gene silencing of ATG5 and ATG7 in *L. esculentum* plants exposed to heat stress (Zhou et al. 2014). It was suggested that heat stress induces autophagy by provoking endoplasmic reticulum stress. Endoplasmic reticulum stress stems from the unfolded proteins accumulation in endoplasmic reticulum, and formation of protein aggregates (Yang et al. 2016). Some of the studies have suggested that both micro- and macro-autophagy play a key role in the formation of anthocyanin vacuolar inclusions under stressful conditions (Masclaux-Daubresse et al. 2014; Chanoca et al. 2015; Sun et al. 2018b). ATG mutant *Arabidopsis* plants have also shown decreased accumulation of anthocyanin under nitrogen starvation (Masclaux-Daubresse et al. 2014), and ATG18a overexpression in *M. domestica* encouraged accumulation of anthocyanin under nitrogen starvation (Sun et al. 2018b). It is suggested that the abiotic stress condition activated ROS production (Baxter et al. 2014), and anthocyanin possibly works as an antioxidant and mitigates the damage caused by ROS, and thus facilitates stress tolerance. In mammalian cells, selective autophagy is mediated by a receptor such as Neighbor of BRCA1 (NBR1) (Svenning et al. 2011). In plants, NBR1 homologs have been linked to selective autophagy under stress, but it is uncertain how they influence the selective autophagy under non-stressed situations (Jung et al. 2020). Svenning et al. (2011) reported that NBR1 binds to ubiquitin in *Arabidopsis* plants, as in the mammalian counterpart. In *Arabidopsis* plants exposed to heat stress condition, NBR1 expression was upregulated, and GFP-NBR1 puncta gathered in the wild-type plants under heat stress, but not in ATG7 mutants; the representative puncta formation was autophagy-dependent (Zhou et al. 2013). Taken together, it was found that the NBR1 mutants were hypersensitive under heat, oxidative, and salt stress

conditions in comparison to wild-type plants. Under heat stress, NBR1 mutants exhibited ubiquitin-positive, non-soluble protein aggregates accumulation and the part of NBR1-bound insoluble proteins was augmented in ATG7 mutants (Zhou et al. 2013). Zhou et al. (2014) reported the same in *L. esculentum* in which NBR1 was silenced by virus-induced gene silencing. They found that silencing of *L. esculentum* ATG5, ATG7, or NBR1 compromised heat-induced expression of not only the targeted genes but also other autophagy-related genes. In another experiment, Sedaghatmehr et al. (2019) identified autophagy as a key negative regulator of thermomemory and, hence, tolerance to successive heat stresses in *Arabidopsis*. The authors suggested that autophagy mediates the degradation of specific heat-shock proteins (HSPs) at later stages of the thermorecovery phase, leading to protein-aggregates accumulation after the second heat stress and facilitates heat tolerance. Autophagy mutants retained HSPs longer than wild type and concurrently showed better thermomemory. Guillaumot et al. (2009) reported a membrane-spanning protein (Tryptophan-rich sensory protein/peripheral-type benzodiazepine receptor-TSPO/MBR), which expressed under salt/osmotic stress and abscisic acid exposure. Vanhee et al. (2011) reported that TSPO binds free heme and acts as a heme-scavenger, and also regulates heme levels in cells. In another study, it was suggested that TSPO binds the plasma membrane aquaporin, PLASMA MEMBRANE INTRINSIC PROTEIN 2;7 (PIP2;7). Expression of both proteins reduced PIP2;7 levels and autophagy inhibition stopped this reduction. Thus, Hachez et al. (2014) suggested that TSPO controls the uptake of water by the cell during the abiotic stress associated with water-deficit conditions. However, TSPO overexpression under salinity showed hypersensitivity, though *tspo* mutants remained unaffected in comparison to wild-type plants (Guillaumot et al. 2009). Perhaps, it could be due to aquaporins over-degradation and hence damaged regulations of cell water status. Further, Nolan et al. (2017) reported that DOMINANT SUPPRESSOR OF KAR 2 (DSK2—a ubiquitin binding receptor) interacted with ATG8 and BRI1-EMS SUPPRESSOR 1 (BES1), a brassinosteroid (BR) pathway regulator. BES1 levels decreased under drought stress. Also, the DOMINANT SUPPRESSOR OF KAR 2 (DSK2)-RNAi *Arabidopsis* showed enhanced sensitivity under stress, which was due to augmented BES1 levels in comparison to wild-type plants. This was also reported in ATG7 mutants. This investigation also revealed opposite expression of drought-related genes in the DSK2-RNAi plants. It was suggested that by controlling BES1 levels via autophagic degradation, DSK2 may downregulate BR signals to switch cells from growth to stress mode (Nolan et al. 2017). Thus, this report revealed the cross talk among autophagy and hormonal signaling in plants under stress conditions.

Thus far, autophagy was considered a phenomenon of promoting plant survival under various abiotic stress conditions. Nonetheless, Bárány et al. (2018) have shown that autophagy functions in promoting PCD during microspore embryogenesis in *Hordeum vulgare*. Formation of autophagosome was observed in microspores as well as PCD on exposure to stress (at 4 °C). Further, autophagy inhibitors treatment reduced the microspore cell death. These observations have revealed the dual role of autophagy under abiotic stress conditions, depending on the type of

stress, plant organ, and the developmental phase. Further, a recent investigation has shown that BRs act as a positive regulator of NBR1-dependent selective autophagy in response to chilling stress in tomato plants (Chi et al. 2020). It was noted that cold and BRs induced the stability of BRASSINAZOLE-RESISTANT1 (BZR1), which upregulates *ATG2*, *ATG6*, *NBR1a*, and *NBR1b* expression by binding to their promoters, thus resulting in increased autophagy and increased levels of NBR1 protein. The upsurge in autophagy and the selective autophagy receptor NBR1 increased photoprotection via greater accumulation of functional proteins (PsbS, VDE, and D1) and encouraged the degradation of stress-damaged ubiquitinated protein aggregates, thus leading to increased tolerance to cold (Fig. 3).



**Fig. 3** A proposed model for the induction of cold tolerance by BZR1 through the activation of autophagy in tomato. Both cold and brassinosteroids can induce the stability of BRASSINAZOLE RESISTANT 1 (BZR1), which activates the transcription of the autophagy genes *ATG2*, *ATG6*, *NBR1a*, and *NBR1b* by directly binding to their promoters, subsequently enhancing autophagy. The increase in autophagy promotes photoprotection via greater accumulation of functional proteins (PsbS, VDE, and D1) and increases the degradation of stress-damaged insoluble ubiquitinated protein aggregates via the selective autophagy receptor NBR1. Arrows denote positive regulation; bar ends denote negative regulation (adopted from Chi et al. 2020)

### 3 Hormonal Interaction

The cross talk between phytohormones and autophagy under stress conditions has been verified many times, yet the precise molecular mechanism is unknown. Abscisic acid (ABA) work as an endogenous messenger under stressful conditions (Raghavendra et al. 2010). ABA was known to prevent the activity of plant target of rapamycin (TOR), which may facilitate the autophagy induction under stress. However, the exact molecular mechanism is still unclear. The role of ABA under abiotic stress was revealed to affect the TSPO expression (Guillaumot et al. 2009). Further, Honig et al. (2012) reported that the *ATI1/2* knockdown seeds showed reduced germination due to ABA exposure, which suggests an interplay between ABA and autophagy. Yoshimoto et al. (2014) suggested that the early senescence phenotype of ATG mutants was arbitrated by salicylic acid (SA) accumulation, and autophagy was revealed to control SA signaling during senescence and also under biotic stress. Slavikova et al. (2008) have reported that GFP-ATG8f-HA *Arabidopsis* plants showed a different performance on exposure to cytokinin, in comparison to the wild-type plants, as verified by changes in root architecture and the production and accumulation of anthocyanin, testifying that autophagy could regulate this process. However, no changes were seen between GFP-ATG8f-HA plants and wild-type plants under IAA exposure (Slavikova et al. 2008). Auxins function in TOR kinase-dependent autophagy induction under specific abiotic stresses (Pu et al. 2017). TOR kinase works as a global integrator of metabolic and environmental signals to increase or decrease the growth, and one of its important functions is the negative autophagy regulation (Liu et al. 2012; Rexin et al. 2015). Autophagy also regulates phytohormone synthesis. For instance, Nolan et al. (2017) have shown BR signaling regulated by autophagy. They have suggested that selective autophagy may be involved in the regulation of phytohormone signaling and biosynthesis, thus modulating plant responses under changing/adverse and or abiotic environmental conditions.

### 4 Conclusion

Autophagy, a eukaryotic catabolic mechanism, participates in processes of plant growth and development, and responses to numerous biotic and abiotic stresses. It is important for the degradation of unnecessary and dysfunctional cellular components at some stages of growth/development and under adverse environmental conditions. In recent years, investigation associated with autophagy has been expanded from *Arabidopsis* to other crop plants. So far, many ATGs associated with the autophagy pathway have been recognized. A better understanding of increased ATGs expression could be beneficial for the agricultural sector. Thus far, the regulatory mechanisms of autophagy and the hormonal cross talk under adverse environmental conditions at the molecular level are poorly understood, and deserve further in-depth exploration.

## References

- Ahmad A, Khan I, Anjum NA, Diva I, Abdin MZ, Iqbal M (2005) Effect of timing of sulfur fertilizer application on growth and yield of rapeseed. *J Plant Nutr* 28(6):1049–1059
- Anjum NA, Gill SS, Ahmad I, Tuteja N, Soni P, Pareek A, Umar S, Iqbal M, Pacheco M, Duarte AC, Pereira E (2012) Understanding stress-responsive mechanisms in plants: an overview of transcriptomics and proteomics approaches. In: Tuteja N, Tiburcio AF, Singh S et al (eds) Improving crop resistance to abiotic stress—omics approaches. Wiley-VCH Verlag GmbH & Co, Germany, pp 337–355
- Anjum NA, Aref IA, Pereira E, Ahmad A, Iqbal M (2014) Glutathione and proline can coordinately make plants withstand the joint attack of osmotic and metal(loid) stresses. *Front Plant Sci* 5(662):4. <https://doi.org/10.3389/fpls.2014.00662>
- Aref IM, Khan PR, Al-Sahli AA, Husen A, Ansari MKA, Mahmooduzzafar, Iqbal M (2016) Response of *Datura innoxia* Linn. to gamma rays and its impact on plant growth and productivity. *Proc Nat Acad Sci, India (Biol Sci)* 86(3):623–629
- Bagheri R, Ahmad J, Bashir H, Iqbal M, Qureshi MI (2017) Changes in rubisco, cysteine-rich proteins and antioxidant system of spinach (*Spinacia oleracea* L.) due to sulphur deficiency, cadmium stress and their combination. *Protoplasma* 254:1031–1043
- Baillo EH, Kimotho RN, Zhang Z, Xu P (2019) Transcription factors associated with abiotic and biotic stress tolerance and their potential for crops improvement. *Genes (Basel)* 10:771
- Bárány I, Berenguer E, Solís MT, Pérez-Pérez Y, Santamaría ME, Crespo JL, Risueño MC, Díaz I, Testillano PS (2018) Autophagy is activated and involved in cell death with participation of cathepsins during stress-induced microspore embryogenesis in barley. *J Exp Bot* 69:1387–1402
- Bashir F, Iqbal M (2014) Lambda-cyhalothrin-induced oxidative stress alters ascorbate-glutathione cycle in *Glycine max* (L.) Merr. *Trends Biosci* 7(9):703–710
- Bashir F, Mahmooduzzafar, Siddiqi TO, Iqbal M (2007) The antioxidative response system in *Glycine max* (L.) Merr. exposed to Deltamethrin, a synthetic pyrethroid insecticide. *Environ Pollut* 147:94–100
- Bashir F, Mahmooduzzafar, Siddiqi TO, Iqbal M (2014) Alphamethrin (a synthetic pyrethroid)-induced oxidative stress and antioxidant-defence mechanism in *Glycine max* (L.) Merr. *Int J Agric Sci* 5(1):27–41
- Bassham DC, Laporte M, Marty F, Moriyasu Y, Ohsumi Y, Olsen LJ, Yoshimoto K (2006) Autophagy in development and stress responses of plants. *Autophagy* 2:2–11
- Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signalling. *J Exp Bot* 65:1229–1240
- Bechtold U, Field B (2018) Molecular mechanisms controlling plant growth during abiotic stress. *J Exp Bot* 69:2753–2758
- Bitá CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Front Plant Sci* 4:273. <https://doi.org/10.3389/fpls.2013.00273>
- Burssens S, Himanen K, van de Cotte B, Beeckman T, Van Montagu M, Inzé D, Verbruggen N (2000) Expression of cell cycle regulatory genes and morphological alterations in response to salt stress in *Arabidopsis thaliana*. *Planta* 211:632–640
- Caplin N, Willey N (2018) Ionizing radiation, higher plants, and radioprotection: from acute high doses to chronic low doses. *Front Plant Sci* 9:847. <https://doi.org/10.3389/fpls.2018.00847>
- Chanoca A, Kovinich N, Burkel B, Stecha S, Bohorquez-Restrepo A, Ueda T, Eliceiri KW, Grotewold E, Otegui MS (2015) Anthocyanin vacuolar inclusions form by a microautophagy mechanism. *Plant Cell* 27:2545–2559
- Chen L, Liao B, Qi H, Xie LJ, Huang L, Tan WJ, Zhai N, Yuan LB, Zhou Y, Yu LJ, Chen QF, Shu W, Xiao S (2015) Autophagy contributes to regulation of the hypoxia response during submergence in *Arabidopsis thaliana*. *Autophagy* 11:2233–2246

- Chi C, Li X, Fang P, Xia X, Shi K, Zhou Y, Zhou J, Yu J (2020) Brassinosteroids act as a positive regulator of NBR1-dependent selective autophagy in response to chilling stress in tomato. *J Exp Bot* 71:1092–1106
- Colebrook EH, Thomas SG, Phillips AL, Hedden P (2014) The role of gibberellin signalling in plant responses to abiotic stress. *J Exp Biol* 217:67–75
- Ding Y, Ding L, Xia Y, Wang F, Zhu C (2020) Emerging roles of microRNAs in plant heavy metal tolerance and homeostasis. *J Agric Food Chem* 68:1958–1965
- Doelling JH, Walker JM, Friedman EM, Thompson AR, Vierstra RD (2002) The APG8/12-activating enzyme APG7 is required for proper nutrient recycling and senescence in *Arabidopsis thaliana*. *J Biol Chem* 277:33105–33114
- dos Reis SP, Lima AM, de Souza CRB (2012) Recent molecular advances on downstream plant responses to abiotic stress. *Int J Mol Sci* 13:8628–8647
- Embiale A, Hussein A, Husen A, Sahile S, Mohammed K (2016) Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. *J Agron* 15:45–57
- Esnault M-A, Legue F, Chen C (2010) Ionizing radiation: advances in plant response. *Environ Exp Bot* 68(3):231–237
- Fukuda H (1996) Xylogenesis: initiation, progression, and cell death. *Annu Rev Plant Physiol Plant Mol Biol* 47:299–325
- Ganie AH, Yousuf PY, Ahad A, Pandey R, Ahmad S, Aref IM, Iqbal M (2016) Quantification of phenolic acids and antioxidant potential of inbred, hybrid and composite cultivars of maize under different nitrogen regimes. *J Environ Biol* 37(6):1273–1279
- Ganie AH, Ahmad A, Yousuf PY, Pandey R, Ahmad S, Aref IM, Iqbal M (2017) Nitrogen-regulated changes in total amino acid profile of maize genotypes having contrasting response to nitrogen deficit. *Protoplasma* 254(6):2143–2153
- Getnet Z, Husen A, Fetene M, Yemata G (2015) Growth, water status, physiological, biochemical and yield response of stay green sorghum (*Sorghum bicolor* (L.) Moench) varieties—a field trial under drought-prone area in Amhara Regional State, Ethiopia. *J Agron* 14:188–202
- Ghori N, Ghori T, Hayat MQ, Imadi SR, Gul A, Altay V, Ozturk M (2019) Heavy metal stress and responses in plants. *Int J Environ Sci Technol* 16:1807–1828
- Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol Biochem* 48:909–930
- Guillaumot D, Guillon S, Deplanque T, Vanhee C, Gummy C, Masquelier D, Morsomme P, Batoko H (2009) The *Arabidopsis* TSPO-related protein is a stress and abscisic acid-regulated, endoplasmic reticulum-Golgi-localized membrane protein. *Plant J* 60:242–256
- Haak DC, Fukao T, Grene R, Hua Z, Ivanov R, Perrella G, Li S (2017) Multilevel regulation of abiotic stress responses in plants. *Front Plant Sci* 8:1564
- Hachez C, Veljanovski V, Reinhardt H, Guillaumot D, Vanhee C, Chaumont F, Batoko H (2014) The *Arabidopsis* abiotic stress-induced TSPO-related protein reduces cell-surface expression of the aquaporin PIP2;7 through protein-protein interactions and autophagic degradation. *Plant Cell* 26:4974–4990
- Han B, Xu H, Feng Y, Xu W, Cui Q, Liu A (2020) Genomic characterization and expressional profiles of autophagy-related genes (*ATGs*) in oilseed crop castor bean (*Ricinus communis* L.). *Int J Mol Sci* 21:562
- Hanamata S, Sawada J, Ono S, Ogawa K, Fukunaga T, Nonomura K-I, Kimura S, Kurusu T, Kuchitsu K (2020) Impact of autophagy on gene expression and tapetal programmed cell death during pollen development in rice. *Front Plant Sci* 11:172
- Harding TM, Morano KA, Scott SV, Klionsky DJ (1995) Isolation and characterization of yeast mutants in the cytoplasm to vacuole protein targeting pathway. *J Cell Biol* 131:591–602
- He M, He CQ, Ding NZ (2018) Abiotic stresses: general defenses of land plants and chances for engineering multistress tolerance. *Front Plant Sci* 9:1771
- Hofius D, Li L, Hafren A, Coll NS (2017) Autophagy as an emerging arena for plant-pathogen interactions. *Curr Opin Plant Biol* 38:117–123

- Honig A, Avin-Wittenberg T, Ufaz S, Galili G (2012) A new type of compartment, defined by plant-specific Atg8-interacting proteins, is induced upon exposure of Arabidopsis plants to carbon starvation. *Plant Cell* 24:288–303
- Husen A (1997) Impact of air pollution on the growth and development of *Datura innoxia* Mill. M.Sc. Dissertation, Jamia Hamdard, Hamdard Nagar, New Delhi, India
- Husen A (2010) Growth characteristics, physiological and metabolic responses of teak (*Tectona grandis* Linn. f.) clones differing in rejuvenation capacity subjected to drought stress. *Silva Genet* 59:124–136
- Husen A, Iqbal M (2004) Growth performance of *Datura innoxia* Mill. under the stress of coal-smoke pollution. *Ann For* 12:182–190
- Husen A, Ali ST, Mahmooduzzafar, Iqbal M (1999) Structural, functional and biochemical responses of *Datura innoxia* Mill. to coal-smoke pollution. *Proc Acad Environ Biol* 8:61–72
- Husen A, Iqbal M, Aref MI (2014) Growth, water status and leaf characteristics of *Brassica carinata* under drought stress and rehydration conditions. *Braz J Bot* 37:217–227
- Husen A, Iqbal M, Aref IM (2016) IAA-induced alteration in growth and photosynthesis of pea (*Pisum sativum* L.) plants grown under salt stress. *J Environ Biol* 37:421–429
- Husen A, Iqbal M, Aref IM (2017) Plant growth and foliar characteristics of faba bean (*Vicia faba* L.) as affected by indole-acetic acid under water-sufficient and water-deficient conditions. *J Environ Biol* 38:179–186
- Husen A, Iqbal M, Sohrab SS, Ansari MKA (2018) Salicylic acid alleviates salinity-caused damage to foliar functions, plant growth and antioxidant system in Ethiopian mustard (*Brassica carinata* A. Br.). *Agric Food Secur* 7:44
- Husen A, Iqbal M, Khanum N, Aref IM, Sohrab SS, Meshresa G (2019) Modulation of salt-stress tolerance of niger (*Guizotia abyssinica*), an oilseed plant, by application of salicylic acid. *J Environ Biol* 40:94–104
- Hussein M, Embiale A, Husen A, Aref IM, Iqbal M (2017) Salinity-induced modulation of plant growth and photosynthetic parameters in faba bean (*Vicia faba*) cultivars. *Pak J Bot* 49:867–877
- Iqbal M, Jacob M, Mehta S, Mahmooduzzafar (2000) Plant responses to particulate matters suspended in the air. In: Iqbal M, Srivastava PS, Siddiqi TO (eds) *Environmental hazards: plants and people*. CBS Publishers, New Delhi, pp 80–112
- Iqbal M, Mahmooduzzafar, Nighat F, Khan PR (2010) Photosynthetic, metabolic and growth responses of *Triumfetta rhomboidea* to coal-smoke pollution at different stages of plant ontogeny. *J Plant Interact* 5(1):11–19
- Jaspers P, Kangasjärvi J (2010) Reactive oxygen species in abiotic stress signaling. *Physiol Plant* 138:405–413
- Jung H, Lee HN, Marshall RS, Lomax AW, Yoon MJ, Kim J, Kim JH, Vierstra RD, Chung T (2020) Arabidopsis cargo receptor NBR1 mediates selective autophagy of defective proteins. *J Exp Bot* 71:73–89
- Kazan K (2015) Diverse roles of jasmonates and ethylene in abiotic stress tolerance. *Trends Plant Sci* 20:219–229
- Kosová K, Vítámvás P, Urban MO, Prášil IT, Renaut J (2018) Plant abiotic stress proteomics: the major factors determining alterations in cellular proteome. *Front Plant Sci* 9:122
- Lai ZB, Wang F, Zheng ZY, Fan BF, Chen ZX (2011) A critical role of autophagy in plant resistance to necrotrophic fungal pathogens. *Plant J* 66:953–968
- Le Gall H, Philippe F, Domon JM, Gillet F, Pelloux J, Rayon C (2015) Cell wall metabolism in response to abiotic stress. *Plants (Basel)* 4:112–166
- Li F, Vierstra RD (2012) Autophagy: a multifaceted intracellular system for bulk and selective recycling. *Trends Plant Sci* 17:526–537
- Liao CY, Bassham DC (2020) Combating stress: the interplay between hormone signaling and autophagy in plants. *J Exp Bot* 71:1723–1733
- Liu YM, Xiong Y, Bassham DC (2009) Autophagy is required for tolerance of drought and salt stress in plants. *Autophagy* 5:954–963



- Liu Y, Burgos JS, Deng Y, Srivastava R, Howell SH, Bassham DC (2012) Degradation of the endoplasmic reticulum by autophagy during endoplasmic reticulum stress in *Arabidopsis*. *Plant Cell* 24:4635–4651
- Locato V, De Gara L (2018) Programmed cell death in plants: an overview. In: De Gara L, Locato V (eds) *Plant programmed cell death*. Methods in molecular biology, vol 1743. Humana Press, New York, pp 1–8
- Loreti E, van Veen H, Perata P (2016) Plant responses to flooding stress. *Curr Opin Plant Biol* 33:64–71
- Luo L, Zhang P, Zhu R, Fu J, Su J, Zheng J, Wang Z, Wang D, Gong Q (2017) Autophagy is rapidly induced by salt stress and is required for salt tolerance in *Arabidopsis*. *Front Plant Sci* 8:1459
- Majid U, Mahmooduzzafar, Siddiqi TO, Aref IM, Iqbal M (2013) Quantitative changes in proteins, pigments and sennosides of *Cassia angustifolia* Vahl. treated with Mancozeb. *Pak J Bot* 45(5):1509–1514
- Marshall RS, Vierstra RD (2018) Autophagy: the master of bulk and selective recycling. *Annu Rev Plant Biol* 69:173–208
- Masclaux-Daubresse C, Clément G, Anne P, Routaboul JM, Guiboileau A, Soulay F, Shirasu K, Yoshimoto K (2014) Stitching together the multiple dimensions of autophagy using metabolomics and transcriptomics reveals impacts on metabolism, development, and plant responses to the environment in *Arabidopsis*. *Plant Cell* 26:1857–1877
- May AI, Devenish RJ, Prescott M (2012) The many faces of mitochondrial autophagy: making sense of contrasting observations in recent research. *Int J Cell Biol* 431684:1–18
- Miller G, Shulaev V, Mittler R (2008) Reactive oxygen signaling and abiotic stress. *Physiol Plant* 133:481–489
- Moinuddin, Umar S, Iqbal M (2004) Plants in relation to excess of heavy metals. In: Hemantaranjan A (ed) *Advances in plant physiology*. Scientific Publishers, Jodhpur, pp 319–346
- Nahar K, Hasanuzzaman M, Ahamed KU, Hakeem KR, Ozturk M, Fujita M (2015) Plant responses and tolerance to high temperature stress: role of exogenous phytoprotectants. In: Hakeem KR (ed) *Crop production and global environmental issues*. Springer, Cham, pp 385–435
- Nolan TM, Brennan B, Yang M, Chen J, Zhang M, Li Z, Wang X, Bassham DC, Walley J, Yin Y (2017) Selective autophagy of BES1 mediated by DSK2 balances plant growth and survival. *Dev Cell* 41:33–46
- Papini A (2018) Investigation of morphological features of autophagy during plant programmed cell death. In: De Gara L, Locato V (eds) *Plant programmed cell death*. Methods in molecular biology, vol 1743. Humana Press, New York, pp 9–19
- Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. *Curr Opin Plant Biol* 14:290–295
- Podlešáková K, Ugena L, Spíchal L, Doležal K, De Diego N (2019) Phytohormones and polyamines regulate plant stress responses by altering GABA pathway. *New Biotechnol* 48:53–65
- Pu Y, Luo X, Bassham DC (2017) TOR-dependent and -independent pathways regulate autophagy in *Arabidopsis thaliana*. *Front Plant Sci* 8:1204
- Rafferty AE, Zimmer A, Frierson DMW, Startz R, Liu P (2017) Less than 2°C warming by 2100 unlikely. *Nat Clim Chang* 7:637
- Raghavendra AS, Gonugunta VK, Christmann A, Grill E (2010) ABA perception and signalling. *Trends Plant Sci* 15:395–401
- Rexin D, Meyer C, Robaglia C, Veit B (2015) TOR signalling in plants. *Biochem J* 470:1–14
- Sedaghatmehr M, Thirumalaikumar VP, Kamranfar I, Marmagne A, Masclaux-Daubresse C, Balazadeh S (2019) A regulatory role of autophagy for resetting the memory of heat stress in plants. *Plant Cell Environ* 42:1054–1064
- Selinski J, Scheibe R, Day DA, Whelan J (2018) Alternative oxidase is positive for plant performance. *Trends Plant Sci* 23:588–597
- Siddiqi KS, Husen A (2016) Engineered gold nanoparticles and plant adaptation potential. *Nanoscale Res Lett* 11:400

- Siddiqi KS, Husen A (2017a) Plant response to strigolactones: current developments and emerging trends. *Appl Soil Ecol* 120:247–253
- Siddiqi KS, Husen A (2017b) Plant response to engineered metal oxide nanoparticles. *Nanoscale Res Lett* 12:92
- Siddiqi KS, Husen A (2019) Plant response to jasmonates: current developments and their role in changing environment. *Bull Natl Res Cent* 43:153
- Signorelli S, Tarkowski ŁP, Van den Ende W, Bassham DC (2019) Linking autophagy to abiotic and biotic stress responses. *Trends Plant Sci* 24:413–430
- Singh S, Husen A (2019) Role of nanomaterials in the mitigation of abiotic stress in plants. In: Husen A, Iqbal M (eds) *Nanomaterials and plant potential*. Springer, Cham, pp 441–471
- Singh S, Husen A (2020) Behavior of agricultural crops in relation to nanomaterials under biotic and abiotic stress conditions. In: Husen A, Jawaid M (eds) *Nanomaterials for agriculture and forestry applications*. Elsevier Inc., 50 Hampshire St., 5th Floor, Cambridge, MA 02139, USA, pp 219–256
- Slavikova S, Ufaz S, Avin-Wittenberg T, Levanony H, Galili G (2008) An autophagy-associated Atg8 protein is involved in the responses of *Arabidopsis* seedlings to hormonal controls and abiotic stresses. *J Exp Bot* 59:4029–4043
- Sun X, Wang P, Jia X, Huo L, Che R, Ma F (2018a) Improvement of drought tolerance by overexpressing MdATG18a is mediated by modified antioxidant system and activated autophagy in transgenic apple. *Plant Biotechnol J* 16:545–557
- Sun X, Jia X, Huo L, Che R, Gong X, Wang P, Ma F (2018b) MdATG18a overexpression improves tolerance to nitrogen deficiency and regulates anthocyanin accumulation through increased autophagy in transgenic apple. *Plant Cell Environ* 41:469–480
- Svenning S, Lamark T, Krause K, Johansen T (2011) Plant NBR1 is a selective autophagy substrate and a functional hybrid of the mammalian autophagic adapters NBR1 and p62/SQSTM1. *Autophagy* 7:993–1010
- Tang J, Bassham DC (2018) Autophagy in crop plants: what's new beyond *Arabidopsis*? *Open Biol* 8:180162
- Thompson AR, Vierstra RD (2005) Autophagic recycling: lessons from yeast help define the process in plants. *Curr Opin Plant Biol* 8:165–173
- Thumm M, Egner R, Koch B, Schlumpberger M, Straub M, Veenhuis M, Wolf DH (1994) Isolation of autophagocytosis mutants of *Saccharomyces cerevisiae*. *FEBS Lett* 349:275–280
- Todde V, Veenhuis M, van der Klei IJ (2009) Autophagy: principles and significance in health and disease. *Biochim Biophys Acta* 1792:3–13
- Tsukada M, Ohsumi Y (1993) Isolation and characterization of autophagy-defective mutants of *Saccharomyces cerevisiae*. *FEBS Lett* 333:169–174
- Umar S, Anjum NA, Ahmad P, Iqbal M (2018) Drought-induced changes in growth, photosynthesis, and yield traits in mungbean: role of potassium and sulfur nutrition. In: Ozturk M, Hakeem KR, Ashraf M, Ahmad MSA (eds) *Crop production technologies for sustainable use and conservation: physiological and molecular advances*. Apple Academic Press, Waretown, pp 79–89
- Vanhee C, Zapotoczny G, Masquelier D, Ghislain M, Batoko H (2011) The *Arabidopsis* multi-stress regulator TSPO is a heme binding membrane protein and a potential scavenger of porphyrins via an autophagy-dependent degradation mechanism. *Plant Cell* 23:785–805
- Wang Y, Cai S, Yin L, Shi K, Xia X, Zhou Y, Yu J, Zhou J (2015) Tomato HsfA1a plays a critical role in plant drought tolerance by activating ATG genes and inducing autophagy. *Autophagy* 11:2033–2047
- Wang P, Sun X, Jia X, Wang N, Gong X, Ma F (2016) Characterization of an autophagy-related gene *MdATG8i* from apple. *Front Plant Sci* 7:720
- Wang P, Sun X, Jia X, Ma F (2017) Apple autophagy-related protein MdATG3s afford tolerance to multiple abiotic stresses. *Plant Sci* 256:53–64
- Xiong Y, Contento AL, Nguyen PQ, Bassham DC (2007) Degradation of oxidized proteins by autophagy during oxidative stress in *Arabidopsis*. *Plant Physiol* 143:291–299

- Yang X, Srivastava R, Howell SH, Bassham DC (2016) Activation of autophagy by unfolded proteins during endoplasmic reticulum stress. *Plant J* 85:83–95
- Yang M, Bu F, Huang W, Chen L (2019) Multiple regulatory levels shape autophagy activity in plants. *Front Plant Sci* 10:532
- Yoshimoto K (2012) Beginning to understand autophagy, an intracellular self-degradation system in plants. *Plant Cell Physiol* 53:1355–1365
- Yoshimoto K, Shibata M, Kondo M, Oikawa K, Sato M, Toyooka K, Shirasu K, Nishimura M, Ohsumi Y (2014) Organ-specific quality control of plant peroxisomes is mediated by autophagy. *J Cell Sci* 127:1161–1168
- Yousuf PY, Ahmad A, Aref IM, Ozturk M, Hemant, Ganie AH, Iqbal M (2016a) Salt-stress-responsive chloroplast proteins in *Brassica juncea* genotypes with contrasting salt tolerance and their quantitative PCR analysis. *Protoplasma* 253:1565–1575
- Yousuf PY, Ahmad A, Ganie AH, Iqbal M (2016b) Salt stress-induced modulations in the shoot proteome of *Brassica juncea* genotypes. *Environ Sci Pollut Res* 23:2391–2401
- Yu J, Zhen X, Li X, Li N, Xu F (2019) Increased autophagy of rice can increase yield and nitrogen use efficiency (NUE). *Front Plant Sci* 10:584
- Zhen X, Li X, Yu J, Xu F (2019) *OsATG8c*-mediated increased autophagy regulates the yield and nitrogen use efficiency in rice. *Int J Mol Sci* 20:4956
- Zhou J, Wang J, Cheng Y, Chi YJ, Fan B, Yu JQ, Chen Z (2013) NBR1-mediated selective autophagy targets insoluble ubiquitinated protein aggregates in plant stress responses. *PLoS Genet* 9:e1003196
- Zhou J, Wang J, Yu JQ, Chen Z (2014) Role and regulation of autophagy in heat stress responses of tomato plants. *Front Plant Sci* 5:174
- Zhou W, Chen F, Meng Y, Chandrasekaran U, Luo X, Yang W, Shu K (2020) Plant waterlogging/flooding stress responses: from seed germination to maturation. *Plant Physiol Biochem* 148:228–236
- Zhu JK (2001) Cell signaling under salt, water and cold stresses. *Curr Opin Plant Biol* 4:401–406
- Zhu T, Zou L, Li Y, Yao X, Xu F, Deng X, Zhang D, Lin H (2018) Mitochondrial alternative oxidase dependent autophagy involved in ethylene mediated drought tolerance in *Solanum lycopersicum*. *Plant Biotechnol J* 16:2063–2076

# Abscisic Acid and Plant Response Under Adverse Environmental Conditions



**Jorge Gonzalez-Villagra, Carla Figueroa, Ana Luengo-Escobar, Melanie Morales, Claudio Inostroza-Blancheteau, and Marjorie Reyes-Díaz**

## Abbreviations

A	Photosynthetic rate
AAO3	Abscisic-aldehyde oxidase
AAO3	Aldehyde oxidase 3
ABA	Abscisic acid
ABCG	ATP-Binding Cassette subfamily G
ABI1	ABA-insensitive1
ABI2	ABA-insensitive2

---

J. Gonzalez-Villagra · C. Inostroza-Blancheteau  
Departamento de Ciencias Agropecuarias y Acuícolas, Facultad de Recursos Naturales,  
Universidad Católica de Temuco, Temuco, Chile

Núcleo de Investigación en Producción Alimentaria, Facultad de Recursos Naturales,  
Universidad Católica de Temuco, Temuco, Chile

C. Figueroa  
Carrera de Bioquímica, Facultad de Ingeniería y Ciencias, Universidad de La Frontera,  
Temuco, Chile

A. Luengo-Escobar  
Center of Plant, Soil Interaction and Natural Resources Biotechnology, Scientific and  
Technological Bioresource Nucleus (BIOREN-UFRO), Universidad de La Frontera,  
Temuco, Chile

M. Morales  
Department of Evolutionary Biology, Ecology and Environmental Sciences,  
Faculty of Biology, University of Barcelona, Barcelona, Spain

M. Reyes-Díaz (✉)  
Center of Plant, Soil Interaction and Natural Resources Biotechnology, Scientific  
and Technological Bioresource Nucleus (BIOREN-UFRO), Universidad de La Frontera,  
Temuco, Chile

Departamento de Ciencias Químicas y Recursos Naturales, Facultad de Ingeniería y Ciencias,  
Universidad de La Frontera, Temuco, Chile  
e-mail: [marjorie.reyes@ufrontera.cl](mailto:marjorie.reyes@ufrontera.cl)

AIT1	(ABA)-importing transporter 1
ALMT1	Aluminum-activated malate transporter 1
APX	Ascorbate peroxidase
BAM1-3	Barely any meristem 3
bZIP	Basic leucine zipper
CLE	Clavata3/embryo-surrounding region-related
CPKs	Ca <sup>2+</sup> -dependent protein kinases
DREB/CBF	Dehydration-responsive element binding/core binding factor
DTX	Detoxification efflux carriers
E	Transpiration rate
ERF	Ethylene responsive factor
GPx	Glutathione peroxidase
GR	Glutathione reductase
gs	Stomatal conductance
HAB1	Hypersensitive to ABA1
IRT1	Iron-regulated transporter 1
LCYb	Lycopene $\beta$ -cyclase
LEA	Late embryogenesis abundant
MATE1	Multidrug and toxin extrusion protein 1
MCSU	Molybdenum cofactor sulfurase
MDA	Malondialdehyde
MEP	Methylerythritol phosphate
NCED3	Nine- <i>cis</i> -epoxycarotenoid dioxygenase 3
NPF	Nitrate peptide transporter
ORE1	ORESARA1
P5CS	Pyrroline-5-carboxylate synthetase
PP2Cs	2C Protein phosphatases
PYR/PYL/RCAR	Pyrabactin resistance/pyrabactin resistance-like/regulatory component of ABA receptors
RCAR	Regulatory component of ABA receptor
ROS	Reactive oxygen species
SAG12	Senescence associated gene12
SDR/ABA2	Short-chain alcohol dehydrogenase/reductase
SnRK2s	Sucrose nonfermenting 1-related protein kinase type 2
SOD	Superoxide dismutase
UFGT	UDP-glucose:flavonoid 3-Oglucosyl transferase
WOX5	Wuschel related homeobox5
XDH	Xanthine dehydrogenase
ZEP	Zeaxanthin epoxidase

## 1 Introduction

Climate change impacts have imposed challenges to search tools that allow improving plant growth, development, and crop yield under abiotic stresses (Wani and Kumar 2015; Dar et al. 2017; Sah et al. 2016). Therefore, identifying the mechanisms by which plants respond to the abiotic stresses is one of the critical challenges leading to sustainable agriculture, including the development of climate-smart crops and resilient to climate change (Ma et al. 2015; Sah et al. 2016; Dar et al. 2017). According to several studies, abiotic stresses trigger many physiological, biochemical, and molecular responses, influencing various cellular processes in plants (Wang et al. 2001, 2003; Sah et al. 2016; Dar et al. 2017). To cope abiotic stresses, phytohormones have been proposed as a novel and dynamic engineering approach, which could improve the productivity of plants as they are the key regulators of plant growth and development, mediating environmental stress responses (Sreenivasulu et al. 2012; Sah et al. 2016; Trivedi et al. 2016; Checker et al. 2018). Among phytohormones, abscisic acid (ABA) is the central regulator of abiotic stress resistance in plants, coordinating several functions of plants to cope with different stresses (Finkelstein 2013; Wani and Kumar 2015; Sah et al. 2016; Dar et al. 2017). In addition, ABA also plays important roles in the synthesis of biomolecules, embryogenesis, stomatal closure, leaf senescence, germination, seed development, and root architecture (Zeevaart and Creelman 1988; Trivedi et al. 2016).

Under osmotic stress, ABA stimulates short-term responses as stomatal closure, regulating water balance and long-term growth responses, regulating stress-responsive genes in plants (Sah et al. 2016; Trivedi et al. 2016; Dar et al. 2017). The ABA level significantly increases via ABA biosynthesis under environmental stress conditions, changing gene expression and physiological responses (Kim et al. 2010; Dar et al. 2017), showing induction in the level of the enzymes associated with ABA biosynthesis and relative induction in mRNA leading to ABA accumulation. On the other hand, the upregulation of expression levels of several ABA synthesis genes like *zeaxanthin epoxidase (ZEP)*, *aldehyde oxidase (AAO3)*, *9-cis-epoxycarotenoid dioxygenase (NCED3)*, and *molybdenum cofactor sulfurase (MCSU)* have been studied under stress conditions, which can be expressed either through an ABA-dependent or ABA-independent pathway (Dar et al. 2017). The major transcription factor families such as bZIP, MYB, MYC, NAC, ERF, and DREB/CBF further control their regulation (Verma et al. 2016). Thus, the role of ABA in stress response has been extensively studied and reviewed (Hashiguchi and Komatsu 2016; Sah et al. 2016; Verma et al. 2016; Dar et al. 2017); therefore, the chapter attempts to underline the biosynthesis, signaling, and transport of ABA and its role in different physiological, biochemical, and molecular responses of plants under adverse environmental conditions.