Plant in Challenging Environments 3

Dharmendra K. Gupta
José Manuel Palma *Editors*

Plant Growth and Stress Physiology

Springer

Plant in Challenging Environments

Volume 3

Series Editors

Dharmendra K. Gupta, Ministry of Environment, Forests and Climate,
New Delhi, India
José Manuel Palma, Estación Experimental del Zaidín, Granada, Granada, Spain
Francisco J. Corpas, Estación Experimental del Zaidín, Granada, Spain

This book series provides recent advancements in wide areas related to higher plants and how they adapt/evolve under environmental changes in a scenario of climate change. It investigates plants under the complementary point of views, including agronomy aspects (vegetables and fruits), nutrition and health (food security), “omics,” epigenetics, contamination by heavy metals, environmental stresses (salinity, drought, high and low temperatures), interaction with beneficial or pathogenic microorganisms, and application of exogenous molecules (nitric oxide, melatonin, chitosan, silicon, etc.) to palliate negative effects. It also includes changes due to climatic condition (high/low rainfall) taking into account that the climate change is often the reason why plants evolve in a challenging environment.

This book series also covers molecular-/cellular-level responses of plants under different climatic reasons. Families of molecules derived from hydrogen peroxide (H_2O_2), nitric oxide (NO) and hydrogen sulfide (H_2S) designated as reactive oxygen, nitrogen and sulfur species (ROS, RNS and RSS, respectively) are included since, depending on the production level, they function both as signal molecules and as a mechanism of response against adverse/changing environmental conditions that can produce multiple cellular damages, alter the redox state or even trigger cell death. During these ensued metabolic processes, some anti-oxidative/oxidative enzymes are also disturbed or triggered abruptly, but there are adequate mechanisms of regulation/homeostasis in the different subcellular compartments to keep these enzymes under control.

In the last decades, the progression in this field has been enormous, but still there is so much in this field to understand the plethora of phenomena behind.

More information about this series at http://www.springer.com/series/16619

Dharmendra K. Gupta • José Manuel Palma
Editors

Plant Growth and Stress Physiology

Springer

Editors
Dharmendra K. Gupta
Ministry of Environment, Forests and Climate Change
New Delhi, India

José Manuel Palma
CSIC
Estación Experimental del Zaidín
Granada, Spain

ISSN 2730-6194 ISSN 2730-6208 (electronic)
Plant in Challenging Environments
ISBN 978-3-030-78419-5 ISBN 978-3-030-78420-1 (eBook)
https://doi.org/10.1007/978-3-030-78420-1

© 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 license 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

Preface

Plants are sessile organisms that have adapted continuously their physiology to a changing environment to ensure their survivor. It implicates a versatile metabolism which allow plants to face-threatening situations such as salinity, drought, flooding, high and low temperatures, radiation, contamination by heavy metals and metalloids (Cd, Hg, Pg, As, and others) and xenobiotics from diverse nature, pests and other pathogens.

All these perspectives make necessary a good knowledge of how plants function under normal conditions and which mechanisms and strategies are used by them to cope with the above unfavorable conditions. Of course, this implies a global view of each species in its surrounding medium where climatologic conditions may drive the final response of the plant. This gains relevance in a scenario of climate change already installed on our planet.

Such knowledge will be decisive to improve our crops and to face the dramatic situations of millions of people who still suffer hunger. More and better Agriculture is indispensable to provide the necessary amount and quality of food for those people who find in the scientific community an ally to solve their nutritional needs. Especially, when contamination, increasing temperatures of the planet, and elevated costs of design agriculture may impose some asymmetric distribution of wealth.

This book compiles much science on “Plant Growth and Stress Physiology”, and provides substantial knowledge on how plants reorganize their metabolism to adapt to unwanted conditions. It means acclimation, but the term resilience is used increasingly to describe how plants not only adapt but also finally get benefit from hostile conditions. A team of good experts from all over the world have contributed to update many issues regarding plant growth and stress physiology in this volume.

Thus, general aspects of the growth and development of plants and their adaptation to unfavorable conditions will be addressed. Several situations which impose to plants stressful situations such as water deficit and contamination by heavy metals, and how plants deal with them (accumulation and phytoremediation strategies), will be also depicted in this book. The molecular sensing mechanisms and those which involve cross-talk and signaling events (nitric oxide and hydrogen peroxide) within the plant tissues and with their surroundings, especially with the bacterial community in the rhizosphere are also subject of the present work. Finally, practices to improve yield and quality of plant products through either management of plant-associated microorganisms, organic fertilization or revegetation will be visited as well.

The target of this book is not only experts in plant biology and the overall scientific community but also teachers and students from any discipline since it has been written by authors with expertise in their scientific field and in disseminating science. The editors are deeply acknowledged to all of them and want to also highlight their enthusiasm and disinterested availability with this work at any time.

New Delhi, India — Dharmendra K. Gupta

Granada, Spain — José M. Palma

Contents

Chapter 1
Plant Stress, Acclimation, and Adaptation: A Review

**Anindita Mitra, Sampriti Kataki, Aditya N. Singh, Apoorva Gaur,
B. H. N. Razafindrabe, Piyush Kumar, Soumya Chatterjee,
and Dharmendra K. Gupta**

Abstract Plant stress impacts a detrimental effect on growth. Stress component may be promoted by either abiotic (physical, chemical or environmental) or biotic (biological agents or pathogen) factors. Stresses are the important reason for persistent losses in the agrarian produces which badly affects the biomass production and survivability in most crops. Heavy metals activate a wide range of physiological and metabolic variations affecting the enzymatic processes. To counteract the stress, plants develop strategies like accumulating organic compounds, solutes, osmolytes, stress proteins and detoxifying enzymes. Diverse signalling pathways/genes regulating the response of plants against abiotic and biotic stress are contributing to stress responses. This review represents plant stress tolerance in general based on the up-to-date research data.

Keywords Heavy metal · Metallothiothein · Stress proteins · Abiotic · Pathogen

---

A. Mitra
Bankura Christian College, Bankura, West Bengal, India

S. Kataki · S. Chatterjee
Defence Research Laboratory, DRDO, Tezpur, Assam, India

A. N. Singh · A. Gaur · D. K. Gupta (✉)
Ministry of Environment, Forest and Climate Change, Indira Paryavaran Bhavan, Aliganj,
New Delhi, India
e-mail: gupta.dharmendra@gov.in

B. H. N. Razafindrabe
Faculty of Agriculture University of the Ryukyus, Okinawa, Japan

P. Kumar
Paryavaran Complex, New Delhi, India

D. K. Gupta, J. M. Palma (eds.), *Plant Growth and Stress Physiology*, Plant in
Challenging Environments 3, https://doi.org/10.1007/978-3-030-78420-1_1

1.1 Introduction

Plant stresses may be defined as any detrimental impact on plant growth and development, triggered by either an environmental or biological factor, or by both. Plants undergo a range of biotic and abiotic stresses due to ever-changing climatic conditions such as global warming, sporadic but heavy rainfall and exhaustion of productive land and water resources (Ahmad et al. 2019). Abiotic stresses enforced upon plants may be sourced either from physical or chemical environmental factors and biotic stresses are imposed by any biological agents and pathogen (Verma et al. 2013). Injuries caused by mild stress for a short duration can be overcome by plants while severe stresses for a longer duration lead to several hazardous effects such as delayed or hindered flowering and fruit setting, seed formation and enhanced senescence (Verma et al. 2013). Abiotic stresses are also reported to promote outbreaks of pests, pathogens, insects and weeds (Ziska et al. 2010; Peters et al. 2014; Ahmad et al. 2019). However, in natural field condition, plants generally confront collateral abiotic stresses such as drought and salinity or drought and heat that are more pernicious to global crop production. Ample evidences are available on the cross-tolerance of plants to a diversity of abiotic stresses (Hossain et al. 2018; Harshavardhan et al. 2018; Shiri et al. 2015). Plant responses to different abiotic stresses follow common signalling pathways and hence plants tolerant to one type of abiotic stress become acclimatized to other different types of abiotic stresses, known as cross-tolerance (Zhu 2016). Apart from encountering a range of abiotic stresses, plants also experience several biotic stresses, commonly through pathogens (fungi, virus, bacteria, nematodes), pest (insects, mites) or herbivore attack concomitantly or consecutively (Ahmad et al. 2019). The causative agents for biotic stresses endorse various types of diseases, infections and damage to plants and thus impose a great pressure on plant productivity (Gull et al. 2019).

Plants may encounter a single (only one stress), multiple individuals (two or more stresses occurring without any overlap), concurrent (two or more stresses occurring simultaneously with a little overlap), and repetitive stresses (single stress or multiple stresses followed by recovery periods, last for shorter or longer duration) depending on the number of interacting factors (Ahmad et al. 2019). However, the tolerance capacity of the plants towards multiple stress factors may either improve or predispose the plant toward a wide range of stresses (Ahmad et al. 2019). For example, concurrent drought and cold stress in North China results in a severe reduction in the productivity of *Vitis vinifera* (Su et al. 2015). Similarly, plants confronted with concurrent biotic stresses (such as combinations of fungal and bacterial attack) are more acutely mutilated than by individual pathogen infection (Lamichhane and Venturi 2015). The effects of abiotic stresses in plants may impart positive or negative impacts in developing susceptibility or resistance to biotic stresses such as powdery mildew, rust, and wilt depending on the timing and severity of drought and/or salinity stress. Niakoo et al. (2019) reported that a diverse set of gene expression is upregulated in response to concurrent stresses to produce secondary metabolites (e.g. phenolics) to mitigate the effects of a broad range of stresses. Plants also express distinctive responses in addition to general responses and also can modify their responses to concurrent stress factors. This chapter aims to summarize the different stresses in plants and the general response of plants to these stresses to cope up.

1.2 Stresses in Plants

Different types of environmental factors like drought, salinity, high concentration of heavy metals in soil, and extreme heat are the major abiotic stresses that prevail in modern agriculture. Reduction in crop yield of about 50–70% has been attributed to abiotic stresses depending upon the intensity and duration of stresses, type of plant and the phase of growth (Jaleel et al. 2008). Abiotic stresses are the leading cause for persistent losses in the agricultural production throughout the world as it adversely affects the survivability, biomass production, and grain yield in the majority of crops (Athar and Ashraf 2009). Plant responses to different abiotic stresses include altered gene expression, anatomical and morphological changes, attenuated photosynthetic efficiency, reduced nitrogen-fixing capability and modulation in the enzymatic activities related to a metabolic reaction.

Drought or water stress is one of the acute abiotic stresses and is responsible for declined agricultural production worldwide. Drought has a negative impact on plant growth and development and induces loss of membrane integrity, stomatal closure, altered pigment content, osmotic alterations and reduced water retention capacity. It adversely affects photosynthetic activity by limiting CO_2 influx, reduces the accumulation of abscisic acid (ABA), osmolytes proline, mannitol, sorbitol and thus hindering the formation of free radical scavenging compounds (ascorbate, glutathione, α-tocopherol, etc.), suppressing the synthesis of new proteins and mRNAs (Osakabe et al. 2014), reducing carboxylation and efficiency of electron transport chain of the chloroplasts inside the mesophyll cells (Feller and Vaseva 2014).

Salinity is another destructive stress following drought which reduces crop productivity. Soil salinity may be increased due to anthropogenic activities sourced from deforestation, over grassing, water-borne and air-borne salts deposition in soils and chemical contamination. Due to increased salinity, the basic structure of the soil is disrupted with higher sodium content as well as other salts that ensues reduced soil porosity and soil aeration and poor water conductance. Plants exposed to high salt concentration in soil face interference in the process of seed germination, seedling growth and vitality, vegetative growth, flowering and fruit set, leading to lower yield and quality production (Pandey et al. 2020). Salinity induces osmotic stress and ionic toxicity (Munns and Tester 2008; Porcel et al. 2012) as elevated salt in the soil promotes higher osmotic pressure in soil solution than the plant cells, thus, restraining the plant uptake of water and essential minerals (like K, Ca, and Mn) due to creation of water potential deficit zone in the soil (Pandey et al. 2020). Persistent accumulation of salts leads to a further adverse situation called ‘physiological drought’ when plants are unable to uptake water present in the soil (Porcel et al. 2016). Depending on the genotype, adaptability and other physiological features, plants respond differently to the salinity that may be reflected in the plant growth and development. For example, Salt sensitive plants such as *Zea mays*, *Oryza sativa*, *Phaseolus vulgaris*, and *Glycine max* (glycophytes) cannot endure the higher levels of salt concentration, while halophytes, for instance, *Medicago sativa*, *Atriplex amnicola*, and *Lepidium* species can well-flourish in high salinity levels. Osmotically stressed plants express some secondary effects at the physiological, biochemical, and molecular level such as reduced cell expansion, receded membrane function, impaired cytosolic metabolism and increased reactive oxygen species (ROS) production (Mushtaq et al. 2020). Like other stress responses, modulation of enzymatic activities is found under salt stress conditions as proved by the enhanced activities of the antioxidative enzymes like superoxide dismutase, peroxidase, and catalase, as well as of phenylalanine ammonia-lyase and tryptophan decarboxylase (Gao et al. 2008; Mishra et al. 2013). It is assumed that global warming due to anthropogenic emission of CO_2 would worsen the problem of salt stress and desertification (Lavania et al. 2015). In the presence of excess CO_2, the inflated electrons generated can react with O_2, resulting in the formation of detrimental ROS, that causes photoinhibition. The overproduction of ROS ultimately promotes the loss of cellular integrity by imposing pernicious effects on cell membranes and other cell organelles (mitochondria, chloroplasts, and peroxisomes) and major biomolecules like proteins and lipids (Mittler 2002; Ahmad et al. 2008).

Over the last few decades excessive increase of atmospheric CO_2 and CH_4, chlorofluorocarbons and nitrous oxides concentration has triggered negative consequences to global warming. As a result, heat stress has become the primary limiting factor) for crop production and food security worldwide (Friedlingstein et al. 2010; Lobell et al. 2011; Abdelrahman et al. 2017; Hassan et al. 2020). It has been presumed that heat stress has reduced wheat (*Triticum aestivum* L.) global productivity by more than 6% per degree Celsius rise in temperature (Asseng et al. 2015). Although heat stress has some positive impacts on productivity in colder climatic regions (Challinor et al. 2014), it can severely affect different aspects of plant physiology including seed germination, growth, development, photosynthesis and reproduction which ultimately affect total productivity (Hasanuzzaman et al. 2012). Heat stress induces poor seed germination by perturbing the activity of starch digesting enzymes and abscisic acid (ABA) synthesizing enzymes (Essamine et al. 2010) as well as by impairing protein synthesis in seed embryo (Riley 1981). As reported by Akman (2009), the growth of coleoptile was found to stop completely at temperatures above 37 °C. Stunted growth, reduced tiller and dry biomass production were observed in wheat and sugarcane due to heat stress (Mitra and Bhatia 2008; Srivastava et al. 2012). Additionally, heat stress results in various morphological abnormalities such as leaf scorching, sun burning of stems, branches, leaves and twigs, leaf rolling, damage of leaf tips, discoloration of fruits, leaf senescence and abscission (Rodríguez et al. 2005; Omae et al. 2012). Plant growth is hindered due to a reduction in nutrient and water uptake at high temperature (Huang et al. 2012) and restriction of nutrient transport from root to shoot (Huang et al. 2008). The most eminent process in plant physiology, the photosynthesis, is greatly impeded by high temperature. Heat stress promotes abated water content in leaf, compromised stomatal conductance as well as inter-cellular CO_2 concentration (Greer and Weedon 2012). Crucial enzymatic activities related to the photosynthetic process (such as phosphate synthase, ADP-glucose pyrophosphorylase, and invertase) are also curtailed by high temperature leading to reduction of starch production (Djanaguiraman et al. 2009).

Heavy metal (HM) stress is another important abiotic stress in plants that mostly stemmed from anthropogenic processes due to immoderate use of fertilizers, pesticides combined with sewage irrigation, and solid waste from mines, industries, urban activities and agricultural practices (Sharma et al. 2014). Some HMs such as cadmium, lead, chromium, arsenic, mercury, etc. are non-essential elements and do not have any biological role (Chetia et al. 2011). Coupled with essential materials (water, nutrients, minerals) needed for their growth, plants take up non-essential HMs from soil and groundwater through their roots and survive by mitigating the toxic effects through diverse detoxification mechanisms within their system (Singer 2006; Chatterjee et al. 2013). Metal toxicity in organisms is imparted through oxidative stress by the production of excessive free radicals or ROS and intruding the function of essential cellular enzymes (especially in the case of metalloenzymes) (Prasad and Freitas 2003). Plant root rhizosphere plays a significant role in developing metal tolerance, where, soil microflora in the rhizospheric region have the ability to get rid of several contaminants along with HMs from the surroundings by a range of enzymatic processes (Mitra et al. 2017b). Phytotoxicity elicited by different metals triggers a wide range of physiological and metabolic modulations (Villiers et al. 2011). The visible toxic responses of plants induced by different HMs include reduced plant growth, leaf chlorosis, necrosis, turgor loss, poor rate of seed germination, and deformed photosynthetic apparatus, often correlated with progressing senescence processes or with the plant death (Dalcorso et al. 2010).

Combined biotic stresses are very common in plants. For example, brown apical necrosis of *Juglans regia* caused by combined biotic stress from simultaneous attacks by bacterial (*Xanthomonas arboricola*) and fungal (*Fusarium* spp., *Alternaria* spp., *Cladosporium* spp., *Colletotrichum* spp., or *Phomopsis* spp.) pathogens (Belisario et al. 2002). Primarily fungi, bacteria, nematodes and viruses are disease-causing pathogens. Two types of fungal parasites are known viz. *nectrotrophs* that kill host cells by releasing toxins, and *biotrophs* that along with bacteria cause vascular wilts, leaf spots and cankers among other symptoms, and can spread the infection to different parts of the plant body (Gimenez et al. 2018). Nematodes consume the plant cells content and plant-parasitic nematodes are responsible for soil-borne diseases and attack plants' root system. Nematode infection results in nutrient deficiency, wilting or stunting in plants. Viruses cause local lesions and systemic damage that ultimately lead to stunting, chlorosis and malformations affecting different parts of the plant. On the other hand, insects and mites damage plants through feeding or egg-laying or as vectors for transmitting pathogens (Schumann and D'Arcy 2006). Plants exposed to different abiotic and biotic stresses are schematically represented in Fig. 1.1.

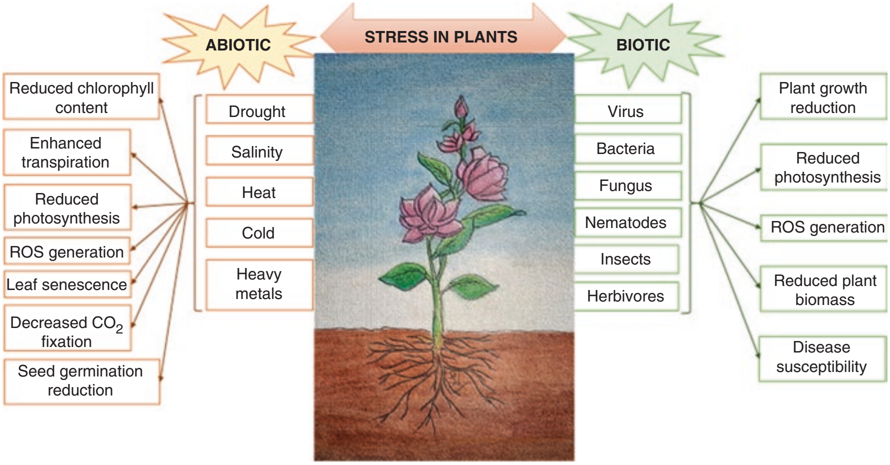

Fig. 1.1 Impact of different abiotic (drought, salinity, heat, cold, heavy metals) and biotic (pathogen, insect pest, herbivores) stresses in plant physiology

1.3 Plant Responses Against Multiple Stressors to Develop Tolerance

The intricate interplay between abiotic and biotic stresses induces complex counter-responses to different stressors in plants for protecting them from multiple aggressors (Pastori and Foyer 2002; Rasmussen et al. 2013). These responses may be through synthesizing secondary metabolites (e.g., alkaloids, terpenoids etc), phytohormones, changes in ion influx, inducing an antioxidative system for combating the stresses by triggering metabolic reprogramming towards defense (Yasuda et al. 2008; Bartoli et al. 2013). The common regulatory pathway under biotic stress and abiotic stress responses of plants are represented in Fig. 1.2.

1.4 Acclimation and Adaptation Against Multiple Stressors Through Different Signalling Pathways

1.4.1 Redox Signalling

A rapid outburst of reactive oxygen species is generally found following different stress exposure in plants triggering oxidative stress (Wojtaszek 1997; Foyer and Noctor 2013). Although ROS are fatal for organisms, the ROS generation is delicately balanced in plants to escape tissue damage for regulating the plant's stress responses (Mori and Schroeder 2004; Choudhury et al. 2013). In plants, low levels of ROS have an important role in cell signalling (acting as second messengers)

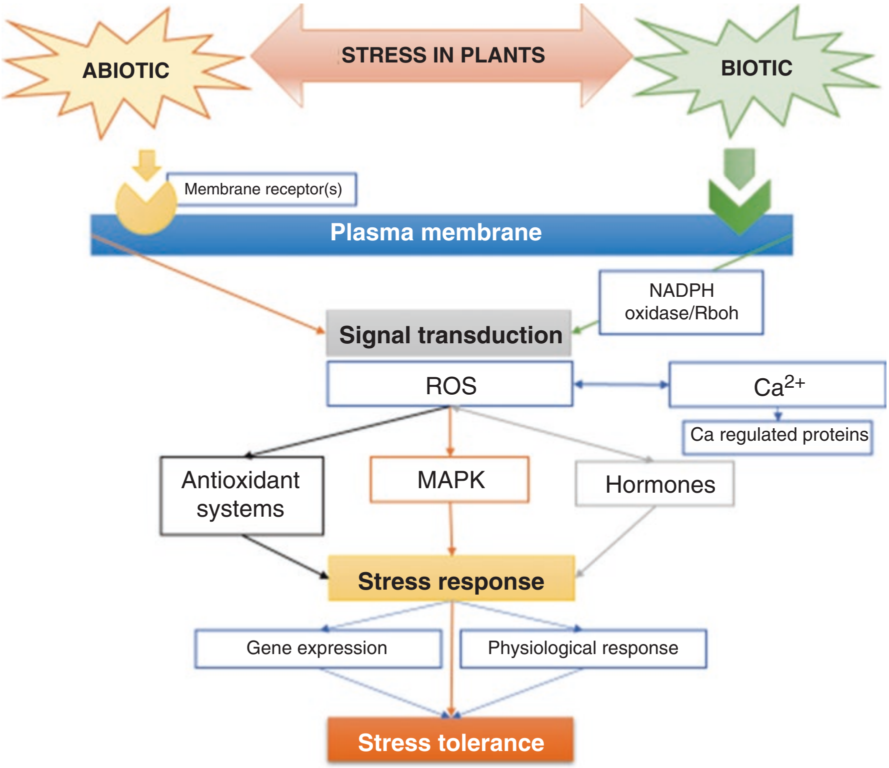

Fig. 1.2 The common signalling pathway under biotic stress and abiotic stress in plants to develop tolerance. Stress-induced ROS generation triggers the activation of the MAPK signalling pathway, phytohormone release and activation of the antioxidant system which in turn alters the gene expression and physiological responses for developing tolerance in plants. (Modified from Wang et al. 2016)

regulating plant stress responses, while high levels are deleterious to the plants (Garg and Manchanda 2009). Abiotic stresses promote ROS production through disbalancing the electron transfer reactions in plants (Gill and Tuteja 2010; Mitra et al. 2017a) while under biotic stress, membrane-bound NADPH oxidases (and NADPH oxidase-like also called respiratory burst oxidase homologs, RBOHs) or peroxidases intentionally induce ROS generation to kill or restrict the pathogen propagation through hypersensitive response (HR) (Zurbriggen et al. 2010). ROS play a significant role in cell signalling under biotic stress. For example, ROS help to increase the drought tolerance in *Arabidopsis thaliana* by inducing *de novo* xylem formation to enhance water flow when infected with the vascular pathogen *Verticillium* spp. (Xia et al. 2009). A crucial role is played by ROS to develop cross-tolerance in plants to combat abiotic and biotic stresses, especially through ABA signalling pathway. In *Arabidopsis,* NADPH oxidase in guard cell, induces *AtrbohD* and *AtrbohF* genes mediating ROS generation leading to ABA-mediated stomatal closure, cytosolic upsurge of Ca^{2+} ion, and HR to pathogen attack (Ichimura et al. 2000; Chinchilla et al. 2007). Another redox signalling mechanism embraces oxidation of glutathione (GSH) pool in association with the rise in total GSH under abiotic stresses, which is considered as one of the key players in H_2O_2-induced heavy metal tolerance (Chandrakar et al. 2016b). In plants, an upsurge of GSH following heavy metal exposure thereby reduces the negative impacts of oxidative damage.

1.4.2 MAP Kinase Pathway

Mitogen-activated protein kinases (MAPKs), which is highly conserved in the eukaryotic system and mediate signal transduction in several cellular processes, are known to be involved in different biotic/abiotic or combined stress responses (Samajova et al. 2013; Rejeb et al. 2014; Ramegowda et al. 2020). In response to heavy metal stress, released ROS play a vital role in activating the MAPK signalling pathway (Chandrakar et al. 2020). Two leading MAPK cascades (MEKK1-MKK4/5-MPK3/6 and MEKK1-MKK2-MPK4/6) involved in both abiotic and biotic stress signaling have been noticed to control the levels of ROS in *A. thaliana* (Pitzschke et al. 2009; Jalmi and Sinha 2015). In Arabidopsis, *GbRLK* gene (receptor-like kinase from *Gossypium barbadense*) was shown to downregulate the stress-responsive genes to combat against salinity and drought by reducing water loss and thus enhancing tolerance (Zhao et al. 2013). Salicylic acid (SA) mediated activation of MAPK pathways following pathogen attack in plants and consequent expression of *PR* genes for defense reactions has been reported (Xiong et al. 2003). Likewise, protein kinases activated by salicylic acid during salt stress confers osmotic tolerance in Arabidopsis (Feng et al. 2015). Studies by Chinchilla et al. (2007) reported that pathogen-associated molecular patterns (PAMPs) like flagellin stir up MAPK cascades to initiate pathogen response signalling. MAPK signalling synergistically interacts with ROS mediated and ABA signalling pathways to boost up plant defense and to produce cross-acclimation to both abiotic and biotic stress (Lu et al. 2002; Miura and Tada 2014; Zhou et al. 2014). In rice, *MAPKs* (known as *OsMPK5*) are overexpressed to develop the ABA-mediated resistance against the necrotrophic brown spot pathogen *Cochliobolus miyabeanus* and abiotic stress tolerance (De Vleesschauwer et al. 2010). In plants, heavy metal (Cd, Cu, and As) induced activation of MAPKs has been reported by several scientists (Jaspers and Kangasjarvi 2010; Karuppanapandian et al. 2011; Kreslavski et al. 2012; Baxter et al. 2014). In *O. sativa* an increased number of transcripts of *OsMSRMK2* (*OsMPK3* homolog), *OsMSRMK3* (*OsMPK7* homolog), and *OsWJUMK1* (*OsMPK20–4* homolog) under Cu and Cd exposures has been observed (Yeh et al. 2007; Rao et al. 2011).

1.4.3 Role of Phytohormones and Growth Regulators in Stress Signalling Pathway

Plant hormones are known to play important roles in developing tolerance to a range of biotic and abiotic stress in addition to regulating all phases of plant growth and development (Davies 2010; Ramegowda et al. 2020). The specific phytohormones such as (ABA, SA, jasmonic acid (JA), and ethylene (ET) form the baseline pathway that triggers signalling cascade after perceiving the abiotic and biotic stresses (Verma et al. 2016).

ABA is the multifunctional phytohormone involved in different stages of the life cycle in plants and also in the perception of abiotic stress and adverse environmental situation (Bücker-Neto et al. 2017; Sytar et al. 2018). ABA interacts synergistically and antagonistically at different levels regulating both biotic and abiotic stress responses (Fujita et al. 2006). ABA signalling pathway is mediated by ABA receptors namely PYR/PYL/RCAR (pyrabactin resistance 1/PYR1-like regulatory component), phosphatase 2Cs (PP2Cs), and Snf1-related kinases 2 (Klingler et al. 2010). Under Cu and Zn stress, three genes namely *PYL*, *PP2C*, and *SnRK2* are responsible for ABA signal transduction during seed germination in *C. sativus* (Wang et al. 2014). In *O. sativa* Cd and Cu exposure boosted MAPK signalling and ABA level providing increased Cd and Cu tolerance (Yeh et al. 2003, 2004). Similarly, an increased amount of ABA was detected in *Empetrum nigrum* and *Cicer arietinum*, following exposure to Cu and Pb (Monni et al. 2001; Atici et al. 2005). As a secondary effect, increased synthesis of ABA under abiotic stresses triggers the stomatal closure, that prevents the invasion of pathogens through these passive ports (Melotto et al. 2006). Hence, in such circumstances plant develops cross-tolerance against both biotic and abiotic stresses (Lim et al. 2015; Berens et al. 2017). Some plants can regulate the pathogen entry by stomatal movement after detecting microbe-associated molecular patterns (MAMPs) such as flagellin and chitin (Zeng and Hey 2010). For example, In Arabidopsis, tomato and moss (*Physcomitrella patens*), MAMP-triggered stomatal closure was found to be regulated by ABA (Melotto et al. 2017).

SA promotes the development of the systemic acquired resistance (SAR) and regulation of plant defense responses against biotrophic and hemibiotrophic pathogens, while JA and ET mainly control the defense responses against necrotrophic pathogens and insect pest and herbivores attack (Dong 1998). In plants, synthesis of SA is induced in response to pathogen attack and SA signalling is initiated involving its receptors and regulators NPR1 (non-expressor of PR-genes 1), and NPR3 and NPR4 to protect the undamaged part of the plants distant from the site of pathogen attack (broad-spectrum plant defense called SAR) (Dong 1998). Additionally, SA is known to protect the plants against a variety of abiotic stresses like heavy metals, extreme temperature, salinity, osmotic stress, drought, ozone, and

UV-irradiation (Zhang et al. 2015; Nazar et al. 2015; Naser et al. 2014; Khan et al. 2013). For example, in *O. sativa* and *G. max,* following exposure to arsenic (As), the metalloid-exerted oxidative injury is effectively reduced via strengthening the antioxidant defense mechanism (Singh et al. 2015; Chandrakar et al. 2016a). During heavy metal stress, SA reduces the contents of ROS, osmolytes/ionsleakage, and lipid peroxidation reaction, while it augments the total chlorophyll content, total lipids, and linolenic acid (Chandrakar et al. 2020).

The JA signalling is mediated by its receptor (COI1, a F-box protein) and co-ordination of a number of transcription factors [such as Jasmonate Insensitive 1 (JIN1)/MYC2] and ethylene response factor ERF1, ERF2, ERF5, and ERF6 (members of AP2/ERF family)] regulating the JA responsive marker gene plant defensin 1.2 (Deshaies 1999; Moffat et al. 2012). Like other phytohormones, JA is also responsible for plant defense against abiotic stress such as salinity, drought, high or low temperature, heavy metals, ozone, and UV-irradiation (Yan et al. 2015; Hu et al. 2017; Per et al. 2018).

Ethylene, a gaseous hormone that plays vital role in fruit ripening and senescence, is also involved in biotic stress response against necrotrophic, biotrophic, and hemibiotrophic pathogens (Ramegowda et al. 2020). The role of ET in developing resistance in plants against abiotic stress such as cold and freezing, salinity, drought, heavy metal exposure, heat, and flooding has been studied in detail (Kazan 2015). ET signalling is mediated through different ethylene receptors such as ETR1, ETR2, Ethylene Response Sensor 1 (ERS1) and ERS2. These receptors activate a membrane protein Ethylene Insensitive 2 (EIN2). Downstream to the EIN2 are transcription factor EIN3 and Ethylene Insensitive 3-Like 1 (EIL1) in the nucleus triggering the activation of ET responsive genes (Yang et al. 2015). ET acts synergistically with SA, JA, and ABA in the plant's defense against pathogens (Ramegowda et al. 2020). Several authors reported the upsurge in the number of transcripts of ethylene biosynthesis-related genes (*ACS1*, *ACS2*, *ACO4*, and *ACO5*) in the roots of *O. sativa* exposed to Cr, suggesting their involvement in developing Cr resistance (Steffens 2014; Trinh et al. 2014). Likewise, Cd stress in *A. thaliana* was found to induce the ethylene biosynthesis through upregulation of *ACS2* and *ACS6* genes (Schellingen et al. 2014).

Auxin (indole-3-acetic acid, IAA) is an essential phytohormone having manifold activities in regulating the growth and development of plants exposed to various abiotic stresses (Sytar et al. 2018). Srivastava et al. (2013) observed the unaffected growth of *B. juncea* under As stress if IAA applied exogenously. A similar report of the exogenous application of an IAA precursor, L-tryptophan in the *O. sativa* radicles shows improved growth and yield under Cd stress in comparison to seedlings raised without IAA precursor in Cd-contaminated soil (Farooq et al. 2015a, b).

1.5 Tolerance to Heavy Metals

1.5.1 Synthesis of Metal Chelators

One of the sophisticated strategies against metal stress employed by plants is through chelation and sequestration of metals by high-affinity metal binding ligands such as phytochelatins (PCs) and metallothioneins (MTs). PC synthesis is stimulated by a wide range of metal cations (such as Cd, Cu, Zn, Ag, Au, Pb, Hg) and anions (As) due to transpeptidation of (γ-glutamyl-cysteinyl)-glycine from GSH by the action of PC synthase (PCS) (Gasic and Korban 2007). A number of studies have suggested that PC–metal complexes are sequestered into vacuoles (Shukla et al. 2016).

Metallothioneins are low molecular weight Cys-rich peptides present in both animals and plants. They are capable of high-affinity binding with heavy metal ions via Cys residues and play a significant role in essential heavy-metal homeostasis in plants (Sharma et al. 2014). MTs play a vital role in carrying out a series of activities such as sequestration of toxic metals, transportation of Zn and Cu, precluding interaction of toxic metals with other biomolecules, thereby reducing phytotoxicity (Shukla et al. 2016).

1.5.2 Secretion of Organic Acids in Root Exudates

Plants grown in heavy metal contaminated soil secrete organic acids (such as oxalic acid, citric acid, malic acid, tartaric acid and succinic acid) in root exudates for chelating metals to reduce the bioavailability of such toxic metals (Yu et al. 2019). Carboxyl groups present in the organic acids chelate with heavy metals to convert them into non-toxic immobilized form. For example, organic acids in the root exudates of *Phyllostachys pubescens*was was found to precipitate lead and reduce Pb availability to plant (Chen et al. 2016). A significant increase in the secretion of organic acids (about 1.76–2.43 times) in the roots of cadmium-accumulator rice was observed in comparison to Cd-sensitive varieties (Fu et al. 2017).

1.6 Tolerance to Heat Stress

Heat tolerance in plants varies among species and different short term and long-term strategies are adopted by plants to survive under heat stress. The major pathways include ion transport, abundance of late embryogenesis proteins, presence of osmo-protectants, and antioxidant defense system (Rodríguez et al. 2005). Short term mechanisms of heat tolerance in plants are avoidance and acclimation as well as some morphological adaptation such as leaf rolling, small size leaves or alteration in leaf position and lipid composition in the membrane, and cooling through transpiration (Fitter and Hay 2002; Sarieva et al. 2010). Long term morphological changes in response to heat stress include increased density of leaf stomata and hair, and larger vessels (Srivastava et al. 2012). Plants are highly susceptible to a higher temperature during the active growth stages. When exposed to high temperature, plants are capable of reducing the rate of light absorption through small hairs on the leaf blade that act as protective surface cover. Some types of low molecular weight compounds called osmolytes are found to accumulate in plant tissue to develop heat tolerance and increase survival by conserving the cell structure (Hare et al. 1998; Sakamoto and Murata 2002). Different osmolytes such as sugars, proline, ammonium, sulphonium and glycine-betaine compounds are synthesized under heat stress (Sairam and Tyagi 2004). However, osmolyte concentration varies among species and genotypes (Ashraf and Foolad 2007). Similarly, plants also accumulate several secondary metabolites to combat heat stress (different phenolic compounds, such as flavonoids and phenylpropanoids).

1.7 Tolerance to Salt Stress

Regulation of ion homeostasis within the cell is important for the maintenance of membrane potential and proper functioning of the enzymes involved in the metabolic reaction under abiotic stresses (Hasegawa 2013). Plants can efflux the redundant salt ions from cytosol through transporters (H^+-ATPase, vacuolar H^+-ATPase, H^+-Pyrophosphate, and Ca^{2+}-ATPase) to retain low concentration of Na^+ ions within cytosol as high concentrations are deleterious for cell (Farooq et al. 2015a, b). The signalling pathway coordinating the activities of several transporters under salt stress is the ‘salt overly sensitive’ (SOS) stress signalling pathway that involves three proteins, SOS1, SOS2, and SOS3 (a Ca^{2+} ion binding protein and sensor for calcium signal) (Zhu 2003).

1.8 Plant Immune Response Against Biotic Stress

To deal with biotic stresses plants have evolved a well responsive immune system (Gimenez et al. 2018). Passive immunity is the first line of defense in plants which is endorsed by waxy leaf or stem surface, thick cuticles and specialized trichomes to prevent insects or pathogens. Plants also release chemical compounds (secondary metabolites such as phenolics, alkaloids, flavonoids, terpenoids) to safeguard themselves against herbivory and pathogen infection (Taiz and Zeiger 2006). Further, plants possess two levels of pathogen recognition system to trigger immune responses: the first level of recognition involves Pattern Recognition Receptors (PRRs) that recognize pathogen-associated molecular patterns (PAMPs) as described in the previous section, activating PAMP-triggered immunity (PTI)

(Monaghan and Zipfel 2012). In the second level of plant immune response known as effector-triggered immunity (ETI), the key player is a plant resistance protein (PRP), that recognizes specific effectors from pathogens or pests (Avr proteins) and invigorates plant defense mechanisms in a much more specific way (Kaloshian 2004; Spoel and Dong 2012). ETI actually triggers the hypersensitive responses (HR) that consequences to programmed cell death of the infected cells and the surrounding areas (Mur et al. 2007).

1.9 Antioxidant Defense System

Under different abiotic stresses, excess ROS are produced in plants causing oxidative stress. Plants recruit antioxidant system to protect cellular and subcellular compartments from this fatal impact using antioxidant enzymes as well as non-enzymatic compounds.

1.9.1 Enzymatic Antioxidative System

The role of different enzymes acting as ROS scavengers such as superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione reductase (GR), ascorbate peroxidase (APX), and catalase (CAT) to protect cells from the toxic effects of ROS under both abiotic and biotic stresses have been well studied (Samajova et al. 2013).

SODs are members of the metalloenzyme family that safeguards the cells from oxidative stress by catalyzing the dismutation of superoxide radicals ($O_2^{\bullet-}$) to H_2O_2 with the aid of diverse metals as cofactors (Li et al. 2017). Hydrogen peroxide is another highly reactive oxidizing agent later detoxified by CAT and the ascorbate–glutathione cycle, both of which regulate H_2O_2 level (Shigeoka et al. 2002). The tetrameric, heme-containing enzyme CAT is a H_2O_2 scavenger, located exclusively in peroxisomes (Mitra et al. 2018), which rapidly degrades H_2O_2 into water and molecular oxygen without consuming cellular reducing equivalents (Sharma 2012). The presence of a heme prosthetic group has been reported with CAT. APX, an active scavenger of the H_2O_2, are members of class I heme-peroxidases found as different subcellular isoforms catalysing the reduction of H_2O_2 into water and two molecules of monodehydroascorbate (Anjum et al. 2016). GR, which functions in coordination with APX and is broadly located in diverse cell organelles, mediates the reduction of glutathione disulphide (GSSG) to glutathione (GSH) (using NADPH as an electron donor) and sustains a highly reduced state of GSH/GSSG and ascorbate/monodehydroascorbate and thus preserves the redox intracellular level as well during oxidative stress (Anjum et al. 2012). GPX, another member of a large peroxidase family having a broad substrate spectrum, catalyses the reduction of H_2O_2, organic and lipid hydroperoxides using the GSH pool directly as a reducing agent, thereby protecting the cells against oxidative damage (Anjum et al. 2010).

1.9.2 Non-enzymatic Antioxidative System

Plants have a well-developed antioxidative system for combating the adverse environmental stresses by producing low molecular weight thiols, such as GSH, that plays a role in biosynthetic pathways, ROS detoxification of xenobiotics and antioxidant chemistry (Mitra et al. 2018). GSH is a nonprotein thiol synthesized from glutamate (Glu), cysteine (Cys) and glycine (Gly) by two adenosine triphosphate (ATP)-dependent reactions catalysed by gamma-glutamylcysteine synthetase (γ–ECS) and glutathione synthetase (GS). The accumulation of glutathione was observed in different plants exposed to various stresses such as salinity, drought, extreme temperatures (cold and heat), heavy metal toxicity, herbicides and air pollutants (Waśkiewicz et al. 2014).

Ascorbate (AsA), synthesized in mitochondria but commonly found in the stroma of chloroplast, apoplast, cytosol, mitochondria and peroxisomes of the plant cell, is the most copious antioxidant in plants, which reacts with a range of ROS such as H_2O_2, $O_2^{\bullet-}$ and singlet oxygen ($^1O_2$). Ascorbate is the most substantial reducing substrate for the discharge of H_2O_2 via the ascorbate-glutathione cycle (Singh et al. 2006) and restoration of membrane-bound carotenoids and α-tocopherol in plant cells (Sharma 2012). Exogenous application of AsA was found to be effective in alleviating the adverse effects of different abiotic stresses such as salinity, drought by enhancing chlorophyll, carotenoids, proline accumulation, and leaf area, improving water status and soluble protein while decreasing H_2O_2 levels in plant tissue (Akram et al. 2017).

1.10 Conclusion and Future Prospects

Plants are exposed to a variety of stresses including abiotic and biotic stresses throughout their lifetime and accumulate low-molecular-weight organic compounds, compatible solutes or osmolytes, stress-specific proteins, heat-shock proteins, phytochelatins, metallothioneins, and activate many detoxification enzymes to acclimatize under a stressful situation. The thresholds of stress tolerance vary from species to species, and a few of them can successfully thrive under severe stresses completing their life cycles. However, most of the cultivated crop species are highly vulnerable and either dies or becomes less productive after being exposed to long periods of stress. Thus, knowledge about the enhancement of stress tolerance in plants not only presents a challenging basic research problem but could also have a significant impact on the benefit of agricultural productivity. Recent researches are gaining insight into the different signalling pathways/genes that regulate the plants response to abiotic and biotic stress and are directly or indirectly associated with multiple stress responses. These association may be synergistic or antagonistic in action leading to developing cross-tolerance. Furthermore, the integration of multiple omics (such as transcriptomics, proteomics or metabolomics) technologies will be very helpful to find a broad and precise view about the regulatory hubs in developing stress tolerance in plants in the near future.

References

Abdelrahman M, El-Sayed M, Jogaiah S, Burritt DJ, Tran L (2017) The stay-green trait and phytohormone signaling networks in plants under heat stress. Plant Cell Rep 36:1009–1025

Ahmad P, Sarwat M, Sharma S (2008) Reactive oxygen species, antioxidants and signaling in plants. J Plant Biol 51:167–173

Ahmad B, Raina A, Khan S (2019) Impact of biotic and abiotic stresses on plants, and their responses. In: Wani S (ed) Disease resistance in crop plants. Springer, pp 1–19

Akman Z (2009) Comparison of high temperature tolerance in maize, rice and sorghum seeds, by plant growth regulators. J Anim Vet Adv 8:358–336

Akram NA, Shafiq F, Ashraf M (2017) Ascorbic acid-a potential oxidant scavenger and its role in plant development and abiotic stress tolerance. Front Plant Sci 8:613

Anjum NA, Umar S, Chan MT (2010) Ascorbate-glutathione pathway and stress tolerance in plants. Springer, Dordrecht

Anjum NA, Ahmad I, Mohmood I, Pacheco M, Duarte AC, Pereira E, Umar S, Ahmad A, Khan NA, Iqbal M, Prasad MN (2012) Modulation of glutathione and its related enzymes in plants' responses to toxic metals and metalloids – a review. Environ Exp Bot 75:307–324

Anjum NA, Sharma P, Gill SS, Hasanuzzaman M, Khan EA, Kachhap K, Mohamed AA, Thangavel P, Devi GD, Vasudhevan P, Sofo A (2016) Catalase and ascorbate peroxidase-representative H_2O_2-detoxifying heme enzymes in plants. Environ Sci Pollut Res 23:19002–19029

Ashraf M, Foolad MR (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot 59:206–216

Asseng S, Ewert F, Martre P, Rotter RP, Lobell DB, Cammarano D, Kimball BA, Ottman MJ, Wall GW, White JW, Reynolds MP (2015) Rising temperatures reduce global wheat production. Nat Clim Chang 5:143–147

Athar HR, Ashraf M (2009) Strategies for crop improvement against salinity and drought stress: an overview. In: Ashraf M, Ozturk M, Athar H (eds) Salinity and Water Stress. Springer, Dordrecht, pp 1–16

Atici Ö, Agar G, Battal P (2005) Changes in phytohormone contents in chickpea seeds germinating under lead or zinc stress. Biol Plant 49:215–222

Bartoli CG, Casalongué CA, Simontacchi M, Márquez-García B, Foyer CH (2013) Interactions between hormone and redox signaling pathways in the control of growth and cross-tolerance to stress. Environ Exp Bot 94:73–88

Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signaling. J Exp Bot 65:1229–1240

Belisario A, Maccaroni M, Corazza L, Balmas V, Valier A (2002) Occurrence and etiology of brown apical necrosis on Persian (English) walnut fruit. Plant Dis 86:599–602

Berens ML, Berry HM, Mine A, Argueso CT, Tsuda K (2017) Evolution of hormone signaling networks in plant defense. Annu Rev Phytopathol 55:401–425

Bücker-Neto L, Paiva ALS, Machado RD, Arenhart RA, Margis-Pinheiro M (2017) Interactions between plant hormones and heavy metals responses. Genet Mol Biol 40:373–386

Challinor AJ, Watson J, Lobell DB, Howden SM, Smith DR, Chhetri N (2014) A meta-analysis of crop yield under climate change and adaptation. Nature Clim Change 4:287–291

Chandrakar V, Naithani SC, Keshavkant S (2016a) Arsenic-induced metabolic disturbances and their mitigation mechanism in crop plants: a review. Biologia 71:367–377

Chandrakar V, Dubey A, Keshavkant S (2016b) Modulation of antioxidant enzymes by salicylic acid in arsenic exposed *Glycine max* L. J Soil Sci Plant Nutr 16:662–676

Chandrakar V, Yadu B, Xalxo R, Kumar M, Keshavkant S (2020) Mechanisms of plant adaptation and tolerance to metal/metalloid toxicity. In: Hasanuzzaman M (ed) Plant ecophysiology and adaptation under climate change: mechanisms and perspectives II. Springer, Singapore, pp 107–135

Chatterjee S, Datta S, Halder Mallick P, Mitra A, Veer V, Mukhopadhyay SK (2013) Use of wetland plants in bioaccumulation of heavy metals. In: Gupta DK (ed) Plant-based remediation processes. Edited by Springer-Verlag, Berlin, Heidelberg, pp 117–139

Chen J, Shafi M, Wang Y (2016) Organic acid compounds in root exudation of Moso bamboo (*Phyllostachys pubescens*) and its bioactivity as affected by heavy metals. Environ Sci Pollut Res Int 23:20977–20984

Chetia M, Chatterjee S, Banerjee S, Nath MJ, Singh L, Srivastava RB, Sarma HP (2011) Groundwater arsenic contamination in Brahmaputra river basin: a water quality assessment in Golaghat (Assam), India. Environ Monit Assess 173:371–385

Chinchilla D, Zipfel C, Robatzek S, Kemmerling B, Nürnberger T, Jones JD, Felix G, Boller T (2007) Flagellin-induced complex of the receptor FLS2 and BAK1 initiates plant defence. Nature 448:497–500

Choudhury S, Panda P, Sahoo L, Panda SK (2013) Reactive oxygen species signalling in plants under abiotic stress. Plant Signal Behav 8:e23681

Dalcorso G, Farinati S, Furini A (2010) Regulatory networks of cadmium stress in plants. Plant Signal Behav 5:1–5

Davies PJ (2010) The plant hormones: their nature, occurrence, and functions. In: Davies PJ (ed) Plant hormones. Springer, pp 1–15

De Vleesschauwer D, Yang Y, Cruz CV, Hofte M (2010) Abscisic acid-induced resistance against the brown spot pathogen *Cochliobolus miyabeanus* in rice involves MAP kinase-mediated repression of ethylene signaling. Plant Physiol 152:2036–2052

Deshaies RJ (1999) SCF and Cullin/Ring H_2-based ubiquitin ligases. Annu Rev Cell Dev Biol 15:435–467

Djanaguiraman M, Sheeba JA, Devi DD, Bangarusamy U (2009) Cotton leaf senescence can be delayed by nitrophenolate spray through enhanced antioxidant defense system. J Agron Crop Sci 195:213–224

Dong X (1998) SA, JA, ethylene, and disease resistance in plants. Curr Opin Plant Biol 1:316–323

Essamine J, Ammar S, Bouzid S (2010) Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussion and mechanisms of defense. J Biol Sci 10:565–572

Farooq H, Asghar HN, Khan MY, Saleem M, Zahir ZA (2015a) Auxin-mediated growth of rice in cadmium-contaminated soil. Turk J Agric For 39:272–276

Farooq M, Hussain M, Wakeel A, Siddique KHM (2015b) Salt stress in maize effects resistance mechanisms and seedling vigor as affected by seed priming in coarse rice. Can J Bot 84:1196–1202

Feller U, Vaseva II (2014) Extreme climatic events: impacts of drought and high temperature on physiological processes in agronomically important plants. Front Environ Sci 2:39

Feng J, Li J, Lavania Z, Lu Y, Yu J, Zheng Q, Yan S, Zhang W, He H, Ma L (2015) SKIP confers osmotic tolerance during salt stress by controlling alternative gene splicing in Arabidopsis. Mol Plant 8:1038–1052

Fitter AH, Hay RK (2002) Environmental physiology of plants, 3rd edn. Academic, London

Foyer CH, Noctor G (2013) Redox signaling in plants. Antioxid Redox Signal 18:2087–2090

Friedlingstein P, Houghton RA, Marland G, Hackler J, Boden TA, Conway TJ, Canadell JG, Raupach MR, Ciais P, Le Quéré C (2010) Update on CO_2 emissions. Nat Geosci 3(12):811–812

Fu H, Yu H, Li T, Zhang X (2017) Influence of cadmium stress on root exudates of high cadmium accumulating rice line (*Oryza sativa* L.). Ecotoxicol Environ Saf 150:168–175

Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 9:436–442

Gao S, Ouyang C, Wang S, Xu Y, Tang L, Chen F (2008) Effects of salt stress on growth, antioxidant enzymeand phenylalanine ammonia-lyase activities in *Jatropha curcas* L. seedlings. Plant Soil Environ 54:374–381

Garg N, Manchanda G (2009) ROS generation in plants: boon or bane? Plant Biosyst 143:81–96

Gasic K, Korban SS (2007) Transgenic Indian mustard (*Brassica juncea*) plants expressing an *Arabidopsis* phytochelatin synthase (*AtPCS1*) exhibit enhanced As and Cd tolerance. Plant Mol Biol 64:361–369

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Gimenez E, Salinas M, Manzano-Agugliaro F (2018) Worldwide research on plant defense against biotic stresses as improvement for sustainable agriculture. Sustainability 2:391

Greer DH, Weedon MM (2012) Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate. Plant Cell Environ 35:1050–1064

Gull A, Lone AA, Wani NU (2019) Biotic and abiotic stresses in plants. In: De Oliveira A (ed) Abiotic and biotic stress in plants. Intech Open, London

Hare PD, Cress WA, Staden JV (1998) Dissecting the roles of osmolyte accumulation during stress. Plant Cell Environ 21:535–553

Harshavardhan VT, Govind G, Kalladan R, Sreenivasulu N, Hong CY (2018) Cross-protection by oxidative stress: improving tolerance to abiotic stresses including salinity. In: Kumar V, Wani SH, Suprasanna P, LSP T (eds) Salinity responses and tolerance in plants, vol 1. Springer, pp 283–305

Hasanuzzaman M, Nahar K, Alam MM, Fujita M (2012) Exogenous nitric oxide alleviates high temperature induced oxidative stress in wheat (*Triticum aestivum* L.) seedlings by modulating the antioxidant defense and glyoxalase system. Aust J Crop Sci 6:1314–1323

Hasegawa PM (2013) Sodium (Na^+) homeostasis and salt tolerance of plants. Environ Exp Bot 92:19–31

Hassan MU, Chattha MU, Khan I, Chattha MB, Barbanti L, Aamer M, Iqbal MM, Nawaz M, Mahmood A, Ali A, Aslam MT (2020) Heat stress in cultivated plants: nature, impact, mechanisms, and mitigation strategies—a review. Plant Biosyst 3:1–24

Hossain MA, Li Z-G, Hoque TS, Burritt DJ, Fujita M, Munné-Bosch S (2018) Heat or cold priming induced cross-tolerance to abiotic stresses in plants: key regulators and possible mechanisms. Protoplasma 255:399–412

Hu Y, Jiang Y, Han X, Wang H, Pan J, Yu D (2017) Jasmonate regulates leaf senescence and tolerance to cold stress: crosstalk with other phytohormones. J Exp Bot 68:1361–1369

Huang D, Wu W, Abrams SR, Cutler AJ (2008) The relationship of drought-related gene expression in Arabidopsis thaliana to hormonal and environmental factors. J Exp Bot 59:2991–3007

Huang B, Rachmilevitch S, Xu J (2012) Root carbon and protein metabolism associated with heat tolerance. J Exp Bot 63:3455–3465

Ichimura K, Mizoguchi T, Yoshida R, Yuasa T, Shinozaki K (2000) Various abiotic stresses rapidly activate Arabidopsis MAP kinases ATMPK4 and ATMPK6. Plant J 24:655–665

Jaleel CA, Gopi R, Panneerselvam R (2008) Growth and photosynthetic pigments responses of two varieties of *Catharanthus roseus* to triadimefon treatment. C R Biol 331:272–277

Jalmi SK, Sinha AK (2015) ROS mediated MAPK signaling in abiotic and biotic stress-striking similarities and differences. Front Plant Sci 6:769

Jaspers P, Kangasjarvi J (2010) Reactive oxygen species in abiotic stress signaling. Physiol Plant 138:405–413

Kaloshian I (2004) Gene-for-gene disease resistance: bridging insect pest and pathogen defense. J Chem Ecol 30:2419–2438

Karuppanapandian T, Moo J, Kim C, Manoharan K, Kim W (2011) Reactive oxygen species inplants, their generation, signal transduction, and scavenging mechanisms. Aust J Crop Sci 5:709–725

Kazan K (2015) Diverse roles of jasmonates and ethylene in abiotic stress tolerance. Trend Plant Sci 20:219–229

Khan MIR, Iqbal N, Masood A, Per TS, Khan NA (2013) Salicylic acid alleviates adverse effects of heat stress on photosynthesis through changes in proline production and ethylene formation. Plant Signal Behav 8:e26374

Klingler JP, Batelli G, Zhu JK (2010) ABA receptors: the START of a new paradigm in phytohormone signalling. J Exp Bot 61:3199–3210

Kreslavski VD, Los DA, Allakhverdiev SI, Kuznetsov V (2012) Signaling role of reactive oxygen-species in plants under stress. Russ J Plant Physiol 59:141–154

Lamichhane JR, Venturi V (2015) Synergisms between microbial pathogens in plant disease complexes: a growing trend. Front Plant Sci 6:385

Lavania D, Siddiqui MH, Al-Whaibi MH, Singh AK, Kumar R, Grover A (2015) Genetic approaches for breeding heat stress tolerance in faba bean (*Vicia faba* L.). Acta Physiol Plant 37:17–37

Li Z, Han X, Song X, Zhang Y, Jiang J, Han Q, Liu M, Qiao G, Zhuo R (2017) Overexpressing the *Sedum alfredii* Cu/Zn superoxide dismutase increased resistance to oxidative stress in transgenic Arabidopsis. Front Plant Sci 8:1010

Lim C, Baek W, Jung J, Kim JH, Lee S (2015) Function of ABA in stomatal defense against biotic and drought stresses. Int J Mol Sci 16:15251–15270

Lobell DB, Schlenker W, Costa-Roberts J (2011) Climate trends and global crop production since 1980. Science 333:616–620

Lu C, Han MH, Guevara-Garcia A, Fedoroff NV (2002) Mitogen-activated protein kinase signalling in postgermination arrest of development by abscisic acid. Proc Natl Acad Sci U S A 99:15812–15817

Melotto M, Underwood W, Koczan J, Nomura K, He SY (2006) Plant stomata function in innate immunity against bacterial invasion. Cell 126:969–980

Melotto M, Zhang L, Oblessuc PR, He SY (2017) Stomatal defense a decade later. Plant Physiol 174:561–571

Mishra P, Bhoomika K, Dubey RS (2013) Differential responses of antioxidative defense system to prolonged salinity stress in salt-tolerant and salt-sensitive Indica rice (*Oryza sativa* L.) seedlings. Protoplasma 250:3–19

Mitra R, Bhatia CR (2008) Bioenergetic cost of heat tolerance in wheat crop. Curr Sci 94:1049–1053

Mitra A, Chatterjee S, Moogouei R, Gupta DK (2017a) Arsenic accumulation in rice and probable mitigation approaches: a review. Agronomy 7:67

Mitra A, Chatterjee S, Gupta DK (2017b) Potential role of microbes in bioremediation of arsenic. In: Gupta DK, Chatterjee S (eds) Arsenic contamination in the environment, the issues and solutions. Springer, Cham, pp 195–213

Mitra A, Chatterjee S, Gupta DK (2018) Plants response and tolerance to arsenic-induced oxidative stress. In: Hasanuzzaman M, Nahar K, Fujita M (eds) Mechanisms of arsenic toxicity and tolerance in plants. Springer, Singapore, pp 105–118

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trend Plant Sci 7:405–410

Miura K, Tada Y (2014) Regulation of water; salinity and cold stress responses by salicylic acid. Front Plant Sci 5:e4

Moffat CS, Ingle RA, Wathugala DL, Saunders NJ, Knight H, Knight MR (2012) ERF5 and ERF6 play redundant roles as positive regulators of JA/Et-mediated defense against *Botrytis cinerea* in *Arabidopsis*. PLoS One 7:e35995

Monaghan J, Zipfel C (2012) Plant pattern recognition receptor complexes at the plasma membrane. Curr Opin Plant Biol 15:349–357

Monni S, Uhlig C, Hansen E, Magel E (2001) Ecophysiological responses of *Empetrum nigrum* to heavy metal pollution. Environ Pollut 112:121–129

Mori IC, Schroeder JI (2004) Reactive oxygen species activation of plant Ca^{2+} channels. A signaling mechanism in polar growth, hormone transduction, stress signaling, and hypothetically mechanotransduction. Plant Physiol 135:702–708

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Mur LA, Kenton P, Lloyd AJ, Ougham H, Prats E (2007) The hypersensitive response; the centenary is upon us but how much do we know? J Exp Bot 59:501–520

Mushtaq Z, Faizan S, Gulzar B (2020) Salt stress, its impacts on plants and the strategies plants are employing against it: a review. J App Biol Biotechnol 8:81–91

Naser Alavi SM, Arvin MJ, Manoochehri KK (2014) Salicylic acid and nitric oxide alleviate osmotic stress in wheat (*Triticum aestivum* L.) seedlings. J Pant Interact 9:683–688

Nazar R, Umar S, Khan NA (2015) Exogenous salicylic acid improves photosynthesis and growth through increase in ascorbate-glutathione metabolism and S assimilation in mustard under salt stress. Plant Signal Behav 10:e1003751

Niakoo MI, Dar MI, Raghib F, Jaleel H, Ahmad B, Raina A, Khan FA, Naushin F (2019) Role and regulation of plants phenolics in abiotic stress tolerance: an overview. In: MIR K, Reddy PS, Ferrante A, Khan NA (eds) Plant signalling molecules. Woodhead Publishing, Elsevier, Duxford, pp 157–168

Omae H, Kumar A, Shono M (2012) Adaptation to high temperature and water deficit in the common bean (*Phaseolus vulgaris* L.) during the reproductive period. J Bot 11:13–21

Osakabe Y, Osakabe K, Shinozaki K, Tran LSP (2014) Response of plants to water stress. Front Plant Sci 5:86

Pandey P, Srivastava S, Pandey AK, Dubey RS (2020) Abiotic-stress tolerance in plants-system biology approach. In: Plant life under changing environment. Academic Press, pp 577–609

Pastori GM, Foyer CH (2002) Common components, networks, and oathways of cress-tolerance to stress. The central role of “redox” and abscisic acid-mediated controls. Plant Physiol 129:460–468

Per TS, Khan MIR, Anjum NA, Masood A, Hussain SJ, Khan NA (2018) Jasmonates in plants under abiotic stresses: crosstalk with other phytohormones matters. Environ Exp Bot 145:104–120

Peters K, Breitsameter L, Gerowitt B (2014) Impact of climate change on weeds in agriculture: a review. Agric Sustain Dev 34:707–721

Pitzschke A, Djamei A, Bitton F, Hirt H (2009) A major role of the MEKK1–MKK1/2–MPK4 pathway in ROS signalling. Mol Plant 2:120–137

Porcel R, Aroca R, Ruiz-Lozano JM (2012) Salinity stress alleviation using arbuscular mycorrhizal fungi: a review. Agron Sustain Dev 32:181–200

Porcel R, Aroca R, Azcón R, Ruiz-Lozano JM (2016) Regulation of cation transporter genes by the arbuscular mycorrhizal symbiosis in rice plants subjected to salinity suggests improved salt tolerance due to reduced Na^{+} root to shoot distribution. Mycorrhiza 26:673–284

Prasad MNV, Freitas HMO (2003) Metal hyperaccumulation in plants-biodiversity prospecting for phytoremediation technology. Elect J Biotechnol 6:285–321

Ramegowda V, Da Costa MV, Harihar S, Karaba NN, Sreeman SM (2020) Abiotic and biotic stress interactions in plants: a cross-tolerance perspective. In: Hossain MA, Liu F, Burritt Masayuki Fujita DJ, Huang B (eds) Priming-mediated stress and cross-stress tolerance in crop plants. Academic Press, pp 267–302

Rao KP, Vani G, Kumar K, Wankhede DP, Misra M, Gupta M et al (2011) Arsenic stress activates MAP kinase in rice roots and leaves. Arch Biochem Biophys 506:73–82

Rasmussen S, Barah P, Suarez-Rodriguez MC, Bressendorff S, Friis P, Costantino P, Bones AM, Nielsen HB, Mundy J (2013) Transcriptome responses to combinations of stresses in Arabidopsis. Plant Phyisol 161:1783–1794

Rejeb IB, Pastor V, Mauch-Mani B (2014) Plant responses to simultaneous biotic and abiotic stress: molecular mechanisms. Plan Theory 3:458–375

Riley G (1981) Effects of high temperature on protein synthesis during germination of maize *(Zea mays* L.). Planta 151:75–80

Rodríguez M, Canales E, Borrás-Hidalgo O (2005) Molecular aspects of abiotic stress in plants. Biotechnol 22:1–10

Sairam RK, Tyagi A (2004) Physiology and molecular biology of salinity stress tolerance in plants. Curr Sci 86:407–421

Sakamoto A, Murata N (2002) The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. Plant Cell Environ 25:163–171

Šamajová O, Plíhal O, Al-Yousif M, Hirt H, Šamaj J (2013) Improvement of stress tolerance in plants by genetic manipulation of mitogen-activated protein kinases. Biotechnol Adv 31:118–128

Sarieva GE, Kenzhebaeva SS, Lichtenthaler HK (2010) Adaptation potential of photosynthesis in wheat cultivars with a capability of leaf rolling under high temperature conditions. Russ J Plant Physiol 57:28–36

Schellingen K, Van Der Straeten D, Vandenbussche F, Prinsen E, Remans T (2014) Cadmium-induced ethylene production and responses in *Arabidopsis thaliana* rely on *ACS2* and *ACS6* gene expression. BMC Plant Biol 14:214

Schumann GL, D'Arcy CJ (2006) Essential plant pathology. APS Press, St. Paul

Sharma I (2012) Arsenic induced oxidative stress in plants. Biologia 67:447–453

Sharma S, Chatterjee S, Datta S, Mitra A, Vairale MG, Veer V, Chaurasia A, Gupta DK (2014) In vitro selection of plants for the removal of toxic metals from contaminated soil: role of genetic variation in phytoremediation. In: Gupta DK, Chatterjee S (eds) Heavy metal remediation. Nova Science Publisher, New York, pp 155–178

Shigeoka S, Ishikawa T, Tamoi M, Miyagawa Y, Takeda T, Yabuta Y, Yoshimura K (2002) Regulation and function of ascorbate peroxidase isoenzymes. J Exp Bot 53:1305–1319

Shiri M, Rabhi M, El Amrani A, Abdelly C (2015) Cross-tolerance to abiotic stresses in halophytes: application for phytoremediation of organic pollutants. Acta Physiol Plant 37:209

Shukla D, Trivedi PK, Nath P, Tuteja N (2016) Metallothioneins and phytochelatins: role and perspectives in heavy metal (loid)s stress tolerance in crop plants. In: Tuteja N, Gill SS (eds) Abiotic stress response in plants. Wiley-VCH Verlag GmbH and Co. K GaA, Weinheim

Singer A (2006) The chemical ecology of pollutants biodegradation. In: Mackova M (ed) Phytoremediation and rhizoremediation: theoretical background. Springer, Germany, pp 5–21

Singh N, Ma LQ, Srivastava M, Rathinasabapathi B (2006) Metabolic adaptations to arsenic-induced oxidative stress in *Pteris vittata* L and *Pteris ensiformis L.* Plant Sci 170:274–282

Singh AP, Dixit G, Mishra S, Dwivedi S, Tiwari M, Mallick S, Pandey V, Trivedi PK, Chakrabarty D, Tripathi RD (2015) Salicylic acid modulates arsenic toxicity by reducing its root to shoot translocation in rice (*Oryza sativa* L.). Front Plant Sci 6:1–12

Spoel SH, Dong X (2012) How do plants achieve immunity? Defence without specialized immune cells. Nat Rev Immunol 12:89–100

Srivastava S, Pathak AD, Gupta PS, Shrivastava AK, Srivastava AK (2012) Hydrogen peroxide-scavenging enzymes impart tolerance to high temperature induced oxidative stress in sugarcane. J Environ Biol 33:657–661

Srivastava S, Chiappetta A, Beatrice M (2013) Identification and profiling of arsenic stress-induced miRNAs in *Brassica juncea*. J Exp Bot 64:303–315

Steffens B (2014) The role of ethylene and ROS in salinity, heavy metal, and flooding responses inrice. Front Plant Sci 5:685

Su L, Dai Z, Li S, Xin H (2015) A novel system for evaluating drought–cold tolerance of grapevines using chlorophyll fluorescence. BMC Plant Biol 15:82

Sytar O, Kumari P, Yadav S, Brestic M, Rastogi A (2018) Phytohormone priming: regulator for heavy metal stress in plants. J Plant Growth Regul 38:739