MOLECULAR AND PHYSIOLOGICAL INSIGHTS INTO PLANT STRESS TOLERANCE AND APPLICATIONS IN AGRICULTURE

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Molecular and Physiological Insights into Plant Stress Tolerance and Applications in Agriculture

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FOREWORD

Stress tolerance is a continuing issue for researchers and professionals seeking to increase crop productivity. In the research field of plant science, stress physiology is an intensive topic for researchers, and tons of publications are reported per year to get increasing knowledge about stress tolerance when facing global climate change. In the meantime, the emerging knowledge of plant stress physiology should be applied to the practice of agriculture for sustainable agriculture as well as food security globally. Importantly, there is a high demand for the integration of current knowledge of plant stress physiology. Moreover, a systematic summary of methods in plant stress management also needs to be refined.

This book, “Molecular and Physiological Insights into Plant Stress Tolerance and Applications in Agriculture,” collects the most recent original research and literature reviews for unraveling the physiology of plant stress tolerance. Divided into 21 chapters, it provides in-depth coverage of the recent advances by exploring the unique features of stress tolerance mechanisms, which are essential for better understanding and improving plant response, growth, and development under stress conditions, in particular by exploring knowledge that focuses on the application of plant growth regulators, advanced biotechnologies, high-throughput technologies, multi-omics, bioinformatics, systems biology, and artificial intelligence as well as beneficial microorganisms on the alleviation of plant stress.

The mechanisms covered in this book include the perception of stress, signal transduction, and the production of chemicals and proteins associated with the stress response. The book also offers critical knowledge of the gene networks involved in stress tolerance and how they are used in plant stress tolerance development. Modern genetic studies and useful breeding methods are also covered. It also presents the current challenges and further perspectives. Therefore, this book might largely benefit breeding programs as well as sustainable agricultural production in the future.

The editor, Prof. Jen-Tsung Chen has done an excellent job of bringing together specialists from diverse fields to present the most comprehensive view of current research findings and their implications for plant stress tolerance physiology. Therefore, this book, "Molecular and Physiological Insights into Plant Stress Tolerance and Applications in Agriculture," is an essential resource for academics and professionals working in agronomy, plant science, and horticulture. It is an essential resource for both novices and specialists. It can also be utilized as a resource for courses at the university level for students and Ph.D. students interested in the physiology of plant stress tolerance. I recommend it without reservation!

Christophe Hano
University of Orleans
France

PREFACE

This book is an edited collection of a series of chapters presented by experts in the cross-disciplinary research fields of plant physiology, plant stress, agronomy, agriculture, horticulture, microbiology, molecular biology, multi-omics, plant pathology, and environmental science. To ensure its broad sources of knowledge and transparency, over one thousand invitations were sent by email to experts all over the world together with the announcement of a call for papers in the ResearchGate which attracted over seven hundred "reads" and twenty-five "followers" for about half a year of posting, more than thirty groups express their interest in contributing chapters to this book after two months of communication. The content of the chapters was finished after four to five months of preparation and eventually, twenty-one of them were accepted for publication. So, I would like to thank all the contributors to this book for their time and effort in organizing valuable chapters.

This book consists of five major subtopics, including 1) the fundamental theory of molecular biology and plant stress physiology; 2) microbial dynamics within the rhizosphere of plants and the use of plant growth-promoting bacteria in the improvement of growth and productivity of crops; 3) morphological and physiological responses of plants and the underlying molecular mechanisms under abiotic stress particularly salt, heat and drought, and importantly, several chapters pay their attention to systematic describe molecular aspects of salt tolerance in plants; 4) the current applications of biotechnology and the benefits to sustainable agriculture; 5) the techniques for improving tolerance to biotic stress such as the use of endophytic bacteria.

The contents of this book could enrich our understanding of molecular and physiological mechanisms in plant abiotic and biotic stresses and their interactions. It collects the recent advances through refining the knowledge systematically from a large amount of literature of more than two thousand and five hundred publications and organizes thirty-seven figures and thirty-five comprehensive tables to attract readers. This book could be a critical reference and suitable textbook for researchers, students, teachers, growers, and experts in a broad range of fields such as plant science, agronomy, and agriculture. It contributes to the significant progress in expanding our knowledge in the field of plant stress physiology and the contents benefit in obtaining stress-tolerant crops; enhancing their quality and productivity; and eventually, supporting the sustainability of agriculture and the global food supply.

This book has been divided into two parts. In part I, the emerging knowledge on plant abiotic/environmental stress tolerance was included, which covers stressors including temperature, salt, and drought and their combinations. When faced with global climate change, these abiotic stresses can be worse chiefly due to a rise in temperature. Firstly, the fundamental theory, methods, and applications of stress mitigation technology have been refined in this book. It provides an in-depth discussion on salt stress response and its mitigation strategies, particularly, several chapters focus on recent achievements in significant crops such as sugar beet and rice. In addition, temperature and drought stresses were systematically reviewed and the authors give perspective for the future directions. Part I of this book aims to support the goals of SDGs (Sustainable Development Goals), particularly achieving zero hunger through enhancing agricultural production.

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CHAPTER 1

Influence of Abiotic Stress on Molecular Responses of Flowering in Rice

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Abstract: Rice is a short-day plant, and its heading date (Hd)/flowering time is one of the important agronomic traits for realizing the maximum yield with high nutrition. Theoretically, flowering initiates with the transition from the vegetative stage to shoot apical meristems (SAMs), and it is regulated by endogenous and environmental signals. Under favorable environmental conditions, flowering is triggered with the synthesis of mobile signal florigen in leaves and then translocated to the shoot for activation of cell differentiation-associated genes. In rice, the genetic pathway of flowering comprises *OsGI–Hd1–Hd3a,* which is an ortholog of the *Arabidopsis GI–CO–FT* pathway, and the *Ehd1-Hd3a* pathway. Climate change could affect photoperiod and temperature, which in turn influences heading date and crop yield. In low temperatures and long-day conditions, the expression of the *HD3a* gene analogous to *FT* in *Arabidopsis* deceased, which delays flowering. Similarly, during drought, expression of the *Ehd1* gene is suppressed, resulting in a late-flowering phenotype in rice. Drought affects pollen fertility and reduction in grain yield by reducing male fertility, which affects male meiosis during reproduction, microspore development, and anther dehiscence. In this research field, substantial progress has been made to manipulate flowering-related genes to combat abiotic stresses. Here, we summarize the roles of a few genes in improving the flowering traits of rice.

Keywords: Abiotic stress, Flowering, Florigen, *Hd1*, *Hd3a*, Long-day, Short-day.

1. INTRODUCTION

Rice is an important staple food crop, consumed by more than 50% of the population in world. Rice is grown in puddled conditions in general, however, recently, aerobic rice cultivation has been gaining importance in saving water. Drought is one of the most severe forms of abiotic stress affecting plants, due to global climate change. Due to the high requirement for water, the rice crop is severely affected during drought conditions. Drought negatively affects plant

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growth and grain quality due to hindrances in the physiological and metabolic processes, including respiration, photosynthesis, stomatal opening-closing, *etc*. The Rice plant takes around 3-6 months to grow and consists of vegetative, reproductive, and ripening stages. The reproductive stages in rice begin with booting, which leads to a bulging of the leaf, the stem that conceals the developing panicle, followed by the emergence of the stem that continues to grow. Flowering or heading in rice begins when the panicle is fully grown [1, 2]. Drought affects rice growth at almost every stage, most severe at flowering, followed by booting and grain-filling stages. Drought affects spikelet fertility at the panicle initiation stage, resulting in low grain yield [3, 4]. Another crucial environmental factor affecting plant growth and reproduction is extreme temperatures, leading to a significant decrease in crop yield. An increase in temperature induces floret sterility in rice due to another indehiscence by interfering with pollen grains swelling [1, 2]. Similarly, cold stress in the range of 15–19°C, significantly affects the reproductive stage and reduces rice yield. The reduced temperature at the heading stage in rice causes improper development of microspore, which produces infertile pollen grains, resulting in high spikelet sterility and low nutritional quality grains [3].

Being sessile, plants have evolved many stress adaptation and escape mechanisms. *Arabidopsis* has evolved a drought escape (DE) mechanism by shortening its life cycle to avoid drought [5]. However, when rice is exposed to water-deficit conditions, it can trigger early flowering and reduced tiller numbers or delay in flowering, depending upon drought severity [5]. Reduction in tissue water status during drought stress triggers various signaling molecules such as calcium influx from the extracellular matrix to cytosol, inositol-1, 4, 5-triphosphate (IP3), abscisic acid (ABA), cyclic adenosine diphosphate ribose (cADPR), nitric oxide, *etc*. Secretion of these signaling molecules alters diverse signaling pathways, which play a critical role in determining the flowering and productivity. The environmental cues and these signaling molecules are perceived by a diverse family of receptors, which activate or suppress a cascade of signaling events. Upon perception, receptor-ligand interactions trigger the activation of kinases which affect the expression of diverse transcription factors such as HD-zip/bZIP, AP2/ERF, NAC, MYB, WRKY, and other genes [6 - 10]. The cell fate-determining factors play an important role in flower initiation and transition mechanisms. The mitogen-activated protein kinases (MAPKs), proline (pro), late embryogenesis abundant (LEA), glycine betaine (GB), soluble sugar (SS), proteins and aquaporin (AQP) are upregulated during drought, which favors plant survival in harsh conditions [11]. To develop a climate-resilient rice crop, which can withstand adverse abiotic stresses, it is important to understand the plant responses to environmental factors. Efforts have been made to understand the molecular mechanisms involved in flowering, and attempts have been made to design climate-resilient crops.

1.1. Receptor for Light and Temperature

To adapt to climatic conditions, plants have evolved different photoreceptors such as cryptochrome (*CRY*), phytochrome (*Phy*), and phototropin (*PHOT*) for sensing light which regulates photoperiod (day length). Cryptochromes are flavin-containing photoreceptors that interact with a DNA repair enzyme photolyase, which gets oxidized and activated by blue and UV-A light, leading to the formation of a semiquinone intermediate that can efficiently absorb green (500–600 nm) light. In rice, two cryptochrome genes are present: OsCRY1a and OsCRY2 (formerly known as OsCRY1b), which promote rice flowering time [12, 13]. Mutations in these genes inhibit coleoptile and leaf elongation upon blue light irradiation [12]. *OsCRY1a* and *OsCRY1b* inhibit rice seedling development by physically interacting with Constitutively Photomorphogenic 1 (COP1) protein that inhibits coleoptile development and leaf elongation [12, 14]. *COP1* encodes RING-finger E3 ubiquitin ligase and interacts with the Suppressor of *phyA-105* (SPA) to degrade CONSTANS (CO), a central regulator of flowering. *CO* expression is indirectly regulated by the degradation of GIGANTEA (GI) [15]. Phototropins have two flavin binding domains at the N-terminal and a serine/threonine kinase domain at the C-terminal end. *PHOT1* and *PHOT2* regulate phototropism and stomatal movement in plants. Phytochromes are the best-known blue-green pigment receptors, ranging from PhyA to PhyC, which sense different wavelengths of light from red to far-red. These are cytoplasmic, dimeric, serine/threonine kinases activated in response to red light by absorbing 560 nm wavelength converting inactive Pr (Red) form to active Pfr (far-red) form and Pfr to Pr by absorbing far-red light of ~730 nm wavelength. The inactive form of Pr is present in cytosol as it converts to the active Pfr form translocated to the nucleus, where it interacts with multiple partners to influence the expression of many target genes involved in photomorphogenesis [12]. Phytochromes play a critical role in the process of anthesis, influencing the heading date and overall growth of rice plants. Double mutants of *phyA* and *phyB* show defects in pollen development and anthesis [14]. Phytochromes also play an important role in flowering by regulating the expression of *Hd3a* in rice *via Hd1*. Hd1, in turn, is regulated at the post-translational level by PhyB [16]. PhyB also acts as a thermosensor, and its direct interaction with the promoter region of key target genes in a temperature-dependent fashion has been reported. Phytochromes are involved in the convergence of light and temperature in regulating photomorphogenesis [16].

Phytochromes interact with the basic helix-loop-helix (bHLH) group of transcription factors, *i.e.*, Phytochrome Interacting Factors (PIFs), for maintaining the skotomorphogenic state (development of seedlings in the dark) of plants in dark condition. Phytochromes are activated upon exposure to light and interact

CHAPTER 2

A Peep into the Tolerance Mechanism and the Sugar Beet Response to Salt Stress

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Abstract: Salt stress is one of the main environmental stresses occurring all over the globe. Soil salinity is a serious issue in arid and semi-arid areas, causing significant ecological disruption. Excess salts in the soil have an impact on plant nutrient intake and osmotic equilibrium, causing osmotic and ionic stress. Complex physiological features, metabolic pathways, enzyme synthesis, suitable solutes, metabolites, and molecular or genetic networks all play a role in plant adaptation or tolerance to salinity stress. Sugar beet is a well-known crop in terms of salt tolerance and for reclaiming such soils, even for the growth of other crops. Natural endowments, accumulation of organic solutes, sodium potassium ions accumulation in vacuoles, and osmotic tolerance potential are some of the key mechanisms involved in providing tolerance to sugar beet. A greater understanding of sugar beet tolerance and response to salt stress will open up new avenues for increasing crop performance in these conditions. The mechanisms involved in sugar beet adaptation to salt stress conditions, as well as the response to such conditions, are discussed in this chapter.

Keywords: Osmotic adjustment, Mechanism, SOS Pathway, Sugar beet, Tolerance.

1. INTRODUCTION

Salinity is a severe challenge to modern agriculture, causing crop growth and development to be hampered. Excess salt levels harm around 960 million hectares of fertile land worldwide [1 - 3]. In the current situation, more than 20% of well-irrigated lands around the world are vulnerable to soil saline conditions. Due to the excessive use of water for crop irrigation and rapid barrenness (due to climate change issues), the problem of salt stress has grown [4]. The increasing soil salinity is majorly due to the global variation in temperature, poor irrigation practices, and incorrect fertilizer use. All of these have enhanced the negative impacts of salt increment in soils resulting in an annual salinity increase of 1-2 percent [5]. Munns [6] and Munns [7] described a two-phase growth reaction of

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plants towards salt stress. In the first phase, the effect of salt stress has contributed to osmotic alterations occurring exterior to the salt-affected cells. This, in turn, causes a lower rate of water absorption. The second phase is denoted by salt accumulation in leaves which results in enzymatic activity hindrance and activation of ionic and oxidative stress [8].

Sugar beet, thanks to its sea beet ancestor, has a high salt tolerance capacity [9, 10] of 9.5 m mhos/cm to salt stress [11, 12]. This salt tolerance ability is exceptionally strong when compared to other crops, such as paddy (6.0), sugarcane (4.4), and wheat (2.4). It's a halophyte that scavenges sodium salts in salty soils, removing roughly 500 kg of sodium salts per hectare per season [11]. Several cultivars have obtained salt tolerance traits from their ancestor. Yang *et al.* [9] stated that this crop can withstand 500 mM sodium chloride (NaCl) for seven days without dying. Sugar beet was found to be able to grow in soil containing 85–140 mM salt [13]. According to Peng *et al.* [14], sugar beets grew better in 3 mM NaCl than in 0 mM NaCl. Besides, the production quality had even been reported to be ineffective when the electrical conductivity (EC) of the soil reached 7.0 dS m^{-1} (67 mM NaCl) [15]. However, when EC exceeds the 7.0 dS m^{-1} level, this crop shows reduced yield [16, 17]. Khandil *et al.* [18] reported this crop as an economically farmed crop in saline soils and also helped in reclaiming such soils. Sugar beet is now considered an ideal crop model for understanding salt tolerance mechanisms, thanks to the completion of its genome sequencing [19].

1.1. Characteristics of Halophytes for Salt Stress Condition

Halophytes have a built-in ability to thrive in saline environments. Chenopodiaceous plants have more mitochondria than other plants because they require more energy in high-salt environments [20]. Additionally, these plants aid in the accumulation of sodium and chlorine ions in their cytoplasm. This allows the chloroplasts to withstand even the saline conditions are at extreme [21]. These plants also contain special glands on their leaves that aid in the elimination of salt. These glands prevent salt from reaching the sprout *via* the surface of the leaves [22]. Furthermore, the presence of hydathodes in these plants aid in the excretion of excessive salts. With less stomatal conductance and more transpiration water loss, this happens.

1.2. Salt Stress Tolerance Mechanism in Sugar Beet

The tolerance mechanism in sugar beet for salt stress has been investigated in a number of studies [23, 24]. Osmotic tolerance, ion exclusion, and tissue tolerance are the three identified mechanisms behind the tolerance potential of this plant for such conditions. Osmotic tolerance/ adjustment potential has been prominently seen in this crop with the accrual of sodium and chloride ions in their vacuoles and cytoplasm [25, 26]. It is an essential regulatory mechanism for the crop to adapt to salt conditions [27]. An osmotic gradient is created when salt components from the cytoplasm accumulate in the vacuole. The surge in the solute synthesis that happens in the cytoplasm controls this gradient. Osmotic adjustment is the process of increasing solute production [28]. This is an adaptive approach for plants that have been exposed to a saltwater environment. Various suitable solutes have been discovered. Compatible solutes have features such as increased solubility, low polar charge, and a broad hydration shell [29]. The various features of compatible solutes contribute to cell turgor maintenance and even cause consistency in enzyme structure in the cytoplasm. As a result, the solutes are protected by inorganic ions [30]. Flowers [31] found the absorbing and accumulating capability of sodium ions in the sugar beet leaves for osmotic regulation/adaptation under saline conditions. Flowers and Colmer [32] found that plants grown under salt-stress conditions possess high rates of organic solutes. The production of organic solutes under such a condition causes the plant to maintain its cell turgidity and enzymatic conformation. Proline, in this respect, plays an essential part. It is involved in the protection of the cytomembrane system and sustaining the enzyme structure [33]. Ashraf and Fatima [34] stated that proline production varies with tolerance potential for salt stress. Proline and soluble sugars have long been recognized for their role in osmotic adjustment in plants under salt stress [35].

Zeng *et al.* [36] found that salt-tolerant halophytes had a substantial increase in betaine contents. Wang *et al.* [37] showed that the accumulation of amino acids in salt-stressed sugar beet had much higher rates than proline/choline levels. Wang *et al.* [38] depicted that the higher the organic acid in salt-stressed plants higher the salt tolerance potential. They further stated that organic acid accumulation causes the plant to cope with abiotic stresses. Iqbal *et al.* [39] revealed that protein structure and cell membrane stability are sustained by salt-tolerant sugar beet plants in the osmotic adjustment defense mechanism. This helps in lowering the osmotic potential of cells. Ninety-five redox proteins have been identified in this crop under salt stress conditions depicting its involvement in metabolic activities as well as several other activities related to defense mechanisms for such an environment [40]. Mansour and Ali [41] have shown that all these responses help in giving energy to plants for coping/adapting to the salt stress condition.

Sugar beet has long been known to have a salt stress tolerance capacity. Yang *et al.* [9] revealed that this plant can withstand the salt stress condition of up to 500 mM NaCl for one week and that too without losing its viability. According to Gupta [42], the tolerance power of sugar beet was 9.5 Dsm^{-1}. The absorption of salt by the plant from the soil to the shoots has been documented in this trait. This

CHAPTER 3

The Role of Functional Genomics to Fight the Abiotic Stresses for Better Crop Quality and Production

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Abstract: Plant quality, growth, yield and productivity are repeatedly affected by different abiotic stresses. It sometimes becomes a major upcoming threat to food security when the stress is on some staple crops. Stress-associated gene expression or no expression leads to abiotic stress tolerance, which is an outcome of complex signal transduction networks. Different plants have evolved with diverse, complex signaling networks concerning abiotic stresses. With the advancement of bioinformatics and functional genomics, in particular, many researchers have identified many genes related to abiotic stress tolerance in different crops, which are being used as a promising improvement in abiotic stresses. Different techniques of genome editing also play an important role in combating abiotic stresses. This chapter represents the knowledge regarding stress-tolerant mechanisms using technologies related to the field of functional genomics and may benefit the researchers in designing more efficient breeding programs and eventually for the farmers to acquire stress-tolerant and high-yielding crops to raise their income in the future.

Keywords: Abiotic stress, Crop quality, Crop production, Functional genomics.

1. INTRODUCTION

The extremes of temperature (high or low), drought, radiation, salinity, heavy metals, *etc*., are collectively called abiotic stresses to the plants that strongly affect the plant growth, development, and eventually their quality and yield. Abiotic stress was found to be responsible for major crop losses throughout the world as they reduce yields and deteriorate the quality of the product by showing a negative impact on the actual potential of the crop. These stresses adversely affect crops in all means, in particular, physically and biochemically; also, the molecular expression of crops changes which ultimately affects the production of the crop

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[1 - 3]. It is anticipated that on account of environmental change, abiotic stresses might turn out to be more extreme and incessant. Dry spells and saltiness are turning out to be expanded in numerous places and may cause genuine salinization of over half of all arable terrains continuously by the year 2050. Subsequently, as a result of climbing temperatures and regular flooding for quite a long time, prolific horticultural land and harvest yields might diminish quickly. Moderate evaluations suggest that over 90% of the land in provincial regions is impacted by abiotic stress factors eventually during the developing season.

Details of various abiotic stresses and their effect on plants are well summarized in Table (**1**) [4 - 7].

Table 1. Details of abiotic stresses affecting the regular function of plant metabolism.

Stress	Mechanism	Major Effect on Plants
Drought	Water deficit and cellular dehydration (the decrease of the cell water content)	Reduced growth and metabolic activity with a reduction in yield
Heat	Enzymes inactivation and gradually denatured	Reproduction of plants, flowering, Male sterility, and abnormalities in the spikelets
Salt	Osmotic or water-deficit stress ionic toxicity (osmotic or water potential of the surrounding root zone is decreased by Na^+ and Cl^- solutes)	Inhibits plant growth and reduces the ability to uptake water and nutrients
Cold	Induce water leakage and lead to cell dehydration (inability to transport the water available from the soil to the living cell of leaf mesophyll)	Adversely affects plant growth and development, limits the geographical distribution of plant species

Ongoing innovative advances and the previously mentioned horticultural difficulties have prompted the rise of high-throughput devices to investigate and take advantage of plant genomes for crop improvement. The functional genomics-based approaches mean translating the whole genome, including genic and intergenic locales, which will thus give explicit procedures to have genetic improvement.

1.1. The Use of Functional Genomics in Studying Plant Physiology under Abiotic Stresses

1.1.1. Microarrays and MicroRNAs

The recent development in the field of computational biology with innovative omics techniques and technologies allows the identification of different genetic elements that contribute to various complex processes related to different stresses in crops [8]. In *Arabidopsis*, *AtPARP2* and *AREB1/ABF2,* responsible for the increased tolerance to drought have been studied *via* 24K and 22K Affymetrix microarrays, respectively [9, 10]. The technique of microarrays fills the bridging gap between functional genomics and sequencing data, which helps to understand the involvement of various genes in different regulatory networks and signal transduction pathways associated with tolerance or resistance against multiple abiotic crop stresses [8, 11]. The functional analysis through the method of microarrays reveals a number of signaling, metabolic and cellular pathways which in turn regulate the many biological and developmental processes, *viz*., abiotic stresses. For example, 24K Affymetrix microarray revealed *AtMYB41*control the primary metabolism and negative regulation in *Arabidopsis* [12].

For miRNA analysis among crops, the development of different bioinformatic tools *viz*., RNAhybrid, TarHunter, miRanda, MirGeneDB, and RNA22 [13], can detect miRNA targets and help in structure prediction. In *Arabidopsis*, miR398 was the first-ever reported miRNA to be involved in the regulation of auxin signaling which is related to stress tolerance. In the case of plants at various stages of development, miRNAs proved to be an important regulator of gene expression. Theoretically, Watson-Crick base pairing is hampered with miRNAs that lead to inhibition of translation either by cleavage of the target, which ultimately disrupts the function of genes at both transcriptional and post-transcriptional levels. For salinity stress tolerance, many active genes which are involved in transcription and other metabolic pathways were identified in wheat [14]. Hichri and co-workers [15] proved that the transcription factor SlWRKY3 is involved in salt stress tolerance in tomatoes and revealed that there is a significant relation between salinity stress and transcription factors from the family of the zinc finger. In *Oryza sativa*, miR156, miR158, miR159, miR397, miR398, miR482.2, miR530a, miR1445 on inducible genes, including *SalT* (LOC_Os01g24710) and *OsLEA3* (LOC_Os05g46480), were found to be responsible for drought tolerance, pathogen immune response and heat stress tolerance [16]. Wang and Long [17] found miR402 in *Zea mays* and found it to be responsible for seed germination and growth of seedlings under stress. In the case of wheat, it was observed that miRNAs (miR398) also play a substantial role in the down-regulation of gene expression when needed for adverse environmental stresses and oxidative activities [18]. Different inducible genes or their encoded proteins or transcription factors, including *Rd29A* (At5g52310) and CCAAT-binding transcription factors (*Arabidopsis*); CCAAT Binding Factor (CBF), Growth Regulating Factor (GRF), Cu/Zn superoxide dismutases (CSD1, CSD2) and TIR-NBS-LRR domain protein (*Medicago truncculata*), were found to be responsible for drought tolerance when interacting with different responsive miRNAs *viz*, miR164, miR169, miR389, miR393, miR396, miR397, miR402 (*Arabidopsis*) and miR169, miR396, miR398, miR2118 (*M. truncculata*).

CHAPTER 4

Genetic Enhancement for Salt Tolerance in Rice

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Abstract: Rice is the major and dominant cereal food crop in the world. Salinity stress is the second most abiotic stress next to drought, limiting rice yield. Approximately 953 Mha area of the world is affected by salinity. Genetic improvement of salt tolerance is an efficient approach to achieving yield gain in salt-affected areas. Although high-yielding salt-tolerant rice varieties are developed, it is difficult to generate tailor-made adapted varieties through traditional breeding. Hence various crop improvement approaches are followed, including marker-assisted selection and transgenic technology apart from classical breeding. Numerous QTLs were identified through the molecular marker approach, and specifically, *Saltol* QTL was introgressed into elite lines through marker-assisted back cross-breeding, and improved salt-tolerant varieties were bred. Genetic engineering tools are also amply employed whereby the genes underlying various biochemical/physiological processes such as ion and osmotic homeostasis, antioxidation, signaling, and transcription-associated with increased tolerance were characterized, validated, and used to develop salt-tolerant lines of rice. Yet, a clear relationship between expected gains in salt tolerance *in vitro* has often not been observed in the field in terms of grain yield. Hence, an integrated approach involving molecular breeding and conventional breeding would certainly pave the way to enhance salt tolerance in rice.

Keywords: Rice, Salinity, Alkalinity, Screening techniques, Salt tolerance, Mechanisms of tolerance, Breeding, QTLs, Marker-assisted selection, Transgenics.

1. INTRODUCTION

Rice is the staple and major cereal food crop for the majority of the global population. It is cultivated in an extensive range of climatic conditions and is

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often exposed to multiple abiotic stresses, *viz.,* high temperature, cold, drought, high salinity and alkalinity, submergence, excess water, and mineral deficiency or toxicity. Salt stresses, including salinity and alkalinity stresses, are the most often encountered in problem soils, limiting rice production in irrigated and rainfed ecologies. It is estimated that salinity affects 950 m ha of arable land and more than 20% of irrigated land globally [1, 2]. Salinization of land and water severely affects agricultural productivity [3]. Breeding superior salt-tolerant varieties appear to be the most promising approach to cultivating rice, even in salt-affected lands. The stress-tolerant varieties are expected to provide a yield increase of about 2t ha^{-1} [4].

Although rice varieties with improved salt tolerance are generated through traditional breeding strategy, the genetic gain obtained is not encouraging due to the polygenic nature, involvement of complex mechanisms of salinity tolerance with multiple physiological and biochemical traits, high environmental influence, presence of low genetic variability for salt tolerance [5]. With the intervention of molecular marker analysis, it has become possible to analyze quantitative traits, including salt tolerance, and a number of QTLs were detected for salt tolerance in rice. The *Saltol* QTL derived from Pokkali [6, 7] controlling Na^+/K^+ homeostasis and the *SKC1* gene from Nona Bokra [8] are noteworthy, offering increased seedling stage salinity tolerance. The *Saltol* QTL is introgressed into local popular rice varieties for the accelerated development of a few new salt-tolerant varieties [9 - 13] through marker-assisted back cross-breeding (MABB) with improved salt tolerance. However, the MABB approach could not impart significant expected yield gain under prolonged salt stress during reproductive stage tolerance.

The transgenic approach involves the manipulation of genes that encode the synthesis of compatible organic solutes, antioxidants, Na and K transport proteins, antioxidants, detoxifying genes, and late embryogenesis abundant proteins found to impart salt tolerance in crops [14]. But variety development through a transgenic approach for cultivation needs further investigation. The present review discusses the impact of salt stress in rice production, its effects on the morphological, physiological, biochemical, and genetic characteristics in rice, screening, and mechanisms contributing to salt tolerance, and reviews the progress made in breeding salt tolerance coupled with molecular breeding and genetic engineering strategies to cope up with salt stress.

1.1. Classification of Problem Soils

Broadly the salt-affected problem soils can be classified into two types, *viz*., saline and alkaline. Carbonates and bicarbonates of sodium and magnesium are the dominating anions in alkaline soils, while chlorides and sulfates of sodium and magnesium are often seen in saline soils. Soil salinity is characterized by soluble salts of high concentration and measured in terms of electrical conductivity (ECe). The soil exhibiting >4 dS m^{-1} ECe, <8.5 pH, and <15% exchangeable sodium percentage (ESP) is considered saline soil. The alkaline soils indicate >8.5 pH and < 4 dS m^{-1} ECe and >15% ESP. Saline-sodic soils record > 4 dS m^{-1} ECe and >15 percent ESP with varying pH having both saline and sodic properties [15, 16].

1.2. Halophytes *vs* Glycophytes

1.2.1. Sodium Extrusion

Broadly plants are categorized into halophytes (salt-loving) and glycophytes (salt-sensitive) depending on their ability to withstand high salt levels. Halophytes thrive well under high salt-affected areas, wherein Na Cl content is found to be as high as ~ 500 mM. Glycophytes include vegetable and grain crops that are sensitive to high salinity. Halophytes have certain inherent mechanisms to resist high salt concentrations. Halophytes 1) minimize salt entry into leaves by a preferential accumulation of K^+ and sodium export by salt glands, 2) compartmentalize excessive sodium in old leaves, leaf sheath, and stem as well as extrude salt by plasma membrane or vacuolar Na^+/H^+ antiporters, thus maintaining an increased cytosolic K^+/Na^+, 3) accumulate osmolytes such as glycine, betaine or proline for osmotic adjustment, 4) maintain high metabolism under detrimental salt concentrations, and 5) produce antioxidants to resist the oxidative damage. Glycophytes also show more or less similar strategies of salt tolerance adapted by halophytes but are not so well developed.

A few well-known halophytes are S*alicornia, Avicennia marina, Sesuvium portulacastrum, Suaeda salsa, Mesembryanthemum crystallinum, Thellungiella halophila* and *Porteresia coarctata*. Among them, *M.crystallinum* and *T. halophila* possess a formidable capacity to survive and reproduce at 500 mM NaCl [17] and extreme cold (-15° C). *P. coarctata*, a tetraploid (2n = 4x = 48), is regarded as a model plant among the wild relatives of rice. It is a potential source that can tolerate extended periods of saline water (20 to 40 dS m^{-1}) inundation. It can maintain a low Na^+/K^+ ratio within shoots and pump out excessive sodium through special glands on leaves, and sequester sodium to older and non-functional old leaves. Generally, crops, including rice, are glycophytes that are sensitive to salts even at lower levels of salinity (ECe < 4 dS m^{-1}) and cannot tolerate prolonged exposure to salinity. In extreme conditions of salt stress, glycophytes show mortality.

CHAPTER 5

Morphological and Physiological Responses of Plants Under Temperature Stress and Underlying Mechanisms

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Abstract: During evolution, plants are exposed to a wide range of beneficial and detrimental environmental conditions. Among these, temperature stress could retard plant growth and development, and even threaten survival. In agriculture, due to temperature stress, crop yield might be reduced remarkably and consequently damage food security. Fortunately, to mitigate these losses, plants have evolved various mechanisms for adaptation, avoidance and acclimatization to overcome temperature stress. For example, chilling or freezing injury can lead to the disruption of many physiological processes in plants, *e.g.*, water status, photosynthesis, respiration, and even most of the metabolism, and thus, various adaptative mechanisms could be activated in plants to avoid damage by the ice crystal formation or other chilling damages. These temperature-stress-tolerant mechanisms for high-temperature stress, cold stress, chilling injury, and freezing injury have been intensively revealed by researchers, and this present chapter attempts to summarize them systematically.

Keywords: Cold Stress, Chilling Injury, Cold Tolerance, Freezing Injury, High-Temperature Stress, Heat Tolerance.

1. INTRODUCTION

Plants have a prerequisite of some abiotic factors, including light, temperature, air, water, and some chemical factors, such as organic and inorganic nutrients, which are balanced and accurate at the same time to optimize growth and development. All deviations from the optimal levels of these essential factors for plant growth may cause impacts in the standard functions of the plant giving rise to abiotic stress. Theoretically, abiotic stress can be either elastic (reversible) or plastic (irreversible). Temperature stress is designated as to the metabolic proc-

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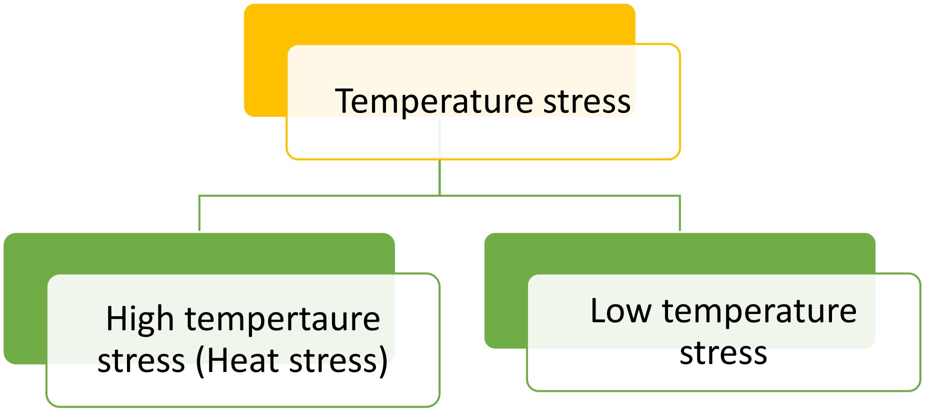
-esses in plants plastic biological stress, as the functions of plants do not return to normal under temperature stress. Temperature is one of the most important biological factors that influence the natural spread of plants. This factor also influences the rise and fall of agricultural crop yields. Temperature is an important abiotic factor for plant photosynthesis, respiration, and transpiration. In various ecosystems, plants differ in their temperature tolerance, which ranges from below 0°C to 60°C. The fluctuation in temperature under different habitats leads to damage to the metabolic processes in plants.

2. TEMPERATURE STRESS

Earth's temperature changes along longitudinal and altitudinal lines and also with the season. Most plants are specially adapted to function over a particular range of temperatures. Fluctuation in temperature above or below this range limits the survival of plants. Climate change is leading plant scientists to increasingly be concerned about temperature stress, mainly due to the potential impact of agriculture [1]. High temperatures caused by global climate change are now considered one of the main abiotic constraints restricting agricultural production [2]. The mean global temperature is now predicted to be 1.7-4.9 °C warmer than the current level by 2,100 due to the impact of the growth of the human population [3]. This prediction is raising scientific concern because temperature stress is known to affect the life cycle of organisms. As a sessile organism, plants cannot demonstrate a movement to favorable conditions. Consequently, gets exposed to lethal conditions due to High Temperature (HT) stress.



3. PLANT RESPONSES TO HIGH TEMPERATURE (HT) STRESS: AN OVERVIEW

High temperature is an environmental stress that occurs due to a hike in temperature for a long period beyond the captivity threshold, causing irreparable damage to the growth and development of plants [4]. The growth and development of plants cover a large number of biological, chemical reactions and sensitivity to high temperatures. Heat stress affects almost all plant processes, from germination to yield [5 - 8]. Severe cellular damage or even cell death occurs within minutes under high temperatures, which leads to the fatal collapse of cellular association [9]. Damage or death caused by HT includes protein degeneration, increased membrane lipid fluidity, and changes in enzyme reaction efficiency, resulting in metabolic imbalances.

3.1. Germination Stage

Germination is the first step of plant development to be impacted. As previously stated, several plant species experience a drop in germination percentage as a result of HT stress. High temperatures also damage plant germination, seedling vigor, and radicle and plumule development [10 - 12]. HT affects seed germination differently depending on the plant species. Heat stress harms a variety of crops during seed germination, albeit the temperature ranges differ per crop type. Heat stress has a variety of negative effects on geminated seedling germination percentage, plant emergence, seedling vigor, radicle and plumule development. Seed germination is also inhibited at high temperatures, which is caused by the induction of ABA. Under HT, Cell size is reduced due to the loss of cell content, and ultimately, growth is affected. Another reason for the relative growth rate (RGR) decline is the reduction in the net assimilation rate (NAR) of HT in corn, wheat, and sugarcane.

3.2. Photosynthesis

One of the heat-sensitive physiological processes in plants is photosynthesis. The photosynthetic capability of C3 plants is significantly higher than that of C4 plants when temperatures are high [13]. Under the influence of HT, the carbon metabolism of stroma and the photochemical reactions of thylakoid lamellae are the main locations of damage to chloroplasts [14]. The thylakoid membrane is extremely vulnerable to HT. Under HT, considerable changes in chloroplasts occur, including thylakoids' structural organization, grana stacking loss and grana inflammation. Photosystem II activity is greatly decreased, if not stopped, at high temperatures. The number of photosynthetic pigments is likewise reduced by HT. Heat resistance is directly linked to plants' ability to stimulate the exchange of leaf gases and the rate of CO_2 assimilation when temperatures are high. The state of the leaf water, the transmission of the leaf stomata and the concentration of CO_2 between the cells are affected by heat stress. Closure of the stomata Photosynthesis is further hampered by high temperatures, which affects intercellular CO_2. Heat stress induces lipid peroxidation in the chloroplast and

CHAPTER 6

Molecular Studies and Metabolic Engineering of Phytohormones for Abiotic Stress Tolerance

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Abstract: Agricultural productivity across the world is affected by varied abiotic stresses, which require the development of crops tolerant to unfavorable conditions without considerable yield loss. In recent times, considerable importance has been given to phytohormones because of their versatile functions in plant responses to environmental constraints and for their role in the regulation and coordination of the growth and development of plants. Research on phytohormones has shed light on the role of classical and new members of phytohormones in alleviating the harmful effects of abiotic stresses on crop plants, so understanding phytohormone metabolism and its engineering could be a potent and novel approach for developing climate-resilient crops. The present chapter presents a short description of classical and new members of phytohormones and their role in alleviating varied abiotic stresses. Furthermore, molecular and genetic engineering efforts undertaken for the development of crops tolerant to abiotic stresses are also presented along with research gaps and challenges for the utilization of phytohormones for the development of abiotic stress-tolerant plants.

Keywords: Auxins, Brassinosteroids, Phytohormones, Phytohormone engineering, Salicylic acid, Strigolactones.

1. INTRODUCTION

The rising human population, coupled with climate changes, is putting unprecedented pressure on the agricultural system, necessitating a significant rise in the production and yield of crops. Several types of abiotic and biotic stresses are the key reasons for low agricultural productivity [1]. Abiotic stresses like drought, salinity, temperature (chilling or freezing), heat, ultraviolet radiations, weak and intense light, and gaseous pollutants of the atmosphere (sulfur dioxide, ozone) are affecting crop productivity to a great extent [2]. By the end of 2050,

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agricultural production would have to increase by 70% to feed an additional nearly two and a half billion people [3]. All these factors have necessitated the development of stress-tolerant cultivars to mitigate a wide array of stresses in different agro-climatic conditions. Plants have distinct and much more complicated systems for environmental stress response and tolerance than animals [4]. Owing to complexity, traditional breeding strategies have had limited success with stress tolerance traits. The development of plant biotechnological tools and the use of genetic engineering has offered an effective solution to address the limitation of conventional plant breeding for the development of plants tolerant to stresses [5]. In the recent past, because of multidimensional functions in response to abiotic stress, phytohormones have received great consideration.

Phytohormones are substances that are produced in very small amounts yet have the ability to control a range of cellular processes in plants. They function as signaling molecules in plant species to convey cellular activity [6]. Phytohormones serve an important function in the regulation of numerous signal transduction pathways at the time of perceived stress. They control both exterior and internal stimuli [7]. Besides classical phytohormones, newer members of phytohormones may offer effective targets for metabolic engineering for developing climate-resilient crops with a higher yield. The present chapter reviewed phytohormones and their functions in various aspects of abiotic stress tolerance, along with their molecular and metabolic engineering efforts undertaken to develop plants to boost agricultural production and productivity.

2. PHYTOHORMONES MEDIATED ABIOTIC STRESS TOLERANCE

To respond to diverse external and internal stimuli, plants must control their development and growth [8]. These responses are mediated by phytohormones, a varied group of signaling chemicals present in minute amounts in cells. Their importance in enabling plant acclimatization to ever-changing environments through nutrient allocation, source/sink transitions, and regulating development and growth has long been recognized [9]. Plant response to abiotic stressors is influenced by a variety of factors, but phytohormones, the most significant endogenous chemicals for influencing molecular and physiological responses, offer adaptive responses for the plant in stressed conditions [9]. Phytohormones can operate at their production location or anywhere in the plant once transported [10]. Plant development and plastic growth rely heavily on phytohormones.

2.1. Abscisic Acid (ABA)

It is an abiotic stress hormone because of its particular and responsive effect on plant adjustment or adaptation to abiotic stresses. It gets its name from its function related to the abscission of plant leaves. The plastidial methylerythritol 4-phosphate (MEP) pathway produces it as an isoprenoid plant hormone. The creation of storage lipids and proteins, embryo morphogenesis, stomatal opening, seed development and dormancy are only a few of the physiological processes and developmental stages in which ABA plays a role [11]. The function of ABA during stress resilience has attracted a lot of interest since it is regarded as an important messenger during adaptive responses of plants to abiotic stress. The rapid increment of endogenous abscisic acid indicates that the plant is responding to environmental stresses by activating certain signaling pathways and altering gene expression levels [12]. ABA upon transcription influences up to 10% of protein-encoding DNA sequences, according to Nemhauser *et al.* [13]. Abscisic acid also serves as an internal stimulus for plants, allowing them to thrive in harsh environments [14]. Under water-stressed situations, ABA is critical for plants to communicate with their shoots about stressful issues near the roots, which leads to water-saving anti-transpirant behavior such as reduced leaf growth and stomatal closure [15]. Under drought stress [16] and nitrogen deprivation [17], abscisic acid is also implicated in vigorous root development and other structural alterations. ABA is involved in the manufacture of protective proteins such as dehydrins and LEA proteins, as well as the translation of various genes that are involved in the stress response [18, 19]. Desiccation tolerance is conferred through the upregulation of mechanisms engaged in the manufacture of antioxidant and osmoprotectant enzymes and cell turgor pressure maintenance by ABA [20]. Zhang *et al.* [21] observed a proportionate rise in abscisic acid concentration in plants that are exposed to salinity.

2.2. Auxins (IAA)

Even though IAA has been researched for almost a century, the production, transport, and signaling routes remain unknown [22]. However, some interconnected routes for auxin production in plants have been proposed so far, including one Trp-independent and four Trp-dependent pathways [23]. Being a multifunctional phytohormone, Indole-3-acetic acid is important for plant development and growth as well as in regulating and coordinating plant development and growth in stressful conditions [24]. The availability of an auxin production, signaling, and transportation system in single-celled green algae has demonstrated auxin's evolutionary relevance in plant adaptation to various terrestrial conditions [25]. Despite recent gains in our knowledge of auxin's role in plant development and growth, its function as a stress response regulator is still unknown [24]. Surprisingly, there is mounting proof that Indole-3-acetic acid has a key role in plant salinity stress response [9, 26]. It promotes shoot and root growth in plants that are exposed to salt or heavy metals [27, 28]. Auxin induces the transcription process of the many numbers of protein-coding genes known as primary auxin response genes, which have been detected and characterized in plants such as soybean, arabidopsis and rice [29]. Auxin is thought to be an important component of defensive responses because it regulates several genes

CHAPTER 7

Living with Abiotic Stress from a Plant Nutrition Perspective in Arid and Semi-arid Regions

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Abstract: Mitigating the negative impacts of abiotic stress is an important approach, especially if climate change scenarios are realized. It is important to develop modern applications to deliver adequate and safe food for human consumption, particularly in arid and semi-arid regions that suffer from environmental and economic stressors. The progress made by scientific research in the field of plant tolerance to stress conditions during the last decade is considerable, but it needs to supply technical support for the application. The development strategy is based on combining more than one technique to achieve the integrated management of plants under different abiotic stresses, as will be described in this chapter.

Keywords: Abiotic stress, Management, Nano-technology, Plant, Soil, Water.

1. INTRODUCTION

The food gap is increasing with the severe increase in population density (the global population will be around 10 billion in 2050) in concomitant to the decrease in food production induced by environmental stress.

Environmental factors include natural forces such as the air, water, land, minerals, and all other external factors that affect a given living organism and influence its life for development and growth, as well as danger and damage at any time. The environment can also be defined as I) everything that is around us, II) the sum of all surroundings; circumstances, conditions, people, animals, plants, things, also abiotic and biotic factors that affect an organism in a particular geographical area.

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Before talking about the environment, three important factors should be determined; I) which kind of environment; natural, biophysical, historical or social environment, *etc*., II) the studied living organisms such as humans, animals, or plants, and III) the specific geographical region; humidity or arid region, *etc*.

Environmental stress is defined as the pressure caused by natural events (Drought) or by peoples' activities (Pollution). Natural environmental stress (Ecological stress) is divided into two main types; biotic (The negative impact induced by living organisms such as parasites and pathogens; bacteria, viruses, nematodes, fungi, or insects) and abiotic (the damage caused by non-living factors) stress. The ability of plants to resist and survive under the stress is termed living with stress.

As well known, most of the newly reclaimed soils in Egypt are affected by more than one ecological stressor. Therefore, this work aims to give an overview of the modern techniques in living with abiotic stress as an important part of natural environmental stress and alleviate its impact on plant production under arid and semi-arid conditions.

2. BACKGROUND AND REVIEW OF LITERATURE

2.1. The Ecological Factors Related to Plant Production

The ecological factors are the summations of different components that affect plant survival, human health, and the economy. These factors can be classified into biotic factors that are related to living organisms (plants, animals, insects, and microorganisms) and abiotic factors which related to climate (temperature, light, precipitation, humidity, wind, and gases), topography (altitude, slope), soil, water, nutrients, *etc*.

The unfavorable ecological pressures are called ecological stressors. Only 3.5% of the global lands are not affected by ecological stress, according to the FAO report 2007 [1].

The ecological stressors are split into two primary kinds; biotic (pathogens and pests) and abiotic stress. Salinity (water or soil), water stress (drought or flooded), temperature (high or low), light (high or low) in addition to soil, water, or atmospheric pollution (heavy metals HMs, organic contaminants, high radiation, sound, magnetic and electrical pollution) caused by worse agriculture practices like unbalanced fertilization and excessive pesticide, the industry's wastes and fires which produced nitrogen oxides, hydrocarbons, hydrogen chloride, sulfur dioxide and dust as very dangerous contaminants Fig (**1**).

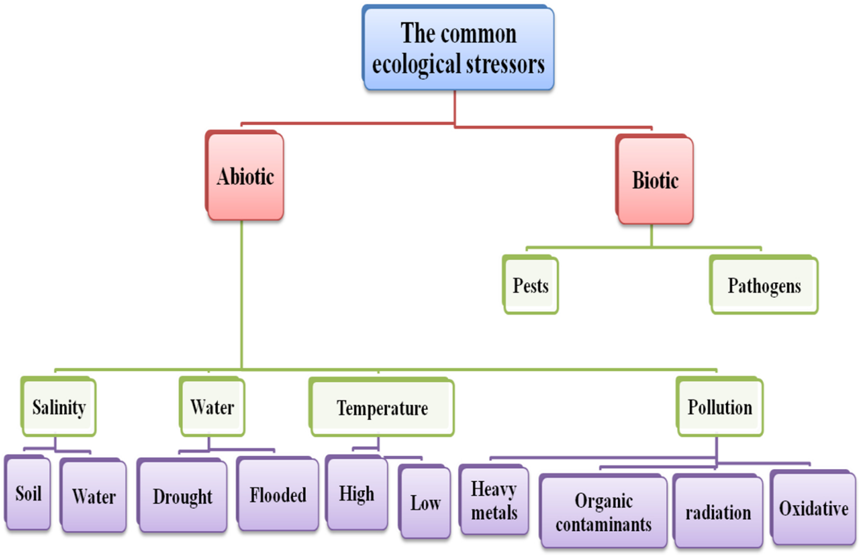

Fig. (1). The common ecological stressors that affect plant survival.

2.2. The Abiotic Stressors Under Arid And Semi-Arid Regions

Abiotic stress is the adverse effect of non-living forces on plant growth and yield below optimum levels in a specific region. The combinations of abiotic stressors are more harmful than occur solely [2].

Salinity, drought, high temperatures, and pollution with HMs are the most common stress on plants in arid and semiarid regions.

2.2.1. Salinity

Salinity is considered the major abiotic stress caused by natural events, for example, salty water, parent rock, oceanic salts, low precipitation, and higher evaporation, or by peoples' activities like incorrect cultivation management [3]. It’s responsible for I) osmotic imbalance, thus low soil water availability for plants, II) ion-specific toxicities or imbalance causing decreasing nutrient uptake, consequently, affecting plant physiology (photosynthesis activity, inhibiting plants metabolism and chlorophyll content) [4]. It is estimated that about eight hundred million hectares of land are salt-affected soils [5]. The categories of saline soils are defined in soil classification literature by The Natural Resources Conservation Service (NRCS), as shown in Table (**1**).

CHAPTER 8

Understanding Molecular Mechanisms of Plant Physiological Responses Under Drought and Salt Stresses

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Abstract: The change in global climate patterns raised issues related to soil salinization, desertification, unseasonal rains, and droughts which directly or indirectly influence agricultural produce. Plants have some level of tolerance towards various stresses, and this tolerance capacity varies among plant species based on their genetic constitution and evolutionary adaptability. Abiotic stress sensing and responses in plants involve complex pathways containing multiple steps and genes. To survive in stressful conditions, plants need to adjust their physiological and metabolic processes. Adjustments in these processes involve complex changes at the molecular level resulting in a plant's adaptation at a morphological and developmental level, which in turn impacts agriculture yields (biomass). Here in this chapter, we are emphasizing molecular dissection of the physiological responses towards salt and drought stress. The study of salt and drought stress responses in plants is also important from an agricultural perspective. We aim to provide up-to-date advancements in the molecular biology field to explain 'stress sensing to stress response' in plants which involves multifaceted pathways and networks. We will be covering the process starting from sensing, transfer of signals, regulation of gene expressions, synthesis of osmolytes-metabolites, ROS scavenging pathways, *etc.*., involved in the survival of plants. This chapter will specifically address information regarding salt and drought stress effects and responses in plants.

Keywords: Drought, Environmental Stress, Molecular Physiology, Salt, Signaling.

1. INTRODUCTION

Different plants belonging to various climatic zones have different stress tolerance potentials, which are based on their genetic constitution and evolutionary evolved adaptability. When plants experience stress, they tend to overcome it by changing physiological and metabolic processes which affect growth and development and

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assist the plants to handle stressful conditions. According to various reports, the agriculture sector would be highly impacted in the near future due to changing climate, which has increased the weather extremities. It has been noted that the number of warms days also increases in a year [1].

Majorly tropical and sub-tropical regions of the world are getting affected by heat stress and interrelated consequences [2]. Salt stress or salinity stress also negatively impacts the overall yield of the crops [3].

There are different reasons for salt stress, like using poor-quality water, which contains a high amount of soluble salts in irrigation [4]. Studies suggest that approximately 800Mha of land is affected by salt stress [5]. It was also reported that the presence of a high amount of salt in soil interferes with the absorption of other nutrients [6]. The major traits affected by salt stress are germination, leaf area, height, reduction in water uptake capacity, root architecture, *etc.*. [7 - 10]. In broad terms, salt stress causes osmotic stress and ionic toxicity. If we compare the osmotic pressure in plant cells and soil solution under normal conditions, the plant cells have high osmotic pressure. In salt stress conditions, the osmotic pressure in soil solution becomes more than that of plant cells. This restricts the flow of water into the plants. This flow of important minerals like K^+ and Ca^{2+} is also restricted. To avoid the ill effects of Na^+ and Cl^-, plants generally adopt sequestration of these ions in a cellular compartment like a vacuole.

Drought or water shortage also has a great impact on the agriculture sector. The change in rainfall patterns due to climate change is a major challenge in the agriculture system [11]. Most agriculture depends upon rainfall for irrigation purposes [12]. Common effects are a decrease in plant height, leaf area, leaf curl, small flowers and fruits, leaf senescence, destruction of photosynthetic pigments, and ultimately, effects on the yield of the crops [13 - 16]. The acclimatization of drought stress doesn't work in many crops as many of them are annual and harvested in a single generation only. To cope with drought stress, we need a better variety of seeds that have stress tolerance capacity and remain minimally affected due to stress conditions. Any kind of stress ultimately impacts the yield of crops. The change in the morpho-physiological form of plants can help them to survive the stress, but that creates huge agroeconomic losses.

In this chapter, we will be covering the process starting from sensing and transfer of stress signals, regulation of gene expressions, synthesis of osmolytes-metabolites, ROS (Reactive Oxygen Species) scavenging pathways, *etc.*

1.1. Signaling Mechanisms Under Salt Stress

Till now, the exact mechanism of salt stress perception/sense is not known.

Whether there is any receptor or sensor present on the plasma membrane is also not known. There are different signaling mechanisms present in plants that get activated under stress.

- Calcium-based pathway: It was reported that during salt stress, the cytosolic concentration of calcium ions increases. The rise of calcium ions initiates further downstream transfer of signals [17]. Calcium-dependent protein kinases (CDPKs), calcineurin B-like proteins (CBLs), and CBL-interacting protein kinases (CIPKs) were also reported to regulate gene expression under hyperosmotic stress [18 - 19]. Besides these, various other TFs are known to be directly activated by the calcium ions like MYBs, GTLs (GT element-binding like proteins), Calmodulin-binding transcription activators (CAMTAs), *etc.*. [20 - 22].
- The protein kinases pathway: The activation of Mitogen-Activated Protein Kinases (MAPKs) is well known in the transduction of signals in stress conditions. The activation of the MAPK pathway affects the expression of various transcription factors involved in stress which alter the gene expression. The MAPK cascade is generally activated by ROS generation due to stress [23].
- Cyclic Nucleotides: The level of cGMP under salt stress gets increased and activates two different cascades with and without calcium involvement. It was also shown that cGMP inhibits sodium influx in the cells [24 - 28].
- SOS (Salt overlay sensitive) signaling pathway: SOS-dependent signaling pathway constitutes a major ion homeostasis maintenance system. It is one of the major cell sodium exporters. The discovery of the SOS system allowed a better understanding of salt stress signaling [29].
- ABA-dependent pathway: salt stress also activates the ABA-dependent pathway. It was also noted that the ABA level increases in plant cells when treated with salt and affects downstream signaling [30]. ABA influences the expression of various stress-responsive transcription factors, which in turn regulate the expression of several genes involved in ABA biosynthesis like zeaxanthin epoxidase, z9-cis-epoxy carotenoid dioxygenase, the aldehyde oxidase gene, *etc.* [31 - 32].
- Lipid pathway: Plasma membrane contains many lipid derivatives. Phospholipids, phosphatidic acid, sphingolipids, *etc.* Most lipid-based molecules act as secondary cellular messengers involved in the signaling cascade [33] Fig (**1**).

CHAPTER 9

Salt Stress and its Mitigation Strategies for Enhancing Agricultural Production

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Abstract: In agriculture, salinity has been a major limiting factor in food security. Soil salinity has been shown to limit land utilization and crop productivity. It is especially crucial to avoid such losses as the ever-increasing global population imposes a tremendous amount of pressure on human populations to produce more food and feed. Salt stress has a negative effect on the whole plant and can be seen at all phases of growth, including germination, seedling and vegetative stages. Tolerance to salt stress, on the other hand, varies with plant developmental processes and even from species and cultivars. Salinity in the agricultural system can be managed by adopting various mitigation strategies. To maintain higher productivity in salt-affected environments, salt-tolerant genotypes must be introduced, as well as precise site-specific production systems. Recent advances in genetics and biotechnology, along with traditional breeding methods, provide the potential to create transgenic cultivars that perform well under stress. Exogenous treatment of certain osmoprotectants and growth regulators, as well as nutrient management and seed rejuvenation strategies, may be beneficial for cost-effective agricultural production in saline soils

Keywords: Acid Soil, Bio-Saline Agriculture, Management Practices, Phytoremediation, Salt-Affected Soil.

1. INTRODUCTION

Since the 21st century, global water resource scarcity, increased salinization, and pollution of soil and water have become major concerns for environmentalists. Problem soils are characterized by where most plants and crops cannot be produced efficiently, and are not fertile or productive, resulting in a significant reduction in cultivated land area, yields and quality. They have substantial physical and chemical constraints on the growth of most plants, like sodicity,

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salinity, acidity, and reduced soil fertility. According to Beltran and Manzur (2005) [1], the total area under salt-affected soils, comprising sodic and saline soils, is 831 mha in the world, whereas, in India, it is about 6.7 mha. Soil acidity affects ~48 M ha of India's 142 M ha of arable land, with 25 M ha having a *p*H below 5.5 [2]. The salt-affected area continues to increase each year, hence, we need to adopt proper agronomic and soil management practices to revive the productivity of problem soils. To alleviate this, lime and/or alternate soil amendment materials, as well as other management strategies, are required. Apart from enhancing production, lime application improves fertilizer efficiency, protects the environment and raises farmers' net profit [3]. Organic amendments, such as biochar, biogas slurry, fly ash, and other organic amendments, on the other hand, have been demonstrated to be beneficial in restoring acid soils. To avoid excessive salt buildup, irrigation water needs to be provided in an excess amount of what is required for crop evaporation. When evapo-transpiration needs are low, in cold weather, and with high humidity, leaching is more efficient in preventing salt accumulation in the root zone. Other options include green manuring, mulching, and salt scraping, along with new technologies such as phytoremediation and bio-saline agriculture offer a way to grow salt-tolerant crops in adverse conditions. Biochar application reduces soil electrical conductivity and exchangeable Na percentage to an acceptable range [4]. The microbial and biological activity of sodic soils has been reported to improve when they are covered by trees, grasses, or any cultivable crops [5]. Those agronomic interventions can improve the biological, physical, and chemical properties of problem soil, which ultimately leads to an increase in crop productivity and sustainable yield. It is necessary to develop salt stress-tolerant crop varieties through breeding and plant genetic modification, but this is a time-consuming process, while agronomic interventions to relieve stress might be a more cost-effective and eco-friendly approach that could be framed in a shorter period. Hence to restore agricultural production under constrained resource conditions, it is necessary to integrate soil, water, forest, and biological resources and adopt these practices in an integrated manner that would be a greater step toward the restoration of problem soils.

2. BACKGROUND

The world population crossed 6 billion in 2000 and is expected to approach 11 billion by 2100. The world's demand for food, fiber, and bio-energy products will grow at an annual rate of 2.5% and that of developing countries at 3.7% [6] as against the annual growth of only 1% in the output. Among the total land resource of 13.5 billion ha in the world, roughly 3.03 billion ha (22%) is potentially available for cultivation, out of which only one-half (1.5 billion ha) is cultivated due to some constraints. Therefore, very limited land is available for cultivation. In comparison to the global scenario, the situation in India is grimmer with a geographical area of 329 M ha (2.3% of the total world's land), supporting about 18% human population and 15% livestock population. The amount of arable land per person is only 0.15 ha, and by 2025, that number is predicted to drop to 0.08 ha.

Owing to increase demographic pressure on the limited soil resource and unscientific practices adopted for short-term gains to meet mounting multiple demands without consideration of long-term sustained productivity, the global economy governed by urbanization, industrialization, and other developmental activities is outpacing the "land capability." As a result, grave worries about environmental and land degradation as well as a slowing rate of productivity growth, have gained prominence recently. Every year, 5-7 million hectares of arable land are lost to deterioration, and 2 billion ha of land have already undergone some form of degradation. According to estimates, soil degradation has a relative impact of 39% in Asia, 25% in Africa, 12% in South America, 11% in Europe, and 5% in Oceania. India is one of the poorest developing nations, with a high population density. The NBSS&LUP estimates that 148.9 million hectares of degraded land are affected by water erosion, followed by 13.5 million by wind erosion, 13.8 million by chemical degradation, and 11.6 million by physical degradation.

The agricultural situation in India is fast changing in response to the numerous stressors that cultivated areas are facing Fig (**1**). The agricultural sector cannot afford to wait and must act now. In the production-to-consumption chain, manage change and meet the rising and diverse needs. Nearly variable rainfall affects 7.0 million acres of agricultural land. In the country, there are various levels of salt concerns. As a result of secondary irrigation commands with salinization and lift irrigated projects, an increase in agriculture's reliance on poor seawater intrusion and brackish water aquaculture in coastal regions, as well as quality waters in semi-arid and desert regions, the problem's location is predicted to worsen shortly. India's anticipated area under salt-affected soils by 2025 is 13 million ha Table (**1**). Problem soils are the soils whose productivity is lowered due to inherent unfavorable soil conditions *viz*., salt content and soil reaction. Through agronomic research, agronomists have played and will continue to play a crucial role in managing these lands and boosting productivity. They have developed a thorough understanding and improved contingency plans based on resource-efficient, socioeconomically viable, and ecologically sound technologies to deal with salt-affected soils in a climate variability scenario.

Numerous studies have been conducted on the characteristics of moisture retention [7, 8]. Studies on water transmission characteristics gained a lot of interest in sodic soils with varied ESP and pH. By this time, soil scientists and agronomists had discovered that cation exchange equilibrium is the most crucial element in determining how salt-affected soils react to reclamation methods. It is a perplexing situation where, on the one hand, the limited soil base must produce more to keep up with the demands of a constantly growing population, but on the other, vast areas are either losing their ability to support agriculture or are

CHAPTER 10

Impact of Heat Coupled with Drought Stress on Plants

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Abstract: Various stages of plant growth and development could greatly be affected by abiotic stresses. Among them, two significant abiotic stressors, including drought and heat, hinder crops' vegetative or reproductive growth stages, which in turn affect sustainable agriculture worldwide. The incidence of drought coupled with heat stress is increasing mainly due to global climate change. It was proved that the effect of drought coupled with heat stress is additive when compared to individual stresses. This chapter focuses on the influence of common dual-stress heat coupled with drought stress on plants. A critical understanding of how different plants respond to heat coupled with drought stress would pave the way to developing suitable agronomic management practices for better crop genotypes with improved productivity.

Keywords: Drought, Drought coupled with heat, Heat stress, Plant stress.

1. INTRODUCTION

Naturally, the climate tends to vary over time depending on the region. Intergovernmental Panel on climate change (IPCC), in its sixth climate change Assessment Report (AR6) stated that human-induced rapid climate change, apart from natural climate variability, imposes a risk to the ecosystem [1]. Climate change aggravates the occurrence, duration, severity and impacts of some types of weather events, such as increased floods, drought, long-duration heat, or dry spells. These intense extreme events have an adverse impact on agriculture and, thus, food availability [2, 3].

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Plants are exposed to either single stresses or multiple stresses in nature. Plant molecular responses to individual or single abiotic stresses, including drought, salt stress, flooding, extreme temperatures, light, and radiation, as well as biotic interactions like pathogen attacks and herbivory, have been studied intensively [4 - 7]. In field conditions, plants may be exposed to more than one stress factor, like simultaneous salt stress and drought, UV and drought, drought and heat, and ozone and drought [8 - 12]. Pollution leads to heavy metal contamination of sites and increased carbon dioxide concentration. Some plants are exposed to elevated CO_2 and drought, elevated CO_2 and heat stress conditions [13, 14]. Plants in contaminated sites are exposed to drought and heavy metal stress, salinity and heavy metal stress [15 - 20]. Nevertheless, more attention has been paid recently to finding the molecular mechanisms beneath interactive impacts between a combination of stresses or multiple stresses which occur simultaneously or in a sequence one after the other [21]. Further, plants may be exposed to concurrent biotic and abiotic stress factors like pathogens and drought [22, 23]. The present situation of environmental factors, besides their adverse effects on all metabolic activities of plants, made several researchers concentrate their investigation on plant stress. Progress has been made in understanding the effect of the combination of stresses to some extent on plant growth. Often, plant responses to combined stresses are not similar to individual stress responses. A combination of stresses can have synergistic or antagonistic effects on plants.

Plants ought to continuously endure a set of abiotic and biotic stressors. The sensitivity of the plants to stress depends upon the intensity and temporal extent of stress in addition to the progressive stage of the plant [24]. Plants defend themselves from stressors by responding rapidly and efficiently. Their ability to cope rests on the quick perception of changes in the environment, signal transduction within the plant, and the expression of various responses for adaptation. Adaptations of plants to stress could progress agricultural production under any adverse conditions [25, 26]. Understanding the elicitation of different signaling pathways to the specific combination of stresses is important as a response to a different combination of stressors is unique and sometimes specific to species, genotypes, and cultivars.

Food crops in arid and semi-arid regions are frequently exposed to drought coupled with heat stress due to erratic precipitation and high temperatures. The co-occurrence of prolonged heat waves with severe dry spells has increased worldwide in recent decades [27 - 34], and further, climatic models predicted drought and heat wave incidence to increase in the future [35]. Simultaneous exposure to acute or prolonged drought and heat waves causes enormous losses in agricultural yield [36, 37]. So far, our current knowledge on plant responses to drought coupled with heat stress is still limited. Understanding vital plant mechanisms responding to drought coupled with heat stress is vital for the production of dual stress-tolerant crops. In this chapter, we focus on the drought coupled with heat stress associated with physiological, morphological, and molecular changes in plants.

1.1. Morpho-physiological Responses to Drought Coupled with Heat Stress

Drought concurrent with heat stress might happen either in the vegetative or reproductive stages of plants with varied effects on the yield along with biomass of different crops [37, 38]. This stress combination has a profound effect on germination, root, tiller, stem and leaf development, root architecture, photosynthesis, carbon assimilation, and dry matter production at the vegetative growth of plants. Floral initiation, pollen fertility, fertilization, panicle exertion, seed growth, and seed filling are the reproduction stages affected by heat coupled with drought stress [39, 40]. Despite that, occasionally, the adverse effects at one stage could be indemnified by the retrieval and also further development of another organ. For example, lesser root emergence was frequently indemnified with enhanced tillering. Plenty of seeds were inhibited by partly filled seeds. Low grain yield has been indemnified by improved grain quality [41]. The reactions of plants to drought coupled with heat stress are given in Fig (**1**).

1.2. Plant Growth

The foremost effect of stress is on the germination and seedling phase of plants. Seeds initiate biochemical changes as soon as the imbibition of water is completed. Seed imbibition of water has relied on soil water accessibility. Drought hinders imbibition and consequently leads to diminished germination rate and germination percentage. Heat stress caused by temperatures above optimum temperatures reduces total germination percentage. Drought, coupled with heat stress, even decreased the germination percentage [42]. Studies on *Arabidopsis thaliana* have shown that drought coupled with heat stress reduces plant growth more than individual stress [43, 44]. The heat coupled with drought stress, decreased the morphological parameters in maize [45]. Leaf temperature increased in combined stress conditions in maize [46]. The desert plant, *Artmesia sieberi alba,* showed a decline in vegetative growth [47].

1.3. Root System

Roots are considered important for plant yield. They provide water and nutrient uptake, anchorage to the plant, and act as storage organs. Root architecture refers to root length, spread, number, and lateral root length that help in the acquisition of resources required for root growth. Root architecture plays an important role in plants' adaptation to abiotic stress. Roots sense the stresses first as they grow underground and alter their genetic program to survive the stress [48]. Root plasticity is triggered through differences in the growth of root constituents, number, placement and extension [49]. These variations in root architecture subsequently influence shoot growth and development [50] by altering carbon allocation to shoots. Drought coupled with heat stress in maize primary roots

SUBJECT INDEX

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