



Water Stress and Crop Plants

Water Stress and Crop Plants

A Sustainable Approach,
Volume 1

EDITED BY

Parvaiz Ahmad

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Dedicated
to



Hakim Abdul Hameed
(1908–1999)
Founder of Jamia Hamdard
(Hamdard University)
New Delhi, India

Contents

List of contributors, ix

About the editor, xiii

Foreword, xiv

Preface, xvi

- 1** Drought stress and photosynthesis in plants, 1
Zoya Siddique, Sumira Jan, Sameen Ruqia Imadi, Alvina Gul, and Parvaiz Ahmad
- 2** The role of crassulacean acid metabolism induction in plant adaptation to water deficit, 12
Ghader Habibi
- 3** Stomatal responses to drought stress, 24
Hadi Pirasteh-Anosheh, Armin Saed-Moucheshi, Hassan Pakniyat, and Mohammad Pesarakli
- 4** Recurrent droughts: Keys for sustainable water management from case studies of tree fruit orchards in central Chile, 41
Estrella Garrido and Enrique Misle
- 5** Global explicit profiling of water deficit-induced diminutions in agricultural crop sustainability: Key emerging trends and challenges, 58
Shweta Singh, Durgesh Kumar Tripathi, Nawal Kishore Dubey, and Devendra Kumar Chauhan
- 6** Sustainable agricultural practices for water quality protection, 75
Fabio Stagnari, Sumira Jan, Galieni Angelica, and Pisante Michele
- 7** Salinity and drought stress: Similarities and differences in oxidative responses and cellular redox regulation, 86
Mohammad Nesar Uddin, Mohammad Anwar Hossain, and David J. Burritt
- 8** Oxidative stress and plant responses to pathogens under drought conditions, 102
Murat Dikilitas, Sema Karakas, Abeer Hashem, E.F. Abd Allah, and Parvaiz Ahmad
- 9** Potential usage of antioxidants, hormones and plant extracts: An innovative approach to taming water stress limitation in crop plants, 124
Sibgha Noreen, Seema Mahmood, Habib-ur-Rehman Athar, Zafar Ullah Zafar, and Muhammad Ashraf
- 10** Water stress in plants: From gene to biotechnology, 142
Kilani Ben Rejeb, Maali Benzarti, Ahmed Debez, Arnould Savouré, and Chedly Abdelly
- 11** Plant aquaporin biotechnology: Challenges and prospects for abiotic stress tolerance under a changing global environment, 150
Syed Sarfraz Hussain, Muhammad Asif Ahsan, Bushra Rashid, and Bu-Jun Shi
- 12** Role of proteins in alleviating drought stress in plants, 165
Kaouther Feki and Faical Brini
- 13** Avenues for improving drought tolerance in crops by ABA regulation: Molecular and physiological basis, 177
Hamid Manzoor, Habib-ur-Rehman Athar, Sumaira Rasul, Tehseen Kanwal, Muhammad Shahzad Anjam, Muhammad Kamran Qureshi, Nahidah Bashir, Zafar Ullah Zafar, Muhammad Ali, and Muhammad Ashraf
- 14** MYB transcription factors for enhanced drought tolerance in plants, 194
Sónia Gonçalves
- 15** Analysis of novel haplotype variation at *TaDREB-D1* and *TaCwi-D1* genes influencing drought tolerance in bread/synthetic wheat derivatives: An overview, 206
Maria Khalid, Fakiha Afzal, Alvina Gul, Mohammad Abass Ahanger, and Parvaiz Ahmad
- 16** Toward integration of a systems-based approach for understanding drought stress in plants, 227
Syed Sarfraz Hussain, Muhammad Asif Ahsan, Pradeep Sornaraj, Muhammad Ali, and Bu-Jun Shi

- 17** miRNA/siRNA-based approaches to enhance drought tolerance of barley and wheat under drought stress, 248
Bu-Jun Shi and Syed Sarfraz Hussain
- 18** MicroRNAs and their role in drought stress response in plants, 261
Narghes Morad-Talab and Roghieh Hajiboland
- 19** Sugar signalling in plants: A novel mechanism for drought stress management, 287
Poonam, Renu Bhardwaj, Neha Handa, Harpreet Kaur, Amandeep Rattan, Shagun Bali, Vandana Gautam, Anket Sharma, Puja Ohri, Ashwani Kumar Thukral, Geetika Sirhindi, and Saroj Arora
- 20** Agricultural, socioeconomic, and cultural relevance of crop wild relatives, in particular, food legume landraces, in Northern Africa, 303
Siham Tellah, Mourad Latati, Mohamed Lazali, Naima Ghalmi, Ghania Ounane, Sidi Mohamed Ounane, Agostino Sorgonà, and Maurizio Badiani

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Editor of 14 volumes (1 with Studium Press Pvt. India Ltd., New Delhi, India, 9 with Springer, New York, 3 with Elsevier USA, and 1 with John Wiley & Sons, Ltd). He is a recipient of the Junior Research Fellowship and Senior Research Fellowship by CSIR, New Delhi, India. Dr. Parvaiz has been awarded the Young Scientist Award under Fast Track scheme in 2007 by the Department of Science and Technology (DST), Govt. of India. Dr. Parvaiz is actively engaged in studying the molecular and physiobiochemical responses of different agricultural and horticultural plants under environmental stress.

Foreword

Humans started their community life nearly 10,000 years back by beginning to gather and cultivate plants and domesticate animals. In this way the foundations for agriculture were laid as an important part of life. A great development has taken place since then, but still a large population is suffering from hunger in different countries. Land degradation is leading to tremendous soil losses and different types of stresses are posing great threat to the soil productivity, which in turn is affecting plant growth and development ending up with decreases in the crop yields.

On the other hand, demographic developments are posing another threat and attempts are to be made to combat this grave situation in order to feed the hungry. Plant scientists are trying hard to develop plants with higher yields and those which can be grown on marginal lands. They are working hard to develop techniques with latest technologies to understand the molecular, physiological, and biochemical pathways in order to meet the global agricultural needs by overcoming the stresses affecting the yield.

Water is the most critical resource for a sustainable agricultural development in the world. It is a must for the agriculture as an important part of our environment. The problems arising from under and overirrigation emphasize the fact that humans cannot continue with the current use and throw away policy with their natural resources; in particular, regarding water. The area of irrigated lands is reaching a level of nearly 500 million ha and approximately 20% of these irrigated lands provide only 50% of the global food supply. Expectations are that the need for irrigation water will increase far more by 2025. Water scarcity will cause stress problems in plants. In view of this we have to look for the possibilities to overcome water shortages in the agriculture so as to increase the water use efficiency, use marginal lands, marginal waters, and techniques to overcome stress problems in plants to feed hungry mouths.

This volume is therefore a compilation of different perspectives from around the globe that directly or

indirectly lead us to understand the mechanism of plant stress tolerance and mitigation of these dangerous stresses through sustainable methods.

Chapter 1 deals with the drought stress and photosynthesis in plants. Here, the authors give details regarding the effect of drought on photosynthesis in plants, stomatal and non-stomatal limitation of photosynthesis during drought stress, resistance of plants to drought stress, and effect of drought stress on leading plants.

Chapter 2 discusses the role of crassulacean acid metabolism induction in plants as an adaptation to water deficit; physiological and metabolic aspects of CAM induction by drought, CAM induction and fitness under water deficit; capability of CAM to improve water-use efficiency, and productivity is also explained clearly.

In Chapter 3 authors enlighten the effect of drought stress on the functioning of stomata, and hormonal, nutritional, as well as genetic aspects under drought stress.

Chapter 4 discusses the case study under the heading of recurrent droughts with details about keys for sustainable water management from case studies of tree fruit orchards in central Chile.

In Chapter 5, global explicit profiling of water deficit-induced diminutions in agricultural crop sustainability is given as a key emerging trend and challenge; defensive mechanisms adopted by crops at whole plant level under specific drought scenarios: perception, sensing, and acclimation is also explained.

The information on sustainable agricultural practices for water quality protection are discussed at length in Chapter 6.

In Chapter 7, salinity and drought stress topics are evaluated including information on the similarities and differences in oxidative responses and cellular redox regulation; similarities and differences in ROS metabolism under salinity and drought, together with water stress \times salt stress effects on plants and possible tolerance mechanisms.

The oxidative stress and plant responses to pathogens under drought conditions are discussed at length in Chapter 8.

In Chapter 9, the potential use of antioxidants, hormones, and plant extracts are reviewed with innovative approaches in taming water stress limitation in crop plants; the authors stress upon the impact of water stress on growth and development, yield, physiological processes, oxidative stress, adaptation strategies, application for osmoprotectants, and plant extracts as antioxidants.

The main topics reviewed in Chapter 10 are water stress in plants, from genes to biotechnology, identifying the genes associated with drought tolerance and engineering drought tolerance.

Chapter 11 analyzes plant aquaporins in abiotic stress tolerance under such headings as; status and prospects, functional diversity of aquaporins in plants, aquaporin gene expression studies under abiotic stresses, and genetic manipulation of aquaporin functions in transgenic plants.

Chapter 12 presents a discussion on the role of proteins in alleviating drought stress in plants, with information on functional and regulatory proteins, QTL analysis, and breeding.

The avenues for improving drought tolerance in crops by ABA regulation with molecular and physiological basis are debated in Chapter 13; whereas MYB transcription factors for enhanced drought tolerance in plants are given in Chapter 14. Here, it also explains the molecular responses to stress, transcription factors – major players in the control of gene expression and MYB transcription factors in drought stress.

Chapter 15 presents an overview dealing with the analysis of novel haplotype variations at *TaDREB-D1* and *TaCwi-D1* genes influencing drought tolerance in bread/synthetic wheat derivatives.

The TFs, master switches with multiple roles in regulatory networks for abiotic stress tolerance, transgenic plants harboring TFs versus drought stress tolerance,

microRNAs and drought stress tolerance, a fact or fiction and systems-based approach for functional genomics in plants is discussed at length in Chapter 16.

Chapters 17 and 18 deal with the role of miRNA/siRNA to enhance drought tolerance of barley and wheat and other crops; whereas Chapter 19 demonstrates sugar signaling in plants, a novel mechanism for drought stress management together with the role of sugars, osmoregulation under drought stress, sugars as signaling molecules, and exogenous application of sugars to alleviate the drought stress.

In Chapter 20, information on agriculture, socio-economic, and cultural relevance of wild relatives of crops, in particular, food legume landraces, in Northern Africa, are well documented.

I am sure that this volume will be beneficial to the students as well as staff of agricultural faculties, agricultural engineers working in the extension services, environmentalists, and also for agro-industry workers. I extend my deepest appreciations to the editor as well as the contributors for the hard labor they have put in producing this excellent volume.

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Preface

Water stress is accepted as one of the major abiotic stresses faced on a global scale. The reasons for this could be less availability of water, which results in drought, or presence of excessive amount of water leading to waterlogging. Drought as well as waterlogging have negative impacts on plant growth and development and ultimately affect the production of crops. The primary stresses imposed here are osmotic and ionic stress, however, prolonged effects can cause secondary stress known as oxidative stress. In the latter case, the generation of reactive oxygen species is evolved, which attack the biomolecules and hamper their normal functions. Although research on impact of water stress on plants is going at high speed at global level, the effects at biochemical and molecular levels are still unclear. To understand the physiological, biochemical, and molecular mechanisms involved in environmental stress perception, transduction, and tolerance is still a challenge facing plant biologists.

Plants are equipped with different resistance mechanisms to survive under these harsh conditions. Scientists are investigating the possibilities to create water resistant crops to bring the marginal lands in to cultivation so that growing population can meet the hunger need. The current book entitled *Water Stress and Crop Plants: A Sustainable Approach* has two volumes covering all aspects of drought and flooding stress, causes and

consequences, mitigation of water stress, modern tools, and techniques to alleviate water stress and production of crop yields under water stress. The first volume includes 20 chapters enlightening the reader to different aspects with the latest knowledge and provides extensive information regarding the crop plants, their growth and development, physiological and molecular responses, together with the adaptability of crop plants to different environmental stresses.

Chapters contributed here have been published whilst keeping intact author's justifications; however, suitable editorial changes have been incorporated wherever considered necessary. We have tried our best to gather the information on different aspects of this volume, however, there is a possibility that some errors still creep in to the book for which we seek reader's indulgence and feedback. We are thankful to the authors for their valuable contributions and to John Wiley & Sons, Ltd, Chichester, particularly Gudrun Walter (Editorial Director, Natural Sciences), Audrie Tan (Project Editor), Laura Bell (Assistant Editor), and all other staff members at Wiley, who were directly or indirectly associated with us in this project for their constant help, valuable suggestions, and efforts in bringing out the timely publication of this volume.

Parvaiz Ahmad

CHAPTER 1

Drought stress and photosynthesis in plants

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1.1 Introduction

Drought is a prolonged period of water deficiency in a particular region. This deficiency can occur either in atmospheric, ground, or surface water. The deficiency of water has significant impact on agriculture of affected land. Duration of drought may vary from days to months and years. Global crop production is estimated to fall by up to 30% by 2025 in comparison to present productivity as per the World economic forum Q2 (Hasanuzzaman *et al.*, 2013). Accordingly, drought stress is enumerated among the significant threat to food security in the prevailing climate change era (Alam *et al.*, 2013). Some of the greatest famines in history mark the crucial importance of presence of water for sustenance of life, including The Great Chinese Famine, which lasted for three years from 1958 to 1961 killing millions of people and The Indian Famine, which took place from 1896 to 1902 claiming about 19 million lives. The Atacama Desert in Chile, the driest place on Earth, has witnessed world's largest drought, which lasted for 400 years from 1571 to 1971. Complex relationship amongst anthropogenic activities, terrestrial productivity, the hydrological cycle, and global demand for ecosystem services will direct amplified strain on ecosystem water demands (Bernacchi and VanLoocke, 2015). The fourth assessment report by IPCC states that a 1.1–6.4°C increase in global surface average temperature is expected during this century, which will pose an intimidating threat for continuity of life all around the globe. Climate-change scenario in many areas of the globe suggest an average increase in aridity that has

accentuated this issue and propelled the research into understanding plant response to water scarcity. Drought, along with high temperature and radiation, is one of the most important environmental constraints to growth, productivity, and plant survival (Arve *et al.*, 2011; Miller *et al.*, 2010). It is observed that when plants are subjected to diverse stress, they rephrase their growth and photosynthesis by indefinite mechanisms (Skirycz *et al.*, 2010). Photosynthesis is one of the key processes that are affected by drought stress by decreased diffusion of carbon dioxide and metabolic constraints. Intensity of drought stress, occurrence of superimposed stress, and the species that are dealing with stress, define the relative impacts of these limitations (Pinheiro and Chaves, 2011). All phases of photosynthesis are affected by drought stress. Photosynthesis mechanism involves photosynthetic pigments and photosystems, electron transport chain, and carbon dioxide reduction pathways. Damage at any level reduces overall synthetic capacity of plants (Ashraf and Harris, 2013).

1.2 Effect of drought on photosynthesis in plants

Water is a necessary factor for survival of plants. Plants must absorb water from soil in which they grow and transport it to all parts of plants in order to carry out photosynthesis. Carbon dioxide from the atmosphere enters the plants through stomata. Water from plants also exudes through stomatal openings. Transpiration pull is the key force, which pulls water upwards through

xylem vessels. As stomata open, carbon dioxide enters the leaves and water transpires. As stomata close, transpiration rate also falls. Plants can control amount of water lost from leaves with the help of stomata to adjust with the environmental conditions (Arve *et al.*, 2011). Photosynthesis is an essential process, which converts light energy into chemical energy. Productivity of plants is dependent on photosynthesis, consequently relying on ability of plants to utilize water. Carbon dioxide assimilation rate determines the speed of photosynthetic reactions occurring in plants (Athar and Ashraf, 2005). Alam *et al.* (2014a,b) observed a significant reduction in fresh, dry weight, chlorophyll content, and alteration in oxidative system and glyoxylase systems in all *Brassica* species. Various limitations are imposed on plant's physiological reactions due to changes in environmental conditions. Availability of water is necessary for plant growth and photosynthetic reactions. Mediterranean ecosystems are expected to face aggravated water scarcity due to fluctuating environmental conditions. Hence, it is imperative to maintain photosynthetic machinery functioning under drought stress. Water stress can limit photosynthesis in plants via two ways; through stomatal and non-stomatal limitations (Grassi and Magnani, 2005). Alam *et al.* (2014a,b) observed diverse response in *Brassica* species with significant decline in plant biomass, chlorophyll content, and relative water content.

Scarcity of water has a direct effect on plants at physiological, morphological, and molecular levels. All biochemical and physiological processes depend on availability of water. Lack of sufficient water limits photosynthesis and consequently affects plant yield all over the world (Flexas *et al.*, 2008). Severity and period of water loss, the stage and age of development, the cell and organ type, the species and genotype all these factors are correlated with plant's response to drought stress (Barnabas *et al.*, 2008). There is a need for understanding the effects of drought stress in plants critical for better breeding practices in agriculture and for predicting the fate of natural vegetation under drastic climate changes (Arve *et al.*, 2011). Photosynthesis and many key metabolic functions are affected by changes in water cycle, leading to consequent effects on agricultural and ecosystem productivity (Xu *et al.*, 2010). Gupta and Thind (2015) investigated the cellular redox status in wheat under drought stress and concluded yield stability and improved tolerance under glycine

betaine application. Drought stress reduces the utilization of water by plants and disturbs plant-water relations by reducing root proliferation affecting stem extension and leaf size (Farooq *et al.*, 2009). Many imminent effects on photosynthetic machinery have been observed during drought stress leading to suppression of photosynthetic genes. Moreover, transcripts encoding some glycolysis and pentose phosphate pathway enzymes are induced, which suggest that sugars are utilized during drought stress period. Elevated leaf temperature, accelerated respiration rate, stomatal closure, and reduction in photosynthetic rate are clearly observed as an effect of drought and heat shock (Rizhsky *et al.*, 2002). Significant drops of 22 and 75% have been observed in light-saturated net photosynthetic rate when extreme drought stress was induced in *Populus nigra* plants, which indicate the correlation of drought stress with a decline of photosynthesis (Xu *et al.*, 2010).

Severity of drought stress treatment controls the extent to which photosynthesis is inhibited in plants. Progressive decline of photosynthesis has been investigated in variety of grapevine cultivars that were induced to drought stress gradually. Values of stomatal conductance can be used as indicator of water stress conditions resisted by leaves; hence the effect of drought on plants can be accurately examined. Reduction of substomatal CO₂ concentration, stomatal conductance, estimated chloroplastic CO₂ concentration, and net photosynthetic rate, have been observed in grapevine cultivars thriving under drought stress conditions, whereas the ETR (Electron transport rate) remains unaffected. Increase in drought stress is accompanied by a decrease in estimated mesophyll conductance and ETR. Significant reductions in mesophyll conductance and stomatal conductance, as well as in ETR, are caused by severe drought conditions (Flexas *et al.*, 2004).

Decline in inorganic phosphate reserves in Calvin cycle could be the cause of declined photosynthetic rate, which occurs by synthesis and accumulation of sugars during drought stress. Over-reduction of the photosynthetic electron chain can be a consequence for drought-induced decline in photosynthetic rate. The excitation energy produced as a result of these events must be dissipated. This energy can be expelled out via non-photochemical quenching by xanthophylls cycle so that photosystem (PS) II can be effectively protected against increased production of

harmful reactive oxygen species (ROS). Incidences of drought stress can inevitably change division of carbon at both leaf and whole plant level by hindering the consumption and production of photo-assimilates. Hence, alterations in size of carbohydrate pool depend on the time period as well as severity of water deficit stress. However, under mild drought stress, decline in starch level is accompanied by accumulation of soluble sugars. This shift in carbon division can be adaptive and may induce ability of osmotic adjustment in plants (Praxedes *et al.*, 2006).

Two oak species (*Quercus robur* and *Q. petraea*) have been investigated for effects of drought stress on photosynthesis, under natural conditions in a 30 year-old stand. A progressive reduction in net assimilation and leaf conductance was observed in both of these species as a response to drought (Epron *et al.*, 1992). In recent research, gradual application of drought-stress on four clones of robusta coffee, representing drought-sensitive and drought-tolerant genotypes, exhibited a marked decline in stomatal conductance, which is associated with remarkable decrease in the internal to atmospheric CO₂ concentration ratio. A significant decrease in amount of starch was observed, which was independent of the amount of drought stress applied. Chlorophyll fluorescence parameters remained unaffected under drought stress in an experiment carried out on alfalfa leaves (Praxedes *et al.*, 2006). The amount of total chlorophyll content (chlorophyll b and chlorophyll a) was remarkably decreased due to drought conditions imposed during vegetative growth of plants. Mesophyll resistance determines photosynthetic rate during drought stress (Mafakheri *et al.*, 2010). Two fundamental enzymes that play a crucial role in sucrose utilization are invertase and sucrose synthase. These enzymes are more active during water scarcity, which may be the cause of accumulation of hexoses during drought stress. SPS is the fundamental enzyme that takes part in sucrose synthesis and exhibits a marked decline during drought. A considerable increase in such enzymes has been observed, which hydrolyzes starch resulting in decline of starch level with a decrease in leaf water (Praxedes *et al.*, 2006). Clauw *et al.* (2015) investigated six *Arabidopsis thaliana* accessions from diverse geographic regions and demonstrated about 354 genes with differential expression thriving in mild drought stress.

1.3 Stomatal and non-stomatal limitation of photosynthesis during drought stress

Stomatal closure is one of the major processes that occur during drought stress (Liu *et al.*, 2010). As stomata close, carbon dioxide supply for metabolism is inhibited. This occurs particularly during mild drought stress, however, according to some studies, non-stomatal factors can significantly contribute to limitation of photosynthesis during drought. These drought stress conditions can directly affect ATP synthase, which results in a restricted supply of ATP. When stomata close, the concentration of carbon dioxide in cellular spaces of leaves falls, which results in improper functioning of metabolic processes, for example, inhibition in sucrose phosphate synthase and nitrate reductase (Praxedes *et al.*, 2006).

Virlouvet and Fromm (2014) hypothesized that the system assists adaptation to upcoming dehydration stress by closing stomata and dropping water losses from homiohydric plants. Though the opening of stomata should be useful when water supplies are sufficient because improved gas exchange assists C accumulation and, therefore, the growth performance of plants oppose one another for restraining resources.

Stomatal limitation is a major factor in reduction in photosynthetic rate during drought stress, whereas non-stomatal limitation contributes to a decline in efficiency of photosynthetic system II photochemistry, unavailability of carbon dioxide in chloroplasts and decrease in Rubisco activity, which is associated with an increase in water stress intensity and duration of drought stress (Zhenzhu *et al.*, 2010). As soon as the leaf water potential falls down, carbon dioxide levels are diminished as a consequence of closure of stomatal openings, which in turn results in a decrease in photosynthetic rate (Eric *et al.*, 2006). Membrane damage and stomatal closure are major factors for declined carbon dioxide assimilation by leaves. Moreover, any disturbance that affects the functioning of enzymes, particularly those playing a part in ATP synthesis and carbon dioxide fixation in leaves, can be a major factor leading to hindrance in photosynthetic reactions (Farooq *et al.*, 2009). Photosynthetic rate in leaves decreases as a result of increase in water stress. This decrease in photosynthesis is a result of both hampered chloroplast activity and stomatal closure resulting in lower diffusion of carbon dioxide. An increased

external supply of carbon dioxide can be helpful for overcoming stomatal limitation to photosynthesis (Praxedes *et al.*, 2006).

1.3.1 Stomatal limitation to photosynthesis during drought

Stomatal conductance is extremely sensitive to physiological and environmental factors. Environmental factors like air humidity and temperature, as well as internal physiological factors like leaf water status, control stomatal opening. Water deficit stress leads to progressive curtailment of photosynthesis, which is a consequence of alteration in carbon and nitrogen assimilation. A strong relationship has been discovered between maximum stomatal conductance and nitrogen concentration in leaves (Lawlor, 2002). A high correlation (87%) was observed between photosynthesis and stomatal conductance in an experiment conducted on grapevines under water stress.

Opening and closing of stomata is regulated by changes in turgor pressure in guard cells that are present in epidermis and, hence, this process protects plants from dehydration and death during fluctuating environmental conditions. There are many factors that control stomatal limitation. Changing membrane permeability and metabolic energy play a major role in determining whether stomatal opening will remain open or closed. Leaf water status, carbon dioxide concentration, intensity of light, and chemical signals can also result in opening or closing of stomata. Hence, a complex set of factors is involved in stomatal response to drought stress (Lawlor *et al.*, 2002). Stomatal limitation leads to constraints in diffusion of carbon dioxide into intercellular spaces in leaves. It is the first major event that occurs in response to drought stress (Grassi and Magnani, 2005). A study on C4 plants indicates that stomatal conductance decreases with decreasing leaf water status, which leads to a decline in photosynthetic rate in these plants (Ghannoum, 2009).

1.3.1.1 Root to leaf chemical signaling (role of abscisic acid and cytokinins)

When the roots of plant are submerged in dehydrated and dry soil, chemical signals in the form of abscisic acid (ABA) travel upward to leaves from root and hence cause stomata to close (Athar and Ashraf, 2005). Other chemical signals besides ABA can also play their role in stomatal regulation by plants. High concentration of cytokinin in xylem vessels can cause plants to become

immune to abscisic acid concentrations, which cause stomata to open directly. Experiments reveal that as the grapevines are subjected to partial dehydration only in root zone, the cytokinin level in roots drop and stomatal conductance also decreases. This regulation of stomatal conductance by ABA is not simple and is controlled by pH level in leaf tissue and xylem sap (Lawlor *et al.*, 2002). Takahashi and Kinoshita (2014) reported that the guard cells responsible for stomatal opening and closing assist in dehydration stress memory and regulate stomatal closure following the period of relief from drought probably by enhancing ABA levels and maintaining the gene regulatory pathways.

1.3.1.2 Decline in intercellular carbon dioxide concentration

An experiment carried out on ericaceous shrub species confirmed that plants exposed to drought conditions show low gas exchange rates compared to plants grown in normal environmental conditions (Llorens *et al.*, 2004). As stomatal opening closes, the amount of carbon dioxide present in mesophyll spaces in leaves also decreases, which results in decline of carbon dioxide to oxygen ratio and a rise in photorespiration rate during water stress. Stomatal openings close completely during severe drought, which causes both photosynthesis and photorespiration rates to lower (Athar and Ashraf, 2005).

1.3.1.3 Effects on mesophyll conductance

Stomatal closure induced by drought inhibits photosynthesis by affecting mesophyll metabolism. Lower diffusion of carbon dioxide across leaf mesophyll may also cause the inhibition of photosynthesis. Studies have confirmed that drought stress cause the decrease in leaf conductance to carbon dioxide diffusion. This decreased leaf conductance may be the consequence of decreased mesophyll conductance, as suggested by decreased carbon dioxide concentration at the carboxylation site of Rubisco. Providing a high concentration of carbon dioxide can help in recovery from increased mesophyll resistance so the rate of photosynthesis can be brought back to normal (Lawlor *et al.*, 2002).

1.3.2 Non-stomatal limitation of photosynthesis during drought

Impairment of photosynthetic metabolism may occur due to low supply of ATP and NADPH, defects in electron transport, and use of assimilation products

(Pessarakli, 2005). Reduction in amount of ribulose-1, 5-bisphosphate regeneration, lesser carboxylation efficiency, decline in amount of functional Rubisco, and inhibition of functional activity in PSII leads to non-stomatal limitation of photosynthesis. Primary photochemical and biochemical processes may become inhibited as a consequence of these metabolic changes (Zlatev and Lidon, 2012). The key non-stomatal factors that lead to inhibition of photosynthesis include inhibition of nitrate assimilation, induction of early aging in plants, declined activity of photosynthetic enzymes, and changes in the leaf anatomy (Ghannoum, 2009).

1.3.2.1 Impairment of RuBP regeneration and ATP synthesis

In an experiment conducted on wheat cultivars subjected to drought stress, it was observed that the RuBP and ATP content decrease during the early stages of drought when stomatal conductance is relatively high. Therefore, both processes that include RuBP regeneration and ATP synthesis are impaired during water deficit. Photochemistry and Rubisco activity are particularly decreased as a result of drought stress and water deficit (Khakwani *et al.*, 2013). Boyer and his coworkers concluded that inhibition of ATP synthesis is a major cause of drought-induced inhibition of photosynthesis in sunflower leaves (Athar and Ashraf, 2005).

Lower levels of ATP and imbalance in NADPH status greatly affect cell metabolism (Lawlor *et al.*, 2002). In a study on sunflower plants, it was suggested that impaired phosphorylation due to low activity of chloroplast ATPase is the main factor that inhibits photosynthetic reactions in plants facing extreme drought stress. Immediately after this study, others workers confirmed that impaired Rubisco activity and RuBP regeneration also occur during periods of drought stress (Flexas *et al.*, 2012).

1.3.2.2 Impaired carbon assimilation

In an experiment carried out on grapevines grown under drought stress in fields, a progressive decline in stomatal conductance has been observed along with a sharp decline in carbon dioxide assimilation. A shift from stomatal limitation to non-stomatal limitation was observed followed by marked decline in maximum photosynthetic rate (Escalona *et al.*, 1999). Moreover, in experimental studies on mesophytic plants, drought stress significantly decreases the photosynthetic carbon dioxide assimilation (Lawlor and Cornic, 2002). Hasibeder *et al.* (2015) concluded that plants thriving

under drought regimes demonstrate that the usage of fresh photosynthates is transferred from metabolic activity to osmotic adjustment and storage compounds. There are two general types of relation of Apot to RWC (relative water content); Type 1 and Type 2. In some cases, photosynthetic potential (Apot), under saturated carbon dioxide level, is not affected by minor loss of relative water content. It becomes gradually more inhibited and is less stimulated by the increased amount of carbon dioxide, below a threshold RWC (This is type 1 response). The type 1 response consists of a decrease in stomatal conductance as a consequence of stomatal closure during mild drought stress. The photosynthetic capacity is affected only when RWC is very low. In other studies, Apot and the stimulation of carbon dioxide assimilation by elevated carbon dioxide decrease gradually with the decrease in relative water content (this is a type 2 response) (Lawlor *et al.*, 2002). This type 2 response consists of a simultaneous decrease in stomatal conductance and photosynthetic capacity as relative water content drops (Flexas *et al.*, 2012).

1.3.2.3 Increased photorespiration

Increase in density of light is accompanied by an increase in the rate of photorespiration. During drought stress, plant requirement for light is significantly decreased and excess light can damage the photosynthetic machinery leading to photoinhibition. The main target of this damage by excessive light is PS II because PSI is more stable than PS II to increase light intensity. Photorespiration or thermal dissipation are means to get rid of excess light, hence the rate of these processes also significantly increases during drought stress (Athar and Ashraf, 2005).

1.3.2.4 Production of ROS (reactive oxygen species) and damage to chloroplast ATPase

Under drought stress, the amount of reactive oxygen species also rises due to excess energy, which leads to oxidative damage in photosynthetic machinery. These ROS can be hydrogen peroxide, superoxide, or free hydroxyl radicals. ROS harm entire plant cell biopolymers, resulting in their dysfunction. They trigger plasma membrane Ca^{2+} -permeable and K^{+} -permeable cation channels plus annexins, catalyzing Ca^{2+} signaling events, K^{+} leakage, and triggering programmed cell death (Demidchik, 2015). Antioxidant molecules present in different parts of plant cells are used for scavenging these free radicals and protecting vital photosynthetic machinery (Lawlor *et al.*, 2002). A hypothesis suggests

that damage caused by ROS species to chloroplast ATPase results in a decreased rate of photosynthesis in plants during periods of low carbon dioxide and excess light (Flexas *et al.*, 2012). Shen *et al.* (2015) observed that the immense membrane damage indicates lipid peroxidation and osmolytes leakage in soybean and maize.

1.3.2.5 Shifting to carbon dioxide uptake mechanisms

Studies suggest that C4 photosynthesis is highly responsive to drought stress. The main aspect of C4 photosynthesis is the functioning of carbon dioxide concentration mechanism in leaves, which leads to the saturation of photosynthesis and suppression of photorespiration. A high carbon dioxide concentration increases the effect of water stress on plant productivity by improving plant water status and soil moisture due to decrease in leaf transpiration and stomatal conductance in C4 plants under drought stress (Ghannoum, 2009). This evolution has led to efficient use of water in these plants and increased rate of photosynthesis, and has been the cause of ecological success of these plants.

CAM plants also have a unique mechanism to deal with drought stress. CAM plants absorb carbon dioxide through stomata during the night and fix this carbon dioxide into carbohydrates during the day time, which has greatly increased the survival chances of these plants in arid regions. Inducible CAM plants exhibit exclusive machinery to deal with drought stress. These plants normally use C4 photosynthetic pathway but when they are exposed to drought stress, they switch to water-efficient CAM photosynthesis. Drought stress results in upregulation of some genes and downregulation of others in order to accumulate a set of enzymes that help in favorable occurrence of CAM photosynthesis (Lawlor *et al.*, 2002).

1.3.2.6 Changes in chlorophyll and chlorophyll fluorescence

Severe drought stress can lead to changes in chlorophyll fluorescence in many species of plants. An experiment on oak leaves suggests fluctuation in chlorophyll fluorescence when the intensity of water deficit stress in growth medium exceeded 30% (Athar and Ashraf, 2005). During the periods of severe water stress, photosynthetic capacity is badly affected. Chlorophyll and protein contents are significantly decreased during this period (Flexas *et al.*, 2012).

1.4 Resistance of plants to drought stress

Many different mechanisms are taken up by plants to resist adverse effects of drought stress. Efficient uptake of water with productive, enhanced, and deep root systems, restricted loss of water by increased diffusive resistance, and smaller leaves to reduce the transpirational loss are some of the strategies that are beneficial for plants during drought (Farooq *et al.*, 2009). The run away, avoidance, and tolerance strategies are used by plants to cope with harsh conditions during drought (Chaves *et al.*, 2003). Growth patterns are altered by some plants during drought to withstand unfavorable environmental conditions. Different plants have different ways of dealing with high drought stress, which include differences in rate of transpiration and water potential of leaves. It is also observed that stomatal conductance is normally higher in mycorrhizal plants due to higher water uptake. This results in higher water content and accelerated photosynthetic rate in mycorrhizal plants compared to nonmycorrhizal plants (Zhu *et al.*, 2011).

Highly complex mechanisms are adopted by plants during water deficit at molecular, physiological, and ecosystem levels. These mechanisms include drought avoidance through improved capacity of water absorbance by improved root system and increased leaf surface area, drought avoidance through early completion of plant life cycle, drought resistance through altering metabolic pathway (e.g., increased antioxidant metabolism), drought tolerance through osmotic adjustment, and drought avoidance by discarding any part of the plant (e.g., shedding of leaves due to water stress conditions) (Xu *et al.*, 2010). Gibberellins, salicylic acid, cytokinin, abscisic acid, and auxins are some of the plant growth substances that regulate plant behavior under drought stress (Farooq *et al.*, 2009).

Abscisic acid is a prominent plant hormone that serves as a long-term signal during drought. As abscisic acid is transported in xylem and travels through shoot, stomata close, and reduction in leaf expansion occurs, which prevents dehydration of leaf tissues. Abscisic acid also plays a role in transport and movement of reserves during drought stress (Xiong and Zhu, 2003). If drought stress is induced during grain filling, reduction in plant water level, and decline in photosynthetic rate during this period results in accretion of sugar in grains and production of soluble sugars from stem reserves (Barnabas *et al.*, 2008).

Moreover, recovery capacity of affected plants and resistance to drought stress can be intensified by functional activity of photosystem II photochemistry, regardless of cultivars and species (Zhenzhu *et al.*, 2010). Responses of plants towards drought stress include reduction in stomatal density, stomatal aperture, and transpiration rate and water loss. It leads to high chlorophyll content and photosynthetic rate (Dong *et al.*, 2014).

1.5 Effect of drought stress on leading plants

1.5.1 *Arabidopsis thaliana*

Drought is the most adverse stress that affects growth and productivity of the crops. Drought stress is known to decrease carbon dioxide assimilation rate, which is associated with reduced stomatal conductance. Drought stress is observed to induce reduction in activity of carbon reduction cycle enzymes during photosynthesis. The key photosynthetic enzyme inhibited by drought stress is ribulose-1,5-bisphosphate carboxylase/oxygenase (Reddy *et al.*, 2004). *Arabidopsis thaliana* plants exposed to ultraviolet-B radiation show an increase in proline content and a decrease in stomatal conductance. This aspect can be used as a source of resistance to drought stress. *Arabidopsis* plants exposed to UVB light, when treated with drought stress show increased tolerance to drought compared to plants that are not exposed to UV- B (Poulson *et al.*, 2006). Water deficit stress significantly decreases the rate of photosynthesis and stomatal conductance in *Arabidopsis thaliana* plants (Zhang *et al.*, 2008).

Exposure of *Arabidopsis* plants to heat and drought stress results in reduction of biomass and inhibition of photosynthesis with an increase in stress conditions. Lipophilic antioxidants and membrane protecting enzymes are highly enhanced as a result of drought stress. Elevated levels of carbon dioxide mitigate the effect of drought, which is apparent in the reduction of biomass, inhibition of photosynthesis, decline in chlorophyll fluorescence, production of hydrogen peroxide, and oxidation of proteins (Wituszyńska *et al.*, 2013; Zinta *et al.*, 2014). It is observed that during natural senescence under drought conditions, extensive cell death, and yellowing of leaves occur in autophagy mutants of *Arabidopsis*. Under mild stress conditions, these mutants retain high levels of chlorophyll pigments

and photosystem proteins. They also maintain normal chloroplast structure (Sakuraba *et al.*, 2014).

Leaf water content decreases with an increase in water deficit stress. Sugar and proline concentrations are observed to increase with decrease in leaf water content. Young leaves show less water loss under mild and moderate stress and accumulates high levels of metabolites as compared to older mature leaves. Acclimation of young *Arabidopsis* leaves to drought stress is due to increased accumulation of sugars, enhanced proline synthesis, decreased proline metabolism, and decreased NADPH/NADP⁺ ratio (Sperdoui and Moustakas, 2014).

1.5.2 *Triticum aestivum* (wheat)

Drought is known to cause a decrease in rate of photosynthesis in different wheat cultivars. This decrease is more pronounced in drought sensitive cultivars as compared to drought tolerant cultivars. Reduction in photosystem II photochemical efficiency is observed in wheat as a result of drought (Loggini *et al.*, 1999; Nakabayashi *et al.*, 2014). Plants exposed to drought stress after anthesis show a decrease in photosynthesis, stomatal conductance, viable leaf area, shoot mass, grain mass, weight, and water use efficiency. Consequences of drought on plants are more pronounced at high temperatures as compared to low temperatures (Shah and Paulsen, 2003; Sperdoui and Moustakas, 2012). Under drought conditions, wheat yield and productivity are highly dependent on rate and efficiency of photosynthesis and transpiration (Monneveux *et al.*, 2006).

Drought is considered to be one of the major factors that affect the yield of wheat by distressing the rate of photosynthesis during grain filling period (Bazargani *et al.*, 2011; Hummel *et al.*, 2010; Harb *et al.*, 2010). As a result of drought stress, the level of amino acids including proline, tryptophan, leucine, isoleucine, and valine significantly alter in bread wheat (Bowen *et al.*, 2012).

1.5.3 *Oryza sativa* (rice)

Leaf water potential in rice plants exposed to drought stress is known to decrease. This decrease is more notable after midday. As water content in soil slide down the threshold value predawn leaf water potential is significantly decreased. This is associated with a distinct decline in photosynthesis and stomatal conductance.

Net photosynthetic rates in severe water deficit are known to lower by 50% (Hu *et al.*, 2004). Water deficit in rice causes a decrease in leaf gas exchange by three mechanisms. These mechanisms include leaf rolling, reduced stomatal conductance, and non-stomata 1 inhibition (Dingkuhn *et al.*, 1989). In rice, a decrease in efficiency of Rubisco is observed as the drought stress approaches. Inhibition in photosynthesis as a result of drought stress is due to diffusive and metabolomic limitations. Metabolic limitations are caused due to adverse effects of drought on some metabolic processes related to photosynthesis and oxidative damage to chloroplasts (Zhou *et al.*, 2007). A transcription factor named HYR (Higher Yield Rice) enhances the ability of rice to withstand drought stress by activating photosynthetic genes, a cascade of transcription factors and other downstream genes that are involved in photosynthetic carbon metabolism. This leads to stability of yield in rice plants (Ambavaram *et al.*, 2014).

1.5.4 *Gossypium barbadense* (cotton)

Water stress reduces the net leaf photosynthetic carbon assimilation through stomatal effects and non-stomatal effects. Stomatal effects reduce leaf internal carbon dioxide concentration whereas non-stomatal effects result in decreased carbon assimilation during photosynthesis. Drought treatment to cotton reduces the chloroplast levels in leaves (Ennahli and Earl, 2005). Cotton plants subjected to water stress exhibited decreased stomatal conductance at ambient external carbon dioxide concentrations, increased stomatal sensitivity to high concentrations of carbon dioxide, decreased mesophyll conductance, and increased abscisic acid content (Radin, 1981).

Drought stress applied to cotton plants shows a decrease in rate of plastoquinone re-oxidation. This results in reduced primary photosystem II electron acceptor Q4. Photosystem I mediated electron transport is also inhibited by drought stress (Genty *et al.*, 1987). As a result of drought stress, the wilted leaves, which have zero turgor potential, are recognized to exhibit minimal diffusive resistance. Decrease in rate of photosynthesis is recognized in both vegetative and reproductive leaves of cotton. Declining leaf water potentials have diverse effects on photosynthetic rates in different leaves. Reduction of photosynthesis is not associated with stomatal closure (Ackerson *et al.*, 1977).

1.5.5 Other Crops

A decrease in photosynthetic fixation of carbon dioxide is observed with the onset of water deficit stress. Concentration of chlorophyll, soluble proteins and nitrate are known to get lowered in first leaves of drought subjected plants. Photosynthesis is seen to decrease by 11% on application of drought stress. Plants having a large leaf area show maximum effects of drought.

Under water deficit stress, carbon exchange rate, and stomatal conductance are decreased in a non-linear way in the *Saccharum* species. Chlorophyll content and total soluble protein in leaves of sugarcane are also decreased. Changes in chlorophyll content and total soluble protein levels are highly associated with carbon exchange rates. Stomatal and non-stomatal limitations are involved in decline of carbon exchange rates. Inhibition of non-stomatal photosynthesis results in diminished orthophosphate dikinase activity (PPDK) (Suriyan and Chalermopol, 2009).

Severely water stressed plants of maize are recognized to have lower photosynthetic capacity as a result of drought (Wolfe *et al.*, 1988). Stomatal conductance and carbohydrate metabolism are known to reduce during drought stress in *Zea mays* (maize) plants. These reductions are associated with a decrease in leaf photosynthetic rate (Pelleschi *et al.*, 1997).

1.6 Conclusion and future prospects

Drought resistance and tolerance are imperative aspects for the life cycle of plants. As the soil water starts depleting, profuse and deep root systems accompanied with maintenance of leaf surface area are the attributes of drought-resistant plants. There is an immediate need for better understanding of methods and techniques that enable plants to adjust under shortage of water as well as to sustain growth and production under drought. This will ultimately result in better and improved selection of drought tolerant clones in near future. In future, more studies on drought stress and photosynthesis are required so that plant life cycles and physiological mechanisms can be implicated efficiently. Responses of plants towards combination of different stresses are unique. As in field conditions, plants usually experience more than one type of stress so these responses cannot be directly extrapolated from plants, responses towards individual stresses. A high degree of complexity is

observed in plant responses towards stresses. Mechanisms by which these plants respond to single or multiple stresses need to be understood in future to increase the knowledge of impact of varied kinds of stress on plant growth. It is the need of the hour to model plants under water deficit stress and design them for breeding programs.

A better understanding of signaling components like transcription factors and protein kinases, especially mitogen activated protein kinases, is required in future to analyze responses towards such stresses and to determine acclimation strategies for these stresses. Transgenic plants should be made in future that include drought tolerant genes integrated into the genome of drought sensitive plants to enhance the acclimation of plants toward drought conditions. Bioengineering is one branch of science that can offer plausible and rapid solutions to effects of drought stress in plants. Transgenic plants produced as a result of bioengineering are observed to possess tolerance against different abiotic stresses. These approaches should be implemented in future for designing plants with tolerance to drought stress and to achieve sustainability and stability of environment.

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CHAPTER 2

The role of crassulacean acid metabolism induction in plant adaptation to water deficit

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2.1 Introduction

Crassulacean acid metabolism (CAM) is found in some 23 different families of flowering plants and ferns. CAM plants are found in many different ecosystems such as hot and arid climates (e.g., deserts), semi-arid regions with seasonal water availability (e.g., Mediterranean climates), or microclimates characterized by intermittent water availability. In CAM plants, CO₂ intake happens during the night and CO₂ is combined with phosphoenolpyruvate (PEP) by PEP-carboxylase (PEPC) to produce oxaloacetate, which is reduced to malate. Accumulation of malate leads to a marked acidification of plant cells at night. This organic acid is decarboxylated during daytime, leading to the formation of CO₂ and is assimilated through the action of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) in the stroma.

CAM plants show a wide degree of plasticity in their expression of the CAM pathway. These include: (i) obligate CAM, with high nocturnal CO₂ fixation; (ii) C₃/CAM intermediate, facultative or inducible CAM, with a continuous net uptake of CO₂ over 24 h; (iii) CAM-cycling, with net CO₂ uptake during the day but the stomata are closed at night, and respiratory CO₂ being released to produce malic acid; (iv) CAM-idling, with a continuous stomatal closure during the day and night but recycling of carbon skeletons behind closed stomata.

Facultative CAM species that are generally found within the *Aizoaceae*, *Crassulaceae*, *Portulacaceae*, and *Vitaceae*, can readily switch from C₃ to CAM and back to C₃. These plants perform C₃ photosynthesis to increase growth at times of sufficient water supply but during

periods of limited water supply, they employ almost exclusively the CAM mode as a means of reducing water loss while maintaining photosynthetic integrity.

Therefore, CAM is an effective strategy for improving water use efficiency, survival, and productivity under stress in semi-arid and arid regions of the world. Since climatic changes endanger agricultural sustainability worldwide, improving our understanding of the diverse metabolic and ecological manifestations of CAM pathway in both intermittently and seasonally dry habitats is expected to have broad importance. The aim of the current chapter is to provide an overview of the biochemical, molecular, and physiological components of inducible CAM in species that engage this metabolic adaptation to avoid water limitation.

2.2 Adaptation of plant photosynthesis to drought stress

Photosynthesis occurs in all green plants as well as in photosynthetic bacteria (Taiz and Zeiger, 2010; Pan *et al.*, 2012). In light reactions of photosynthesis, light energy is conserved by converting to reducing potential, in the form of NADPH and ATP, and oxygen is released. In dark reactions, CO₂ is incorporated into carbohydrate is known as carbon fixation or the photosynthetic carbon reduction (PCR) cycle by consumption of ATP and NADPH (Ceusters *et al.*, 2010; Dulai *et al.*, 2011; Taiz and Zeiger, 2010). Environmental stress conditions cause reduction in the activity of photosynthesis in all its phases. Water deficit causes an increase in abscisic