Emerging Technologies and Management of Crop Stress Tolerance

Volume II A Sustainable Approach

Edited by

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Water Stress and Crop Plants

Water Stress and Crop Plants

A Sustainable Approach, Volume 1

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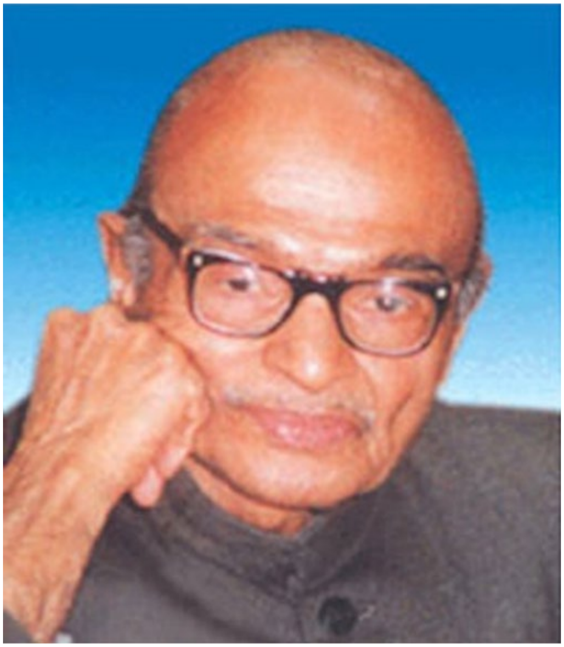

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Foreword

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 agricultutal 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, mariginal 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 × 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, socioeconomic, 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 27

Drought stress and morphophysiological responses in plants

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27.1 Introduction

Plants are one of the most abundant groups of living organisms present on Earth and face a number of drastic alterations in their domestic as well as wild habitat (Kuiper, 1998). Technological developments have led to climate change resulting in a number of biotic and abiotic stress factors with drastic disturbance to ecosystems. Biotic stresses are mostly induced by microorganisms like bacteria, viruses, and some species of fungi. The effects caused by pathogenic microorganisms on plants are devastating and are considered the main threat to both crop and wild plants. Abiotic stresses include heat, drought, and salinity resulting in a decline in crop yield as well as the quality. Among abiotic stresses, drought stress, or water deficiency is the major factor, which causes severe damage to plants. Global warming, less precipitation, low ground water table, and reduction in the level of soil water are the main factors responsible for the development of drought condition in field crops (Mishra and Cherkauer, 2010; Vadez *et al.*, 2012). The models designed to estimate the severity of drought stress as a threat to plants have also indicated an increase in drought conditions under the current changing environmental conditions (Walter *et al.*, 2011). Another simulation model has indicated that an average rise of temperature from 2–5 °C could lead to the reduction in precipitation by 15% by the year 2100 (Ciscar, 2012). The temperature of Earth is continuously rising each year leading to excessive transpiration of water from plant leaves leading to water deficit (Farooq *et al.*, 2012). Most of the crops rely on water coming from either melting of glaciers or precipitation. Decline in both of these main water resources has led to critical effects on plants in terms of yield and quality (Hussain *et al.*, 2004; Moayedi *et al.*, 2010). Economic loss was observed in US during the year 2012 due to the crop yield being affected by drought (USDA, 2014). Drought stress not only affects the physiological aspects of plants but also their internal metabolic system and gene expression. A severe water deficit situation can lead to the decrease in plant membrane stability and transport activity along the membrane (Rahdari *et al.*, 2012). Other important biochemical alterations, like accumulation of proline, reduction in chlorophyll content, protein content, and soluble sugar level, have also been reported in plants under drought stress (Bandurska and Jozwiak, 2010; Kazama *et al.*, 2014). The main physiological processes affected by drought stress are transpiration, photosynthesis, and stomatal conductance (Anjum *et al.*, 2011a). Cell-water relationship is also affected by water deficiency, as insufficient water may reduce water potential and relative water content in leaf and stem (Aref *et al.*, 2013). Drought induced oxidative stress, that is, production of reactive oxygen species (ROS) can cause membrane damage and degrade certain enzymes

Water Stress and Crop Plants: A Sustainable Approach, Volume 2, First Edition. Edited by Parvaiz Ahmad.

(Zlatev and Lidon, 2012). ROS production mostly takes place in the chloroplast. Accumulation of ROS leads to the inactivation of chloroplast enzymes involved in ATP production resulting in reduced ATP formation (Foyer and Shigeoka, 2011). In water deficient soil, roots of plant become clumped and hence the ability of water uptake is reduced making plant vulnerable to severe structural problems (Couso and Fernandez, 2012).

Plant responses against drought stress not only involve the physical adaptation of roots and leaves to enhance water absorption and minimize water loss respectively, but they are also accompanied by a series of gene encoding regulatory proteins that are involved in signaling and enhancing the expression of a number of certain other genes (Waseem *et al.*, 2011). Drought induced qualitative and quantitative changes in protein content also affect the expression of certain genes ultimately affecting the protein production. Some proteins are specifically synthesized under water deficit conditions like osmoprotectants, proteases, and transcription factors like WRKY, NAC, and so on (Seyed *et al.*, 2012). Plants are quite adaptive in nature as they can alter their metabolic and physiological functions in order to minimize the harmful effects caused by the stress in order to maximize their survival (Thapa *et al.*, 2011). A number of transcription factors have been identified, which enhance the expression of genes specifically related to the stress. The expression of these transcription factors is enhanced under stress to make plants more tolerant to the stress (Liu *et al.*, 2013).

27.2 Drought stress in plants

Plants being an integral part of ecosystem and motionless organisms face a number of adverse conditions during their life cycle due to the changes in their surrounding environment. These stresses have somehow evolved plants to tackle these environmental changes by making changes in their metabolic pathways and gene expression. Drought is one of the major stresses that adversely affect the agriculture sector by reducing the yield and quality (Farahani *et al.*, 2009). Under water deficit conditions, plants undergo certain physiological and morphological changes to reduce their growth for survival (Rahdari and Hoseini, 2012). Major crops are at a greater risk of yield and quality loss due to water deficiency. Drought is considered the major stress that affects the productivity of crops (Lambers *et al.*, 2008). As drought stress limits the production of crops, the study of ability of plants to withstand drought conditions is of utmost importance (Seyed *et al.*, 2012). Important staple crops like wheat, rice, and maize have been focused on for the study of responsive mechanisms against drought to minimize the loss of yield, which is estimated to reach 30% compared to the current situation (Fischer and Polle, 2010; Grando *et al.*, 2010).

On the basis of water availability, water stress has been categorized into two types: water deficit and water logging. Both of these types are the main cause of loss in crop yield throughout the world. Continuously varying climate and threatening levels of global warming have been making water stress even more severe leading to massive losses in productivity.

27.2.1 Water deficit

Water deficit stress arises due to low rainfall leading to low water level in soil, which leads to low water potential in leaves and stems. In drought, the loss of water from leaves exceeds the water absorption from soil through roots (Knox, 2005). In case of low availability of water, plants adapt themselves to minimize the water loss through transpiration and also strive to expand roots to achieve the maximum possible absorption of water.

27.2.2 Water logging

Water logging stress is another major factor responsible for the reduction in yield of major staple crops worldwide. This condition arises when water levels in soil exceed the normal level. Plants require certain amount of oxygen (O_2) through the soil for proper development but due to the excessive water levels, O_2 levels decline in soil leading to stress for plants (Sairam *et al.*, 2008). In the state of hypoxia, reduction in root respiration results in inhibition of energy production in plant root (Ashraf *et al.*, 2012). Plants that are adaptive develop adventitious roots to gain maximum air trapped within the pores of soil. Hormones like ethylene and auxin facilitate the formation of adventitious roots making plants resistant to such conditions (Akhtar and Nazir, 2013). Plants are severely affected in the germination stages under water logging stress conditions, which leads to inhibition of respiration, ATP formation, and transport of electrons (Hsu *et al.*, 2000). In regions where crops are irrigated through rivers and canals, serious stress is faced as ground water tables have been rising continuously causing flooding to crops (Singh, 2013).

27.3 Ecological factors responsible for water stress

A number of natural cycles get disturbed due to continuously changing climate of Earth's atmosphere. Both modern technologies and rapid industrialization have played a key role in adversely affecting the balanced climate of ecosystem. A lot of attention is now being given to the climate change and its impact on major crops like wheat, maize, and rice. Low precipitation and flooding are the two main reasons that are responsible for drought in plants leading to massive yield loss. The major cause of imbalance in the natural cycles is global warming.

27.3.1 Global warming

Earth is an optimum place for all living organisms to live and reproduce but human activities have been horrifically disturbing the natural balance. A number of gases like ozone (O_3), carbon dioxide (CO_2), and methane (CH_4) form a thick layer around the Earth's surface making it difficult to dissipate the Sun's rays, leading to an increase in overall temperature around the globe. Atmospheric CO_2 is somehow beneficial to plants, as an elevated level of photosynthesis has been reported at its higher concentration (Widodo *et al.*, 2003; Lazzarotto *et al.*, 2010). An increase in temperature is leading to rapid defrosting of glaciers making land areas more vulnerable to floods. With the passage of time, water reservoirs are also shrinking due to rapid melt down, leading to unavailability of enough water for crops. Global warming is also responsible for the lowering of annual precipitation in number of areas where the sole source of water is rainfall. These regions are known as "rainfed" areas. Higher temperature is leading to heat stress to plants making water loss from leaves to maximum level hence creating water deficit conditions for plants. It has been estimated that if the global warming elevates by 2 °C more than the present temperature by 2100, about one-fifth of the population will have to face a severe water deficit (Schiermeier, 2014). An increase in global warming has already started influencing crop production and yield negatively in many areas of different continents (Rosenzweig *et al.*, 2011).

27.3.2 Insufficient precipitation

Irrigated land often faces less stress as compared to areas that are entirely dependent on rainfall. Rainfed areas, which are dependent on precipitation, have high chances of being affected by drought stress (Schlenker and Roberts, 2009; Seager *et al.*, 2010; Knutti and Sedlacek, 2013). Anthropogenic activities are the major sources to altering natural cycles and precipitation pattern. Urbanization, deforestation, and industrialization are the leading human activities that are making the climate warmer and more drastic in the context of water availability to plants (Lobell and Gourdji, 2012).

27.3.3 Monsoon weather system

This system is a source of precipitation in most of the regions of Asia during summer. It is also linked with an increase in temperature and it is predicted that, by the twenty-second century, the amount of rainfall caused by monsoon will reduce by 70% leading to shortage of water in rainfed areas for summer crops (Schewe and Levermann, 2012; Lee and Wang, 2012). It is also estimated that rainfall will increase in the coming years in India and Pakistan due to an increasing level of CO_2 in atmosphere, which will cause massive flooding and destruction to the agricultural sector in the region (Turner, 2013).

27.3.4 Meltdown of glaciers

Short winter seasons reduce the quantity of snowfall on mountains like Himalayas hence causing the water shortage even in the irrigated areas of Asia. It is predicted predicted that Himalayan glaciers will disappear in the next 20–30 years resulting in a massive drought in India, China, Pakistan, Nepal, and Bhutan. Another perspective of melting of glaciers is that the lakes are getting larger and this might lead to flooding in most of the regions close to these mountains (Malone, 2010).

27.4 Impact and adaptive mechanism of water stress on plants

Crops in arid and semi-arid regions face heat stress, which affects the growth, development, quality, and quantity of crops resulting in low yield (Tuna *et al.*, 2010). Although plants respond to stress by various means, there is always a reduction in plant growth and productivity (Massonnet *et al.*, 2007). This is mainly due to changes in growth, yield, photosynthetic ability, electrolyte leakage, and chlorophyll content (Praba *et al.*, 2009). Crops facing water stress often undergo changes in the relative water content, chlorophyll index, and stomatal conductance (Bahari, 2014; Bolat *et al.*, 2014).

Plants cope with drought stress by alteration in their transcription factors and expression of drought responsive genes. Transcription factors like WRKY, NAC, ZAT, and MYB are mostly expressed under severe stress conditions. Moreover, carbohydrate deposition, increase in active oxygen species (AOS), and antioxidative enzymes are also observed in plants exposed to drought stress (Tuna *et al.*, 2010). Despite all, today's on-going progression in urbanization and industrialization may lead to water shortages if not controlled, which will bring more drastic effects to agriculture (Haro von Mogel, 2013).

27.4.1 Morphological impact of water stress on crops

A cumulative effect of water stress appears in the morphological characters of plants. These include relative root-shoot length, fresh weight, dry weight, and total biomass of stressed plants. Water stress also affects the germination rate (Bolat *et al.*, 2014). Variation in plant height, leaf count, and leaf diameter has also been reported when plants are exposed to drought stress. Growth and yield are two of the most severely affected physical attributes of crops. Stem length is another factor that is reduced by the induction of water deficit conditions (Sankar *et al.*, 2008). Experiments done on wheat varieties in order to study the impact of drought showed reduction in thousand grain weight, number of grains per spike, spike length, and yield per hectare (Khan and Kabir *et al.*, 2014; Allahverdiyev *et al.*, 2015). In addition, water deficit conditions also reduce the pod weight and pod number in crop plants.

27.4.1.1 Plant height

Under water deficit conditions, shortening of stem length and plant height has been reported in many crop varieties (Parent *et al.*, 2010). In case of cotton, the stem length is reduced by 12% under water deficit conditions as compared to irrigated conditions (Ahmad *et al.*, 2013). Rice (*Oryza Sativa*) showed reduction in height when grown in water deficient environments. Due to limited availability of water, plants minimize the water loss by limiting the further growth of shoots or leaves; instead, they expand their root systems in order to absorb maximum water from the soil.

27.4.1.2 Relative root-shoot length

Shoots are the main channel for movement of water throughout the plant body by means of xylem tissue. The shoot system is solely dependent on the root system that facilitates the absorption of water from the soil and its uptake in order to fulfill the plant's water requirement. Under water deficit conditions, changes in the root properties and traits make it even more adaptive to stress conditions, hence making plants tolerant to drought. Roots of most of the herbaceous plants have a fibrous system with fine lateral roots to enhance deep penetration for absorption of water (Fitter, 2002). In addition to these lateral roots, another type of root that arises from the lower part of stem provides additional characteristics to plants enabling them to show wider responses to water stress (Rostamza *et al.*, 2013). In case of drought stress, an increase in root length was observed compared to shoot length. Under drought conditions, growth of shoot regions is reduced and roots expanded, helping more water absorption by the plant. Hence an increased root:shoot ratio is observed when plants face severe drought conditions (Nejad, 2011).

27.4.1.3 Total biomass of plants

Plants that face severe water deficit conditions are subjected to a reduction in their total biomass. Shedding of leaves is a well-known response in order to protect extra loss of water in the form of transpiration. Plants also lose turgor, leading to death of tissues and thereby reducing the biomass of plants. Drought induced inhibition of physiological and biochemical processes negatively affects concentration of biomolecules and growth, which ultimately causes a reduction in biomass of plants (Tsuchihashi and Goto, 2004; Ghaffaripour and Samson, 2015).

27.4.1.4 Leaf rolling

This has been observed in a number of crops like wheat, maize, and rice. This effect is mostly reported in the case of rice, which is more susceptible to water deficit compared to other crops (Lafitte *et al.*, 2004). Leaf rolling occurs to minimize the water loss through leaves during severe dehydration (Kadioglua *et al.*, 2012). Leaf rolling has been described as an important characteristic of crops that helps in improving photosynthetic efficiency, decreasing transpiration rate, an increasing grain yield (Fang *et al.*, 2012). But under severe drought conditions, excessive leaf rolling leads to retardation in growth and yield of crops. Transcription factors have been reported to stimulate and enhance the phenomena of leaf rolling making plants more adaptable to water deficit conditions (Yang *et al.*, 2014a).

27.4.1.5 Relative water content

Water levels in leaves provide the osmotic strength and shape to facilitate maximum absorption of sunlight. Under water deficit conditions, relative water content is significantly reduced leading to severe effects on growth and yield of crops like wheat. It is reported that under irrigated conditions, relative water (RW) content is observed as much as 90% but after applying water deficit stress, it is reduced significantly to a very low level (Rahimi *et al.*, 2010). In another study it was found out that water absorption through roots significantly affects the leaf water potential under water deficit conditions (Alvarez *et al.*, 2011). Growth of a plant is solely dependent on the ability of its leaves to maintain its proper structure and photo-absorption. If leaves of plant lose their water content, it severely affects the crop growth and yield as observed in cow pea (Hayatu *et al.*, 2014).

27.4.2 Morphological adaptations in plants under water deficit conditions

27.4.2.1 Decrease in number of leaves

Most water loss is through the process of transpiration that causes evaporation of water from the stomata of leaves. Plants in arid or semi-arid conditions minimize the transpiration rate through their leaves under drought conditions. The reduction in transpiration is usually achieved by adaptive alteration in their morphology like shedding their leaves thus decreasing number of leaves, leaf size, and minimizing the branches (Fahn, 1964).

27.4.2.2 Alternate growth pattern

Growth is a complex event, which includes a number of processes like cell division, cell differentiation, and cell elongation, involving various biochemical, genetic, and morphological factors. Reduction in turgor pressure due to scarce water availability leads to major impact on plants and some of these are in fact adaptive strategies of plants against drought stress (Taiz and Zeiger, 2006). Elongating cells require a continuous flow of water in and out of them but under stress the interruption of water through the xylem results in inhibition of this process. Plants adopt the alternate pattern of cell growth to survive under water deficit conditions.

27.4.2.3 Structural alternations in plants

Plants under water stress conditions bring about structural alterations mainly for reduction of water loss and enhancement of water storage by thickening their tissues (De Micco and Aronne, 2007). In case of continuous prevalence of drought, there is a very quick evolution in the reduction of their life cycle making plants more adaptive. Studies on desert plants have shown that when severe drought is imposed on them, they rapidly evolve themselves by reducing the period of their growth leading to early seed maturation and flowering (Aronson *et al.*, 1992). Plants often try to reduce their leaf volume by compacting themselves and subsequent stomatal conductance is also reduced to minimize water loss by transpiration.

Diameter of the stem is reduced under drought stress in order to minimize the unnecessary utilization of water and direct the available water to key processes going on inside them. Plants that have been growing in desert habitat are continuously facing water deficit conditions and they have adapted themselves by transforming their leaves into spikes and designing extra water storing organs that store water for a very long period. Another adaptation is that they have a thick cuticle layer that minimizes the excessive loss of water from spikes and stems. Leaf shedding is an important adaptation to get rid of the excessive load of water suckers (Cherubini *et al.*, 2003).

27.4.2.4 Changes in stomatal distribution and structure

Drought is a major cause of seed mortality at the germination stage (Moles and Westoby, 2004; Arena *et al.*, 2008). Drought conditions also affect the stomatal structure and physiology; such as a decrease in stomata size to minimize the loss of water. Stomata are the gateway of plants that help in gaseous exchange and water conductivity. Some of the wheat varieties have been reported to keep their stomata open, even under severe drought conditions. This trait can be considered as drought tolerance because keeping their stomata opened does not inhibit growth and photosynthesis (Baloch *et al.*, 2012). Studies have been done regarding the effect of drought on stomata, which clearly state that under moderate drought conditions, density of stomata increase but when severe drought is imposed, this results in significant reduction in density (Xu and Zhou, 2008). Leaves play a critical role in adaptive mechanism of plants under water deficit environment. Plants that have undergone a long lasting drought conditions have modified their leaves into xeromorphic leaves with a thick cuticle layer. Water flow through cuticle depends on the thickness and its chemical composition. These characteristics are mostly controlled by genetic factors and plants have undergone extensive evolutionary process to overcome impact of water deficiency (Riederer and Schreiber, 2001). The cuticle is composed of important chemicals that help in inhibiting the irradiation from sun and thus reducing water loss from leaves. Some plants also develop water storage layer along with multilayered epidermis. Parenchyma cells help in extra storage of water under water deficit conditions thus enhancing the use of water effectively by aquaporin proteins (Tattini *et al.*, 2000).

27.4.2.5 Alternation in water conduction

Transport of water from roots to leaves is another trait considered as an adaptive response against drought stress. Structure of stem plays a key role in hydraulic conductivity and biomechanics of plants (Baas *et al.*, 2004). Some of the crops have shown adaptations by their phenotypic traits like smaller plants, reduced leaf area, and early maturity. Smaller plants require less quantity of water for stable growth and to fulfill basic requirements. Roots are the first to come in contact with water deficit conditions. Under stress conditions, shoots are the most affected part of plants compared to roots. Roots penetrate deep into the soil to capture maximum moisture and hence an increase in root:shoot ratio is observed. Water conductance is also changed due to leaf rolling during scarcity of water. Reduction in the plant height is another adaptive mechanism to deal with water deficit conditions. Under scarce water, plants minimize the requirement of water by reducing the activities, which involve the utilization of water. Plants that undergo reduction in height somehow try to increase the seed size, which ultimately results in higher yield (Singh *et al.*, 1995).

In most of the crops like wheat and rice, drought studies have mainly been focused on the impact of stress on yield and growth rate. Peduncle length is considered as an important attribute in defining the yield of crops. Wheat often undergoes changes in peduncle length when subjected to water deficit conditions (Kaya *et al.*, 2002). Similarly, a study conducted on the durum wheat to determine the major adaptive trait responsible for increasing the yield and grain number shows that the leaf posture and rolling play a significant role in the survival of plant. Those cultivars, which showed significant leaf rolling and posture, yielded higher compared to others with no adaptive traits (Bogale *et al.*, 2011).

27.4.2.6 Delayed leaf rolling

Leaf rolling has been exhibited by many crop species under water deficit conditions. This adaptive event helps plants to maintain their internal water status essential for normal growth (Subashri *et al.*, 2008). Leaf rolling occurs by the alteration in water status of hypodermal and schlerenchyma cells. When water availability is too low, it causes tissues to lose turgor pressure causing leaves to roll whereas leaves remain flat under normal conditions (Kadioglu *et al.*, 2007). Hypodermis cells that are present just beneath the epidermis have also been reported to play a key role in leaf rolling under drought stress. In rice, schlerenchyma cells are also involved in rolling of leaf, which is controlled by genetic factors. Mutants that lack a specific sequence helping in modulating leaf rolling have shown excessive leaf rolling resulting in the death of plants (Zhang *et al.*, 2009a). Plants that have delayed leaf rolling are more tolerant to drought as the flag leaf plays an important role in photosynthesis. Plants with erect leaves remain unaffected under drought stress for longer periods, hence increased growth and grain yield are observed. Flag leaf area is considered as an important indicator for the drought stress severity in a variety of crops. Any kind of adaptive mechanism that results in structural changes in plants is mostly regulated by the genome of that plant.

27.4.2.7 Increased root length

Along with leaves, roots are also considered as a key player in adapting to stress conditions. Plants undergo rapid root deepening into the soil in order to absorb maximum amount of water from deep soil (Mackill *et al.*, 1996). Cultivars that have a deep root system are positively correlated to the xylem vessel area, which plays a key role in conductance of water from roots to leaves. Root hair present on the root segments are vital for the absorbance of nutrients and trapping moisture from soil. An expanded network of roots defines the biomass of whole plant. Plants that have higher dry biomass are more tolerant and have more chances of survival under harsh conditions.

27.4.3 Biochemical impacts of water stress on crops

Biochemical properties of plants are greatly affected by paucity of water. Drought induced oxidative stress may result in the production of reactive oxygen species (ROS) that are damaging for plant cells, proteins and DNA (Farooq *et al.*, 2009). Inadequate amount of water causes alteration in concentration and structure of biomolecules, hindering various metabolic pathways of plants.

27.4.3.1 Oxidative burst

Oxidative Burst is the term coined for the release of ROS species such as O^-, H_2O_2, and OH. These three free radicals are quite devastating for any cell or tissue because they severely damage the proteins, lipids, and nuclear proteins present in the cell. Under water deficit conditions, plant induces oxidative stress, which further triggers the responses against drought. Increased production of ROS leads to the accumulation of melanodialdehyde (MDA) and hydrogen peroxide, which are the indicators of damage caused to plants by reactive oxygen species (ROS) (Anjum *et al.*, 2011a,b, Hasanuzzaman, 2013).

27.4.3.2 Lipid peroxidation

During oxidative stress, lipids being an integral part of the membrane are degraded by free radicals released in stress. This peroxidation leads to the decrease in membrane stability ultimately damaging the whole cell and tissues (Cunhua *et al.*, 2010). Lipid peroxidation acts as an indicator for the occurrence of radical reaction in tissues. It has been reported that the degree of lipid peroxidation increases four-fold with the induction of drought stress in plants (Moran *et al.*, 1994).

27.4.4 Biochemical adaptation in plats against water stress

27.4.4.1 Enzymatic antioxidant defense system

In order to cope with oxidative stress induced by drought stress, plants use their own defensive mechanism, which can be either enzymatic or non-enzymatic (Horváth *et al.*, 2007). Enzymatic antioxidants include superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) (Sharma, 2012). These three enzymes play a significant role in minimizing the damage from free radicals and their expression is increased manifold under drought stress. All three enzymes either directly control the free radicals or are involved in the production of other non-enzymatic antioxidants. Studies have reported that the level of these enzymes in plants under drought stress is greater than in un-stressed plants (Yang *et al.*, 2010; Mohammadi *et al.*, 2014; Mohammadi, 2015). An increase in two major antioxidant enzymes, peroxidase and glutathione reductase, has also been reported in plants under water deficit conditions by Gill and Tuteja (2010). Similarly, Bahari *et al.* (2015) also reported that drought treated seedlings showed elevated levels of oxidative stress, and simultaneous increase in the activities of the enzymes catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), peroxidase (POD), and polyphenol oxidase (PPO) when compared to control plants.

27.4.4.2 Non-enzymatic oxidants

In case of severe water deficit conditions, a group of chemicals helps in tackling the free radicals to minimize the destructive effect of oxidative burst. Glutathione, carotene, and ascorbate are the main antioxidants that are produced in greater amounts under drought stress (Wang *et al.*, 2012). By increasing or maintaining the level of antioxidants, it is possible for plants to become even more adaptive to such conditions.

27.4.4.3 Proline accumulation

Plants accumulate various solutes like proline, sucrose, soluble carbohydrates, glycinebetaine, and others to maintain turgidity in the cell wall under drought stress (Rhodes and Samaras, 1994).

Proline, being an essential amino acid, plays a key role in maintaining the osmotic potential of cells and protecting them from severe dehydration (Zhang *et al.*, 2009b; Anjum *et al.*, 2011b; Brossa *et al.*, 2013). Higher levels of proline help in overcoming the adverse effects of drought and it also minimizes the damage caused by ROS to cells. Proline level is associated with the ability of plants to tolerate the drought; hence, the higher the level of proline, the more tolerant plant will be to drought (Da Man *et al.*, 2011). Compared to any other amino acid present in plants, proline is the one that is accumulated at far higher levels under water deficit conditions (Ghaderi and Siosemardeh, 2011; Boudjabi *et al.*, 2015). Proline works as a signaling molecule to regulate mitochondria, cell production, and cell death. Moreover, it also plays a key role in buffering cellular redox potential (Hanci and Cebeci, 2014).

27.4.4.4 Photosynthetic pigments

Chlorophyll is an essential component of plant and plays a key role in growth and development by the process of photosynthesis (Rahdari *et al.*, 2012). Chlorophyll pigments like chlorophyll a, chlorophyll b, and carotenoids are involved in the absorbance of light from the sun and utilization of this energy results in the production of glucose that is distributed in number of pathways of biosynthesis. Under drought conditions, a decline in these pigments have been reported, making plant vulnerable to die (Astorga and Melendez, 2010).

27.4.5 Physiological impacts of water stress on crops

Factors that are responsible for causing water deficit conditions are mostly natural and hence almost impossible to overcome. The only strategy left with us is to minimize the losses as much as possible. Species and duration dependent impact and response have both been observed in plants exposed to water deficiency. Plants usually face drastic effects on photosynthesis, respiration, growth and developmental processes, and stomatal conductance. The decline in the functioning ability of any one of these processes leads to the reduction in yield and quality of plants on a large scale.

27.4.5.1 Photosynthesis

Photosynthesis is the only way of synthesizing sugars essential for growth and development. When affected by water deficit, there is no way out for the survival of plants except for the expression of adaptive traits to minimize the effects of drought. Photosynthesis is mostly dependent on light, concentration of CO_2, and stomatal opening and closure (Flexas *et al.*, 2004). It is also affected by metabolic changes or a reduction in important components essential for effectively carrying out this process. Studies suggest that the reduction in rubilose bisphosphate (RuBP) and rubisco protein level is responsible for decreasing the rate of photosynthetic process resulting in reduced growth and yield in plants exposed to drought. Plants tend to keep their stomata closed in order to avoid transpiration but simultaneous blockage of gaseous exchange results in decreased photosynthetic rate (Cornic, 2000). The photosynthetic pathway is also disturbed by the oxidative damage caused by ROS to the chloroplasts in plants (Zhou *et al.*, 2007). According to a study on potatoes, it has been reported that the stomatal limitation factor, damage to photosystem II, and the antioxidant enzyme system are responsible for the decrease in the rate of photosynthesis in drought sensitive plants (Li *et al.*, 2015).

27.4.5.2 Respiration

Respiration is another physiological process affected by severe water deficit reducing the yield and growth of plants. It is necessary to focus on respiration because photosynthesis occurs only during daylight and in green parts of the plant, whereas each part of plants respires continuously. Mitochondria, being the powerhouses of cells, require an adequate supply of gases and are the main contributors to the growth and survival of plants (Gifford, 2003). Despite being a key process, still respiration is not well studied under drought conditions (Ribas-Carbo *et al.*, 2005). The gaseous exchange through stomata is reduced in water deficit due to closed stomata, which limits both respiration and photosynthesis. The rate of respiration is mostly dependent and regulated by the events that utilize the respiratory product. The reduction of ATP, NADH, and Krebs Cycle components lead to a decreased rate of respiration in stressed plants. In some cases, an increased rate of respiration has also been identified under water deficit conditions, which leads to an elevation in intracellular CO_2 level. Sanhueza *et al.* (2013) reported that respiration rate increases in plants in the drought tolerant *Nothofagus* species. Mitochondria and chloroplasts are very closely interrelated in metabolic processes. Leaf mitochondria in crops act as buffers and avoid damage caused by drought stress by changing their metabolic activities (Atkin and Machere, 2009).

27.4.6 Physiological adaptation in plants under water stress

Plants may survive the drought by minimizing its adverse effects, that is combating the stress by developing the capacity to tolerate the stress conditions (Puijalon *et al.*, 2011). Plants improve their survival by enhancing their root density, and reducing their transpiration rate, low stomatal conductance, leaf rolling, slow wilting, and delayed senescence. Expression of major osmoprotectants and transcription factors also helps plants to increase their tolerance to water deficit.

27.4.6.1 Increased root grow

Plants adapt to water deficit by stimulating the growth of roots to absorb the maximum moisture from soil. They sometimes expand their roots to a greater depth, especially in cases when water is at a deeper level. Most of the time, drying of soil takes place in an upward to downward direction. Having a deeper root system helps the plant in absorbing soil moisture from lower levels of soil (Prasad *et al.*, 2008). Crops with deeper root systems are more tolerant to water deficit compared to those with shallow root systems (Hudak and Patterson, 1996). The crops with deep root systems have direct access to both deeper and shallow water so the depletion in shallow water does not render the plant vulnerable to drought stress at later stages of its reproduction or flowering. According to Chimungu *et al.* (2014), a decline in root cortical cell number improves drought tolerance in maize by reducing the metabolic activities, improving stomatal conductance, leaf CO_2 assimilation, and relative water content.

27.4.6.2 Transpiration efficiency

Plants require specific amount of water to absorb through their root system. Under drought conditions, limited water availability leads to closing of stomata to avoid transpiration. But closing of stomata also reduces the intake of CO_2 necessary for photosynthesis, subsequently resulting in decline in growth and total biomass of plants. Water use efficiency (WUE) calibrates the plant net water usage into biomass (Prasad *et al.*, 2008). By efficiently absorbing the water from soil, it is possible to avoid decline in photosynthetic process due to stomatal closure. Plants have a very diverse genetic background. It has been noted that some wheat varieties have higher WUEs compared to others. A crop grown on soil with 100% moisture has a higher level of WUE compared to one grown in water deficient soil.

27.4.6.3 Osmotic adjustment

The cell-water relationship is a key factor of survival for the plant cell. Osmotic adjustment plays an important role to maintain this relationship under drought stress in plants (Yang *et al.*, 2014b). It has been suggested that KUP potassium transporter family has a significant role in osmotic adjustment and turgor dependent cell growth in plants. Studies in Arabidopsis mutants using 86 radioactive rubidium ion ($86Rb^+$) indicate that these transporters are regulated by abscisic acid (ABA) and auxin. The potassium uptake (KUP) transporter may regulate K^+ efflux in root cells, stomatal closing, and ABA signaling complexes in plant cells exposed to drought stress (Rizhsky *et al.*, 2004; Osakabe *et al.*, 2013). A greater degree of osmotic adjustment is helpful in increasing the yield and biomass of plants (Blum, 2005). This adjustment also helps in maintaining higher leaf water content leading to increased growth even under drought conditions. It also leads to the accumulation of osmolytes in the root section, which facilitates the root expansion into deeper soil resulting in absorbance of water from deeper parts of soil (Serraj and Sinclair, 2002). Lowering of water potential to a certain level helps the survival of plants under low levels of soil moisture. This adaptation has led plants to become more tolerant to drought conditions resulting in less damage to plants. Some crop varieties have also shown such mechanism under drought stress including wheat and barley. (Basu *et al.*, 2010; Morgan, 2000; González and Ayerbe, 2011). Many studies have reported that osmotic adjustment and plant growth and yield are somehow associated with each other (Guóth *et al.*, 2010).

27.4.6.4 Hormonal regulation

Plants have a diverse hormonal system that enables them to adapt to a number of stress conditions. Under water deficit stress, induction of abscisic acid (ABA) synthesis takes place in roots. ABA is then transported to leaves where they cause closing of stomata and limit the growth of plants to make them more adaptive to stress (Wilkinson and Davies, 2010). In crops like barley, a five-fold increase in ABA level has been reported in drought tolerant varieties as compared to the susceptible ones, thereby confirming that ABA plays an essential role in making plant adaptable to water deficit (Thameur *et al.*, 2011). Aquaporin proteins that are involved in efficient water translocation from one cell to another have also been reported to be regulated by ABA (Parent *et al.*, 2009). ABA also helps in regulating other hormones like ethylene, which cause senescence. Under higher ABA levels, ethylene production is inhibited leading to a reduction in the development of plant (Sujata and Awant, 2013).

27.4.6.5 Delayed senescence

Delayed senescence also plays a significant role in assisting plants to cope with drought stress. Plants have adapted themselves in order to stay green for a longer period to prolong photosynthetic activity, which ultimately results in increased yield and growth rate. On the other hand, the loss of the green color of leaves is another mechanism for carrying out floral development because the degradation of chlorophyll results in the release of important nutrients required for enhancing the growth of florets in crops (Lim *et al.*, 2007). Under stress conditions, plants often reduce the thickness of their leaf as an adaptive response to avoid negative effects of stress. Although reduction in leaf thickness is mainly due to reduction in number and size of mesophyll cells, such changes are somehow favorable in plant tolerance against drought stress.

Plants mostly face accelerated senescence under water deficit conditions leading to the decline in yield of crops. Crops like wheat, rice, and cotton are often subjected to drought throughout the world leading to massive losses in yields and to farmers as well. Some perennial plants have adapted themselves to delay their senescence to tolerate the water deficient conditions. It has been hypothesized that the accelerated senescence occurs due to the triggering of programmed cell death signal that ultimately results in the death of plant (Rivero *et al.*, 2007). Plants that are tolerant to drought stress have adapted themselves by delaying their senescence period, hence helping them survive under extreme conditions. The physiological basis of how these evergreen plants survive such extreme conditions is still not well-understood.

27.5 Alteration in signaling pathway

Plants can sense and respond to water deficit by complex signaling cascade composed of a suite of stress receptors, signal transduction systems, and transcriptional regulatory networks (Kuromori *et al.*, 2014). Various groups of researchers are working on the drought-stress regulatory networks and the development of drought-tolerant transgenic rice plants (Fukao and Xiong, 2013; Voesenek and Bailey-Serres, 2013). Their reports suggest that drought tolerant rice may be developed by the alteration of signaling pathway related to the regulatory gene for transcription factors, protein kinases, phytohormone biosynthesis, and the action of osmoregulators (Todaka *et al.*, 2015). Uga *et al.* (2013) reported that changes in root structure play an important role in the tolerance against water deficit conditions. It has been proved that the QTL *Deeper Rooting 1 (DRO1)* increased the root growth angle in rice, leading to high-yield performance under drought conditions.

It has also been reported that the overexpression of *OsOAT* gene leads to the increase in the level of proline and glutathione in crops exposed to drought stress (You *et al.*, 2012). *OsOAT* gene regulates ornithine δ-aminotransferase enzyme, which is a key factor of proline and arginine metabolism. Similarly, overexpression of OsSDIR1 (*O. sativa* salt-and drought-induced ring finger 1) and *OSRIP18* (a rice ribosome-inactivating protein 18 gene) show tolerance against water deficit conditions via improved stomatal closing in rice plants (Bae *et al.* 2011; Gao *et al.*, 2011; Jiang *et al.*, 2012). Hennig *et al.* (2015) reported that protoplast fusion lines of drought resistant poplar hybrids showed a higher concentration of carbohydrate and reduced plant height, which makes them tolerant against drought stress. Photosynthesis and respiration have key elements, namely chlorophyll and heme. These two basic biochemicals are made up of tetrapyrrols. Recent reports show that modified tetrapyrrol biosynthesis leads to wilting avoidance by organellar retrograde signaling (Dilrukshi *et al.*, 2015). It has also been observed that drought stress signaling is triggered by oxidative burst (Tripathy and Oelmüller, 2012), which activates Ca^{++} ion channels and protein kinase enzymes and alters the expression of a nuclear gene involved in heme biosynthesis.

27.6 Plant life stages and drought sensitivity

The impact of drought on plants is dependent on the severity of stress, its duration, and the plant growth stage. Mostly the drought stress is less damaging to plants at early seedling stage while its sensitivity to drought increases gradually as the crop matures particularly at flowering and seed development stage. The most sensitive stage to drought stress is the panicle or cereal flowering stage. Most studies on drought stress have been done before flowering or at the flowering stage (Valliyodon and Nguyen, 2006). Studies on rice have shown that the drought stress at the anthesis stage causes the largest loss in yield as compared to other stages (O'Toole, 1982).

Plants are more sensitive to drought at the reproductive stage because the reproductive organs have no adaptive mechanisms like the production of osmolytes to tolerate drought stress (Akram, 2011).

27.7 Conclusion and future prospects

Understanding the causes of drought stress might be helpful in effective planning to avoid stress and increase the yield of crops. Drought stress affects the morphological, biochemical, and physiological attributes, and, in severe cases leads to cell death. With better understanding of factors responsible for low yield and quality, drought tolerance can be improved by both traditional and modern methodologies. Some of the drastic effects caused by drought can be overcome by the application of external supplies, leading to the survival of plants. Plants show diverse reactions in response to stress at various stages of growth period. Understanding those factors responsible for making that specific stage tolerant and other stage susceptible would help in overcoming drought susceptibility.

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