

Sharad Vats *Editor*

# Biotic and Abiotic Stress Tolerance in Plants

 Springer

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# Foreword

Throughout evolution, plants have faced extreme variations in environment. Yet, they have survived and adapted themselves in different ecological niches. However, it is foreseen that in the ensuing period of present day global climatic changes, the impact on the domesticated crops, which feed the humanity, will result in negative growth and productivity. Scientists will have to develop new varieties, either through classical breeding tools or using new genomic approaches like molecular assisted breeding or developing biotech crops using transgenic or genome editing technologies. To achieve success in this direction it is essential to understand, at the biochemical and molecular level, the mechanisms of plant perception to abiotic and biotic stresses, the signaling pathways, and the identification of genes that respond to confer stress tolerance. The present book is an attempt to line up different chapters to illustrate the knowledge that has accumulated in some of the domains in the area of biotic and abiotic stress tolerance in plants.

One of the chapters broadly cover plant responses to drought in particular, to illustrate how the stress affects the physiology and biochemistry of the plants. How plants can be made to survive short drought conditions is an important aspect of future plant biotechnology studies. Using either phenomics or genomics based approaches one should get plants which can produce more per drop of water, which is going to be more scare for agriculture with increasing population and urbanization. More specifically, one of the chapters deals with impact of abiotic stresses on photosynthesis, which is the fundamental process that needs to be protected in order for the plants to survive and grow. It has been seen that senescence and chlorophyll breakdown ensues following stress conditions, which lowers photosynthesis and hence yield. A few chapters deal with the role of signaling molecules like nitric oxide, reactive oxygen species, and salicylic acid in modulating and adapting to stress environment and also in inducing cell death. These signals are produced in addition to changes in abscisic acid and calcium, etc., whose role has been well studied in stress physiology. One of the important molecule that also plays

a very significant role is glutathione. Modulation of GSH and GSSG seems to be one of the key parameters that senses and transduces stress signals. In view of this, the role of glutathione transferases and phosphite in adaptation is also discussed in two chapters.

Air, water, and soil pollution influence plant growth and development. Two chapters are devoted to pollution as a stress for plants where effect of insecticides and also biomonitoring have been presented. Among other changes that occur in plants following stress perception, role of bioactive compounds has been presented in a separate chapter. In order to assess the overall molecular changes under stress environment, a chapter deals with changes in miRNA and another on the availability of bioinformatic resources. One chapter on breeding for stress has been included using *Capsicum* as a test case.

Overall, the editor has effectively used his experience and knowledge to incorporate experts from various parts of the globe to write chapters covering important aspects of plant stress biology. The information compiled in this volume will be useful to students and researchers of molecular plant physiology in general and to those working in stress physiology in particular.

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# Preface

Plants, being sedentary, are highly exposed to environmental stress (biotic and abiotic). However, they have developed several mechanisms to tolerate adverse conditions, which are rather complex to decipher. Global climatic changes, pollution, ever-increasing population, resistant pests, and other related factors have even worsened the current environmental situation, having a direct negative impact on the world's crop production. Thus, understanding the effects and various tolerance mechanisms of plants under stress is of prime importance to the scientific fraternity. The present work is an attempt to incorporate some of the biochemical, physiological, and molecular aspects of plant stress with latest updates.

The book is organized into 14 chapters written by eminent experts from different parts of the globe. The first chapter focuses on the physiological, biochemical, and molecular response of the plants under drought stress, which is one of the most predominant abiotic stresses. The second chapter highlights the effect of abiotic stress on the photosynthetic apparatus of the plants. The strategies involved to safeguard this apparatus have been discussed, which could help in the development of plants with effective photosynthetic machinery under stress. This is followed by a chapter which emphasizes on the ecotoxicological effects of insecticides on plants with special reference to germination and other phytotoxicity tools. The Chaps. 4 and 5 explore the variations of plant bioactive compounds and the role of salicylic acid in modulating salinity stress. Chapters 6, 7, 8 and 9 bring to light the involvement of beneficial elements, glutathione-S-transferase, phosphite, and nitric oxide, respectively, in the adaptive response of plants under stress and as a stimulator of better plant performance. Stress induced programmed cell death (PCD) in plants as a survival strategy and the role and cross-talk of reactive species of oxygen and nitrogen in activating PCD in plants have been efficiently described in the chapter "Involvement of Reactive Species of Oxygen and Nitrogen in Triggering Programmed Cell Death in Plants." In the Chap. 11, the research progress toward *Capsicum*, a commercially important plant, against stress tolerance has been compiled from classical breeding to the recent use of large-scale transcriptome and genome sequencing technologies. This is followed by a chapter, which underlines

the role of small RNAs in the plant development and stress mitigation. Apart from knowing the adaptive mechanisms of the plants it is also very important to identify some biological agents that monitor the level of environmental stress. Viewing the same, Chap. 13 has been included, which specifies the significance of the liliptians of the plant kingdom (Bryophytes) as biomonitors/bioindicators. The last chapter focuses on various general and specialized bioinformatics resources useful for people working in the field of plant stress biology. Overall, the book includes the latest developments in the field of plant stress biology supplemented with related figures and tables, which can be useful for students and research scholars.

I am extremely grateful to the publisher (Springer), contributors, and reviewers for their support and meticulous assessment of the book chapters. I would like to state that the encouragement and unconditional support of my parents, my wife, and my beloved daughter (Vaibhavi) were the guiding factors behind the effective completion of this work. I am also thankful to Prof. S. K. Sopory for providing his guidance and consent to write the foreword of this book.

Rajasthan, India

Sharad Vats



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# Plant Responses to Drought Stress: Physiological, Biochemical and Molecular Basis



Sanjay Kumar, Supriya Sachdeva, K. V. Bhat, and Sharad Vats

**Abstract** Drought is one of the most serious threats to crop production all over the world and is likely to worsen with anticipated changes in the climate. Drought impairs normal growth, disturbs water relations and reduces water-use efficiency in plants. Plants, however, have a variety of physiological and biochemical responses at cellular and organism levels, making it a more complex phenomenon. Researchers have been trying to understand and dissect the mechanisms of plant tolerance to drought stress using various approaches. The present chapter describes the strategies used by plants to adapt to low water potential at physiological, biochemical and molecular levels. This chapter also describes the strategies involving genetic engineering used by breeders in order to obtain crop varieties with improved drought tolerance, some of which show great promise. Modern genomic and genetic approaches coupled with breeding methodologies are expected to more effectively identify the genes and metabolic pathways that confer drought tolerance in crops.

**Keywords** Abiotic stress · Photosynthesis · Reactive oxygen species · Regulatory genes · Stress tolerance · Transgenic plants

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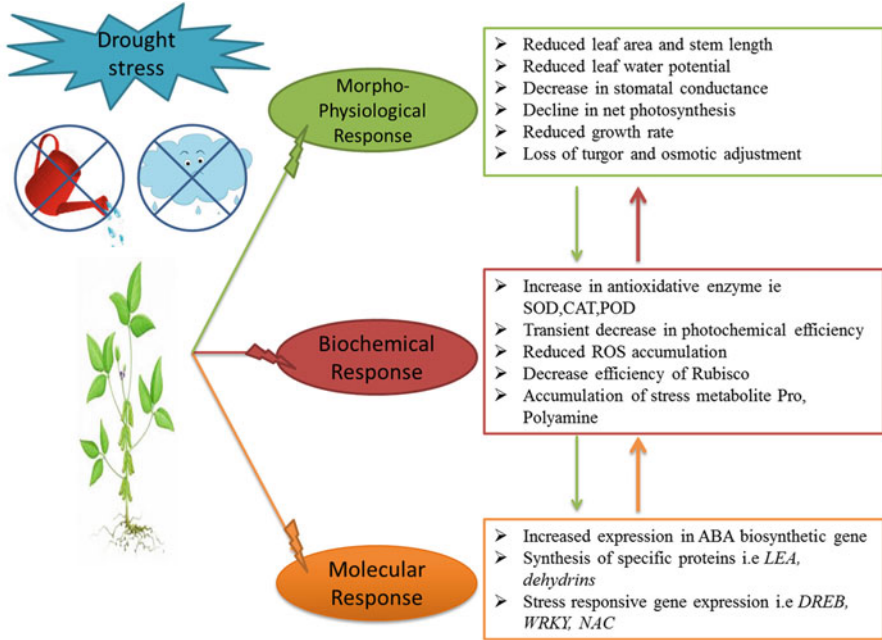
## 1 Introduction

Global climatic change and ever increasing population necessitates the need for developing stress-resistant crops. Drought is one of the major phenomena that limit crop production and yield worldwide. It is estimated that 70% of crop yield loss can be attributed to abiotic stresses, especially drought (Bray et al. 2000). Traditional breeding for drought tolerance has been a basic approach, and success has been achieved in few crops such as maize (Hoisington et al. 1996) and wheat (Zhao et al. 2000). Incorporation of functional, comparative and structural genomics would greatly enhance the success of traditional breeding efforts. Application of modern genomic tools in traditional breeding programmes is becoming common because of its great potential. Modern genetic and genomic technologies and advancement in breeding and phenotyping have helped in identifying candidate genes and metabolic pathways functional in drought-tolerant crops (Ishitani et al. 2004; Cattivelli et al. 2008; Mir et al. 2012). However, a large gap remains between crop yields in ideal and stress conditions.

Drought is a physiological form of water deficit where soil water available to the plant is inadequate, which adversely affects the plant's metabolism. However, plants possess multiple morphological (reduced leaf area, reduced stem length, leaf moulding, wax content, efficient rooting system, stability in yield and number of branches), physiological (transpiration, water-use efficiency, stomatal activity and osmotic adjustment) and biochemical responses (accumulation of proline, polyamine, trehalose, increasing of nitrate reductase activity and storage of carbohydrate at cellular and organism levels) under drought stress, making it a more complex phenomenon to decipher (Haworth et al. 2013; Ammar et al. 2015; Conesa et al. 2016) (Fig. 1). Of various plant responses to water scarcity, enhanced abscisic acid (ABA) accumulation is one of the key mechanisms of adaptation to water stress (Esther et al. 2000; Bano et al. 2012; Brodribb and McAdam 2013). The plant growth regulator, ABA, plays an important role in the response and tolerance against dehydration. It seems that dehydration triggers production of ABA, which induces expression of genes like *rd22* (Abe et al. 1997); *RD29A*, *RD29B*, *KIN2* and *RAB18* (Yao et al. 2012); and *PYL8* (Lim et al. 2013). There are genes that are induced by dehydration and not responsive to exogenous ABA treatments suggesting the existence of ABA independent in addition to ABA-dependent signalling pathways between initial signal of drought stress and expression of specific genes (Shinozaki and Yamaguchi-shinozaki 1997; Yoshida et al. 2010; Ding et al. 2016).

Stomatal response, ROS scavenging, metabolic changes and photosynthesis are majorly affected when plants are exposed to water stress. Thus, in order to acclimatize to abiotic stresses, plants accumulate biomolecules that are harmless and do not interfere with plant processes. They may include protective proteins such as dehydrins; heat shock proteins (HSPs); late embryogenesis abundant (LEA) proteins (Vierling 1991; Lipiec et al. 2013); osmolytes like proline, trehalose and sugars (Zhang et al. 2010; Hayat et al. 2012; Ilhan et al. 2015); glycine; and betaine (Sakamoto and Murata 2002; Wang et al. 2010; Chen and Murata 2011). Some





**Fig. 1** Plants’ responses under drought stress

signalling molecules include polyamines (Roy and Wu 2002; Navakouidis et al. 2003; Capell et al. 2004; Wi et al. 2006; Liu et al. 2007; Wen et al. 2008; Cheng et al. 2009; Gill and Tuteja 2010; Alcazar et al. 2010; Rangan et al. 2014), inositol (Xiong et al. 2001; Sengupta et al. 2008) and hormones like abscisic acid (Davies and Zhang 1991; Saradhi et al. 2000), ethylene (Quan et al. 2010; Xiong et al. 2013) and methyl jasmonate (Bartels and Sunkar 2005; Vincour and Altman 2005; Wu et al. 2008; Jan et al. 2013). Changes in membrane fluidity and protein composition of membranes help to maintain the cellular integrity of plants (Bohnert et al. 1995). Accumulation of LEA proteins is correlated to improved tolerance under drought, salinity and cold (Imai et al. 1996; Close 1996; Xu et al. 1996; Juszczak and Bartels 2017). The accumulating solute appears to act in protein solubilisation (ectoine, glycine, betaine), and uncharged solutes (mannitol, pinitol) may act as scavengers of reactive oxygen species (ROS) (Ashraf and Foolad 2007). Overexpression of Fe-binding ferritin resulted in increased tolerance to removal of free iron which participates in ‘Fenton’s reaction’ and produces hydroxyl radicals (Shen et al. 1996). Nitric oxide has also proved to be protective against oxidative stress conditions. These collective responses are controlled by complex regulatory events intervened by ABA, ion transport and transcription factors (TFs) involved in the regulation of stomatal responses, which are integrated into coordinated molecular networks, enabling plants to adapt and survive.

Osmolytes increase tolerance to environmental stresses in several plants (Wang et al. 2003; Hochberg et al. 2013). Drought-tolerant transgenic rice lines were developed showing tissue or stress-inducible accumulation of trehalose, which accounted for higher levels of soluble carbohydrate, a higher capacity of photosynthesis and concomitant decline in photo-oxidative damages and more favourable mineral balance mutually under stress and non-stress conditions, with no negative effects (Garg et al. 2002). Several studies have identified traits for which presence or expression is linked to plant adaptability to drought conditions (Table 1). Amongst them, traits such as small plant size, reduced leaf area, early maturity and prolonged stomatal closure lead to reduction in the total seasonal evapotranspiration and the yield potential (Fischer and Wood 1979; Karamanos and Papatheohari 1999). Stay-green plants are characterized by a post-flowering drought resistance phenotype that gives plants resistance to premature senescence, stalk rot and lodging when subjected to drought during grain filling. As a result, stay green has been extensively used to improve yield potential and yield stability under water-stressed environments in various breeding programmes (Campos et al. 2004; Tollenaar and Wu 1999). Genomics and crop physiology have led to new insights in drought tolerance providing breeders with new tools for plant improvement (Tuberosa and Salvi 2006). The plant drought stress can be managed by adopting strategies such as mass screening and breeding, marker-assisted selection and exogenous application of hormones and osmo-protectants to seeds or plants, as well as engineering for drought resistance. This chapter provides an outline of plant drought stress, its effects on plant's resistance mechanisms and management strategies to cope with this global challenge.

## 2 Desiccation and Dehydration

Water deficit can affect plants in several ways. A mild water deficit leads to small changes in the water status of plants, and plants cope with such a situation by reducing water loss and/or by increasing water uptake (Bray 1997). The most severe form of water deficit is desiccation, when most of the protoplasmic water is lost and only a very small amount of firmly bound water remains in the cell. Desiccation is drying out of an organism that is exposed to air. Most flowering plants cannot survive exposure to a water deficit equivalent to less than 85–98% (v/v) relative humidity during their vegetative growth phase although desiccation is an essential part of the developmental process of most higher plants with reference to seed formation (Gaff 1971). Desiccation tolerance seemingly depends on the ability of cells to maintain the integrity of cell membranes and to prevent denaturation of proteins. Tolerance in organs such as seeds and pollen is widespread amongst higher plants, and partial desiccation is a precondition for completing lifecycle in most species producing seeds. Desiccation-tolerant plants comprise monocotyledonous and dicotyledonous species within the angiosperms in the so-called resurrection plants (Gaff 1971), and certain ferns, algae, lichens and bryophytes possess

**Table 1** Physiological and biochemical responses of plants under drought stress

Sr. No.	Plant traits	Yield-related effects on plant	Variation in stress	References
1.	Net photosynthesis, total leaf area, plant dry weight	To recover the net photosynthesis after well watered	Selected cultivar resistant to drought stress	Fini et al. (2013)
2.	Amino acid, C/N ratio and osmolality	Change in water potential and metabolic changes in plant cause yield decrease under stress	Water scarcity causes the increase in amino acid and osmolality and lowers C/N ratio	Hochberg et al. (2013)
3.	Electrolyte leakage, peroxidase activities	Increase in water stress reduction in budding success	Phenol and peroxidase activities increase, but chlorophyll and relative water content decrease under stress	Bolat et al. (2014)
4.	Membrane stability and chlorophyll content	Reduced membrane stability, relative water content and total carotenoid content in all the cultivars, whereas total chlorophyll content increased	Water deficit stress at pod development stage proved to be more damaging than at pegging stage	Chakraborty et al. (2015)
5.	Root water absorption, leaf relative water content and antioxidative enzyme	Increase tuber yield and activities of antioxidative enzyme higher under water stress condition	Drought resistant increases under stress conditions in selected cultivars	Shia et al. (2015)
6.	Transpiration rate	Variation in leaf area and stomatal conductance	Few landraces show tolerance	Nakhforoosh et al. (2016)
7.	Photosynthesis rate, leaf carbon isotopes	Water-use efficiency increases with stomatal conductance	Increase water deficit tolerance capacity	Bota et al. (2016)
8.	Relative water content, grain yield and leaf area index	Total biomass and yield increase under water deficit in selected genotype	Tolerant under water deficit stress	Panda et al. (2016)
9.	Water-use efficiency	Total yield increase under water deficit	Drought tolerant	Djurovic et al. (2016)
10.	Photosynthetic rate, conductance of stomata	High degree of photosynthetic rate and increased biomass gain under drought	Resistance under stress	Haworth et al. (2017) and Sapeta et al. (2013)
11.	Fruit dry matter, total soluble solids, total ascorbic acids	Increased fruit dry matter and total soluble solid/total ascorbic acid	Improve fruit quality and water deficit capacity	Guida et al. (2017)
12.	Carotenoids and photosynthetic pigments	Decreased amount of chlorophylls, carotenes and neoxanthin, the	Major effect on the concentration of some	Mibei et al. (2017)

(continued)

**Table 1** (continued)

Sr. No.	Plant traits	Yield-related effects on plant	Variation in stress	References
		concentration of zeaxanthin increased with water deficit	carotenoids and photosynthetic pigments	
13.	Leaf area, root length	High leaf area, increased root-to-above ground ratio	Survive under severe drought condition	Silva et al. (2017)
14.	Shoot fresh and dry weights, stomatal conductance and photosynthetic capacity	Less decrease shoot fresh and dry weights, stomatal conductance and photosynthetic capacity	Shows drought stress tolerance in selected species	Aboughadareh et al. (2017)

desiccation-tolerant vegetative tissues. So far, no gymnosperms have been found to be desiccation tolerant (Bartels 2005). Desiccation tolerance is the ability of the plant to survive periods during which the cells are water-stressed and the plant dries up; all its metabolic systems undergo dehydration. The attainment of desiccation tolerance is the result of complex interactions of different cellular processes due to multiple stresses imposed on plant tissues during severe dehydration. The speed of water loss and the events before dehydration appear to be critical for survival, such that if the speed of dehydration is too fast, plants do not acquire tolerance to desiccation. This observation suggests acquisition of desiccation tolerance is an active process and requires explicit biochemical changes and the synthesis of desiccation-related molecules. The intricacy of desiccation tolerance proposes that the gene products induced at the time of dehydration can be correlated with signal transduction pathways and regulation of stress-specific transcription, with carbohydrate metabolism or with cellular protection (Phillips and Bartels 2000). In order to understand the molecular basis of desiccation tolerance, numerous approaches may be used. One strategy is the developing genetic model system to study desiccation tolerance in vegetative tissue. Transposon tagging or insertional mutagenesis via T-DNA could be used in inferring the function of genes in genetic model systems. Secondly, natural allelic variation has been shown to be effective for identifying genes involved in plant development. Quantitative trait locus (QTL) analysis of plant accessions that exhibit extensive variation for desiccation tolerance may be a means of identifying genes in complex regulatory networks.

### 3 Gene Expression and Dehydration

Molecular responses to unfavourable environment include a series of genes and signal transduction pathways that are highly regulated and enable plants to survive the stress conditions. Although much of this regulation is at transcriptional, post-transcriptional

and post-translational levels, the majority of the focus remains at the transcriptional level involving modification and remodelling of chromatin, *cis*-acting elements located upstream and downstream the coding region of the gene and transcription factors (Luo et al. 2012).

Physiological studies on stress responses reveal that the recent progress in plant molecular biology has assisted the detection of many genes governing stress tolerance (Table 2). Functional genes include the cell protection (enzymes for generating protective metabolites and proteins) and regulatory genes which regulate stress response (such as protein kinases and transcription factors). Thus, these genes have been categorized as functional proteins and regulatory proteins (Fig. 2). Functional proteins function in stress tolerance and regulatory proteins function in signal transduction and gene expression to stress response. Variety of drought-inducible genes in plants suggests the complex nature of drought stress. These gene products are involved in drought tolerance and stress response. Mostly the drought-inducible genes respond to cold stress as well except a few. The DNA sequences involved in stress sensing, transduction of the signal and regulation and function of the downstream gene induction and repression mechanism are largely conserved (Serrano 1996; Shinozaki and Yamaguchi-shinozaki 1997; Zhu et al. 1997; Ishitani et al. 1997). A 9 bp conserved sequence, TACCGACAT, named the dehydration responsive element (DRE) is vital for the regulation of induction of *rd29A* under low-temperature, drought and high salt stress conditions, however not as an ABA-responsive element (Kasuga et al. 1999). The *rd29A* promoter which functions in response to ABA also contains ABRE. DRE-related motifs have been found in promoter region of several genes induced under drought and low temperature (Yamaguchi-shinozaki and Shinozaki 1994).

These results show that the DRE-related motifs including C-repeat (CRT) and low-temperature-responsive elements (LTRE) which contain a CCGAC core motif are involved in ABA-independent gene functions in response to drought and cold stress.

Liu et al. (1998) cloned five independent DRE/CRT binding proteins using yeast hybrid assay and classified them into two groups: CBF1/DREB1 and DREB2. The *DREB1A* gene and its two homologs (*DREB1B*=*CBF1*, *DREB1C*) are expressed under low-temperature stress, but the *DREB2A* gene and its homologue (*DREB2B*) are expressed under dehydration (Shinwari et al. 1998). Overproduction of the *DREB1A* and *CBF1/DREB1B* cDNA driven by the 35S CaMV promoter in transgenic plants markedly improved stress tolerance to drought and freezing (Yoshida et al. 2010). However, the *DREB1A* transgenic plants revealed severe growth retardation under normal conditions. The *DREB1A* cDNA driven by the stress-inducible *rd29A* promoter was expressed at low level under unstressed controlled conditions and strongly induced by dehydration, salt and cold stresses (Kasuga et al. 1999). The *rd29A* promoter reduced the negative effects on growth of plants to minimum, whereas the 35S CaMV promoter severely retarded growth under normal growth conditions. Moreover, this stress-inducible promoter enhanced tolerance to drought, salt and freezing as compared to 35S CaMV promoter (Kasuga et al. 1999). Polygenic inheritance of root characters was reported by Ekanayake et al. (1985),

**Table 2** Relevant examples of genes conferring drought tolerance

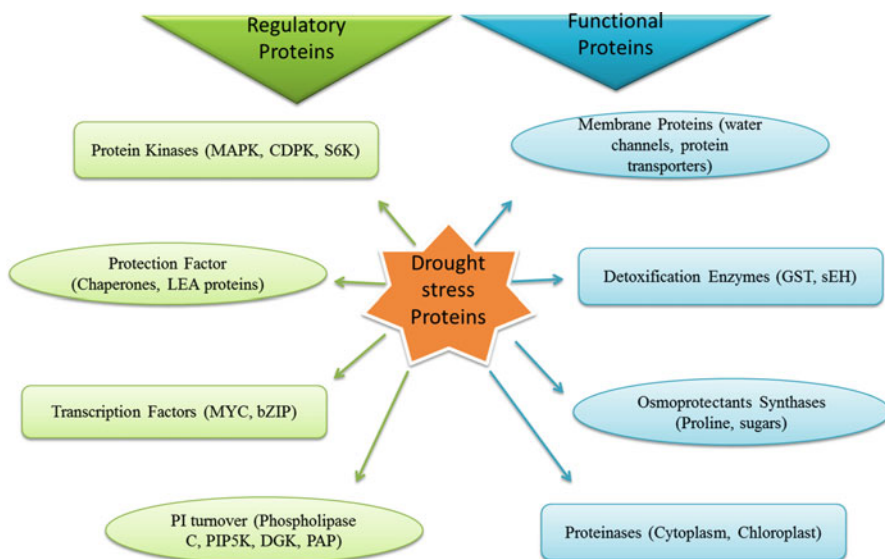
Sr. No	Genes	Function during drought	Mechanism of action	References
1.	<i>CKX1/WRKY6</i>	Enhanced abscisic acid catabolism and regulate stomatal conductance	Modulation of cytokinin with decrease in leaf osmotic potential and proline biosynthetic gene <i>P5CSA</i> raised during stress	Mackova et al. (2013)
2.	<i>GsZFP1</i>	Relative membrane permeability, malondialdehyde (MDA) content and more free proline and soluble sugars accumulated	Gene overexpression enhanced the salt/drought stress tolerance	Tang et al. (2013)
3.	<i>SNAC1</i>	Regulating photosynthesis rate and transpiration rate	Overexpression of <i>SNAC1</i> improved tolerance to drought and salt in cotton through enhanced root development and reduced transpiration rates	Liu et al. (2014a)
4.	<i>DREB2A/NAC5</i>	Transcription factors were enhanced by stress	Silicon- and selenium-pretreated plant under water stress showed increase in proline content and glycine betaine in both shoots and roots. Enhanced the expression of drought-specific genes, OsCMO coding rice choline monoxygenase and dehydrin OsRAB16b	Khattab et al. (2014)
5.	<i>MaPIP1;1</i>	Reduced expression of ABA-responsive genes and high cytosolic K <sup>+</sup> /Na <sup>+</sup> ratio under stress	Increased primary root elongation, root hair numbers and reduced membrane injury and improved osmotic adjustments due to overexpression of gene in banana	Xu et al. (2014)
6.	<i>BdWRKY36</i>	Controlling ROS homeostasis and regulating transcription of stress-related genes	Overexpression enhance lesser ion leakage (IL) and reactive oxygen species (ROS) accumulation, but higher contents of chlorophyll, relative water content (RWC) and activities of antioxidant enzyme under drought condition	Sun et al. (2015)
7.	<i>popW</i>	Primed antioxidant responses	Significant increase in peroxidase, superoxide dismutase, catalase activities and ascorbic acid content, and overexpression also enhanced the relative transcript levels of oxidative stress-responsive	Liu et al. (2016)

(continued)

**Table 2** (continued)

Sr. No	Genes	Function during drought	Mechanism of action	References
			genes <i>NtAPX</i> , <i>NtCAT1</i> , <i>NtGST</i> and <i>NtCu/Zn-SOD</i> under drought stress	
8.	<i>AtWRKY57</i>	Stress-induced transcription factors	Enhanced drought/salt tolerance by decreased electrolyte leakage, malondialdehyde content; increased proline and reactive oxygen content in transgenic rice	Jiang et al. (2016)
9.	<i>OsNRRB</i>	Stress-induced transcription responses	Positively regulate drought stress tolerance through upregulating stress-responsive genes <i>OsZIP23</i> , <i>OsDREB2A</i> , <i>OsP5CS</i> and <i>OsLea3</i> by overexpression of <i>OsNRRB</i> , which increase drought tolerance in rice	Zhang and Chen (2017)
10.	<i>MpCYS4</i>	ABA hypersensitivity and enhanced stomatal closing	Enhanced stomatal closure and upregulation of the transcriptional levels of ABA and drought-related genes during drought	Tan et al. (2017)
11.	<i>LEA</i>	Decrease of photosynthetic activity and activation of antioxidant systems	Increased water deficit stress tolerance	Juszczak and Bartels (2017)
12.	<i>PgRab7</i>	Regulating Na <sup>+</sup> ion homeostasis, altered expression of transporter genes, including <i>OsVHA</i> , maintenance of photosynthetic rate	Overexpression induced the salt/drought stress tolerance	Tripathy et al. (2017)
13.	<i>ThDREB</i>	Stress enhancing the antioxidase activity and managing ROS level	Expression of <i>ThDREB</i> higher germination rates, fresh weights and root lengths under NaCl and mannitol treatments. The total chlorophyll content, superoxide dismutase (SOD) and peroxidase (POD) activities are also higher	Yang et al. (2017)

where the dominant alleles governed long and more numbers of roots whereas recessive alleles governed the thick root tip (Gaff 1980). Leaf moulding and osmotic adjustment showed monogenic inheritance. Tomar and Prasad (1996) reported a drought resistance gene, *Drt1* in rice, which is linked with pigmentation, hull colour, plant height and pleiotropic effects on the root system.



**Fig. 2** Drought-inducible proteins in stress tolerance and responses

Numerous stress-related genes have been isolated and characterized in a number of crop species in the last eras (Cattivelli et al. 2002, 2008; Prabha et al. 2011; Joshi et al. 2016). Three coding single nucleotide polymorphisms (SNPs) and one haplotype identified in the *OsDREB1F* gene are likely to be related to drought tolerance in rice (Singh et al. 2015). Six different *OsDREB1F* protein variants were identified based on translated amino acid residues amongst the orthologs. Deletions in coding region trimmed five protein variants which were found to be susceptible to drought stress. Association study revealed that three coding SNPs of this gene were considerably associated with drought tolerance. One *OsDREB1F* variant in the activation domain of *OsDREB1F* gene that has an amino acid change from aspartate to glutamate was found to be associated with drought tolerance. The natural allelic variants mined in the *OsDREB1F* gene can be used in translational genomics in the future for improving the water-use efficiency in rice (Singh et al. 2015). Expression of the *SHINE* and *HARDY* genes were found to confer water-use efficiency in rice, although their phenotypic effects have not yet been evaluated under field conditions (Karaba et al. 2007). Transgenic plants with either upregulated stress responses or specific metabolic processes related to drought tolerance have been developed by classical physiological studies (Cattivelli et al. 2008). Few reports on transgenic rice overexpressing *NAC1* transcription factor (Hu et al. 2006; Tran et al. 2004) and *OsLEA3* gene (Xiao et al. 2007) showed higher yield under drought conditions due to increased spikelet fertility. Under stress conditions, ectopic expression of *OsCDPK7* gene encoding a calcium-dependent protein kinase improved levels of stress-responsive genes that contribute to improved salt and drought tolerance in rice (Saijo et al. 2000). *CBF3/DREB1A* gene in transgenic rice also increased drought tolerance without affecting growth undesirably (Oh et al. 2005).



Numerous transcription factors initiate stress responses and establish plant stress tolerance by regulating stress-inducible genes. Transcription factors (TFs) are basically proteins that recognize and bind to the cis-acting elements in promoter region and regulate transcription, by activating or inhibiting the expression of particular genes. Overexpression of some transcription factors, including bZIP, ERF/AP2 family, DOF, HDZIP, MYB, NAC, WRKY and Zn-finger (Dubouzet et al. 2003; Yang et al. 2012; Jan et al. 2013), and genes like *CDPKs*, *HAP/CAAT*, *HSPs-LEA* family and *MAPKKK* (Vierling 1991; Kazuko and Shinozaki 2006; Lipiec et al. 2013) have proved to be promising candidates as stress modulators. Members from each transcription factor family show protective phenotypes against multiple stresses such as cold, drought and excess salt (Shukla and Mattoo 2013; Mattoo et al. 2014). For example, in rice, *OsWRKY89* improved tolerance to UV irradiation and fungal infection (Wang et al. 2007), and *OsWRKY45* is found to be highly expressed under cold, heat, salt and dehydration. The overexpression of *OsWRKY11* enhanced heat and drought tolerance (Wu et al. 2008). *AtMYB60* and *AtMYB96* regulate stomata movement in the ABA signalling cascade in response to drought stress (Cominelli et al. 2005). *AtMYB13*, *AtMYB15*, *AtMYB33* and *AtMYB101* are also involved in ABA-mediated responses to environmental stresses (Reyes and Chua 2007). In rice, the *OsISAP1* gene having zinc-finger domain was highly expressed in effect of stress induced by dehydration, cold, salinity and heavy metals (Mukhopadhyay et al. 2004). Several studies reveal transcription factors control various defence mechanisms; therefore, they are being considered of great importance in breeding programmes that aim mechanisms of tolerance to abiotic stresses.

## 4 Biochemical Aspects of Dehydration Tolerance

Seemingly, most of the plants employ multiple mechanisms to ensure dehydration tolerance. At present, our knowledge on the metabolic changes that lead to dehydration tolerance is partial, but information about the biochemical processes governing dehydration tolerance is essential for successful engineering of dehydration tolerance in crop plants.

### 4.1 HSPs

HSPs are widely distributed in nature and accumulate during stress. They are commonly known as molecular chaperones involved in protein folding and assembly, removal and disposal of nonfunctional proteins (Wang et al. 2004). HSPs are induced by drought and salinity stress (Alamillo et al. 1995; Campalans et al. 2001), and in vivo evidences propose that HSPs inhibit thermal aggregation of proteins, thus easing the recovery of cell functions after abiotic stress (Lee et al. 1995). They are classified according to their molecular weight: Hsp70 family (family DnaK);

chaperonins, namely, GroEL and Hsp60; the Hsp90 family; the Hsp100 family; and the small Hsp family (Wang et al. 2004). Cyclophilin is a chaperon protein involved in protein folding, highly induced under drought stress; overexpression of *cyclophilin* gene confers manifold abiotic stress tolerance (Gottschalk et al. 2008; Sekhar et al. 2010). An increase in cysteine protease activity has also been observed during drought conditions (Koizumi et al. 1993; Seki et al. 2002). HSF (heat shock factor) family members bind to the promoter region of few chaperones known as heat shock proteins (Pelham 1982). These TFs are located in the cytoplasm when in their inactive state (Baniwal et al. 2004; Hu et al. 2009) and have a C-terminal portion and 3N-terminal portions, besides the amino acid leucine (Schuetz et al. 1991). Various reports suggest the presence of at least 21 HSFs in *A. thaliana* (Baniwal et al. 2004; Nover and Baniwal 2006), 30 in corn, 24 in *Brachypodium*, 25 in rice, 27 in tomato and 52 in soybean (Scharf et al. 2012), supporting the idea that, in plants, there are many duplications, which make HSFs extremely complex. Rice mutants demonstrated the performance of HSFs as the response to abiotic stresses. Overexpression of OsHsfA7 mutant in rice and *A. thaliana* promoted a tolerance of 42 °C, resulting in the survival of more than 50% of the mutants when stressed, twice the value of the results obtained by the control (Liu et al. 2009). Another report established the higher expression of HSPs and HSFs under heat stress in rice, showing that the regulation of abiotic stress induces numerous genes and HSPs that act together in different cascades to combat the problems of abiotic stress (Chandel et al. 2013). These studies highlight the importance of transcription factors and HSFs in the regulation of metabolic pathways responsive to abiotic stress so one can consider them as good candidates in breeding programmes targeting mechanisms of tolerance to abiotic stresses.

## 4.2 BiP

The bZIP family of TFs is abundant, with its orthologs in several species, which include 17 in yeast, 56 in humans, 75 in *Arabidopsis*, 89 in rice, 92 in sorghum, 125 in maize and 131 in soybean (Jakoby et al. 2002; Wei et al. 2012). Elevated levels of binding protein (BiP) have been associated to a variety of abiotic and biotic stresses such as water stress, fungal manifestations, nutritional stress, cold acclimation, insect attack and elicitors of the plant pathogenesis response (Anderson et al. 1994; Denecke et al. 1995; Kalinski et al. 1995; Fontes et al. 1996, 1999; Figueiredo et al. 1997). The rice gene *OsISAP1*, a bZIP family, when overexpressed in tobacco, conferred tolerance to cold, dehydration and salt stress at the seed germination (Mukhopadhyay et al. 2004). OsbZIP71, a TF in rice, was found to be strongly induced by drought, PEG and ABA treatments and repressed by salinity, signifying its regulatory role in ABA-mediated drought and salt tolerance (Liu et al. 2014b).

### 4.3 Protein Kinase

Protein kinases belonging to calcium-dependent protein kinase (CDPK), mitogen-activated protein kinase (MAPK) families and calcineurin B-like protein-interacting protein kinases (CIPK) are thought to be majorly involved in drought tolerance.  $\text{Ca}^{2+}$  cytosolic levels increase rapidly in plant cells in response to environmental stresses, namely, drought and salinity (Sanders et al. 1999). This  $\text{Ca}^{2+}$  influx is probably mediated by a combination of protein phosphorylation/dephosphorylation cascades involving members of the CDPK family. In rice, overexpression of *OsCDPK7* (under the control of the 35S promoter) resulted in increased seedling recovery rate after a salt treatment (Saijo et al. 2000). Transgenic rice overexpressing three *CIPK* genes (*OsCIPK03*, *OsCIPK12* and *OsCIPK15*) showed enhanced tolerance to cold, drought and salt stress, respectively (Xiang et al. 2007). Overexpression of *OsMAPK5a* gene in rice lead to an increase in kinase activity and enhanced tolerance to drought and salt stresses (Xiong and Yang 2003). Overexpression of *OsMAPK44* gene resulted ERA1 in increased tolerance to salt stress in rice (Jeong et al. 2006). Recently, overexpression in rice of DSM1 (drought-hypersensitive mutant1), a well-accepted MAPK kinase kinase (*MAPKKK*) gene, increased the water stress tolerance at seedling level (Ning et al. 2010). It was suggested that DSM1 might be operating as an early signalling component in controlling mechanisms of ROS scavenging in rice. Expression of a *MAPKKK* gene was proved to trigger an oxidative signal cascade and led to tolerance to environmental stress in transgenic tobacco (Shou et al. 2004). In yeast, the catalytic domain of *Nicotiana* protein kinase 1 (NPK1) activated a bypass of BCK1-mediated signal transduction pathway, which was found to be conserved amongst different organisms (Banno et al. 1993). NPK1 was reported to be upstream of oxidative pathways inducing expression of heat shock proteins and glutathione-S-transferases (GST) (Kovtun et al. 2000). Constitutive overexpression of the tobacco *MAPKKK* in maize enhanced the drought tolerance of the transgenic plants (Shou et al. 2004). The transgenic plants maintained significantly higher photosynthesis rates and kernel weight as compared with wild-type plants under drought conditions. However, the effect of NPK1 on yield components was less apparent.

### 4.4 Nuclear Factor Y-B Subunit

NF-Y is a conserved hetero-trimeric complex consisting of NF-YA (HAP2), NF-YB (HAP3) and NF-YC (HAP5) subunits (Mantovani 1999). In *Arabidopsis*, AtNF-YB1, a nuclear factor Y (NF-Y complex), was found to regulate transcription through CCAAT DNA elements and confer abiotic stress tolerance when constitutively expressed in *Arabidopsis* (Nelson et al. 2007). In maize, an ortholog of NF-YB gene was found showing similar response to drought (Wei et al. 2012).

## 4.5 NAC Proteins

Several NAC domain proteins [word derived from the first alphabet of three genes *NAM* (No Apical Meristem), *ATAF* (*Arabidopsis* transcription activation factor) and *CUC* (cup shaped cotyledon)], which are one of the largest plant TF families, have been found to be associated with abiotic stresses (Riechmann et al. 2000). Amongst the 150 members of the NAC family identified in rice that recognizes the cis-acting drought-responsive element NACRS, the expression of about 40 NAC genes increased during drought or salinity stress (Sakuma et al. 2006).

Twofold increase was observed in 20 genes during stress, and a majority of them comprise the SNAC (stress-responsive NAC) group (Fang et al. 2008). Overexpressing *SNAC1* improved biomass accumulation at the vegetative stage in rice plants under both salinity and drought stress due to increased stomatal closure and ABA sensitivity in the transgenic plants (Hu et al. 2006). It was found that the rice genes *ONAC19*, *ONAC55*, *ONAC72* and *ONAC045* were induced by drought and *ONAC045* by high salt, low-temperature and ABA treatment (Zeng et al. 2009). Of late, the overexpression of *OsNAC10* under the control of the constitutive promoter *GOS2* and the root-specific promoter *RCc3* improved tolerance to drought and salinity of the transgenic rice plants at the vegetative stage. However, only the root-specific overexpression of *OsNAC10* enhanced drought tolerance significantly during the reproductive phase, increasing grain yield (25–42%) under drought conditions due to the larger root diameter, which were almost 20% larger than both the wild-type and *PGOS2::OsNAC10* plants (Jeong et al. 2010).

## 4.6 LEA Proteins

Late embryogenesis abundant (LEA) proteins are low-molecular weight proteins that accumulate at higher levels in embryos (Dure et al. 1981; Galau et al. 1986). LEA proteins accumulate in plants in response to water stress and have various functions in drought tolerance. They act synergistically with trehalose to prevent protein aggregation during water deficit (Goyal et al. 2005). Genes encoding LEA-type proteins are diverse RD (responsive to dehydration), ERD (early response to dehydration), KIN (cold inducible), COR (cold regulated) and RAB (responsive to ABA). Five LEA groups have been identified based on structural domains, group 3 and 5 form dimmers with a coiled-coil conformation that manage the ions during stress (Dure et al. 1989). Dehydrins, also known as group 2 LEA proteins, accumulate in response to dehydration and low temperature (Close 1997). The overexpression of *OsLEA3-1* under the control of strong constitutive promoters (35S and Actin1) and a stress-inducible promoter (HVA1-like promoter isolated from the upland rice IRAT109) improved drought tolerance in the drought-sensitive Japonica (lowland) rice (Xiao et al. 2007). Increasing *LEA* gene expression under stress, and presumably LEA protein abundance, has also been accomplished indirectly, with the

overexpression of NAC genes. The overexpression of the stress-responsive proteins OsNAC5 and OsNAC6 enhanced stress tolerance by upregulating the expression of stress-inducible gene *OsLEA3* in rice.

#### 4.7 *Aquaporins*

Aquaporins are central membrane proteins that govern the transport of water, small neutral solutes and CO<sub>2</sub> (Tyerman et al. 2002). The regulatory role of aquaporins in cellular water transport had been demonstrated (Knepper 1994). The expression of the aquaporin, RWC3, a member of the plasma membrane intrinsic protein 1 (PIP1) subfamily, induced under stress resulted in improved water status of lowland rice (Lian et al. 2004). Transgenic rice plants constitutively overexpressing a barley plasma membrane aquaporin, HvPIP2, displayed more sensitivity (reduction in growth rate) to salinity stress (Katsuhara et al. 2003).

#### 4.8 *Other Transcription Factors*

Multiple transcription factors (TFs) have been well characterized in various plant species, but transcriptional reprogramming under drought and stress is not fully understood. Transgenic rice plants overexpressing *AtMYB2* gene conferred salt stress tolerance, with higher biomass and decreased ion leakage under the control of an ABA-inducible promoter (Malik and Wu 2005). Overexpression of WRKY domain containing TF, OsWRKY11 under the control of a *HSP101* promoter, with slower leaf wilting and higher survival rate of green parts of plants conferred heat and drought tolerance at the seedling stage (Wu et al. 2008). It was shown that the constitutive overexpression of bacterial RNA chaperones, CspA and CspB, conferred abiotic stress tolerance to transgenic *Arabidopsis*, rice and maize (Castiglioni et al. 2008). The transgenic maize plants under water-stressed environment showed increase in yield up to 15% (0.75 t/ha) in comparison to the non-transgenic controls that indicates chaperone molecules may be good targets for enhancing abiotic stress tolerance in crop plants (Castiglioni et al. 2008).

### 5 *Oxidative Stress*

Free oxygen radicals produced as a consequence of various environmental stresses are very dangerous for cell components and must be regulated precisely. All plants have developed several antioxidant systems to scavenge these deadly compounds which include catalases (CAT), superoxide dismutase (SOD), peroxidases (POD), ascorbate peroxidases (APX), glutathione reductase (GR) and monodehydroascorbate reductase

(MDAR) (Yang et al. 2017). Besides, there are antioxidant molecules such as ascorbic acid (AA), glutathione, tocopherols, flavanones, carotenoids and anthocyanins (Liu et al. 2016). Some osmolytes (e.g. proline), proteins (e.g. peroxiredoxin) and amphiphilic molecules (e.g. tocopherol) have ROS scavenging function and might function as the antioxidant (Mattoo et al. 2014). Non-enzymatic plant antioxidants are either AA-like scavengers or pigments multifunctional in nature acting as the enzyme cofactor and as a donor/acceptor of electron (Chakraborty et al. 2015). The degree of activities of antioxidant systems under drought stress is exceptionally variable owing to variation in plant species, in the cultivars of the same species, development and the metabolism of the plant and the duration and intensity of the stress.

## 6 Conclusion and Future Prospects

More than 50% yield losses occur in major crop plants owing to different abiotic stresses especially drought (Lipiec et al. 2013). A tremendous effort has to be done to elucidate the stress response pathways, which include interpretation of the function and characterization of various genes and gene families responsible for stress tolerance.

Understanding the molecular basis of plant responses to water stress and their concomitant growth adjustments shall help us to increase plant productivity under water stress conditions. The diversity and specificity of TFs make key components for triggering signalling cascades. Further studies identifying gene variants associated with the significant agronomic traits will assist the molecular engineering of plants with increased tolerance to severe environmental stresses.

In summary, it is vital to integrate crop physiology, genomics and breeding approaches to dissect complex traits, understand the molecular basis of drought tolerance and develop the next-generation crops for our changing climate. Though research is continuing in some major crops, it is predicted that integrated physiology, genomics and breeding approaches will be accelerated in the orphan crops that are essential for food security in many developing countries.

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