Chapter 7
Drought Stress Responses and Signal Transduction in Plants

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Abstract Nature provides all necessary components for healthy growth and development of plants in the form of air, water, light, nutrients, and soil. Any imbalance in the environmental harmony may cause stress to them. Stresses encountered by plants can broadly be categorized into biotic and abiotic stresses. Biotic stresses are mainly caused by pathogens and herbivory, whereas abiotic stresses include the threat imposed by drought, salinity, and extremes of temperature, heavy metals, and pollution. Drought stress is a major cause of yield instability in crops across diverse eco-geographic regions worldwide. A variety of biochemical, molecular, and physiological changes are manifested by plants in response to drought stress. The cellular abscisic acid (ABA) concentration increases on water deficit leading to the activation of a number of stress-responsive genes and the patterns of expression of these genes are very complex, with some genes being induced early while others respond slowly. In general, drought-responsive genes respond to salt and cold stresses as well as to exogenous ABA treatment. However, there are several genes, which express themselves in an ABA-independent manner suggesting that both ABA-dependent and -independent signal transduction cascades exist for drought stress perception, response, and adaptation. Drought stress response and adaptation in plants involves an array of pathways for signal perception, transduction, gene expression and synthesis of proteins, and other stress metabolites. Drought-responsive genes can mainly be classified into two groups. First group constitutes genes whose products provide osmotolerance and protection to plants thus directly functioning in tolerance to stress, while the second group includes genes playing a role in signal transduction as well as regulation of gene expression. This chapter summarizes the complex molecular mechanisms of drought stress response and adaptation in plants, highlighting the transcriptional regulation of stress-responsive

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gene expression. It also focuses on the recent advances in analyzing various stress-responsive pathways with prime emphasis on ABA-dependent and -independent pathways.

Keywords Abscisic acid • Cross talk • Drought • Gene expression • Signal transduction • Transcription factors

7.1 Introduction

Plants are continually challenged by innumerable adverse environmental stresses that affect their growth and productivity. These environmental stresses are of two types, viz. biotic and abiotic. The biotic stresses indicate the stresses caused by living organisms like pathogens and herbivory while abiotic stresses usually comprise moisture deficit or drought, salinity, heat, and low temperature or cold stresses. Irrespective of the type, all these stresses elicit a complex molecular response in plants, starting with perception of stress, initiation of signal transduction, and its manifestation at cellular, physiological, and developmental levels. Of note, these processes rely on the stress duration, genotype, severity of stress, developmental stage, and factors conferring the stress (Bray 1994). Plants are equipped with different strategies to adapt or acclimatize to these environmental stresses, and hence studying these mechanism(s) by which plants perceive stress signals, respond, and adapt to them is of prime importance in biology in order to understand the complex stress regulatory pathways. This knowledge would assist the plant research community to generate elite crop species with enhanced stress tolerance.

The term “drought” comes with several connotations ranging from impaired yields due to too little water according to agronomists, to sudden severe water deficits as defined by molecular biologists (Passioura 2007). In the scenario of global warming, drought is indeed considered to be one of the most important abiotic stresses that adversely affect the plant growth and development, and ultimately questions the food security (Anjum et al. 2011a, b, c; Shao et al. 2009). Limited water supply to roots and/or higher transpiration rate due to elevated atmospheric temperature induces drought stress, which severely impairs growth, yield, and also causes disrupted membrane integrity, reduced pigment content and photosynthetic activity, and changes in osmotic balance (Praba et al. 2009). Plants in turn are equipped with sophisticated stress-responsive mechanisms to circumvent the water deficit stress (Duan et al. 2007; Anjum et al. 2011a, b, c). Therefore, understanding the molecular mechanism of drought stress signal transduction pathway in crop plants is crucial for sustained advancement of rational crop breeding and transgenic approaches to improve stress tolerance in crops of economic importance. This chapter thus aims to summarize various responses of plants to drought stress along with some common characteristics of drought stress signal transduction. It also attempts to analyze some studies on the signaling components.

7.2 Drought Stress Responses

7.2.1 Morphological, Physiological, and Biochemical Responses

7.2.1.1 Growth and Yield

The effects of drought stress largely depend upon severity, duration, and developmental stages. Water deficit stress is more vulnerable at the germination and early seedling growth stages of plants. Reduced or impaired germination and poor seedling stand are some of the early signs of drought stress (Harris et al. 2002; Farooq et al. 2009). A reduction in germination potential, hypocotyls length, and root and shoot length have been reported in several crops (Zeid and Shedeed 2006; Manikavelu et al. 2006; Baloch et al. 2012; Singh and Lata 2013, unpublished). Water stress led to increased root growth in *Helianthus* (Tahir et al. 2002) and *Catharanthus* (Jaleel et al. 2008). Fresh and dry biomasses of crop plants are also greatly affected by water deficit (Zhao et al. 2006). Similarly, Sečenji et al. (2010) reported a decrease in root mass as well as biomass of aerial parts in wheat genotypes during drought stress. In addition, among the physiological processes, the most sensitive process to get affected by water deficit is the cell growth (Farooq et al. 2006). A reduction in turgor pressure due to water deficit limits cell growth while cell elongation of higher plants is inhibited by interrupted water flow from xylem to the surrounding elongating cells (Nonami 1998; Taiz and Zeiger 2006). Further, severe water deficiency imposes reduction in photosynthesis and suppression of leaf expansion, which lead to reduce leaf area (Rucker et al. 1995). A cumulative effect of reduction in growth-related traits, viz. plant height, leaf area, number of leaves per plant, cob length, shoot fresh, and dry weight due to drought stress was reported in maize (Kamara et al. 2003).

Further, several yield determining physiological and developmental processes are also affected by water stress. Disruption in leaf gas exchange properties limit the size of source and sink, impairs phloem loading, nutrient uptake, and dry matter partitioning in plants, thus severely declining yield traits (Farooq et al. 2009). For example, pre-anthesis water stress reduced time to anthesis while a post-anthesis stress decreased the grain-filling duration in several triticale genotypes (Estrada-Campuzano et al. 2008). Reduced grain filling occurs due to decreased assimilate segregation and activities of sucrose and starch biosynthesis enzymes (Anjum et al. 2011c). Drought at flowering stage in pearl millet is more damaging than at vegetative stage (Yadav et al. 2011). Drought stress at tasseling stage in maize leads to considerable decline in yields and yield-related traits in maize (Anjum et al. 2011a). These evidences indicate that dehydration stress directly impairs the growth and yield of several crop plants.

7.2.1.2 Water and Nutrient Uptake

Plant–water relations are largely determined by several physiological characteristics including leaf water potential (LWP), leaf and canopy temperature, relative water content (RWC), stomatal resistance, and transpiration rate (Tr). Water-stressed wheat, rice, and foxtail millet plants had lower RWC as compared to the control plants (Siddique et al. 2001; Lata et al. 2011a). Siddique et al. (2001) reported a decline in LWP, RWC, and Tr with a simultaneous increase in leaf temperature in drought-stressed wheat and rice plants. RWC, turgor potential, transpiration, stomatal conductance, and water use efficiency decreased in drought-stressed *Hibiscus* plants (Egilla et al. 2005). In fact, closing and opening of stomata is badly affected by reduced water availability as compared to other components of plant–water relations. Furthermore, variation in leaf temperature could be a significant factor in regulating leaf water status during water deficit stress (Farooq et al. 2009).

Total nutrient uptake including absorption and translocation is also greatly affected by reduced water availability. Water stress induces an increase in nitrogen (N), a drastic decrease in phosphorus (P), and no significant effects on potassium (K) uptake (Garg 2003). However, several reports indicated that uptake of inorganic ions gets declined under the influence of drought stress in crop plants (McWilliams 2003; Peuke and Rennenberg 2004). Limited availability of energy for assimilation of NO^{3-}/NH^{4+}, PO_4^{3-}, and SO_4^{2-} may also be correlated to the influence of drought on plant nutrition (Grossman and Takahashi 2001). Drought stress thus reduces availability, uptake, translocation, and metabolism of nutrients; however, crop yields can even then be considerably improved by enhancing nutrient-use-efficiency, as there is a significant interaction between soil moisture deficit and nutrient acquisition (Farooq et al. 2009).

7.2.1.3 Photosynthesis and Pigment Content

Water deficit stress has a profound adverse effect on photosynthesis, photosynthetic apparatus, and pigment content (Wahid and Rasul 2005). A considerable decline in net photosynthesis has been reported in drought-stressed maize in contrast to well-watered control plants (Anjum et al. 2011a). With a decrease in RWC and LWP, the foliar photosynthetic rate in higher plants is also observed to decline (Lawlor and Cornic 2002). Severe water stress has also been reported to decline the activity of the most important photosynthetic enzyme RuBisCO, and thus limiting photosynthesis (Bota et al. 2004). Several research groups reported reduced photosynthetic activity under conditions of drought stress because of stomatal or non-stomatal mechanisms (Del Blanco et al. 2000; Samarah et al. 2009; Farooq et al. 2009). However, in sunflower, it has been observed that photosynthesis reduction during dehydration through metabolic damage is more complex than stomatal limitations and is mainly through reduced photosynthetic pigment contents (Reddy et al. 2004). Water deficit-induced loss of chlorophyll content is considered to be the main cause of reduced photosynthesis and the reduction in pigment contents has also been attributed to acute swelling, appearance of lipid droplets, loss of chloroplast membranes, and the distortion of lamellae vesiculation (Kaiser et al. 1981). This is supported by the reports on reduced concentration of chlorophyll and carotenoids in plant tissues (Kiani et al. 2008) primarily due to drought-induced reactive oxygen species (ROS) production in the thylakoids (Reddy et al. 2004). Similar reduction in chlorophyll content due to drought stress has been reported in several crop plants (Manivannan et al. 2007; Massacci et al. 2008; Jaleel et al. 2008; Kiani et al. 2008; Jain and Chattopadhyay 2010). A changed ratio of chlorophyll "a" and "b" and carotenoids due to water stress has also been reported by Farooq et al. (2009) and Anjum et al. (2011b). These reports justified the drought-inhibition of photosynthesis, which threatens the survival of crop plants.

7.2.1.4 Accumulation of Osmolytes

In order to maintain cell turgor, plants accumulate various types of solutes into the cytosol thus balancing the osmotic pressure (Rhodes and Samaras 1994). The process of accumulation of various solutes such as proline, glycine betaine, glutamate, sucrose, and soluble carbohydrates in the cytoplasm is known as osmotic adjustment, by which the plant maintains leaf turgor under drought stress (Anjum et al. 2011c). These compounds prevent membrane damage and enzyme inactivation at low water activity environment and thereby assist in maintaining normal cellular activities during dehydration (Rampino et al. 2006). Proline is one of the most important osmolytes involved in membrane stabilization. Infact plants exposed to water stress tend to primarily accumulate proline in order to reduce cell injury. Several studies have reported the accumulation of proline under progressive drought stress (Claussen 2004; Rampino et al. 2006; Anjum et al. 2011b; Singh and Lata 2014, unpublished). Proline is a key molecule responsible for stabilization of subcellular structures, removal of free radicals, and buffering cellular redox potential during stress (Demiral and Turkan 2004; Ashraf and Foolad 2007). In addition, proline is also thought to act as a signaling molecule in modulating various cellular events such as mitochondrial function, cell proliferation, cell death, and specific gene expression which help cells in recovering from stress (Anjum et al. 2011b). In several species, higher accumulation of proline in tolerant genotypes during stress is related with stress tolerance of those genotypes (Anjum et al. 2011c).

7.2.1.5 Generation of ROS

Generation of ROS such as superoxide anions, hydroxyl radical, hydrogen peroxide, and singlet oxygen is probably one of the earliest biochemical responses of plants exposed to environmental stresses including water stress. Though ROS is a normal by-product of regular oxygen metabolism, it also acts as secondary messengers to elicit specific defense cell signaling or redox signal transduction during severe environmental stresses. Under drought stress, ROS may react with lipids, proteins, and nucleic acids to cause oxidative damage and ultimately hampers the normal cellular functions or even result in cell death (Anjum et al. 2011c; Lata et al. 2011a). It has also been reported that ROS can cause widespread protein denaturation, mutation of nucleic acids, peroxidation, and de-esterification of membrane lipids (Bowler et al. 1992). In plants, ROS are generated in chloroplast, mitochondria, and peroxisomes. Excessive ROS generation in chloroplast membrane makes them extremely sensitive to oxidative stress damage (Mahajan and Tuteja 2005). It has been reported that drought-induced overproduction of ROS increases malonaldehyde (MDA) content, which is an indicator of oxidative damage and also a suitable marker for membrane lipid peroxidation caused by ROS (Anjum et al. 2011c; Lata et al. 2011a). Decreased membrane stability indicates the extent of lipid peroxidation and also shows the prevalence of free radicals in affected tissues. Several reports have shown increased levels of lipid peroxidation with drought stress (Yang and Miao 2010; Lata et al. 2011a).

7.3 Molecular Responses

Water deficit or drought stress induces a plethora of molecular, biochemical, and physiological responses in plants. It is a well-recognized fact that tolerance to dehydration stress is a complex phenomenon comprising the combined action of several genes (Farooq et al. 2009). Numerous responses to water deficit stress are controlled by an array of genes with diverse functions whose expression may change (up- or downregulation) under such adverse conditions. In order to compensate water loss from the cell, regulatory processes are initiated to fine-tune cellular metabolism to new cellular conditions (Bray 1993). Simultaneously, inhibited growth and altered developmental pathways lead to changes in gene expression. It is anticipated that genes expressed during water deficit stress promote cellular tolerance against dehydration either through providing osmotic homeostasis or through stress damage control and repair or through growth control and regulating gene expression (Bray 1993; Zhu 2002). Thus, drought stress signaling can be classified into three functional categories: (1) osmotic signaling to reestablish cellular homeostasis; (2) detoxification signaling for repairing and damage control; and (3) cell division and expansion signaling (Zhu 2002). Stress signal perception and transmission, preferably called stress signal transduction is crucial for gene expression regulation.

7.4 General Stress Signaling Pathways

A general signal transduction pathway commences with stress perception by receptor(s). These receptors are plasma membrane proteins, which bind and interact with the extracellular molecules, known as ligands or elicitors. The stress signal is then transduced downstream resulting in the generation of the second messengers such as ROS and inositol phosphates that can modulate intracellular Ca^{2+} levels. This perturbation is sensed by calcium sensors, which after changing their conformation often initiate a phosphorylation cascade that finally targets stress-responsive genes. These stress-responsive genes could be directly implicated in cellular protection or transcription factors (TFs) that regulate the expression of downstream stress-regulated genes (Mahajan and Tuteja 2005; Xiong et al. 2002). The products of these stress-responsive genes not only help plants to adapt and survive adverse environmental conditions but may also participate in the generation of phytohormones like abscisic acid (ABA), salicylic acid (SA), and ethylene. These hormones act as regulatory molecules in amplifying the initial signal and also initiating a second round of signaling that can follow the same generic pathway or involve on the whole different signaling components. There are also certain components known as accessory molecules, which may not directly participate in stress signaling but may help in modification, delivery, or assembly of various signaling components and thus are crucial for precise stress signal transmission. These accessory molecules include protein modifiers such as enzymes for glycosylation, methylation, myristoylation, and ubiquitination; scaffold proteins and adaptors (Xiong and Zhu 2001).

The products of major stress-inducible genes may be largely classified into two groups: first group comprises proteins that are directly involved in stress tolerance such as water channel proteins and late embryogenesis abundant (LEA) proteins. The second group constitutes regulators of intracellular signaling and stress-inducible gene expression such as protein kinases, phosphatases, *cis*-regulatory elements, and TFs (Hirayama and Shinozaki 2010).

7.5 Aquaporins and Stress Proteins

Aquaporins are intrinsic membrane proteins which simplify and control passive exchanges of water molecules across plant membranes. In plants, they are widely found in plasma and vacuolar membranes. Several studies have been performed on aquaporins and plant–water relations, which showed the vital roles of aquaporins in transcellular water transport. Hence, aquaporins are found to be abundantly expressed in root, where they mediate soil water uptake (Javot and Maurel 2002). The study by Javot and Maurel (2002) had also showed the decrease of root hydraulic conductivity in the presence of mercury, which is reported to be a potential inhibitor of aquaporins, thus hampering overall root water uptake.

Several drought-induced gene products are found to shield the cellular structures from dehydration. Since most of the drought-induced gene products such as stress proteins are water soluble, they provide hydration to cellular structures and thereby confer stress tolerance (Wahid et al. 2007). LEA proteins are the most abundant stress proteins that are linked to both water and cold stress in plants. These proteins are active in seeds that contain high ABA levels (Tunnacliffe and Wise 2007). In plants, six groups of *LEA* genes have been identified of which group 3 and 5 LEA proteins are predicted to play important roles in ion sequestration during cellular dehydration or water deficit (Bray 1993). Group 1 LEA proteins are predicted to possess enhanced water-binding capability while group 4 LEA proteins may participate in replacing water to protect cellular structures (Bray 1993). Dehydrins are also a group of LEA proteins that are known to accumulate during water deficit stress. Transgenic rice plants expressing barley group 3 LEA genes, *HVA1* were able to maintain relatively high RWC and showed less electrolyte leakage from cells suggesting that this protein may play crucial roles in protecting cell membranes from damage during osmotic stress (Rohila et al. 2002; Babu et al. 2004). This gene when expressed in wheat was also capable of conferring improved growth and higher WUE (Sivamani et al. 2000). Similarly, Group 1 and 2 LEA proteins from wheat provide protection against dehydration stress when expressed in rice (Cheng et al. 2002).

7.6 Protein Kinases in Drought Signaling

Protein phosphorylation, the core theme in cell signaling has also been found to be involved in stress adaptation (Zhu 2002). Several protein kinases are reported to express in response to osmotic stress. Mitogen-activated protein kinase (MAPK) cascades constitute one of the major cellular signaling components in eukaryotic cells and are generally activated in response of hyperosmotic stress (Hirayama and Shinozaki 2010). A large number of MAPKs, MAPKKs, and MAPKKKs have been identified in various plant species, which are shown to function in several various processes thus making complex networks. Transcript levels of many protein kinases including various members of MAPK signaling have been found to be increased under osmotic stress. This ultimately resulted in accumulation of osmolytes that help in reestablishing osmotic balance and protects the cells from stress damage by induction of several stress proteins such as LEA (Zhu 2002; Mahajan and Tuteja 2005).

Sucrose non-fermentation 1 (SNF1)-related kinases are also found to be induced in response to hyperosmotic stresses. Several of these kinases such as *Arabidopsis SRK2D/SnRK2.2*, *SRK2I/SnRK2.3*, and *SRK2E/OST1/SnRK2.6* are strongly ABA responsive are essential for ABA signaling thus establishing the fact that SnRK2-type kinases may play crucial roles in transducing the signals which activate them (Hirayama and Shinozaki 2010).

Calcium-dependent protein kinases (CDPK) are another important group of kinases that are activated in response to osmotic stress and are found to activate calcium signaling (Zhu 2002). In a study in maize protoplast transient expression system showed that a constitutively active CDPK mutant activated the expression of the reporter gene, which was normally responsive to osmotic stress, cold, and ABA while its negative form was capable of inhibiting the stress or ABA induction of the gene (Sheen 1996). CDPK genes, CPK3, and CPK6 regulate ABA activity in guard cells (Mori et al. 2006) while CPK4 and CPK11 positively regulates ABA responses. In addition, they were also able to phosphorylate AREB/ABF TFs in an ABA-dependent manner (Zhu et al. 2007).

7.7 Phospholipid Signaling

Membrane phospholipids not only comprise an active system that produces a large number of signal molecules such as inositol 1, 4, 5-triphosphate (IP_3), diacylglycerol (DAG), and phosphatidic acid (PA) but also serve as important structural elements during stress responses (Zhu 2002). Phospholipid signaling systems are categorized according to the phospholipases that catalyze the formation of lipid and other signal messengers. Among these signaling systems, the phospholipase C (PLC) pathway is well characterized. PLC catalyzes the hydrolysis of phosphatidylinositol 2, 5-biphosphate (PIP_2) into second messengers IP_3 and DAG. IP_3 releases Ca^{2+} from cellular reserves, whereas DAG activates protein kinase C. Drastic increase in IP_3 levels have also been shown in response to hyperosmotic stress in several plant systems (DeWald et al. 2001; Takahashi et al. 2001). In guard cells, IP_3-induced Ca^{2+} increase in the cytoplasm led to stomatal closure and thus enables the cells to retain water (Sanders et al. 1999). An increased cytoplasmic Ca^{2+} could lead to the expression of several osmotic stress-responsive genes (Wu et al. 1997). In fact elevated IP_3 accumulation in *Arabidopsis fry1* mutant has been correlated with, super induction of ABA- and stress-responsive gene transcription (Xiong et al. 2001). Other inositol phosphates such as IP_6 and IP_3 also help in releasing Ca^{2+} from internal stores and thus assist in IP_3 signaling. DAG signaling may be indirect in plants as it can be rapidly phosphorylated to PA.

Increase in phospholipase D (PLD) activity was also evidenced during osmotic stress in various plants (Munnik et al. 2000). PLD is responsible for cleavage of membrane phospholipids to phosphatidic acid (PA) and free head groups wherein PA acts as second messengers in animal cells. PLD was found to be rapidly activated in various plant cells (Frank et al. 2000; Katagiri et al. 2001) and also its activity was higher in drought-sensitive plants than the tolerant ones (El Maarouf et al. 1999). Blocking its activity reduced stress injury and improved stress tolerance, which suggests that its activation results in lipolytic membrane disintegration under stressed condition. On the other hand, application of PA mimics ABA in inducing stomatal closure thus helping to mitigate stress injury (Jacob et al. 1999).

7.8 Role of ABA and Transcription Factors in Osmotic Stress Signaling

ABA carries out a vital role in regulation of many physiological and developmental processes in plants (Lata and Prasad 2011) (Fig. 7.1). It has also been found to be a main physiological signal in inducing drought and high salinity responses (Farooq et al. 2009; Lata and Prasad 2011). The role of ABA is not only in the regulation of developmental pathways but also for controlling many stress adaptation responses like activating genes responsible for osmotic adjustment, ion compartmentalization,

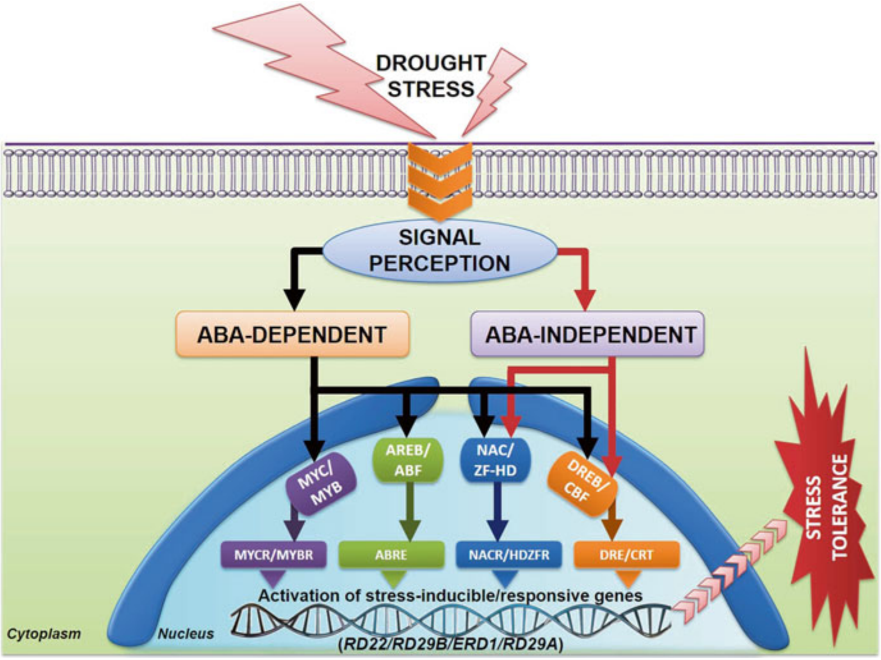

Fig. 7.1 Schematic representation of drought stress tolerance mechanism in plants mediated by several transcription factors (modified from Lata et al. 2011c)

root hydraulic conductivity, regulation of shoot and root growth, limiting transpiration rate and wilting, and ultimately reducing water loss in the plants (Verslues and Zhu 2005; Pospíšilová et al. 2009). It is also involved in modification of gene expression and upregulation of various stress-responsive genes during osmotic imbalance (Ingram and Bartels 1996). Even though many genes are expressed in response to drought stress on exogenous ABA treatment, contrarily some genes do not respond to such treatments. This proposes the existence of two types of pathways: ABA-dependent and -independent signal transduction cascades in crop plants (Hirayama and Shinozaki 2010; Lata and Prasad 2011). ABA-dependent signaling pathway mediates the plant's acclimatization to stress by activating two different regulons: (1) the AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor), and (2) the MYC/MYB regulon. The ABA-independent regulons are: (1) the CBF/DREB (Cold-binding factor/dehydration-responsive element binding) regulon; and (2) the NAC and ZF-HD (zinc-finger homeodomain) regulon (Saibo et al. 2009; Lata and Prasad 2011). Although these different stress response pathways usually function independently, occurrence of pathway cross talks are also possible at some levels.

7.8.1 The AREB/ABF Regulon

The AREB or ABFs belong to the bZIP (basic leucine zipper) transcription factor family which recognizes the ABRE motif thereby activating ABA-dependent gene expression (Uno et al. 2000) (Fig. 7.1). In studies related to ABA-deficient aba2 and ABA-insensitive abi1 mutants, these proteins showed less activity as compared to ABA-hypersensitive *Arabidopsis* era1 mutant (Uno et al. 2000). The ABA-dependent phosphorylation of the AREB/ABF proteins could be a possible mechanism for this response (Shinozaki and Yamaguchi-Shinozaki 2007). The ABFs/AREBs are grouped under group A AtbZIPs (Jakoby et al. 2002), which generally function in ABA signaling during seed maturation as well as under stress conditions (Lata et al. 2011c). Reports indicate that these ABFs play a role in diverse stress signaling pathways, viz. drought, cold, heat, salt, and glucose (Kim et al. 2004; Fujita et al. 2005).

For instance, OsABI5 was found to be induced by ABA and high salinity, and downregulated by dehydration and cold stress in seedlings, while its overexpression led to improved salinity tolerance in rice (Zou et al. 2008; Nakashima et al. 2009). Overexpression of ABF3 and ABF4 led to reduction in transpiration and enhanced drought tolerance (Kang et al. 2002). AREB1/ABF2 is a crucial component of glucose signaling whose overexpression improved drought stress tolerance (Kim et al. 2004). Overexpression of *OsbZIP23* considerably enhanced drought and high salinity tolerance in rice at the reproductive stage (Xiang et al. 2008). Further, upregulation of LEA-class genes and ABA- and dehydration-stress-inducible regulatory genes such as linker histone H1 and AAA ATPase was also evidenced.

7.8.2 The MYC/MYB Regulon

MYC/MYB TFs play active roles in the stress signaling by ABA-dependent pathway and upregulate abiotic stress-responsive genes. *AtMYB2* and *AtMYC2* together act as transcriptional activators in the dehydration- and ABA-inducible expression of *RD22* (Urao et al. 1993; Abe et al. 2003). *AtMYB102* assimilates dehydration, salinity, osmotic, ABA, and wound-signaling pathways (Denekamp and Smeekens 2003). *AtMYB44* confers abiotic stress tolerance by facilitating stomatal closure in an ABA-independent manner (Jung et al. 2008). *AtMyb41* of *Arabidopsis* is transcriptionally regulated under conditions of drought, salinity, drought, and ABA responses.

The overexpression of MYB15 in *Arabidopsis* was found to improve drought and salt tolerance (Ding et al. 2009). Increase in the expression levels of AtMYB2, or AtMYC2 independently or together enhanced ABA sensitivity and improved osmotic tolerance (Abe et al. 2003). *OsMYB4* transgenic lines of *Arabidopsis* exhibited improved chilling and freezing tolerance with a dwarf phenotype (Vannini et al. 2004), the tomato transgenic showed enhanced tolerance to drought stress (Vannini et al. 2007), while an improved drought and cold tolerance was evidenced in the transgenic apple (Pasquali et al. 2008). Transgenic potato overexpressing *StMYB1R-1* showed higher tolerance to drought stress with no significant effects on other agricultural traits (Shin et al. 2011).

7.8.3 The CBF/DREB Regulon

The CBF/DREB TFs play a significant role in the ABA-independent pathways, inducing the expression of stress-responsive genes. The two main subgroups of DREB subfamily: DREB1 and DREB2 are included in two separate signal transduction pathways under low temperature and dehydration, respectively (Lata and Prasad 2011). In rice, *OsDREB1A* and *Os-DREB1B* were observed to get induced immediately (within 40 min) after cold exposure, but did not respond to ABA treatment (Dubouzet et al. 2003). *Ca-DREBLP1* from hot pepper was rapidly induced by dehydration and high salinity stresses and to a lesser degree by mechanical wounding (Hong and Kim 2005). In another study, *Arabidopsis DREB2A* and its homolog *DREB2B* were induced by dehydration and salinity stresses, but not by cold stress and ABA (Liu et al. 1998; Nakashima et al. 2000). Likewise ABA, mannitol, and cold treatments had meager effect on the expression of *DREB2C* (Lee et al. 2010). *OsDREB2A* accumulated to the highest levels under control conditions and was induced marginally by high temperature, drought, and high salinity treatments (Matsukura et al. 2010). Foxtail millet *SiDREB2* was also evidenced to be upregulated by drought and high salinity treatments (Lata et al. 2011b).

DREB1B/CBF1 or *DREB1A/CBF3* overexpression lines of *Arabidopsis* under a constitutive promoter showed durable tolerance to extreme cold, drought, and high salinity stresses indicating that DREBs/CBFs regulates multiple genes involved in stress tolerance (Jaglo-Ottosen et al. 1998; Liu et al. 1998; Kasuga et al. 1999). Overexpression of *OsDREB1A* in transgenic *Arabidopsis* and rice plants also exhibited tolerance to low temperatures, high salinity, and drought (Dubouzet et al. 2003; Ito et al. 2006). Improved dehydration tolerance was reported in overexpression wheat lines possessing RD29A::*DREB1A/CBF3* constructs (Pellegrineschi et al. 2004). A constitutive overexpression of *CBF3/DREB1A* and *ABF3* showed enhanced dehydration and salt tolerance in transgenic rice without any phenotypic aberrations or yield penalties (Oh et al. 2005). Overexpression of *OsDREB1F* significantly improved high salinity, drought, and low-temperature tolerance of both rice and *Arabidopsis* transgenics (Wang et al. 2008). These reports support the fact that DREB transcription factors are crucial for regulation of abiotic stress-related genes and thereby play a prime role in imparting stress endurance to plants.

7.8.4 The NAC Regulon

The NAC (NAM, ATAF, and CUC) family is one of the plant-specific TF family whose members are involved in plant developmental programs and disease resistance (Lata et al. 2011c). Many of these genes were also found to respond to various environmental stresses (Lata et al. 2011c; Puranik et al. 2012). *SNAC1*, a stress-responsive NAC is activated primarily in guard cells under dehydration (Hu et al. 2006). *ERD1* (early responsive to dehydration stress 1) promoter analysis revealed that the NAC ZF-HD transcription factors are vital for activation of the ERD1 gene (Tran et al. 2007). *GmNAC2*, *GmNAC3*, and *GmNAC4* were found to be strongly activated by osmotic stress (Pinheiro et al. 2009). OsNAC045 was induced by drought, salinity, low temperature, and ABA in leaves and roots (Zheng et al. 2009). *TaNAC4* was found to be induced by cold, salt, wounding, ABA, ethylene, and MeJA, indicating a considerable cross talk between abiotic and biotic stress conditions (Xia et al. 2010). cDNA microarray led to the identification of several target genes of the AtNAC019, AtNAC055, and AtNAC072 transcriptional activators in the *Arabidopsis* transgenic plants (Tran et al. 2004). These transgenic plants also exhibited enhanced drought tolerance. The *OsNAC6* transgenic plants exhibited the upregulation of various abiotic and biotic stress-responsive genes (Nakashima et al. 2007). The transgenics were also tolerant to dehydration and high salt stresses. Rice plants overexpressing *OsNAC045* showed enhanced tolerance to drought and salt stresses (Zheng et al. 2009). Further, genome-wide analysis of NAC TF family members in foxtail millet and its expression profiling during various abiotic stresses and hormonal treatments revealed a stimulus-specific and time-dependent responses of these TFs (Puranik et al. 2013). The above reports suggest that NAC TFs play a very important role in physiological adaptation of plants for successful growth in stress conditions.

7.9 Functional Genomics Studies on Drought Stress Response and Signaling

Knowledge acquired from the genetic and functional genomic studies of model plants such as *Arabidopsis*, rice, and foxtail millet and also of the plant species that thrive in extreme environmental conditions such as resurrection plant has provided crucial information on drought stress tolerance mechanism(s). Other than model plants, drought tolerance response mechanism has also been elucidated in crops of economic importance such as wheat, maize, and poplar using either gene-by-gene approach or transcriptome, proteome, or metabolome profiling studies (Li et al. 2012; Pérez-Clemente et al. 2013). Typically, a gene-by-gene approach has been used to study plant responses to stress. Overexpression and gene silencing have been major strategies to study stress tolerance mechanisms in different crop plants. Some of the genes, which are involved in drought stress responses and signaling in plants, are listed in Table 7.1.

Table 7.1 Summary of gene(s) involved in drought stress responses and signaling in plants (last 5 year reports were summarized)

Plant	Gene(s)	Gene source	ABA response	Reference
Glycine max and *Nicotiana tabacum*	The endoplasmic reticulum (ER)-resident molecular chaperone BiP (binding protein)	*G. max*	No	Valente et al. (2009)
Oryza sativa	Core-binding factor (*CBF3*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	Salt Overly Sensitive 2 (*SOS2*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	9-cis-epoxycarotenoid dioxygenase 2 (*NCED2*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	Nicotiana protein kinase 1 (*NPK1*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	Molybdenum cofactor sulfurase (*LOS5*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	C2H2-EAR zinc-finger protein (*ZAT10*)	*O. sativa*	Yes	Xiao et al. (2009)
O. sativa	Na(+)/H(+) exchanger (*NHX1*)	*O. sativa*	Yes	Xiao et al. (2009)
N. tabacum	Ethylene response factor 3 (*ERF3*)	*G. max*	Yes	Zhang et al. (2009)
Arabidopsis thaliana	MYB transcription factor (*MYB15*)	*A. thaliana*	Yes	Ding et al. (2009)
O. sativa	β-carotene hydroxylase (*BCH*)	*O. sativa*	Yes	Du et al. (2010)
Solanum lycopersicum	Osmotin	*N. tabacum*	No	Goel et al. (2010)
O. sativa	Ethylene response factor 3 (*JERF3*)	*O. sativa*	No	Zhang et al. (2010)
O. sativa	Ethylene response factor 1 (*ERF1*)	*S. lycopersicum*	Yes	Quan et al. (2010)
A. thaliana	ABA-responsive elements (ABREs) binding factors (*ABF3*)	*A. thaliana*	Yes	Abdeen et al. (2010)
A. thaliana	Phospholipase D (*PLDα1*)	*Setaria italica*	Yes	Peng et al. (2010)
A. thaliana	Ubiquitin-conjugating enzyme gene 2 (*UBC2*)	*G. max*	No	Zhou et al. (2010)
S. lycopersicum	Xyloglucan endo-trans-gluco-sylase/hydrolase (*XTH3*)	*C. annuum*	No	Choi et al. (2011)
O. sativa	RING domain-containing protein (*RDCP1*)	*O. sativa*	Yes	Bae et al. (2011)
O. sativa	Salt- and drought-induced ring finger 1 (*SDIR1*)	*O. sativa*	Yes	Gao et al. (2011)

(continued)

Table 7.1 (continued)

Plant	Gene(s)	Gene source	ABA response	Reference
O. sativa	No apical meristem [NAM], Arabidopsis transcription activation factor [ATAF], and cup-shaped cotyledon [CUC] (NAC) [*NAC5*]	*O. sativa*	Yes	Song et al. (2011)
O. sativa	Drought-responsive ethylene response factor (*DREF1*)	*O. sativa*	No	Wan et al. (2011)
Ralstonia solanacearum	MYB transcription factor (PIMP1)	*Triticum aestivum*	Yes	Liu et al. (2011)
A. thaliana	Dehydration-responsive element-binding protein 3a (*DREB3a*)	*Leymus chinensis*	Yes	Xianjun et al. (2011)
S. tuberosum	R1-type MYB-like transcription factor (*MYB1R-1*)	*S. tuberosum*	Yes	Shin et al. (2011)
A. thaliana	Vacuolar H+-pyrophosphatase gene (*AVP1*)	*A. thaliana*	No	Pasapula et al. (2011)
O. sativa	A bZIP transcription factor OsbZIP46 with a deletion of domain D (*OsbZIP46CA1*)	*O. sativa*	Yes	Tang et al. (2012)
N. tabacum	Aquaporin (*AQP7*)	*T. aestivum*	No	Zhou et al. (2012b)
S. lycopersicum	Endoplasmic reticulum (ER)-localized really interesting new genes (RING) E3 Ub ligase (*Rma1H1*)	*Capsicum annuum*	No	Seo et al. (2012)
O. sativa	Heat shock proteins (*Hsp17.0* and *Hsp23.7*)	*O. sativa*	No	Zou et al. (2012)
A. thaliana	C2H2-type zinc-finger protein 1 (ZFP1)	*G. soja*	No	Luo et al. (2012)
A. thaliana	SUMO-conjugating enzyme 9 (*Sce9*)	*Spartina alterniflora*	Yes	Karan and Subudhi (2012a)
A. thaliana	Nascent polypeptide associated complex gene (*βNAC*)	*S. alterniflora*	No	Karan and Subudhi (2012b)
A. thaliana and *Lotus corniculatus*	Dehydration-responsive element-binding protein (*DREB*)	*P. euphratica*	Yes	Zhou et al. (2012a)
O. sativa	Drought-induced lipid transfer protein (*DIL*)	*O. sativa*	Yes	Guo et al. (2013)

(continued)

Table 7.1 (continued)

Plant	Gene(s)	Gene source	ABA response	Reference
T. aestivum	NAC transcription factor (*NAC1*)	*O. sativa*	Yes	Saad et al. (2013)
A. thaliana	Late embryogenesis abundant gene (*LEA*)	*Jatropha curcas*	No	Liang et al. (2013)
A. thaliana	Expansin 4 (*EXPA4*)	*rosa hybrida*	Yes	Lü et al. (2013)
A. thaliana	Acyl-CoA-binding protein 2 (*ACBP2*)	*A. thaliana*	No	DU et al. (2013)
A. thaliana and *G. soja*	Receptor-like cytoplasmic kinase (*RLCK*)	*G. soja*	Yes	Sun et al. (2013)
A. thaliana	Nuclear factor YA (NF-YA)	*G. max*	Yes	Ni et al. (2013)
A. thaliana	Seven In Absentia 2 (SINA2)	*A. thaliana*	Yes	Bao et al. (2014)
A. thaliana	Adenosine diphosphate-ribosylation factors (*ARF*)	*S. alterniflora*	No	Karan and Subudhi (2013)
A. thaliana	Receptor-like kinase (*RLK*)	*Gossypium barbadense*	Yes	Zhao et al. (2013)
O. sativa	DUF966-stress-repressive gene 2 (*DSR2*)	*O. sativa*	Yes	Luo et al. (2013)
A. thaliana	Arabidopsis Response Regulator 22 (*ARR22*)	*A. thaliana*	No	Kang et al. (2013)
A. thaliana	RING E3 ligase (*CTR1*)	*O. sativa*	Yes	Lim et al. (2013)
A. thaliana	Mg-chelatase H subunit (*CHLH*)	*A. thaliana*	Yes	Tsuzuki et al. (2013)
A. thaliana	Calcium-dependent protein kinase (*CPK10*)	*Populus euphratica*	Yes	Chen et al. (2013a)
S. tuberosum	Dehydration-responsive element-binding protein 1 (*DREB1*)	*S. tuberosum*	Yes	Bouaziz et al. (2013)
Gentiana triflora	Dehydrin 1 and 2 (*DHN1* and *DHN2*)	*G. triflora*	No	Imamura et al. (2013)
A. thaliana	Vacuolar pyrophosphatase type I (*EVP1*)	*Eucalyptus globulus*	No	Gamboa et al. (2013)
Zea mays	Molybdenum cofactor sulfurase (*LOS5*)	*Arabidopsis thaliana*	Yes	Lu et al. (2014)
T. aestivum	Ethylene response factor 3 (*ERF3*)	*T. aestivum*	Yes	Rong et al. (2014)

However, functional genomics approach allows large-scale gene function analysis using high-throughput technologies and also helps in establishing function and interaction of gene products at cellular and whole plant level. Also the information generated through next-generation sequencing programs also contribute towards analyzing stress-responsive genes. The large-scale availability of expressed sequence tags (ESTs) and cDNA sequences also compensates for those plant species, which are yet not sequenced. As for example, in *Arabidopsis* several research groups have conducted transcriptome studies to decipher mechanisms regulating stress perception, signaling, and tolerance (Shinozaki et al. 2003; Shinozaki and Yamaguchi-Shinozaki 2007; Rasmussen et al. 2013). The dehydration tolerance mechanism in foxtail millet, a model plant for Panicoid species, has been dissected using transcriptomics approach (Lata et al. 2010). Few of the important transcriptome studies on drought stress response in model plants and different crops have been enlisted in Table 7.2.

One of the basic purposes of studying drought stress response and signaling in crop plants is to generate improved stress-tolerant crops by means of genetic manipulation. The outcome of basic molecular and genetic research using model plants especially *Arabidopsis* have been applied to improve stress tolerance of several other plant species including crop plants. Several agronomic traits are quantitative and are controlled by multiple genes, which may interact with each other. Trait(s) controlled by many genes acting together are known as Quantitative trait locus (QTL). Therefore, QTL analyses among tolerant and susceptible crop species has also received wider attention in recent times as such approaches not only help in identifying stress tolerance QTLs but also enable development of stress-tolerant crops by combining or pyramiding various stress tolerance QTLs (Hirayama and Shinozaki 2010; Pérez-Clemente et al. 2013).

In foxtail millet, a synonymous SNP at the 558th bp position (A/G transition) was identified in the *SiDREB2* gene from dehydration-tolerant (A) and -sensitive (G) cultivars (Lata et al. 2011b). Based on the identified SNP, an allele-specific marker (ASM) for dehydration tolerance was developed. The data on segregation of the ASM along with both the lipid peroxidation (LP) data, and RWC data of 170 foxtail millet accessions were recorded for conducting the single marker regression analyses (Lata et al. 2011b). The regression of LP and RWC on the *SiDREB2*-ASM were highly significant, thus indicating an association between the marker and the traits (Lata and Prasad 2013, 2014). The R^2 values of 0.27 and 0.19 for LP and RWC, respectively, suggested that the *SiDREB2* associated trait contributed to ~27 % and ~20 % of the total variation in LP and RWC among 170 and 122 accessions correspondingly. This suggested that the ASM is tightly linked with LP and RWC, which are important biochemical markers for assessing dehydration-induced oxidative stress tolerance in foxtail millet (Lata and Prasad 2014). Similarly, an SNP associated with drought tolerance in wheat *TaMYB2* was identified and an ASM was developed for the same (Garg et al. 2012). The use of these ASMs might be faster, cheaper, and reproducible than other SNP genotyping methods, thus enabling allele-mining and marker-aided breeding of crop varieties for drought tolerance.

Table 7.2 List of important transcriptome studies on drought stress response in crop plants reported in last 2 years

Crop	Strategy	Platform	Nature of study	Reference
Gossypium herbaceum	Transcriptome sequencing	GS-FLX pyrosequencer	Transcriptome of two *G. herbaceum* cultivars contrastingly differing in their tolerance to drought stress was studied by sequencing the RNA content of leaves from respective cultivars	Ranjan et al. (2012a)
G. hirsutum	Microarray	Affymetrix cotton GeneChip Genome array	Genome-wide transcriptome analysis using microarray was performed in developing fibers of *G. hirsutum* under drought stress	Padmalatha et al. (2012)
G. herbaceum	Microarray; transcriptome sequencing	Affymetrix gene chip; GS-FLX pyrosequencer	Comprehensive transcriptome analysis was performed among four genotypes of *G. herbaceum* exposed to drought stress	Ranjan et al. (2012a, b)
Coffea canephora	Electronic northern; macroarray; 2D gel electrophoresis	Hoefer SE600 Ruby system	Identification and analysis of differentially expressed genes and proteins upon drought acclimation in tolerant and sensitive genotypes of *C. canephora* was performed	Marraccini et al. (2012)
Populus euphratica	Microarray	Affymetrix gene chip	Transcriptomics of *P. euphratica* responsive to long-term drought was characterized using microarray and expression profiling was studied using qRT-PCR	Yan et al. (2012)

(continued)

Table 7.2 (continued)

Crop	Strategy	Platform	Nature of study	Reference
Glycine max	Microarray	Affymetrix Soybean Array GeneChip	Microarray analysis of leaf tissues of soybean plants, which were subjected to drought stress from late vegetative V6 and from full bloom reproductive R2 stages was performed	Le et al. (2012)
Ammopiptanthus mongolicus	Transcriptome sequencing	GS XLR70 Titanium pyrosequencer	Transcriptome sequencing of *A. mongolicus* root was performed and analyzed	Zhou et al. (2012a, b, c)
G. hirsutum	Transcriptome sequencing	Illumina HiSeq 2000	Total RNA from the toot tissues of drought stressed and control plant of *G. hirsutum* was sequenced and analyzed	Bowman et al. (2013)
G. arboretum	mRNA sequencing	Illumina HiSeq 2000	Total mRNA from the leaf, stem (including hypocotyl), and root tissues of drought stressed and control plant of *G. arboretum* was sequenced and analyzed	Zhang et al. (2013)
Lablab purpureus	SSH; cDNA sequencing	Information not available	SSH libraries generated from root tissues of the drought-stressed *L. purpureus* under water–stress and control conditions were sequenced and the ESTs were analyzed	Yao et al. (2013)
P. euphratica	Transcriptome sequencing	454-GS FLX Titanium System	The total RNA of non-stressed control and drought-stressed *P. euphratica* leaves was sequenced and analyzed for identifying the differentially expressed genes	Tang et al. (2013)

(continued)

Table 7.2 (continued)

Crop	Strategy	Platform	Nature of study	Reference
Oryza sativa	Microarray	GreenGene Biotech	Microarray experiments using mRNA from air-dried leaves and roots of rice were performed to investigate the genes involved in acute dehydration response.	Minh-Thu et al. (2013)
Glycine max	Digital gene expression tag profiling (DGE)	Illumina HiSeq 2000	Using DGE, the expression profiles between two soybean genotypes were analyzed for identifying drought-responsive genes	Chen et al. (2013a, b)
Chrysanthemum morifolium	Transcriptome sequencing	Illumina HiSeq 2000	The total RNA of *C. morifolium* exposed to drought stress was sequenced and analyzed	Xu et al. (2013)
Macrotyloma uniflorum	Transcriptome sequencing	Illumina HiSeq 2000	The RNA content of shoot and root tissues of control and drought-stressed samples of drought-sensitive genotype and drought-tolerant genotype was isolated and sequenced	Bhardwaj et al. (2013)
Setaria italica	Transcriptome sequencing	Illumina HiSeq 2000	Transcriptome sequencing of *S. italica* shoot tissue was performed and analyzed	Qi et al. (2013)
Hylocereus undatus	SSH; cDNA microarray	*Custom made*	SSH cDNA libraries were constructed using in vitro shoots of *H. undatus* exposed to drought stress and control. Comparative analysis was performed using microarray	Fan et al. (2014)

(continued)

Table 7.2 (continued)

Crop	Strategy	Platform	Nature of study	Reference
Solanum tuberosum	Transcriptome sequencing	Illumina HiSeq 2000	Transcriptome analysis in drought-stressed potato leaf tissues was performed. A subset of differentially expressed genes associated with drought response was examined using qRT-PCR	Zhang et al. (2014)
Pinus halepensis	Transcriptome sequencing	Illumina HiSeq 2000	Transcriptome sequencing of two phenotypically divergent *P. halepensis* accessions was performed and analyzed	Pinosio et al. (2014)

7.10 Conclusion and Future Perspectives

Drought stress is a major threat for agriculture globally with its direct impact on crop production, quality, and productivity. The situation has become worse with recent global climate change. Stress duration, severity, developmental stage, and genotype of the crop undeniably play crucial roles in understanding how plants respond to water deficit stress. Plants respond and adapt to drought stress by exhibiting various molecular, biochemical, physiological, and morphological responses. Many genes are expressed in response to drought stress, and their products impart stress tolerance to plants. Therefore, identifying the mechanism of plant responses to drought stress at the molecular level is of fundamental importance, since it would proffer the research on improving stress tolerance and productivity of crop plants. This chapter summarizes various responses of plants to drought and role of various signaling components including important TFs, viz. ABRE, MYC/MYB, CBF/DREBs, and NAC, which regulate the expression of various stress-responsive genes (Fig. 7.1). Further, these TFs play crucial roles in providing tolerance and adaptation to plants against multiple stresses in both ABA-dependent and -independent manner. These signaling components and transcription factors can be genetically modified to generate transgenics with higher tolerance to drought and abiotic stresses. Their functional analysis will thus be helpful in providing more information on the complex regulatory networks involved in stress responses and adaptation of plants and the cross talk between different signaling pathways. Additionally, considering these components as candidate genes in plant breeding programs will provide a better understanding of signal transduction events pertaining to abiotic stresses. Eventually, this would assist in developing crop varieties with enhanced stress tolerance through genetic manipulation.

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