

Chapter 14

Transcription Factors in Abiotic Stress Responses: Their Potentials in Crop Improvement

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Abstract Abiotic stresses, especially drought, high salinity, flooding, and extreme temperatures, have become a big concern due to their high frequency of occurrence and usually beyond human control capacity, as well as their severe impacts on agricultural crop productivities. Under the pressures of climate change and reduction in total cultivated land worldwide for other purposes, sustaining food security to feed an increasing human population while coping with these environmental constraints is a greater challenge than ever. Generating new varieties with better traits based on gene exchange from available sources via conventional breeding methods currently no longer provides an adequate solution in coping with abiotic stresses. Therefore, another research theme attracting the scientists over the past 20 years has been to elucidate molecular mechanisms that the plants employ to defend and adapt to stress conditions. The final aims are to identify and characterize the function of important genes involved in plant responses to stress that can be used for genetic manipulation. Thanks to advances in molecular biotechnology, including gene transfer techniques such as particle bombardment, microinjection, and *Agrobacterium*-mediated transformation, new varieties with better stress tolerance and yield production could be made by this strategy; thus, in combination with traditional approaches, development of new lines with improved traits has become more practical. According to our current knowledge, transcription factors (TFs) have been recognized to play essential roles in regulating plant responses against adverse abiotic factors. Many TFs belonging to families AP2/EREBP, bZIP, MYB, WRKY, and NAC have been

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reported to participate in plant responses to various stressors. A number of TFs whose encoding genes are appropriately altered in expression level have shown enhanced tolerance capacity toward drought, salt, and suboptimal temperatures in transgenic model and crop plants. In this chapter, we summarize our current understanding about TF activities in plants under adverse stress conditions and their use in crop improvement.

Keywords Abiotic stress · Transcriptional factor · Stress tolerance · Genetic engineering · Crop improvement

1 Introduction

Abiotic stress is defined as a “non-living environmental factor that can negatively or even harmfully affect the growth and productivity of plant” (Ku et al. 2013). Among the abiotic stressors, drought is the biggest threat to plants in general and to crops in particular. Shortage of water supply leads to reduction of photosynthesis due to lack of intracellular CO₂ availability because of stress-induced stomatal closing and reduction of root capacity to absorb nutrients in soil, and thus total energy production of the plant is decreased (Lawlor and Cornic 2002; Lawlor and Tezara 2009; Aroca et al. 2012). Excessive light can exacerbate stress in plants by affecting its photosynthesis. When chloroplasts are exposed to excessive light, photooxidation is induced, which results in the increased production of reactive oxygen species (ROS), such as hydrogen peroxide, superoxide anion, and hydroxyl radicals (Grassi and Magnani 2005; Aguado-Santacruz 2006; Zhou et al. 2007; Miller et al. 2010; Osakabe et al. 2014). These biological molecules can cause negative effects on plant productivity. Moreover, water deficit triggers the stomata closure and a decrease in leaf water potential as well as the downregulation of photosynthesis-related genes and slow diffusion of CO₂ (Osakabe et al. 2014). More severe drought exposures can finally lead to plant death.

The invasion of salinity into mainland and higher frequency of flooding as a consequence of ice melt or urbanization process make these the second- and third-ranked concerns to sustainable agriculture. Under high salinity, susceptible plants suffer ion toxicity due to excessive entry of ions, particularly Na⁺, into the cells, resulting in homeostatic disruption, water loss, and oxidative stress, and thereof inhibition of photosynthesis and enzyme activities, cell division, and plant growth (Munns et al. 2006; Munns and Tester 2008; Parvaiz and Satyawati 2008; Shabala and Munns 2012). It is projected that by 2050, more than half of arable land would encounter salinity problem (Wang et al. 2003; Setia et al. 2011). Opposite to water deficit, waterlogging is another type of water stress whereby it prevents plants, or at least their root part, from accessing oxygen supplied from environment (Mahajan and Tuteja 2005; Calvo-Polanco et al. 2012; Kreuzwieser and Rennenberg 2014). The consequences of this are negative effects on root functions in respiration and taking up nutrients (Mahajan and Tuteja 2005). Meanwhile, exposure to nonoptimal

temperature conditions, such as cold (chilling and frost) and heat (high temperature), may cause injuries to cellular structure and functions, and thus significantly affecting plant metabolism, development, and reproduction (Yadav 2010; Theocharis et al. 2012; Hasanuzzaman et al. 2013). For example, cellular ice formation, dehydration, and fluidity movement reduction in the phospholipid membrane are among early effects caused by low temperatures (Mahajan and Tuteja 2005; Wang et al. 2006).

It has been known that chilling, freezing, heat, drought, and salinity all lead to hyperosmotic condition as a secondary stress in plants. Depletion in cellular water is the common consequence caused by each of these stress factors. Hyperosmosis is explained as a condition in which there is an increase in concentration of extracellular solutes due to water deficit, and thus triggering the movement of water out of the cells into the environment (Aguado-Santacruz 2006). As a result, cellular turgor cannot be maintained and intracellular concentration of solutes is increased (Aguado-Santacruz 2006; Solanke and Sharma 2008; Chaves et al. 2009). It is important to mention that although some of the molecular responses to these types of stressors overlap as they produce similar effects in the water status of cells, stress-specific responses are also present depending on which particular stress the plant is facing with (Aguado-Santacruz 2006).

In addition to the well-mentioned abiotic stressors, such as drought, salinity, heat, cold, and flooding, there are other abiotic stressors appearing with less frequency, including UV radiation, heavy metal toxicity, and inorganic nutrient deficiency (Clemens 2006; Hossain et al. 2012; Hideg et al. 2013; Liang et al. 2013). Nowadays, abiotic stresses are not purely considered as natural causes since their occurrence and severity are under the influence of human activities such as not only inappropriate practices in agriculture like intensive land use without break and excessive organic fertilization but also in other areas, such as deforestation and industrial gas release into the atmosphere. As a consequence of these human errors, climate change has been a hot topic for discussion, and of course this exacerbates unpredictability of abiotic stresses, making them more serious threats to the food security of humankind.

To reduce agricultural loss by the impact of abiotic stresses, scientists have been trying to widen our current understanding of the mechanisms of plant tolerance to various abiotic stressors by using different methodologies. Although how expression of genes alters under stress conditions can be easily determined, working out their roles in the stress responses and identifying their relationship with other members in the whole picture of stress acclimation are not easy tasks (Chaves et al. 2009). That may be the reason why the number of successes in the development of crop plants coping with the major stressors, including water scarcity, salinity, and temperature stresses, is still limited. To accelerate this process, a combination of modern techniques in molecular biology, advances in phenotyping, quantitative trait locus (QTL) mapping, and conventional breeding strategies has been used. The purposes of this chapter are to summarize our current knowledge about stress-adaptive mechanisms in plants, mainly focusing on major abiotic stresses (drought, salinity, and extreme temperatures) and transcription factors (TFs)—important members in

the stress-adaptive pathways—and then review the progress in applications of TFs in improving abiotic stress tolerance in crop plants.

2 Mechanisms in Plant Responses to Abiotic Stresses

It is predicted that abiotic stresses will continue to be major constraints affecting global crop yields (Sharma and Lavanya 2002; Osakabe et al. 2013b), and thus, through evolution plants have developed various mechanisms to cope with them. These mechanisms have been classified into three groups: (1) stress escape by adjusting plant development and reproduction in accordance with the environmental conditions; (2) stress avoidance by developing morphologically and physiologically advantageous traits; and (3) stress tolerance by regulating morphological, physiological, biochemical, and molecular activities to minimize the stress impact (Turner et al. 2001; Mittler 2002; Chaves et al. 2003). The last defending strategy attracts the largest research attention and hence will be discussed in detail later in this section.

2.1 *Physiological and Biochemical Responses*

Adaptation to abiotic stress is undoubtedly one of the most complex biological processes in plants since it involves multigenic traits. Responses that are usually seen at the physiological level are closure of stomata, shedding of leaves, decrease in light absorbance and photosynthetic activities, adjustment in relative water content, increase in root growth, and reduction in shoot growth (Manavalan et al. 2009; Shanker and Venkateswarlu 2011; Thu et al. 2014; Ha et al. 2013). For example, under high CO₂ and abiotic stress conditions, excess C may favor root growth over that of photosynthetic organs (Hachiya et al. 2014). Shoot-growth restriction could be considered as an advantage to help plants preserve limited carbohydrate resource for maintaining the most important metabolism activities to ensure their survival over the stress period and their capacity to recover quickly after the demission of the stress (Aguado-Santacruz 2006). In contrast, continuation of root growth is favorably promoted to search for water from deeper soil layers (Alsina et al. 2011; Aroca et al. 2012). Examination of various root characteristics, such as dry weight, total length, and number of lateral roots, enables us to quickly assess the tolerant capacity of a particular plant variety under stress conditions (Liu et al. 2005; Gowda et al. 2011; Kumar et al. 2012). Other physiological symptoms can be observed under abiotic stress, including decrease in leaf expansion, wilting, discoloration, chlorosis, surface lesion and/or sterility at reproduction stage, senescence, stunted shoots, and lower biomass production (Wen et al. 2002; Yadav 2010; Jaarsma et al. 2013). Hence, many common parameters, such as survival rate, productivity, and relative

growth rate, are used for the evaluation of plant tolerance to various stresses (Ashraf and Harris 2004; Parvaiz and Satyawati 2008).

The most important, commonly seen response of plants to major abiotic stresses at biochemical level is perhaps the osmotic adjustment. A wide variety of solutes are involved in this regulation, including amino acids and amino acid-associated compounds (proline, aspartate, glutamate, and glycine betaine etc.), sugars (sucrose, fructose, fructans, and trehalose etc.), and polyols (mannitol, and sorbitol etc.) (Chaves et al. 2003; Koyro et al. 2012). These metabolites are also called osmo-protective substances that contribute to maintaining the cell turgor and prevention of water loss. Additionally, increase of other products, such as antioxidant substances (e.g., ascorbate, glutathione, carotenoids, anthocyanins, and α -tocopherol), detoxifying enzymes (e.g., catalase, superoxide dismutase, peroxidase, ascorbate peroxidase, glutathione peroxidase, and glutathione reductase), heat shock proteins (HSPs), and late embryogenesis abundant (LEA) proteins, is also observed under stresses (Goyal et al. 2005; Chakrabortee et al. 2010; Aguado-Santacruz 2006). Moreover, under stress conditions, such as drought and salinity, transportation activities of anions and cations, including Cl^- , Na^+ , and K^+ , as well as the participation of water transport systems play important roles to maintain an ion balance between tissues and cells in stress adaptation (Osakabe et al. 2013a; Osakabe et al. 2014).

2.2 Signal Perception, Transduction, and Regulating Pathways Involved in Plant Responses to Abiotic Stresses

Regulation of molecular activities such as gene expression is considered the most critical factor determining the response degree of a plant as a whole toward a specific stress condition. In this process, being able to sense changes in the surrounding environment is the first important step for plants to respond, survive, and adapt to living conditions. Disruption of normal intracellular homeostasis in plants caused by stress is regarded as early alerting signals that include alterations of cellular size, solute concentration, and cellular turgidity and/or increase in ROS levels (Loutfy et al. 2012; Suzuki et al. 2012). A number of stress detectors have been identified in plants and most of them are located on the cell membrane (Mahajan and Tuteja 2005). Under cold, drought, or salinity stress conditions, Ca^{2+} ions have been shown to be shuttled into the cell cytoplasm, indicating participation of Ca^{2+} permeable channels in the stress-responsive networks as stress signal receptors (Boudsocq and Sheen 2013). Calcium ions have been indicated to interact with kinase enzymes, including Ca-dependent protein kinases (CDPKs), calmodulin-binding protein kinases, and Ca^{2+} /calmodulin-dependent protein kinases that are known to participate in signaling pathways via phosphorylation activities. Taking a strategy used by plants to cope with salt stress as an example, the salt overly sensitive (SOS)-responsive pathway, which aids the reestablishment of intracellular ionic balance, includes a sensor Ca-binding protein SOS3 that is able to mediate the activity of kinase SOS2 (Boudsocq and Laurière 2005; Thapa et al. 2011). These activated kinases will in

turn directly regulate activities of TFs in the downstream transduction pathway (Chinnusamy et al. 2004). It was reported that an increase in ROS concentration during stress also led to the enhancement of activity of these Ca channels (Mori and Schroeder 2004).

Another type of membrane protein sensors involved in the perception of drought, high salinity, and low temperature, which deserves to be mentioned, is histidine kinases (HKs) that are members of two-component system (TCS). In *Arabidopsis thaliana*, a number of HKs (AHKs) have been identified (Schaller et al. 2008). HKs functioning as osmosensors, such as Sln1 and Sho1, are also present in yeast in which both of them are membrane spanning but have no similarity in structure. In *Arabidopsis*, a homolog of Sln1, AtHK1/AHK1, has been identified which is able to suppress the salt-sensitive phenotype of the yeast double-mutant *sln1Δ sho1Δ* that lacked both osmosensors (Urao et al. 1999). The interaction between AHK1 and the downstream *Arabidopsis* histidine phosphotransfers (AHPs) in the multistep phosphorelay has been identified (Urao et al. 2000; Kumar et al. 2013). In addition to these above-described sensors, G protein-associated receptors may function in the perception of a secondary signal derived from these stresses (Perfus-Barbeoch et al. 2004; Misra et al. 2007). They might also serve as a kind of membrane-bound receptors for abscisic acid (ABA; Pandey et al. 2009).

It is important to emphasize that a specific abiotic stress can generate more than one type of signals that can be detected by one or more sensors (Gong et al. 2013). For example, drought causes both osmotic and oxidative stresses to plants. Oxidative stress and appearance of photorespiration as secondary stress effects from drought can lead to increased production of ROS, possibly deriving from organelles such as chloroplasts, mitochondria, glyoxysomes, and peroxisomes, and from activities of β -oxidation of lipids and several different oxidases (Apel and Hirt 2004; Miller et al. 2010; Voss et al. 2013). ROS inhibits the function of many enzymes, increases protein and DNA susceptibility to degradation due to structural modifications, reduces permeability of plasma membrane, and stimulates the activity of Ca-dependent proteases and nucleases (Sharma et al. 2012).

The participators working as second messengers can be divided into three groups, including: (1) diacylglycerol, inositol triphosphate, such as IP₃, and phosphate inositol (group of hydrophobic molecules) which are located on the membrane and are able to pass the signal to membrane-associated effector proteins; (2) cAMP, cGMP, sugars, such as sucrose, glucose, and fructose, and Ca²⁺ (group of hydrophilic molecules) which are presented within the cytosol; and (3) nitric oxide and carbon monoxide (group of gas molecules) which can diffuse through cytosol and cellular membranes (Bhargava and Sawant 2013; Aguado-Santacruz 2006; Chaves et al. 2009). Additionally, ROS can also be assigned as another member of second messenger since its damage effects to cellular components during stress switch on specific genes involved in the activation of mitogen-activated protein kinase (MAPKs) as well as the production of antioxidants, HSPs, and ROS-scavenging enzymes.

Several second messengers, such as IP₃, can regulate intracellular Ca²⁺ levels, while the Ca²⁺ ion itself is also regarded as a second messenger. Ca²⁺ has been known

to be involved in the closure of stomatal aperture (Zhang et al. 2011a), and often initiates a protein phosphorylation cascade that regulates expression of downstream regulatory and functional genes, contributing to stress tolerance (Gong et al. 2013). It is noticed that in order to successfully transfer the signal message through the whole signal transduction pathway, extra assistants that are in charge of modification, delivery, or assembly of signaling components are required as well. Examples of these molecules are protein modifiers involved in protein lipidation, methylation, glycosylation, and ubiquitination; scaffolds; and adaptors (Xiong et al. 2002).

A great variety of other elements are also recruited in the networks, leading to acclimative reactions to stress, such as plant growth regulators, including phytohormones, polyamines, and Ca, and various proteins, including CDPKs, MAPKs (including MAPKKs, MAP kinase kinase kinases; MAPKKs, MAP kinase kinases), and TFs (Ohnishi et al. 2008; Huang et al. 2012). Particularly, involvement of ABA and its induced biosynthesis in response to various abiotic stresses, such as salinity, drought, and cold, have been well reported in literature (Fujita et al. 2011; Danquah et al. 2014). Many stress-responsive functional genes, such as *RD22* (responsive to dehydration 22), *RD29A*, *COR15* (cold responsive 15), *COR47*, and *P5CS* (Δ -1-pyrroline-5-carboxylate synthase), and regulatory genes, including dehydration-responsive element-binding protein (DREB), ABA-responsive element (AREB), myeloblastosis (MYB), and NAC (NAM, no apical meristem; ATAF, *Arabidopsis* transcription activation factor; and CUC, cup-shaped cotyledon), whose expression is regulated by ABA, have been identified to be involved in regulating plant responses to stresses (Xiong et al. 2001; Dalal et al. 2009; Fujita et al. 2011; Nakashima et al. 2009; Tran et al. 2010).

Protein phosphorylation is an important and effective mechanism that plants use in the signal transduction process to trigger stress responses as quickly as possible. In plants, in addition to the TCSs, activities of the two classes of stress-activated protein kinases, MAPKs and CDPKs, are also performed via phosphorylation at specific amino acid residues present in the structure (Schaller et al. 2008; Huang et al. 2012). In the working module of MAPK members, an MAPKKK is activated by phosphorylation which in turn phosphorylates the activity of MAPKK (Bhargava and Sawant 2013). At the end of the phosphorylation cascade, activation of a cytoplasmic MAPK often results in its translocation into the nucleus to regulate gene expression via controlling TFs also by phosphorylation (Danquah et al. 2014). Alternatively, these terminal MAPKs remain in the cytoplasm where they phosphorylate enzymes or cytoskeleton components (Danquah et al. 2014).

In further progression of the signaling process, TFs should be highlighted as the key participants. They work as final transducers in the transduction module and directly mediate gene expression since they can bind to regulatory regions of specific promoters (e.g., *cis*-acting elements). There is a fact that expression of a gene can be regulated by several mechanisms of which some are still unknown (Weake and Workman 2010). Nonetheless, the regulation of gene expression via the interaction of TFs and promoters are well documented (Yamaguchi-Shinozaki and Shinozaki 2006). Detailed information about TFs will be discussed in the next section of this chapter.

3 Plant TFs and their Roles in Abiotic Stress Responses

In plant genomes, approximately 7% of the coding sequences are assigned to TFs (Udvardi et al. 2007), which are divided into families based on their distinct signatures in structure. Major families are well known to be involved in various abiotic stresses either in ABA-dependent (MYB/MYC, bZIP) (Zhang et al. 2009a; Fujita et al. 2011), ABA-independent pathway (WRKY) (Chen et al. 2012; Rushton et al. 2008; Umezawa et al. 2006), or in both pathways (NAC, AP2/EREBP) (Souer et al. 1996; Olsen et al. 2005; Nakashima et al. 2012; Puranik et al. 2012). With the aim to generate new varieties, which are able to cope with abiotic stress(es) more efficiently, genetic engineering has been considered as a powerful approach in addition to conventional breeding methods. Thanks to recent advances in technologies, including real-time quantitative polymerase chain reaction (RT-qPCR), omic technologies, cloning, transformation, gene overexpressing and silencing, and other biochemical, molecular, and physiological methods employed in stress-response analyses at physiological and molecular levels, essential candidate genes contributing to plant adaptation to stress have been identified. These genes include those encoding members functioning in various stages of stress signal transduction cascade. Among these, TFs have drawn particular attention due to their important function in stress regulation and their potential in genetic engineering. Therefore, numerous attempts have been made all around the world, mainly by overexpressing the TF-encoding genes, and several promising results have been reported. Table 14.1 summarizes a number of studies using TFs to create transgenic model and crop plants with improved abiotic stress tolerance within the past 5 years.

3.1 The AP2/EREBP Family

In plants, AP2/EREBP (APETALA2/ethylene-responsive element-binding protein) has been known as a large family of TF genes which contains the highly conserved AP2/ethylene-responsive element-binding factor (ERF) DNA-binding domain (Riechmann and Meyerowitz 1998), and has been identified in various species, such as *Arabidopsis*, tobacco (*Nicotiana tabacum*), and tomato (*Solanum lycopersicum*) (Fischer and Dröge-Laser 2004; Oñate-Sánchez and Singh 2002; Tournier et al. 2003). Based on the number of AP2/ERF domains and the gene structure, the AP2/EREBP gene family can be divided into four subfamilies AP2, RAV (related to ABI3/VP1), DREB, and ERF (Sakuma et al. 2002; Sharoni et al. 2011). Among these, the ERF and DREB TF subfamilies were discovered in various plant species, including rice (*Oryza sativa*) (Quan et al. 2010), *Arabidopsis* (Sakuma et al. 2006), and tobacco (Agarwal et al. 2010), and their functions in the plant responses to biotic and abiotic stresses have been extensively studied (Agarwal et al. 2006; Agarwal et al. 2010).

The DREB-type TFs contain a conserved DNA-binding domain of 58–60 amino acids, and thus are able to bind to the PyCCGACAT *cis*-elements named

Table 14.1 Studies on abiotic stress tolerance improvement in crop plants using transcription factors over the past 5 years

| Family | Gene | Source of isolation | Transgenic host | Gene manipulation | Stress tolerance | References |
|------------------|-----------------|-----------------------------|--------------------|---|---------------------|----------------------------|
| <i>AP2/EREBP</i> | <i>AtDREB1A</i> | <i>Arabidopsis thaliana</i> | Rice | Stress-inducible overexpression | Drought↑ | (Ravikumar et al. 2014) |
| | <i>GmERF3</i> | <i>Glycine max</i> | Tobacco | Constitutive overexpression | Drought↑, salinity↑ | (Zhang et al. 2009b) |
| | <i>GmERF7</i> | <i>Glycine max</i> | Tobacco | Constitutive overexpression | Salinity↑ | (Zhat et al. 2013) |
| | <i>HARDY</i> | <i>Arabidopsis thaliana</i> | Clover | Constitutive overexpression | Drought↑, salinity↑ | (Abogadallah et al. 2011) |
| | <i>JERF3</i> | <i>Solanum lycopersicum</i> | Rice | Constitutive overexpression | Drought↑ | (Zhang et al. 2010) |
| | <i>LcDREB3a</i> | <i>Leymus chinensis</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑, salinity↑ | (Peng et al. 2011) |
| | <i>LcDREB2</i> | <i>Leymus chinensis</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity↑ | (Peng et al. 2013) |
| | <i>OsAP23</i> | <i>Oryza sativa</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity↓ | (Zhuang et al. 2013) |
| | <i>OsDREB2A</i> | <i>Oryza sativa</i> | Rice | Stress-inducible overexpression | Drought↑, salinity↑ | (Mallikarjuna et al. 2011) |
| | <i>OsDREB2A</i> | <i>Oryza sativa</i> | Soybean | Constitutive overexpression | Salinity↑ | (Zhang et al. 2013) |
| | <i>OsERF4a</i> | <i>Oryza sativa</i> | Rice | Constitutive and ABA-inducible overexpression | Drought↑ | (Joo et al. 2013) |
| | <i>SlDREB1</i> | <i>Solanum tuberosum</i> | Potato | Constitutive overexpression | Salinity↑ | (Bouaziz et al. 2013) |
| | <i>TaERF3</i> | <i>Triticum aestivum</i> | Wheat | Constitutive overexpression | Drought↑, salinity↑ | (Rong et al. 2014) |
| | | | | Constitutive knockdown | Drought↓, salinity↓ | |
| | <i>TaPIE1</i> | <i>Triticum aestivum</i> | Wheat | Constitutive overexpression | Cold↑ | (Zhu et al. 2014) |
| | <i>TaPIE1</i> | <i>Triticum aestivum</i> | Wheat | Constitutive knockdown | Cold↓ | (Zhu et al. 2014) |
| | <i>TSRF1</i> | <i>Solanum lycopersicum</i> | Rice | Constitutive overexpression | Drought↑ | (Quan et al. 2010) |

Table 14.1 (continued)

| Family | Gene | Source of isolation | Transgenic host | Gene manipulation | Stress tolerance | References |
|----------------|--------------------------|-----------------------------|----------------------------------|---|--|-------------------------|
| bZIP | <i>ABF9</i> | <i>Zea mays</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑, salinity↑, cold↑ | (Zhang et al. 2011b) |
| | <i>AbZIP1</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Knockout | Drought↓, salinity↓ | (Sun et al. 2012) |
| | <i>GmbZIP1</i> | <i>Glycine max</i> | <i>Arabidopsis</i> | Constitutive and ABA-inducible overexpression | Drought↑, salinity↑, cold↑ | (Gao et al. 2011) |
| | <i>GmbZIP1</i> | <i>Glycine max</i> | Wheat | Constitutive overexpression | Drought↑, salinity↑, cold↑ | (Gao et al. 2011) |
| | <i>GmbZIP1</i> | <i>Glycine max</i> | Tobacco | Constitutive and ABA-inducible overexpression | Drought↑, salinity↑, cold↑ | (Gao et al. 2011) |
| | <i>LrbZIP</i> | <i>Nelumbo nucifera</i> | Tobacco | Constitutive overexpression | Salinity↑ | (Cheng et al. 2013a) |
| | <i>OsZIP72</i> | <i>Oryza sativa</i> | Rice | Constitutive overexpression | Drought↑ | (Lu et al. 2009) |
| | <i>OsZIP71</i> | <i>Oryza sativa</i> | Rice | Constitutive overexpression Constitutive knockdown | Drought↑, salinity↑ Salinity↓ | (Liu et al. 2014a) |
| | <i>Pt-ABF</i> | <i>Poncirus trifoliata</i> | Tobacco | Constitutive overexpression | Drought↑ | (Huang et al. 2010) |
| | <i>ZmbZIP72</i> | <i>Zea mays</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑, salinity↑ | (Ying et al. 2012) |
| NAC | <i>AhNAC5</i> | <i>Arachis hypogaea</i> | Tobacco | Constitutive overexpression | Drought↑ | (Liu et al. 2013) |
| | <i>BaNAC5</i> | <i>Brassica napus</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity↑ | (Zhong et al. 2012) |
| | <i>EcNAC</i> | <i>Eleusine coracana</i> | Tobacco | Constitutive overexpression | Salinity↑ | (Ramegowda et al. 2012) |
| | <i>JcNAC1</i> | <i>Jatropha curcas</i> | Model woody | Constitutive overexpression | Drought↑ | (Qin et al. 2014) |
| | <i>ONAC063</i> | <i>Oryza sativa</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity↑ | (Yokotani et al. 2009) |
| | <i>OsNAC5</i> | <i>Oryza sativa</i> | Rice | Constitutive overexpression Constitutive knockdown | Drought↑, salinity↑, cold↑ Drought↑, salinity↓, cold↓ | (Song et al. 2011) |
| | <i>ONAC045</i> | <i>Oryza sativa</i> | Rice | Constitutive overexpression | Drought↑, salinity↑ | (Zheng et al. 2009) |
| | <i>OsNAC52</i> | <i>Oryza sativa</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑ | (Gao et al. 2010) |
| | <i>OsNAP</i> | <i>Oryza sativa</i> | Rice | Constitutive overexpression | Drought↑, salinity↑, cold↑ | (Chen et al. 2014) |
| | <i>SNAC1</i> | <i>Oryza sativa</i> | Cotton | Constitutive overexpression | Drought↑, salinity↑ | (Liu et al. 2014b) |
| <i>SNAC1</i> | <i>Oryza sativa</i> | Wheat | Constitutive overexpression | Drought↑, salinity↑ | (Saad et al. 2013) | |
| <i>TaNAC2a</i> | <i>Triticum aestivum</i> | Tobacco | Constitutive overexpression | Drought↑ | (Tang et al. 2012) | |
| <i>TaNAC67</i> | <i>Triticum aestivum</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑, salinity↑, cold↑ | (Mao et al. 2014) | |
| <i>TaNAC69</i> | <i>Triticum aestivum</i> | Wheat | Drought-inducible overexpression | Drought↑ | (Xue et al. 2011) | |
| <i>ZmSNAC1</i> | <i>Zea mays</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought↑ | (Lu et al. 2012) | |

Table 14.1 (continued)

| Family | Gene | Source of isolation | Transgenic host | Gene manipulation | Stress tolerance | References |
|--------|-------------------|-----------------------------|--------------------|-------------------------------|---------------------|-------------------------|
| MYB | <i>AtMYB14</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Constitutive knockdown | Cold† | (Chen et al. 2013a) |
| | <i>AtMYB44</i> | <i>Arabidopsis thaliana</i> | Soybean | Constitutive overexpression | Drought†, salinity† | (Seo et al. 2012) |
| | <i>AtMYBR1</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought‡ | (Jaradat et al. 2013) |
| | <i>GmMYB11</i> | <i>Glycine max</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought†, cold† | (Su et al. 2014) |
| | <i>LcMYB1</i> | <i>Leymus chinensis</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity† | (Cheng et al. 2013b) |
| | <i>MYB15</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought†, salinity† | (Ding et al. 2009) |
| | <i>TaPIMP1</i> | <i>Triticum aestivum</i> | Tobacco | Constitutive overexpression | Drought†, salinity† | (Liu et al. 2011b) |
| | <i>AtWRKY28</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity† | (Babitha et al. 2013) |
| | <i>AtWRKY30</i> | <i>Arabidopsis thaliana</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity† | (Scarpeci et al. 2013) |
| | <i>GhWRKY39</i> | <i>Gossypium hirsutum</i> | Tobacco | Constitutive overexpression | Salinity† | (Shi et al. 2014) |
| WRKY | <i>MusaWRKY71</i> | <i>Musa</i> spp. | Banana | Constitutive overexpression | Salinity† | (Shekhawat et al. 2011) |
| | <i>OsWRKY11</i> | <i>Oryza sativa</i> | Rice | Heat-inducible overexpression | Drought†, heat† | (Wu et al. 2009) |
| | <i>OsWRKY45</i> | <i>Oryza sativa</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought†, salinity† | (Qiu and Yu 2009) |
| | <i>TaWRKY10</i> | <i>Triticum aestivum</i> | Tobacco | Constitutive overexpression | Drought†, salinity† | (Wang et al. 2013) |
| | <i>TaWRKY79</i> | <i>Triticum aestivum</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought†, salinity† | (Qin et al. 2013) |
| | <i>VvWRKY11</i> | <i>Vitis vinifera</i> | <i>Arabidopsis</i> | Constitutive overexpression | Drought† | (Liu et al. 2011a) |
| | <i>ZmWRKY33</i> | <i>Zea mays</i> | <i>Arabidopsis</i> | Constitutive overexpression | Salinity† | (Li et al. 2013) |

as DRE/C-repeat (CRT) motifs located in the promoter regions of target genes to activate or suppress their transcription for achieving stress adaptation (Park et al. 2001; Ito et al. 2006; Jaglo et al. 2001; Kasuga et al. 1999; Liu et al. 1998; Agarwal et al. 2006; Sakuma et al. 2002). According to Sakuma et al. (2002), DREB subfamily has been further classified into six subgroups termed A-1 to A-6, of which A-1 and A-2 are the two largest groups. DREB1/C-repeat-binding factor (CBF; A-1) subgroup of *Arabidopsis* with three major regulator factors, DREB1A/CBF3, DREB1B/CBF1, and DREB1C/CBF2, has shown its importance in plant responses to cold stress. Overexpression of *RD29A:DREB1* or *35S:CBF* genes showed significantly improved tolerance to freezing, drought, and high salinity in *Arabidopsis* (Jaglo-Ottosen et al. 1998; Liu et al. 1998; Mizoi et al. 2012). Furthermore, the DREB1s can be used to produce transgenic crops with higher tolerance to drought, high salt, high temperature, and cold stress. Bouaziz et al. (2013) reported that transgenic potato plants overexpressing *35S:StDREB1*, which had been isolated from potato (*S. tuberosum*) and classified in the A-4 group of DREB subfamily based on multiple sequence alignments and phylogenetic characterization, had enhanced salt and drought tolerance. Moreover, *StDREB1* was significantly induced by NaCl, drought, low temperature, and ABA conditions in potato. In *Populus trichocarpa*, the development of *Populus* varieties with a greater tolerance to many adverse environments has been aided by understanding the characterization of the *DREB* subfamily (Chen et al. 2013b). Based on the expression analysis of 15 selected *PtrDREB* genes under abiotic stress conditions in *Populus*, Chen et al. (2013b) claimed that there were 14 genes with induced expression under different abiotic stresses. *GmDREB2* isolated from soybean is a novel *DREB* gene of A-5 subgroup which was found to have induced expression by drought, high salt, and low temperature stresses (Chen et al. 2007). Overexpression of *GmDREB2* by constitutive *35S* promoter or stress-inducible *RD29A* promoter resulted in upregulation of downstream genes in transgenic *Arabidopsis* (Chen et al. 2007). As a result, the transgenic plants showed enhanced tolerance to drought and high salinity without any growth retardation even with constitutive overexpression (Chen et al. 2007), as was observed with constitutive overexpression of *OsDREB1A* (Dubouzet et al. 2003). *LeDREB2* was discovered from tomato genome and classified into an A-2 group member of the *DREB* family. The expression of this gene was induced by high salinity, drought, and cold (Islam and Wang 2012). In another independent research on expression analysis in *Pisum sativum*, *PsDREB2A* was reported to be induced in pea roots and leaves under water deficit (Jovanovic et al. 2013). Mallikarjuna et al. (2011) developed transgenic rice lines overexpressing *OsDREB2A* under control of stress-inducible *RD29A* promoter, which resulted in the enhanced growth performance and significant tolerance to osmotic, salt, and dehydration stresses during simulated stress conditions as compared with the wild type. Later on, Zhang et al. (2013) used this gene to enhance salt tolerance of soybeans. The authors reported that salt tolerance was enhanced in the *35S:OsDREB2A* transgenic soybean plants due to accumulation of osmolytes, such as soluble sugars and free proline, as well as induced expression of several stress-responsive TFs and key genes (Zhang et al. 2013). *LcDREB3a* from the drought-tolerant forage grass

Leymus chinensis was shown to function in the improvement of drought and salt tolerance in *Arabidopsis* overexpressing *35S:LcDREB3a* without causing growth retardation by inducing expression of stress tolerance genes when compared to control (Peng et al. 2011). Besides, transgenic expression of another *LcDREB* member (*LcDREB2*) in combination with its downstream gene (S-adenosyl-methionine decarboxylase, *LcSAMDC2*,-encoding gene) obtained from *L. chinensis* under the control of the *35S* promoter could improve the salt tolerance in *Arabidopsis* (Peng et al. 2013). In *Malus domestica*, RT-qPCR analysis showed significant upregulation of some putative *MdDREB* genes under various abiotic stress treatments, which proved their vital roles during stress adaptation (Zhao et al. 2012).

In another subfamily of AP2/EREBP TFs, ERFs have been indicative of their participation in plant responses to biotic and abiotic stresses by recognizing the *cis*-acting element AGCCGCC, known as the GCC box (Hao et al. 1998; Ohme-Takagi and Shinshi 1995; Fujimoto et al. 2000). Based on the phylogenetic analyses of 125 *AP2/ERF* members in *Arabidopsis*, the ERF subfamily could be divided into six subgroups, from ERF-B1 to ERF-B6 (Sakuma et al. 2002). In wheat (*Triticum aestivum*), 47 ERF-encoding genes have already been identified (Zhuang et al. 2011). Among these, constitutively overexpressing *TaPIE1* controlled by maize *ubiquitin* promoter in wheat exhibited significantly enhanced resistance to both pathogen (triggered by *Rhizoctonia cerealis*) and freezing stress, whereas constitutive knockdown wheat plants by a recombinant construct between barley stripe mosaic virus (BSMV) and *TaPIE1* were more susceptible to both stresses relative to control plants (Zhu et al. 2014). Functional analysis of *TSRF1*, a member of tomato ERF TFs, demonstrated that overexpression of *35S:TSRF1* improved the osmotic and drought tolerance of rice seedlings without growth retardation as indicated by physiological analyses of root and leaf growth, leaf water loss, and survival rate under stress conditions compared to control (Quan et al. 2010). In another study in rice, Joo et al. (2013) reported that *ERF* genes, including *OsERF4a* and *OsERF10a*, had an important contribution in conferring drought stress tolerance. Both constitutive and ABA-inducible expression of the ERF-associated amphiphilic repression (EAR) domain-containing protein-encoding *OsERF4a* showed increased drought tolerance as a consequence of suppression of a putative repressor *Silent information regulator 2* (*Sir2*) involved in response to drought. By using a yeast-one hybrid system, *OsAP23* belonging to the B3 group of the *ERF* subfamily was isolated from rice (Zhuang et al. 2013). When exposed to high salt concentrations, several stress-responsive genes were induced significantly in the wild-type lines compared to *Arabidopsis* overexpressing *35S:OsAP23*, suggesting a negative regulatory role of *OsAP23* in salt stress response (Zhuang et al. 2013). Besides, characterization of an *ERF* gene from soybean, *GmERF3*, showed its inducible expression in soybean by high salinity, drought, ABA, salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and soybean mosaic virus (SMV), whereas *GmERF3* mRNA was not significantly accumulated under cold stress treatment (Zhang et al. 2009b). Transgenic tobacco plants with overexpressed *35S:GmERF3* displayed not only enhanced resistance against infection by *Ralstonia solanacearum*, *Alternaria alternata*, and tobacco mosaic virus (TMV) but also higher tolerance to high salinity and dehydration.

Functional analyses of a tomato *ERF* (*JERF3*-jasmonate and ethylene responsive factor 3) in transgenic tobacco overexpressing *35S:JERF3* indicated that expression of this gene could enhance the tolerance to salt, drought, and freezing (Wang et al. 2004; Wu et al. 2008). Also in further report of this group, transgenic rice plants overexpressing *35S:JERF3* exhibited better tolerance to drought and osmotic stress in comparison with non-transgenic rice seedlings (Zhang et al. 2010).

3.2 The bZIP Family

The bZIP (basic leucine zipper) family is another large group of TFs in plants. At present, most reports on stress responses have shown that bZIP TFs regulate stress response in ABA-dependent manner through interaction with specific ABA-responsive *cis*-acting elements (ABRE) to promote transcription of downstream target genes (Kobayashi et al. 2005; Kim 2006; Zou et al. 2008; Shinozaki and Yamaguchi-Shinozaki 2007; Uno et al. 2000). In *Arabidopsis*, *AtbZIP1*-knockout mutants showed a decrease in salt and osmotic stress tolerance, suggesting its positive regulation of plant response to these stresses (Sun et al. 2012). Transgenic *Arabidopsis* overexpressing the maize *ABP9* gene under the control of *35S* promoter, which encodes a bZIP TF, enhanced tolerance to multiple stresses (Zhang et al. 2011b). Another *bZIP* from maize was identified as *35S:ZmbZIP72* whose overexpression improved drought and partial salt tolerance of transgenic *Arabidopsis* plants (Ying et al. 2012). Meanwhile, expression analysis of *LrbZIP* in tips of lotus roots (*Nelumbo nucifera*) showed strong upregulation by low temperature, salt, and ABA treatments (Cheng et al. 2013a). Transgenic tobacco transformed with *35S:LrbZIP* exhibited higher salt tolerance comparing to the control under salt stress (Cheng et al. 2013a). Lu et al. (2009) identified *OsbZIP72* as a positive regulator whose constitutive overexpression increased hypersensitivity to ABA and transcript level of ABA-responsive genes to improve drought tolerance in transgenic rice. Several soybean bZIPs, including *GmbZIP44*, *GmbZIP62*, and *GmbZIP78*, displayed notable roles in stress acclimation. These TFs functioned as negative regulators of ABA signaling and plant responses to salt and freezing tolerance (Liao et al. 2008b). Gao et al. (2011) also indicated the positive role of *GmbZIP1* in the enhancement of multiple abiotic stress tolerance, including drought, salinity, and cold stresses in transgenic *Arabidopsis* by stimulating the expression of ABA- or stress-related genes. Overexpression of this gene by *ubiquitin* promoter also resulted in enhanced drought, salt, and freezing tolerance in transgenic wheat (Gao et al. 2011). The authors indicated that *Arabidopsis* and tobacco overexpressing *GmbZIP1* by stress-inducible *RD29A* or *35S* promoter also showed increased tolerance under similar stresses. *ScAREB1*, *SpAREB1*, and *SlAREB1* belonging to the *bZIP* family of *S. chilense*, *S. peruvianum*, and *S. lycopersicum*, respectively, were upregulated by salt stress (Yáñez et al. 2009). Moreover, expression of *SlAREB1* was induced by other stresses, such as drought and cold, and ABA in *S. lycopersicum*, and its encoded TF upregulated stress-responsive genes in *35S:SlAREB1*-overexpressing transgenic tobacco and tomato plants (Yáñez et al. 2009).

3.3 The MYB Family

The MYB TFs have also been known to form one of the largest TF families, which interact with one or more of the two stress-inducible *cis*-elements known as MYB-binding sites (MBS) that contain consensus sequences CNGTT(A/G) (MBSI) or C(G/T)T(A/T)GTT(A/G) (MBSII) to activate their downstream genes (Abe et al. 1997; Pabo and Sauer 1992; Riechmann and Ratcliffe 2000). The MYB TFs possess a MYB domain containing 1–4 imperfect tandem repeats (MYB repeat) located near the N-terminus and thus showing their distinctive characteristics (Ambawat et al. 2013). Based on the number of adjacent repeat(s) in the MYB domain, the MYB family is divided into different types, including 4R-MYB (four repeats), 3R-MYB (R1R2R3-MYB) (three consecutive repeats), R2R3-MYB (two repeats), and the MYB-related type with just a single repeat (Rosinski and Atchley 1998; Jin and Martin 1999; Dubos et al. 2010). Members belonging to this family have been found in different plant species, such as 204 members in *Arabidopsis*, 218 members in rice, 279 members in grapevine, and 197 members in *Populus* (Wilkins et al. 2009; Velasco et al. 2007; Chen et al. 2006). The roles of MYB proteins have been indicated in many physiological and biochemical processes which include regulation of primary and secondary metabolism, control of cell development and cell cycle, hormone synthesis, and signal transduction. The MYBs are also involved in plant responses to various biotic and abiotic stresses (Dubos et al. 2010; Feller et al. 2011; Stracke et al. 2001). Mochida et al. (2009) also found approximately 160 *Gm*-MYBs in soybean, of which 43 out of 48 analyzed genes showed expression changes at least by one of the following treatments: ABA, high salinity, drought, and cold.

A number of studies have indicated the potential of MYB TFs in genetic engineering for improved stress tolerance. When the rice *OsMYB3R-2* and the wheat *TaPIMP1* genes were overexpressed in *Arabidopsis* and tobacco using 35S promoter, respectively, the transgenic lines displayed increased drought tolerance (Liu et al. 2011b; Dai et al. 2007). Besides, salt and freezing tolerance was elevated significantly in *Arabidopsis* overexpressing either 35S:*GmMYB76* or 35S:*GmMYB177* (Liao et al. 2008a). In addition, while *GmMYB177* was upregulated by both drought and NaCl treatments, *GmMYB76* was induced by NaCl treatment only. Jaradat et al. (2013) characterized the function of *AtMYBR1* by using *mybr1*-mutant and 35S:*AtMYBR1*-overexpressing *Arabidopsis* lines. Its negative regulatory functions in drought response and senescence, as well as in the downregulation of many ABA-responsive genes involved in abiotic stresses, were revealed in their study. Moreover, expression of *Arabidopsis AtMYB44* gene has been shown to improve salt and drought stress tolerance in soybean and *Arabidopsis* by preventing excessive ROS accumulation (Persak and Pitzschke 2014; Seo et al. 2012). Expression analysis of the *OsMyb4* in rice suggested that this gene might be involved in rice response to dehydration and cold stress (Baldoni et al. 2013). Moreover, the authors found induction of *OsMyb4*-like genes in wheat and *Arabidopsis* under similar stress treatments. Overexpression of 35S:*OsMyb4* in apple could improve adaptive responses to drought and cold stresses (Pasquali et al. 2008).

3.4 The WRKY Family

The WRKY TFs were first reported in the study of Ishiguro and Nakamura (1994) and the name WRKY (pronounced “worky”) was coined with the identification of WRKY1, WRKY2, and WRKY3 from parsley (*Petroselinum crispum*) (Rushton et al. 1996). The WRKY family is among the largest families of TFs in higher plants (Rushton et al. 2010). The WRKY domain is about 60 residues in length, and based on the number of WRKY domains, WRKY TFs were divided into three groups, group I (two domains), group II (one domain), and group III (one domain with structure of zinc fingers C2HC) (Eulgem et al. 2000). Till date, the functions of WRKY TFs have been intensively studied in not only biotic stress responses but also abiotic stress responses, as well as in seed germination, flower development, and senescence (Tripathi et al. 2014; Rushton et al. 2012; Thao and Tran 2012).

Overexpression of the heat- and drought-inducible rice *OsWRKY11* gene mediated using the heat-inducible *HSP101* promoter showed significant heat and drought tolerances in transgenic rice plants (Wu et al. 2009). Mochida et al. (2009) identified more than 210 putative WRKY TF-encoding genes in soybean. Under various abiotic stresses, 24 of 64 examined *GmWRKY* genes were found to be induced by drought (Zhou et al. 2008). Zhou et al. (2008) reported that 35S:*GmWRKY21*-overexpressing *Arabidopsis* plants exhibited improved tolerance to cold stress in comparison with wild type. The same authors also demonstrated that transgenic *Arabidopsis* plants overexpressing 35S:*GmWRKY54* were more tolerant to drought and salt stress, whereas those overexpressing 35S:*GmWRKY13* were more sensitive to salt stress (Zhou et al. 2008), suggesting these two WRKY TFs have opposite functions in plant responses to salt stress. Overexpression of the rice 35S:*OsWRKY45* enhanced salt and drought tolerance of *Arabidopsis* transgenic plants in addition to increased disease resistance (Qiu and Yu 2009). The grapevine VvWRKY11 TF played a role in osmotic stress tolerance as improved tolerance of 35S:*VvWRKY11*-overexpressing transgenic *Arabidopsis* seedlings to mannitol-induced osmotic stress was observed in comparison with wild-type plants (Liu et al. 2011a). Recently, overexpression of the 35S:*AtWRKY30* in *Arabidopsis* showed enhanced abiotic stress tolerance during early growth stages due to the binding of the TF to W-boxes in the promoter region of many stress/development-related genes, leading to the activation of their expression (Scarpeci et al. 2013). Results of RT-qPCR analyses showed that *ZmWRKY33* of maize belonging to the group I subfamily was induced by high salt, dehydration, cold, and ABA treatments. Overexpression of this gene under control of 35S promoter in *Arabidopsis* activated stress-responsive genes, such as *RD29A*, under both normal growth and stress conditions, thereby improving tolerance of transgenic plants to salt stress (Li et al. 2013). Babitha et al. (2013) overexpressed 35S:*AtWRKY28* in *Arabidopsis* and observed enhanced tolerance of transgenic plants to high NaCl, high mannitol, and oxidative stress. Additionally, higher root growth was observed in transgenic lines under mannitol-induced stress conditions. These transgenic plants showed their capacity in growth recovery to normal level after an 8-day drought exposure period followed by 6 days of rewatering.

3.5 The NAC Family

The plant-specific NAC TF family was initially described in *Petunia* and *Arabidopsis* more than 15 years ago (Aida et al. 1997; Souer et al. 1996). In plants, the NAC TFs have been reported to regulate diverse biological processes, such as flowering (Yoo et al. 2007), regulation of secondary cell wall synthesis and cell division (Zhong et al. 2007), embryo development (Duval et al. 2002), auxin signaling and lateral root formation (Xie et al. 2000), senescence (Kjaersgaard et al. 2011), as well as biotic and abiotic stress responses (Olsen et al. 2005; Puranik et al. 2012). The typical features of an NAC TF include an N-terminal conserved DNA-binding domain involving nucleus-oriented localization and a variable domain located at the C-terminal end which is essential for transcriptional activation (Fang et al. 2008; Riechmann and Ratcliffe 2000; Hao et al. 2011). Alignments of *Arabidopsis* and rice NAC domains suggested eight NAC subfamilies (from NAC-a to NAC-h), mainly distinguished by their unique structures in motif at the C-terminal of NAC domain (Fujita et al. 2004; Fang et al. 2008; Shen et al. 2009). Till date, NAC TFs have been systematically identified in many plant species thanks to the availability of their sequenced genomes. For instance, at least 117, 151, 163, 152, and 200 NAC genes have been identified in *Arabidopsis*, rice (Nuruzzaman et al. 2010), poplar (Hu et al. 2010), tobacco (Rushton et al. 2008), and soybean (Mochida et al. 2009), respectively. In drought signaling, NAC TFs were reported to function in both ABA-dependent and ABA-independent pathways (Shinozaki and Yamaguchi-Shinozaki 2007). The role of NACs in relation to drought response was initially proposed in a study of overexpression of either *ANAC019*, *ANAC055*, or *ANAC072* in *Arabidopsis* which led to considerable increase in drought tolerance of transgenic plants (Tran et al. 2004). Thereafter, stress-related NAC genes have been detected in other plant species, such as rice (*OsNAC5*, *OsNAC6*, *SNAC1*, and *ONAC45*) (Puranik et al. 2012; Nakashima et al. 2007; Hu et al. 2006; Zheng et al. 2009; Song et al. 2011; Takasaki et al. 2010), wheat (*TaNAC4*, *TaNAC69*, and *TaNAC2a*) (Xue et al. 2011; Tang et al. 2012; Xia et al. 2010), oilseed rape (*Brassica napus*) (*BnNAC2* and *BnNAC5*) (Zhong et al. 2012), and peanut (*Arachis hypogaea*) (*AhNAC3*) (Liu et al. 2013), which showed strong potential for genetic engineering of improved biotic and/or abiotic stress-tolerant crops.

Transgenic *Arabidopsis* displayed enhanced tolerance to drought stress without growth retardation when overexpressing the rice *OsNAC52* using 35S promoter (Gao et al. 2010). In another independent study of rice, *ONAC063* expression was highly induced in roots by high salinity as well as by high osmotic pressure and ROS levels (Yokotani et al. 2009). 35S:*ONAC063*-overexpressing transgenic *Arabidopsis* also displayed enhanced tolerance to high salinity and osmotic pressure (Yokotani et al. 2009). In a study of Lu et al. (2012), a maize NAC gene, *ZmSNAC1*, was cloned and functionally characterized. Low temperature, high salinity, drought stress, and ABA treatment strongly induced the expression of this gene. Overexpression of 35S:*ZmSNAC1* in *Arabidopsis* resulted in hypersensitivity of transgenic plants to ABA and osmotic stress at the germination stage, but enhanced dehydra-

tion tolerance at the seedling stage as compared with non-transgenic control (Lu et al. 2012). Recently, a novel TF named *JcNAC1* from the new model woody plant, *Jatropha curcas*, was reported to have function in responses to abiotic stresses and pathogen infection as overexpression of this gene under control of 35S promoter not only changed the expression of stress-related genes but also increased tolerance of transgenic *J. curcas* to drought (Qin et al. 2014). Another novel NAC TF, *EcNAC* from finger millet (*Eleusine coracana*), was overexpressed under control of either 35S promoter or synthetic 4xABRE stress-inducible promoter in tobacco, and both transgenic lines led to enhanced tolerance to various abiotic stresses, including stresses induced by polyethylene glycol (PEG) and mannitol, as well as high salinity (Ramegowda et al. 2012). In alfalfa (*Medicago sativa*), a NAC TF involved in response to abiotic stress was identified, and the expression of this gene was shown to be induced by drought, high salinity, and ABA (Wang 2013). Results revealed that transgenic *Arabidopsis* overexpressing this TF using 35S promoter had better drought tolerance than the wild type (Wang 2013). Baloglu et al. (2012) performed expression analysis of *TaNAC69-1* and *TtNAMB-2* in durum wheat (*T. turgidum*) under different abiotic stress conditions. Specifically, *TaNAC69-1* was upregulated after 3 h of salt treatment, and the highest level of expression was observed at 24 and 48 h of post-treatment with heat and salinity respectively. On the other hand, *TtNAMB-2* was significantly induced by salt and low temperature stresses. In soybean, the first *GmNAC* genes identified were *GmNAC1-6* in a study conducted by Meng et al. (2007). Subsequently, expression of these genes in response to various stress and hormone treatments, including ABA, JA, high salinity, and PEG-induced osmotic stress, was analyzed in detail by another group (Pinheiro et al. 2009). Later on, Tran et al. (2009) initiated a study of the *GmNAC* family at a wider scale, covering the expression analysis of 31 *GmNAC* genes at seedling stage and under different abiotic stress conditions, including dehydration, salinity, cold, and ABA treatment, as well as examination of their transcriptional activity. According to the results, nine genes were shown to be upregulated by at least one of the tested treatments. Except *GmNAC028*, all remaining genes (*GmNAC002*, *003*, *004*, *010*, *012*, *013*, *015*, and *020*) also had transcriptional activation activity as shown by a yeast one-hybrid assay. More recently, Tran's laboratory studied 152 *GmNAC* genes, which could be detected in soybean genome with full-length cDNA, and proposed a comprehensive nomenclature for the *GmNAC* members (Le et al. 2011). Furthermore, the authors reported that 31 genes displayed significantly altered expression upon dehydration, with 25 up- and 6 downregulated genes. Additionally, the same research group demonstrated the complexity in the dynamics of drought-responsive expression of the *GmNAC* genes as they indicated that expression of several *GmNAC* genes were tissue- and/or development stage-dependent (Le et al. 2012). More recently, Thao et al. (2013) found differential expression of a subset of drought-responsive *GmNACs* in soybean cultivars differing in drought tolerance, and identified positive correlation between *GmNAC* expression levels in these cultivars and their drought-tolerant degree. On the basis of their results, the authors also suggested a number of promising candidate *GmNAC* genes with potential application in genetic engineering of improved drought-tolerant soybean varieties (Thao et al. 2013).

4 Conclusions and Future Perspectives

Given the fact that using conventional breeding methods to create better stress-tolerant cultivars is not really effective since it is applied for varieties with close relationship only, creating transgenic plants by genetic technologies is a much more powerful approach. Thanks to advanced development in molecular cloning and plant transformation methods, barriers in gene transfer across species can be easily overcome. Therefore, the main challenge for scientists is to gain more and more in-depth understanding of mechanisms that plants employ to respond to stresses, especially to conditions similarly to the field environment. By doing this, important genes involved in plant adaptation to environmental stresses can be identified and used for crop improvement. Till date, many genes have been assigned as crucial contributors and uncountable attempts have been made to evaluate their roles in transgenic plants regarding the tolerance capacity toward abiotic stresses. The results of applications of TF-encoding genes so far have been quite promising. Accordingly, TFs bear a high potential for crop improvement using genetic engineering, and thus their characterization should deserve even more attention from the research community in the coming years.

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