***Pak. J. Bot.*, 51(6): 2037-2045, 2019.** **DOI: http://dx.doi.org/10.30848/PJB2019-6(17)**

NAC VS: ABIOTIC STRESSES, CURRENT UNDERSTANDING AND PERSPECTIVE, WITH SPECIAL REFERENCE TO THE CROPS OF POACEAE FAMILY

NASEEM SAMO[1], XUECHUN WANG[1*], MUHAMMAD IMRAN[1], HADI BUX[2],
SHABEER AHMED[1] AND YUNGAO HU[1*]

[1]College of Life Science and Engineering, Southwest University of Science and Technology Main Yang,
Sichuan Province 621010, China
[2]Institute of Plant Sciences, University of Sindh Jamshoro, Pakistan
**Corresponding author's email: xuechunwang@swust.edu.cn*

Abstract

Abiotic stresses are one of the major challenges for crop growth and productivity, and climate change has the potential to further worsen the scenario. The identification and characterization of unique genes, and the understanding their molecular mechanisms, are critical for the development of abiotic-stress-resistant crops with improved yield. NAC is one of the largest families of transcription factors (TFs) unique to plants and is a key player in the defense against harsh environmental conditions. NAC TFs also play a crucial role in the physiological processes of plants, including the formation of secondary walls and roots, leaf senescence, phytohormone homeostasis, the formation of embryos, and flowers. The Poaceae family encompasses many primary sources of food, including rice, wheat, maize, and barley. Being a model plant several NAC TFs characterized from rice, however, a large number remain unidentified or functionally analyzed yet. Far fewer NAC TFs have been identified in other crops than in rice. The exploration and in-depth analyses on NAC TFs from crops will help to identify novel NAC members, which can be used to induce tolerance in crops. In this review, we have summarized the functionally analyzed NAC TFs specific to rice, wheat, maize, and barley. Through this review, we demonstrate that NAC TFs have a crucial role in abiotic stress tolerance mechanisms. We believe further investigation and in-depth studies on NAC TFs are necessary to engineer stress tolerance in crops and provide food security to a growing population.

Key words: Abiotic stresses; Poaceae; NAC; transcription factors; Genetic engineering.

Introduction

Due to their immobile nature, plants are often exposed to various environmental stressors such as temperature, salinity, and drought, which can reduce their growth and productivity (Umezawa *et al*., 2006; Nakashima *et al*., 2012; Zhou *et al.,* 2019; Shafiq *et al.,* 2019). To cope with these environmental stressors, plants have developed a complex network to perceive signals and respond appropriately (Smékalová *et al*., 2014). These responses occur through a series of complex signaling pathways through which plants utilize enzymes, hormones, transcription factors (TFs), and secondary messengers to activate various genes that confer stress tolerance (Smékalová *et al*., 2014). TFs are a key player in these signaling pathways. When plants are exposed to stressors, the stress-responsive TFs are induced, which bind with cis-elements to the promoter of the target stress-related genes and modulate their expression to confer the stress tolerance (Whittaker *et al*., 2001; Cramer *et al*., 2011; Nakashima *et al*., 2012; Puranik *et al*., 2012; Hernandez-Garcia and Finer, 2014; Singh and Laxmi, 2015). Utilization of the TFs to modulate the expression of specific genes is a promising strategy to induce tolerance in plants (Yang *et al*., 2010). It has been reported that approximately 6–10% of genes in the plant genome encode TFs (Franco-Zorrilla *et al*., 2014). These include several families of stress-responsive TFs, including bZIP, AP2/EREBP, ZF, MYB, NAC, and WRKY, which have been well elucidated for their role in a wide range of environmental stress tolerance mechanisms (Abe *et al*., 1997; Ito *et al*., 2006; Nakashima *et al*., 2007; Amir Hossain *et al*., 2010; Puranik *et al*., 2012; Wang *et al*., 2013, 2015; Jia *et al*., 2015).

NAC is one of the largest families of stress-responsive TFs that are specific to plants (Li *et al*., 2016). NAC TFs exhibit an organ-specific expression, and the level of expression is greatly affected by environmental stimuli, which suggests that members of NAC family play an important role in environmental stress tolerance mechanisms (Puranik *et al*., 2012; Wang *et al*., 2013; Zhu *et al*., 2014; Jia *et al*., 2015; Wang *et al*., 2015), as well as the growth and development of plants (Souer *et al*., 1996; Xie *et al*., 2000; Zhong *et al*., 2006, 2007; Yang *et al*., 2011).

The expression of NAC genes primarily depends on their promoters, and at least one upstream promoter sequence of every NAC gene contains a cis-element (Lv *et al*., 2016). You *et al*., (2015) identified 101 BdNAC genes from *Brachypodium distachyon* and analyzed their 1 kb promoter sequence. The analysis determined that nearly every BdNAC gene contained one or more cis-element in the promoter region. Furthermore, they profiled the expression of BdNAC genes under different types of stressors and hormone treatments. Their results revealed that in response to stress, an average of 63% of genes differentially expressed under at least one treatment, and the rest of the genes differentially expressed under more than one treatment. Conversely, in response to a phytohormones treatment, an average 34% of genes differentially expressed under one phytohormone treatment, while the remainder of genes differentially expressed under more than one phytohormone treatment (You *et al*., 2015). These outcomes suggested that NAC genes were involved in complex phytohormones signaling pathways and played a vital role in abiotic stress tolerance. Several other reports illustrated the role of NAC TFs in different environmental stress tolerance mechanisms as well (Addie Nina Olsen *et al*., 2005; Nuruzzaman *et al*., 2012, 2013; Puranik *et al*., 2013; Oh, 2017).

The identification and expression analysis of NAC genes is critical to understanding their networks and modulate their expression during the development of cultivars. Various climate models have predicted that continued changes in climate will lead to a more erratic and harsh growing environment for field crops, which are an important source of food. Thus, there is an urgent need to produce crops with enhanced tolerance to harsh environments. We review recent studies on functionally analyzed NAC TFs from crops in the Poaceae family, including rice, wheat, maize, and barley. As the NAC TFs are a primary regulator of molecular reprogramming and play a key role in abiotic stress tolerance mechanisms, further examination and in-depth studies on NAC TFs are essential.

NAC TFs structure: As a superfamily of TFs, NAC exists in plants only and was named after identification of three proteins: no apical meristem (NAM) from Petunia, Arabidopsis transcription activation factor 1 and 2 (ATAF1 and ATAF2), and cup-shaped cotyledon 2 (CUC2) from Arabidopsis having similar DNA binding domain structure (Aida, 1997). NAM proteins are essential for the formation of the shoot apical meristem, ATAF1 and ATAF2 proteins activate the CaMV35S promoter in yeast, and CUC2 is responsible for the normal development of the carpel margin meristems and the initiation of shoot meristems (Souer *et al*., 1996; Kikuchi *et al*., 2000; Duval *et al*., 2002; Liu *et al*., 2014). The NAC proteins contain a conserved DNA binding domain at the N-terminal and a diverse activation domain at the C-terminal (Addie N. Olsen *et al*., 2005; Fang *et al*., 2008; Puranik *et al*., 2012). The conserved DNA binding domain is roughly 150–160 amino acid residues that are further separated into five subdomains (A–E). The specific amino acids and inserted gaps make each subdomain distinguishable. The subdomains C and D are mainly composed of basic amino acids and responsible for nuclear localization signals, while D and E are positioned near the 60 amino acid region and are responsible for DNA-binding properties (Souer *et al*., 1996; Kikuchi *et al*., 2000; Duval *et al*., 2002; Addie N. Olsen *et al*., 2005; Nuruzzaman *et al*., 2013; Cenci *et al*., 2014). The C-terminal region is divergent in sequence and length, and it is responsible for the activation and repression of transcriptional activity (Ooka *et al*., 2003; He *et al*., 2005; Puranik *et al*., 2012; Ma *et al*., 2013; Cenci *et al*., 2014). The variable C-terminal is very large and displays protein binding properties (Kim *et al*., 2007).

NAC TFs origin: The NAC proteins are not found in unicellular and multicellular algae and have only been reported in land plants (You *et al*., 2015). A limited number of NAC TFs have been found in mosses and lycophytes, but in angiosperms, NAC TFs are found in huge numbers (You *et al*., 2015). It can be postulated from this that NAC proteins may have originated when plants transitioned from water to land and that they are instrumental in environmental adaptation. A different number of NAC proteins exist among plant species. For example, 30 have been reported in lower plants, and up to 453 in hexaploid wheat (Cenci *et al*., 2014; Borrill *et al*., 2017). Genome-wide sequence analysis carried out in different plant species has reported 105 NAC members in Arabidopsis (Ooka *et al*., 2003), 151 in rice (Nuruzzaman *et al*., 2010), 163 in poplar (Hu *et al*., 2010), 152 in soybean (Le *et al*., 2011), 147 in foxtail millet (Puranik *et al*., 2013), 101 in tomato (Jin *et al*., 2014), 106 in pepper (Kim *et al*., 2014), 96 in cassava (Hu *et al*., 2015), 101 in stiff brome (You *et al*., 2015), 152 in tobacco (Rushton *et al*., 2008), and 167 in banana (Cenci *et al*., 2014). The existence of high numbers of NAC proteins in plants is an indication of their functional diversity.

NAC TFs function and mechanism: NAC TFs have a complicated signal transduction network that plays a crucial role in stress tolerance mechanisms via ABA-dependent and ABA-independent pathways. Overexpression of RD26/ANAC072, ATAF1/ANAC002, JUB1/ANAC042 ANAC096, ANAC2, and VNI2/ANAC083 greatly enhances resistance to abiotic stresses in Arabidopsis (He *et al*., 2005; Wu *et al*., 2009; Yang *et al*., 2011; Wu *et al*., 2012; Xu *et al*., 2013). Two TFs in caragana indica, CiNAC3 and CiNAC4, decreased ABA sensitivity and increased salt tolerance in transgenic Arabidopsis at the seed germination stage (Han *et al*., 2015). EcNAC67 from finger millet (Eleusine coracana L.) greatly enhanced tolerance to salinity and drought in transgenic rice (Rahman *et al*., 2016). MusaNAC042 improved drought and salt tolerance capacity, increased the chlorophyll content of leaves, and decreased the malondialdehyde (MAD) content in transgenic banana (Tak *et al*., 2016). Besides the abiotic stress tolerance, NAC TFs are also involved in plant growth and developmental processes such as secondary wall formation, leaf senescence, phytohormones homeostasis, root development, and the formation of the embryo and flower (Sablowski and Meyerowitz, 1998; Souer *et al*., 1996; Xie *et al*., 2000; Umezawa *et al*., 2006; Zhong *et al*., 2006, 2007; Yang *et al*., 2011; Nakashima *et al*., 2012; Puranik *et al*., 2012; Huang *et al*., 2015).

Poaceae crops: Poaceae is one of the most important and the largest families of monocotyledonous plants. Poaceae crops are a vital source of food worldwide and include wheat, rice, barley, and maize. Nearly 55% of carbohydrates are provided by wheat (Gill *et al*., 2004), and more than half of the world's population depends on rice as their primary food source (Cui *et al*., 2016). Barley is the fourth most cultivated cereal crop and is primarily used as a forage crop and in the brewing industry (Shen *et al*., 2016). Maize used as food, feed, and industrial purposes, and most recently, for the production of fuel (Ranum & Pe, 2014).

Impact of abiotic stress on food crops of Poaceae family: Poaceae crops show distinct behavior under different kinds of abiotic stress. Rice and wheat are sensitive and less productive under water-deficient and saline soil conditions. Barley tends to have a natural resistance to drought and salinity, distinguishing it as the most resilient cereal crop in the Poaceae family. Due to this, barley is often used as a model plant to study stress physiology in crops (Gürel *et al*., 2016; Shen *et al*., 2016). However, a number of barley genotypes developed by breeding approaches show greater sensitivity under abiotic stress due genetic variation (Ahmed *et al*., 2013). From 1980 to 2008, climatic changes have led to dramatic reductions in crop yields in the Poaceae family. Rice production reduced to a large extent in some developing countries including China. Globally, wheat and maize production have declined by 5.5% and 3.8%, respectively (Lobell *et al*., 2011). It can be concluded from the above studies that it is critical to study stress physiology in these economically important crops to develop applicable approaches for the development of resistant cultivars.

NAC TFs in major crops of Poaceae family

Rice NAC TFs: A genome-wide survey of NAC TFs has been performed in rice, and approximately 151 members of this family were identified (Nuruzzaman *et al*., 2010). The expression pattern analysis revealed that 46 non-redundant OsNAC genes were up- or down-regulated under one or more abiotic stressors (Nuruzzaman *et al*., 2010). More NAC family genes from model plants, such as rice, have been characterized and functionally analyzed than in other crops within the Poaceae family (Table 1). A large number of NAC members remain to be characterized and functionally analyzed. In rice, NAC TFs have been reported in a number of abiotic stress tolerance mechanisms. The expression of *SNAC1* was induced under salt, drought, ABA, and cold treatment in rice. During drought stress, *SNAC1* was induced predominantly in guard cells, and the overexpressed transgenic rice genotypes had a 22–34% improvement in drought tolerance at the reproductive stage. At the vegetative stage, the transgenic plants displayed tolerance to both drought and salt stress. The transgenic rice lines also exhibited greater sensitivity to ABA and lost water content more slowly compared to the wild type (WT). Moreover, the expression of some marker genes was upregulated in the overexpressed lines as compared with the WT (Hu *et al*., 2006). The overexpression of *SNAC1* in transgenic wheat increased ABA sensitivity and significantly enhanced tolerance to salinity and drought stress for multiple generations. The transgenic plants had a higher chlorophyll and water content in their leaves and a greater fresh and dry weight of both roots and shoots compared with the WT. Furthermore, the expression of three stress-related marker genes (sucrose phosphate synthase, 1-phosphatidylinositol-3-phosphate 5-kinase, and regulatory components of the ABA receptor) was upregulated, while the expression of one gene (type 2C protein phosphatases) was suppressed (Saad *et al*., 2013).

In cotton, the overexpression of *SNAC1* improved drought and salt tolerance by enhancing root development and reducing the transpiration rate (Liu *et al*., 2014). An *et al.,* (2015) performed the functional analysis of *SNAC1* in ramie, and their findings suggested that overexpression of *SNAC1* greatly enhanced salt and drought tolerance at the seedling, fiber maturation, and rapid growth stages. Recently, Parvin *et al.,* (2015) reported that *SNAC1* significantly increased drought and salt tolerance in transgenic rice. Ghosh *et al.,* (2016) findings suggested that *OsNAC1* was involved in low temperature tolerance.

Hu *et al.,* (2008) investigated the role of *SNAC2* in rice, and their results revealed that *SNAC2* is a chief regulator in the defense to multiple abiotic stresses. Overexpressed plants remained vigorous (50%) in severe cold (4–8°C), while all the WT plants died. Additionally, the transgenic plants exhibited higher membrane stability under cold stress. During salt stress, overexpressed rice plants exhibited a higher germination and growth rate, moreover, enhanced tolerance to polyethylene glycol (PEG), and reduced sensitivity to ABA. Similarly, Shen *et al.,* (2017) stated that *OsNAC2* was strongly induced by ABA, salt, and drought stress, and rice lines overexpressing the gene had a significant tolerance to salt stress at the vegetative and flowering stage compared to WT. It has also been observed that under salt stress, *OsNAC2* predominantly expressed in leaves, while during drought stress, the highest expression levels were recorded in roots. Additionally, the overexpressed lines did not show any significant increase in yield compared with WT. Conversely, RNAi lines showed higher drought and salinity resistance, and plants maintained high yield under drought conditions. Gene expression analysis found that *OsNAC2* overexpression down-regulated ABA-dependent stress-related marker genes. These findings suggest that *OsNAC2* acts as an inhibitor to the drought and salinity response pathways. When the *OsNAC2* target genes were further explored using ChIP and yeast-one-hybrid analyses, data suggested that *OsNAC2* has a new function and regulation mechanism in abiotic stress responses and directly regulated *OsLEA3* (LATE EMBRYOGENESIS ABUNDANT 3) and *OsSAPK1* (Stress-Activated Protein Kinases 1). Therefore, *OsNAC2* may act as a connection point in the ABA-dependent pathway and abiotic stress response.

The expression of *OsNAC5* induced under high salinity, drought, cold, methyl jasmonic acid, and ABA in overexpressed lines resulted in enhanced tolerance to salt stress. *OsNAC5* improved tolerance to abiotic stresses by inducing expression of various stress-responsive genes such as *OsLEA*. Moreover, *OsNAC5* appears to interact with *OsNAC6* and *SNAC1* and shows the functional homology with *OsNAC6,* except for growth retardation (Takasaki *et al.,* 2010). Song *et al.,* (2011) further evaluated the physiological mechanism of *OsNAC5* to confer drought and salt stress tolerance. The authors generated overexpressed and suppressed *OsNAC5* lines and determined that *OsNAC5* confers tolerance against drought and salinity by regulating Na+ accumulation, antioxidant system, and synthesis of soluble sugars and Proline.

Recently, Lee *et al.,* (2017) examined the molecular mechanisms of *OsNAC6* and stated that overexpressed rice lines had improved drought tolerance by mediated root structure adaptation, including root number and root diameter. Meanwhile, *OsNAC6* mutants exhibited drought susceptibility. Their examination unveiled that *OsNAC6* can be utilized for the development of highly productive crops, and it allows crops to flourish in water-stressed conditions.

Table 1. Functionally analyzed NAC TFs from rice.

Transcription factor	Induction	Function	Reference
SNAC1	Drought, salt, cold, and ABA	Salt, Drought, Stress tolerance	(Hu *et al*., 2006) (Saad *et al*., 2013) (Liu *et al*., 2014). (An *et al*., 2015) (Parvin *et al*., 2015)
OsNAC1	Low-temperature	Low-temperature Stress tolerance	(Ghosh *et al*., 2016)
SNAC2	drought, salinity, cold, wounding and ABA	Cod, PEG, Salt, stress tolerance	(Hu *et al*., 2008)
OsNAC2	ABA, salt, and drought stress	Salt and drought stress tolerance	(Shen *et al*., 2017)
OsNAC5	drought, salt, cold, MeJA and ABA	Drought, salt and cold stress tolerance and enhance yield	(Takasaki *et al*., 2010) (Song *et al*., 2011)
OsNAC6	Drought, salt, cold, ABA, JA and wounding	drought and salt stress tolerance and enhance yield	(Lee *et al*., 2017)
OsNAC9	Drought	drought stress tolerance and enhance yield	(Redillas *et al*., 2012)
OsNAC10	Drought, salt, cold, ABA	Drought, salt and cold stress tolerance and enhance yield	(Jeong *et al*., 2010)
OsNAC22	Drought, salt, ABA	Drought and salt stress tolerance	(Hong *et al*., 2016)
OsNAC95	Drought and cold	Drought and cold stress tolerance	(Huang *et al*., 2016)

Table 2. Functionally analyzed NAC TFs from wheat, maize, and barley.

Transcription factor	Induction	Function	Reference
TaNAC2	Drought, salt, cold and ABA	Drought, salt, and freezing stress tolerance	(Mao *et al*., 2012)
TaNAC2a	Drought and salt	Drought Stress tolerance	(Tang *et al*., 2012)
TaNAC2L	Heat	Heat stress tolerance	(Guo *et al*., 2015)
TaNAC29	salt, H_2O_2, PEG and ABA	Drought and salt Stress tolerance	(Huang *et al*., 2015) (Xu *et al*., 2015)
TaNAC47	salt, cold, PEG and ABA	Drought, salt, and freezing stress tolerance	(Zhang *et al*., 2016)
TaNAC67	Drought, salt, cold and ABA	Drought, salt, and freezing stress tolerance	(Mao *et al*., 2014)
TaNAC69	Drought	Drought Stress tolerance	(Xue *et al*., 2011)
ZmSNAC1	drought, cold, high salinity, and ABA	Drought tolerance	(Lu *et al*., 2012)
ZmSNAC55	drought, cold, high salinity, and ABA	Drought tolerance	(Mao *et al*., 2016)
ZmSNAC111	Drought	Drought tolerance	(Mao *et al*., 2015)
HvNAC1	Drought	Drought Stress tolerance	(Al Abdallat *et al*., 2014)

The overexpressed lines of *OsNAC9* and *OsNAC10* under the control of a root-specific promoter displayed thicker roots and a higher grain yield during drought conditions compared with control plants. Microarray analysis suggested that *OsNAC9* modified the expression of the downstream genes, including *NCED* and calcium-transporting ATPase, while *OsNAC10* modulated the expression of various downstream genes, including *P450, Zn-finger, HAK5, 2OG-Fe* (II), *NCED, NAC,* and *KUP3* (Jeong *et al*., 2010; Redillas *et al*., 2012). These findings suggest that *OsNAC9* and *OsNAC10* play a vital role in the defense of multiple abiotic stresses.

OsNAC022 is a stress-related NAC TF, and the transcription level of *OsNAC022* has been induced under high salinity, drought, and ABA treatments. The overexpression of *OsNAC022* mediates drought and salt resistance in transgenic rice through the ABA-dependent pathway (Hong *et al*., 2016). *OsNAC095* plays a dual role in cold and drought stress, as it acts as the positive regulator of cold stress responses and the negative regulator in drought responses in transgenic rice (Huang *et al*., 2016). These findings highlight that rice NAC TFs play a key role in the defense against a broad range of abiotic stress. The characterization of members of NAC TFs in rice provides a theoretical basis for understanding the mechanisms underlying stress tolerance and the development of resistant varieties using biotechnological approaches.

Wheat NAC TFs: Recently, genome-wide analysis of the NAC TFs was performed in the polyploid wheat genome (Borrill *et al*., 2017). A total of 453 NAC TFs were identified, as compared with rice studies on characterization and functional analysis of NAC TFs from wheat are scarce (Table 2). The overexpression of *TaNAC2a* enhanced drought tolerance in transgenic tobacco while enhancing the fresh and dry weight of plants (Tang *et al*., 2012). The overexpression of *TaNAC2L* in Arabidopsis improved tolerance to heat stress (Guo *et al*., 2015). *TaNAC69* conferred drought tolerance in transgenic wheat lines by upregulating the expression of stress-related genes (Xue *et al*., 2011). In Arabidopsis, the overexpression of *TaNAC2, TaNAC47*, *TaNAC67*, and *TaNAC29* conferred drought tolerance. The overexpression of *TaNAC2* induced the expression of ten stress-related marker genes (*DREB1A*, *DREB2A*, *CBF1*, *CBF2*, *RD29A*, *RD29B*, *RD22*, *COR15*, *COR47*, and *Rab18*) and four ABA synthesis/response genes (*ABA1*, *ABI1*, *ABI2*, and *ABI5*) (Mao *et al*., 2012). Similarly, overexpression of *TaNAC47* induced the expression of six stress-related marker genes (*RD29A*, *RD29B*, *COR47*, *RD20*, *GSTF6*, and *P5CS1*) (Mao *et al*., 2014). Additionally, the overexpression of *TaNAC67* induced the expression of five stress-related marker genes (*DERB1A*, *RD29B*, *RD29A*, *RAB18*, and *ABI5*) (Zhang *et al*., 2016). In contrast, the overexpression of *TaNAC29* significantly reduced the expression level of some key

ABA signaling regulators and senescence-associated genes (*RD29B*, *SAG13*, *SAG113*, *AIB1*, *ERD11*, and *ABI5*) (Huang *et al*., 2015). Interestingly, in another study, *TaNAC29* conferred salt tolerance by enhancing the expression of some stress-related marker genes (*RD29A, RD29B,* and *KINI*) (Xu *et al*., 2015). These findings demonstrate that wheat NAC TFs are involved in a broad range of abiotic stresses and may confer tolerance by activating or repressing downstream genes.

Maize NAC TFs: A genome-wide survey of NAC TFs was performed in maize (*Zea mays* L.), and a total 148 non-redundant NAC genes (*ZmNAC1–ZmNAC148*) were identified (Peng *et al*., 2015). Based on the phylogenetic relationship identified, genes were subdivided into 12 groups (a–l). Microarray examination found that most of the maize NAC genes were expressed during different developmental stages. Evolutionary relationships and sequence comparative analysis revealed that 19 ZmNAC genes shared homology with published stress-related marker genes. Furthermore, under a drought stress treatment, 14 of the 19 genes showed an enhanced expression level (*ZmNAC16*, *ZmNAC28*, *ZmNAC39*, *ZmNAC42*, *ZmNAC44*, *ZmNAC68*, *ZmNAC69*, *ZmNAC70*, *ZmNAC71*, *ZmNAC81*, *ZmNAC96*, *ZmNAC102*, *ZmNAC126*, and *ZmNAC137*) (Peng *et al*., 2015). These findings suggested that these particular genes may play a vital role in stress regulation mechanisms. Studies on the functional analysis of maize NAC TFs are limited (Table 2). *ZmSNAC1* is strongly upregulated under high salinity, drought, cold, and ABA treatments but down-regulated by salicylic acid treatment. The overexpression of *ZmSNAC1* in Arabidopsis enhanced ABA sensitivity and conferred drought stress tolerance (Lu *et al*., 2012). Increasing the expression of *ZmNAC111* in transgenic Arabidopsis improved tolerance to drought stress at the seedling stage and water use efficiency by upregulating drought-responsive genes under water-stressed conditions (Mao *et al*., 2015). Another maize NAC gene, *ZmNAC55*, was also induced under high salinity, drought, cold, and ABA treatment. The overexpression of *ZmNAC55* in Arabidopsis resulted in increased sensitivity to ABA at the germination stage and enhanced tolerance to drought stress compared to WT. Moreover, transcriptome analysis revealed that numerous stress-related genes were differentially expressed, including 12 drought responsive marker genes (*DREB2A*, *RD29A*, *RD29B*, *LEA14*, *RD26*, *RD17*, *PP2CA*, *ZAT10*, *RAB18*, *ANAC019*, *NCED3*, and *RD20*) (Mao *et al*., 2016). These findings suggest that maize NAC TFs have a positive regulatory role in abiotic stress tolerance mechanisms, and they have potential applications for the development of stress-tolerant crops.

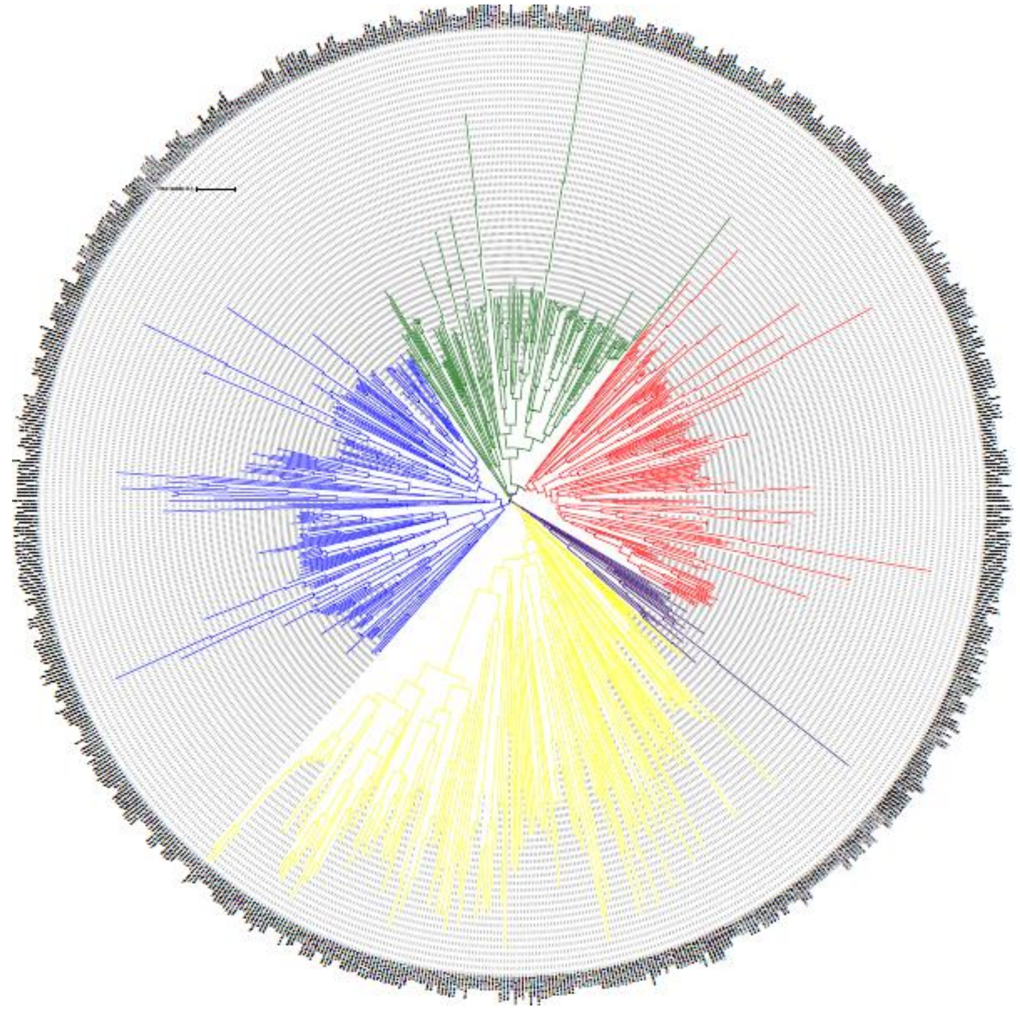

Fig. 1. Phylogenetic analysis performed between the Arabidopsis, rice, wheat, maize and Barley. The full-length amino acid sequences, 133 from Arabidopsis, 150 from rice (BGIOSGA), 204 from wheat (Traes), 168 from maize (GRMZM) and 150 from barley (MLOC) was used to construct phylogenetic tree by geneious software using default parameters.

Barley NAC TFs: The barley (*Hordeum vulgare* L.) genome has not yet been fully sequenced, but Christiansen *et al.,* (2011) identified 48 NAC genes, 43 of which were full coding sequences. Phylogenetic analysis revealed that barley NAC genes include members from eight NAC subfamilies, including Arabidopsis and rice, although numerous HvNAC genes still need to be identified. They also reported that the expression profile and comparative analysis revealed that HvNAC genes may play a vital role in leaf senescence, root and seed development, secondary cell wall biosynthesis, and hormone-regulated stress responses. The stress-responsive NAC gene *HvNAC1* was functionally analyzed by Al Abdallat *et al.,* (2014) showed that *HvNAC1* is induced by exposure to drought (Table 2). The overexpression of *HvNAC1* in transgenic barley resulted in an improved resistance to drought stress at different growth stages compared with the WT plants. Additionally, the transgenic plant had an enhanced water status and greater photosynthetic activity, and water loss was reduced under drought stress. A higher grain yield was also harvested from transgenic plants. Collectively, these results indicate that HvNAC TFs also play a vital role in abiotic stress tolerance and can be utilized for the development of resistant cultivars.

Conclusion

The development of stress-resistant crops is essential to ensuring food security. As global food demand is increasing each day in the face of a growing population and climate change, it is essential to identify and characterize members of the NAC family in crops. Doing so will assist in the engineering of cultivars that are more tolerant of stressful environments. To date, a very limited number of NAC TFs have been characterized and functionally analyzed in crops (Fig. 1). Given that the NAC TFs are the primary regulators of growth, development, and stress response in plants, further studies on NAC TFs are necessary.

Acknowledgments

This work is supported by National Key Research and Development Program of China (2017YFD0100201); Sichuan Science and Technology Program (2018HH0039; 2018NZZJ001). We would like to thank the reviewers who provided suggestions to improve this paper.

References

Abe, H., K. Yamaguchi-Shinozaki, T. Urao, T. Iwasaki, D. Hosokawa and K. Shinozaki. 1997. Role of arabidopsis MYC and MYB homologs in drought- and abscisic acid-regulated gene expression. *Plant Cell,* 9(10): 1859-1868.

Ahmed, I.M., F. Cao, M. Zhang, X. Chen, G. Zhang and F. Wu. 2013. Difference in yield and physiological features in response to drought and salinity combined stress during anthesis in tibetan wild and cultivated barleys. *PLoS One,* 8(10): p.e77869.

Aida, M. 1997. Genes Involved in Organ Separation in Arabidopsis: An Analysis of the cup-shaped cotyledon Mutant. *Plant Cell Online*, 9(6): 841-857.

Al Abdallat, A.M., J.Y. Ayad, J.M. Abu Elenein, Z. Al Ajlouni and W.A. Harwood. 2014. Overexpression of the transcription factor HvSNAC1 improves drought tolerance in barley (*Hordeum vulgare* L.). *Mol. Breed.,* 33(2): 401-414.

Amir Hossain, M., Y. Lee, J.I. Cho, C.H. Ahn, S.K. Lee, J.S. Jeon, H. Kang, C.H. Lee, G.An and P.B. Park. 2010. The bZIP transcription factor OsABF1 is an ABA responsive element binding factor that enhances abiotic stress signaling in rice. *Plant Mol. Biol.*, 72: 557-566.

An, X., Y. Liao, J. Zhang, L. Dai, N. Zhang, B. Wang, L. Liu and D. Peng. 2015. Overexpression of rice NAC gene SNAC1 in ramie improves drought and salt tolerance. *Plant Growth Regul.,* 76: 211-223.

Borrill, P., S.A. Harrington and C. Uauy. 2017. Genome-Wide Sequence and Expression Analysis of the NAC Transcription Factor Family in Polyploid Wheat. *G3: Genes Genomes Genetics,* 7(9): 3019-3029.

Cenci, A., V. Guignon, N. Roux and M. Rouard. 2014. Genomic analysis of NAC transcription factors in banana (*Musa acuminata*) and definition of NAC orthologous groups for monocots and dicots. *Plant Mol. Biol.,* 85: 63-80.

Christiansen, M.W., P.B. Holm and P.L. Gregersen. 2011. Characterization of barley (*Hordeum vulgare* L.) NAC transcription factors suggests conserved functions compared to both monocots and dicots. *BMC Res. Notes*., 4(1): 302.

Cramer, G.R., K. Urano, S. Delrot, M. Pezzotti and K. Shinozaki. 2011. Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol.,* 11: 163.

Cui, Y., M. Wang, H. Zhou, M. Li, L. Huang, X. Yin, G. Zhao, F. Lin, X. Xia and G. Xu. 2016. OsSGL, a Novel DUF1645 Domain-Containing Protein, Confers Enhanced Drought Tolerance in Transgenic Rice and Arabidopsis. *Front. Plant Sci.,* 7: 2001.

Duval, M., T.F. Hsieh, S.Y. Kim and T.L. Thomas. 2002. Molecular characterization of AtNAM: A member of the Arabidopsis NAC domain superfamily. *Plant Mol. Biol.,* 50: 237-248.

Fang, Y., J. You, K. Xie, W. Xie and L. Xiong. 2008. Systematic sequence analysis and identification of tissue-specific or stress-responsive genes of NAC transcription factor family in rice. *Mol. Genet. Genomics*., 280: 547-563.

Franco-Zorrilla, J.M., I. López-Vidriero, J.L. Carrasco, M. Godoy, P. Vera and R. Solano. 2014. DNA-binding specificities of plant transcription factors and their potential to define target genes. *Proc. Natl. Acad. Sci.,* 111: 2367-2372.

Ghosh, T., M. Rai, W. Tyagi and C. Challam. 2016. Seedling stage low temperature response in tolerant and susceptible rice genotypes suggests role of relative water content and members of OsSNAC gene family. *Plant Signal. Behav.*, 11: 1-5.

Gill, B.S., R. Appels, A.M. Botha-Oberholster, C.R. Buell, J.L. Bennetzen, B. Chalhoub, F. Chumley, J. Dvořák, M. Iwanaga, B. Keller, W. Li, W.R McCombie, Y. Ogihara, F. Quetier and T. Sasaki. 2004. A workshop report on wheat genome sequencing: International genome research on wheat consortium. *Genetics*, 168(2): 1087-1096.

Guo, W., J. Zhang, N. Zhang, M. Xin, H. Peng, Z. Hu, Z. Ni and J. Du. 2015. The wheat NAC transcription factor TaNAC2L is regulated at the transcriptional and post-translational levels and promotes heat stress tolerance in transgenic arabidopsis. *PLoS One,* 10: 1-11.

Gürel, F., Z.N. Öztürk, C. Uçarlı and D. Rosellini. 2016. Barley Genes as Tools to Confer Abiotic Stress Tolerance in Crops. *Front. Plant Sci.,* 7: 1137.

Han, X., Z. Feng, D. Xing, Q. Yang, R. Wang, L. Qi and G. Li. 2015. Two NAC transcription factors from Caragana intermedia altered salt tolerance of the transgenic Arabidopsis. *BMC Plant Biol.,* 15: 208.

He, X.J., R.L. Mu, W.H. Cao, Z.G. Zhang, J.S. Zhang and S.Y. Chen. 2005. AtNAC2, a transcription factor downstream of ethylene and auxin signaling pathways, is involved in salt stress response and lateral root development. *Plant J.*, 44: 903-916.

Hernandez-Garcia, C.M. and J.J. Finer. 2014. Identification and validation of promoters and cis-acting regulatory elements. *Plant Sci.,* 217-218: 109-119.

Hong, Y., H. Zhang, L. Huang, D. Li and F. Song. 2016. Overexpression of a Stress-Responsive NAC Transcription Factor Gene ONAC022 Improves Drought and Salt Tolerance in Rice. *Front. Plant Sci.*, 7: 1-19.

Hu, H., J. You, Y. Fang, X. Zhu, Z. Qi and L. Xiong. 2008. Characterization of transcription factor gene SNAC2 conferring cold and salt tolerance in rice. *Plant Mol. Biol.,* 67: 169-181.

Hu, H., M. Dai, J. Yao, B. Xiao, X. Li, Q. Zhang and L. Xiong. 2006. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proc. Natl. Acad. Sci.,* 103: 12987-12992.

Hu, R., G. Qi, Y. Kong, D. Kong, Q. Gao and G. Zhou. 2010. Comprehensive Analysis of NAC Domain Transcription Factor Gene Family in Populus trichocarpa. *BMC Plant Biol.*, 10(1): 145.

Hu, W., Y. Wei, Z. Xia, Y. Yan, X. Hou, M. Zou, C. Lu, W. Wang and M. Peng. 2015. Genome-wide identification and expression analysis of the NAC transcription factor family in cassava. *PLoS One*, 10: 1-25.

Huang, L., Y. Hong, H. Zhang, D. Li and F. Song. 2016. Rice NAC transcription factor ONAC095 plays opposite roles in drought and cold stress tolerance. *BMC Plant Biol.*, 16: 203.

Huang, Q., Y. Wang, B. Li, J. Chang, M. Chen, K. Li, G. Yang and G. He. 2015. TaNAC29, a NAC transcription factor from wheat, enhances salt and drought tolerance in transgenic Arabidopsis. *BMC Plant Biol.,* 15: 268.

Ito, Y., K. Katsura, K. Maruyama, T. Taji, M. Kobayashi, M. Seki, K. Shinozaki and K. Yamaguchi-Shinozaki. 2006. Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. *Plant Cell Physiol.,* 47: 141-153.

Jeong, J.S., Y.S. Kim, K.H. Baek, H. Jung, S.H. Ha, Y. Do Choi, M. Kim, C. Reuzeau and J.K. Kim. 2010. Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. *Plant Physiol.,*153: 185-197.

Jia, H., C. Wang, F. Wang, S. Liu, G. Li and X. Guo. 2015. GhWRKY68 reduces resistance to salt and drought in transgenic Nicotiana benthamiana. *PLoS One,* 10(3): e0120646.

Jin, J., H. Zhang, L. Kong, G. Gao and J. Luo. 2014. PlantTFDB 3.0: A portal for the functional and evolutionary study of plant transcription factors. *Nucleic Acids Res.,* 42(D1): D1182-D1187.

Kikuchi, K., M. Ueguchi-Tanaka, K.T. Yoshida, Y. Nagato, M. Matsusoka and H.Y. Hirano. 2000. Molecular analysis of the NAC gene family in rice. *Mol. Gen. Genet.,* 262: 1047-1051.

Kim, S., M. Park, S.I. Yeom, Y.M. Kim, J.M. Lee, H.A. Lee, E. Seo, J. Choi, K. Cheong, K.T. Kim, K. Jung, G.W. Lee, S.K. Oh, C. Bae, S.B. Kim, H.Y. Lee, S.Y. Kim, M.S. Kim, B.C. Kang, Y.D. Jo, H.B. Yang, H.J. Jeong, W.H. Kang, J.K. Kwon, C. Shin, J.Y. Lim, J.H. Park, J.H. Huh, J.S. Kim, B.D. Kim, O. Cohen, I. Paran, M.C. Suh, S.B. Lee, Y.K. Kim, Y. Shin, S.J. Noh, J. Park, Y.S. Seo, S.Y. Kwon, H.A. Kim, J.M. Park, H.J. Kim, S.B. Choi, P.W. Bosland, G. Reeves, S.H. Jo, B.W. Lee, H.T. Cho, H.S. Choi, M.S. Lee, Y. Yu, Y. Do Choi, B.S. Park, A. Van Deynze, H. Ashrafi, T. Hill, W.T. Kim, H.S. Pai, H.K. Ahn, I. Yeam, J.J. Giovannoni, J.K.C. Rose, I. Sørensen, S.J. Lee, R.W. Kim, I.Y. Choi, B.S. Choi, J.S. Lim, Y.H. Lee and D.Choi. 2014. Genome sequence of the hot pepper provides insights into the evolution of pungency in Capsicum species. *Nat. Genet.,* 46: 270-278.

Kim, S.G., S.Y. Kim and C.M. Park. 2007. A membrane-associated NAC transcription factor regulates salt-responsive flowering via FLOWERING LOCUS T in Arabidopsis. *Planta*, 226: 647-654.

Le, D.T., R. Nishiyama, Y. Watanabe, K. Mochida, K. Yamaguchi-Shinozaki, K. Shinozaki and L.S.P. Tran. 2011. Genome-wide survey and expression analysis of the plant-specific NAC transcription factor family in soybean during development and dehydration stress. *DNA Res.,* 18: 263-276.

Lee, D.K., P.J. Chung, J.S. Jeong, G. Jang, S.W. Bang, H. Jung, Y.S. Kim, S.H. Ha, Y. Do Choi and J.K. Kim. 2017. The rice OsNAC6 transcription factor orchestrates multiple molecular mechanisms involving root structural adaptions and nicotianamine biosynthesis for drought tolerance. *Plant Biotechnol. J.,* 15: 754-764.

Li, X.D., K.Y. Zhuang, Z.M. Liu, D.Y. Yang, N.N. Ma and Q.W. Meng. 2016. Overexpression of a novel NAC-type tomato transcription factor, SlNAM1, enhances the chilling stress tolerance of transgenic tobacco. *J. Plant Physiol.,* 204: 54-65.

Liu, G., X. Li, S. Jin, X. Liu, L. Zhu, Y. Nie and X. Zhang. 2014. Overexpression of rice NAC gene SNAC1 improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton. *PLoS One,* 9(1): e86895.

Lobell, D.B., W. Schlenker and J. Costa-Roberts. 2011. Climate trends and global crop production since 1980. *Science,* 333: 616-620.

Lu, M., S. Ying, D.F. Zhang, Y.S. Shi, Y.C. Song, T.Y. Wang and Y. Li. 2012. A maize stress-responsive NAC transcription factor, ZmSNAC1, confers enhanced tolerance to dehydration in transgenic Arabidopsis. *Plant Cell Rep.,* 31: 1701-1711.

Lv, X., S. Lan, K.M. Guy, J. Yang, M. Zhang and Z. Hu. 2016. Global Expressions Landscape of NAC Transcription Factor Family and Their Responses to Abiotic Stresses in Citrullus lanatus. *Sci. Rep.,* 6: 30574.

Ma, N.N., Y.Q. Zuo, X.Q. Liang, B. Yin, G.D. Wang and Q.W. Meng. 2013. The multiple stress-responsive transcription factor SlNAC1 improves the chilling tolerance of tomato. *Physiol. Plant.,* 149: 474-486.

Mao, H., H. Wang, S. Liu, Z. Li, X. Yang, J. Yan, J. Li, L.S.P Tran and F. Qin. 2015. A transposable element in a NAC gene is associated with drought tolerance in maize seedlings. *Nat. Commun.,* 6: 8326.

Mao, H., L. Yu, R. Han, Z. Li and H. Liu. 2016. ZmNAC55, a maize stress-responsive NAC transcription factor, confers drought resistance in transgenic Arabidopsis. *Plant Physiol. Biochem.,* 105: 55-66.

Mao, X., H. Zhang, X. Qian, A. Li, G. Zhao and R. Jing. 2012. TaNAC2, a NAC-type wheat transcription factor conferring enhanced multiple abiotic stress tolerances in Arabidopsis. *J. Exp. Bot.,* 63: 2933-2946.

Mao, X., S. Chen, A. Li, C. Zhai and R. Jing. 2014. Novel NAC transcription factor TaNAC67 confers enhanced multi-abiotic stress tolerances in Arabidopsis. *PLoS One,* 9(1): e84359.

Nakashima, K., H. Takasaki, J. Mizoi, K. Shinozaki and K. Yamaguchi-Shinozaki. 2012. NAC transcription factors in plant abiotic stress responses. *Biochim. Biophys. Acta - Gene Regul. Mech.,* 1819: 97-103.

Nakashima, K., L.S.P. Tran, D. Van Nguyen, M. Fujita, K. Maruyama, D. Todaka, Y. Ito, N. Hayashi, K. Shinozaki and K. Yamaguchi-Shinozaki. 2007. Functional analysis of a NAC-type transcription factor OsNAC6 involved in abiotic and biotic stress-responsive gene expression in rice. *Plant J.,* 51: 617-630.

Nuruzzaman, M., A.M. Sharoni and S. Kikuchi. 2013. Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants. *Front. Microbiol.,* 4: 248.

Nuruzzaman, M., A.M. Sharoni, K. Satoh, A. Moumeni, R. Venuprasad, R.Serraj, A. Kumar, H. Leung, K. Attia and S. Kikuchi. 2012. Comprehensive gene expression analysis of the NAC gene family under normal growth conditions, hormone treatment, and drought stress conditions in rice using near-isogenic lines (NILs) generated from crossing Aday Selection (drought tolerant) and IR64. *Mol. Genet. Genomics*., 287: 389-410.

Nuruzzaman, M., R. Manimekalai, A.M. Sharoni, K. Satoh, H. Kondoh, H. Ooka and S. Kikuchi. 2010. Genome-wide analysis of NAC transcription factor family in rice. *Gene*, 465: 30-44.

Oh, S.T. and K. Sang. 2017. Biological roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in solanaceous crops. *J. Plant Biotechnol.,* 44(1): 1-11.

Olsen, A.N., H.A. Ernst, L. Lo Leggio and K. Skriver. 2005. DNA-binding specificity and molecular functions of NAC transcription factors. *Plant Sci.,* 169: 785-797.

Olsen, A.N., H.A. Ernst, L.L. Leggio and K. Skriver. 2005. NAC transcription factors: Structurally distinct, functionally diverse. *Trends Plant Sci.,* 10: 79-87.

Ooka, H., K. Satoh, K. Doi, T. Nagata, Y. Otomo, K. Murakami, K. Matsubara, N. Osato, J. Kawai, P. Carninci, Y. Hayashizaki, K. Suzuki, K. Kojima, Y. Takahara, K. Yamamoto and S. Kikuchi. 2003. Comprehensive Analysis of NAC Family Genes in Oryza sativa and Arabidopsis thaliana. *DNA Res.,* 10: 239-247.

Parvin, S., S. Biswas, S. Razzaque, T. Haque, S.M. Elias, R.S. Tammi and Z.I. Seraj. 2015. Salinity and drought tolerance conferred by in planta transformation of SNAC1 transcription factor into a high-yielding rice variety of Bangladesh. *Acta Physiol. Plant.,* 37: 1-12.

Peng, X., Y. Zhao, X. Li, M. Wu, W. Chai, L. Sheng, Y. Wang, Q. Dong, H. Jiang and B. Cheng. 2015. Genomewide identification, classification and analysis of NAC type gene family in maize. *J. Genet.,* 94: 377-390.

Puranik, S., P.P. Sahu, P.S. Srivastava and M. Prasad. 2012. NAC proteins: Regulation and role in stress tolerance. *Trends Plant Sci.,* 17: 369-381.

Puranik, S., P.P. Sahu, S.N. Mandal, S.K. Parida and M. Prasad. 2013. Comprehensive genome-wide survey, genomic constitution and expression profiling of the NAC transcription factor family in foxtail millet (*Setaria italica* L.). *PloS one,* 8(5): e64594.

Rahman, H., V. Ramanathan, J. Nallathambi, S. Duraialagaraja, R. Muthurajan, W. Wang, B. Vinocur, A. Altman, P. Gepts, H. Athar, M. Ashraf, R. Mittler, E. Blumwald, S. Singla-Pareek, M. Reddy, S. Sopory, R. Yadav, A. Solanke, P. Kumar, D. Pattanayak, N. Yadav, P. Kumar, S. Turan, K. Cornish, S. Kumar, G. Khong, F. Richaud, Y. Coudert, P. Pati, C. Santi, C. Périn, K. Nakashima, H.Takasaki, J. Mizoi, K. Shinozaki, K. Yamaguchi-Shinozaki, J. Zhu, N. Yadav, J. Taunk, A. Rani, B. Aneja, R. Yadav, P. Agarwal, P. Agarwal, M. Reddy, S. Sopory, H. Shen, C. Liu, Y. Zhang, X. Meng, X. Zhou, C.Chu, Q. Xie, M. Duval, T. Hsieh, S. Kim, T. Thomas, H. Ernst, A.N. Olsen, K. Skriver, S. Larsen, L. Lo-Leggio, H. Hu, M. Dai, J. Yao, B. Xiao, X. Li, Q. Zhang, L. Xiong, J. Jin, H. Zhang, L. Kong, G. Gao, J. Luo, E. Souer, A. Houwelingen, D. Kloos, J. Mol, R. Koes, R. Zhong, T. Demura, Z. Ye, R. Zhong, E. Richardson, Z. Ye, S. Yang, P. Seo, H. Yoon, C. Park, L. Sun, D. Li, H. Zhang, F. Song, M. Nuruzzaman, A. Sharoni, S. Kikuchi, V. Ramegowda, M. Senthil-Kumar, K. Nataraja, M. Reddy, K. Mysore, M. Udayakumar, L. Tran, R. Nishiyama, K. Yamaguchi-Shinozaki, K. Shinozaki, M. Fujita, Y. Fujita, K. Maruyama, M. Seki, K. Hiratsu, M. Ohme-Takagi, Y. Jiang, M. Deyholos, Y. Fang, J. You, K. Xie, W. Xie, L. Xiong, K.Mochida, T. Yoshida, T. Sakurai, K. Yamaguchi-Shinozaki, K. Shinozaki, L. Tran, K. Nakashima, L. Tran, D. Van-Nguyen, M. Fujita, K. Maruyama, D.Todaka, G. Liu, X. Li, S. Jin, X. Liu, L. Zhu, Y. Nie, J. Jeong, Y. Kim, K. Baek, H. Jung, S. Ha, Y. Do-Choi, M. Kim, C. Reuzeau, J. Kim, X. Mao, S. Chen, A. Li, C. Zhai, R. Jing, P. Mehta, K. Sivaprakash, M. Parani, G. Venkataraman, A.Parida, R. Mishra, P. Reddy, S. Nair, G. Markandeya, A. Reddy, S. Sopory, R. Garg, M. Verma, S. Agrawal, R. Shankar, M. Majee, M. Jain, K. Devos, M. Gale, H. Shailaja, S. Thirumeni, S. Agarwal, A. Kumar, P. Singh, A. Singh, H. Rahman, N. Jagadeeshselvam, R. Valarmathi, B. Sachin, R. Sasikala, N. Senthil, D. Sudhakar, S. Robin, R. Muthurajan, K. Livak, T. Schmittgen, Y. Hiei, T. Komari, E. Southern, X. He, R. Mu, W. Cao, Z. Zhang, J. Zhang, S. Chen, H. Hu, J. You, Y. Fang, X. Zhu, Z. Qi, L. Xiong, S. Puranik, P. Sahu, P. Srivastava, M. Prasad, M. Nuruzzaman, R. Manimekalai, A. Sharoni, K. Satoh, H. Kondoh, H. Ooka, S. Puranik, P. Sahu, S. Mandal, B. Suresh, S. Parida, M. Prasad, A. Singh, V. Sharma, A. Pal, V. Acharya, P. Ahuja, Z. Chen, X. Guo, Z. Chen, W. Chen, D. Liu, Y. Zheng, H. Huang, Y. Wang, S. Wang, X. Wu, K. Yang, Y. Niu, J. Ma, F. Wang, M. Li, Q. Jiang, G.Tan, A. Xiong, G. Pinheiro, C. Marques, M. Costa, P. Reis, M. Alves, C. Carvalho, K. Shiriga, R. Sharma, K. Kumar, S. Yadav, F. Hossain, N. Thirunavukkarasu, J. You, L. Zhang, B. Song, X. Qi, Z. Chan, X. Zheng, B. Chen, G. Lu, B. Han, L. Tran, K. Nakashima, Y. Sakuma, S. Simpson, Y. Fujita, K. Maruyama, A. Alizadeh, A. Alqudah, N. Samarah, R. Mullen and R. Daniel. 2016. Over-expression of a NAC 67 transcription factor from finger millet (*Eleusine coracana* L.) confers tolerance against salinity and drought stress in rice. *BMC Biotechnol.,* 16: 35.

Ranum, P., J.P. Peña-Rosas and M.N. Garcia-Casal. 2014. Global maize production, utilization, and consumption. *Annals of the New York Academy of Sciences,* 1312(1): 105-112.

Redillas, M.C.F.R., J.S. Jeong, Y.S. Kim, H. Jung, S.W. Bang, Y.D. Choi, S.H. Ha, C. Reuzeau and J.K. Kim. 2012. The overexpression of OsNAC9 alters the root architecture of rice plants enhancing drought resistance and grain yield under field conditions. *Plant Biotechnol. J.,* 10: 792-805.

Rushton, P.J., M.T. Bokowiec, S. Han, H. Zhang, J.F. Brannock, X. Chen, T.W. Laudeman and M.P. Timko. 2008. Tobacco Transcription Factors: Novel Insights into Transcriptional Regulation in the Solanaceae. *Plant Physiol.,* 147: 280-295.

Saad, A.S.I., X. Li, H.P. Li, T. Huang, C.S. Gao, M.W. Guo, W. Cheng, G.Y. Zhao and Y.C. Liao. 2013. A rice stress-responsive NAC gene enhances tolerance of transgenic wheat to drought and salt stresses. *Plant Sci.,* 203-204: 33-40.

Sablowski, R.W.M. and E.M. Meyerowitz. 1998. A homolog of NO APICAL MERISTEM is an immediate target of the floral homeotic genes APETALA3/PISTILLATA. *Cell*., 92: 93-103.

Shafiq, S., N.A. Akram and M. Ashraf. 2019. Assessment of physio-biochemical indicators for drought tolerance in different cultivars of maize (*Zea mays* L.). *Pak. J. Bot.,* 51(4): 1241-1247.

Shen, J., B. Lv, L. Luo, J. He, C. Mao, D. Xi and F. Ming. 2017. The NAC-type transcription factor OsNAC2 regulates ABA-dependent genes and abiotic stress tolerance in rice. *Sci. Rep.,* 7: 40641.

Shen, Q., L. Fu, F. Dai, L. Jiang, G. Zhang and D. Wu. 2016. Multi-omics analysis reveals molecular mechanisms of shoot adaption to salt stress in Tibetan wild barley. *BMC Genomics,* 17(1): 889.

Singh, D. and A. Laxmi. 2015. Transcriptional regulation of drought response: a tortuous network of transcriptional factors. *Front. Plant Sci.,* 6: 1-11.

Smékalová, V., A. Doskočilová, G. Komis and J. Šamaj. 2014. Crosstalk between secondary messengers, hormones and MAPK modules during abiotic stress signalling in plants. *Biotechnol. Adv.,* 32(1): 2-11.

Song, S.Y., Y. Chen, J. Chen, X.Y. Dai and W.H. Zhang. 2011. Physiological mechanisms underlying OsNAC5-dependent tolerance of rice plants to abiotic stress. *Planta,* 234: 331-345.

Souer, E., A. Van Houwelingen, D. Kloos, J. Mol and R. Koes. 1996. The no apical Meristem gene of petunia is required for pattern formation in embryos and flowers and is expressed at meristem and primordia boundaries. *Cell*, 85: 159-170.

Tak, H., S. Negi and T.R. Ganapathi 2016. Banana NAC transcription factor MusaNAC042 is positively associated with drought and salinity tolerance. *Protoplasma,* 254: 803-816.

Takasaki, H., K. Maruyama, S. Kidokoro, Y. Ito, Y. Fujita, K. Shinozaki, K. Yamaguchi-Shinozaki and K. Nakashima. 2010. The abiotic stress-responsive NAC-type transcription factor OsNAC5 regulates stress-inducible genes and stress tolerance in rice. *Mol. Genet. Genomics.,* 284: 173-183.

Tang, Y., M. Liu, S. Gao, Z. Zhang, X. Zhao, C. Zhao, F. Zhang and X. Chen. 2012. Molecular characterization of novel TaNAC genes in wheat and overexpression of TaNAC2a confers drought tolerance in tobacco. *Physiol. Plant.,* 144: 210-224.

Umezawa, T., M. Fujita, Y. Fujita, K. Yamaguchi-Shinozaki and K. Shinozaki. 2006. Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. *Curr. Opin. Biotechnol.,* 17: 113-122.

Wang, C., P. Deng, L. Chen, X. Wang, H. Ma, W. Hu, N. Yao, Y. Feng, R. Chai, G. Yang and G. He. 2013. A Wheat WRKY Transcription Factor TaWRKY10 Confers Tolerance to Multiple Abiotic Stresses in Transgenic Tobacco. *PloS one,* 8(6): e65120.

Wang, X., J. Zeng, Y. Li, X. Rong, J. Sun, T. Sun, M. Li, L. Wang, Y. Feng, R. Chai, M. Chen, J. Chang, K. Li, G. Yang and G. He. 2015. Expression of TaWRKY44, a wheat WRKY gene, in transgenic tobacco confers multiple abiotic stress tolerances. *Front. Plant Sci.,* 6: 1-14.

Whittaker, A, A. Bochicchio, C. Vazzana, G. Lindsey and J. Farrant. 2001. Changes in leaf hexokinase activity and metabolite levels in response to drying in the desiccation-tolerant species Sporobolus stapfianus and Xerophyta viscosa. *J. Exp. Bot.,* 52: 961-9.

Wu, A., A.D. Allu, P. Garapati, H. Siddiqui, H. Dortay, M.I. Zanor, M.A. Asensi-Fabado, S. Munne-Bosch, C. Antonio, T. Tohge, A.R. Fernie, K. Kaufmann, G.P. Xue, B. Mueller-Roeber and S. Balazadeh. 2012. JUNGBRUNNEN1, a Reactive Oxygen Species-Responsive NAC Transcription Factor, Regulates Longevity in Arabidopsis. *Plant Cell Online.,* 24: 482-506.

Wu, Y., Z. Deng, J. Lai, Y. Zhang, C. Yang, B. Yin, Q. Zhao, L. Zhang, Y. Li and Q. Xie. 2009. Dual function of Arabidopsis ATAF1 in abiotic and biotic stress responses. *Cell Res.,* 15: 15.

Xie, Q., G. Frugis, D. Colgan and N.H. Chua. 2000. Arabidopsis NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. *Genes Dev.,* 14: 3024-3036.

Xu, Z., Gongbuzhaxi, C. Wang, F. Xue, H. Zhang and W. Ji. 2015. Wheat NAC transcription factor TaNAC29 is involved in response to salt stress. *Plant Physiol. Biochem.,* 96: 356-363.

Xu, Z.Y., S.Y. Kim, D.Y. Hyeon, D.H. Kim, T. Dong, Y. Park, J.B. Jin, S.H. Joo, S.K. Kim, J.C. Hong, D. Hwang and I. Hwang. 2013. The Arabidopsis NAC Transcription Factor ANAC096 Cooperates with bZIP-Type Transcription Factors in Dehydration and Osmotic Stress Responses. *Plant Cell,* 25: 4708-4724.

Xue, G.P., H.M. Way, T. Richardson, J. Drenth, P.A. Joyce and C.L. McIntyre. 2011. Overexpression of TaNAC69 leads to enhanced transcript levels of stress up-regulated genes and dehydration tolerance in bread wheat. *Mol. Plant.,* 4: 697-712.

Yang, S., B. Vanderbeld, J. Wan and Y. Huang. 2010. Narrowing down the targets: Towards successful genetic engineering of drought-tolerant crops. *Mol. Plant.,* 3(3): 469-490.

Yang, S.D., P.J. Seo, H.K. Yoon and C.M. Park. 2011. The *Arabidopsis* NAC Transcription Factor VNI2 Integrates Abscisic Acid Signals into Leaf Senescence via the *COR* / *RD* Genes. *Plant Cell,* 23: 2155-2168.

You, J., L. Zhang, B. Song, X. Qi and Z. Chan. 2015. Systematic analysis and identification of stress-responsive genes of the NAC gene family in Brachypodium distachyon. *PLoS One.,* 10: 1-20.

Zhang, L.L., L.L. Zhang, C. Xia, G. Zhao, J. Jia and X. Kong. 2016. The Novel Wheat Transcription Factor TaNAC47 Enhances Multiple Abiotic Stress Tolerances in Transgenic Plants. *Front. Plant Sci.,* 6: 1174.

Zhong, R., E.A. Richardson and Z.H. Ye. 2007. Two NAC domain transcription factors, SND1 and NST1, function redundantly in regulation of secondary wall synthesis in fibers of Arabidopsis. *Planta,* 225: 1603-1611.

Zhong, R., T. Demura and Z.H. Ye. 2006. SND1, a NAC Domain Transcription Factor, Is a Key Regulator of Secondary Wall Synthesis in Fibers of Arabidopsis. *Plant Cell Online*., 18: 3158-3170.

Zhou, J., N. Ahmed, Y. Cheng, C. Qin, P. Chen, C. Zhang and L. Zhang. 2019. Effect of inoculation of strains with acc deaminase isolated from vermicompost on seed germination and some physiological attributes in maize (*Zea mays* L.) Exposed to salt stress. *Pak. J. Bot.,* 51(4): 1169-1177.

Zhu, M., G. Chen, S. Zhou, Y. Tu, Y. Wang, T. Dong and Z. Hu. 2014. A new tomato NAC (NAM ATAF1/2/CUC2) transcription factor, SlNAC4, functions as a positive regulator of fruit ripening and carotenoid accumulation. *Plant Cell Physiol.,* 55: 119-135.

(Received for publication 19 July 2018)