

# NAC Transcription Factors in Drought and Salinity Tolerance



Xuan Lan Thi Hoang, Yen-Nhi Hoang Nguyen, Nguyen Phuong Thao and Lam-Son Phan Tran

**Abstract** Water deficit and salinity are known as the top serious abiotic stresses affecting quality and productivity of many crop plants. Expanding knowledge in plant science and advances in plant biotechnology have brought more practical opportunities to improve plant tolerance capacity toward drought and/or salinity conditions in a number of major crops. Compared with manipulating a functional gene, manipulation of a regulatory gene like transcription factor-encoding gene could alter more plant characteristics, and these changes together can protect plants against either single or multiple stresses. The purpose of this chapter is to update the readers with the latest reports on the involvement of NAC (NAM, ATAF1/2, and CUC2) transcription factors in drought- and salinity-responsive regulation. Although most studies have focused on laboratory-scale experiments, the present findings are expected to provide an overview about the progress on our understanding of NAC transcription factors-associated mechanisms underlying plant responses to drought and salinity, as well as to evaluate the potential applications of the recently characterized NAC transcription factors in development of transgenic plants with improved tolerance to water scarcity and/or salinity.

## Abbreviations

ABA	Abscisic acid
ARF	Auxin response factor
AP2/ERF	APETALA2/ethylene-responsive element binding factor

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X. L. T. Hoang (✉) · Y.-N. H. Nguyen · N. P. Thao  
Applied Biotechnology for Crop Development, School of Biotechnology, International University,  
Ho Chi Minh City 700000, Vietnam  
e-mail: [htlxuan@hcmiu.edu.vn](mailto:htlxuan@hcmiu.edu.vn)

Vietnam National University, Ho Chi Minh City 700000, Vietnam

L.-S. P. Tran  
Stress Adaptation Research Unit, RIKEN Center for Sustainable Resource Science, 1-7-22,  
Suehiro-cho, Tsurumi, Yokohama 230-0045, Japan  
e-mail: [son.tran@riken.jp](mailto:son.tran@riken.jp)

bZIP	Basic leucine zipper
LEA	Late embryogenesis abundant proteins
MDA	Malondialdehyde
MeJA	Methyl jasmonate
MYB	Myeloblastosis
NAC	NAM, ATAF1/2, and CUC2
NACBS	NAC binding site
NACRS	NAC recognition sequence
ROS	Reactive oxygen species
RT-qPCR	Reverse transcription-quantitative polymerase chain reaction
TF	Transcription factor

## 1 Introduction

A major challenge for current agricultural production is the inability to keep in pace with the increasing food demand to satisfy the growing world population (Tester and Langridge 2010). Dramatic losses of cultivable land and severe soil destruction are a few reasons among the causes of this inability (Golldack et al. 2011). What is more, abiotic and biotic stresses can also decrease crop yields and quality with various extents (Zhu 2016). Among the abiotic stressors, drought and salinity are the two common ones that have negative effects on most aspects of plant physiology and metabolism (de Oliveira et al. 2013). These stressors prevent plants to get sufficient water accommodating their needs while triggering the over-production of intracellular reactive oxygen species (ROS), which in turn results in oxidative stress to plants. The non-manageable high levels of ROS production cause cell damage (Miller et al. 2010), cellular homeostasis disruption (Fleury et al. 2010; Shabala and Munns 2012), and cellular activity impediment (Anjum et al. 2011). Therefore, the consequences of either drought or salinity are abnormal plant growth and development, lower biomass accumulation, lower plant productivity, and even plant death in severe cases (de Oliveira et al. 2013).

In general, plant stress response is the outcome of a three-stage process, beginning with perception of the external stimulus (e.g., the stressor), followed by the transduction of the signal from membrane receptors toward the nucleus through different mediators, and finally the regulation of gene expression activities to improve stress adaptation/acclimatization (Hoang et al. 2014). Under drought or salinity conditions, plant defense activities include minimizing homeostasis fluctuation, preventing cellular injuries, and redirecting plant growth and developmental processes (Roychoudhury et al. 2013). Among the phytohormones, abscisic acid (ABA) has been identified as a key signaling molecule playing important role in regulating expression of many osmotic stress-responsive genes, which can be functional or regulatory genes (Finkelstein 2013; Yoshida et al. 2014). Examples for several stress-responsive components that are under ABA regulation are LEA (late embryogenesis abundant) proteins,

kinases, phosphatases, water transporters like aquaporins, detoxifying enzymes like peroxidase, catalase and superoxide dismutase, and transcription factors (TFs) like those belonging to basic leucine zipper (bZIP), APETALA2/ethylene-responsive element binding factor (AP2/ERF), myeloblastosis (MYB) and NAM/ATAF1/2/CUC2 (NAC) TF families (Fujita et al. 2011; Nakashima et al. 2012; Hoang et al. 2014; Vishwakarma et al. 2017). In the signal transduction cascades, TFs are usually the terminal signal transducer. Their capability to interact with promoter regions to synchronously regulate the expression of downstream genes makes them the key components determining the successful responses or adaptations of plants to the ever-changing environmental conditions (Liang et al. 2016; Hoang et al. 2017). Members of various TF families have been identified and characterized for their mode of action in mediating plant responses to environmental stresses. In this chapter, we focus on the TFs belonging to the NAC family, which have been identified to play key regulatory functions in plant responses to drought and/or salinity. Some of the latest findings on stresses-related functions of NAC TFs are summarized in Table 1.

## 2 NAC TFs—An Overview

NACs are unique plant TFs. In addition to analyses of NAC TFs in common model and crop plant species (Thao et al. 2013), whole genome search for genes encoding NAC TFs including membrane-bound NACs has been recently performed in *Camellia sinensis* (tea, 45 genes found) (Wang et al. 2016b), *Raphanus sativus* (radish, at least 98 found) (Karanja et al. 2017), *Triticum turgidum* (durum wheat, 168 found) (Saidi et al. 2017); *Cucumis sativus* (cucumber, 82 found) (Zhang et al. 2017), *Sesamum indicum* (sesame, 87 found) (Zhang et al. 2018), *Pyrus pyrifolia* (Asian pear, 185 found) (Ahmad et al. 2018), groundnut (*Arachis* species, 76 found) (Suchithra et al. 2018) and *Fragaria vesca* (wild strawberry, 112 found) (Moyano et al. 2018). Moreover, specific NAC expression patterns in various plant organs in responses to various stresses have also been comprehensively examined by using RNA-sequencing and reverse transcription-quantitative polymerase chain reaction (RT-qPCR) in a number of plants species, such as soybean (*Glycine max*) (Le et al. 2011), chickpea (*Cicer arietinum*) (Ha et al. 2014), Asian pear (Ahmad et al. 2018), and rice (*Oryza sativa*) (Chung et al. 2018).

Structurally, the NAC proteins consist of a highly conserved N-terminal DNA-binding domain and a variable C-terminal regulatory domain (Tran et al. 2010). The binding specificity of different NAC TFs might be defined by the sequences flanking the core site in the promoters of target genes (Shao et al. 2015). The NAC TFs bind to a consensus sequence called NAC recognition sequence (NACRS) or NACRS-like sequence containing the “CACG” core-DNA binding motif in the promoters of downstream genes (Shao et al. 2015). Additionally, other *cis*-elements containing the core sequence “CGT(G/A)”, “GCTT” or “(T/A)NN(C/T)(T/C/G)TNNNNNNA(A/C)GN(A/C/T)(A/T)” are also reported as NAC-binding sites (NACBS) (Zhong et al. 2010; Puranik et al. 2012; Olins et al.

**Table 1** The NAC (NAM/ATAF1/2/CUC2) transcription factors that were reported to be involved in plant responses to drought and/or salinity

TF origin	Gene name	Responses to stresses (in wild-type plants)	Genetically modified plant system	Characterized TF functions using transgenic/mutant plants	References
<b><i>In planta</i> studies using homologous plant systems</b>					
<i>Arabidopsis</i>	<i>ANAC032</i>	Salinity, mannitol	<i>Arabidopsis</i>	Promotes senescence and accumulation of H <sub>2</sub> O <sub>2</sub> , regulates expression of senescence-related genes like <i>AtNYE1</i> , <i>SAG113</i> and <i>SAUR36/SAG201</i>	Mahmood et al. (2016)
Rice	<i>OsNAC6</i>	Drought, salinity	Rice	Positive regulator of drought response: increases root system development and yield, regulates genes related to nicotianamine production, glycosylation, membrane and transportation activities, and carbohydrate metabolism	Lee et al. (2017), Chung et al. (2018)
	<i>ONAC066</i>	Polyethylene glycol, salinity, H <sub>2</sub> O <sub>2</sub>	Rice	Positive regulator of drought response: decreases water loss rate, increases proline and soluble sugar contents	Yuan et al. (2019)
	<i>ONAC022</i>	Drought, salinity	Rice	Positive regulator of responses to drought and salinity: lowers Na <sup>+</sup> accumulation, reduces transpiration, increases proline and soluble sugar contents	Hong et al. (2016)
	<i>OsNAC2</i>	Drought, salinity	Rice	Negative regulator of responses to drought and salinity: decreases yield, down-regulates <i>LEA3</i> , GTPase-related genes (e.g. <i>RAB21</i> , <i>RAB16C</i> and <i>RAB16D</i> ) and kinase-related genes (e.g. <i>SAPK1</i> and <i>SAPK10</i> )	Shen et al. (2017)

(continued)

**Table 1** (continued)

TF origin	Gene name	Responses to stresses (in wild-type plants)	Genetically modified plant system	Characterized TF functions using transgenic/mutant plants	References
Tomato	<i>SINAC11</i>	Dehydration, salinity, cold, heat	Tomato	Positive regulator of responses to drought and salinity: <i>SINAC11</i> -RNAi tomato plants became less tolerant, had lower chlorophyll content and germination rate, higher malondialdehyde (MDA)	Wang et al. (2017)
	<i>SIJUB1</i>	Dehydration, polyethylene glycol, salinity, H <sub>2</sub> O <sub>2</sub>	Tomato	Positive regulator of drought response: reduces cellular damage, regulates expression of <i>DREBs</i> and <i>DELTA</i>	Thirumalaikumar et al. (2018)
Banana	<i>MusaNAC042</i>	Drought, salinity	Banana	Positive regulator of responses to drought and salinity: increases chlorophyll content, lowers MDA content	Tak et al. (2017)
Poplar	<i>PeNAC045</i>	Drought, salinity	Poplar	Negative regulator of responses to drought and salinity: inhibits root growth, lowers photosynthesis	Lu et al. (2018)

***In planta* studies using heterologous plant systems**

Tomato	<i>SINAC35</i>	Dehydration, salinity	Tobacco	Positive regulator of responses to drought and salinity: promotes root development, reduces reactive oxygen species (ROS) levels, increases anti-oxidative enzyme activities	Wang et al. (2016a)
Trifoliolate orange	<i>PtrNAC72</i>	Drought, cold	Tobacco	Negative regulator of drought response: increases water loss rate, levels of MDA and electrolyte leakage (EL)	Wu et al. (2016)

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**Table 1** (continued)

TF origin	Gene name	Responses to stresses (in wild-type plants)	Genetically modified plant system	Characterized TF functions using transgenic/mutant plants	References
<i>Suaeda liaotungensis</i>	<i>SINAC8</i>	Drought, salinity	<i>Arabidopsis</i>	Positive regulator of responses to drought and salinity: increases proline content, chlorophyll fluorescence and activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), lowers MDA and EL; up-regulates <i>RD20</i> , <i>GSTF6</i> , <i>COR47</i> , <i>RD29A</i> , <i>RD29B</i> and <i>NYC1</i>	Wu et al. (2018)
Pumpkin	<i>CmNAC1</i>	Salinity, dehydration, cold, H <sub>2</sub> O <sub>2</sub>	<i>Arabidopsis</i>	Positive regulator of responses to multiple stresses: promotes root growth; reduces Na <sup>+</sup> accumulation in leaves under salinity, increases survival rate under drought	Cao et al. (2017)
Chickpea	<i>CarNAC4</i>	Drought, salinity, H <sub>2</sub> O <sub>2</sub>	<i>Arabidopsis</i>	Positive regulator of responses to drought and salinity: increases proline content, lowers water loss rate and MDA content	Yu et al. (2016)
Maize	<i>ZmNAC55</i>	Drought, salinity	<i>Arabidopsis</i>	Positive regulator of drought response: lowers water loss rate, up-regulates ABA-responsive genes (e.g. <i>RD17</i> , <i>PP2CA</i> , <i>RAB18</i> and <i>NCED3</i> )	Mao et al. (2016)
Foxtail millet	<i>SiNAC110</i>	Dehydration, salinity	<i>Arabidopsis</i>	Positive regulator of responses to dehydration and salinity: increases germination rate, root growth, plant fresh and dry weights	Xie et al. (2017)

(continued)

**Table 1** (continued)

TF origin	Gene name	Responses to stresses (in wild-type plants)	Genetically modified plant system	Characterized TF functions using transgenic/mutant plants	References
Pearl millet	<i>PgNAC21</i>	Salinity	<i>Arabidopsis</i>	Positive regulator of response to salinity: increases germination rate, fresh weight and root length, up-regulates <i>GSTF6</i> , <i>RD20</i> and <i>COR47</i>	Shinde et al. (2019)
Finger millet	<i>EcNAC67</i>	Salinity	Rice	Positive regulator of responses to drought and salinity: increases root length, shoot biomass, relative water content, post-stress recovery rate and yield	Rahman et al. (2016)
<i>Miscanthus lutarioriparius</i>	<i>MINAC10</i>	Drought, salinity	<i>Arabidopsis</i>	Positive regulator of responses to drought and salinity: increases proline content and anti-oxidative enzyme activities, reduces ROS and MDA accumulation	He et al. (2019)
	<i>MINAC9</i>	Drought, salinity, cold	<i>Arabidopsis</i>	Positive regulator of responses to drought and salinity: increases activities of SOD, CAT and POD, lowers MDA accumulation	Zhao et al. (2016)
Cotton	<i>GhSNAC3</i>	Drought, salinity	Tobacco	Positive regulator of responses to drought and salinity: increases primary root length and fresh weight	Liu et al. (2018)
Soybean	<i>GmNAC085</i>	Dehydration	<i>Arabidopsis</i>	Positive regulator of drought response: increases activities of SOD, CAT and peroxidase ascorbate, enhances glutathione-dependent detoxifications of ROS and methylglyoxal, reduces water loss rate and biomass reduction rate	Nguyen et al. (2018a, b)

(continued)

**Table 1** (continued)

TF origin	Gene name	Responses to stresses (in wild-type plants)	Genetically modified plant system	Characterized TF functions using transgenic/mutant plants	References
Poplar	<i>PeNAC034</i>	Drought, salinity	<i>Arabidopsis</i>	Negative regulator of responses to drought and salinity; inhibits root development, down-regulates <i>COR47</i> , <i>RD29B</i> , <i>ERD11</i> , <i>RD22</i> and <i>DREB2A</i>	Lu et al. (2018)
	<i>PeNAC036</i>	Drought, salinity	<i>Arabidopsis</i>	Positive regulator of responses to drought and salinity; promotes root development, up-regulates <i>COR47</i> , <i>RD29B</i> , <i>ERD11</i> , <i>RD22</i> and <i>DREB2A</i>	

The table listed only those reported from 2016

2018). Therefore, NAC TFs can potentially regulate a large number of downstream genes. Many studies have documented divergent functions of NACs associated with various biological processes in plant growth and development (Zhong et al. 2010; Bollhöner et al. 2012; Nakashima et al. 2012; Hussey et al. 2013) as well as plant responses to a wide range of biotic and abiotic stresses (Puranik et al. 2012; Nuruz-zaman et al. 2013; Thu et al. 2014). These features make NAC TF family a highly potential resource of valuable candidates for genetic engineering.

### 3 Drought- and Salinity-Related NAC TF Characterization Using Homologous Plant Systems

Early attempts in identification and functional analyses of stress-related NAC genes, such as *ANAC019*, *ANAC055* and *ANAC072* (Tran et al. 2004), and *AtNAC2* (*ANAC092/ORE1*) (He et al. 2005), have been conducted in the model plant *Arabidopsis thaliana*. Following the identification of the regulatory role of *AtNAC2* in regulating ethylene-/auxin-dependent pathways, root development (He et al. 2005) and leaf senescence (Balazadeh et al. 2010) in response to salinity in *Arabidopsis*, ectopic expression of *AtNAC2* gene in groundnut (*A. hypogaea*) could provide the transgenic plants with an enhanced drought and salinity resistance as evidenced by significantly higher chlorophyll stability index, lower rate of water loss, better growth and yield characteristics (Patil et al. 2014). *ANAC032* was a more recently characterized *Arabidopsis* NAC member. The expression analysis of *ANAC032* showed that this gene was induced by various abiotic stresses, including salinity (Mahmood et al. 2016). Also from this study, overexpression of *ANAC032* was reported to promote



senescence process in responses to osmotic stress and salinity conditions and accumulate higher level of hydrogen peroxide ( $H_2O_2$ ) in the transgenic lines. Meanwhile, the chimeric-repression *Arabidopsis* lines of *ANAC032* displayed a more tolerant phenotype to salinity and lower accumulation of  $H_2O_2$  compared with the wild-type plants.

In rice, the model monocot crop plant, many NAC members have been shown to play a part in plant responses to drought and salinity, such as *SNAC1* (Stress-responsive NAC1) (Hu et al. 2006), *OsNAC10* (Jeong et al. 2010), *OsNAC9* (Redillas et al. 2012), *ENAC1* (early NAC-domain protein induced by abiotic stress 1) (Sun et al. 2012) and *SNAC3* (Fang et al. 2015). Among these, *SNAC1*, a drought-inducible NAC gene found to express mainly in rice guard cells, has been well documented to be an excellent candidate for genetic manipulation (Hu et al. 2006). The employment of *SNAC1* overexpression was reported to enhance the drought and salinity adaptations in various crop plants, including rice (Hu et al. 2006), wheat (*T. aestivum*) (Saad et al. 2013), cotton (*Gossypium hirsutum*) (Liu et al. 2014) and ramie (*Boehmeria nivea*) (An et al. 2015). Recently, Hong et al. (2016) found that the presence of overexpressed *ONAC022* in the transformed rice could equip the plants with a better drought and salinity resistance abilities, at least due to lowered  $Na^+$  accumulation in the root and shoot tissues compared with that in the non-transgenic plants. Likewise, molecular analysis of *ONAC066* illustrated that this gene was induced significantly by polyethylene glycol and NaCl, and *ONAC066*-overexpressing transgenic rice showed higher tolerance to drought as indicated by decreased ROS accumulation and water loss rate, and increased proline and soluble sugar contents (Yuan et al. 2019). Examination on *OsNAC6* function also revealed that this rice NAC TF is a positive regulator of plant response to drought. Overexpression of *OsNAC6* specifically in the root tissues could enlarge the stele and aerenchyma cells in the root tissues of the transgenic rice, and thus enable the plants to be more resistant to water deficit under both laboratory and field testing conditions (Lee et al. 2017). Analyzing the gene expression to identify its downstream genes revealed that *OsNAC6* is likely the direct regulator of certain genes associating with membrane-transporter proteins, vesicle, phytohormones and carbohydrate metabolism (Lee et al. 2017; Chung et al. 2018). In contrast, the rice *OsNAC2* was demonstrated to function as a negative regulator. *OsNAC2* expression was up-regulated by osmotic stress conditions; however, its overexpression led to reduced resistance and yields of the transgenic rice plants under drought and salinity (Shen et al. 2017).

In tomato (*Solanum lycopersicum*), *SINAC11* was recently found to function as a stress-responsive TF. Molecular analyses revealed that *SINAC11* had significantly increased expression patterns by various abiotic stresses, including dehydration (Wang et al. 2017). *SINAC11*-silencing tomato plants became more vulnerable under drought as well as salinity conditions, as they displayed lower photosynthetic performance and higher stress-induced levels of cellular injuries than their non-transgenic counterparts (Wang et al. 2017). Similarly silencing of another drought-inducible tomato NAC gene (the so-called *Jungbrunnen1* (*JUB1*)) made the tomato plants more susceptible to drought with escalation of ion leakage and  $H_2O_2$  levels, and the reduction in transcriptional levels of drought-responsive *DREB* and *DELLA*

genes (Thirumalaikumar et al. 2018). From a study in banana (*Musa acuminata*), Tak et al. (2017) reported that the expression of *MusaNAC042* gene was positively associated with banana resistance to salinity and drought. According to their results, the *MusaNAC042*-overexpressing transgenic banana displayed higher contents of proline and chlorophyll, and lower level of malondialdehyde (MDA) compared with the control plants under the stress conditions.

#### 4 Drought- and Salinity-Related NAC TF Characterization Using Heterologous Plant Systems

It is well noted that the employment of NACs from other plants species could produce similar levels of enhanced tolerance as observed in the tested transgenic plant systems. Tomato *SINAC35* appeared to be a positive regulator of plant responses to drought and salinity as ectopic expression of *SINAC35* in the transgenic tobacco stimulated the root development under these stress conditions, suggestively due to modulating *auxin response factor (ARF)* expression, and thus the auxin signaling pathway (Wang et al. 2016a). In chickpea, ectopic expression of *CarNAC4* in *Arabidopsis* could increase the tolerance of transgenic plants to both drought and salinity, indicating that *CarNAC4* functions as a positive mediator (Yu et al. 2016). Meanwhile, in maize (*Zea mays*), the expression analysis of *ZmNAC55* showed that this gene was induced by drought and high salinity (Mao et al. 2016). Ectopic expression of *ZmNAC55* in *Arabidopsis* demonstrated its involvement in the ABA-mediated pathway as the seed germination was more sensitive to ABA treatment and a number of ABA-responsive genes were shown to be up-regulated. The positive regulatory role of *ZmNAC55* in lowering transpiration rate under drought conditions was also elucidated (Mao et al. 2016). In a recent study, functional characterization of the dehydration-inducible *GmNAC085* isolated from soybean revealed the positive role of this TF in drought response by controlling the ROS removal-related activities. Specifically, ectopic expression of this gene in *Arabidopsis* led to improved drought tolerance of the transgenic lines, which was associated with mitigation of drought-induced oxidative stress through enhanced activities of antioxidant enzymes like superoxide dismutase, catalase and ascorbate peroxidase (Nguyen et al. 2018a), and glutathione-dependent detoxifications of ROS and methylglyoxal (Nguyen et al. 2018b).

In *Miscanthus lutarioriparius*, *MINAC10* was indicated to have important role in enhancing drought and salinity tolerance of the transgenic *Arabidopsis* plants ectopically expressing *MINAC10* by increasing proline content and antioxidant enzyme activities, and reducing ROS and MDA accumulations (He et al. 2019). Searching for stress-related *NAC* genes in upland cotton revealed that *GhNAC18* gene was up-regulated by drought (Evans et al. 2016). Additionally, phylogenetic analysis revealed that *GhNAC18* was a close relative of the wheat *TaNAC67*, which was known as a positive regulator of *Arabidopsis* plant responses to drought and salinity (Mao et al.

2014; Evans et al. 2016). A more recent report indicated that transgenic tobacco plants ectopically expressing *GhSNAC3* showed enhanced tolerance by promoting primary root elongation under drought and salinity conditions (Liu et al. 2018). Another stress-related NAC confirmed by *in planta* study was the finger millet (*Eleusine coracana*) *EcNAC67* (Rahman et al. 2016). Genetic analysis of *EcNAC67* showed that this gene is involved in regulating plant responses to drought and high salinity. Transgenic rice ectopically expressing *EcNAC67* was reported to have longer root, higher relative water content, better shoot biomass and post-stress recovery as well as higher yields under these adverse conditions (Rahman et al. 2016). In trifoliate orange (*Poncirus trifoliata*), *PtrNAC72* was defined as a repressor for drought tolerance as ectopic expression of *PtrNAC72* in tobacco induced higher levels of water loss, electrolyte leakage and MDA in the transgenic lines under drought or dehydration treatment (Wu et al. 2016). In pumpkin (*Cucurbita moschata*), *CmNAC1* was indicated as a potential candidate with positive role in root growth and salinity stress tolerance in transgenic *Arabidopsis* plants (Cao et al. 2017). In foxtail millet (*Setaria italica*), *SiNAC110* was illustrated to improve the tolerance of *SiNAC110*-expressing transgenic *Arabidopsis* to drought and high salinity as evidenced by their better seed germination rate, root growth, fresh and dry weights of the whole plant by controlling various cell regulation pathways (Xie et al. 2017). In pearl millet (*Pennisetum glaucum*), *PgNAC21* was revealed as a potential candidate in improving salinity stress tolerance. The transgenic *Arabidopsis* plants ectopically expressing *PgNAC21* exhibited several better physiological and phenotypic traits, including enhanced seed germination, plant fresh weight and root length (Shinde et al. 2019). It is also worth noting that a number of studies on stress-responsive NAC genes have been conducted using perennial trees in order to learn how plants deal with a long duration of drought or salinity. For example, an investigation in a poplar species living in desert (e.g., *Populus euphratica* Olivier) showed that the expression of the three genes *PeNAC034*, *36*, and *45* was differentially altered in responses to drought and salinity (Lu et al. 2018). Detailed studies of these three genes using overexpression and mutant systems (*Arabidopsis* for *PeNAC034* and *36*, poplar for *PeNAC045*) demonstrated that *PeNAC036* acts as a positive regulator, whereas *PeNAC034* and *PeNAC045* function as negative regulators of plant responses to drought and salinity (Lu et al. 2018).

## 5 Conclusions and Perspectives

Within recent decades, a large number of NAC TFs from various plant species have been reported to be involved in mediating plant responses to drought and salinity. Their important roles and diverse mode of actions under abiotic stress have been demonstrated. Functional characterization studies revealed many of them acting as positive regulators, which can be used for genetic engineering. However, it has to be admitted that the majority of *in planta* studies only have attempted to resolve the acting mechanisms of the TFs in regulating plant responses to environmental stresses, while values of agronomic traits in genetically modified plants, especially

testing the plant performance and yield production under field conditions, have not been much achieved. Therefore, to more practically employ NAC TFs in generating elite crop cultivars with improved stress tolerance and minimized yield losses, more application-oriented research should be designed and conducted.

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