



## Role of NAC Gene Transcription Factors in the Regulation of Abiotic Stress Responses in Cereal Crops

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### ABSTRACT

NAC transcriptional regulators are plant-specific proteins involved in various developmental stages and tissues. The NAC acronym is derived from three genes initially discovered to contain a specific domain called the NAC domain: NAM (No apical Meristem), ATAF, and CUC (cup-shaped cotyledon). This family represents one of the largest groups of transcriptional regulators in plants, and their members have been implicated in the regulation of transcriptional reprogramming during plant stress responses. This review aims to explore the regulation of stress-responsive NAC genes involved in conferring resistance to various stresses. It provides a comprehensive summary of the current knowledge regarding NAC gene transcription factors' response to abiotic stresses, including drought, cold, salinity, osmotic stress, temperature stress, nutrient efficiency, and phytohormone signaling pathways. The review highlights the crucial role of NAC genes in abiotic stress tolerance, and their overexpression has the potential to enhance stress tolerance through biotechnological approaches.

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### INTRODUCTION

Cereal crops have been predominantly used as staple food around the globe since the time immemorial and are widely cultivated and produce annually, 1800 to 1900 million tonnes of food grains worldwide. Cereals also represent 60% of the calories and proteins consumed by human beings, they include a variety of crops including rice, maize, wheat, oats, barley, rye, etc., but excluding millets like pearl millet and other minor millets. However, efforts in meeting the food requirements on sustainable basis for ever increasing population are seriously being hampered due to biotic and abiotic stresses. Abiotic factors (like drought, salinity and temperature), are most important accounting for about 70% reductions in yield of the cereal crops (Mueen *et al.*, 2013).

Abiotic stresses trigger a wide range of plant responses, from the alteration of gene expression and cellular metabolism to changes in plant growth and development of crop yields.

Transcription factors (TFs) and cis-elements function in the promoter region of different stress-related genes, and the over expression or suppression of these genes may improve the plant's tolerance to both types of stress. The NAC acronym is derived from three genes that were initially discovered to contain a particular domain (the NAC domain): NAM (for no apical meristem), ATAF, and CUC2 (for cup-shaped cotyledon) (Aida *et al.*, 1997). The NAC genes constitute one of the largest families of plant-specific TFs and are present in a wide range of species. Extensive investigation aided by the availability of several complete plant genomic sequences has identified 117 NAC genes in Arabidopsis, 151 in rice, 79 in grape, 26 in citrus, 163 in poplar, and 152 each in soybean and tobacco (Hu *et al.*, 2012). Numerous NAC genes are involved in the response of plants to abiotic stresses, such as drought, salinity, cold, and submergence (Nuruzzaman *et al.*, 2012). Genes in the NAC family have been shown to regulate a

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wide range of developmental processes, including seed development (Sperotto *et al.*, 2009), embryo development, shoot apical meristem formation, fiber development, leaf senescence and cell division (Kim *et al.*, 2009). Additionally, expression of the *AtNAC1* gene is induced by lateral root development, which in turn is regulated by the hormone auxin (Xie *et al.*, 2000).

NAC are plant specific transcriptional regulators that are in various developmental stages and tissues. Transcription factors (TFs) are proteins that control the rate of transcription of genetic information from DNA to RNA by binding a specific DNA sequences, (TFs) turn on/off the transcription of the appropriate genes in order to make sure that, the genetic information are expressed in the right cell at the right time, throughout the life of the cell of an organism (Jin *et al.*, 2014). In many plants that adapt to abiotic stresses, a set of genes are transcriptionally activated, leading to the accumulation of new proteins in seeds and vegetative organs and greater tolerance to drought (Baker *et al.*, 1988). Abiotic stresses is the most important constraint reducing cereal yield in rain fed areas, the understanding of molecular basis of genes tolerance to drought stress will help to breed elite cereals cultivars under lower water requirements (Nguyen *et al.*, 2010).

### STRUCTURAL FEATURES OF THE NAC PROTEINS

The N-terminus of NAC proteins is a highly homologous region containing the DNA-binding NAC domain. NAC proteins commonly possess a conserved NAC domain at the N-terminus that consists of approximately 150–160 amino acids and is divided into five sub-domains (A to E) (Ooka *et al.*, 2003). The function of the NAC domain has been associated with nuclear localization, DNA binding, and the formation of homodimers or heterodimers with other NAC domain-containing proteins (Olsen *et al.*, 2005). The structure of the DNA-binding NAC domain of Arabidopsis ANAC019 has been solved by X-ray crystallography and the functional dimer formed

by the NAC domain was identified in the structural analysis.

The NAC domain structure of a rice stress-responsive NAC protein (SNAC1; STRESS-RESPONSIVE NAC 1) was also reported (Chen *et al.*, 2011) and shares structural similarity with the NAC domain from Arabidopsis ANAC019. In contrast, the C-terminal regions of NAC proteins are highly divergent (Ooka *et al.*, 2003) and are responsible for the observed regulatory differences between the transcriptional activation activity of NAC proteins (Jensen *et al.*, 2010). The divergent C-terminal region of these proteins generally operates as a functional domain, acting as a transcriptional activator or repressor (Kim *et al.*, 2007). The C-terminal region is large and possesses protein-binding activity.

### DROUGHT, SALINITY, COLD, AND OSMOTIC STRESS

Abiotic stress triggers a wide range of plant responses, from the alteration of gene expression and cellular metabolism to changes in plant growth, development, and crop yield. Thus, understanding the complex mechanism of drought and salinity tolerance is important for crop production. Interestingly, many NAC genes have been shown to be involved in plant responses to drought and salinity stress. In transgenic rice, the Os01g66120/OsNAC2/6 and Os11g03300/OsNAC10 genes were found to enhance drought and salt tolerance and Os03g60080/SNAC1 increased grain yield under drought stress (Nakashima *et al.*, 2009). Udupa *et al.* (1999) reported that comparative gene expression profiling is an efficient way to identify the pathways and genes regulating a stress response under different stress conditions. The Arabidopsis NAC gene ANAC092 demonstrates an intricate overlap of ANAC092-mediated gene regulatory networks during salt-promoted senescence and seed maturation (Balazadeh *et al.*, 2010). Lan *et al.* (2005) found that a large portion of the genes regulated by dehydration are also up-regulated by fertilization; indeed, pollen is a major site of variations in the expression levels for many genes (Czechowski *et al.*, 2005). Related conclusions have been drawn from

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analyses based on promoter-GUS fusions of cold-inducible Os01g66120/SNAC2/6, Os11g03300/OsNAC10, RD29A, COR15A, KIN1, and COR6.6 in rice and arabidopsis genes that are regulated during plant development (root, leaf, and pollen) under both stress (drought and cold) and non-stress conditions (Jeong *et al.*, 2010). You *et al.* (2013) reported that OsOAT is a direct target of the stress-responsive NAC transcription factor SNAC2, and OsOAT over expression in rice resulted in significantly enhanced drought and osmotic stress tolerance. Plants over expressing GmNAC085 show enhanced drought tolerance whereas the over expression of GmNAC11 led to increased sensitivity to salt and mannitol stresses (Hao *et al.*, 2011). Microarray profiling of the roots and leaves of drought-treated rice revealed the induction of 17 NAC genes by severe or mild drought treatment (Nuruzzaman *et al.*, 2012). SiNAC is also simultaneously induced by dehydration, salinity, ethephon, and methyl jasmonate treatments (Puranik *et al.*, 2011). Similarly, the expression of TaNAC2 and EcNAC1 were strongly induced by NaCl and drought stresses in transgenic tobacco plants (Tang *et al.*, 2012).

#### PHYTOHORMONE SIGNALING PATHWAY

The expression of members of the OsNAC gene family under hormone treatment requires extensive cross-talk between the response pathways, and it is likely that substantial physiological connections exist between NAC protein production and phytohormone treatment. Phytohormones are involved in influencing signaling responses by acting in conjunction with or in opposition to each other to maintain cellular homeostasis (Miller *et al.*, 2008). NAC gene such as ANAC019 and ANAC055 are involved in both ABA- and JA-mediated regulation (Jensen *et al.*, 2010). A number of NAC genes (e.g., AtNAC2 and OsNAC5) in plants are affected by auxin, ethylene and ABA (Sperotto *et al.*, 2009). In Arabidopsis, NAC TF NTL8 regulates GA3-mediated salt signaling in seed germination (Kim *et al.*, 2009). ABA plays a major role in mediating the adaptation of a plant to stress, and this

hormone can stimulate root growth in plants that need to increase their ability to extract water from the soil. OsNAC5/ONAC009/ONAC071 and OsNAC6 are homologs that are induced by abiotic stress, such as drought and high salinity, and ABA (Takasaki *et al.*, 2010). AtNAC1 and AtNAC2 are induced by auxin and ABA, respectively, and AtNAC1 mediates auxin signaling to promote lateral root development in arabidopsis (He *et al.*, 2005). ABA signaling induces the expression of genes encoding proteins that protect the cells in vegetative tissues from damage when they become dehydrated. These well-known ABA responses are less sensitive to ABA in NPX1-overexpressing plants (Kim *et al.*, 2009).

The expression of the RD26 gene is induced by drought and also ABA and high salinity (Fujita *et al.*, 2004). NAC TFs regulate many target genes by binding to the CATGTG motif in the promoter region of the target gene to activate transcription in the response to drought stress, a transcriptional regulatory system that is known as a regulon (Nakashima *et al.*, 2007). ABA is produced under conditions of drought stress and plays a crucial role in drought tolerance in plants (Shinozaki *et al.*, 2013). In addition to NAC and other regulons, OsDREB2 responds to dehydration in rice; the dehydration-responsive element binding protein 1 (DREB1)/C-repeat-binding factor (CBF) and DREB2 regulators function in ABA-independent gene expression, whereas the ABA-responsive element (ABRE)-binding protein (AREB)/ABRE-binding factor (ABF) regulon functions in ABA-dependent gene expression. ABA-activated OSRK1 protein kinases phosphorylate and activate AREB/ABF-type proteins in rice (Chae *et al.*, 2007). Both ABA-independent and ABA-dependent signal transduction pathways convert the initial stress signal into cellular responses (Hu *et al.*, 2006). The expression of OsNAC6 is induced by ABA and abiotic stresses, including cold, drought, and high salinity (Nakashima *et al.*, 2007). Together, these data provide evidence that different NAC genes play differential roles in the specific responses to different phytohormone treatments. Thus, gene expression profiles under

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both biotic and abiotic stresses to determine the vital role of NAC genes in plant growth and stress responses and the identification of target genes for TFs involved in stress responses are important.

### TEMPERATURE STRESS

In crop production, high or low temperature acts as a major negative factor limiting crop production. Indeed, tremendous work has been performed in the past two decades to reveal the complex molecular mechanism in the plant responses to extreme temperature, and there is increasing evidence that NAC proteins are involved in responses to both heat and cold stresses. For example, an NAC TF gene (OsNAC063) in rice roots responds to a combination of high-temperature stress (Yokotani *et al.*, 2009). Another example is that transgenic arabidopsis plants over expressing ANAC042 show increased tolerance to heat stress when compared to the wild-type plants (Shahnejat *et al.*, 2012). Moreover, the over expression of ZmNAC1 enhanced the tolerance to drought and low-temperature stress compared to the control (Lu *et al.*, 2012). The expression of OsNAC10, SNAC2/OsNAC6, TaNAC4, NTL6, TaNAC2a, TaNAC4a, TaNAC6, TaNAC7, TaNAC13, and TaNTL5 is induced by low temperature in plants (Tang *et al.*, 2012). Yoo *et al.* (2007) reported that the phenotype resulting from the over expression of an NAC-domain protein gene (At2g02450) is related to the control of flowering time and cold responses. The importance of NAC proteins in plant development, transcription regulation, and regulatory pathways involving protein-protein interactions is being increasingly recognized. Taken together, NAC proteins function in plants adaption to temperature variations through the transcriptional reprogramming of downstream stress-related genes.

### NUTRIENT-USE EFFICIENCY

Various nutrient elements are required for the normal growth and development of plants. Boron (B) is an essential micronutrient for higher plants, but excessive amounts of B inhibit growth (B toxicity). As the optimal range of B

concentration in tissues is narrow, B toxicity occurs in many plants at levels only slightly above that required for normal growth (Mengel *et al.*, 2001). The Os04g0477300 gene encodes an NAC-like TF, and the function of the transcript is abolished in B toxicity-tolerant cultivars. Transgenic plants in which the expression of Os04g0477300 is abolished by RNA interference acquire a tolerance to B toxicity (Ochiai *et al.*, 2011). In a transcriptome analysis using Arabidopsis plants under B toxicity, nine genes encoding multidrug and toxic compound extrusion transporters, a zinc-finger family TF, a heat-shock protein-like protein, NAC-like TF, and unknown proteins were induced though the functions of these proteins are not yet known.

A sufficient supply of inorganic phosphate (Pi) is vital to plants, and the low bioavailability of Pi in soils is often a limitation to growth and development. Consequently, plants have evolved a range of regulatory mechanisms to adapt to phosphorus-starvation to optimize the uptake and assimilation of Pi. Recently, significant progress has been achieved in elucidating these mechanisms, revealing that the coordinated expression of a large number of genes is important for many of these adaptations with a focus on the Arabidopsis transcriptome (Kasajima *et al.*, 2007). Nilsson *et al.* (2010) reported common findings that indicate new groups of putative regulators, including the NAC, MYB, and WRKY families. With a number of new discoveries of regulatory elements, a complex regulatory network is emerging. They evaluate the contribution of the regulatory elements to P-responses and present a model comprising the factors directly or indirectly involved in transcriptional regulation. Thus, NAC genes appear to respond to several aspects of nutrient excess and deficiency-induced stresses, implicating their diverse functions in these signaling pathways.

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## CONCLUSION

In many plants that adapt to abiotic stresses, a set of genes are transcriptionally activated, leading to the accumulation of new proteins in seeds and vegetative organs and greater tolerance to drought (Baker *et al.*, 1988).

The worldwide production of cereal crops is frequently impacted by abiotic stresses such as drought, salinity, cold and osmotic stress of cereal crops in breeding programs, while NAC TFs transcription factors have been demonstrated to play essential role in regulating abiotic stresses and has been proposed as important arbitrators of various plant processes and have been subjected to intensive investigations, especially in well-known model plants.

## RECOMMENDATION

The responses to the environment are specialized through the diversification of the structure of stress-response regulators of NAC TFs, which are involved in stress-response pathways via binding motifs (CATGTG) in their target genes. Thus, the components and regulatory structure of specific pathways must be delimited for an understanding of the evolutionary genetics of environmental stress responses much better.

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