

NAC TRANSCRIPTION FACTORS ROLE IN VARIOUS BIOTIC AND ABIOTIC STRESSES

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ABSTRACT

NAC transcription factors are considered as main family of transcriptional regulators in plants. NAC gene family members play significant contribution in regulating transcriptional reprogramming in plants related to plant stress response. These proteins possess highly conserved DNA binding domains and play a diverse functions in several plants. NAC gene is related to several stress factors including biotic and abiotic factors. NAC transcription factors controls several interrelated processes and their protein products can function as negative or positive regulators in many cellular processes. These regulatory functions are also controlled by NAC proteins such as auto and cross regulation. These regulatory proteins are regarded as a central regulator for the interaction of phyto hormones in various stress signaling pathways. This review highlights the role of NAC transcription factors in modulating gene expression and their role in various biotic and abiotic stress tolerance in plants.

Key Words:

Transcription factor, *NAC*, stress response, biotic stress, abiotic stress.

INTRODUCTION

Transcription factors (TFs) and their interaction with promoter regulatory sequences are necessary to regulate gene expression in plants and animals. There are about 2500 genes in

Arabidopsis genome encode for various transcription factors (1). There are large numbers of transcription factors related to regulation of genes in plants. The main families include NAC {No apical meristem (NAM), Arabidopsis transcription activation factor (ATAF), Cup-shaped cotyledon (CUC)}. Various isoforms of NAC family have been recognized and categorized in model plants like *Arabidopsis* (2,3), crops like *Oryza sativa*(4,5)soybean (*Glycinemax*) (6,7,8) and wheat (*Triticum species*) (9) and in certain typical tree classes like *Populus trichocarpa* (10) and citrus (*Citrus sp.*) (11,12).Extensive research supported by the study of genomic sequences of various plants identified 117 NAC genes in *Arabidopsis*, 79 in *Vitis vinifera*, 151 in rice, 163 in *Populus trichocarpa* and 152 in tobacco and soybean, making them a major group of TF's in plants.

Structural Characteristics

Typically, NAC proteins consist of two motifs located at both N and C- termini. N-terminal motif is conserved and comprise of 150 amino acids while C-terminal transcription regulatory (TR) regions are highly variable (Figure 1 (i))(13). Along with these structural motifs, some uncommon modifications in NAC assembly has also been observed [Fig 1 (ii–vi)]. One domain of NAC codes for 1 NAC protein (14,15) and two tandem repeated NAC domains(16). SOG1 genes are extended by the N-terminal motif (16,17) and are made up of NAC and Vascular plant One-Zinc finger proteins, which includes DNA binding (db), zinc finger, C-terminal NAC region and N-terminal TR region(13,16).

NAC Domains

NAC domain is recognized by its DNA binding ability and is divided into 5 subdomains (A-E, Fig 1). Each subdomain is highly conserved and have diverse properties related to structure. Functional analysis reveal that subdomain A is involve in the synthesis of functional dimer, subdomain B and E are distinct and shows the functional variation in NAC genes in different plants. Subdomain C contains positively charged amino acids and is highly conserved domain while subdomain D has ability to bind the DNA (16,18). According to a report,15 variants (A-O) of NAC protein have been identified in rice that are different in their structures based on their amino acid domains(19).Type A - E contains five motifs that are present in standard NACDNA binding domain, and type F - O consists of a distinct motif conformation in ' NAC-like ' proteins. Due to structural variations in various motifs, these proteins shows possibly diverse functions and have unidentified specificities.

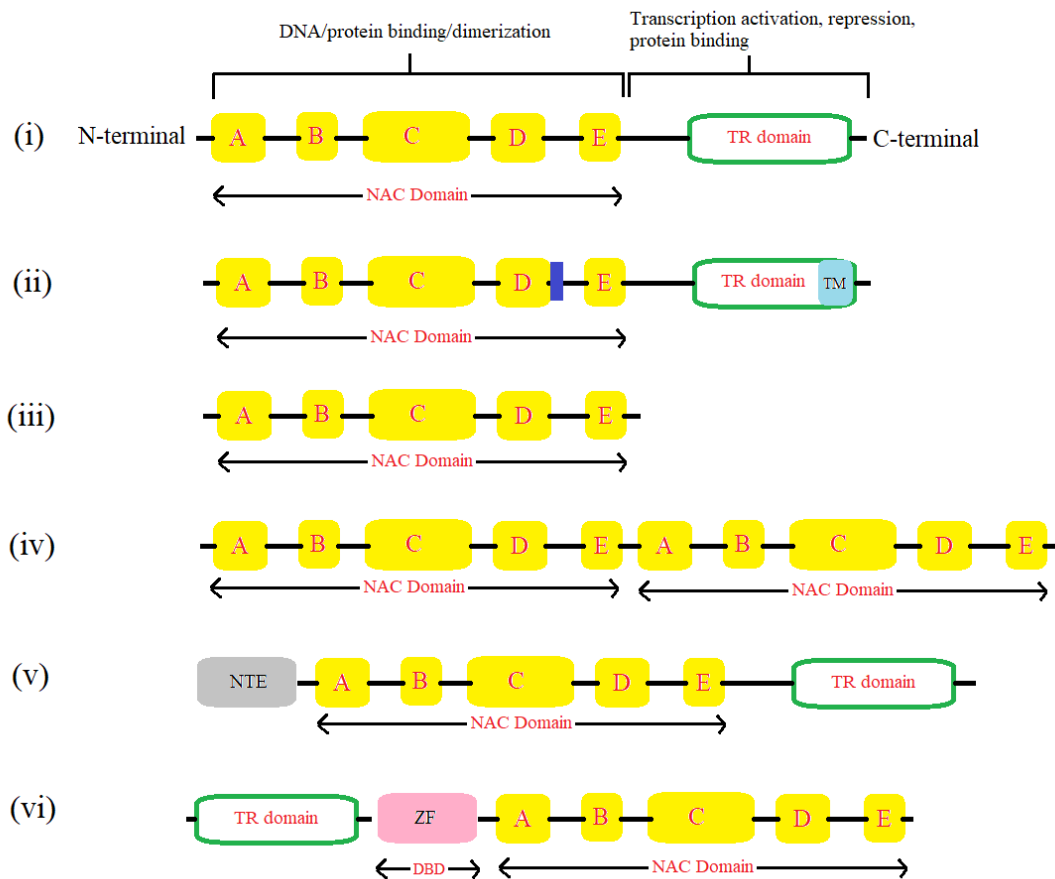


Figure 1: Structure and regulation of NAC proteins: Diagrammatic description demonstrate (i) a standard NAC protein at the N-region with an extremely conserved NAC motif that is sub-divided into five conserved subdomains (A – E). This zone contains DNA binding ability that follows protein binding and dimerization. C-terminal is diverse and supports an activator or repressor-functional transcriptional regulatory (TR) dominant domain which may often carry protein binding activity. (ii) In various circumstances a trans membrane motif (TM) in the C-terminal is found in the NAC domain and a blue shaded negative control domain. Changes in standard NAC proteins contain those programming (iii) the NAC motifs, (iv) two tandemly repeated NAC motifs, (v) a N-terminal extended area (NTE) moving towards NAC domain (vi) Vascular plant One-Zinc finger proteins (VOZ), where the NAC region is located at the C terminal and the TR region is located at the N-end with a zinc finger motif (ZF) working as a conserved DNA binding domain.

X-ray Crystal Structure

After studying crystallography and *in silico* investigation in *Setaria italica* *SiNAC*, *Arabidopsis thaliana* *AtNAC019* and in *Oryza sativa* stress-responsive *NAC1* (*SNAC1*) proteins, it is revealed that these transcription factors are comprised of a twisted β -sheet ($\beta 1-6/7$) that are antiparallel, used for DNA binding and positioned between an N-extreme of α turn and a short helix (18,20). Amino acid composition of DB domain reveals that 19 to Serine183, $\beta 4$ to 6 zone D – E, Lysine123 and Lysine126, $\beta 4-5$ zone D and Lysine79, Arginine85 and Arginine88,

b1–2 zone C (13,18). In DNA binding affinities, Lysine79 and Arginine85 are distinct so that they are exchangeable residues whereas Arginine is 88 is retained in all NAC proteins (16).

In fact, the protein binding action of NAC transcription factors regulates the fate and role of the NAC protein(13,24). These interactions are important between plants and pathogens as well as in stress tolerance (21). The D subunit is extremely hydrophobic negative regulatory domain (NRD) in some NAC proteins, which limits transcriptional activity [Fig 1 (ii)]. Even other TF families such as DNA-binding with one finger (Dof), WRKY and AP2/DRE can be suppressed by the NRD-like sequences (8).

NAC Transcription Regulatory Regions (TRRs)

Structural analysis reveal that transcription regulatory regions (TRRs) are usually located at C-terminal (Figure 1 (i)). These regions can stimulate (22) or suppress the rate of transcription of various genes (23,24). The Transcriptional regulatory regions have conserved amino acid sequences that are abundant in Ser-Thr, Pro-Glu repeats or acidic amino acids. It is identified that ten TRR regions are present in NAC proteins in rice(19). It has shown that these regions are similar for subgroups of NAC subdivision but there is variation across different subdivision(14). Thus, TTRs shows modifications according to specific roles of NAC proteins in different plants. Due to the less complicated sequences, transcription regulatory region contains a high level of intrinsic dysfunction (ID) and it does not contain any stable 3D structure (16, 25). This flexibility facilitates the formation of model proteins by interacting them with different target proteins for structural and TF functional analysis. The TTR's of some NAC proteins have the ability to bind several proteins with it (25). The pattern of alpha-helical trans membrane (TM) found in some NAC proteins (named NTLs) is responsible for anchoring the cell membrane or ER membrane (Fig 1(ii)) (26).

NAC Function and Expression

NAC transcription factors have role in a number of processes, including plant development(13), secondary wall synthesis (27) maturity (25,28), biotic (13,29) and abiotic stresses(30,31). The genome-wide transcriptome study and bioinformatics study shows 20 to 25 percent of NAC genes working at least in one stress response or another (19,32).

Diversity of molecular mechanisms regulates the localization of eukaryotic transcription factors, one of which by allowing nuclear localization of the transcription factor. Precursor cleavage have two mechanisms , one is regulated intramembrane proteolysis and other is regulated ubiquitin—proteasome dependent processing (95). Some transmembrane prediction programs predict that TIP consist of transmembrane region. Nucleocytoplasmic shuttling guided by nuclear localization signals (NLSs) (96) and nuclear export signals (NESs) (97) can also regulate the activity of transcription factors. Five NAC proteins have been shown to localize to the nucleus (3, 94). Several NAC sequences are predicted to contain an NLS when analysed by PredictNLS (98) and PSORT (99). Though, no single conserved NLS site is visible with these prediction tools. Using the NES prediction tool NetNES (100), some NAC sequences are predicted to have an NES in a region of the NAC domain that is rich in conserved hydrophobic amino acids e-g residues 43-51 in AC019.

Box 1. Regulation of nuclear localization of NAC transcription factors

NAC Regulation and Activity

Transcriptional regulation

Transcription factors have role in regulation level of transcription (Figure 2). Studies of leaf to protoplasmic evolution indicated that multi-potential advances includes triggering multiple silent *NAC* genes (33,34). Other example is the *NACnrp1*, endosperm, controlled by genomic imprinting .Patrilineal transferred alleles are therefore suppressed, permitting maternal regulation of the production of endosperm (35).

Post-transcriptional regulation

miRNAs are small RNAs with a regulatory association to the targeted mRNAs which allow the targets to be repressed after transcription (36). Computer analysis shows that transcription factors implicated in the determination of cell-fate are the primary objectives of miRNAs in plants(37). Initially, a subclass of *Arabidopsis* *NAC* mRNAs including *CUC1*, *CUC2*, *Nac1*, *5g07680* mRNA's and *CUC1* and *CUC2* were estimated as a targeting component of the miR164 gene family, and their additional miR164 sites were blocked (38). However, the miR164 expression resistant for *CUC1* and *CUC2* mRNA's and miR164 overexpression showed that miR164 is compulsory in order to regulate the *CUC1* and *CUC2* correctly. miR164-directed *NAC1*, At5g07680 and At5g61430 were identified by representing the significance of post-transcription regulation of different *NAC* genes (39, 40). Another regulation point at the RNA level is the long term phloem transference of the *NAC* mRNA *CmNACP* in *Cucurbita maxima*. A pathway that integrates physiological processing in the

distant organs with development in meristematic tissue, *CmNACP* mRNA is shifted from plant body to shooting apex (41) (Figure 2).

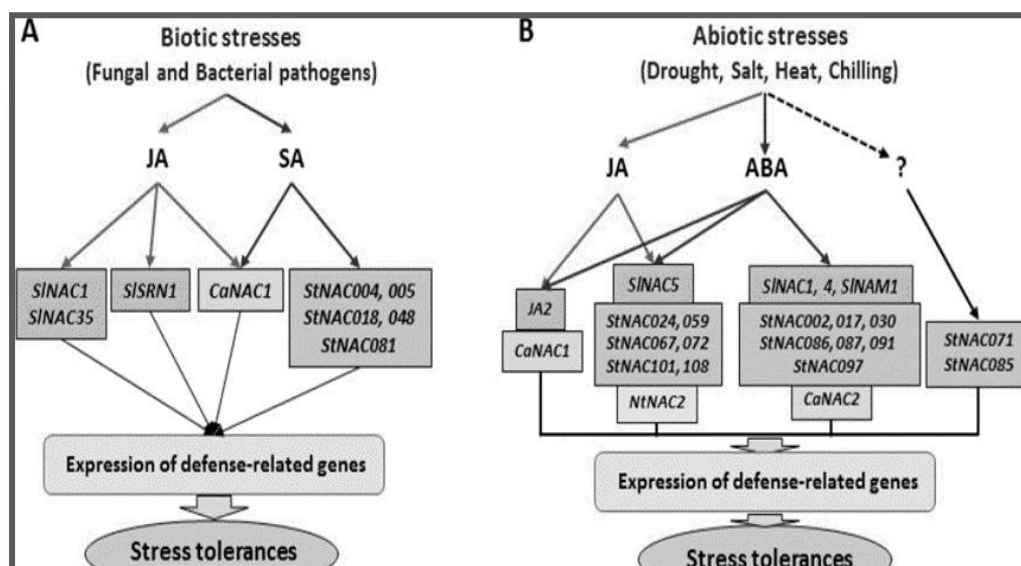


Figure 2: The function of NAC TF's in the signaling pathway for herbivores / biotic and abiotic.

Post-translational regulation

Post translation regulation by ubiquitine-mediated protein degradation is also used to control the *NAC* activity (42). The degradation of proteins is targeted by the poly ubiquitination of the proteins E1, E2 and E3 by sequential action (43). *SINAT5* (*Arabidopsis thaliana* 5 SINA) was established as an interaction partner of *NAC1* with a yeast 2 hybrid screening(42). *SINAT5* has been demonstrated to act as an E3 protein ligase and targeted for *NAC1* in order to degrade proteasomes (Fig. 2).

NAC Function in Abiotic Stress

During stress response in plants, the NAC TF's acts as an important component of various signaling pathways. Various plants have moderately a huge range of NAC transcription factors and shows their diverse and unknown functions under various environmental stimuli, and finding their role in abiotic stress is considered a major challenge. In recent studies, NAC protein may have been indirectly involved in abiotic stresses from transcription modeling and functional studies. In general, the facts presented here summarizes the role of various NAC

transcription factors in controlling transcriptional reprogramming to plant's abiotic stresses (Fig. 3, Table 1).

During plant stress response, NAC proteins act as an important component in the diverse signaling pathways. Various plants have relatively large numbers of NAC transcription factors and their diverse and unknown roles in complex environmental stimuli and finding their role in abiotic stress is considered as big challenge. The strict modulation of *NAC* in plant stress conditions participate in the development of diverse signaling networks and prospective candidates for stress tolerance are the significant function of *NAC* for herbal abiotic stress responses.

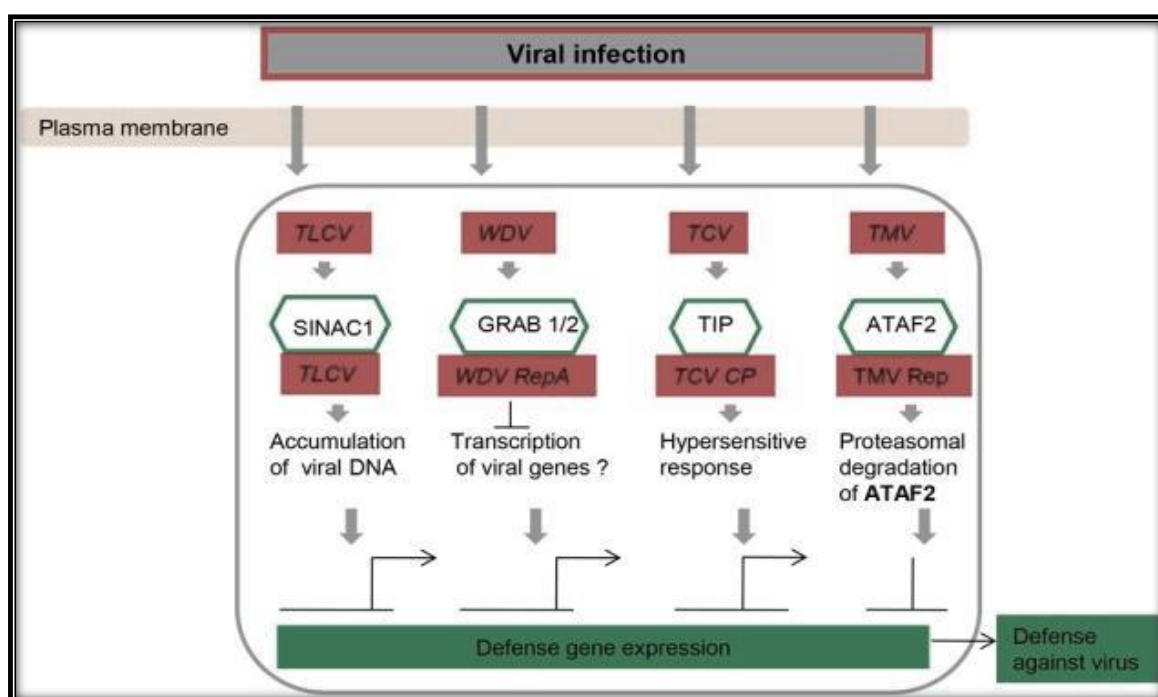


Figure 3: Factors of NAC transcription are key components of gene expression transcriptional regulation in viral diseases.

Abbreviations: WDV (wheat dwarf geminivirus), TCV(turnip crinkle virus); TIP (TCV-interacting protein). TLCV (tomato leaf curl virus), TMV (tobacco mosaic virus).

Abiotic stresses cause a wide spread range of reaction in plants, from changes in the expression of gene and cell metabolism to modifications in plant progress, reproduction and yield performance. Desiccation and NaCl sensitivity in transgenic *Oryza Sativa* has been increased after overexpression of *Os01g66120/OsNAC2/6* and *Os11g03300/OsNAC-10* (44, 45). It has

also reported that overexpression of *Os03G60080/SNAC1* resulted in improvement of plant growth from 21 to 34 % under low water availability (4). Comparative expression studies of genes has been identified as an effective method to recognize stress response pathways and genes under different stress conditions (46). A complete relationship has been identified in the *Arabidopsis* NAC gene *ANAC092* (47), during seed maturation and salt-promoting senescence. Various studies revealed that a significant part of dehydration-regulated genes are also fertilization-regulated; pollen is still the main spot of variability in rates of expression among various genes (48, 49). Subsequent studies focused on the GUS-promoter fusions for rice and *Arabidopsis* of cold inducing genes (*Os01g66120/SNAC2/6*, *Os11g03300/OsNAC10* and *RD29A*, *COR15A* and *COR6.6*) were found to upregulated under both stressed and under stressed conditions and during the plant growth (45, 50). *OsOAT* is a target gene of NAC stress inducing transcription factor. *SNAC2* and *OsOAT* overexpression in *Oryza Sativa* has contributed to a significantly increased during drought and osmotic stress conditions (51). Plants that over-express *GmNAC085* show increased tolerance to drought (7) while *GmNAC11* overexpression has directed to increase NaCl and mannitol stress tolerance (8). The activation of 17 NAC genes under low water potential has been reported by microarray analysis in rice roots (52). Over expression of *SiNAC* from foxtail millet has also resulted during various stresses including drought, high salt concentration, and methyl jasmonate (20). Transgenic Tobacco (*Nicotiana tabacum*) transformed with various NAC genes including *DgNAC1*, *TaNAC2a* and *EcNAC1* isolated from bacteria and higher plants showed tolerance to salinity and drought conditions (53, 54, 55).

NAC Role in Biotic Stress

Various studies regarding NAC transcription factor show the significance of various members of the multigene family in the transcriptional reprogramming of the plant immunized response. The research has been reviewed extensively and will therefore be briefly examined here. Apparently, the NAC TF's are the main elements of different characteristics in the innate immune system, essential defense and complete resistance of a crop. This is an important field of research that has been thoroughly examined and is thus only mentioned shortly here. Apparently, NAC TF's are essential components for many aspects of the endogenous, fundamental and systemic immune system in plants. 4; Table 2) (16, 56, 57). In order to assess function of NAC transcription factors (*ONAC122* and *ONAC131*) in *M. grisea* resistance disease, Sun and

co-workers used VIGS systems (58). Virus-induced gene silencing is a valuable tool for fast genetic feature investigation in plants (59, 60). Virus-induced gene silencing have been established for dicot species, in which the tobacco virus based VIGS vector for *Solanum*, tobacco and the tomato is a most successful model (61). The VIGS vector of barley stripe mosaic virus is used to elucidate the role of several genes in wheat and barley disease resistance (50). Researchers have created a brome mosaic vector based VIGS, which has been shown to be a powerful method to rapidly evaluate the gene function of barley, rice and maize (62, 63).

There are several cases of overexpression or low NAC gene expression influencing plant defence, which have enabled some components of the signal pathway to be resolved (Figures 3, In germinating rice seedlings 19 and 13 genes have been upregulated after RSV and RTSV inflammations at several days of inoculations, respectively (32). Many NAC proteins have been shown to over expressed as a result of attacks by viruses, various fungal elicitor and bacteria that may both increase or decrease the viral growth by interacting with virus-encrypted proteins and increase in NAC expression levels (9,64,65,66). The interaction of NAC proteins with different regulatory network is a consequence of this dual regulation in plant defense. *OsNAC4* is the main positive regulator for hypersensitive plant cell death, with dramatically declining hypersensitive cell mortality as a consequence of non-infectious bacterial strains on *OsNAC4* knock-down line. *OsNAC4* will be transferred to the nucleus according to the phosphorylation after inducing virulent pathogens perceiving signal.

On the other side, the *OsNAC6* overexpression does not result in hypersensitive cell mortality (67), while *OsNAC6* over-sensitive *Oryza sativa* plants has the ability to tolerate blast disease (68). An increased sensitivity of *ATAF2* overexpression against the parasitic infection *Fusarium oxysporum* during proper situations due to pathogenesis associated suppression (69), which contributed to an enhanced vulnerability for pathogenesis-related (PR) genes caused to the non-sterile aggregation of tobacco mosaic viruses (66). The role of NAC transcription factors in several plant-patent association has also been identified in RNA interference and overexpression analysis (67, 70). The role of *ATAF1* and its Barley Homolog *HvNAC6* has also been shown to positively control penetration susceptibility to *Blumeria graminis*.sp. biotrophic fungus RNA studies and over-expression findings. The aim is to reduce resistance for various diseases, including Bacterial, and fungal diseases (56, 57).

Table 1: NAC TF's families involved in abiotic stress-responsive pathways in plants

Species	Genes	Functions	Method	References
<i>O. sativa</i>	<i>OsNAC5/Os11g08210</i>	ABA, salt, cold tolerance, grain filling	Overexpression	(76)
<i>O. sativa</i>	<i>ONAC04/Os11g033005</i>	Drought, salt, cold tolerance	Overexpression	(77)
<i>O. sativa</i>	<i>OsNAC10/Os11g03300</i>	Root, panicle, drought, salt, ABA	Overexpression	(45)
<i>O. sativa</i>	<i>Ostil1</i>	Shoot branching	Overexpression	(101)
<i>O. sativa</i>	<i>SNAC1/Os03g60080</i>	Stomata close, higher seed setting	Overexpression	(4)
<i>O. sativa</i>	<i>SNAC2/OsNAC6/Os01g66120</i>	Salt, drought, disease resistance drought, salinity, cold, wounding, and abscisic acid (ABA) treatment	Overexpression	(50)
<i>O. sativa</i>	<i>RIMI/Os03g02800</i>	JA pathway signaling	Mutant	(78)
<i>O. sativa</i>	<i>Os07g04560, Os10g38834</i>	Root, severe drought	Microarray	(52)
<i>N. tabacum</i>	<i>TaNAC2a</i>	Drought tolerance	Overexpression	(55)
<i>N. tabacum</i>	<i>DgNAC1</i>	ABA, NaCl, drought and cold	Overexpression	(53)
<i>G. max, A. thaliana</i>	<i>GmNAC20, DREB1A/CBF3, KIN2/cor6.6, Cor15A, RD29A/cor78, ARF19, LBD12, AIR1</i>	Salt and freezing tolerance	Overexpression	(8)
<i>A. thaliana</i>	<i>NTL8</i>	Salt tolerance, GA, and ABA pathway	Gene expression	(79)
<i>A. thaliana</i>	<i>ANAC019, ANAC055</i>	Defense disease, JA pathway	Overexpression	(80)
<i>A. thaliana</i>	<i>anac092-1, ANAC083, ANAC041, ANAC054, ANAC084</i>	Positive regulator of seed germination under salinity	Mutant	(47)
<i>A. thaliana</i>	<i>ntl8-1</i>	Positive regulator of seed germination under salinity	Mutant	(79)
<i>A. thaliana</i>	<i>ATAF1, COR47, ERD10, KIN1, RD22, RD29A</i>	Positive regulator of drought tolerance	<i>knockouts (ataf1-1/2)</i>	(81)
<i>T. aestivum</i>	<i>TaNAC2a, TaNAC4a, TaNAC6, TaNAC7, TaNAC13 and TaNTL5</i>	Dehydration, salinity and low temperature	Transgenic	(9)
<i>T. aestivum</i>	<i>TaNAC4</i>	Environmental stimuli, including high salinity, wounding, and low-temperature also induced	Transcription	(82)
<i>G. max</i>	<i>GmNAC11, DREB1A, ERD11, Cor15A, ERF5, RAB18, KAT2</i>	Salt tolerance in soybean transgenic hairy roots	Overexpression	(8)
<i>G. max</i>	<i>GmNAC</i> glycoside hydrolases, defensins and glyoxalase I family proteins	Drought stress	Soybean array GeneChip	(7)

In comparison to *ATAF2*, transcription-activators are *ATAF1* and *HvNAC6* and can potentially control PR repression through imaginary negative regulators. Therefore, it seems that the ATAF subfamily has a retained but not obsolete role in regulating reactions to different pathogenic agents. The immune reaction in pathogen-borne plant species is defined by several

defensive responses that are controlled by the various types of TF such as the production of the significant number of resistance associated genes (71). *Arabidopsis* NAC genes that are stress-responsive, including RD26 relate to JA, a well-known phytohormone that works to improve plant damage (3, 72).

Table 2: Role of NAC transcription factors in stress response

Species	Genes	Functions	Method	References
<i>Oryza (O) sativa</i>	<i>OsNAC4</i>	Inducer of HR cell death upon <i>Acidovorax avenae</i> infection, loss of plasma membrane integrity, nuclear DNA fragmentation	Overexpression/knockdown	(67)
<i>O. sativa</i>	<i>OsNAC6</i> , <i>PR protein 1</i> , <i>Probenazoleinducible proteins (PBZ1s)</i> , <i>DUF26- like Ser/Thr protein kinase</i> , <i>Thioredoxin</i> , <i>Peroxidase</i> , <i>Lipoxygenase</i> ,	Slightly increased tolerance to rice blast disease	Overexpression	(68)
<i>O. sativa</i>	<i>Os02g34970</i> , <i>Os02g38130</i> , <i>Os11g03310</i> , <i>Os11g03370</i> , <i>Os11g05614</i> , <i>Os12g03050</i>	RSV, RTSV infections	Microarray	(32)
<i>O. sativa</i>	<i>OsNAC19</i>	Disease resistance	Infection	(83)
<i>O. sativa</i>	<i>ONAC122</i> and <i>ONAC131</i> bromo mosaic virus (BMV)	Defense responses against <i>Magnaporthe grisea</i>	---	(58)
<i>G. max</i>	<i>GmNAC6</i>	Responses to biotic signals, osmotic stress-induced	Transcription	(84)
<i>S. tuberosum</i>	<i>Stprx2</i> , <i>StNAC</i>	Wounding and pathogen response	Transcriptome	(85)
<i>A. thaliana</i>	<i>ATAF2</i> , <i>NIT2</i>	Defense hormones, pathogen infection	Overexpression/knockout	(86)
<i>A. thaliana</i>	<i>ANAC019</i> , <i>ANAC055</i>	Defense disease, JA pathway	Overexpression	(80)
<i>A. thaliana</i>	<i>ATAF2</i> , <i>PR1</i> , <i>PR2</i> , <i>PDF1.2</i>	OX = Reduced tobacco mosaic virus accumulation, increased pathogenesis-related genes	Overexpression/knockout	(65)
<i>A. thaliana</i>	<i>ATAF2</i> , <i>PR1</i> , <i>PR2</i> , <i>PR4</i> , <i>PRS</i> , <i>PDF1.1</i> , <i>PDF1.2</i>	<i>ATAF2</i> negatively regulates resistance to <i>F. oxysporum</i> , represses pathogenesis-related proteins	Overexpression/knockout	(69)
<i>A. thaliana</i>	<i>ANAC042</i> , <i>P450</i>	Regulation of camalexin biosynthesis, pathogen infection	β - Glucuronidase (GUS)-reporter assays	(87)
<i>A. thaliana</i>	<i>NTL4</i>	ROS under abscisic acid, leaf senescence	Transgenic	(88)
<i>A. thaliana</i>	<i>NTL9</i>	Osmotic stress responses, leaf senescence	Overexpression/knockout	(89)
<i>M. truncatula</i>	<i>MtNAC969</i>	Symbiotic nodule senescence	Overexpression	(90)
<i>A. thaliana</i>	<i>VNI2</i> , <i>OR/RD</i>	Leaf senescence	Transcription	(91)

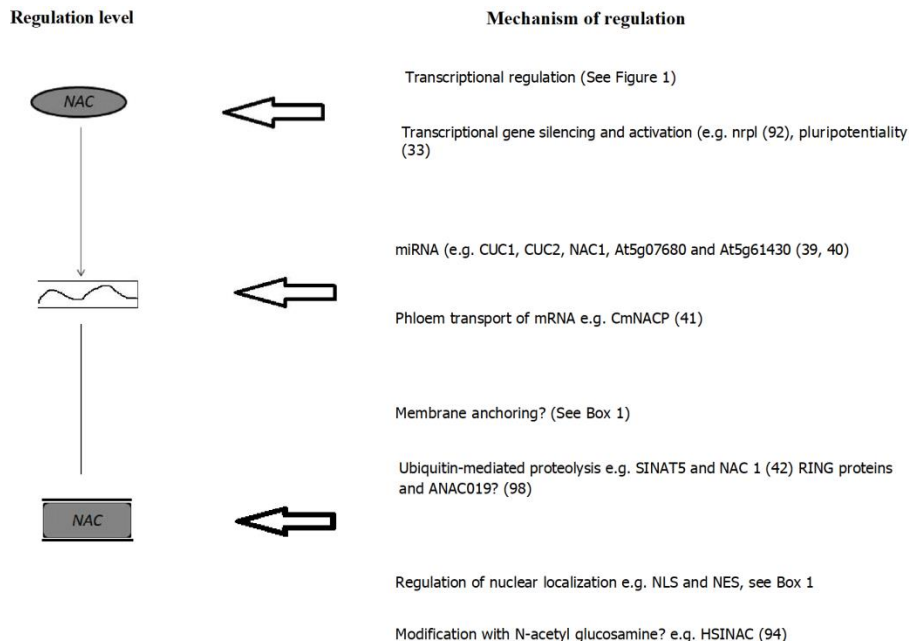


Figure 4. Regulation and location of NAC protein. The regulatory pathway shows the affect of levels of NAC proteins or the position of the protein are described at right side, with the arrows showing the level of DNA, mRNA or protein regulation. Abbreviation: NES (nuclear export signal), HSINAC (HvSPY-interacting NAC), NLS (nuclear localization signal).

Prospects for Future Research

After the identification of the NAC transcription factor family the study of the physiological and molecular roles of NAC proteins was extended further. However, it is still the beginning of this area of research. The occurrence of broad NAC gene families in an extensive variety of plants represents a challenging task in assessing the roles of NAC.

In addition, NAC work would definitely benefit from specific functional review approaches. It is of huge attention to identify targeted NAC genes. One important technique is the overexpression of NAC genes in association with microarray investigation. The TF binding sites of genomic DNA are shown by microarrays in combination with chromatin immunoprecipitation (73). Many knockout mutants are likely to be helpful due to their functional stability. Alternatively, RNA silencing (35) and chimeric repressor silencing (3, 74) could also be used. In functional genomics, further analysis of the molecular roles of these transcription factors is important for a better function of NAC protein.

This will also include a detailed examination of NAC protein interactions with DNA and other proteins. In addition to TCP transcription factors, viral proteins and RING proteins, the study of protein-protein interactions can provide important information on plant defense mechanisms, controlled protein degradation and plant growth. In addition, consideration

should be given to the association of the regulated NAC protein regions with the transcriptional mechanism. The relationship between NAC protein and TCP transcription factors and its ability to dimerize homo and hetero indicates a combinatorial modulation of transcription factor activity (75). So it is obvious that NAC proteins function with other transcription factors at both upstream and downstream regions. Therefore, a major aim of research on NAC proteins is to brighten up their role in networks of transcription factor.

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