

ATAF NAC transcription factors

Regulators of plant stress signaling

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NAC proteins are one of the largest classes of plant-specific transcriptional regulators. Since the first NAC gene NO APICAL MERSITEM (NAM) was identified from petunia in 1996,¹ NAC genes have been implicated in important plant developmental processes like boundary cell formation in shoot apical meristems,^{1,2} secondary cell wall formation,³ and lateral root development.⁴ However, recent work indicates that NAC genes are also important regulators in stress responses. Nowhere is this more evident than the ATAF subgroup of NAC domain transcription factors. This mini-review aims at highlighting recent evidence of the importance of the ATAF-like NAC group in a diverse array of stress related signaling processes.

NAC Domain Family of Transcription Factors

NAC domain proteins share a conserved N-terminal DNA binding domain originally found in four genes (NAM, ATAF1, ATAF2 and CUC2). Subsequent analysis on the genome sequence of plants has indicated that NAC domain proteins are a large family of at least 94 members in Arabidopsis and over 100 members in rice.⁵⁻⁷ The NAC domain consists of five N-terminal conserved domains (designated A–E), with domains A and B exhibiting a net negative charge while the others are positive,¹⁷ (Fig. 1). Domains A, C and D are highly conserved among members from different species while B and E are more diverse.⁶ Crystallographic analysis has shown that the NAC domain consists of a novel twisted β -sheet surrounded by

helical elements and that one face of the NAC domain is rich in positive charges that could be involved in DNA binding.⁸ The DNA binding ability of NAC proteins was first demonstrated by the activation of the cauliflower mosaic virus 35S promoter by ATAF1 and ATAF2 and the core consensus binding sequence has been determined to be CGT[G/A].⁹ Binding sequence determinants are located on subdomains D and E.^{4,10}

The C terminal region of several NAC proteins have been experimentally shown to function as a transcriptional activation region (TAR).^{4,10-14} Motif analysis by Ooka et al.⁶ showed at least 13 common TAR motifs and that in general TARs were conserved in parallel with NAC domain structures. A common feature of the TAR is a bias towards simple amino acid repeats and regions rich in serine and threonine, proline and glutamine, or acidic residues characteristic of transcriptional activation regions in eukaryotes.^{2,10,13,15-18} NAC proteins have been found to be localized to the nucleus, as expected for a transcriptional regulator,^{4,11,14-16,18-23} but the targeting signals responsible are largely unknown.

NAC expression is controlled at multiple levels that hint at the complex nature of the interactions in which they are involved. Knowledge of the direct regulation of NAC genes by transcription factors is currently limited, but canonical sequences of well characterized transcription factors are present in most NAC promoters.^{5,14} Studies on the transition from leaf cells to protoplasts have shown activation of several silent NAC genes, indicating that some NACs may be regulated by changes

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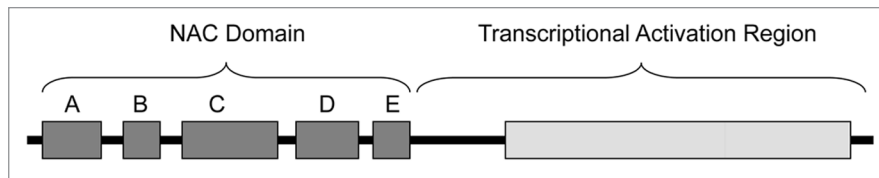


Figure 1. The generalized structure of a NAC domain protein, containing five N-terminal sub-domains that comprise the conserved NAC-domain (indicated with the letters A–E), and the C-terminal functions as a transcriptional activation region.

in chromatin structure.²⁴ A subset of NAC mRNAs are controlled post-transcriptionally by microRNAs.^{25,26} The activity of other NACs is post-transcriptionally modulated either by proteolytic processing and release from a membrane-bound state for subsequent nuclear import,²⁷ by binding of co-factors like calmodulin,²⁸ or by post-translational modification with N-acetylglucosamine.²¹ Ubiquitination-mediated proteolysis also plays an important role in regulating the stability of the NAC1 and ANAC019 factors.²⁹

NAC proteins form homo- and heterodimers^{4,8,9,13,30} via the NAC domain, although the C-terminal regions can also play some role.¹³ The NAC domain can also interact with non NAC proteins; both the TURNIP CRINKLE VIRUS-INTERACTING (ANAC109)³¹ and wheat GEMINIVIRUS REP A-BINDING¹⁷ proteins interact with viral proteins to impair viral replication. In contrast the tomato SINAC1 protein that was isolated on its ability to interact with geminivirus replication enhancer proteins, is thought to enhance the replication of the *Tomato leaf curl virus*.¹⁸ These protein-protein interactions add another level of complexity to NAC-domain regulatory functions.

Phylogenetic analysis of the NAC domains from known NAC family proteins and putative Arabidopsis and rice NACs have separated them into 18 subgroups based on the conservation of the NAC domain in conjunction with the C-terminal TAR.⁶

ATAF NAC Subgroup

The ATAF subgroup of NAC proteins contains proteins with highly conserved B and E domains and a motif designated (v) in the TAR.⁶ This group consist of 4 genes in Arabidopsis, at least 8 in rapeseed

(*Brassica napus*)¹³ two in rice⁶ and representatives from tomato (*Solanum lycopersicum*), cayenne pepper (*Capsicum annuum*),³² sugarcane (*Saccharum officinarum*),³³ soybean (*Glycine max*),¹¹ barley (*Hordeum vulgare*)¹⁵ and cotton (*Gossypium hirsutum* L.).³⁴

ATAF1 and ATAF2 from Arabidopsis were some of the first described NAC members. The sequences of these genes were first deposited in Genbank in 1993 (Hirst H, University of Vienna) and were named because of their ability to activate the cauliflower mosaic virus 35S promoter in yeast (*Arabidopsis thaliana* activation factor), although the work was never formally published. In Arabidopsis the ATAF group consists of ATAF1 (At1g01720;ANAC002), ATAF2 (At5g08790;ANAC081), ANAC032 (At1g77450) and ANAC102 (At5g63790). Three of the Arabidopsis genes belonging to the ATAF subgroup have been characterized and all are involved in plant stress responses.

ATAF NACs and Stress Responses

The first report of a stress responsive ATAF-like gene was the potato StNAC gene that is induced upon infection with *Phytophthora infestans*.³⁵ Due to its close homology to ATAF1 and ATAF2 in Arabidopsis, Collinge and Boller tested and found that ATAF1 and ATAF2 genes were also wound inducible. Since that study, numerous gene expression surveys have implicated ATAF-like NAC genes in a wide range of plant stresses^{11,13-15,32,33,36-39} (see Fig. 2 for a summary). In Arabidopsis, Seki et al.⁴⁰ found that ANAC102 was induced by cold, drought and salinity, whereas ATAF1 was induced by drought and salinity. Work by two groups showed that ATAF2, ANAC102 and ANAC032

were regulated by nitric oxide (NO) an important regulator of plant stress responses, as well as seed germination and development.^{41,42} ANAC102 was also found to be low oxygen inducible.⁴³ The connection of these ATAF-like NACs to stress by gene expression analyses instigated reverse genetic studies to functionally characterize members for stress associated phenotypes.

To date only a few functional analyses on ATAF NACs using plants either lacking a functional gene product or constitutively overexpressing the factors have been performed, but all have implicated these NACs as important regulators of plant stress. The first comprehensive functional analysis of an ATAF-like NAC was ATAF2 by Delessert et al.³⁶ ATAF2 is induced early and locally in the wound response. Plants without a functional allele of ATAF2 did not show any observable morphological changes, whereas constitutive overexpression resulted in a complex phenotype that consisted of larger cells and yellowing of leaves similar to that observed by ectopic expression of the barley homolog of ATAF1, BnNAC14.¹³ Microarray analysis revealed that overexpression of ATAF2 repressed several well characterized pathogen-associated genes whereas the loss of ATAF2 resulted in higher levels of expression of those genes than in wild type, implicating ATAF2 as a negative regulator of plant defence. Subsequently, plants overexpressing ATAF2 were found to have increased susceptibility to the necrotrophic fungal pathogen *Fusarium oxysporum*, although resistance was unchanged in plants with ATAF2 T-DNA insertions. ATAF2 is therefore an important transcriptional integrator between mechanical damage and pathogen defence.

ATAF1 has also been found to be an important integrator of biotic and abiotic stresses. Like ATAF2, ATAF1 is negative regulator of defense responses against different type of pathogens. Overexpression of the *ATAF1* resulted in increased susceptibility to a range of pathogens (*Botrytis cinerea*, *Pseudomonas syringae* pv. *tomato* DC3000 and *Alternaria brassicicola*) while plants expressing an ATAF1 chimeric dominant repressor construct exhibited enhanced resistance.⁴⁴ Jensen et al.¹⁵ found that Arabidopsis ATAF1 and its barley

ATAF NACs		ABA	Wounding	Drought	Salt	Cold	Pathogen
Arabidopsis	ATAF1						
	ATAF2						
	ANAC032						
Rice	ANAC102						
	OsNAC5						
Sugarcane	OsNAC6						
	SsNAC23						
Cotton	GhNAC1	▨			▨		
	GhNAC2						
	GhNAC3						
Barley	HvNAC6						
Cayenne pepper	CaNAC1						
	SiNAC						
Potato	SINAC						
Tomato	SINAC						
	BnNAC1-1						
Rapeseed	BnNAC3						
	BnNAC5-1						
	BnNAC5-7						
	BnNAC5-8						
	BnNAC5-11						
	BnNAC14						
Soybean	BnNAC18						
	GmNAC2						

Figure 2. Expression of ATAF NAC domain genes in response to different stresses. Solid filled squares represent induction of transcription in response to the stress treatments listed, whereas hatched squares represent downregulation. White squares indicate either that the result is unknown or that there is no change.

homologue HvNAC6 plays a role in penetration resistance in Arabidopsis against the non-host pathogen, *Blumeria graminis* f. sp. *hordei*, and in barley against virulent *B. graminis* f. sp. *hordei*.^{15,45} In addition to its role in plant defence, ATAF1 also negatively regulates drought responsive gene expression in Arabidopsis.¹² Plants lacking a functional ATAF1 gene exhibited a higher recovery rate from drought than wild-type plants which was correlated with the enhanced expression of stress responsive marker genes.¹²

ANAC102 was found to play a part in growth stage specific responses to low-oxygen stress. ANAC102 is rapidly induced under low oxygen treatment in germinating seeds, and in adult root and shoot tissues.⁴⁶ Overexpression of *ANAC102* altered the expression of a number of other genes including many previously identified as being low-oxygen

responsive. Loss of *ANAC102* expression had no effect on global gene transcription in adult plants, but did alter expression patterns in low oxygen stressed seeds. *ANAC102* is not required for normal growth and development as neither overexpression nor decreased-expression had a visible phenotype in the absence of stress. Decreased *ANAC102* expression significantly decreased germination efficiency following low oxygen, but increased expression had no effect on germination.⁴⁶ Although *ANAC102* is also induced by cold drought and salinity,⁴⁰ germination was unaffected by salt or osmotic stresses in plants with decreased *ANAC102*. It is not yet understood how decreased *ANAC102* expression reduces seed germination, but it is likely that *ANAC102* is an important regulator of seed germination under low oxygen, possibly regulated by NO.⁴⁷

In rice, the only well characterised ATAF-like NAC is OsNAC6 (SNAC2, Os01g66120). Similar to what has been observed in Arabidopsis, OsNAC6 is an important integrator of biotic and abiotic stresses as it is induced by both abiotic and biotic stresses (rice blast infection). In contrast to ATAF1 and ATAF2, OsNAC6 positively regulates stress responses; plants overexpressing OsNAC6 are more tolerant to cold, dehydration, high-salt stresses, and have slightly improved tolerance to rice blast disease.^{14,48} Tolerance is correlated with overexpression of genes associated with abiotic and biotic stresses such as peroxidases.

Regulation of ATAF NACs

The complex transcriptional regulation of ATAF NACs does not appear to be due to regulation by miRNAs, but instead looks to be dependent on upstream regulation by

other transcription factors. Analysis of the 4 Arabidopsis ATAF NAC promoter regions reveals over-representation of both a ABA-responsive element (YACGTGGC) and G-box (CACGTG), implicating regulation by bZIP transcription factors and providing some explanation of their ABA and stress responsiveness. However, post-transcriptional regulation of ATAF NAC translation is suggested, at least for ANAC102, by the discordance between RNA and protein levels observed for an ANAC102::*GUS* fusion construct under low oxygen stress and that ANAC102 low-oxygen induction can occur in the absence of protein synthesis.⁴⁶ Changes in chromatin structure and methylation are also important in the regulation of stress responses⁴⁹ and it is interesting to note that both ATAF1 and ANAC032 are upregulated in the transition from leaf cell to protoplast.²⁴

Analysis of protein interactions has shown that the ATAF NACs like other NAC proteins are capable of complex protein interactions, forming homo- and hetero-dimers^{15,30} and binding to non-NAC proteins.¹⁸ Recently ATAF1 was shown to interact with SNF1-related kinases AKIN10 and AKIN11 indicating possible post-translational regulation by phosphorylation.⁵⁰

Conclusion

The minority of plant ATAF-like NACs that have been characterised indicate that this group is an important regulator of plant stress responses. Due to their propensity to be regulated by diverse stimuli and ability to form multiple protein complexes the ATAF-like NACs are capable of integrating the response between multiple stresses. This suggests that further characterisation of this group will yield important information on how plants integrate and respond to different stresses. The ability to control the expression of these genes may therefore prove to be a practical way of engineering multiple stress tolerance into crops.²³

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