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NAVIGATING STRESS AND DEVELOPMENT: THE MULTIFACETED ROLES OF NAC TRANSCRIPTION FACTORS IN PLANTS

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ABSTRACT

NAC (NAM, ATAF1/2, and CUC2) transcription factors constitute one of the largest plant-specific transcription factor families, playing essential roles in diverse biological processes. These include plant development, hormone signaling, and responses to both biotic and abiotic stresses. Structurally, NAC proteins are characterized by a highly conserved N-terminal DNA-binding NAC domain and a variable C-terminal domain responsible for transcriptional regulation, contributing to their functional diversity. Recent advances in genomics and transcriptomics have deepened our understanding of their regulatory networks, uncovering their involvement in key pathways such as senescence, secondary wall formation, drought tolerance, and pathogen defense. This review summarizes the molecular structure, functional classification, and regulatory mechanisms of NAC transcription factors, emphasizing their potential for crop improvement through genetic engineering and molecular breeding strategies.

KEYWORDS: NAC transcription factor, Abiotic stress, Biotic stress, Hormone signalling, Plant development

As sessile and non-motile organisms, plants must adapt to changing environmental conditions to survive, often relying on hormone-dependent responses to overcome stress (Anderson et al., 2004). Environmental cues play a crucial role in shaping plant growth, development, and overall crop productivity (Nuruzzaman et al., 2013; Chen C. et al., 2016; Mao et al., 2017). Transcription factors (TFs) act as molecular switches that regulate gene expression in response to various internal and external signals. Several TF families, such as NAC, WRKY, AP2/ERF, MYB, and bZIP, have been extensively characterized in various crops (Srivastava et al., 2014).

NAC proteins contain a conserved N-terminal DNA-binding domain and a variable C-terminal domain involved in transcriptional regulation. These proteins belong to a large plant-specific gene family, including members of the NAC (No Apical Meristem), NAM (*Arabidopsis* Transcription Activation Factor), and CUC (Cup-Shaped Cotyledons) superfamily. The first *NAC* gene was isolated from petunia (Souer et al., 1996). In Arabidopsis, the *CUC1* and *CUC2* genes, which function redundantly, are essential for shoot apical meristem formation and floral organ differentiation (Aida et al., 1997). Similarly, ATAF1 and ATAF2 are induced by pathogen attack and wounding (Collinge and Boller, 2001). *NAC* genes such as *ANAC019*, *ANAC055*, *RhNAC3* and *ANAC072* are responsive to osmotic, drought, salinity, and low temperatures, and their overexpression in Arabidopsis confers enhanced tolerance to these abiotic stresses (Fujita M et al., 2004; Jiang et al., 2014;).

NAC TFs participate in a wide range of developmental and physiological processes, including shoot and root development (Gunapati S. et al., 2016), senescence (Balazadeh S et al., 2011), cell division (Kim et al., 2006; Gall et al., 2015) and abiotic stress responses (You J et al., 2013; Shao et al., 2015; Tweneboah et al., 2017). These proteins can bind to the CATGTG motif in the promoters of target genes (Tran et al., 2004).

Extensive investigations, supported by the availability of complete plant genome sequences, have led to the identification of 117 *NAC* genes in Arabidopsis, 151 in rice, 79 in grape, 26 in citrus, 163 in poplar, and 152 each in soybean and tobacco (Nuruzzaman et al., 2010, Le DT et al., 2011). This review provides a detailed summary of the functional characterization of NAC (NAM, ATAF, and CUC) transcription factors. It highlights their diverse roles in plant development, stress responses, and other physiological processes, offering insights into the molecular mechanisms through which these transcription factors regulate gene expression and contribute to plant growth and environmental adaptation.

Structure of NAC Transcription Factors

NAC proteins possess two distinct domains: a highly conserved N-terminal domain and a diversified C-terminal transcriptional regulatory domain (Figure 1). The first structural elucidation of the DNA-binding NAC domain (ANAC019) was reported by Ernst et al 2004. using X-ray crystallography. The NAC domain monomer consists of a twisted antiparallel β-sheet, which is flanked by an N-terminal α-helix on one side and a shorter α-helix on the other. The rest of the structure comprises loops between the main secondary structural elements, with only sporadic and short stretches of additional secondary structures. The N-terminal domain of NAC has been further subdivided into five subdomains, designated A to E. Subdomain A is responsible for

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dimerization, while subdomains B and E contribute to the functional diversity of NAC proteins. Subdomains C and D form the highly conserved region involved in DNA binding. The Val119 to Ser183 region, encompassing subdomains D and E, along with specific residues such as Lys123 and Lys126 (subdomain D) and Lys79, Arg85, and Arg88 (subdomain C), is biochemically critical for DNA binding (Chen Q et al., 2011). Notably, Arg88 is conserved across all NAC proteins. Additionally, the NAC domain contains either a mono or bipartite nuclear localization signal (NLS) and a lysine residue within subdomain D, both of which are essential for nuclear transport (Hao et al., 2010). In some NAC proteins, the N-terminal domain also harbours an NAC Repression Domain (NARD), which functions as a suppressor of transcriptional activity. The LVFY motif within this region may contribute to its repression function. Ultimately, the interaction between the NARD and the C-terminal activation domain plays a key role in determining the regulatory potential of NAC family proteins (Hao et al., 2010).

The C Terminal Regulatory Domain

The divergent C terminal regions of NAC proteins function as regulatory domains that act either as transcriptional activators or repressors. These regions are relatively large and exhibit protein-binding activity. In Arabidopsis, the C terminal domains of NAC proteins have been shown to interact with calmodulin proteins (Kim et al., 2006), suggesting the presence of complex mechanisms underlying NAC-mediated transcriptional regulation. Most studies indicate that NAC proteins primarily function as transcriptional activators of target gene expression. For example, AtNAM, AtATAF1, AtNAC2, and AtNAC3 were reported to act as transcriptional activators in yeast hybrid assay systems (He et al., 2005). Similarly, ANAC019, ANAC055, and ANAC072 (RD26) were identified as transcriptional activators in plant protoplast assay systems (Tran et al., 2004). The transcriptional regulatory regions (TRRs) located within the C terminal domain exhibit a high degree of intrinsic disorder and lack a stable three-dimensional structure, which contributes to their functional flexibility and diversity.

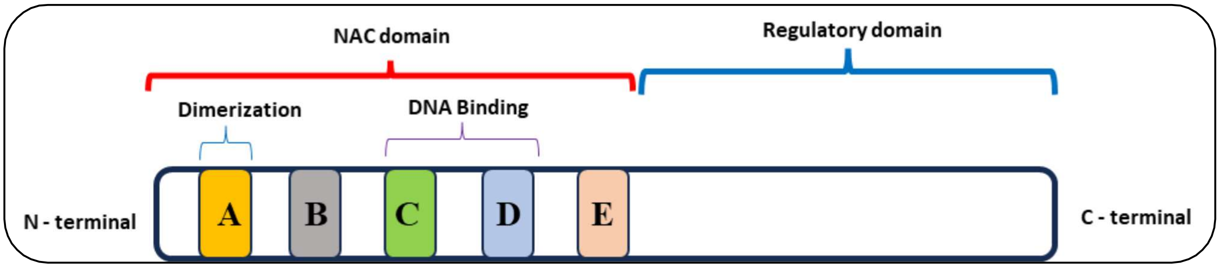

Figure 1. Schematic representation of a NAC transcription factor. Subdomain A is responsible for functional dimer formation. Subdomains B and E contribute to the diverse functions of the transcription factor. Subdomains C and D are involved in DNA binding.

Transcriptional and Post-transcriptional Regulation of NAC Transcription Factors

Transcriptional Regulation

The initial step in gene expression regulation involves the binding of specific transcription factors to regulatory elements within gene promoters. *NAC* gene promoters contain several recognition sequences, including various stress-responsive cis-acting elements. These include ABREs (ABA-responsive elements), DREs (dehydration-responsive elements), LTREs (low-temperature-responsive elements), MYB and MYC binding sites (associated with Myeloblastosis and Myelocytomatosis, respectively), W-box elements (jasmonic acid-responsive), and salicylic acid-responsive elements (Nakashima et al., 2009). The tight regulation of *NAC* gene expression by these elements ensures appropriate transcriptional responses to a wide range of environmental stresses.

Post-transcriptional Regulation

Post-transcriptional regulation plays a crucial role in fine-tuning gene expression after transcription. One of the key mechanisms involves microRNA (miRNA)-mediated cleavage or translational repression of target mRNAs. miRNAs recognize and bind to complementary sequences within mRNA transcripts, resulting in their degradation or inhibition of translation. Several studies have shown that both miRNAs and small interfering RNAs (siRNAs) are involved in the post-transcriptional regulation of *NAC* genes and other transcription factor families (Li Y et al., 2011). These small RNA pathways are vital for modulating stress responses, development, and other essential physiological functions in plants.

Post-translational Regulation

NAC transcription factors are also regulated post-translationally through various mechanisms, including ubiquitin-mediated protein degradation, protein-protein interactions, and dimerization (Puranik et al., 2011). Moreover, the SNF1-related protein kinase 1 (SnRK1) has been shown to regulate NAC proteins directly or indirectly during stress conditions. Membrane-bound NAC transcription factors (NTLs) are activated via stress-induced proteolytic cleavage by intramembrane proteases, leading to their release and translocation to the nucleus. This activation mechanism is triggered by environmental stresses such as high salinity, cold, and osmotic stress (Kim S.G. et al., 2008; Seo P.J. et al., 2010; Xu et al., 2015; Jin et al., 2017).

The Role of NAC Proteins in Development and Stress Responses

Several studies have suggested that NAC transcription factors play diverse and multifaceted roles in regulating a wide range of plant processes, including growth, development, and responses to various biotic and abiotic stresses. NAC proteins function primarily by orchestrating transcriptional reprogramming, influencing the expression of numerous downstream genes involved in these processes. Their regulatory activities are crucial for coordinating plant responses to environmental cues as well as internal developmental signals. In this review, we summarize some of the key plant programs and pathways that are modulated by NAC transcription factors, highlighting their central role in plant adaptation and survival.

Role of NAC TFs in Plant Growth and Development

NAC transcription factors (TFs) regulate various developmental processes, including plant growth, root and leaf development, seed germination, wood formation, seed setting, and grain filling. In poplar, the NAC domain gene *PtrWND* plays a key role in regulating wood formation (Ohtani et al., 2011). In rice, overexpression of *OsNAC2* led to reduced plant height and delayed flowering by modulating the gibberellin (GA) pathway (Chen et al., 2015). In cotton, *GhNAC2* regulates root and seed development while also conferring tolerance to drought stress (Ganapati et al., 2016). Overexpression of *SNAC1* and *OsNAC5* resulted in enhanced seed setting and grain filling, respectively (Guo et al., 2005; Sperotto et al., 2009). In Arabidopsis, genes such as *NTL8-1*, *ANA083*, *CarNAC3, ANAC041*, *ANAC054*, and *ANAC084* have been shown to negatively regulate seed germination (Kim et al., 2008; Peng et al., 2009; Balazadeh et al., 2011) (Table-1).

Table 1: Function of NAC transcription factors in growth and development

Genes	Functions	Species	Reference
NAC1	Root development	*A. thaliana*	Guo et al., 2005
SNAC1	Higher seed setting	*O. sativa*	Hu et al., 2006
ONAC020/23/26	Seed size	*O. sativa*	Mathew et al., 2016
OSNAC5/6	Growth, yield and abiotic stress	*O. sativa*	Takasaki et al., 2010
OSNAC10	Root	*O. sativa*	Jeong et al., 2010
OSTIL1	Shoot branching	*O. sativa*	Mao et al., 2007
ANAC1,	Lateral root formation	*Arabidopsis*	D'haeseleer et al., 2011
TaNAC2-5A	Root growth and yield	*Triticum aestivum*	He et al., 2015
EcNAC 67	Root and shoot	*Eleusine coracana*	Rahman et al., 2016
CARNAC3	Root growth	*Cicer arietinum*	Movahedi et al., 2015
OsSWN1	Cell wall development	*Oryza sativa*	Chai et al., 2015
NTL8-1	Seed germination under salinity	*A. thaliana*	Kim et al., 2008
GhNAC2	Root growth, seed size, and drought	*A. thaliana*	Gunapati S et al., 2016
SND2	Secondary cell wall	*A. thaliana and Eucalyptus*	Hussey et al., 2011

Biotic Stress

Biotic stress triggers transcriptional reprogramming that is associated with plant immune responses aimed at mitigating the effects of such stress. Numerous studies have suggested that NAC transcription factors (TFs) play a central role in various aspects of the plant's innate immune system, basal defense mechanisms, and systemic acquired resistance. Several reports indicate that both overexpression and knockdown of NAC gene expression can significantly impact plant defense responses (Collinge and Boller, 2001; Delessert et al., 2005; He et al., 2005; Jensen et al., 2008) (Table

1). Additionally, increased expression of a NAM-like gene has been linked to the downregulation of *miR164* following infection with Tomato leaf curl New Delhi virus (ToLCNDV) in tomato plants (Naqvi AR et al., 2010).

NAC Regulation by Pathogen Infection

The Virus-Induced Gene Silencing (VIGS) system has been employed to explore the role of NAC transcription factors (TFs), specifically ONAC122 and ONAC131, in disease resistance against Magnaporthe grisea (Sun et al., 2013). The barley stripe mosaic virus (BSMV)-based VIGS vector has also been utilized to characterize various genes involved in disease resistance in wheat and barley (Sindhu et al., 2008). In rice seedlings, 19 and 13 *NAC* genes were found to be upregulated after infection with Rice streak virus (RSV) and Rice tungro spherical virus (RTSV), respectively, at different time points post-inoculation (Nuruzzaman et al., 2012). Several NAC proteins can either promote or inhibit virus replication through direct interactions with virus-encoded proteins (Jeong et al., 2008; Yoshii et al., 2009). Kaneda et al. (2009) demonstrated that OsNAC4 is a key positive regulator of hypersensitive cell death in plants, and this response is notably reduced in OsNAC4-knockdown lines infected with avirulent bacterial strains. In contrast, overexpression of *OsNAC6* does not induce hypersensitive cell death (Kaneda et al., 2009). Furthermore, overexpression of *ATAF2* leads to increased susceptibility to the necrotrophic fungus Fusarium oxysporum under sterile conditions, due to the repression of pathogenesis-related (PR) genes (Delessert et al., 2005). Several NAC proteins have been found to positively regulate plant defense responses by activating PR genes, which are modulated by various types of TFs. NAC, ERF, and WRKY family TFs have been identified as key players in these regulatory processes (Eulgem and Somssich, 2007). Arabidopsis stress-responsive NAC genes, such as RD26, are involved in hypersensitive response (HR) and cell death at infection sites (Kaneda et al., 2009; Seo et al., 2010). Plant immune responses upon pathogen infection are characterized by the activation of multiple defense pathways, including the expression of a wide array of defense-related genes (van Loon et al., 2006), which are regulated by jasmonic acid (JA), a key phytohormone involved in wound and biotic stress responses (Fujita et al., 2006). The application of exogenous phytohormones like JA, salicylic acid (SA), and ethylene (ET) has been shown to induce NAC gene expression across multiple plant species (Tran et al., 2004; Nakashima et al., 2007; Nuruzzaman et al., 2012). These findings suggest that NAC TFs serve as central hubs in the plant stress response network (Table 2).

Senescence

Leaf senescence is a distinct developmental process marked by extensive programmed cell death and the recycling of nutrients. This process can be triggered by pathogen infection. Several *NAC* genes from the ATAF subfamily, such as *ATAF1, ATAF2*, and *RD26*, are upregulated during leaf senescence in Arabidopsis (Guo et al., 2004). More recently, other *NAC* genes, including *NTL4* and *MtNAC969*, have been shown to delay senescence when overexpressed (Lee et al., 2012).

Table 2: Function of NAC transcription factors in biotic stress

Genes/target genes	Functions	Species	Reference
PR1, PR2, PR4, PR5, PDF1.1, PDF1.2	Negatively regulates *P. syringae, B. cinerea, A. brassicicola* infection	*A. thaliana*	Delessert et al., 2005
ATAF1, PR1	Negatively regulates resistance to *B. cinerea*	*A. thaliana*	Wu et al., 2009
PR-1, PR-5, NPR1, PDF1.2	Negatively regulates resistance to *P. syringae, B. cinerea, A. brassicicola*	*A. thaliana*	Wang et al., 2009
SlNAC35	Biotic and Abiotic stress	*Solanum lycopersicum*	Wang et al., 2016
NIT2	Pathogen Infection	*A. thaliana*	Huh et al., 2012
ANAC019, ANAC055	Defence, disease, JA pathway	*A. thaliana*	Bu et al., 2008
NTL6, PR1, PR2, PR5	Positive regulator against *P. syringae*	*A. thaliana*	Seo et al., 2010
ANAC042	Regulation of camalexin biosynthesis, pathogen infection	*A. thaliana*	Saga et al., 2012
NTL4	Leaf senescence	*A. thaliana*	Lee et al., 2012
NTL9	Osmotic stress, leaf senescence	*A. thaliana*	Yoon et al., 2008

VNI2	Leaf senescence	*A. thaliana*	Yang et al.,2011
AtNAP	Leaf senescence	*A. thaliana*	Guo and Gan, 2006
OsNAC4	Loss of membrane integrity	*O. sativa*	Kaneda et al., 2009
OsNAC6	Rice blast disease tolerance	*O. sativa*	Nakashima et al., 2007
RIM1-1	Resistance toward rice dwarf virus and susceptibility to RTYV and RSV	*O. sativa*	Yoshii et al., 2009
OsNAC19	Disease resistance	*O. sativa*	Lin et al., 2007
ONAC122 **and** ***NAC131***	*Magnaporthe grisea* resistance	*O. sativa*	Sun et al., 2013
Os07g37920	Senescence	*O. sativa,*	Distelfeld et al., 2012
SlNAC1	Susceptible to tomato leaf curl virus	*N. benthamiana*	Selth et al., 2005
GRAB1, GRAB2	Reduced wheat dwarf virus infection	*T. monococcum*	Xie et al., 1999
PpNAC2/3	Wounding and salinity	*Pinus pinaster*	Pascual et al., 2015
PpNAC2 and PpNAC3	Tobacco mosaic virus	*Tobacco*	Wang et al., 2009
SlNAC1	Upregulated during pseudomonas infection	*S. lycopersicum*	Huang et al., 2012
CaNAC1	Defense responses against pathogen	*C. arietinum*	Oh et al., 2005
GmNAC6	Osmotic stress-induced	*G. max*	Faria et al., 2011
TLCV, SlNAC1	Susceptible to viral infection	*L. esculentum*	Selth et al., 2005
BnNAC14, BnNAC485,	Biotic and abiotic stresses and wounding	*L. esculentum*	Hegedus et al., 2003
SlNAC61	TYLCV infection	*S. lycopersicum*	Huang et al., 2017
MtNAC969	Nodule senescence	*M. truncatula*	de Zélicourt et al., 2012

Abiotic Stress

Abiotic stress triggers a broad spectrum of plant responses, ranging from alterations in gene expression and cellular metabolism to changes in growth, development, and crop yield. Therefore, understanding the complex mechanisms of drought and salinity tolerance is crucial for agricultural production. In transgenic rice, the *Os01g66120/OsNAC2/6* and *Os11g03300/OsNAC10* genes have been shown to enhance tolerance to drought and salinity (Nakashima et al., 2009; Jeong et al., 2010), while *SNAC1* has been linked to increased grain yield (21–34%) under drought conditions (Hu et al., 2006). Conversely, overexpression of *GmNAC11* resulted in heightened sensitivity to salt and mannitol stress (Hao et al., 2011). Similarly, the expression of *DgNAC1*, was significantly induced by NaCl and drought stresses in transgenic tobacco plants (Tang et al., 2012). Furthermore, overexpression of *ZmSNAC1* enhanced tolerance to both drought and low-temperature stress compared to controls (Lu et al., 2012). The expression of *OsNAC6* is induced by abscisic acid (ABA) and various abiotic stresses, including cold, drought, and high salinity (Nakashima et al., 2007). In rice roots, the expression of *ONAC063* is responsive to high-temperature stress (Yokotani et al., 2009). Additionally, the expression of genes like *OsNAC10, SNAC2/OsNAC6, TaNAC4, NTL6, TaNAC2a, TaNAC4a, TaNAC6, TaNAC7, TaNAC13,* and *TaNTL5* is induced by low temperatures in plants (Xia et al., 2010; Tang et al., 2012), while a gene expressing a *CsNAM*-like protein is induced by heat stress in tea plants (Paul et al., 2012). Promoter activity analysis of *SNAC2* suggests that this gene is upregulated by low-temperature stress. NAC proteins play a pivotal role in plant adaptation to stress by regulating the transcriptional reprogramming of stress-related genes (Table 3).

Table 3: Function of NAC transcription factors in abiotic stress

Genes	Functions	Species	Reference
TaNAC8	Salt and Biotic stress	*T. aestivum*	Xia et al., 2010
RD26, RD20	Drought, salt, and ABA	*A. thaliana*	Fujita et al., 2004
COR47, ERD10, KIN1, RD22, RD29A	Drought tolerance	*A. thaliana*	Lu et al., 2007
ADH1, RD29A, COR47,	Drought tolerance	*A. thaliana*	Wu et al., 2009

ONAC063	Seed germination under high salinity and osmotic stress	*A. thaliana*	Yokotani et al., 2009
ANAC102	Water logging	*A. thaliana*	Christianson et al., 2009
GmNAC20	Salt and freezing tolerance	*A. thaliana*	Hao et al., 2011
NTL8	Salt tolerance	*A. thaliana*	Kim et al., 2008
ANAC042	Heat and biotic stress	*A. thaliana*	Shahnejat- Bushehri et al., 2012
XND1	Programmed cell death	*A. thaliana*	Zhao et al., 2008
LOV1	Cold response	*A. thaliana*	Yoo et al., 2007
NTL6, SnRK2.8	Drought-stress response	*A. thaliana*	Kim et al., 2012
TaNAC2	Drought, salt, and freezing	*A. thaliana*	Mao et al., 2012
ANAC2/AT3G15510	Salt and ABA stress tolerance	*A. thaliana*	He et al., 2005
SNAC2/OsNAC6	Salt, drought, salinity, cold, and wounding	*O. sativa*	Sindhu et al., 2008
TaNAC67	Drought, salt and freezing stress	*T. aestivum*	Mao et al., 2014
SNAC2	Drought and oxidative stress	*O. sativa*	You et al., 2013
ONAC063	Drought and salinity	*O. sativa*	Yokotani et al., 2009
GmNAC20	Salt and freezing tolerance	*G. max,*	Hao et al., 2011
GmNAC085	Dehydration stress	*G. max*	Le et al., 2011
TaNAC2a	Drought tolerance	*N. tabacum*	Tang et al., 2012
DgNAC1	Salt, drought, and cold	*N. tabacum*	Liu et al., 2011
EcNAC1	Drought and salt	*N. tabacum*	Ramegowda et al., 2012
TaNAC69	PEG-induced dehydration	*T. aestivum*	Xue et al., 2011
TaNAC2a, TaNAC4a, TaNAC6, TaNAC7, TaNAC13, TaNTL5	Dehydration, salinity, and cold	*T. aestivum*	Tang et al., 2012
TaNAC4	Salinity, Wound, and cold	*T. aestivum*	Xia et al., 2010
DgNAC1	Salt, drought, and cold	*N. tabacum*	Wang et al., 2017
ZmSNAC1	Cold, high-salinity, and drought	*Z. mays*	Lu et al., 2012
miR319, AsNAC60	Drought and salinity stress	*Agrostis stolonifera*	Zhou et al., 2014
AhNAC2	Salt	*Arachis*	Liu et al., 2011
RhNAC2	Dehydration tolerance	*R. hybrida*	Dai et al., 2012
ClNAC	Salt, drought, and cold	*C. lavandulifolium*	Huang et al., 2012
CsNAM	Drought, osmotic, and salt	*C. sinensis*	Paul et al., 2012
SiNAC	Drought, salt and cold stress	*S. italica*	Puranik et al., 2011
MlNAC9	Drought, salt and cold stress and ABA	*Miscanthus*	Zhao et al., 2016
GhATAF1	Abiotic and biotic stress	*Gossypium hirsutum*	He et al., 2016

Conclusion

NAC transcription factors play pivotal roles in orchestrating plant growth, development, and responses to a wide range of environmental stresses. Their ability to regulate key hormonal pathways, control gene expression networks, and integrate developmental and stress-related signals underscores their functional versatility. As plants continuously face changing environmental conditions, NAC TFs emerge as critical components in ensuring survival and adaptation. Advancements in functional genomics and biotechnological approaches have begun to reveal the full potential of these regulators, offering promising avenues for crop improvement. Future research aimed at elucidating their precise molecular mechanisms and interactions will further enhance our capacity to engineer stress-resilient and high-yielding plants.

Conflicts of Interest: The authors declare no conflicts of interest.

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