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Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants

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NAC transcription factors are one of the largest families of transcriptional regulators in plants, and members of the *NAC* gene family have been suggested to play important roles in the regulation of the transcriptional reprogramming associated with plant stress responses. A phylogenetic analysis of *NAC* genes, with a focus on rice and Arabidopsis, was performed. Herein, we present an overview of the regulation of the stress responsive *NAC SNAC*/(*IX*) group of genes that are implicated in the resistance to different stresses. SNAC factors have important roles for the control of biotic and abiotic stresses tolerance and that their overexpression can improve stress tolerance via biotechnological approaches. We also review the recent progress in elucidating the roles of NAC transcription factors in plant biotic and abiotic stresses. Modification of the expression pattern of transcription factor genes and/or changes in their activity contribute to the elaboration of various signaling pathways and regulatory networks. However, a single *NAC* gene often responds to several stress factors, and their protein products may participate in the regulation of several seemingly disparate processes as negative or positive regulators. Additionally, the NAC proteins function via auto-regulation or cross-regulation is extensively found among *NAC* genes. These observations assist in the understanding of the complex mechanisms of signaling and transcriptional reprogramming controlled by NAC proteins.

Keywords: phylogenetic analysis, motif, NAC transcription factors, defense signaling pathways, biotic infections, abiotic stresses

INTRODUCTION

Biotic and 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 and crop yields. Transcription factors (TFs) and *cis*-elements function in the promoter region of different stress-related genes, and the overexpression 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), ATAF1 and −2, and CUC2 (for cup-shaped cotyledon) (Souer et al., 1996; 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(Rushton et al., 2008; Hu et al., 2010; Nuruzzaman et al., 2010, 2012a; Le et al., 2011).

In the past decade, significant progress has been achieved in determining the molecular mechanisms of innate immune responses in rice, host recognition of pathogens, recognition-triggered early signaling events, and signaling pathways and their involvement in activating defense responses (Skamnioti and Gurr, 2009; Liu et al., 2010; Valent and Khang, 2010). To date, numerous studies have elucidated the regulatory mechanism of innate immune response in rice against blast disease, which is caused by *Magnaporthe* (M) *oryzae*. Multiple disease resistance genes (*R* genes) have been cloned and characterized (Liu et al., 2010). Similar to Arabidopsis, the salicylic acid (SA) and ethylene (ET)/jasmonic acid (JA)-mediated signaling pathways are critical in activating innate immune responses in rice and can operate in concert using some common components or biochemical events (Chern et al., 2005; Qiu et al., 2007; Yuan et al., 2007; Li et al., 2011). A number of regulatory proteins, including several TFs (e.g., OsNAC6), function in regulating defense responses against *M. grisea* (Nakashima et al., 2007). However, a complete understanding of the molecular network regulating the rice immune responses against pathogens remains unclear. Microarray profiling after biotic treatments [rice stripe virus (RSV) and rice tungro spherical virus (RTSV)] in rice seedlings has revealed six *OsNAC* genes induced by both virus infections (Nuruzzaman et al., 2010). Rice plants with a mutation in *rim1-1* are resistant to infection by dwarf virus (Yoshii et al., 2009; Satoh et al., 2011). The *StNAC* (*Solanum tuberosum*) gene is induced in response to *Phytophthora infestans* infection (Collinge and Boller, 2001). Furthermore, numerous *NAC* genes are involved in the response of plants to abiotic stresses, such as drought, salinity, cold, and submergence (Hu et al., 2006; Jeong et al., 2010; Nuruzzaman et al., 2012b).

Genes in the NAC family have been shown to regulate a wide range of developmental processes, including seed development (Sperotto et al., 2009), embryo development (Duval et al., 2002), shoot apical meristem formation (Kim et al., 2007a), fiber development (Ko et al., 2007), leaf senescence (Guo et al., 2005; Breeze et al., 2011), and cell division (Kim et al., 2006). 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).

Regardless, few of these genes have been characterized to date. Indeed, most of the NAC family members have yet to be characterized, even though these genes are likely to play important roles in plant physiology, and substantial experimental work will be required to determine the specific biological function of each *NAC* gene. Based on phylogenetic analyses, it is apparent that this large family of TFs consists of groups that are closely related to each other (Kranz et al., 1998; Reyes et al., 2004; Tian et al., 2004). The focus of this review is the phylogeny of *NAC* genes with respect to resistance pathways. We also present an overview of the regulation of the *SNAC*/(*IX*) group of genes that are implicated in the resistance to different stresses. Furthermore, we will emphasize on the roles of *NAC* TFs genes in plant biotic and abiotic stresses.

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 (Ernst et al., 2004), 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 (Xie et al., 2000; Yamaguchi et al., 2008; 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 (Tran et al., 2004; Hu et al., 2006; Kim et al., 2007b). The C-terminal region is large and possesses protein-binding activity.

STRUCTURAL CONSERVATION OF SNAC GROUP

The evolutionary analysis of developmental processes of *NAC* genes through the correlation of function and phylogeny is a well-known approach in plant research (**Figure 1**; Nuruzzaman et al., 2010, 2012a). The NAC TF family has experienced extensive expansion through gene duplication events. Although NAC structural diversity has been constrained within the 60-amino acid conserved domain, which comprises a unique DNA-interacting β-sheet structure, structural conservation outside this conserved domain is extremely limited. Additional highly conserved motifs can be identified only within specific groups (e.g., SNAC, TIP, and SND), and most members in the same group share one or more motifs outside the NAC domain (Nuruzzaman et al., 2012a). A phylogeny of the SNAC group, which includes the *ANAC019* and *OsNAC6* genes, indicates the existence of multiple co-orthologs in dicots and monocots (**Figure 1**). Indeed, the SNAC group has some highly conserved motifs (**Figure 2**) within regions outside the conserved domain. A 28-amino acid (WVLCR) motif (RSARKKNSLRLDDWVLCRIYNKKGGLEK in OsNAC) is found amino-terminal to the conserved DNA-binding domain in monocots and in dicots. We first identified putative conserved motifs outside of the NAC domain in rice and compared with those of Arabidopsis and citrus. Outside of the NAC domain, rice specific conserved motifs were detected (Nuruzzaman et al., 2012a). These conserved motifs are likely to be involved in the recruitment of proteins that are involved in activating gene expression or perhaps in the control of protein stability. It is notable that only some of these motifs are conserved in both dicots and monocots, suggesting that protein function has both diverged and been conserved even within this evolutionarily conserved NAC family. Further analysis of motif function via protein-interaction analyses of TF complexes is needed.

ROLES PLAYED BY NAC TRANSCRIPTION FACTORS

Since the early research into NAC TFs, it was evident that these factors play roles in regulating several different plant processes. For convenience, some of these processes are discussed individually below. The recent data presented here provided new insight, namely, that it is common for a single NAC NF to regulate transcriptional reprogramming that is associated with multiple plant programs: the dynamic web of signaling in which NAC factors operate has multiple inputs and outputs.

NAC FUNCTION IN BIOTIC STRESS

The majority of reports concerning NAC TFs have indicated that numerous members of the multigene family play roles in the transcriptional reprogramming associated with plant immune responses. This is an active research area that has been extensively reviewed and therefore will only be briefly considered here. To date, it is clear that NAC NFs are central components of many aspects of the plant innate immune system, basal defense, and systemic acquired resistance. There are many examples in which the overexpression or knockdown of *NAC* gene expression has effects on plant defense, observations that have allowed the resolution of some components of the web of signaling pathways (**Figures 3–5**; **Table 1**) (Collinge and Boller, 2001; Delessert et al., 2005; He et al., 2005; Jensen et al., 2007, 2008, 2010).

REGULATION OF NAC TFs BY PATHOGEN INFECTION

Sun and co-workers applied Virus-induced gene silencing (VIGS) system to investigate the function of NAC TFs (ONAC122 and ONAC131) in disease resistance against *M. grisea* (Sun et al., 2013). VIGS is a useful tool for the rapid analysis of gene function in plants (Liu et al., 2002; Purkayastha and Dasgupta,

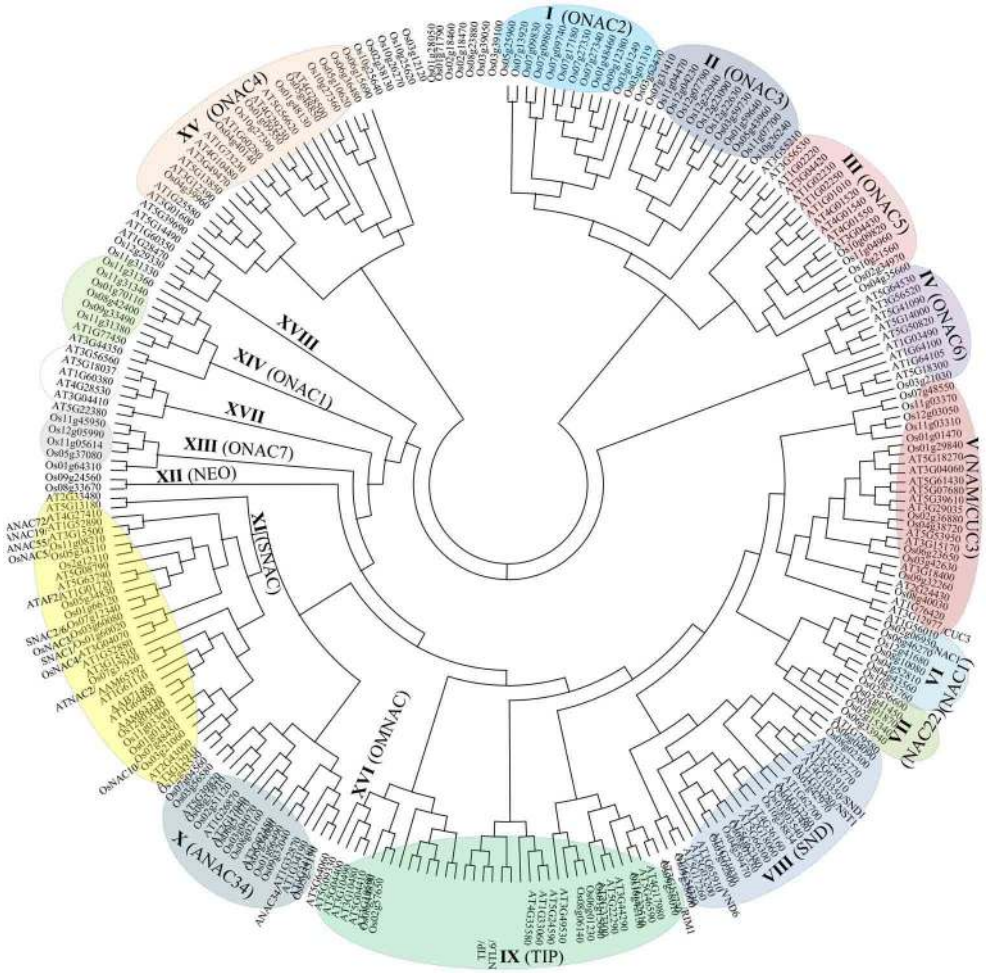

FIGURE 1 | An unrooted phylogenetic tree of the NAC transcription factors of rice and Arabidopsis. The amino acid sequences of the NAC domain of 135 rice NAC family proteins and 117 Arabidopsis NAC proteins were aligned by ClustalW, and the phylogenetic tree was constructed using MEGA 4.0 and the NJ method. Bootstrap values from 1000 replicates were used to assess the robustness of the trees. The classification by Nuruzzaman et al. (2010) is indicated in parentheses.

2009; Scofield and Nelson, 2009). Some VIGS vectors have been developed for dicotyledonous plants among which the tobacco rattle virus (TRV)-based VIGS vector is the most successful example for members of Solanaceae, such as *Nicotiana benthamiana* and *Lycopersicon esculentum* (Liu et al., 2002; Chakravarthy et al., 2010). The barley stripe mosaic virus (BSMV)-based VIGS vector was used to characterize multiple genes for their roles in disease resistance in wheat and barley (Hein et al., 2005; Scofield et al., 2005; Zhou et al., 2007; Sindhu et al., 2008). Several scientists have developed a brome mosaic virus (BMV)-based VIGS vector, and this vector was demonstrated to be a versatile tool for rapid gene function analysis in barley, rice, and maize (Ding et al., 2006; Pacak et al., 2010; van der Linde et al., 2011; Biruma et al., 2012). In rice seedlings, 19 and 13 *NAC* genes were up-regulated after RSV and RTSV infection, respectively, at different days after inoculation (Nuruzzaman et al., 2010). Several NAC proteins can either enhance or inhibit virus multiplication by directly interacting with virus-encoded proteins (**Figure 3**; Xie et al., 1999; Ren et al., 2000, 2005; Selth et al., 2005; Jeong et al., 2008; Yoshii et al., 2009), and increases in the expression level of *NAC* genes have been monitored in response to attack by viruses, several fungal elicitors, and bacteria (**Figures 3**, **4**; Xie et al., 1999; Ren et al., 2000; Collinge and Boller, 2001; Mysore et al., 2002; Hegedus et al., 2003; Oh et al., 2005; Selth et al., 2005; Jensen et al., 2007; Lin et al., 2007; Jeong et al., 2008; Wang et al., 2009a,b; Xia et al., 2010a,b). Such dual modulation in plant defense implies the association of NAC proteins with distinct regulatory complexes.

Kaneda et al. (2009) reported that *OsNAC4* is a key positive regulator of hypersensitive cell death in plants, and hypersensitive cell death is markedly decreased in response to avirulent bacterial strains in *OsNAC4*-knock-down lines. After induction by an avirulent pathogen recognition signal, *OsNAC4* is translocated into the nucleus in a phosphorylation-dependent manner. Conversely, the overexpression of *OsNAC6* does not lead to hypersensitive cell death (Kaneda et al., 2009), whereas transgenic rice plants overexpressing *OsNAC6* exhibited tolerance to

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AAM65392          156  1.10e-28 NLSTAAKPPD LTTTRKNSLRLDDWVLCRIYKKNSSQRP TMERVLLRED
AAB71483          153  1.10e-28 NLSTAAKPPD LTTTRKNSLRLDDWVLCRIYKKNSSQRP TMERVLLRED
Os01g66120        138  2.10e-27 MHEYRLADVD RSARKKNSLRLDDWVLCRIYNKKGGLEK PPAAAVAAAG
AT1G01720         136  3.73e-27 HEYRLADVDR SVRKKKNSLRLDDWVLCRIYNKKGAERR GPPPPVVYGD
AT5G63790         179  6.51e-27 EYRLANVDRS ASTNKKNNLRLDDWVLCRIYNKKGTMEK YLPAAAEKPT
Os05g34830        147  7.81e-27 MHEYRLADVD RSARKKNTLRLDDWVLCRIYNKKGGVEK PSGGGGGERS
AT3G15510         155  1.89e-26 ENKPNNRPPG CDFGNKNSLRLDDWVLCRIYKKNNASRH VDNDKDHDMI
Os03g60080        149  7.19e-26 EYRLADAGRA AAGAKKGSLRLDDWVLCRLYNKKNEWEK MQQGKEVKEE
Os07g48450        156  4.56e-25 AAANTYKPSS SSRFRNVSMRLDDWVLCRIYKKSGQASP MMPPLAADYD
AT5G08790         137  9.38e-25 EYRLANVDRS ASVNKKNNLRLDDWVLCRIYNKKGMEKY FPADEKPRTT
AAM63330          140  1.24e-24 HEYRLHDSRK ASTKRSGSMRLDEWVLCRIYKKRGASKL LNEQEGFMDE
AT1G61110         154  3.25e-24 GNLSTAAKPP DLTTTRKSLRLDDWVLCRIYKKNSSQRP TMERVLLRED
AT1G52880         154  4.24e-24 RLTDNKPTHI CDFGNKKSLRLDDWVLCRIYKKNNSTAS RHHHHLHHIH
Os11g08210        145  1.05e-23 DVDRSAAARK LSKSSHNALRLDDWVLCRIYNKKGVIER YDTVDAGEDV
Os12g03040        151  4.63e-23 TSANNTTTTK QRRASSMTMRLDDWVLCRIHKKSNDFNS SDQHDQEPEG
Os11g03300        151  4.63e-23 TSANSTTTTK QRRASSMTMRLDDWVLCRIHKKSNDFNS SDQHDQEPEE
Os01g01430        177  4.63e-23 SNMKQLASSS SSSSSSASMRLDEWVLCRIYKKKEANQQ LQHYIDMMMD
AT1G69490         139  9.42e-23 HEYRLHDSRK ASTKRNGSMRLDEWVLCRIYKKGASKLL NEQEGFMDEV
AT3G04070         163  1.19e-22 SGGSEVNNFG DRNSKEYSMRLDDWVLCRIYKKSHASLS SPDVALVTSN
Os07g12340        149  1.19e-22 EYRLAKKGGA AAAAGAGALRLDDWVLCRLYNKKNEWEK MQSRKEEEEA
Os03g21060        152  2.10e-22 ADAHAANTYR PMKFRNTSMRLDDWVLCRIYKKSSHASP LAVPPLSDHE
Os01g60020        154  9.84e-22 HEYRLADADR APGGKKGSQKLDEWVLCRLYNKKNNWEK VKLEQQDVAS
AT1G52890         140  1.86e-21 NWIMHEYRLI EPSRRNGSTKLDDWVLCRIYKQSSAQKQ VYDNGIANAR
AT4G27410         140  2.54e-21 NWIMHEYRLI EHSRSHGSSKLDDWVLCRIYKTSGSQRQ AVTPVQACRE
Os07g37920        179  1.57e-20 TTRRPPPPIT GGSKGAVSLRLDDWVLCRIYKKTNKAGA GQRSMECEDS
Os05g34310        152  7.16e-17 GGSTASHPSL SSSTAHPSVKLDEWVLCKIFNKSPEPDN TAPPSNVVSR
AT2G33480         138  5.05e-14 NWVLHEYRLV DSQQDSLYGQNMNWVLCRVFLKKSNSNS KRKEDEKEEV
                                                WVLCR
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FIGURE 2 | Conserved motifs outside of the NAC domain of the SNAC/(IX) group in rice and Arabidopsis.

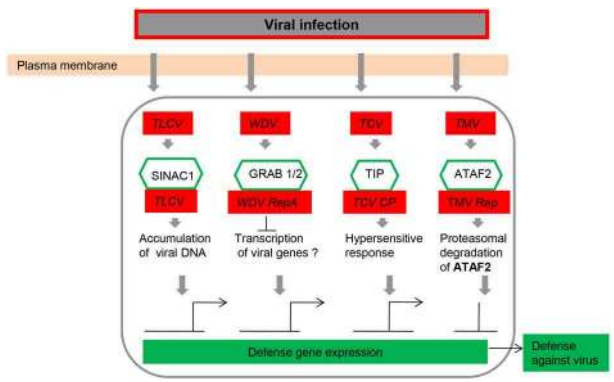

FIGURE 3 | NAC transcription factors as key components in the transcriptional regulation of gene expression during virus infection. Abbreviations: TCV, turnip crinkle virus; TIP, TCV-interacting protein; TLCV, tomato leaf curl virus; TMV, tobacco mosaic virus; WDV, wheat dwarf geminivirus.

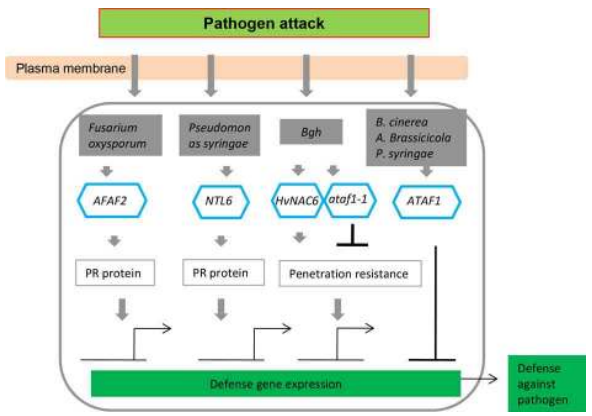

FIGURE 4 | NAC transcription factors as key components in transcriptional regulation of gene expression during pathogen attack, integrating both positive (arrows) and negative (bars) regulatory mechanisms.

blast disease (Nakashima et al., 2007). *ATAF2* overexpression resulted in increased susceptibility toward the necrotrophic fungus *Fusarium oxysporum* under sterile conditions due to the repression of pathogenesis-related (*PR*) genes (Delessert et al., 2005) but induced *PR* genes, reducing tobacco mosaic virus accumulation in a non-sterile environment (Wang et al., 2009b). RNA interference and overexpression studies have also revealed the function of NAC TFs in various plant–pathogen interactions (**Figure 4**). A number of NAC proteins may positively regulate plant defense responses by activating *PR* genes, inducing a hypersensitive response (HR), and cell death at the infection site (**Figure 4**; Jensen et al., 2007, 2008; Kaneda et al., 2009; Seo et al., 2010). *ATAF1* and its barley homolog *HvNAC6* positively regulate penetration resistance to the biotrophic fungus *Blumeria graminis* f.sp. *hordei* (*Bgh*) (Jensen et al., 2007, 2008) but attenuate the resistance to other pathogens, such as *Pseudomonas syringae*, *Botrytis cinerea*, and *Alternaria brassicicola* (Wang et al., 2009a; Wu et al., 2009). Unlike *ATAF2*, *ATAF1* and *HvNAC6* are transcriptional activators and may indirectly regulate the repression of *PR* genes via a hypothetical negative regulator (**Figure 4**). Hence, the ATAF subfamily clearly appears to have a conserved but non-redundant function in regulating the responses to different pathogens. The immune response in plants elicited upon pathogen infection is characterized by activation of multiple defense responses including expression of a large set of defense-related genes (van Loon et al., 2006), which are regulated by different types of TFs. Many TFs belonging to the NAC, ERF, and WRKY families have been identified (Eulgem and Somssich, 2007;

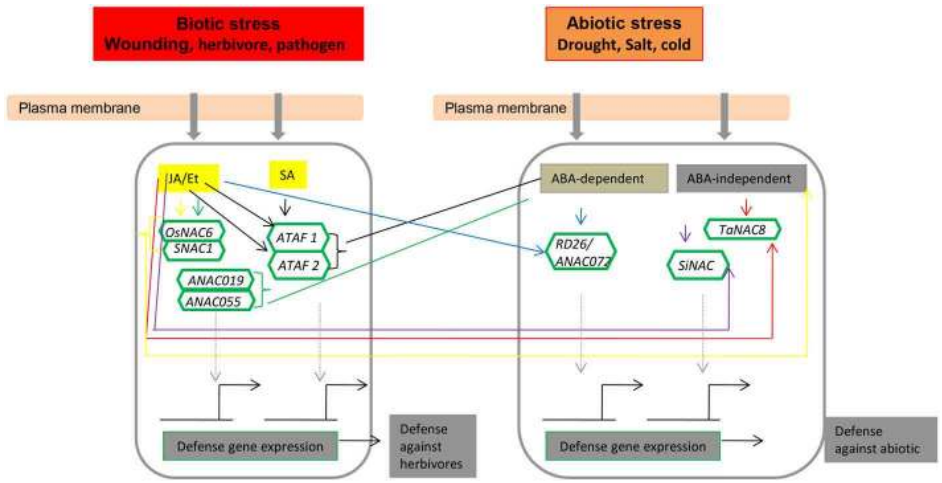

FIGURE 5 | The role of NAC transcription factors in the herbivore/biotic and abiotic response signaling pathway. Key to all colors: OsNAC6/SNAC1, yellow; ANAC019/ANAC055, green; ATAF1/ATAF2, black; TaNAC8, red; SiNAC, purple; RD26/ANAC072, blue. Abbreviations: ABA, abscisic acid; ANAC, *Arabidopsis thaliana* NAC; JA, jasmonic acid; Et, ethylene; and SA, salicylic acid.

Gutterson and Reuber, 2004) and revealed to play important roles in regulating expression of defense-related genes.

Arabidopsis stress-responsive *NAC* genes, such as *RD26*, respond to JA, a well-described phytohormone that is functionally involved in regulating wounding and biotic stress responses (Fujita et al., 2004, 2006). Hence, it is reasonable to consider that JA-responsive SNAC factors might function in both biotic and abiotic stress responses. In rice, most of the genes in the SNAC group respond to JA. Among them, *SNAC1*, *OsNAC3*, *OsNAC4*, *OsNAC5*, *OsNAC6*, and *OsNAC10* are present in the same phylogenetic SNAC/(IX) group (**Figure 1**). In particular, the SNAC group (**Figure 1**) comprises several genes that regulate disease resistance pathways, as inferred from the increased resistance to pathogens upon overexpression under the control of a constitutive promoter. Data indicate that NAC TFs also have an important role in the regulation of plant defense responses to different pathogens in addition to wounding and insect feeding (**Figure 5**). The application of exogenous phytohormones, such as JA, SA, and ET, has also been shown to induce *NAC* genes in several species (Tran et al., 2004; He et al., 2005; Hu et al., 2006; Sindhu et al., 2008; Lu et al., 2007; Nakashima et al., 2007; Yokotani et al., 2009; Zheng et al., 2009; Xia et al., 2010a,b; Yoshii et al., 2010; Nuruzzaman et al., 2012b). Hence, NAC TFs can possibly modulate the phytohormonal regulation of the biotic stress cellular network for convergent and divergent adaptive pathways.

NAC TFs IN ROS AND SENESCENCE SIGNALING PATHWAYS

Reactive oxygen species (ROS) is an active molecule in most biotic plant stress. Such ROS as H_2O_2 act as important signal transduction molecules, mediating the acquisition of tolerance to various stresses (Bhattacharjee, 2005; Davletova et al., 2005). In rice, *OsNAC6* gene is involved in both response and tolerance to biotic stress (Nakashima et al., 2007). In Arabidopsis, ATAF subfamily (*ATAF1*, *ATAF2*, and *RD26*) is also involved in biotic stress. The expression of *RD26* is induced by JA and H_2O_2, and pathogen infections (Fujita et al., 2004; Zimmermann et al., 2004). Large-scale transcriptiome analysis with both types of mutants revealed that *RD26*-regulated genes are involved in the detoxification of ROS, defense, and senescence (Fujita et al., 2004; Balazadeh et al., 2011). The role of stress-responsive NAC proteins in senescence is poorly understood. Recently, the *NTL4*, (Lee et al., 2012), *MtNAC969* (de Zélicourt et al., 2012), *Os07g37920*, wheat *GPC* (Distelfeld et al., 2012) genes were found to be induced senescence in different plants. Leaf senescence is a unique developmental process that is characterized by massive programmed cell death and nutrient recycling. Leaf senescence is induced by pathogen infection (Dhindsa et al., 1981; Buchanan-Wollaston et al., 2003; Gepstein et al., 2003). *AtNAP* gene, which belongs to the closest NAC subfamily of the ATAF subfamily, has been shown to be involved in senescence (Guo and Gan, 2006). In addition all ATAF subfamily *NAC* genes, including *ATAF1*, *ATAF2*, and *RD26*, are upregulated during senescence in Arabidopsis leaves (Guo et al., 2004). These findings suggest that *RD26* may function at the node of convergence between the pathogen defense and senescence signaling pathways. Taken together, these results support the notion that ROS and senescence may be closely related to NAC-mediated stress responses.

NAC FUNCTION IN ABIOTIC STRESS

The NAC TFs function as important components in complex signaling progresses during plant stress responses. Considering the relatively large number of NAC TFs from different plants and their unknown and diverse roles under complex environmental stimuli, it remains a considerable challenge to uncover their roles in abiotic stress. Until recently, the possible involvement of TF NAC proteins in abiotic stress responses was deduced indirectly from transcription profiling; recent functional analyses, however, have provided some direct evidence. The recent data presented here mainly summarize the function of most NAC TFs in regulating the transcriptional reprogramming associated with plant

Table 1 | Function of NAC transcription factors in biotic infections.

Genes/target genes	Functions	Method	Species	References
HvNAC6	*HvNAC6* positively regulates penetration resistant toward *Bl. gramini f.sp. hordei (Bgh)* attack	Knockdown/overexpression	*H. vulgare*	Jensen et al., 2007
ataf1-1	Loss-of-function mutants have attenuated penetration resistance toward *Bgh* attack	Knockout	*A. thaliana (At)*	Jensen et al., 2008
ATAF1, PR1	ATAF1 negatively regulates resistance to *B. cinerea*	Overexpression/*ataf1-1* and *ataf1-2*, knockout	*A. thaliana*	Wu et al., 2009
ATAF1, PR-1, PR-5, NPR1, PDF1.2	ATAF1 negatively regulates resistance to *P. syringae*, *B. cinerea*, *A. brassicicola*	Overexpression/*ataf1-2*, knockout	*A. thaliana*	Wang et al., 2009a
ATAF2, PR1, PR2, PR4, PR5, PDF1.1, PDF1.2	ATAF2 negatively regulates resistance to *F. oxysporum*, represses pathogenesis-related proteins	Overexpression/knockout	*A. thaliana*	Delessert et al., 2005
ATAF2, PR1, PR2, PDF1.2	OX = Reduced tobacco mosaic virus accumulation, increased pathogenesis-related genes	Overexpression/knockout	*A. thaliana*	Wang et al., 2009a
ATAF2, NIT2	Defense hormones, pathogen infection	Overexpression/knockout	*A. thaliana*	Huh et al., 2012
ANAC019, ANAC055	Defense disease, JA pathway	Overexpression	*A. thaliana*	Bu et al., 2008
NTL6, PR1, PR2, PR5	Positive regulator of pathogen resistance against *P. syringae*	Gene silencing/overexpression	*A. thaliana*	Seo et al., 2010
ANAC042, P450	Regulation of camalexin biosynthesis, pathogen infection	β- Glucuronidase (GUS)-reporter assays	*A. thaliana*	Saga et al., 2012
SlNAC1	Increased tomato leaf curl virus (TLCV) DNA accumulation	Transient overexpression	*N. benthamiana*	Selth et al., 2005
OsNAC4	Inducer of HR cell death upon *Acidovorax avenae* infection, loss of plasma membrane integrity, nuclear DNA fragmentation	Overexpression/knockdown	*Oryza (O) sativa*	Kaneda et al., 2009
OsNAC6, PR protein 1, Probenazoleinducible proteins (PBZ1s), DUF26- like Ser/Thr protein kinase, Thioredoxin, Peroxidase, Lipoxygenase,	Slightly increased tolerance to rice blast disease	Overexpression	*O. sativa*	Nakashima et al., 2007
rim1-1	Resistance to rice dwarf virus (RDV), susceptible to *rice* transitory yellowing virus (RTYV) and RSV	Knockout	*O. sativa*	Yoshii et al., 2009
Os02g34970, Os02g38130, Os11g03310, Os11g03370, Os11g05614, Os12g03050	RSV, RTSV infections	Microarray	*O. sativa*	Nuruzzaman et al., 2010
OsNAC19	Disease resistance	Infection	*O. sativa*	Lin et al., 2007
GRAB1, GRAB2	Inhibited wheat dwarf virus replication	Transient Overexpression	*T. monococcum*	Xie et al., 1999
ATAF2	Tobacco mosaic virus	Transgenic	*Tobaco*	Wang et al., 2009b
ONAC122 and *ONAC131* brome mosaic virus (BMV)	Defense responses against *Magnaporthe grisea*	–	*O. sativa*	Sun et al., 2013
SlNAC1	Upregulated during pseudomonas infection	Pathogen infection	*S. lycopersicum*	Huang et al., 2012
CaNAC1	Defense responses against pathogen	Infection	*C. arietinum*	Oh et al., 2005
GmNAC6	Responses to biotic signals, osmotic stress-induced	Transctiption	*G. max*	Faria et al., 2011
TLCV, SlNAC1	Enhances viral replication	Overexpression	*L. esculentum*	Selth et al., 2005
BnNAC14, BnNAC485, ATAF1 or ATAF2	Response to biotic and abiotic stresses including wounding	cDNA libraries	–	Hegedus et al., 2003
Stprx2, StNAC	Wounding and pathogen response	Transcriptome	*S. tuberosum*	Collinge and Boller, 2001

(Continued)

Table 1 | Continued

Genes/target genes	Functions	Method	Species	References
NT L4	ROS under abscisic acid, leaf senescence	Transgenic	*A. thaliana*	Lee et al., 2012
NTL9	Osmotic stress responses, leaf senescence	Overexpression/knocout	*A. thaliana*	Yoon et al., 2008
MtNAC969	Symbiotic nodule senescence	Overexpresion	*M. truncatula*	de Zélicourt et al., 2012
VNI2, OR/RD	Leaf senescence	Transcription	*A. thaliana*	Seo and Park, 2011
Os07g37920, Wheat GPC	Senescence	Overexpression/RNAi	*O. sativa, T. aestivum*	Distelfeld et al., 2012
AtNAP	Leaf senescence	Overexpression/RNAi	*A. thaliana*	Guo and Gan, 2006

abiotic responses (**Figures 5**, **6**; **Table 2**). The tight regulation and fine-tuning of *NAC* genes during plant stress responses contribute to the establishment of complex signaling webs, and the important roles of *NAC* genes in plant abiotic stress responses make them potential candidates for imparting stress tolerance.

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 agriculture 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 (**Figure 5**; Nakashima et al., 2009; Jeong et al., 2010), and *Os03g60080/SNAC1* increased grain yield (21–34%) under drought stress (Hu et al., 2006). 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 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 (Sindhu et al., 2008; 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* overexpression in rice resulted in significantly enhanced drought and osmotic stress tolerance. Plants overexpressing *GmNAC085* show enhanced drought tolerance (Le et al., 2011), whereas the overexpression 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., 2012b). *SiNAC* is also simultaneously induced by dehydration, salinity, ethephon, and methyl jasmonate treatments (Puranik et al., 2011). Similarly, the expression of *DgNAC1*, *TaNAC2a* and *EcNAC1* were strongly induced by NaCl and drought stresses in transgenic tobacco plants (Liu et al., 2011; Ramegowda et al., 2012; Tang et al., 2012). Several genes, such as *ZmSNAC1* (Lu

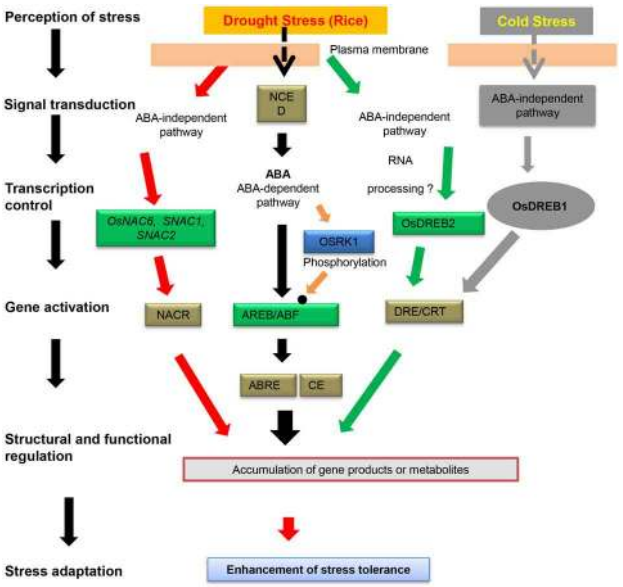

FIGURE 6 | Transcriptional regulatory networks of the *cis*-elements and NAC transcription factors involved in abiotic stress-induced gene expression in rice. The *cis*-elements involved in stress-responsive transcription are shown in white boxes. TFs controlling stress-inducible gene expression are shown in green boxes. Protein kinases involved in the phosphorylation of TFs are shown in blue boxes. The small solid black circle indicates TF modification, i.e., through phosphorylation, in response to stress signals.

Table 2 | Function of NAC transcription factors in abiotic stresses.

Genes	Functions	Method	Species	References
ANAC019/AT1G52890	Drought, high salinity, ABA signaling	Overexpression	*A. thaliana*	Tran et al., 2004
ANAC055/AT3G15500	Drought, high salinity, ABA signaling	Overexpression	*A. thaliana*	Tran et al., 2004
ANAC072/AT4G27410	Drought, high salinity, ABA signaling	Overexpression	*A. thaliana*	Tran et al., 2004
RD26, RD20, Glyoxalase, Glutathione, transferase, Aldo/keto reductase, senesence associated gene13, cinnamil-alcohol dehydrogenase	Drought, salt and ABA response	Overexpression	*A. thaliana*	Fujita et al., 2004
ANAC019, COR47, RD29b, FER1, ERD11	Cold, ABA signaling	Overexpression	*A. thaliana*	Jensen et al., 2010
anac092-1, ANAC083, ANAC041, ANAC054, ANAC084	Positive regulator of seed germination under salinity	Mutant	*A. thaliana*	Balazadeh et al., 2010
ntl8-1	Positive regulator of seed germination under salinity	Mutant	*A. thaliana*	Kim et al., 2008
ATAF1, COR47, ERD10, KIN1, RD22, RD29A	Positive regulator of drought tolerance	*knockouts (ataf1-1/2)*	*A. thaliana*	Lu et al., 2007
ATAF1, ADH1, RD29A, COR47	Positive regulator of drought tolerance	Overexpression	*A. thaliana*	Wu et al., 2009
ONAC063	Higher seed germination under high salinity and osmotic stress	Overexpression	*A. thaliana*	Yokotani et al., 2009
AhNAC2, RD29A, RD29B, RAB18, ERD1, AtMYB2, AtMYC2, COR47, COR15a, KIN1, AREB1, CBF1	Drought and salt tolerance	Overexpression	*A. thaliana*	Liu et al., 2011
GmNAC20, DREB1A/CBF3, KIN2/cor6.6, Cor15A, RD29A/cor78, ARF19, LBD12, AIR1	Salt and freezing tolerance	Overexpression	*G. max, A. thaliana*	Hao et al., 2011
NTL8	Salt tolerance, GA, and ABA pathway	Gene expression	*A. thaliana*	Kim et al., 2008
ANAC019, ANAC055	Defense disease, JA pathway	Overexpression	*A. thaliana*	Bu et al., 2008
XND1	Programmed cell death	Overexpression	*A. thaliana*	Zhao et al., 2008
LOV1	Cold response, photoperiod pathway	Overexpression	*A. thaliana*	Yoo et al., 2007
NAC1	Auxin, root development	Overexpression	*A. thaliana*	Guo et al., 2005
ZmSNAC1	Low temperature, high-salinity, drought stress, and abscisic acid (ABA)	Transgenic	*Z. mays*	Lu et al., 2012
NTL6, SnRK2.8	Drought-stress response	Overexpression/ RNAi	*A. thaliana*	Kim et al., 2012
ANAC019, ANAC055 and *ANAC072, ICS1* and *BSMT1*	Inhibits salicylic acid accumulation	Transgenic	*A. thaliana*	Zheng et al., 2012
TaNAC2	Drought, salt, and freezing stresses	Overexpression	*A. thaliana*	Mao et al., 2012
ANAC2/AT3G15510	Salt and ABA stress tolerance	Overexpression	*A. thaliana*	He et al., 2005
SNAC1/Os03g60080	Stomata close, higher seed setting	Overexpression	*O. sativa*	Hu et al., 2006
SNAC2/OsNAC6/Os01g66120	Salt, drought, disease resistance drought, salinity, cold, wounding, and abscisic acid (ABA) treatment	Overexpression	*O. sativa*	Sindhu et al., 2008
OsNAC5/ Os11g08210	ABA, salt, cold tolerance, grain filling	Overexpression	*O. sativa*	Sperotto et al., 2009
ONAC04/Os11g033005	Drought, salt, cold tolerance	Overexpression	*O. sativa*	Zheng et al., 2009
OsNAC10/Os11g03300	Root, panicle, drought, salt, ABA	Overexpression	*O. sativa*	Jeong et al., 2010
Ostil1	Shoot branching	Overexpression	*O. sativa*	Mao et al., 2007
RIM1/Os03g02800	JA pathway signaling	Mutant	*O. sativa*	Yoshii et al., 2010
Os07g04560, Os10g38834	Root, severe drought	Microarray	*O. sativa*	Nuruzzaman et al., 2012b

(Continued)

Table 2 | Continued

Genes	Functions	Method	Species	References
Os01g28050, Os01g29840	Leaf, severe drought	Microarray	*O. sativa*	Nuruzzaman et al., 2012b
Os03g12120, *Os03g59730*, *Os06g15690*, *Os08g06140*, *Os08g33670*	Panicle, severe drought	Microarray	*O. sativa*	Nuruzzaman et al., 2012b
Os12g41680, *Os07g48550*, *Os11g03300*, *Os12g03040*, *Os01g66120*, *Os05g34830*,	Cold, drought, submergence, laidown-submergnece	Microarray	*O. sativa*	Nuruzzaman et al., 2010
Os02g34970, *Os07g48450*, *Os01g01430*, Os01g48460	Drought, submergence, laidown-submergnece	Microarray	*O. sativa*	Nuruzzaman et al., 2010
OsOAT, *SNAC2*	Drought and oxidative stress tolerance	Overexpression	*O. sativa*	You et al., 2013
SNAC1, *OsSRO1c*	Oxidative stress tolerance	Overexpression	*O. sativa*	You et al., 2013
TaNAC69	PEG-induced dehydration	Overexpression	*T. aestivum*	Xue et al., 2011
GmNAC11, *DREB1A*, *ERD11*, *Cor15A*, *ERF5*, *RAB18*, *KAT2*	Salt tolerance in soybean transgenic hairy roots	Overexpression	*G. max*	Hao et al., 2011
GmNAC glycoside hydrolases, defensins and glyoxalase I family proteins	Drought stress	Soybean array GeneChip	*G. max*	Le et al., 2011
GmNAC085	Dehydration stress	Soybean Affymetrix array	*G. max*	Le et al., 2011
TaNAC2a	Drought tolerance	Overexpression	*N. tabacum*	Tang et al., 2012
DgNAC1	ABA, NaCl, drought and cold	Overexpression	*N. tabacum*	Liu et al., 2011
CarNAC3	Seed germination, drought, ethephon, ABA, IAA signaling	Transcriptome	*C. arietinum*	Peng et al., 2009
miR319, AsNAC60	Drought and salinity stress		*Agrostis stolonifera*	Zhou et al., 2013
EcNAC1	Water-deficit and salt stress	Overexpression	*N. tabacum*	Ramegowda et al., 2012
AhNAC2	Salt	Overexpression	Arachis	Liu et al., 2011
RhNAC2 or *RhEXPA4*	Dehydration tolerance	Transgenic	*R. hybrida*	Dai et al., 2012
ClNAC	Hormonal treatments including salt, drought, cold, heat, abscisic acid and salicylic acid treatments	Reverse transcriptase polymerase chain reaction	*C. lavandulifolium*	Huang et al., 2012
CsNAM	Drought, osmoticum, salt, heat and hydrogen peroxide		*Camellia sinensis*	Paul et al., 2012
Os04g0477300	Boron-toxicity tolerance	RNA interference	*O. sativa*	Ochiai et al., 2011
SiNAC	Dehydration, salinity, ethephon, and methyl jasmonate.	Transcription	*S. italica*	Puranik et al., 2011
ANAC102	Waterlogging	Overexpression	*A. thaliana*	Christianson et al., 2009
HSImyb and *HSINAC*	Gibberellin response	Transcript	*H. vulgare*	Robertson, 2004
ANAC042 it is also in biotic	Heat stress	Overexpression	*A. thaliana*	Shahnejat-Bushehri et al., 2012
TaNAC2a, *TaNAC4a*, *TaNAC6*, *TaNAC7*, *TaNAC13* and *TaNTL5*	Dehydration, salinity and low temperature	Transgenic	*T. aestivum*	Tang et al., 2012
TaNAC4	Environmental stimuli, including high salinity, wounding, and low-temperature also induced	Transcription	*T. aestivum*	Xia et al., 2010a
ONAC063	High-temperature and high-salinity	Transactivation	*O. sativa*	Yokotani et al., 2009

et al., 2012), *TaNAC69* (Xue et al., 2011), *CarNAC3* (Peng et al., 2009), *miR319, AsNAC60* (Zhou et al., 2013), *AhNAC2* (Liu et al., 2011), *RhNAC2* or *RhEXPA4* (Dai et al., 2012), *ClNAC* (Huang et al., 2012), *CsNAM* (Paul et al., 2012), *SiNAC* (Puranik et al., 2011), *HSImyb* and *HSINAC* (Robertson, 2004), and *TaNAC2a, TaNAC4a, TaNAC6*, and *TaNAC4* (Tang et al., 2012; Xia et al., 2010a), were increased by drought and NaCl (**Figure 5**; **Table 2**).

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 (Fujita et al., 2006; Miller et al., 2008). The NAC TFs form a complex but interesting group of important arbitrators of this process (**Figure 5**). *ANAC019* and *ANAC055* are involved in both ABA- and JA-mediated regulation (Greve et al., 2003; Bu et al., 2008, 2009; Jensen et al., 2010). The ATAF subfamily TFs are another group of NAC proteins that act at the convergence point of biotic and abiotic stress signaling (Delessert et al., 2005; He et al., 2005; Jensen et al., 2007). Because *ATAF1* alleles expedite drought perception at the cost of optimal basal defense, ATAF1 acts as a negative regulator of ABA signaling but induces JA/ET-associated defense signaling marker genes (Jensen et al., 2008). Conversely, *ATAF2* expression was induced by dehydration, JA, and SA (**Figure 5**; Delessert et al., 2005). We have proposed the participation of *SiNAC* in the ABA-independent pathway of abiotic stress and in regulating biotic stress via an antagonistic JA and SA pathway (Puranik et al., 2011). A number of *NAC* genes (e.g., *AtNAC2*) in plants are affected by auxin, ethylene (Xie et al., 2000; He et al., 2005), and ABA (e.g., *OsNAC5*; Sperotto et al., 2009). In Arabidopsis, NAC TF *NTL8* regulates GA3-mediated salt signaling in seed germination (Kim et al., 2008). 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 (Xie et al., 2000; 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 (Nakashima et al., 2007), a transcriptional regulatory system that is known as a regulon. ABA is produced under conditions of drought stress and plays a crucial role in drought tolerance in plants (**Figure 6**; Shinozaki et al., 2003). In addition to NAC and other regulons, *OsDREB2* responds to dehydration in rice (Dubouzet et al., 2003); the dehydration-responsive element binding protein 1 (DREB1)/C-repeat-binding factor (CBF) and DREB2 regulons 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 (**Figure 6**; Chae et al., 2007). Both ABA-independent and ABA-dependent signal transduction pathways convert the initial stress signal into cellular responses (**Figures 5**, **6**). The TF family members involved in both ABA-independent (AP2/ERF, bHLH, and NAC) and ABA-dependent (MYB, bZIP, and MYC) pathways are up-regulated in rice; the TFs belonging to this family interact with specific *cis*-elements and/or proteins, and their overexpression confers stress tolerance in heterologous systems (Fujita et al., 2004; Tran et al., 2004; 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 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 agriculture, 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 (*ONAC063*) in rice roots responds to a combination of high-temperature stress (Yokotani et al., 2009). Another example is that transgenic Arabidopsis plants overexpressing *ANAC042* show increased tolerance to heat stress when compared to the wild-type plants (Shahnejat-Bushehri et al., 2012). Moreover, the overexpression of *ZmSNAC1* 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 (Jeong et al., 2010; Xia et al., 2010a; Tang et al., 2012), and a gene expressing a CsNAM-like protein is induced by heat in tea plants (Paul et al., 2012). Northern blot and SNAC2 promoter activity analyses suggest that the *SNAC2* gene is induced by low temperature. Additionally, a microarray analysis of rice *NAC* genes has revealed that 8 of the 14 analyzed *OsNAC* genes are regulated by severe or mild drought stress (Nuruzzaman et al., 2012b), showing distinct expression patterns upon high-temperature treatment. Yoo et al. (2007) reported that the phenotype resulting from the overexpression 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 adaptions 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 (Blamey et al., 1997), B toxicity occurs in many plants at levels only slightly above that required for normal growth (Mengel and Kirkby, 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, an NAC-like TF, and unknown proteins were induced (Kasajima and Fujiwara, 2007), 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. These studies provide a valuable basis for the identification of new regulatory genes and promoter elements to further the understanding of Pi-dependent gene regulation. With a focus on the Arabidopsis transcriptome, 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.

ONE NAC FOR MULTIPLE PROCESSES

Numerous studies have demonstrated that a single TF may function in several seemingly disparate signaling pathways, as can be deduced from their induced expression profiles by various stress factors. *OsNAC6* was induced by JA, a plant hormone that activates defense responses against herbivores and pathogens (**Figures 5**, **6**; Ohnishi et al., 2005). Studies on an *NAC* gene (*Os04g0477300*) showed that it functions in at least three different processes, including pathogen defense, senescence, and responses to phosphate and boron deficiency (Uauy et al., 2006; Waters et al., 2009; Nilsson et al., 2010; Ochiai et al., 2011). A number of *NAC* genes (e.g., *AtNAC2*) in plants are affected by auxin, ethylene (Xie et al., 2000; He et al., 2005), and ABA (e.g., *OsNAC5*; Sperotto et al., 2009). *Os05g34830* (SNAC group, **Figure 1**) was specifically induced in the roots of a tolerant line under severe and mild drought conditions and was activated by ABA treatment (Nuruzzaman et al., 2012b). *OsNAC5*/*ONAC009*/*ONAC071* and *OsNAC6* are homologs that are induced by pathogen infection and such abiotic stresses 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 (Xie et al., 2000; He et al., 2005). The *TaNAC4* gene functions as a transcriptional activator involved in wheat responses to abiotic and biotic stresses (Xia et al., 2010a). *SiNAC* transcripts mostly accumulate in young spikes and were strongly induced by dehydration, salinity, ethephon, and methyl jasmonate (Distelfeld et al., 2012). These data demonstrate that a single *NAC* gene can function as regulator of several different processes and may also mediate the cross-talk between different signaling pathways.

CONCLUSION

The responses to the environment are specialized through the diversification of the structure of stress-response regulators, 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. This review summarizes the current knowledge of the genes and NAC TFs that comprise a portion of this network. Interestingly, all of the SNAC sequences known to play a role in disease resistance responses are in one group of the NAC family. Much progress in NAC TF functional research has been attained over the past decade. However, most of these advances are related to the involvement of biotic stress. The identification of NAC functions in biotic and abiotic stresses will remain a substantial challenge in the coming years. To achieve a better understanding of their role during both types of stress, it is very important to identify the interacting partner of NAC proteins that cooperates in regulating the transcription of downstream target genes under a specific condition. It is also crucial to identify the key components of the signal transduction pathways with which these factors physically interact. Applying data obtained from microarrays could help to directly determine the specific NAC DNA-binding sites on a global scale under conditions of biotic and abiotic stress. Accordingly, we may then appreciate the complex mechanisms of signaling and transcriptional reprogramming controlled by NAC proteins and the plant processes in which they participate. Certainly, further molecular studies of NAC NFs under different stresses will clarify the fine-tuning mechanisms that are controlled by NAC proteins in plants, with economical benefits to agricultural production.

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