

REVIEW

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Plant NAC transcription factors in the battle against pathogens

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Abstract

Background The NAC transcription factor family, which is recognized as one of the largest plant-specific transcription factor families, comprises numerous members that are widely distributed among various higher plant species and play crucial regulatory roles in plant immunity.

Results In this paper, we provided a detailed summary of the roles that NAC transcription factors play in plant immunity via plant hormone pathways and reactive oxygen species pathways. In addition, we conducted in-depth investigations into the interactions between NAC transcription factors and pathogen effectors to summarize the mechanism through which they regulate the expression of defense-related genes and ultimately affect plant disease resistance.

Conclusions This paper presented a comprehensive overview of the crucial roles that NAC transcription factors play in regulating plant disease resistance through their involvement in diverse signaling pathways, acting as either positive or negative regulators, and thus provided references for further research on NAC transcription factors.

Keywords NAC transcription factor, Plant immunity, Hormone, ROS, Effector

Background

Due to the increasing severity of global climate change, plants are facing more challenges, and plant diseases are becoming more common worldwide. Over time, plants have evolved a series of complex defense strategies to combat infection by pathogens, including bacteria, fungi, viruses, oomycetes, etc. Transcriptional regulation is one of the important regulatory methods. Transcription factors (TFs) activate or repress the expression of relevant genes during plant immunity and subsequently cause a stress response to withstand the detrimental effects inflicted by pathogens. Notably, members of the NAC transcription factor family participate in plant immunity via diverse signaling pathways. In this review, we summarized the recent research progress on the mechanism of NAC transcription factors in the regulation of disease resistance in various plants and elaborated upon the

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intricate roles of NAC transcription factors played in the complex regulatory network governing plant immunity.

NACs as important components in plant immunity

Plant diseases occur worldwide and seriously affect the yield and quality of food crops. Some rare plant species are also on the verge of extinction due to biotic stress, which causes severe damage to plant diversity. By studying plant immunity, scientists can understand the mechanism of interaction between plants and pathogens, thereby revealing the operational mechanism of plant immune systems, which plays an important role in disease-resistance breeding. As reported, in the arms race against pathogens, plants have evolved powerful immune systems. The immune system of plants can be divided into two main layers. The initial layer is the immune response triggered by pathogen-associated molecular patterns (PAMPs), termed as PAMP-triggered immunity (PTI); this layer comprises a series of immune responses activated by pattern recognition receptors (PRRs) on the surface of plant cells that recognize PAMPs. Pathogens employ a variety of strategies to counteract PTI, including the secretion of toxic effectors. In response, plants have evolved nucleotide-binding leucine-rich repeat receptor (NLR) proteins to monitor effectors and repress their activity and thus enhance their resistance; therefore, this layer of immunity is called effector-triggered

immunity (ETI) [1]. In plants, disease resistance proteins act as major immune receptors that are responsible for detecting pathogens and initiating robust defense mechanisms. For example, the disease resistance protein HopZ-activated resistance 1 (ZAR1) and other proteins in plants are transformed into a highly ordered protein complex called the “resistosome”, which detects invading pathogens and thus triggers cell death and immune responses [2–4] (Fig. 1A).

During the long-term evolutionary process between plants and pathogens, PTI and ETI constitute the two main lines of active defense in plants. Studies have demonstrated that the two immune pathways, known as PTI and ETI, collaborate synergistically to contribute to plant disease resistance through calcium signals, hormones, reactive oxygen species (ROS), and other pathways [5–8]. In the interaction between plants and pathogens, transcription factors, as key elements in the responses to pathogen infection, transmit signals to genes related to the defense response and thereby activate or repress gene expression. This process enables plants to mount stress responses, which help them resist the damage caused by pathogen infection. Plants have many transcription factors, such as AP2/ERF, MYB, bZIP, WRKY, bHLH, NAC, etc., which are involved in the transcriptional regulation of plant defense-related genes [9–11]. Notably, the NAC transcription factor family, which is recognized as one

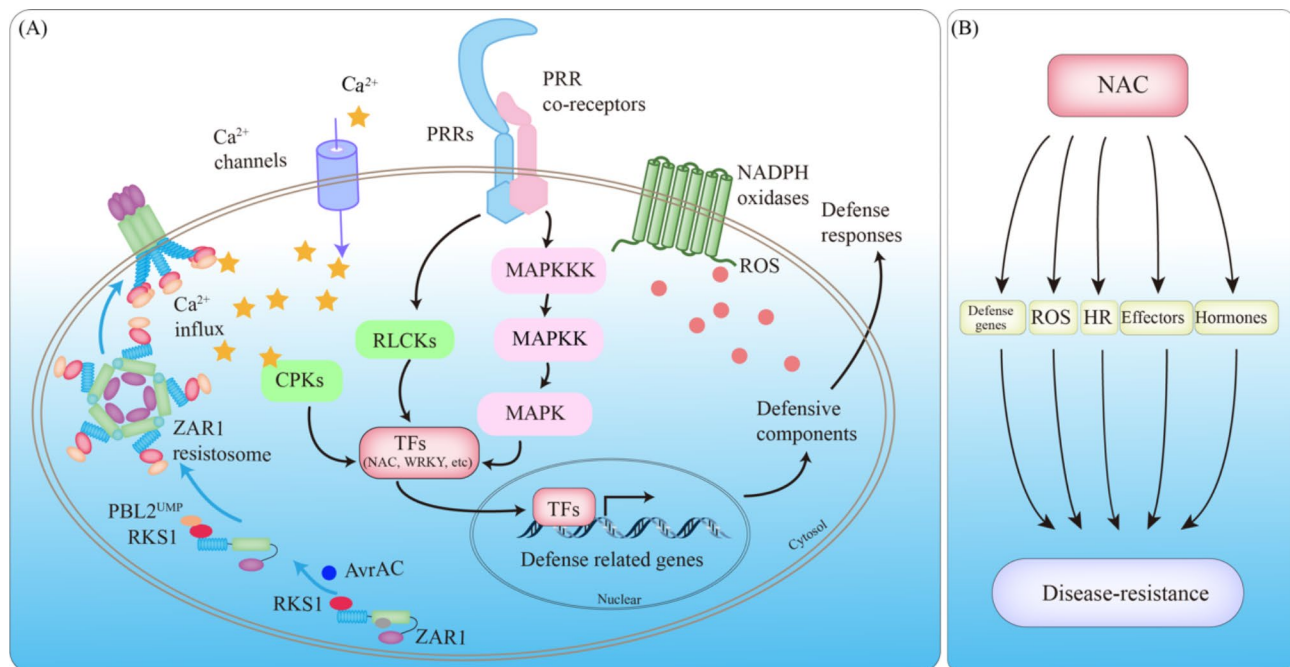


Fig. 1 Important regulatory components in plant immunity. (A) Different components regulate resistance in plants. PRRs, pattern recognition receptors; CPKs, calcium-dependent protein kinases; RLCKs, receptor-like cytoplasmic kinases; PBL2, a receptor-like cytoplasmic kinase; PBL2^{UMP}, uridylylated PBL2; RKS1, resistance-related kinase 1; ZAR1, HopZ-activated resistance 1; TFs, transcription factors; MAPK, mitogen-activated protein kinase; MAPKK, MAPK kinase; MAPKKK, MAPKK kinase; ROS, reactive oxide species. (B) Different pathways of NAC transcription factors are involved in plant disease resistance regulation. HR, hypersensitivity response

of the largest plant-specific transcription factor families, comprises numerous members that are widely distributed among various higher plant species. According to statistics from the Plant Transcription Factor Database (<http://planttfdb.gao-lab.org/>) [12], researchers have found 138 NAC members in *Arabidopsis thaliana*, 328 members in *Oryza sativa*, 263 members in *Triticum aestivum*, 189 members in *Zea mays*, and 411 members in *Brassica napus*. Vranic et al. conducted transcriptome sequencing of wheat tissues infected with several major fungal pathogens and found that 146 *TaNACs* were affected by fungal infection [13], indicating that NAC transcription factors occupy a large proportion of the total population and play important roles in the immune regulatory system of plants. In the battle against various pathogens, NAC transcription factors participate in the regulation of resistance to diseases in different ways, such as by directly regulating defense genes, plant hormone signaling, ROS, the hypersensitivity response (HR), and interactions with effectors from pathogens (Fig. 1B). Besides, other pathways, such as endoplasmic reticulum homeostasis, were recently reported to participate the rice blast disease resistance by the HVA22-like protein 1-NAC with transmembrane motif-like 6(OsHLP1-OsNTL6) complexes [14]. In this paper, we mainly summarized the research progress of NAC transcription factors in protein structure, classification, interactions with effectors from pathogens, crop improvement and roles played in pathways related to hormone signaling, ROS, and HR.

Structure and classification of NAC transcription factors

The NAC transcription factor was named after the acronym for NAM (No Apical Meristem) in *Petunia hybrida*, ATAF1/2 (Arabidopsis transcription activation factor 1/2) and CUC1/2 (cup-shaped cotyledon 1/2) in *A. thaliana*. In 1996, Souer et al. successfully cloned the first NAC gene, *NAM*, from *Petunia hybrida*. The mutant *nam* line exhibited an inability to form apical meristems, resulting in the failure of the plants to develop into stems and leaves [15]. Subsequently, ATAF1/2 and CUC1/2, which possess a structure similar to that of NAM, were discovered in *A. thaliana* [16]. These proteins share a common structural characteristic in their sequence, namely the presence of a NAC domain consisting of approximately 150 amino acids located in the N-terminal region of the NAC transcription factor (Fig. 2A). This particular domain is usually divided into five subdomains, namely A, B, C, D, and E, and sequence alignment of NAC domains in *A. thaliana* and *Oryza sativa* reveals the amino acid sequence characteristics of the five subdomains (Fig. 2B). In *Oryza sativa*, overexpression of some NACs, such as *OsNAC066* [17], *OsNAC096* [18], *OsNAC6* [19], and *OsNAC111* [20], increased resistance to blast disease as shown in the pictorial representation

in the Fig. 2C. Among these subdomains, the A, C, and D domains are relatively conserved, with C and D containing nuclear localization signal sequences, and these sequences are associated with the structure of promoter *cis*-acting elements specific to certain genes. The B and E domains exhibit variability and lack conservation among various NAC proteins, which may account for the functional diversity of different NAC proteins [21]. An X-ray diffraction analysis of the NAC-conserved domains of the ANAC019 and OsNAC1 transcription factors reveals a unique three-dimensional crystal structure, and unlike the typical helix-angle-helix structure, this new structure consists of several α -helices surrounded by a twisted inverse parallel β -fold [22, 23]. The C-terminal region of NAC proteins is highly diverse and functions as a transcriptional regulatory region capable of activating or repressing transcription. A common characteristic of this region is the frequent occurrence of some simple amino acids, including serine, threonine, proline, glutamic acid, or acidic amino acid residues [24]. As reported, proteins belonging to the same subgroup exhibit a higher degree of structural similarity and are likely to have similar biological functions [25].

Through a comprehensive analysis of NAC family genes, Ooka et al. divided them into two major groups based on the predicted and known sequence similarity of NAC domains and further subdivided them into 18 subgroups. Group I comprises 14 subclasses, namely TERN, ONAC022, SENU5, NAP, ATNAC3, ATAF, OsNAC3, NAC2, ANAC011, TIP, OsNAC8, OsNAC7, NAC1 and NAM, and Group II contains four subclasses ANAC001, ONAC003, ONAC001, and ANAC063 [25]. Based on the NAC transcription factor sequences of *Oryza sativa* subsp. *japonica* and *A. thaliana* in the Plant Transcription Factor Database, we constructed a phylogenetic tree to analyze the groups of transcription factors. Currently, the transcription factors included in the database are classified into reported groups, and new subfamilies have emerged (Fig. 2D). With the gradual discovery of NAC family transcription factors, the classification of transcription factor subfamilies is also being updated. Fang et al. conducted a systematic sequence analysis of 140 NAC or NAC-like genes in rice and categorized the NAC family members into five distinct groups (I~V), and the majority of the reported NAC genes associated with stress were classified as class III [26]. Pereira-Santana et al. subsequently performed an evolutionary analysis using 2016 nonredundant sequences from 24 different green plants to divide the NAC family members into six major subgroups, and the third subgroup, also known as the transmembrane motifs (TMM) group, encompasses all NTL sequences identified in *Arabidopsis thaliana*; these sequences are involved mainly in the responses to environmental factors and stress signals [27]. Through

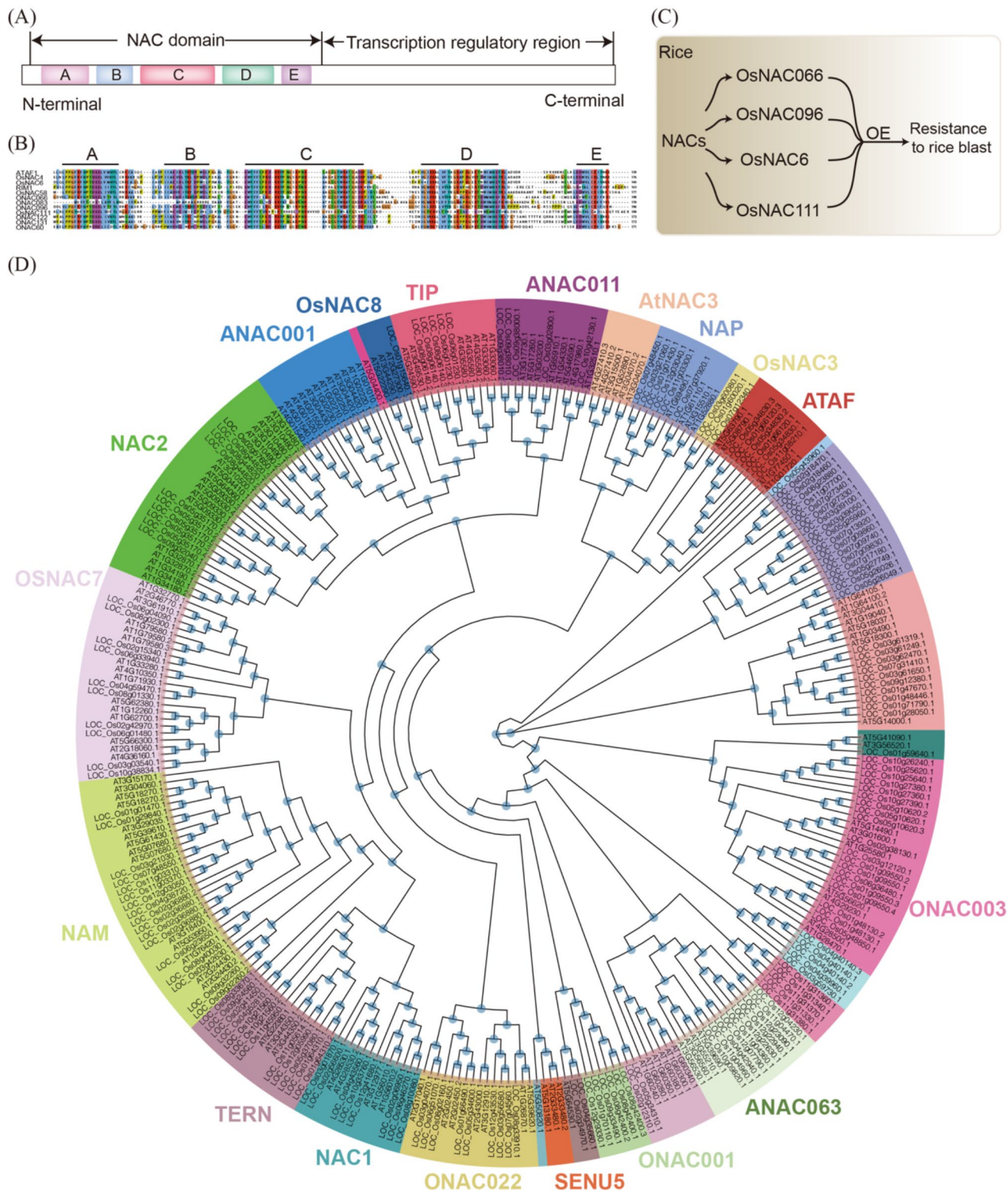


Fig. 2 Structural analysis and classification of NAC proteins. (A) Schematic diagram of the typical NAC protein structure. NAC proteins consist of a relatively conserved NAC domain located at the N-terminal region and a variable transcriptional regulatory region located at the C-terminal region. (B) Sequence alignment of NAC domains of some NAC genes involved in resistance to pathogen in *A. thaliana* and *Oryza sativa*. The NAC domain is divided into five main subdomains (A~E). (C) Pictorial representation for transgene technology of rice for resistance to blast disease. OE, overexpression of NAC gene in rice. (D) Phylogenetic tree of the NAC family TFs in *Oryza sativa* and *A. thaliana*. MUSCLE software (version 3.8) [29] was used for multiple sequence alignment, and a rootless evolutionary tree analysis was then performed using TreeBest software. The phylogenetic tree was visualized with the 'ggtree' package (version 3.2.1) [30] in R (version 4.1.2)

a phylogenetic analysis of garden asparagus (*Asparagus officinalis*) and *A. thaliana*, Li et al. divided the 85 NAC genes identified in *A. officinalis* into 14 subgroups. By examining the *cis*-acting elements in the promoter region, researchers observed that genes with similar gene structures and motif distributions were classified into the same group, and the *cis*-acting elements could be roughly divided into four categories: light response, stress response, hormone response, and plant growth and development related elements [28].

In summary, despite significant variations in the protein structure of NAC transcription factors across different members, there remains a discernible pattern. Specifically, differences in protein structure are responsible for variations in their respective biological functions. Therefore, future investigations of the structure of NAC proteins hold significant reference values for the analysis and exploration of their functional mechanism.

NACs participate in disease resistance via phytohormones

Phytohormones serve as crucial signal molecules that play pivotal roles in the signal transduction process of plant disease resistance. The hormones involved in plant disease responses include salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), ethylene (ETH), etc. NAC transcription factors are involved in many processes, and after receiving direct or indirect stimulation from pathogen invasion, different members of the NAC transcription factor gene family bind to corresponding *cis*-acting elements in promoter regions to regulate the expression of genes related to different hormone synthesis or hormone signal transduction pathways and thus enhance the plant defense response (Table 1).

SA signaling pathway

SA is one of the most widely reported plant hormones involved in plant responses to biological stress. As a mobile signaling molecule, SA plays an important role in the local and systemic acquired immunity of plants against pathogens [56]. Many studies have shown that NAC transcription factors participate in stress responses through the SA-mediated immune pathway. The specific manifestations are mainly related to the transcriptional regulation of SA biosynthesis and SA signaling pathway response-related genes. In *Arabidopsis*, NTL9 enhances the endogenous level of SA in plants and mediates stomatal immunity by positively regulating the genes that encode the key enzyme isochlorogenic acid synthase 1 (ICS1) involved in SA biosynthesis and two other SA synthesis-related enzymes, phytoalexin-deficient 4 (PAD4) and enhanced disease susceptibility 1 (EDS1), to restrict the rapid invasion of pathogens [31]. In addition, ANAC019/ANAC055 (AT3G15500)/ANAC072 inhibit *ICS1* and

activate *benzoic acid and salicylic acid methyltransferase 1 (BSMT1)* and salicylic acid glucosyltransferase 1 (*SAGT1*), while reducing the biosynthesis of SA and enhancing the metabolism of SA, thereby reducing the accumulation of SA in plants and negatively regulating the resistance to *Pseudomonas syringae* [32]. Another recent study showed that NAC3 (AT3G29035) can activate the transcription of *ICS1*, thus enhancing the ability of plants to resist bacteria and viruses. However, excessive immunity affects plant growth and development. In the process of pathogen infection, a long noncoding RNA (lncRNA) called salicylic acid biogenesis controller 1 (SABC1) can reduce the transcription of *NAC3* through H3K27me3, thus decreasing the production of SA. The regulatory mechanism helps maintain hormones at a homeostatic level and maintains the growth and immune balance in plants [36].

JA signaling pathway

JA is reportedly involved in plant growth and development processes such as seed germination, root growth, stamen development, and senescence, as well as in stress responses, especially resistance to pathogenic invasion [57]. Bu et al. investigated the involvement of two NAC genes in the signal transduction of JA and found that *ANAC019* acts downstream of myelocytomatosis protein 2 (AtMYC2) and plays a positive role in enhancing the resistance against *B. cinerea* [33]. Wheat powdery mildew caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*) is widely prevalent worldwide. Zhou et al. identified the differentially expressed NAC genes *TaNAC6-A*, *TaNAC6-B*, and *TaNAC6-D* in wheat and found these *TaNAC6s* could be significantly induced by methyl jasmonate (MeJA), which in turn regulated the JA signaling pathway through a feedback mechanism, and The results of inoculation of pathogens with *TaNAC6s*-overexpressing and *TaNAC6s*-knockdown lines showed that *TaNAC6s* positively regulated broad-spectrum resistance to wheat powdery mildew [44]. The NAC transcription factor rice dwarf virus multiplication 1 (RIM1) has been identified in rice, and *rim* mutants show upregulated expression of several JA biosynthesis pathway genes, such as *lipoxygenase (LOX)*, *alleneoxidase 2 (AOS2)*, and *12-oxophytodienoic acid reductase 7 (OPR7)*, which increases the resistance to rice dwarf virus [47]. In poplar, the JA signaling suppressor JA-ZIM-domain protein 5 (PtoJAZ5) forms complexes with the NAC transcription factor wood-associated NAC domain transcription factors 6 A (WND6A) or the MYB transcription factor MYB3 to regulate the expression of genes involved in lignin and secondary cell wall synthesis, which mediates JA-induced plant immunity [46]. The NAC transcription factor CmNAC083 was recently identified in chrysanthemum. Transcriptomic sequencing data from wild-type

Table 1 NAC transcription factors mediate plant immunity through hormone signaling

Species	Transcription factor	Hormone	Mechanism	Function	References
<i>Arabidopsis thaliana</i>	NTL9	SA	Positive regulation of <i>ICS1</i> , <i>PAD4</i> and <i>EDS1</i>	Positive regulation of stomatal immunity	[31]
<i>Arabidopsis thaliana</i>	ANAC019/ ANAC055/ ANAC072	SA, JA, ABA	Repression of <i>ICS1</i> and activation of <i>BSMT1</i> ; positive regulation of <i>VSP1</i> and <i>LOX2</i> ; H3K-27me3 level regulated by the PRC2 complex	Negative regulation of resistance to <i>Pseudomonas syringae</i> ; positive regulation of resistance to <i>Botrytis cinerea</i>	[32–35]
<i>Arabidopsis thaliana</i>	NAC3	SA	Activation of <i>ICS1</i>	Positive regulation of resistance to <i>Pseudomonas syringae</i> and <i>TuMV</i>	[36]
<i>Arabidopsis thaliana</i>	NST1	ABA	Interaction with SnRK2.2/3/6	Regulation of secondary cell wall synthesis	[37]
<i>Arabidopsis thaliana</i>	ATAF1	SA, JA, ETH, ABA	Repression of <i>PRs</i> ; negative regulation of <i>AAO3</i>	Negative regulation of resistance to <i>P. syringae</i> pv. <i>Tomato (Pst)</i> DC3000, <i>B. cinerea</i> and <i>Alternaria brassicicola</i> ; positive regulation resistance to <i>Blumeria graminis</i> f. sp. <i>Hordei (Bgh)</i>	[38–40]
<i>Arabidopsis thaliana</i>	ATAF2	SA, JA	Repression of the expression of defense genes such as <i>PR1</i> and <i>PDF1.2</i>	Negative regulation of resistance to <i>Fusarium oxysporum</i>	[41]
<i>Arabidopsis thaliana</i>	ANAC032	SA, JA	Repression of <i>MYC2</i> , <i>NIMIN1</i> and activation of <i>PDF1.2A</i>	Positive regulation of resistance to <i>Pst</i>	[42]
<i>Triticum aestivum</i>	TaNAC1	SA, JA, ETH	Suppression of <i>PR1</i> , <i>PR2</i> and <i>AtWRKY70</i>	Negative regulation of resistance to <i>Pst</i> and <i>Puccinia striiformis</i> f. sp. <i>tritici</i>	[43]
<i>Triticum aestivum</i>	TaNAC6s	JA	Induction of expression by MeJA and feedback regulation of the JA signaling pathway	Positive regulation of broad-spectrum resistance to wheat powdery mildew	[44]
<i>Triticum aestivum</i>	TaNACL-D1	JA, ABA	Overexpression plants show increased expression of genes involved in detoxification, the immune response, secondary metabolism, hormone biosynthesis and signaling	Positive regulation of resistance to <i>Fusarium head blight (FHB)</i> disease	[45]
<i>Populus tomentosa</i>	WND6A	JA	Interaction with PtoJAZ5	Regulation of lignin and secondary cell wall synthesis	[46]
<i>Oryza sativa</i>	RIM1	JA	<i>LOX</i> , <i>AOS2</i> and <i>OPR7</i> are upregulated in the rim1 mutants	Participation in the multiplication of rice dwarf virus	[47]
<i>Oryza sativa</i>	ONAC122, ONAC131	SA, JA, ETH	Positive regulation of the expression of <i>OsLOX</i> , <i>OsPR1a</i> , <i>OsWRKY45</i> and <i>OsNH1</i>	Positive regulation of resistance to rice blast	[48]
<i>Oryza sativa</i>	ONAC066	ABA	Repression of <i>LIP9</i> and <i>NCED4</i>	Positive regulation of resistance to rice blast and bacterial blight	[17]
<i>Hordeum vulgare</i>	HvNAC6	ABA	Positive regulation of <i>HvNCED1</i> and <i>HvNCED2</i> , and negative regulation of <i>HvBG7</i>	Positive regulation of resistance to <i>Bgh</i>	[49]
<i>Gossypium spp.</i>	GhATAF1	ABA, SA, JA	Repression of JA-mediated signals and activation of SA-mediated signals	Negative regulation of resistance to <i>V. dahliae</i> and <i>B. cinerea</i>	[50]
<i>Solanum lycopersicum</i>	JA2, JA2L	ABA, JA, SA	JA2 positively regulates <i>SINCE1</i> , and JA2L positively regulates SA metabolism-related genes	Regulation of stomatal closure and reopening	[51]
<i>Solanum lycopersicum</i>	SINAP1	SA, ABA, GA	Negative regulation of <i>SIGA2ox3</i> , positive regulation of <i>SIPAL3</i> and <i>SINCE1</i>	Positive regulation of resistance to <i>Pst</i> and <i>Ralstonia solanacearum</i>	[52]
<i>Musa acuminata</i>	MaNAC5	SA, JA	Interactions with MaWRKY1 and MaWRKY2, activation of <i>MaPR1-1</i> , <i>MaPR2</i> , <i>MaPR10c</i> and <i>MaCHIL1</i>	Positive regulation of resistance to <i>Colletotrichum musae</i>	[53]
<i>Chrysanthemum morifolium</i>	CmNAC083	JA	Activation of JA synthesis pathway-related genes, such as <i>CmLOX2</i> , <i>CmAOC</i> , <i>CmOPR1</i> , <i>CmOPR2</i> , and <i>CmJMT</i> .	Positive regulation of resistance to <i>Alternaria alternata</i>	[54]
<i>Malus hupehensis</i>	MhNAC21/22	JA	miR164 inhibits <i>MhNAC21/22</i> expression and regulates JA signaling pathway	Positive regulation of resistance to <i>Alternaria alternata</i> apple pathotype	[55]

and overexpression plants showed that CmNAC083 can increase the resistance of *Chrysanthemum morifolium* to black spot disease caused by *Alternaria alternata* by activating the expression of genes involved in the JA biosynthesis pathway [54]. Apple leaf spot is also a

serious disease caused by the *Alternaria alternata* apple pathotype and affects apple planting. The expression of *MhNAC21/22* is significantly induced during pathogen infection, and *MhNAC21/22*-overexpression transgenic

plants exhibit increased resistance and enhanced expression of JA signaling-related genes [55].

ABA signaling pathway

ABA has been extensively studied due to its involvement in the response to abiotic stresses such as salt stress, cold stress, and drought stress. However, scarce research has investigated its role in biological stress. As a physical barrier in plants, the cell wall plays an important role in resisting pathogens and infection. In the model plant *Arabidopsis*, several core kinases, Snf1 (sucrose nonfermenting 1)-related kinases (SnRK2.2/3/6), in the ABA signaling pathway physically interact with NAC secondary wall thickening promoting factor 1 (NST1) to phosphorylate NST1, thereby influencing the transcriptional activation of the downstream secondary cell wall (SCW) synthesis genes. Consequently, the normal thickness of the cell wall is affected [37]. ONAC066 in rice can bind to the promoters of the ABA-responsive gene *low-temperature-inducible protein 9 (LIP9)* and the ABA biosynthesis gene *9-cis-epoxycarotenoid dioxygenase 4 (NCED4)* and positively regulate the disease resistance of rice blast and bacterial blight by inhibiting ABA signaling [17]. Exogenous spraying of ABA in barley results in increased resistance of wild-type plants to the biotrophic pathogen *Blumeria graminis* f. sp. *Hordei (Bgh)* but does not change the resistance of RNAi lines of *HvNAC6*, suggesting that ABA relies on *HvNAC6* as a positive regulator of disease resistance [49]. NAC transcription factors can respond to pathogen infection through epigenetic modification and hormonal cross-pathways. *ANAC019/055/072* in *A. thaliana* can be induced by exogenous ABA application and participate in leaf senescence regulation via the ABA-induced pathway [35]. *CURLY LEAF (CLF)* encodes an H3K27 methyltransferase that performs transcriptional inhibition function. The H3K27me3 level and chromatin status of the NAC transcription factor genes *ANAC019/055/072* can be altered by the polycomb repressive complex 2 (PRC2) complexes. In the absence of CLF, the level of H3K27me3 on the *ANAC019/055/072* genes decreases, and the reduction promotes transcription, resulting in enhanced ABA signaling in plants and stomatal closure, providing a water environment conducive to bacterial invasion in *Arabidopsis* leaf apoplasts [34].

NACs involved in crosstalk among various hormones

The process through which plants participate in immune regulation is usually not a single hormone-mediated transmission of immune signals but is often accompanied by crosstalk among multiple hormone signals. Many studies have demonstrated that NAC transcription factors are involved in the regulation of defense genes in plants, along with gene expression changes in

various plant hormone cross-signaling pathways. In *Arabidopsis*, the expression of *ATAF1*, which belongs to the ATAF subgroup of NAC transcription factors, is regulated by a variety of hormones, such as SA, JA, and ETH. *ATAF1* negatively regulates the resistance to *P. syringae* pv. *tomato* DC3000, *B. cinerea*, and *Alternaria brassicicola* by regulating the expression of *pathogenesis-related (PR)* genes in the SA signaling pathway [38]. In addition, *ATAF1* was previously reported to positively regulate disease resistance to *Bgh* via negatively regulating the ABA synthesis pathway gene *AAO3* [39], which indicates a negative correlation between ABA and plant disease resistance. *GhATAF1*, a protein encoded by a homologous gene in cotton, has been found to be induced by ABA, SA, and MeJA. The overexpression of *GhATAF1* in plants results in the repression of JA-mediated signaling and the activation of SA-mediated signaling, increasing the susceptibility to *V. dahliae* and *B. cinerea* [50]. *ATAF2*, a member of the ATAF subgroup along with *ATAF1*, also exerts a significant regulatory influence on the response to biotic stress. Its expression is induced by JA and SA, and the overexpression of *ATAF2* increases the sensitivity of plants to *Fusarium oxysporum* by suppressing the expression of *PR1*, *plant defensin 1.2 (PDF1.2)*, and other defense genes [41]. *ANAC032* can synergistically regulate the expression of *MYC2* and *NIM1 interacting 1 (NIMIN1)* in the SA signaling pathway and that of *PDF1.2A* in the JA signaling pathway, participating in the regulation of the resistance to the bacterial pathogen *Pseudomonas syringae* pv. *tomato* DC3000 (*Pst*) [42]. *TaNAC1*, which was identified in wheat, serves as a negative regulator of the resistance to *Puccinia striiformis* f. sp. *tritici* and *Pst* DC3000 and can respond to treatment with three types of defense-related hormones, such as SA, MeJA, and ETH [43]. Sun et al. detected the expression of the NAC transcription factors *ONAC122* and *ONAC131* in rice, which are induced by exogenous spraying of SA, JA, and ETH; these genes also positively regulate some defense-related genes, such as *OsLOX*, *OsPR1a*, *OsWRKY45* and *Nonexpressor of Pathogenesis-Related Genes 1 (NPR1) homolog (OsNH1)*; and thus participate in the resistance response of plants to rice blast disease [48]. Two homologous NAC transcription factors, *JA2* and *JA2L*, are found in tomatoes and regulate stomatal closure and reopening via different mechanisms mediated by ABA and JA to control pathogen invasion [51]. Similarly, *SINAP1* directly activates the transcription of genes involved in gibberellin (GA) deactivation and the biosynthesis of both SA and ABA, thus positively regulating the resistance to leaf speck disease and bacterial wilt disease [52]. Banana *MaNAC5* interacts with *MaWRKY1* and *MaWRKY2*, which are associated with the induction of resistance against *Colletotrichum musae* through the SA and MeJA signaling pathways, and

increased resistance is achieved by the direct binding of MaWRKY1 and MaWRKY2 to the promoter region of the *PR* genes [53].

NACs involved in HR and ROS signaling pathways

HR-induced cell death can prevent or delay the further expansion of pathogens, thereby reducing damage to plant cells. This effect is usually accompanied by the burst and accumulation of ROS during this process. The overexpression of *OsNAC4* in rice triggers a hypersensitivity response to bacterial infection, and *OsNAC4* positively regulates cell death by controlling the expression of the related genes *heat shock protein 90 (OsHSP90)* and *immune-related endonuclease (IREN)* [58]. The overexpression of *OsNAC60* in rice enhances programmed cell death (PCD), ROS accumulation, and callose deposition. miR164a targets *OsNAC60* and decreases its expression, and the miR164a/*OsNAC60* regulatory module is conserved in the resistance regulatory networks of rice sheath blight, tomato late blight, soybean root, and stem rot diseases [59]. The overexpression of *BnaNAC56* in *Brassica napus* L. triggers a large accumulation of ROS and cell death, resembling HR, and *BnaNAC56* activates the expression of several genes related to ROS, cell death, and defense in response to pathogen infection [60]. Another transcription factor, *BnaNAC87*, positively regulates ROS metabolism and cell death by directly binding to NAC recognition sequence (NACRS) elements in the promoter regions of the *zinnia endonuclease 1 (ZEN1)*, *zinc finger of Arabidopsis thaliana 12 (ZAT12)*, *harpin inducing 1 (HIN1)*, and *PR5* genes [61]. In addition, studies have shown that *BnaNAC55* and *BnaNAC103* have functions similar to those of *BnaNAC56* or *BnaNAC87*, and both of these transcription factors play roles as positive regulators of ROS metabolism and HR [62, 63]. *NAC4*, the target gene of miR164 in *A. thaliana*, inhibits the expression of negative regulators of cell death, such as *late upregulated in response to Hyaloperonospora parasitica 1 (LURP1)*, *WRKY40*, and *WRKY54*, thereby promoting HR and preventing the invasion of pathogens in plants [64]. Glyoxalase I (GLYI) can detoxify methylglyoxal (MG), which enhances the production of ROS. In grapes, *VvNAC72* binds directly to the promoter region of *VvGLYI-4* via 'CACGTG' elements, thereby inhibiting the transcription of *VvGLYI-4* and enhancing the accumulation of ROS and MG [65]. The leaf rust resistance gene *Rph7* in barley, which encodes a putative NAC transcription factor containing a zinc finger BED domain, similar to the N-terminal region of Arabidopsis ANAC019, was identified by mapping cloning and RNA-seq, and the overexpression of *Rph7* can induce a basic immune response and local cell necrosis in plants [66]. In summary, NAC transcription factors participate

in immune responses by regulating ROS levels and cell death in plants (Fig. 3).

Interactions between NACs and effectors

During the process of infecting plants, pathogens secrete abundant small molecule proteins called effectors to aid invasion. Studies conducted in recent years have shown that effectors can target key transcription factors in plants and transcriptionally reprogram genes by interfering with the activation or inhibition of downstream genes, ultimately promoting the invasion of pathogens. *Phytophthora infestans* secrete the RxLR-type effector Pi03192 into plants during invasion. This effector specifically targets two transcription factors, NAC Targeted by *Phytophthora* (NTP)1 and NTP2 in *Solanum tuberosum*, which are localized on the endoplasmic reticulum (ER) membrane. By preventing their relocation from the ER membrane to the nucleus, effectors block the transcriptional regulation of disease-resistance genes and promote the virulence of pathogens [67]. HopD1, a type III effector from *Pseudomonas syringae*, contributes to the full virulence of pathogens. This effector interacts with NTL9 localized in the ER membrane of plants and reduces their defense capacity by inhibiting the expression of NTL9-related genes during ETI [68]. Two other RxLR effectors, BLR05 and BLR09, in the oomycete *Bremia lactucae*, interact with the transcription factor LsNAC069 in lettuce. Similar to Pi03192, BLR05 and BLR09 hinder the entry of LsNAC069 into the nucleus by obstructing the clearance of the transmembrane domain (TMD) at the C-terminal region of LsNAC069 in response to stress signals, thus affecting the positive regulation of downstream defense genes [69]. The process of pathogen invasion in plants is sometimes accompanied by premature senescence of the plant leaves. Studies have shown that the soil-borne pathogenic fungus *Verticillium dahliae* secretes an effector protein called Protein elicitor from *V. dahliae* 1 (PevD1), which enters the nucleus of plants and interacts with the NAC transcription factor ORESARA1 (ORE1). ORE1 can directly bind to the promoter of the ethylene synthetase gene *1-aminocyclopropane-1-carboxylic acid (ACC) synthase 6 (ACS6)* to promote leaf senescence. Under normal conditions, ORE1 is ubiquitinated by the RING-type E3 ubiquitin ligase nitrogen limitation adaptation (NLA), which prevents the excessive synthesis and accumulation of ethylene. PevD1 promotes leaf senescence and facilitates pathogen infection by stabilizing ORE1 [70]. In addition, certain NAC transcription factors can interact with specific proteins in viruses to enhance host disease resistance by decreasing virus replication and accumulation [71, 72]. Overall, the pathogen achieves successful infection and colonization by targeting key NAC transcription

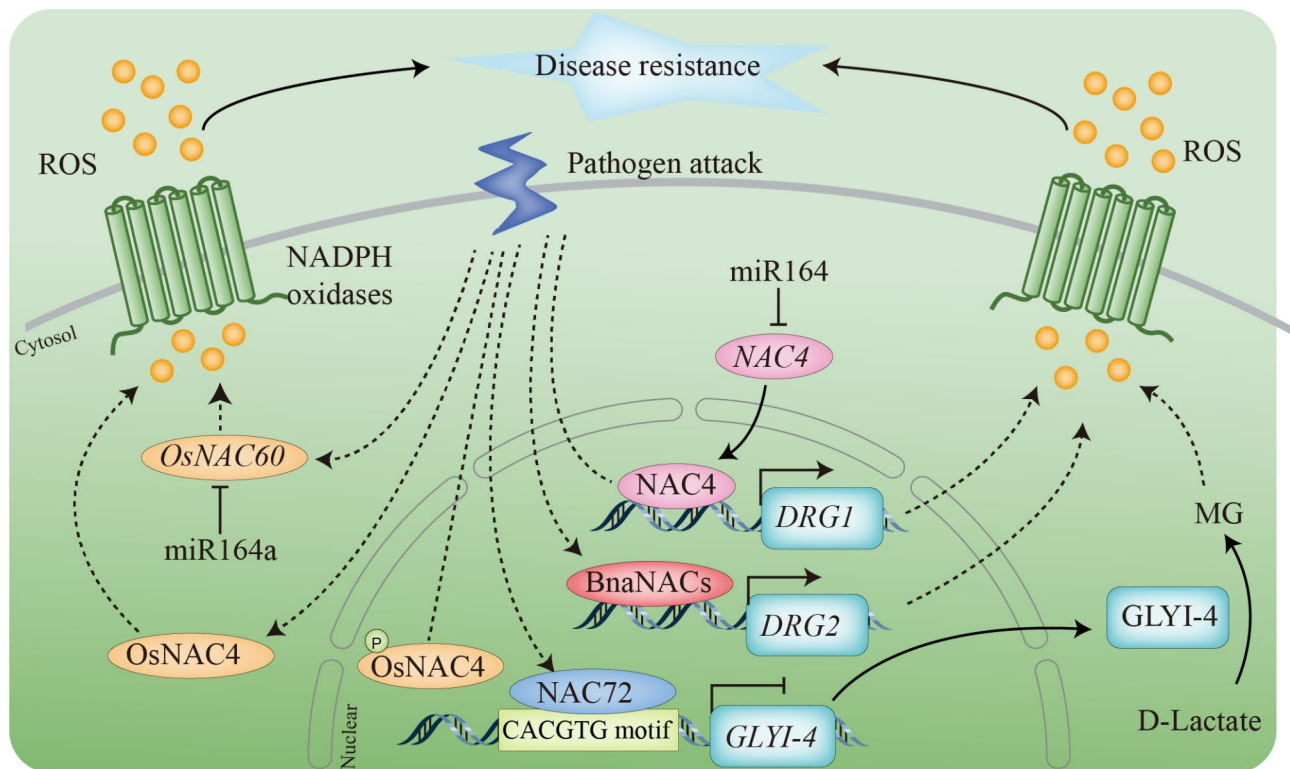


Fig. 3 NAC transcription factors involved in the regulation of ROS homeostasis response to pathogens. The BnaNACs include BnaNAC55, BnaNAC56, BnaNAC87 and BnaNAC103; DRG1, defense-related genes 1, include *OshSP90* and *IREN*; DRG2, defense-related genes 2, include *ZEN1*, *ZAT12*, *HIN1*, and *PR5*; and MG, methylglyoxal. The solid lines represent a direct effect, and the dashed lines represent an indirect effect

factors in the host plant with the help of effectors from the pathogen itself (Fig. 4).

Application of NACs for improving plant disease resistance

According to the research progress described above, it is not difficult to conclude that the NAC transcription factor family is a unique superfamily of transcription factors in plants. Different members of this family positively or negatively regulate the expression of immune-related genes in different pathways at the transcriptional level, forming a complex regulatory network to cope with the challenges posed by bacteria, fungi, viruses, and other microorganisms. With continuous updates and advancements in transgenic technology, the functions of certain NAC transcription factors have demonstrated potential commercial value during the research process and may be utilized for the improvement of germplasm resources. *Artemisinin* is best known for its effectiveness in treating malaria, but its concentration in *Artemisia annua* is relatively low. Lv et al. reported that the overexpression of *AaNAC1* in *Artemisia annua* substantially increases the contents of artemisinin and dihydroartemisinic acid and significantly enhances the resistance to drought and *B. cinerea* [73]. Rice blast disease, caused by *Magnaporthe oryzae*, is one of the most serious diseases in rice, resulting in substantial losses in rice production every

year. Nakashima et al. overexpressed *OsNAC6* in rice to simultaneously improve the tolerance of the plants to salt and their resistance to rice blast [19]. In addition, Bi et al. found that ONAC083 can directly bind to the 'ACG-CAA' elements in the promoter region of the RING-H2 gene *OsRFP2-6*, negatively regulating the resistance to rice blast, and the knockout of *ONAC083* via gene editing technology significantly increases the resistance to rice blast by enhancing pathogen-induced immune responses and chitin-induced PTI [74]. With the mature application of stable genetic transgenic methods for overexpression and gene editing, especially CRISPR/Cas9 technology, the breeding cycle has been greatly shortened, and basic research on these NAC genes with the aim of improving disease resistance traits will become a reality in the future.

Conclusions

NAC transcription factors are widely involved in plant growth, development, and biotic and abiotic response processes. In this review, we summarized the biological roles of NAC transcription factors involved in the regulation of disease resistance in common model plants and several other plant species. Previous studies demonstrated that NACs, which comprise one of the large families of transcription factors unique to plants, can regulate

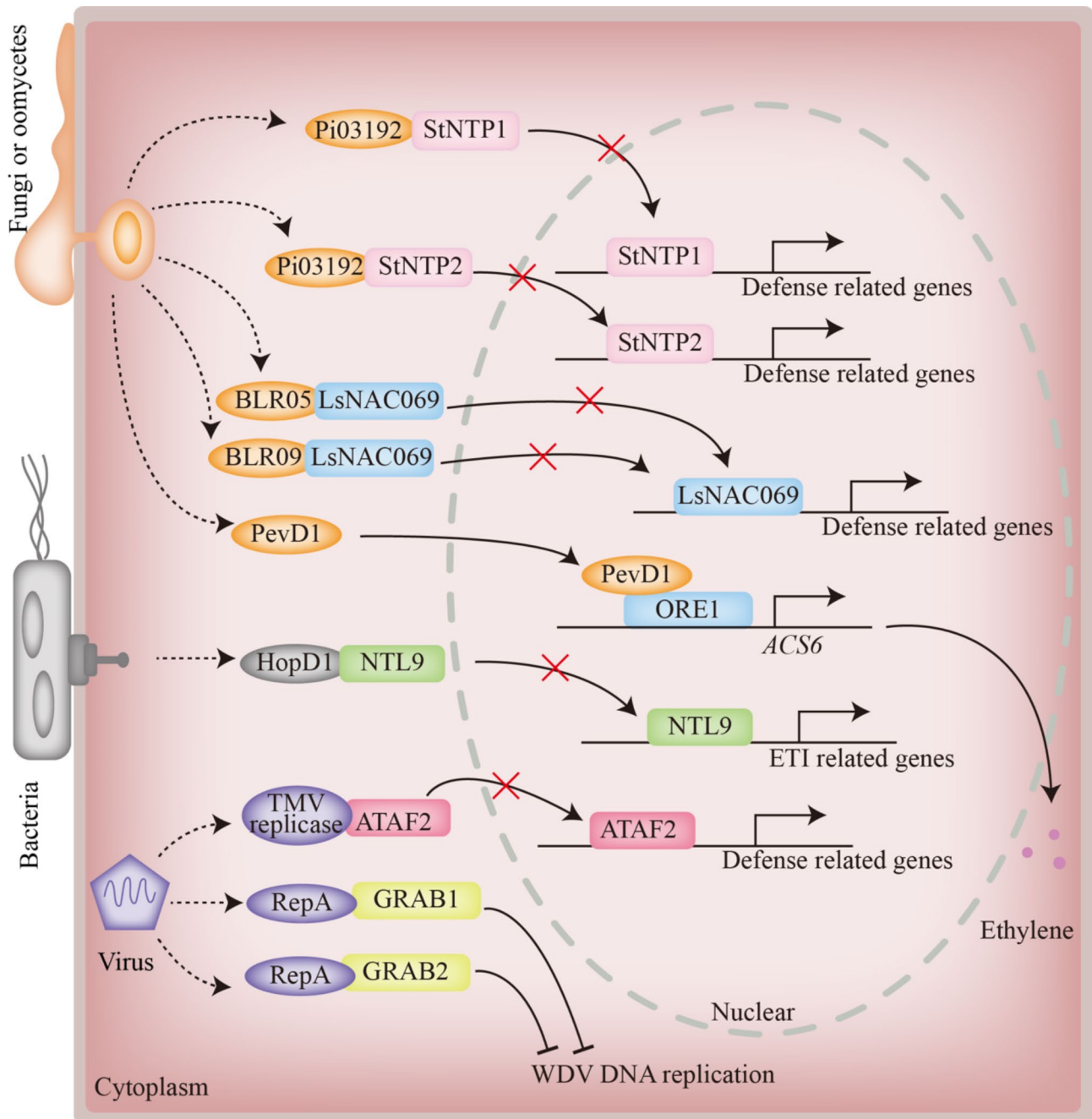


Fig. 4 NAC transcription factors targeted by effectors from pathogens during infection. The figure mainly shows the effectors of bacteria, fungi, oomycetes, and viruses. TMV, tobacco mosaic virus; WDV, wheat dwarf geminivirus

plant disease resistance through a variety of pathways, such as plant hormone signaling, ROS, HR, and effectors, as a positive/negative regulator. However, there remain some problems to be solved: (1) The associations between the protein structure of NAC transcription factors and the mechanism of action in response to disease have rarely been mentioned. (2) As reported, most NACs participated in resistance to a single disease. However, NAC transcription factors with broad-spectrum disease

resistance regulatory functions were less reported. (3) The working mechanisms of NAC transcription factors involved in disease responses need to be studied, but the specific interactions or upstream and downstream targeting factors remain unclear. (4) Epigenetic modifications, such as DNA methylation, histone modification, chromatin remodeling, and noncoding RNA, have become a popular field in recent years and involve changes to phenotype without altering the gene sequence. However, the

current research on the involvement of NAC transcription factors related to plant disease resistance in epigenetic modifications is limited. (5) Multi-omics have been widely used for explaining the biological phenomena, but their application in identification and analyzing the functions of NACs were less reported.

Based on the above, we speculate on the future research trends related to NAC transcription factors as follows: (1) With improvements in structural biology research technology, the crystallographic structures of several proteins have been resolved. In the future, protein structure analyses of NAC transcription factors may rely more on this technology, and the specific three-dimensional structural characteristics related to disease resistance may be identified and summarized by analyzing the crystallographic structural characteristics of NAC transcription factors involved in the regulation of disease resistance. In addition, for NAC transcription factors that are difficult to obtain crystal structures through experimental methods, AlphaFold technologies can be used to assist in prediction. (2) The breeding of excellent varieties that are resistant to most strains of one pathogen or more than one pathogen is the most economical and environmentally friendly disease prevention and control measure [75]. Thus, there is an urgent need to explore broad-spectrum resistance genes. (3) As favorable weapons utilized by pathogens to invade plants, effectors specifically target key transcription factors in plants to achieve transcriptional reprogramming by altering their transcriptional activity or binding ability to the promoters of downstream immune-related genes. However, the specific mechanism underlying the interaction between NAC transcription factors and effectors remains unclear. Future research will originate from the perspective of interactions between microorganisms and plants and identify additional core effectors. Analyses of the specific interactions between effectors and NACs will improve our understanding of the pathogenic mechanism of pathogens or more advanced defense strategies evolved by plants, which could lay a good foundation for the development of biopesticides. (4) To date, epigenetics modification of NACs involved in disease resistance has focused mainly on individual microRNAs [76] and histone methylation [34]. It is widely believed that as technology continues to mature in the future, the modification of NAC transcription factors at the epigenetic level will take on more rich forms. (5) In addition, based on high-throughput sequencing technology, multiple types of omics sequencing data, such as genomic, transcriptomic, proteomic, and metabolomic data, etc. can be obtained, and combined analyses can facilitate the mining of additional key NAC transcription factors and elucidate the functions of NACs. The goal of all these studies pertaining to the function and mechanism of

NAC transcription factors is to improve plants and thus benefit humanity. In the future, the extensive promotion and application of gene editing technology will bring the dawn of theoretical research into reality.

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Author contributions

Y.L., B.D. and G.H. collected the reference data; Y.L., B.D., and W.F. wrote the manuscript; Y.L., B.D., A.S., S.C., J.J., F.C., and W.F. revised the manuscript; Y.L., B.D., G.H., A.S., S.C., J.J., F.C., and W.F. approved the final manuscript.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare no competing interests.

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