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The role of transcription factor in wheat defense against pathogen and its prospect in breeding

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Abstract

The grain yield of a crop represents the expression of many thousands of genes integrated over the life of each of the component plants in the crop in response to environment, as well as severely affected by parasite, including pest and pathogen. Plant has no capacity to elude parasite other than by altering intrinsic gene expression or gene combinations to improve performance under pathogen. Transcriptional control is a crucial part of genes expression, especially in plant response to a range of stresses. Wheat (*Triticum aestivum* L.) is one of the most important cultivated crops, while its production isseverely affected by stripe rust and powdery mildew. Unfortunately, coupled with the loss of genetic diversity in wheat breeding programs, the disease resistance germplasms are more and more scarce due to the frequently variation of epidemic virulent race. Research carried out in the past few years has been productive in identifying TFs for regulating resistance to pathogen stress in wheat and other plant species. The increasing studies showed that Transcription Factors (TFs) are potent positive, negative, cis- and trans-regulators activating the functional gene. Herein, we highlighted the recent progress in elucidating the roles of TFs in wheat defense against pathogen, as well as the potential relationship between transcription factors family with regulating pathogen type, although there should be no expectation that everlasting favorable genes performance will be discovered for variable environments. Furthermore, we discussed new ways to improve varieties' resistance using biotechnology combining with empirical breeding program. This leads to new ideas to enhance wheat resistance or tolerance to disease in virtue of the progress of wheat genetic engineering. This maybe a new way to improve adaptive plasticity of wheat in highly variable environments as aresult of introducing greater diversity of resistance gene pool to cropping systems.

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Introduction

Faced with an accelerating rate of environmental change and the associated need for a more sustainable, low-input agriculture, the urgent new challenge for crop science is to find ways to introduce greater diversity to cropping systems [1]. Wheat is produced on more than 18% of the arable and in the world, and is one of the four major cereals in the world, while its growth and production are severely affected by adverse abiotic and biotic stresses [2]. The development of resistant crops will be essential for agriculture in the many regions worldwide, which has been proved as one of the most effective way to control the disease and to minimize crop losses [3-5]. For disease resistance, the current strategy for developing more durable resistance in cultivars is to use combinations of major all-stage resistance genes, minor additive adult plant resistance genes, or combinations of both, such as powdery mildew resistance gene *Pm21* and Fusarium head blight resistance quantitative trait loci [6,7]. However, the pathogen races are usually faster change and boom than the development of new variety with race-specific resistance. Meanwhile, empirical breeding and even marker assisted selection for resistance to the pathogen has become slowed because the existence of multiple species and races. Therefore, the identification and functional study on resistance genes become increasingly important to elucidate the molecular mechanisms of plant responding topathogen stress. Pathogen stresses such as stripe rust (*Puccinia striiformis* f. sp. *Tritici*, *Pst*), powdery mildew (*Blumeria graminis* f. sp. *tritici*; *Bgt*), head blight (*Fusarium graminearum*), sheath blight (*Rhizoctonia cerealis*) and take-all (*Gaeumannomyces graminis*), similarly with drought and low temperature a biotic stress, lead to wide range of biochemical and physiological responses in plants, resulting from a large number of changes in gene expression [8,9]. Many of the differentially expressed gene products protect plant cells from damage, such as dehydrins and enzymes for the removal of Reactive Oxygen Species (ROS) [10-12]. The production of these functional proteins is widely regulated by specific transcription factors [13-16]. Transcription Factors (TFs) are considered to be the most important regulators that control genes and gene clusters [17,18]. Many families of transcription factors have been demonstrated to play a role in stress responses in plants [19,20]. Among them, the bZIP, WRKY, AP2/ERF,NAC,MYB, C2H2 zinc finger and NF-Y families comprise a high proportion of stress-responsive members, and have been well understand and reviewed in plant responding to abiotic, such as drought and salt tolerance [21,22], and even to engineer enhance drought tolerance in plants [23]. However, the TF's function in plant responding to biotic stresses is still not well reviewed, especially in common wheat. The focus of this review is those transcription factor genes with respect to resistance pathways in wheat. Furthermore, we emphasize on the roles of TF genes in plant pathogen stresses, as well as the prospect in wheat breeding for disease resistance.

bZIP Transcription Factors

The bZIP TFs are characterized by two motifs: a basic region for specific binding to its target DNA, and a leucine zipper required for TF dimerization [24]. Genetic, molecular and biochemical analyses indicate that bZIPs are regulators of many important plant processes such as differentiation, development, nutrient balance control, hormone and sugar signaling [25], oxidative stress [26], and pathogen defence [27,28]. Proteins with bZIP domains are typically bind to DNA sequences with an ACGT core. Plant bZIPs bind to the A-box (TACGTA), C-box (GACGTC) and G-box (CACGTG), although nonpalindromic binding sites are also reported [24]. Based on the sequence similarities of common domains, 102 and 62 bZIP protein members have been identified in *Triticum aestivum* and *Triticum urartu* respectively [29].

Three members of the TGA/OBF family of bZIP transcription factors, AtTGA2, AtTGA3 and TGA5, showed strong affinity for NPR1 (nonexpressor of Pathogenesis-Related (PR) genes) protein [30,31]. NPR1 is a critical component of the Salicylic Acid (SA)-mediated signal transduction pathway leading to the induction of defense genes, such as the *PR1* gene, and enhanced disease resistance [32]. Given the absence of a canonical DNA-binding domain, NPR1 was proposed to regulate PRgene expression as a cofactor of the TGA transcription factors in planta [33,34]. These results directly link NPR1 to SA-induced *PR1* expression through members of bZIP TFs [30] (Figure 1). Under *Pst* stress, Expression analysis showed that *TabZIP1* transcripts were rapidly and highly induced during incompatible interactions, and by exogenously applied methyl jasmonate (MeJA) and Ethylene (ET), but not respond to Salicylic Acid (SA) treatment [35]. Similarly, zhang et al. detected three TGA family of bZIP TFs, numbered T19.62870, T16.17353 and T4.32876, responding to *Bgt* in wheat [8]. *AtbZIP10* is a positive mediator of the uncontrolled cell death observed in lsd1 mutants, and *LSD1* (Lesions simulating disease resistance 1) act antagonistically in both pathogen-induced HR and basal defense responses [28]. However, the bZIP TF superfamily protein showed significant down-regulation in susceptible wheat inoculated with Fusarium head blight [9]. Intriguingly, the bZIP Transcription Factor *Fgap1* plays a key role in the link between oxidative stress responses during interaction with wheat [36]. These results suggest that bZIP factors may serve both negative and positive roles in plant defense responses. The dual roles were similarly with plant responding to a biotic stress observed intrans-dominant mutants [19,37].

NAC Transcription Factors

The NAC domain was characterized based on consensus sequences from Petunia NAM and Arabidopsis ATAF1/2 and CUC2 proteins. Many NAC TFs play important roles in plant development and a biotic stress [38-40]. Similarly, the majority of reports have indicated that NAC TFs play central roles in the transcriptional reprogramming associated with the plant innate immune system, basal defense, and systemic acquired resistance [41,42]. This active research area has been extensively reviewed in plant and therefore will main consider the progress in wheat pathogen stresses here.

To date, 134 NAC genes have been identified from *T.aestivum* in Plant TFDB, whereas, only several of them are implicated in plant responding to pathogen. These mainly function seem to be playing some roles in plant responding to fungal stress. The potato *StNAC* gene shows induced expression in responses to *Phytophthora infestans* infection and wounding treatment [41]. Barley plants with the *HvNAC6* gene knock-down show penetration resistance in epidermal cells when inoculated with virulent isolates of *Blumeria graminis* f. sp. *hordei* [13]. Over expression of rice *OsNAC4* resulted in Hypersensitive Response (HR) cell death; and in the *OsNAC4* knocked down lines, HR cell death was markedly decreased in response to the avirulent bacterial strain [43]. Therefore, it seems that plant NAC TFs play multiple roles in defense responses to pathogen attack.*TaNAC1* acts as a negative regulator of stripe rust resistance in wheat, enhancing susceptibility to *Pseudomonas syringae* [16]. The expression of

TaNAC4 and *TaNAC8* is strongly increased in leaves 24 h post inoculation with *Pst* 32. *TaNAC4* transcript in wheat leaves was also induced by exogenous applied Methyl Jasmonate (MeJA), ABA and ethylene [44]. Yeast one hybrid assays confirmed that TaNAC8's C-terminal region acted as transcriptional activator [45]. Silencing the target of tae-miR164, Feng substantiated that *TaNAC21/22* negatively regulates resistance to stripe rust, and plays an important role in the regulation of wheat resistance to *Pst* [46]. Additionally, some NAC promoters contain several binding sites, such as W-boxes, GCC-boxes and MYB, that are binding to WRKY, ERF and MYB transcription factors respectively [47]. This demonstrated that transcription factors have capacity to regulate the expression of other TFs, and even interactive manipulation (Figure 1).

WRKY Transcription Factors

A WRKY domain of about 60 amino acids is a characteristic of WRKY proteins domain with the absolutely conserved sequence WRKYGQK followed by a zinc finger motif [48]. The WRKY domain binds to the W box (C/TTGACT/C) of target gene promoters to modulate transcription [49,50]. The WRKY TFs of many crops has been large scale identified and well analyzed in crop plants, such as *Oryza sativa* [51], *Brassica napus* [52] and *T. aestivum* [50,53,54]. Although most of WRKY TFs were focused on abiotic stress and exogenous hormone, the view that WRKY transcript factors play an important role in plant immunity response at both transcriptional and post-translational regulation level [55,56] has been well substantiated.

The expression of *TaWRKY1B* showed 146-fold induction in wheat cultivar HD2329 infected with a virulent race of leaf rust fungus [57]. Anorthologue of *TaWRKY2* targeted by tae-miR164 was detected in Xingzi 9104 antagonizing *Pst* CYR 32 using degradome sequencing [58]. The promoter of *NPR1* contains several W boxes, and Arabidopsis plants over expressing *AtWRKY6* have increased *NPR1* expression [59]. This represents that WRKY cooperated with TGA to trigger defense gene in plant. In *Nicotiana benthamiana*, *NbWRKY8* was identified as a substrate of SIPK, WIPK, and the SIPK paralog NTF4. These MAPKs phosphorylated *NbWRKY8* at multisite residues and enhanced DNA-binding and transactivation activities to regulate defense gene [56]. After the attack of the fungal pathogen *Magnaporthe grisea*, the expression of two genes, *OsWRKY45* and *OsWRKY62*, was increased in Salicylic Acid (SA)-treated leaves, while the expression of *OsWRKY10*, *Os-WRKY82* and *OsWRKY85* was increased by Jasmonic Acid (JA) treatment. The *AtWRKY11* and *AtWRKY17* are involved in the regulation of *Pst*-induced JA–dependent responses as negative regulators of basal resistance [60]. *OsWRKY30* and *OsWRKY83* responded to both SA- and JA treatments [61]. *TaWRKY45*, an ortholog of *OsWRKY45*, was upregulated in response to infections with *Fusarium* Head Blight (FHB), *Bgt* and *Pucciniatriticina* (*Puccinia recondita* f. sp. *Tritici*, *Prt*). Constitutive over expression of the *TaWRKY45* transgene conferred enhanced resistance against these fungi [62]. The orthologous TaWRKY78 from monocot wheat and AtWRKY20 from dicot Arabidopsis can cross-activate cognate *PR4* promoters from other species, suggesting WRKY functioning is essentially conserved in these distant plant species [63]. The AtWRKY33 protein interact with MPK4 indirectly to regulate the expression of defense gene *PAD3* (phytoalexin deficient 3) by releasing AtWRKY33 and MKS1 from MPK4–MKS1–AtWRKY33 complex via activating MEKK1–MKK1/2–MPK4 module after bacterial pathogen attack [64], while MPK3/MPK6 direct phosphorylated AtWRKY25/33 in PAD3 regulation [65,66]. Whatever, these indicated that WRKY33 is implicated in the plant immunity response. Two orthologous of *WRKY33* genes from wheat, T13.35253 and T16.5876, were drastically induced and enriched in the plant-pathogen pathway during interaction between wheat and *Bgt* [8]. These observations support the idea that WRKY33 is an important TF in wheat defense though PAMP-triggered immunity (Figure 1). From abovementioned literatures, we can highlight the role of WRKY in plant contributing to the basic resistance to pathogen. This should be the preferred transcription factors used to wheat breeding because this characterization will be beneficial in developing the broad spectrum lasting resistance varieties.

AP2/ERF Transcription Factors

The AP2/ERF superfamily includes three main families, i.e. AP2 family proteins containing two repeated AP2/ERF domains, ERF (ethylene responsive factor) family proteins contain a single AP2/ERF domain, and RAV family proteins contain a B3 domain. Previously, DREB (dehydration responsive element binding protein) was classed into the AP2/ERF super family [67,68]. However, the ERF binds to an AGCCGCC element, named the GCC-box, while members of the DREB subfamily specifically bind in vitro an A/GCCGAC element, which is often associated with ABA, drought and cold responsive genes. Additionally, The ERF proteins contain conserved Alanine-14 and Aspartic acid-19, which were substituted with Valine and Glutamine acid at the corresponding position of CBF/DREB protein [69]. In this review we follow the classification suggested by Licausi taking into account the divergence of DNA-binding affinities between ERF and DREB [70], and then diversified DREB from the AP2/ERF super family. Additionally, largely AP2/ERF TFs have been captured in wheat by in silico analysis [29,71], of which 161 TFs proteins subclassed into ERF family, while 18 proteins belong to AP2 family in wheat. However, the reported pathogen stress-related ERF proteins in wheat are far behind that in abiotic stress.

The ERF regulate and manipulate multistep control of stress responses in monocotyledonous plants [72]. Over-expression of tomato ERF gene, *PTI5*, in Arabidopsis accelerated and increased the expression of specific PR genes only after pathogen infection [73]. Tobacco plants showed enhanced resistance to pathogen attack and osmotic stress when a single ERF gene, Tobacco stress-induced gene 1 (*Tsi*), was over expressed [74]. Interestingly, over expression of Arabidopsis ERF1 enhanced resistance to two different necrotrophic fungi but reduced resistance to *P. syringae* [75]. Overexpression of *GmERF5*, a soybean EAR motif-containing ERF transcription factor, enhances resistance to *Phytophthora sojae* in soybean [76]. An ERF gene from a wheat relative *Thinopyrum intermedium*, *TiERF1*, enhanced resistance to sharp eyespot in the transgenic wheat lines compared with the wild-type and silenced *TiERF1* plants [77]. The expression results suggested that *TaERF3* might be mainly involved in the active defence response to *B. graminis* at an earlier stage through SA signaling, and to *F. graminearum* and *R.cerealis* at a later stage through the ethylene/jasmonic acid signaling pathways [78]. The pathogen-induced wheat ERF1 (*TaPIE1*) mediates host responses to the necrotrophic pathogen *R. cerealis* as well [79]. Microarray and qRT-PCR analyses of *TaPIE1*-overexpressing and -under expressing wheat plants indicated that *TaPIE1* activated a subset of defense- and stress-related genes. Experiment suggest that *TaPIE1* positively regulates the defense responses to *R. cerealis* and freezing stresses by activating defense- and stress-related genes in wheat [79]. These suggested that AP2/ERF transcription factors maybe play a role in wheat against ne-

crotrophic fungal infection.

MYB Transcription Factors

MYB proteins can be classified into three subfamilies depending on the number of adjacent repeats in the MYB domain (one, two or three), and were referred to as MYB1R, R2R3, and MYB3R factors respectively. In contrast to animals, plants contain a MYB-protein subfamily that is characterized by the R2R3-type MYB domain. Experiment showed that *AtMYB59* expression increases in response to phytohormones, especially in leaf and stem tissues [80]. showing its role in hormonal signal pathways in response to biotic stresses. Similarly, several R2R3-type MYB TFs have been proved playing the roles in defense against pathogen attacks in wheat. For example, *TaPIMP1* expressing plants displayed significantly enhanced resistance to *Ralstonia solanacearum* in transgenic tobacco, resistance to *Bipolaris sorokiniana* in transgenic wheat, and exhibited pleiotropy to drought and salt stresses [81,82]. Microarray analysis showed that Pathogenesis-Related (PR) proteins, including PR1a and PR2, were up-regulated in *TaPIMP1*-overexpressing plants, while *TaPIMP1*-underexpressing transgenic wheat showed compromised induction of these defense-responsive genes following ABA and SA treatments [82]. The expression of *TiMYB2R-1* (from *Thinopyrum intermedium*) was significantly induced by *Gaeumannomyces graminis* infection. Overexpression of *TiMYB2R-1* significantly enhanced take-all resistance of wheat and other cereal crops though binding to the MYB-binding site cis-element ACI [83]. So, we suspected that the MYB TFs could be mainly used to defense the pathogen attacking plant root and stem.

NF-Y and C2H2 Transcription Factors

The CCAAT box is one of the most common elements in eukaryotic promoters, and could be recognizedby CCAAT Binding Factor (CBF), also called Heme Activator Protein (HAP) or nuclear factor Y (NF-Y). Multiple trans-acting factors are associated with the CCAAT box, but only Nuclear Factor Y (NF-Y) has an absolute requirement for the pentanucleotide. NF-Y is an important and highly conserved transcription factor across the species [84]. NF-Y has been implicated in human diseases including neurodegenerative diseases, cancer and cardiovascular diseases, as well as immune systems [85]. In *Arabidopsis*, microarray experimentled to the identification of18differentially expressed NF-Y genes after *Botrytiscinerea* infection [86]. At present, a total of 50 NF-Y genes (10 NF-YA, 22 NF-YB, 18 NF-YC) in *T. aestivum* were identified [15,29]. However, only one orthologue of NF-YA-3 (*Zea mays*) was noted in wheat inoculated with *Pst* CYR 32 [58]. This hinted that the big gap in the effect of NF-Y transcription factors on plant-pathogen interaction need to be further filled.

Numerous genes encoding the C2H2 Zinc-Finger (ZF) domain have been characterized from a wide variety of eukaryotes, including plants. The canonical ZF sequence contain two Cysteine (C) and two Histidine (H) that coordinate a zinc atom, creating a compact nucleic acid-binding domain.C2H2-type zinc finger proteins are well elevated under a biotic stress conditions such as low temperature, salt, drought, osmotic stress and oxidative stress [87]. Several C2H2 have been identified for antioxidant defense in plant, especially a natural allele of a C2H2 transcription factor in rice that was evidenced conferring broad-spectrum blast resistance [88]. The expressions of two C2H2-type zinc finger genes, *CAZFP1* [89] and *StZFP1* [90], are enhanced after infection by *Colletotrichum coccodes* and *P. infestans* respectively. Another member of the C2H2-type zinc finger gene family, the tobacco *ZFT1* and Arabidopsis thaliana *STZ* gene, are induced during infection by Tobacco mosaic virus and Cucumber mosaic virus, and both triggering hypersensitive response [91,92]. ABA treatment induced the increases in the expression of *ZFP36* and *ZFP182*, and the activities of Superoxide Dismutase (SOD) and Ascorbate Peroxidase (APX) in rice leaves. The transient gene expression analysis and the RNA interference (RNAi) analysis indicate that *ZFP36* and *ZFP182* are required for ABA-induced antioxidant defense and the expression is regulated by rice MAPKs [93,94]. Unfortunately, the role of the C2H2-type zinc finger proteins in wheat responding to pathogen is still un described. However, proteins with similar domains may have the same or similar biological functions. Therefore, the finding that C2H2 TFs are involved in other plant defence to pathogen infection will be helpful in further detecting the function of C2H2-type zinc finger proteins in wheat.

Conclusion and future prospection of TFs in wheat breeding

Data from the Arabidopsis genome project suggest that more than 5% genes in this plant encode transcription factors [95], i.e., there might be more than 1700 TFs in *Arabidopsis*. According to this ratio, wheat encode more than 6000 TFs of the estimated 120,000 genes in this hexaploid plant species [96]. There has been lots of progress in the past decade in characterizing transcription factors that are involved in stress response, and the evidence of possible networks is starting to emerge in model plant [19]. Several closely related transcription factors have the potential to activate or repress genes through different strategies in plant defense [14,16], including regulation of the other TF promoter [86]. These factors may have closely overlapping functions, which hindered the genetic function of their respective roles. Some transcript factors showed diversified function in different stress, such as TGA transcription factors in disease resistance and nitrate response [97]. Although combinatorial control among different promoter elements and transcription factors for a given promoter is yet not well understood in wheat, the function of TFs in model plant are being brought to bear in deciphering the regulation of pathogen stressed gene expression in hexaploid bread wheat as illustrated in this review. In the next few years, the extensive used genome-wide and reverse-genetic approaches are likely to bring exciting advances to investigate the complete network of genes, especially the breeding and employment of specific near isogenic lines of wheat. Additionally, ChIP technology and improvement of wheat transgenic technology will accelerate to dissect the mechanism of specific transcription factors under various conditions, and help to provide a better understanding in the role of combinatorial controlling or regulating the expression of wheat defense gene against pathogen. The next five years will see an explosion of knowledge of the functional significance of TFs, and understanding its contribution to the complexity of R gene expression will offer new opportunities in approaches to modifying plant function for improved resistance to pathogen.

To develop crop plant with improved characterization, including cold, hot, drought, salt and pathogen stress, a basic understanding of physiological, biochemical and gene regulatory networks is essential. This will be helpful in addressing pleiotropic effects of transcription factor, including deleterious impacts of TFs' over-expression on plant growth and development [98]. Thus, in engineering experiments, an important task is to

restrict transcription factor activity to limit any deleterious effects. Similarly, new technologies must be developed to accelerate breeding through improving genotyping and phenotyping methods and by increasing the available genetic diversity in breeding germplasm [99]. From the perception of stress signals to the expression of stress-responsive genes, transcription factors play an essential role, and then they have emerged as powerful tools for improving stress tolerance though manipulation of complex metabolic pathways in wheat [100]. One example of transcription factors is DREB/CBF that binds to drought responsive cis-acting elements. Transgenic plants have been developed with enhanced stress tolerance by manipulating the expression of DREB/CBF [101]. A particular technological challenge in carrying out targeted genome modification in wheat is polyploidy. Fortunately, Sequence-Specific Nucleases (SSN)-mediated genetic alterations showcase the power for engineering complex plant genomes and for creating polyploidy crops with valuable traits [102]. For example, a mutant line shows strong resistance to powdery mildew that is generated by knocking out all six alleles encoding the mildew-resistance locus protein [103]. Additionally, the breakthrough of transformation technology bring the stable positive transformation efficiencies reaching to 13% in wheat, and the ratio of single transgene loci was more than 50% [104,105]. In a word, therefore, determining the functional role of these TF genes in wheat and tolerance to biotic stresses, and identification of target genes of TFs involved in pathogen responses are one of important current tasks, which will make great contribution to cut loss in wheat breeding because of the improvement of resistance in future.

Figure

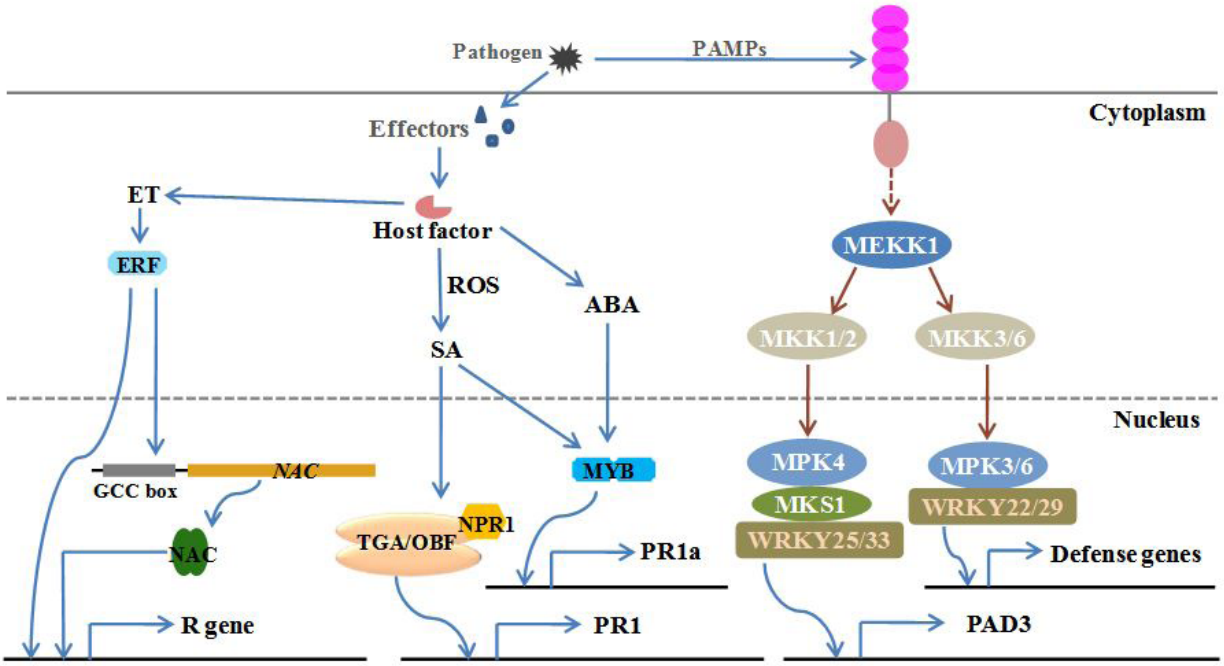

Figure 1: Schematic illustrations of transcription factor in regulating defense gene expression. PAMP perception stimulates the induction of MKK, and then MPK forms a complex with WRKY. Phosphorylation of MKS1 by MPK4 and dissociation of the MKS1-WRKY25/33 complex from MPK4. This leads to the latter complex binds the promoter region of PAD3, which is required for the synthesis of antimicrobial camalexin. Effectors perception stimulates the induction of hormone signal and manipulated ERF, TGA, and MYB TFs to regulate R genes expression directly or indirectly. Some transcription factors could regulate reciprocally by binding to the promoter correspondingly.

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