

# Plant Defense Gene Regulation and Transcription Factor Dynamics

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## Editorial

Plants respond to different pests and pathogens by activating a set of resistance genes that involve in substantial transcriptional reprogramming integrating hormonal, metabolic, and physiological movements [1]. These cumulative downstream defense responses alleviate pathogen and pest by subsequent local or systemic induced resistance. Hormone signaling and trans-acting regulatory factors/Transcription factors (TFs) are the major factors that facilitate downstream defense responses in plants [2]. Approximately, 7% of plant genome coding sequences represent TFs [3]. Among many different type of TFs available in plants, the most common TFs mainly belong to six groups; AP2/ERF, MYB, BZIP, WRKY, MYC and NAC [4]. There is no exact mechanism or correlation between the type of TFs and plant defense signaling. AP2/ERF TFs were found to be mainly involved in Jasmonic acid (JA) and ethylene (ET) signal transduction while, WRKY and bZIP TFs were mostly involved in salicylic acid (SA) mediated signal transduction. TFs encoding genes may be differentially regulated (up or down) by different stresses and substantial overlap occurs in the defense pathways allow integration of different defense signal and thereby, fine tune the Plant defense to pathogen/pest attack.

### AP2/ERF

AP2/ERF (Apetala2/ethylene responsive factor) class of transcription factors constitute plant specific large family of TFs which is well-known for regulating biological responses to environmental stimuli [5]. AP2/ERF TFs constitutes ~163 members in rice and ~140 members in Arabidopsis [5]. The presence of one or two highly conserved 60 amino acid AP2 domain is the characteristic of AP2/ERF transcription factors [6,7]. AP2-like transcription factors are known to contain two AP2 domains while ERF-like factors has one AP2 domain. Ethylene-response elements (ERE), also known as the GCC-box (GCCGCC) binds with AP2/ERF proteins with a single AP2-domain in response to ET [8]. The GCC-box has been identified in many promoters of defense-responsive genes that are inducible by ET. The GCC-box is also found in the promoters of SA-inducible pathogenesis-related (PR) genes, suggesting likely cross-talk between ET and SA pathways. In Arabidopsis, AP2/ERF proteins are also involved in JA-inducible gene expression and known as octadecanoid-responsive AP2/ERF (ORA). Arabidopsis ORA59 positively regulates expression of JA- and ET-mediated defense-related genes [9]. ORA47 regulate JA biosynthetic genes via positive feedback regulation. AP2/ERF proteins, in combination with other transcription factors may regulate the cross-talk and differential defense gene regulation. For example, OsEBP2 (*Oryza sativa* ethylene-responsive-element binding protein 2) expression was identified as a downstream component of a signal transduction pathway in response to rice-blast fungus interaction and also found to be transiently induced by MeJA, ABA and ET treatments [10]. Other TF, OsEREBP1 was reported to be induced in rice and

bacterial pathogen, *Xanthomonas oryzae* pv. *oryzae* (Xoo) interaction. Transcriptome analysis via Microarray and SSH cDNA library showed AP2 transcription factor were differentially up-regulated in incompatible rice-gall interactions [11-13].

### MYB

MYB factors in plants have been implicated in JA signaling pathways that bind to (T/C)AAC(T/G)G and G(G/T)T(A/T) G(G/T)T type of DNA sequences [14]. The role of MYB TFs is mostly documented in regulating the biosynthesis primary and secondary metabolites [15]. Secondary metabolites such as glucosinolates and flavonoid are implicated in hypersensitive response (HR) against herbivores and microorganisms. MYB34/*Arabidopsis* P450 reductase (ATR1) and MYB29/PMG2 have been implicated in the regulation of glucosinolates [16]. AtMYB30 has been implicated as an activator of HR-related cell death and resistance against bacterial pathogen *Xanthomonas campestris* pv. *campestris* [17]. The BOTRYTIS SUSCEPTIBLE 1(BOS1)/AtMYB108 was found to be involved in resistance against necrotrophic pathogens like *B. cinerea* and *A. brassicicola* [18]. MYB transcription factors also play roles in the defense response against insects. AtMYB44 was shown implicated in the plant defense against aphid [19]. Similarly, AtMYB102 has been reported to be effective in defense against the insect herbivore *Pieris rapae* via upregulation of a large number of genes that are involved in cell wall modifications [20]. MYB15 and WRKY40 TFs may play important roles in the transcriptional regulation of carbohydrate metabolism in citrus-HLB interactions [21,22]. AtMYB96-mediated abscisic acid (ABA) signals enhanced pathogen resistance response by inducing SA-biosynthesis via ABA-SA cross-talks [23].

### bZIP

bZIP transcription factors are characterized by their basic leucine zipper (bZIP) domain which is involved in DNA binding [24]. Regularly spaced leucine residues are found in the vicinity of bZIP which are important for the homo and heterodimerization of the bZIP proteins. Lesions simulating disease resistance 1 (LSD1), a plant-specific zinc-finger protein is known to regulate cell death negatively by limiting nuclear translocation of AtbZIP10 [25]. AtbZIP10, a positive regulator of resistance gene-mediated hypersensitivity and reactive oxygen-induced cell death. Arabidopsis TGA family of bZIP transcription factors has been demonstrated in innate immunity [26]. The role of TGA has been documented in systemic acquired resistance (SAR) via SA-regulated redox change which allows interaction with NPR1 [27]. Rice rTGA2.1 has a negative impact on SAR by interacting with OsNPR1 and altering accumulation of the PR genes in response to bacterial pathogen *Xanthomonas oryzae* pv. *oryzae* (xoo) [28]. In contrast, OsbZIP1 may play a positive role in the SA-dependent signal transduction after Magnaporthe grisea attack [29]. Rice-gall midge

incompatible interaction characterized by hypersensitive-mediated and non-hypersensitive related defense pathway [30-33]. Rawat et al. [34] found that TGA domain was mutated in the upstream promoter regions of PR10a in non-hypersensitive gall midge resistance, suggesting its role in HR mediated cell death. Arabidopsis TGA2 and TGA3 have diverse mechanism as TGA2 represses expression of PR-1 promoter in, while TGA3 acts as a transcriptional activator of PR-1 expression, *in vivo* [35].

## WRKY

WRKY proteins represent a large class of DNA-binding proteins in plants and have specific binding affinity for the consensus W-box motif TTGAC(T/C) followed by a typical zinc-finger domain [36]. The genome of rice and *Arabidopsis* contains around 100 *WRKY* genes and 70 *WRKY* genes, respectively. WRKY factors were shown to have strong negative effect conferred by W-box motif for SA-mediated *PR-1* gene expression in *Arabidopsis* [37]. In *Arabidopsis*, PAMP signaling and MAPK cascade (MEKK1–MKK4/MKK5–MPK3/MPK6) involve WRKY22 and WRKY29 proteins as transcriptional regulator after recognition of the flagellin fragment flg22 [38]. These WRKY factors are proposed to augment their expression levels by building a positive feedback loop via several WRKY binding sites in their own promoters. The induced expression of these WRKY factors would then allow induction of resistance to both bacterial and fungal pathogens [38]. WRKY33 is known for positive regulation of JA-induced defense genes and negative regulation of SA-related defense genes. WRKY28 is the only TF that is known to be suppressed by both JA and ET was found up-regulated after flg22 treatment [39]. Eight WRKY proteins (WRKY18, 38, 53, 54, 58, 59, 66, and 70) have been recognized as direct targets of NPR1 [40,41]. Up-regulation of *OsWRKY13* gene in rice, after bacterial blight *Xanthomonas oryzae pv oryzae* (*Xoo*) and fungal blast *Magnaportha grisea* pathogens, leads to enhanced resistance in rice plant [42]. *OsWRKY62* is a negative regulator of both types of plant immunity (PTI and ETI) [43].

## MYC

MYC2 is a member of the basic Helix-Loop-Helix (bHLH) family of TFs that consists ~60 amino acids bipartite bHLH domain [44]. This domain contains a region with a large number of basic residues at the N-terminal side, which is involved in DNA binding. Like ZIP domains, the HLH domain play a role in homo- and/ or heterodimerization. Among various MYC TFs, MYC2 transcription factors is known to regulate JA-dependent physiological processes, drought tolerance, circadian clock and light signaling [45]. However, only a limited number of bHLH transcription factors such as *AtMYC2/JIN1* have been found to be involved in JA- and ABA-regulated signaling induced by wounding and herbivory.

## NAC

NAC (NAM, ATAF1/2, and CUC2) is a plant-specific family of transcription factors include a large family of proteins which contain a variable C-terminal domain and a highly conserved N terminal domain [46]. More than 100 *NAC* genes have been documented in the genomes of *Arabidopsis* and rice. *NAC* proteins appear to be unique transcription factors in plants and no homolog has been identified in other eukaryotes thus far [46]. *NAC* genes have been reported to be induced by pathogen infection in rice, *Arabidopsis* and other plant species [47]. *ATAF1* and its barley homolog *HvNAC6* positively

regulate penetration against fungus *B. graminis f. sp. hordei* [48]. Virus-induced silencing of NAC TFs (*ONAC122* and *ONAC131*) in rice increased susceptibility to blast disease suggesting their positive regulation in disease resistance against *M. grisea* [49]. A number of NAC proteins such as *OsNAC4* have been reported inducing HR and cell death by activating *PR* genes [50].

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