# **Transcription Factors**

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### 1. Transcription Factors (TFs): Modulators of Gene Expression

TFs are regulatory proteins that are responsible for the mechanistic control of gene transcription. Technically, they act as the on/off switch of gene expression and are responsible for the activation and suppression of genes, thereby regulating their function. They are transcribed in the nucleus, translated in the cytoplasm, and returned to the nucleus to search for their targets in the genomic DNA; therefore, they are also called diffusible regulatory molecules [16]. Their re-entry into the nucleus is mediated by nuclear localization sites found in the protein sequences of all TFs [16]. The TFs bind to specific DNA sequences, called *cis*-regulatory elements or TF binding sites (TFBSs), in the promoter region of a gene and have defined DNA-binding domains. TBFs may also be located in the intron region and play regulatory roles. For example, in Arabidopsis thaliana, sequences for cis-regulatory elements of the floral homeotic gene AGAMOUS (AG) are located in the second intron [12]. The second intron contains TFBs for two direct transcriptional activators of AG, i.e., LEAFY (LFY) and WUSCHEL (WUS), and other putative regulatory elements. TFBs are usually highly conserved and are crucial for DNA binding and used to classify TFs into various groups or families [18], such as MADS, WRKY, or APETALA2/ethyleneresponsive factors (AP2/ERF). TFs can also be categorized based on their three-dimensional protein structure and composition, such as basic helix-loop-helix (bHLH), helix-turn-helix, and zinc finger proteins. Sequence-specific TFs are considered vital for the regulation of genes involved in prokaryotic and eukaryotic cellular mechanisms [19]. In prokaryotes and eukaryotes, gene regulation by TFs occurs through different mechanisms: in the former, TFs role is driven by a single protein, while, in the latter, it is a combined process that requires multiple proteins to coordinate and drive gene regulation. The binding of a TF to the promoter of a gene is spatiotemporally dependent. Phillips [18] quoted an interesting example of β-globin (a protein responsible for oxygen exchange in red blood cells) to explain this: the β-globin gene is present in every human cell, but no cell type other than red blood cells expresses this gene. Reddy, et al. [20] studied the beta-globin promoters of different cell types using DNA footprinting. They found that TFs that could bind to beta-globin promoters were only expressed in erythroblasts (immature red blood cells).

TFs have two domains: a DNA-binding domain and an effector domain that regulates interactions with other TFs or proteins necessary for transcription. Most DNA-binding domains are highly conserved within the members of the same family of TFs, while the effector domains evolve more rapidly. TFs mediate many functions, including gene induction, gene repression, and response to signal transduction under various environmental conditions.

## 2. Regulatory Role of TFs in Plant Defense

The two interconnected branches of plant defense, PTI and ETI, are the major defense strategies that plants use immediately after pathogen perception <sup>[6]</sup>. These strategies require well-communicated signal transduction and fine-tuned regulation of gene expression <sup>[21][22][23]</sup>. TFs play a key role in innate plant immunity, primarily by regulating genes involved in PTI, ETI, and hormone and phytoalexin synthesis and pathways. One of the immediate responses to pathogen infection is transcriptional reprogramming. A study using high resolution temporal transcriptomic analyses in *Arabidopsis* demonstrated that approximately one-third of the genome showed differential expression in response to the necrotrophic pathogen *Botrytis cinerea* immediately after infection <sup>[24]</sup>. Thus, transcriptional reprogramming of the plant cell demands significant changes in gene expression to favor defense over other metabolic processes such as growth and development <sup>[23]</sup>. Recent studies also suggested that a metabolic shift is required to mediate the trade-off between growth and immunity to ensure proper resource allocation for plant survival <sup>[25][26][27]</sup>. Many TF families have been reported to play key roles in transcriptional reprogramming. WRKY, bHLH, AP2/ERF, NAM/ATAF/CUC (NAC), and MYB are the major plant TF families <sup>[28]</sup> regulating various biological processes including plant defense.

#### 2.1. WRKY TFs

The WRKY TFs often called "jack-of-various-trades" <sup>[29]</sup>, are one of the largest TF families in plants <sup>[30]</sup>. The detailed composition and mode of action of WRKYs are well explored <sup>[30][31][32][33]</sup>. Here, we will focus on their functional roles, particularly in plant defense.

The regulatory role of WRKYs in plant defense has been extensively studied, particularly in the model plant Arabidopsis thaliana, and are reported to have both negative and positive roles in the regulation of plant defense [34]. Reports suggested that WRKYs regulate PAMP-signaling downstream of the mitogen-activated protein kinase (MAPK) signaling cascade [35]. The MAPK cascade plays a vital role in various defense responses—particularly, in sensing PAMPs or ETI <sup>[36]</sup>. For example, WRKY33 in Arabidopsis is reported to have a role in resistance to necrotrophic fungal pathogens B. cinerea and Alternaria brassicicola [37]. Recent reports using functional genomics revealed that WRKY33 is required for MPK3/MPK6-induced camalexin biosynthesis [38]. They also showed that WRKY33- and pathogen-induced camalexin production was compromised in wrky33 mutants. They further suggested that WRKY33 is a pathogen-inducible TF that acts as a substrate for MPK3/MPK6 to undergo phosphorylation and mutation. WRKY33 also binds to the promoter of phytoalexin deficient 3 (PAD3), which catalyzes the final step in camalexin biosynthesis [28], and to the promoters of 1aminocyclopropane-1-carboxylic acid synthases 2 and 6 (ACS2 and ACS6) in response to B. cinerea [39]. Global expression profiling of wild type and susceptible wrky33 mutants in response to B. cinerea indicated differential transcriptional reprogramming, suggesting that unidentified targets for WRKY33 might be critical for establishing immunity to this necrotrophic pathogen [40]. Similarly, the closest homolog of WRKY33 in Nicotiana benthamiana WRKY8 (NbWRKY8) is also phosphorylated by MAPKs, resulting in the induction of defense-related genes. Furthermore, silencing causes increased susceptibility to the oomycete Phytophthora infestans and the ascomycete fungus Colletotrichum orbiculare [41].

WRKY TFs are also reportedly involved in ETI and interact with plant R proteins. For example, in barley, mildew resistance locus A10 (MLA10) NB-LRR protein, which confers resistance to powdery mildew, interacts with *Hordeum vulgare* WRKY1 (HvWRKY1) and HvWRKY2 in the presence of the AVR<sub>A10</sub> effector <sup>[42]</sup>. Both HvWRKY1 and HvWRKY2 repress basal defenses against the virulent fungus *Blumeria graminis* that causes powdery mildew. Following infection by *B. graminis* (expressing AVR<sub>A10</sub>), MLA10 interacts with HvWRKY1 and HvWRKY2 to activate the defense. Another study reported that rice panicle blast 1 (Pb1), another NB-LRR protein, interacts with *Oryza sativa* WRKY45 (OsWRKY45), mediating the resistance to rice blast caused by the fungus *Magnaporthe oryzae* <sup>[43]</sup>. Similarly, in *Arabidopsis*, WRKY52, also called resistance to *Ralstonia solanacearum* 1 (RRS1), is a TIR-NB-LRR protein with a WRKY domain that shows resistance to the bacterial pathogen *Ralsotonia solanacearum* <sup>[44]</sup>. Using map-based cloning and natural variation analysis, Narusaka, et al. <sup>[45]</sup> reported that RRS1 interacts with RPS4 for dual resistance toward fungal and bacterial phytopathogens. Similarly, *Arabidopsis* WRKY8 (AtWRKY8) negatively regulates basal defenses to *Pseudomonas syringae* pathovar tomato (*Pst*) while positively regulating defense responses to *B. cinerea* <sup>[46]</sup>.

#### 2.2. bHLH TFs

The bHLH TF family reported in animals and plants in 1989 [47](48] and yeast in 1990 [49] comprised of a group of TFs characterized by the so-called "basic helix-loop-helix (bHLH)" domain. The proteins with this domain are known for a broad spectrum of functions that are reviewed in detail by Heim et al. <sup>[50]</sup>. Here we will briefly discuss their role in plant defense. The bHLH domain comprises an N-terminal stretch of hydrophilic basic amino acids followed by an HLH domain predicted to have amphipathic  $\alpha$ -helices with an intervening loop in between, to form dimers [51]. In essence, bHLH TFs bind with E-box sequences (CANNTG) in the promoters of their target genes with variation in binding specificity [52][53]. Studies in mammals have shown that the conserved HLH structure is critical for the formation of bHLH protein dimers [54]. The specificity for a particular protein partner is determined by the  $\alpha$ -helices. In Arabidopsis, the bHLH TF family includes about 160 members (https://www.arabidopsis.org/browse/genefamily/bHLH.jsp). However, only a few of them have been characterized in detail, which has shown that the bHLH might not be directly involved in plant defense, but they have an indirect connection by producing certain metabolites that are required during stress conditions. For example, in Arabidopsis, IAA-LEUCINE RESISTANT3 (ILR3 or BHLH105) represses the production of aliphatic glucosinolates and secondary metabolites produced in response to wounding, insects, or other microbial pathogens [55]. Furthermore, they interact with JA signaling pathway, thus regulating phytohormonal balance which is also critical for plant defense [56]. Song et al. [57] identified members of the bHLH TF family (bHLH3, bHLH13, bHLH14, and bHLH17) to be targeted by JASMONATE-ZEM-Domain (JAZs). Using the loss of function mutants for these bHLH TFs, they showed that bHLH mutants showed sensitivity to JA-inhibited root growth and an increase in JA-induced defense against pathogen infection and insect attack. The transgenic plants overexpressing bHLH13 or bHLH17 showed reduced JA-mediated responses [57]. Another bHLH TF, HBI1 negatively regulates genes that are involved in plant immunity and inhibits PAMP-induced growth

arrest thus mediating the trade-off between growth and PAMP-triggered immunity <sup>[26]</sup>. Similarly, another bHLH TF, ILR3 was reported to regulate iron deficiency, glucosinolate biosynthesis, and pathogen response <sup>[55][58]</sup>. MYC2 another bHLH TF, regulates a subset of plant defense responses in *Nicotiana attenuate* <sup>[59]</sup>.

#### 2.3. AP2/ERF TF

The AP2/ERF is another important plant-specific TF family that regulates stress responses in plants, mostly studied for responses to abiotic stresses <sup>[60]</sup>. Members of this family are characterized by the presence of an AP2 DNA binding domain which comprises 40–70 conserved amino acids <sup>[61][62][63]</sup>. The AP2/ERF TFs regulate genes involved in various biological processes including growth and development, hormone signaling, stress responses both at transcriptional and post-translational levels <sup>[63][64][65][66]</sup>. Studies involving gene expression profiling have shown that most AP2/ERF TFs have a low basal expression and can be induced or reduced by external stress stimuli or hormonal imbalance <sup>[67][68]</sup>. Some of the important AP2/ERFs include DEHYDRATION-RESPONSIVE ELEMENT BINDING proteins (DREBs), members of the RAP2 family, and ABA INSENSITIVE 4 (ABI4), etc. Reports suggested that AP2/ERFs are induced by the *cis*-regulatory elements present in their promotors. These elements include HEAT SHOCK ELEMENT (HSE), ETHYLEN INSENSITVE 3 (EIN3) BINDING SITE (EBS), LOW-TEMPERATURE RESPONSIVE ELEMENT (LRT), and ABA Response Element (ABRE) <sup>[69]</sup>.

Post-translational changes such as phosphorylation also affect the activity and abundance of AP2/ERFs. Other studies have shown that phosphorylation affects AP2/ERF protein stability and transactivity <sup>[69]</sup>. For example, in *Arabidopsis*, the positive regulator of ABA signaling pathway SNF1-related protein kinases (SnRKs) interacts and phosphorylates RAV1 to constrain its transcription repression role <sup>[70]</sup>. Similarly, ERF6 and EFR104 are phosphorylated by mitogen-activated protein kinases (MAPKs) for positive regulation of pathogen responses <sup>[71][72]</sup>. AP2/ERFs are also characterized in plant defense. Mase, et al. <sup>[73]</sup> showed in *Arabidopsis thaliana*, by using a structural analog of AAL, a phytotoxin produced by *Alternaria alternata* <sup>[74]</sup>, that the MODULATOR of ALL CELL DEATH 1 (MACD1), and AP2/ERF TF, was involved in ALL-induced cell death and acted downstream of ethylene.

ERF is one of the large subfamilies of AP2/ERFs. In *Arabidopsis thaliana*, there are about 145 members of the AP2/ERF family <sup>[67]</sup>. Among them, about 65 members are identified as ERFs. Members of the ERF sub-family are characterized for their role in plant defense. In tomato, the Pti4 and Pti5 (ERFs) are phosphorylated by Pto protein when challenged by the virulent *P. syringea*. The *Pst*-induced phosphorylation increases Pti4 and Pti5 binding to their target sequences in defense-related genes <sup>[75]</sup>. Similarly, tomato ERFs Pti4, Pti5, and Pti6 when overexpressed in *Arabidopsis*, induced defense response, and contributed to resistance against *P. syringae* <sup>[76]</sup>. In *Arabidopsis* constitutive expression of ERF1 has been shown to increase resistance against several necrotrophic fungal pathogens. <sup>[77]</sup> Besides, the ERF1 is considered a point of integration between JA and ethylene signaling pathways. A detailed review on the role of AP2/ERF TFs has reported that members of ERFs are enriched in genes regulating disease resistance pathways <sup>[78]</sup> suggesting the significant role of this subfamily in the regulation of plant defense responses.

#### 2.4. MYB TF Family

MYB TF family is one of the largest and most functionally diverse families and is conserved among all eukaryotes. They are also diverse in their structure and are classified based on the presence of a conserved MYB domain that contains two or three imperfect repeats (R1, R2, and R3). The structure, classification, and functional diversity of MYB TFs have been well studied <sup>[79][80][81][82]</sup>. The first plant MYB TF was identified in *Zea mays* <sup>[83]</sup>. Since then, MYB TFs in several other plant species, including *Arabidopsis* <sup>[84]</sup>, have been reported. Although MYB TFs are often implied to be a major player in flavonoid biosynthesis or abiotic stress <sup>[85][86][87][88][89]</sup>, the first MYB gene identified was the oncogene *v-myb* (initially called *mab* or *amv* after the name of avian myeloblastosis virus but later renamed *v-myb*) from the avian myeloblastosis virus <sup>[90][91][92]</sup>. Hence, their role in disease resistance cannot be ignored.

Hypersensitive response (HR), a form of programmed cell death (PCD), is one of the most effective defense strategies of the host plant in response to pathogen infection. MYB TFs are reported to positively regulate the HR response. Daniel, et al. <sup>[93]</sup> showed that, in response to avirulent pathogens such as *Xanthomonas campestris* pv campestris, AtMYB30 showed a rapid and transient expression. Functional genomics study using *Arabidopsis Isd* mutants and their corresponding suppressor *phx* mutants, Daniel, et al. <sup>[94]</sup> reported that MYB30 expression is likely more responsible for the initiation of the HR than for its propagation. Furthermore, overexpression of MYB30 in transgenic plants accelerated the HR following avirulent bacterial pathogen infection and caused HR-like responses to virulent bacterial pathogens <sup>[95]</sup>. Raffaele, et al. <sup>[96]</sup> reported that AtMYB30 regulated HR using long-chain fatty acids and their derivatives. Using microarray analyses of *Arabidopsis* plants overexpressing MYB30 (*MYB30 ox*) or antisense (*MYB30 as*), they reported that MYB30 putatively targeted genes encoding the four enzymes forming the acyl-coA elongase complex that

synthesizes very-long-chain fatty acids <sup>[96]</sup>. Reports have suggested that AtMYB60 and AtMYB96 act through an ABAsignaling cascade, while AtMYB96-mediated ABA signals induce pathogen resistance responses by inducing salicylic acid (SA) biosynthesis in *Arabidopsis* <sup>[97]</sup>. Similarly, AtMYB102/AtM4 and AtMYB41 regulate plant resistance toward the herbivorous insect, *Pieris rape* <sup>[97]</sup>. Some MYB TFs regulate both biotic and abiotic stress; for example, *AtMYB108*, also called the *Botrytis* Susceptible 1 (BOS1), which is an R2R3 type MYB <sup>[99]</sup>. MYB TFs are also reported to contribute to systemic acquired resistance (SAR), a type of plant defense in which the signals broadcast from the site of infection to systemic tissues to warn them of the pathogen attack. Segarra, et al. <sup>[100]</sup> reported that defense pathways triggered by beneficial *Pseudomonas* and *Trichoderma* spp. strains are very similar and that MYB72 functions as an early point of convergence in the signaling pathways induced by these two different species of microorganisms.

However, it seems that MYB TFs are less studied for their role in plant defense compared to other TF families. Microarrayand RNA-seq-mediated studies can be used to identify the candidate MYB TFs that induce defense responses.

#### 2.5. NAC TF Family

The NAC TF family is a key plant-specific TF family. NAC TFs are characterized by the NAC domain, which has a 150 amino acid conserved domain at the N-terminus, and a diversified C-terminal transcription regulatory region (TR) <sup>[101]</sup>. Some NAC TFs also have a transmembrane domain within the TR domain. The NAC domain has been sub-divided into five sub-groups from A to E <sup>[102]</sup>. Genome-wide identification of TFs suggested the presence of NAC TFs in many plant species <sup>[103][104][105][106][107]</sup>.

Like other TFs, NACs also have the DNA-binding ability and can regulate abiotic and biotic stresses, growth, and development. For example, cold-induced NTL6, a plasma membrane-bound NAC TF that is involved in the proteolytic activation of the plasma membrane in *Arabidopsis* <sup>[108]</sup>, is reported to bind directly to the promoter of PR genes to induce resistance against pathogens. Similarly, another NAC TF, ATAF1, that is induced by drought, high salinity, ABA, methyl jasmonate, and wounding has multiple functions in *Arabidopsis* <sup>[109]</sup>. Reports suggested that overexpression of ATAF1 not only enhances drought tolerance but also increases susceptibility to *B. cinerea*, suggesting possible crosstalk between the stressors. Similarly, in rice, JASMONIC ACID 2 (JA2) and JA2-like (JA2L), the two homologous NAC TFs are reported to mediate pathogen-induced stomatal regulation <sup>[110]</sup>, which are considered to be SA- and ABA-dependent processes. These studies suggest that NAC TFs act as interlinking entities in signaling cascades in response to multiple stressors.

Some NAC TFs also act as negative regulators in plant defense responses and are targeted by pathogens to increase susceptibility. As an example, HopD1, a type III effector from *P. syringae*, interacts with NTL9, a membrane-tethered protein at the endoplasmic reticulum, to suppress ETI responses <sup>[111]</sup>. Similarly, in a study involving potato (*Solanum tuberosum*), Block, Toruno, Elowsky, Zhang, Steinbrenner, Beynon and Alfano <sup>[111]</sup> showed that two ER-associated *Solanum tuberosum* NTPs, StNTP1, and StNTP2, interact with an RxLR effector from *P. infestans* to prevent the movement of TFs from the ER to the nucleus and, in doing so, suppress defense responses. Similarly, a type III effector from *P. syringae*, HopD1, interacts with membrane-tethered NTL9 to suppress ETI responses <sup>[111]</sup>. A similar situation was also found in viral pathogenicity, where the TMV replicase protein interreacted with ATAF2, which is an NAC TF, to suppress the basal host defense <sup>[112]</sup>.

Other reports suggested positive regulation of plant defense by NAC TFs. Studies involving RNAi, knockout (KO), and overexpression of genes suggested the role of NAC TFs in various plant-pathogen interactions. NAC TFs are reported to positively regulate plant defense responses by activating PR-related genes and inducing HR at the infection site <sup>[108][113]</sup> <sup>[114][115]</sup>. The ATFAF1 and its ortholog in barley, HvNAC6, is reported to positively regulate penetration resistance toward the biotrophic fungus *Blumeria graminis* <sup>[114][115]</sup>. Thus, NAC TFs appear to be key elements in connecting signal transduction cues from different stressors and can be used to relay between various stresses in plants.

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