Transcription Factors

Subjects: Biochemistry & Molecular Biology

Contributor: Qari Muhammad Imran

Transcription factors (TFs) are regulatory proteins that are responsible for the mechanistic control of gene transcription.

nitric oxide transcription factors

---

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 [17]. 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/ethylene-responsive 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 [6]. These strategies require well-communicated signal transduction and fine-tuned regulation of gene expression [21][22][23]. 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 [24]. 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 [23]. 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 [25][26][27]. 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 [28] regulating various biological processes including plant defense.

2.1. WRKY TFs

The WRKY TFs often called “jack-of-various-trades” [29], are one of the largest TF families in plants [30]. The detailed composition and mode of action of WRKYs are well explored [30][31][32][33]. 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 [36]. 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 1-aminocyclopropane-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_{A10} effector [42]. Both HvWRKY1 and HvWRKY2 repress basal defenses against the virulent fungus *Blumeria graminis* that causes powdery mildew. Following infection by *B. graminis* (expressing AVR_{A10}), 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* [43]. 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* [44]. Using map-based cloning and natural variation analysis, Narusaka, et al. [45] 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* [46].

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. [50]. 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 α-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 α-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 [26]. Similarly, another bHLH TF, ILR3 was reported to regulate iron deficiency, glucosinolate biosynthesis, and pathogen response [55][58]. MYC2 another bHLH TF, regulates a subset of plant defense responses in *Nicotiana attenuate* [59].

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 [60]. Members of this family are characterized by the presence of an AP2 DNA binding domain which comprises 40–70 conserved amino acids [61][62][63]. 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 [63][64][65][66]. 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 [67][68]. 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) [69].

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 [69]. 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 [70]. Similarly, ERF6 and EFR104 are phosphorylated by mitogen-activated protein kinases (MAPKs) for positive regulation of pathogen responses [71][72]. AP2/ERFs are also characterized in plant defense. Mase, et al. [73] showed in *Arabidopsis thaliana*, by using a structural analog of AAL, a phytotoxin produced by *Alternaria alternata* [74], 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 [67]. 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 [75]. Similarly, tomato ERFs Pti4, Pti5, and Pti6 when overexpressed in *Arabidopsis,* induced defense response, and contributed to resistance against *P. syringae* [76]. In *Arabidopsis* constitutive expression of ERF1 has been shown to increase resistance against several necrotrophic fungal pathogens. [77] 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 [78] 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 [79][80][81][82]. The first plant MYB TF was identified in *Zea mays* [83]. Since then, MYB TFs in several other plant species, including *Arabidopsis* [84], have been reported. Although MYB TFs are often implied to be a major player in flavonoid biosynthesis or abiotic stress [85][86][87][88][89], 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 [90][91][92]. 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. [93] 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 lsd* mutants and their corresponding suppressor *phx* mutants, Daniel, et al. [94] 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 [95]. Raffaele, et al. [96] 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 [96]. Reports have suggested that AtMYB60 and AtMYB96 act through an ABA-signaling cascade, while AtMYB96-mediated ABA signals induce pathogen resistance responses by inducing salicylic acid (SA) biosynthesis in *Arabidopsis* [97]. Similarly, AtMYB102/AtM4 and AtMYB41 regulate plant resistance toward the herbivorous insect, *Pieris rape* [97]. 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 [99]. 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. [100] 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. Microarray- and 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) [101]. 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 [102]. Genome-wide identification of TFs suggested the presence of NAC TFs in many plant species [103][104][105][106][107].

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* [108], 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* [109]. 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 [110], 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 [111]. Similarly, in a study involving potato (*Solanum tuberosum*), Block, Toruno, Elowsky, Zhang, Steinbrenner, Beynon and Alfano [111] 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 [111]. 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 [112].

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 [108][113][114][115]. The ATFAF1 and its ortholog in barley, HvNAC6, is reported to positively regulate penetration resistance toward the biotrophic fungus *Blumeria graminis* [114][115]. 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.

References

1. Palmgren, M.G.; Edenbrandt, A.K.; Vedel, S.E.; Andersen, M.M.; Landes, X.; Østerberg, J.T.; Falhof, J.; Olsen, L.I.; Christensen, S.B.; Sandøe, P. Are we ready for back-to-nature crop

breeding? Trends Plant Sci. 2015, 20, 155–164.

2. Oerke, E.C. Crop losses to pests. J. Agric. Sci 2006, 144, 31–43, doi:10.1017/S0021859605005708.
3. Oerke, E.C.; Dehne, H.W. Safeguarding production—losses in major crops and the role of crop protection. Crop. Prot. 2004, 23, 275–285, doi:10.1016/j.cropro.2003.10.001.
4. He, D.C.; Zhan, J.S.; Xie, L.H. Problems, challenges and future of plant disease management: From an ecological point of view. J. Integr. Agric. 2016, 15, 705–715, doi:10.1016/S2095-3119(15)61300-4.
5. Jones, J.D.G.; Dangl, J.L. The plant immune system. Nature 2006, 444, 323–329, doi:10.1038/nature05286.
6. Imran, Q.M.; Yun, B.-W. Pathogen-induced Defense Strategies in Plants. J. Crop Sci. Biotechnol. 2020, 23, 97–105.
7. Dangl, J.L.; Jones, J.D.G. Plant pathogens and integrated defence responses to infection. Nature 2001, 411, 826–833, doi:10.1038/35081161.
8. Ausubel, F.M. Are innate immune signaling pathways in plants and animals conserved? Nat. Immunol. 2005, 6, 973–979, doi:10.1038/ni1253.
9. Zipfel, C.; Felix, G. Plants and animals: A different taste for microbes? Curr. Opin. Plant Biol. 2005, 8, 353–360, doi:10.1016/j.pbi.2005.05.004.
10. Mackey, D.; Holt III, B.F.; Wiig, A.; Dangl, J.L. RIN4 interacts with Pseudomonas syringae type III effector molecules and is required for RPM1-mediated resistance in Arabidopsis. Cell 2002, 108, 743–754.
11. Coaker, G.; Falick, A.; Staskawicz, B. Activation of a phytopathogenic bacterial effector protein by a eukaryotic cyclophilin. Science 2005, 308, 548–550, doi:10.1126/science.1108633.
12. Mackey, D.; Belkhadir, Y.; Alonso, J.M.; Ecker, J.R.; Dangl, J.L. Arabidopsis RIN4 is a target of the type III virulence effector AvrRpt2 and modulates RPS2-mediated resistance. Cell 2003, 112, 379–389, doi:10.1016/S0092-8674(03)00040-0.
13. Day, B.; Dahlbeck, D.; Staskawicz, B.J. NDR1 interaction with RIN4 mediates the differential activation of multiple disease resistance pathways in Arabidopsis. Plant Cell 2006, 18, 2782–2791, doi:10.1105/tpc.106.044693.
14. Day, B.; Dahlbeck, D.; Huang, J.; Chisholm, S.T.; Li, D.H.; Staskawicz, B.J. Molecular basis for the RIN4 negative regulation of RPS2 disease resistance. Plant Cell 2005, 17, 1292–1305, doi:10.1105/tpc.104.030163.

15. van der Hoorn, R.A.L.; Kamoun, S. From Guard to Decoy: A new model for perception of plant pathogen effectors. Plant Cell 2008, 20, 2009–2017, doi:10.1105/tpc.108.060194.
16. Peter, I.S.; Davidson, E.H. Genomic Control Process: Development and Evolution; Academic Press: London, UK; San Diego, CA, USA, 2015; pp. xii, 448p.
17. Hong, R.L.; Hamaguchi, L.; Busch, M.A.; Weigel, D. Regulatory elements of the floral homeotic gene AGAMOUS identified by phylogenetic footprinting and shadowing. Plant Cell 2003, 15, 1296–1309, doi:10.1105/tpc.009548.
18. Phillips, T. Regulation of transcription and gene expression in eukaryotes. Nat. Educ. 2008, 1, 199.
19. Pulverer, B. Sequence-specific DNA-binding transcription factors. Nat. Cell Bio 2005, 13, 1–2.
20. Reddy, P.M.S.; Stamatoyannopoulos, G.; Papayannopoulou, T.; Shen, C.K.J. Genomic Footprinting and Sequencing of Human Beta-Globin Locus—Tissue-Specificity and Cell-Line Artifact. J. Biol. Chem. 1994, 269, 8287–8295.
21. Jalali, B.L.; Bhargava, S.; Kamble, A. Signal transduction and transcriptional regulation of plant defence responses. J. Phytopathol. 2006, 154, 65–74, doi:10.1111/j.1439-0434.2006.01073.x.
22. Van Verk, M.C.; Gatz, C.; Linthorst, H.J.M. Transcriptional Regulation of Plant Defense Responses. Adv. Bot. Res. 2009, 51, 397–438, doi:10.1016/S0065-2296(09)51010-5.
23. Buscaill, P.; Rivas, S. Transcriptional control of plant defence responses. Curr. Opin. Plant Biol. 2014, 20, 35–46, doi:10.1016/j.pbi.2014.04.004.
24. Windram, O.; Madhou, P.; McHattie, S.; Hill, C.; Hickman, R.; Cooke, E.; Jenkins, D.J.; Penfold, C.A.; Baxter, L.; Breeze, E.; et al. Arabidopsis Defense against Botrytis cinerea: Chronology and Regulation Deciphered by High-Resolution Temporal Transcriptomic Analysis. Plant Cell 2012, 24, 3530–3557, doi:10.1105/tpc.112.102046.
25. Lozano-Duran, R.; Macho, A.P.; Boutrot, F.; Segonzac, C.; Somssich, I.E.; Zipfel, C. The transcriptional regulator BZR1 mediates trade-off between plant innate immunity and growth. Elife 2013, 2, e00983, doi:10.7554/eLife.00983.
26. Fan, M.; Bai, M.Y.; Kim, J.G.; Wang, T.N.; Oh, E.; Chen, L.; Park, C.H.; Son, S.H.; Kim, S.K.; Mudgett, M.B.; et al. The bHLH Transcription Factor HBI1 Mediates the Trade-Off between Growth and Pathogen-Associated Molecular Pattern-Triggered Immunity in Arabidopsis. Plant Cell 2014, 26, 828–841, doi:10.1105/tpc.113.121111.
27. Malinovsky, F.G.; Batoux, M.; Schwessinger, B.; Youn, J.H.; Stransfeld, L.; Win, J.; Kim, S.K.; Zipfel, C. Antagonistic Regulation of Growth and Immunity by the Arabidopsis Basic Helix-Loop-Helix Transcription Factor HOMOLOG OF BRASSINOSTEROID ENHANCED EXPRESSION2

INTERACTING WITH INCREASED LEAF INCLINATION1 BINDING bHLH1. Plant Physiol. 2014, 164, 1443–1455, doi:10.1104/pp.113.234625.

28. Seo, E.; Choi, D. Functional studies of transcription factors involved in plant defenses in the genomics era. Brief. Funct. Genom. 2015, 14, 260–267, doi:10.1093/bfgp/elv011.
29. Imran, Q.M.; Lee, S.-U.; Mun, B.-G.; Hussain, A.; Asaf, S.; Lee, I.-J.; Yun, B.-W. WRKYs, the Jack-of-various-Trades, Modulate Dehydration Stress in Populus davidiana—A Transcriptomic Approach. Int. J. Mol. Sci. 2019, 20, 414.
30. Eulgem, T.; Rushton, P.J.; Robatzek, S.; Somssich, I.E. The WRKY superfamily of plant transcription factors. Trends Plant Sci. 2000, 5, 199–206, doi:10.1016/S1360-1385(00)01600-9.
31. Rushton, P.J.; Somssich, I.E.; Ringler, P.; Shen, Q.X.J. WRKY transcription factors. Trends Plant Sci. 2010, 15, 247–258, doi:10.1016/j.tplants.2010.02.006.
32. Cai, M.; Qiu, D.Y.; Yuan, T.; Ding, X.H.; Li, H.J.; Duan, L.; Xu, C.G.; Li, X.H.; Wang, S.P. Identification of novel pathogen-responsive cis-elements and their binding proteins in the promoter of OsWRKY13, a gene regulating rice disease resistance. Plant Cell Environ. 2008, 31, 86–96, doi:10.1111/j.1365-3040.2007.01739.x.
33. Sun, C.X.; Palmqvist, S.; Olsson, H.; Boren, M.; Ahlandsberg, S.; Jansson, C. A novel WRKY transcription factor, SUSIBA2, participates in sugar signaling in barley by binding to the sugar-responsive elements of the iso1 promoter. Plant Cell 2003, 15, 2076–2092, doi:10.1105/tpc.014597.
34. Pandey, S.P.; Somssich, I.E. The Role of WRKY Transcription Factors in Plant Immunity. Plant Physiol. 2009, 150, 1648–1655, doi:10.1104/pp.109.138990.
35. Asai, T.; Tena, G.; Plotnikova, J.; Willmann, M.R.; Chiu, W.L.; Gomez-Gomez, L.; Boller, T.; Ausubel, F.M.; Sheen, J. MAP kinase signalling cascade in Arabidopsis innate immunity. Nature 2002, 415, 977–983, doi:10.1038/415977a.
36. Meng, X.Z.; Zhang, S.Q. MAPK Cascades in Plant Disease Resistance Signaling. Annu. Rev. Phytopathol. 2013, 51, 245–266, doi:10.1146/annurev-phyto-082712-102314.
37. Zheng, Z.Y.; Qamar, S.A.; Chen, Z.X.; Mengiste, T. Arabidopsis WRKY33 transcription factor is required for resistance to necrotrophic fungal pathogens. Plant J. 2006, 48, 592–605, doi:10.1111/j.1365-313X.2006.02901.x.
38. Mao, G.H.; Meng, X.Z.; Liu, Y.D.; Zheng, Z.Y.; Chen, Z.X.; Zhang, S.Q. Phosphorylation of a WRKY Transcription Factor by Two Pathogen-Responsive MAPKs Drives Phytoalexin Biosynthesis in Arabidopsis. Plant Cell 2011, 23, 1639–1653, doi:10.1105/tpc.111.084996.
39. Li, G.J.; Meng, X.Z.; Wang, R.G.; Mao, G.H.; Han, L.; Liu, Y.D.; Zhang, S.Q. Dual-Level Regulation of ACC Synthase Activity by MPK3/MPK6 Cascade and Its Downstream WRKY

Transcription Factor during Ethylene Induction in Arabidopsis. PLoS Genet. 2012, 8, e1002767, doi:10.1371/journal.pgen.1002767.

40. Birkenbihl, R.P.; Diezel, C.; Somssich, I.E. Arabidopsis WRKY33 Is a Key Transcriptional Regulator of Hormonal and Metabolic Responses toward Botrytis cinerea Infection. Plant Physiol. 2012, 159, 266–285, doi:10.1104/pp.111.192641.
41. Ishihama, N.; Yamada, R.; Yoshioka, M.; Katou, S.; Yoshioka, H. Phosphorylation of the Nicotiana benthamiana WRKY8 Transcription Factor by MAPK Functions in the Defense Response. Plant Cell 2011, 23, 1153–1170, doi:10.1105/tpc.110.081794.
42. Shen, Q.H.; Saijo, Y.; Mauch, S.; Biskup, C.; Bieri, S.; Keller, B.; Seki, H.; Ulker, B.; Somssich, I.E.; Schulze-Lefert, P. Nuclear activity of MLA immune receptors links isolate-specific and basal disease-resistance responses. Science 2007, 315, 1098–1103, doi:10.1126/science.1136372.
43. Inoue, H.; Hayashi, N.; Matsushita, A.; Liu, X.Q.; Nakayama, A.; Sugano, S.; Jiang, C.J.; Takatsuji, H. Blast resistance of CC-NB-LRR protein Pb1 is mediated by WRKY45 through protein-protein interaction. Proc. Natl. Acad. Sci. USA 2013, 110, 9577–9582, doi:10.1073/pnas.1222155110.
44. Deslandes, L.; Olivier, J.; Theulieres, F.; Hirsch, J.; Feng, D.X.; Bittner-Eddy, P.; Beynon, J.; Marco, Y. Resistance to Ralstonia solanacearum in Arabidopsis thaliana is conferred by the recessive RRS1-R gene, a member of a novel family of resistance genes. Proc. Natl. Acad. Sci. USA 2002, 99, 2404–2409, doi:10.1073/pnas.032485099.
45. Narusaka, M.; Shirasu, K.; Noutoshi, Y.; Kubo, Y.; Shiraishi, T.; Iwabuchi, M.; Narusaka, Y. RRS1 and RPS4 provide a dual Resistance-gene system against fungal and bacterial pathogens. Plant J. 2009, 60, 218–226, doi:10.1111/j.1365-313X.2009.03949.x.
46. Chen, L.G.; Zhang, L.P.; Yu, D.Q. Wounding-Induced WRKY8 Is Involved in Basal Defense in Arabidopsis. Mol. Plant Microbe Interact. 2010, 23, 558–565, doi:10.1094/Mpmi-23-5-0558.
47. Murre, C.; Mccaw, P.S.; Baltimore, D. A New DNA-Binding and Dimerization Motif in Immunoglobulin Enhancer Binding, Daughterless, Myod, and Myc Proteins. Cell 1989, 56, 777–783, doi:10.1016/0092-8674(89)90682-X.
48. Ludwig, S.R.; Habera, L.F.; Dellaporta, S.L.; Wessler, S.R. Lc, a Member of the Maize R-Gene Family Responsible for Tissue-Specific Anthocyanin Production, Encodes a Protein Similar to Transcriptional Activators and Contains the Myc-Homology Region. Proc. Natl. Acad. Sci. USA 1989, 86, 7092–7096, doi:10.1073/pnas.86.18.7092.
49. Berben, G.; Legrain, M.; Gilliquet, V.; Hilger, F. The Yeast Regulatory Gene Pho4 Encodes a Helix-Loop-Helix Motif. Yeast 1990, 6, 451–454, doi:10.1002/yea.320060510.
50. Heim, M.A.; Jakoby, M.; Werber, M.; Martin, C.; Weisshaar, B.; Bailey, P.C. The basic helix-loop-helix transcription factor family in plants: A genome-wide study of protein structure and functional

diversity. Mol. Biol. Evol. 2003, 20, 735–747, doi:10.1093/molbev/msg088.

51. Murre, C.; Bain, G.; Vandijk, M.A.; Engel, I.; Furnari, B.A.; Massari, M.E.; Matthews, J.R.; Quong, M.W.; Rivera, R.R.; Stuiver, M.H. Structure and Function of Helix-Loop-Helix Proteins. BBA Gene Struct. Exp. 1994, 1218, 129–135, doi:10.1016/0167-4781(94)90001-9.
52. Carretero-Paulet, L.; Galstyan, A.; Roig-Villanova, I.; Martinez-Garcia, J.F.; Bilbao-Castro, J.R.; Robertson, D.L. Genome-Wide Classification and Evolutionary Analysis of the bHLH Family of Transcription Factors in Arabidopsis, Poplar, Rice, Moss, and Algae. Plant Physiol. 2010, 153, 1398–1412, doi:10.1104/pp.110.153593.
53. Fernandez-Calvo, P.; Chini, A.; Fernandez-Barbero, G.; Chico, J.M.; Gimenez-Ibanez, S.; Geerinck, J.; Eeckhout, D.; Schweizer, F.; Godoy, M.; Franco-Zorrilla, J.M.; et al. The Arabidopsis bHLH Transcription Factors MYC3 and MYC4 Are Targets of JAZ Repressors and Act Additively with MYC2 in the Activation of Jasmonate Responses. Plant Cell 2011, 23, 701–715, doi:10.1105/tpc.110.080788.
54. Ferredamare, A.R.; Pognonec, P.; Roeder, R.G.; Burley, S.K. Structure and Function of the B/Hlh/Z Domain of Usf. EMBO J. 1994, 13, 180–189, doi:10.1002/j.1460-2075.1994.tb06247.x.
55. Samira, R.; Li, B.H.; Kliebenstein, D.; Li, C.Y.; Davis, E.; Gillikin, J.W.; Long, T.A. The bHLH transcription factor ILR3 modulates multiple stress responses in Arabidopsis. Plant Mol. Biol. 2018, 97, 297–309, doi:10.1007/s11103-018-0735-8.
56. Goossens, J.; Mertens, J.; Goossens, A. Role and functioning of bHLH transcription factors in jasmonate signalling. J. Exp. Bot. 2017, 68, 1333–1347, doi:10.1093/jxb/erw440.
57. Song, S.S.; Qi, T.C.; Fan, M.; Zhang, X.; Gao, H.; Huang, H.; Wu, D.W.; Guo, H.W.; Xie, D.X. The bHLH Subgroup IIId Factors Negatively Regulate Jasmonate-Mediated Plant Defense and Development. PLoS Genet. 2013, 9, e1003653, doi:10.1371/journal.pgen.1003653.
58. Aparicio, F.; Pallas, V. The coat protein of Alfalfa mosaic virus interacts and interferes with the transcriptional activity of the bHLH transcription factor ILR3 promoting salicylic acid-dependent defence signalling response. Mol. Plant Pathol. 2017, 18, 173–186, doi:10.1111/mpp.12388.
59. Woldemariam, M.G.; Dinh, S.T.; Oh, Y.; Gaquerel, E.; Baldwin, I.T.; Galis, I. NaMYC2 transcription factor regulates a subset of plant defense responses in Nicotiana attenuata. BMC Plant Biol. 2013, 13, 73, doi:10.1186/1471-2229-13-73.
60. Nakano, T.; Suzuki, K.; Fujimura, T.; Shinshi, H. Genome-wide analysis of the ERF gene family in Arabidopsis and rice. Plant Physiol. 2006, 140, 411–432, doi:10.1104/pp.105.073783.
61. Riechmann, J.L.; Meyerowitz, E.M. The AP2/EREBP family of plant transcription factors. Biol. Chem. 1998, 379, 633–646.

62. Sakuma, Y.; Liu, Q.; Dubouzet, J.G.; Abe, H.; Shinozaki, K.; Yamaguchi-Shinozaki, K. DNA-binding specificity of the ERF/AP2 domain of Arabidopsis DREBs, transcription factors involved in dehydration- and cold-inducible gene expression. Biochem. Biophys. Res. Commun. 2002, 290, 998–1009, doi:10.1006/bbrc.2001.6299.

63. Dietz, K.J.; Vogel, M.O.; Viehhauser, A. AP2/EREBP transcription factors are part of gene regulatory networks and integrate metabolic, hormonal and environmental signals in stress acclimation and retrograde signalling. Protoplasma 2010, 245, 3–14, doi:10.1007/s00709-010-0142-8.

64. Mizoi, J.; Shinozaki, K.; Yamaguchi-Shinozaki, K. AP2/ERF family transcription factors in plant abiotic stress responses. BBA Gene Regul. Mech. 2012, 1819, 86–96, doi:10.1016/j.bbagrm.2011.08.004.

65. Licausi, F.; Ohme-Takagi, M.; Perata, P. APETALA2/Ethylene Responsive Factor (AP2/ERF) transcription factors: Mediators of stress responses and developmental programs. New Phytol. 2013, 199, 639–649, doi:10.1111/nph.12291.

66. Gibbs, D.J.; Conde, J.V.; Berckhan, S.; Prasad, G.; Mendiondo, G.M.; Holdsworth, M.J. Group VII Ethylene Response Factors Coordinate Oxygen and Nitric Oxide Signal Transduction and Stress Responses in Plants. Plant Physiol. 2015, 169, 23–31, doi:10.1104/pp.15.00338.

67. Feng, J.X.; Liu, D.; Pan, Y.; Gong, W.; Ma, L.G.; Luo, J.C.; Deng, X.W.; Zhu, Y.X. An annotation update via cDNA sequence analysis and comprehensive profiling of developmental, hormonal or environmental responsiveness of the Arabidopsis AP2/EREBP transcription factor gene family. Plant Mol. Biol. 2005, 59, 853–868, doi:10.1007/s11103-005-1511-0.

68. Li, H.; Wang, Y.; Wu, M.; Li, L.H.; Li, C.; Han, Z.P.; Yuan, J.Y.; Chen, C.B.; Song, W.Q.; Wang, C.G. Genome-Wide Identification of AP2/ERF Transcription Factors in Cauliflower and Expression Profiling of the ERF Family under Salt and Drought Stresses. Front. Plant Sci. 2017, 8, 946, doi:10.3389/fpls.2017.00946.

69. Xie, Z.L.; Nolan, T.M.; Jiang, H.; Yin, Y.H. AP2/ERF Transcription Factor Regulatory Networks in Hormone and Abiotic Stress Responses in Arabidopsis. Front. Plant Sci. 2019, 10, 228, doi:10.3389/fpls.2019.00228.

70. Feng, C.Z.; Chen, Y.; Wang, C.; Kong, Y.H.; Wu, W.H.; Chen, Y.F. Arabidopsis RAV1 transcription factor, phosphorylated by SnRK2 kinases, regulates the expression of ABI3, ABI4, and ABI5 during seed germination and early seedling development. Plant J. 2014, 80, 654–668, doi:10.1111/tpj.12670.

71. Bethke, G.; Unthan, T.; Uhrig, J.F.; Poschl, Y.; Gust, A.A.; Scheel, D.; Lee, J. Flg22 regulates the release of an ethylene response factor substrate from MAP kinase 6 in Arabidopsis thaliana via ethylene signaling. Proc. Natl. Acad. Sci. USA 2009, 106, doi:10.1073/pnas.0810206106.

72. Meng, X.Z.; Xu, J.; He, Y.X.; Yang, K.Y.; Mordorski, B.; Liu, Y.D.; Zhang, S.Q. Phosphorylation of an ERF Transcription Factor by Arabidopsis MPK3/MPK6 Regulates Plant Defense Gene Induction and Fungal Resistance. Plant Cell 2013, 25, 1126–1142, doi:10.1105/tpc.112.109074.
73. Mase, K.; Ishihama, N.; Mori, H.; Takahashi, H.; Kaminaka, H.; Kodama, M.; Yoshioka, H. Ethylene-Responsive AP2/ERF Transcription Factor MACD1 Participates in Phytotoxin-Triggered Programmed Cell Death. Mol. Plant Microbe Interact. 2013, 26, 868–879, doi:10.1094/Mpmi-10-12-0253-R.
74. Wang, H.; Li, J.; Bostock, R.M.; Gilchrist, D.G. Apoptosis: A functional paradigm for programmed plant cell death induced by a host-selective phytotoxin and invoked during development. Plant Cell 1996, 8, 375–391.
75. Zhou, J.; Tang, X.; Martin, G.B. The Pto kinase conferring resistance to tomato bacterial speck disease interacts with proteins that bind a cis-element of pathogenesis-related genes. EMBO J. 1997, 16, 3207–3218.
76. Gu, Y.Q.; Wildermuth, M.C.; Chakravarthy, S.; Loh, Y.T.; Yang, C.M.; He, X.H.; Han, Y.; Martin, G.B. Tomato transcription factors Pti4, Pti5, and Pti6 activate defense responses when expressed in Arabidopsis. Plant Cell 2002, 14, 817–831, doi:10.1105/tpc.000794.
77. Berrocal-Lobo, M.; Molina, A.; Solano, R. Constitutive expression of ETHYLENE-RESPONSE-FACTOR1 in Arabidopsis confers resistance to several necrotrophic fungi. Plant J. 2002, 29, 23–32, doi:10.1046/j.1365-313x.2002.01191.x.
78. Gutterson, N.; Reuber, T.L. Regulation of disease resistance pathways by AP2/ERF transcription factors. Curr. Opin. Plant Biol. 2004, 7, 465–471, doi:10.1016/j.pbi.2004.04.007.
79. Kanei-Ishii, C.; Sarai, A.; Sawazaki, T.; Nakagoshi, H.; He, D.N.; Ogata, K.; Nishimura, Y.; Ishii, S. The tryptophan cluster: A hypothetical structure of the DNA-binding domain of the myb protooncogene product. J. Biol. Chem. 1990, 265, 19990–19995.
80. Jia, L.; Clegg, M.T.; Jiang, T. Evolutionary dynamics of the DNA-binding domains in putative R2R3-MYB genes identified from rice subspecies indica and japonica genomes. Plant Physiol. 2004, 134, 575–585, doi:10.1104/pp.103.027201.
81. Rosinski, J.A.; Atchley, W.R. Molecular evolution of the Myb family of transcription factors: Evidence for polyphyletic origin. J. Mol. Evol. 1998, 46, 74–83, doi:10.1007/Pl00006285.
82. Du, H.; Zhang, L.; Liu, L.; Tang, X.F.; Yang, W.J.; Wu, Y.M.; Huang, Y.B.; Tang, Y.X. Biochemical and molecular characterization of plant MYB transcription factor family. Biochemistry (Moscow) 2009, 74, 1–11, doi:10.1134/S0006297909010015.
83. Paz-Ares, J.; Ghosal, D.; Wienand, U.; Peterson, P.A.; Saedler, H. The regulatory c1 locus of Zea mays encodes a protein with homology to myb proto-oncogene products and with structural similarities to transcriptional activators. EMBO J. 1987, 6, 3553–3558.

84. Dubos, C.; Stracke, R.; Grotewold, E.; Weisshaar, B.; Martin, C.; Lepiniec, L. MYB transcription factors in Arabidopsis. Trends Plant Sci. 2010, 15, 573–581, doi:10.1016/j.tplants.2010.06.005.
85. Ravaglia, D.; Espley, R.V.; Henry-Kirk, R.A.; Andreotti, C.; Ziosi, V.; Hellens, R.P.; Costa, G.; Allan, A.C. Transcriptional regulation of flavonoid biosynthesis in nectarine (Prunus persica) by a set of R2R3 MYB transcription factors. BMC Plant Biol. 2013, 13, 68, doi:10.1186/1471-2229-13-68.
86. Huang, W.J.; Lv, H.Y.; Wang, Y. Functional Characterization of a Novel R2R3-MYB Transcription Factor Modulating the Flavonoid Biosynthetic Pathway from Epimedium sagittatum. Front. Plant Sci. 2017, 8, 1274, doi:10.3389/fpls.2017.01274.
87. Cao, Y.; Li, K.; Li, Y.; Zhao, X.; Wang, L. MYB Transcription Factors as Regulators of Secondary Metabolism in Plants. Biology (Basel) 2020, 9, 61, doi:10.3390/biology9030061.
88. Zhang, T.Q.; Zhao, Y.L.; Wang, Y.C.; Liu, Z.Y.; Gao, C.Q. Comprehensive Analysis of MYB Gene Family and Their Expressions Under Abiotic Stresses and Hormone Treatments in Tamarix hispida. Front. Plant Sci. 2018, 9, 1303, doi:10.3389/fpls.2018.01303.
89. Roy, S. Function of MYB domain transcription factors in abiotic stress and epigenetic control of stress response in plant genome. Plant Signal. Behav. 2016, 11, doi:10.1080/15592324.2015.1117723.
90. Duesberg, P.H.; Bister, K.; Moscovici, C. Genetic structure of avian myeloblastosis virus, released from transformed myeloblasts as a defective virus particle. Proc. Natl. Acad. Sci. USA 1980, 77, 5120–5124.
91. Gonda, T.J.; Sheiness, D.K.; Bishop, J.M. Transcripts from the cellular homologs of retroviral oncogenes: Distribution among chicken tissues. Mol. Cell. Biol. 1982, 2, 617–624, doi:10.1128/mcb.2.6.617.
92. Souza, L.M.; Strommer, J.N.; Hillyard, R.L.; Komaromy, M.C.; Baluda, M.A. Cellular sequences are present in the presumptive avian myeloblastosis virus genome. Proc. Natl. Acad. Sci. USA 1980, 77, 5177, doi:10.1073/pnas.77.9.5177.
93. Daniel, P.T.; Scholz, C.; Essmann, F.; Westermann, J.; Pezzutto, A.; Dorken, B. Dendritic cells inhibit CD95/Fas-triggered apoptosis of activated T lymphocytes by a mechanism upstream of caspase-activation. Blood 1999, 94, 688A.
94. Daniel, X.; Lacomme, C.; Morel, J.B.; Roby, D. A novel myb oncogene homologue in Arabidopsis thaliana related to hypersensitive cell death. Plant J. 1999, 20, 57–66, doi:10.1046/j.1365-313X.1999.00578.x.
95. Vailleau, F.; Daniel, X.; Tronchet, M.; Montillet, J.L.; Triantaphylides, C.; Roby, D. A R2R3-MYB gene, AtMYB30, acts as a positive regulator of the hypersensitive cell death program in plants in response to pathogen attack. Proc. Natl. Acad. Sci. USA 2002, 99, 10179–10184, doi:10.1073/pnas.152047199.

96. Raffaele, S.; Vailleau, F.; Leger, A.; Joubes, J.; Miersch, O.; Huard, C.; Blee, E.; Mongrand, B.; Domergue, F.; Roby, D. A MYB transcription factor regulates very-long-chain fatty acid biosynthesis for activation of the hypersensitive cell death response in Arabidopsis. Plant Cell 2008, 20, 752–767, doi:10.1105/tpc.107.054858.
97. Seo, P.J.; Park, C.M. MYB96-mediated abscisic acid signals induce pathogen resistance response by promoting salicylic acid biosynthesis in Arabidopsis. New Phytol. 2010, 186, 471–483, doi:10.1111/j.1469-8137.2010.03183.x.
98. De Vos, M.; Denekamp, M.; Dicke, M.; Vuylsteke, M.; Van Loon, L.; Smeekens, S.C.; Pieterse, C.M. The Arabidopsis thaliana Transcription Factor AtMYB102 Functions in Defense Against the Insect Herbivore Pieris rapae. Plant Signal. Behav. 2006, 1, 305–311, doi:10.4161/psb.1.6.3512.
99. Mengiste, T.; Chen, X.; Salmeron, J.; Dietrich, R. The BOTRYTIS SUSCEPTIBLE1 gene encodes an R2R3MYB transcription factor protein that is required for biotic and abiotic stress responses in Arabidopsis. Plant Cell 2003, 15, 2551–2565, doi:10.1105/tpc.014167.
100. Segarra, G.; Van der Ent, S.; Trillas, I.; Pieterse, C.M.J. MYB72, a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. Plant Biol. 2009, 11, 90–96, doi:10.1111/j.1438-8677.2008.00162.x.
101. Olsen, A.N.; Ernst, H.A.; Leggio, L.L.; Skriver, K. NAC transcription factors: Structurally distinct, functionally diverse. Trends Plant Sci. 2005, 10, 79–87, doi:10.1016/j.tplants.2004.12.010.
102. Puranik, S.; Sahu, P.P.; Srivastava, P.S.; Prasad, M. NAC proteins: Regulation and role in stress tolerance. Trends Plant Sci. 2012, 17, 369–381, doi:10.1016/j.tplants.2012.02.004.
103. Kou, X.H.; Wang, S.; Wu, M.S.; Guo, R.Z.; Xue, Z.H.; Meng, N.; Tao, X.M.; Chen, M.M.; Zhang, Y.F. Molecular Characterization and Expression Analysis of NAC Family Transcription Factors in Tomato. Plant Mol. Biol. Rep. 2014, 32, 501–516, doi:10.1007/s11105-013-0655-3.
104. Hu, R.B.; Qi, G.A.; Kong, Y.Z.; Kong, D.J.; Gao, Q.A.; Zhou, G.K. Comprehensive Analysis of NAC Domain Transcription Factor Gene Family in Populus trichocarpa. BMC Plant Biol. 2010, 10, 145, doi10.1186/1471-2229-10-145.
105. Nuruzzaman, M.; Manimekalai, R.; Sharoni, A.M.; Satoh, K.; Kondoh, H.; Ooka, H.; Kikuchi, S. Genome-wide analysis of NAC transcription factor family in rice. Gene 2010, 465, 30–44, doi:10.1016/j.gene.2010.06.008.
106. Ooka, H.; Satoh, K.; Doi, K.; Nagata, T.; Otomo, Y.; Murakami, K.; Matsubara, K.; Osato, N.; Kawai, J.; Carninci, P.; et al. Comprehensive analysis of NAC family genes in Oryza sativa and Arabidopsis thaliana. DNA Res. 2003, 10, 239–247, doi:10.1093/dnares/10.6.239.
107. Pinheiro, G.L.; Marques, C.S.; Costa, M.D.B.L.; Reis, P.A.B.; Alves, M.S.; Carvalho, C.M.; Fietto, L.G.; Fontes, E.P.B. Complete inventory of soybean NAC transcription factors: Sequence

conservation and expression analysis uncover their distinct roles in stress response. Gene 2009, 444, 10–23, doi:10.1016/j.gene.2009.05.012.

108. Seo, P.J.; Kim, M.J.; Park, J.Y.; Kim, S.Y.; Jeon, J.; Lee, Y.H.; Kim, J.; Park, C.M. Cold activation of a plasma membrane-tethered NAC transcription factor induces a pathogen resistance response in Arabidopsis. Plant J. 2010, 61, 661–671, doi:10.1111/j.1365-313X.2009.04091.x.
109. Wu, Y.R.; Deng, Z.Y.; Lai, J.B.; Zhang, Y.Y.; Yang, C.P.; Yin, B.J.; Zhao, Q.Z.; Zhang, L.; Li, Y.; Yang, C.W.; et al. Dual function of Arabidopsis ATAF1 in abiotic and biotic stress responses. Cell Res. 2009, 19, 1279–1290, doi:10.1038/cr.2009.108.
110. Du, M.M.; Zhai, Q.Z.; Deng, L.; Li, S.Y.; Li, H.S.; Yan, L.H.; Huang, Z.; Wang, B.; Jiang, H.L.; Huang, T.T.; et al. Closely Related NAC Transcription Factors of Tomato Differentially Regulate Stomatal Closure and Reopening during Pathogen Attack. Plant Cell 2014, 26, 3167–3184, doi:10.1105/tpc.114.128272.
111. Block, A.; Toruno, T.Y.; Elowsky, C.G.; Zhang, C.; Steinbrenner, J.; Beynon, J.; Alfano, J.R. The Pseudomonas syringae type III effector HopD1 suppresses effector-triggered immunity, localizes to the endoplasmic reticulum, and targets the Arabidopsis transcription factor NTL9. New Phytol. 2014, 201, 1358–1370, doi:10.1111/nph.12626.
112. Wang, X.; Goregaoker, S.P.; Culver, J.N. Interaction of the Tobacco Mosaic Virus Replicase Protein with a NAC Domain Transcription Factor Is Associated with the Suppression of Systemic Host Defenses. J. Virol. 2009, 83, 9720–9730, doi:10.1128/Jvi.00941-09.
113. Kaneda, T.; Taga, Y.; Takai, R.; Iwano, M.; Matsui, H.; Takayama, S.; Isogai, A.; Che, F.S. The transcription factor OsNAC4 is a key positive regulator of plant hypersensitive cell death. EMBO J. 2009, 28, 926–936, doi:10.1038/emboj.2009.39.
114. Jensen, M.K.; Rung, J.H.; Gregersen, P.L.; Gjetting, T.; Fuglsang, A.T.; Hansen, M.; Joehnk, N.; Lyngkjaer, M.F.; Collinge, D.B. The HvNAC6 transcription factor: A positive regulator of penetration resistance in barley and Arabidopsis. Plant Mol. Biol. 2007, 65, 137–150, doi:10.1007/s11103-007-9204-5.
115. Jensen, M.K.; Hagedorn, P.H.; de Torres-Zabala, M.; Grant, M.R.; Rung, J.H.; Collinge, D.B.; Lyngkjaer, M.F. Transcriptional regulation by an NAC (NAM-ATAF1,2-CUC2) transcription factor attenuates ABA signalling for efficient basal defence towards Blumeria graminis f. sp hordei in Arabidopsis. Plant J. 2008, 56, 867–880, doi:10.1111/j.1365-313X.2008.03646.x.

Retrieved from https://encyclopedia.pub/entry/history/show/15904