Transcription Factors Involved in Plant Resistance to Pathogens

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Abstract: Phytopathogenic microorganisms have a significant influence on survival and productivity of several crop plants. Transcription factors (TFs) are important players in the response to biotic stresses, as insect attack and pathogen infection. In face of such adversities many TFs families have been previously reported as differentially expressed in plants as a reaction to bacterial, fungal and viral infection. This review highlights recent progresses in understanding the structure, function, signal regulation and interaction of transcription factors with other proteins in response to pathogens. Hence, we focus on three families of transcription factors: ERF, bZIP and WRKY, due to their abundance, importance and the availability of functionally well-characterized members in response to pathogen attack. Their roles and the possibilities related to the use of this knowledge for engineering pathogen resistance in crop plants are also discussed.

Keywords: Plant defense genes, biotic stress, interactions, crosstalk.

1. INTRODUCTION

During their entire life cycle, plants are continuously exposed to multiple biotic stressors like viruses, bacteria, fungi, nematodes and herbivorous insects that greatly influence the entire plant metabolism and adversely affect the growth, development, fertility and productivity of many crops [1]. In order to survive, plants developed efficient strategies to cope with and adapt to pathogen attack, a challenge that requires a coordination of complex physiological, biochemical and molecular processes through elaborate signaling transduction pathways to perceive stress and modulate the regulation and expression of various functional (*e.g.* defensins and protease inhibitors) and regulatory proteins, including transcription factors (TFs) and protein kinases [2].

To date, numerous studies have elucidated two primary means by which plants recognize invading pathogens and induce signaling events (Fig. **1**). The first line of defense in plants against pathogens is the recognition of microbial- or pathogen-associated molecular patterns (MAMPs or PAMPs), such as chitin, flagellin, and elongation factor-tu (EF-Tu). The perception of PAMPs by plant transmembrane pattern recognition receptors (PRRs), which include transmembrane receptor-like kinases (RLKs) and transmembrane receptor-like proteins (RLPs), activate an immune response referred to as MAMPs or PAMPs-triggered immunity (MTI or PTI), providing protection against non-host pathogens [3]. If a pathogen is able to surpass these first lines of defense by injecting a battery of effector proteins (Avr) into the cytoplasm in order to suppress or evade PTI, plants have a repertoire of immune receptors termed disease resistance (R) genes adequate to recognize the Avr proteins or detect changes to an associated host protein brought about by effectors. After recognition, plants carry a second layer of defense called effector-triggered immunity (ETI) that results in the prevention of pathogen infection regulated by interactions between different proteins and transcription factors [4-6]. Usually, PTI and ETI trigger similar defense responses, but ETI is quantitatively stronger and faster than PTI and often involves the development hypersensitive response (HR) a type of localized programmed cell death that limits pathogen spread [7, 8].

Resistance mechanisms of plants against pathogens include local and systemic responses that are controlled through pathways involving the hormones salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), as well as diverse genes encoding enzymes related to biosynthesis of secondary metabolites and pathogenesis related (PR) proteins, which finely control genome-wide transcriptional reprogramming of plant cells to orchestrate multiple defense-

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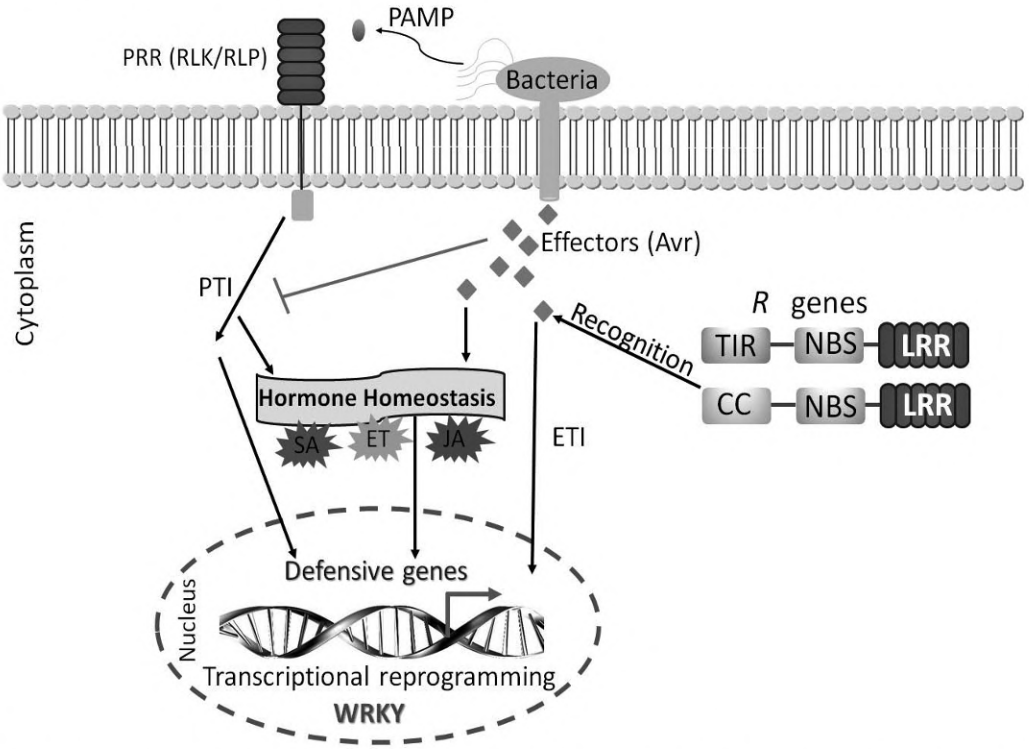

Fig. (1). Modes of plant recognition of a hypothetical invading pathogen and induction of active immune response. Pathogen-Associated Molecular Patterns (PAMPs) are perceived by pathogen recognition receptors (PRRs), which induce signaling cascades and lead to PAMP Triggered Immunity (PTI). To overcome this, bacterial pathogens release effector molecules (Avr) that inhibit the activation of PTI and interfere with the hormonal balance. Effector recognition by R genes leads to Effector-Triggered Immunity (ETI). After recognition, a signaling cascade begins and induces the activation of genes to a robust and quick defense response. ETI response may include altering chromatin configuration that further facilitates access by TF, such as WRKY that is strongly upregulated by pathogen infection.

related processes [9-12]. Transcriptional reprogramming occurs rapidly after pathogen infection. For example in the case of *Arabidopsis thaliana* defense against the necrotrophic fungus *Botrytis cinerea*, a high-resolution temporal transcriptomic analysis demonstrated that approximately one-third of the *Arabidopsis* genome was differentially expressed during the initial stages of infection [13]. Many TFs-families have been suggested to play an important role for transcriptional reprogramming associated to plant stress response. In legumes, transcriptomic analyzes to characterize plant-pathogen interactions revealed that many genes were regulated in a similar way in resistant and susceptible plants. These results indicated that the success of defense is due not only to the activation or suppression of transcription of particular genes in resistant genotypes, but possibly involves a phenomenon of higher degree of gene regulation [14, 15].

Transcription factors constitute key components of plant defense signaling and adaptation mechanisms through sequence-specific interactions with *cis*-regulatory DNA elements in the promoters of target stress-related genes containing binding sites for TFs, specifically activating or repressing expression target genes and directing the expression in a synchronized manner [16]. The binding of TFs to sequence-specific is influenced by conservation of sequences, abundance and conservation of binding domains. Therefore, binding site changes may cause variation in gene expression [17]. In addition, the activity of TFs proteins can be regulated through developmental or exogenous stimuli and by recruiting of host co-regulatory proteins [18].

TFs are generally classified into different families and subfamilies according to the structure of DNA binding domains (DBD), which are conserved among species. To mediate the response to pathogen attack, different transcription factors are up- or downregulated [19-21]. For example, the bZIP factor – that exhibits a prominent function in response to pathogen attack in maize – showed increased expression during *Ustilago maydis* infection [22]. At the present more than 50 different TFs families have been identified based mainly on bioinformatic annotation, rendering TFs one of the most abundant classes of proteins in plants. Some public databases actually provide diverse information to identification and annotation of plant TFs (Table **1**), such as DRTF [23], DPTF [24], TOBFAC [25], GRASSIUS [26], LegumeTFDB [27], PlnTFDB [28], SoyDB [29], AGRIS [30], and PlanTFDB [31].

This review focuses on selected plant TFs families, which play a significant role in defense responses to pathogen attack. We will address aspects of the structure, classification and molecular mechanisms of main TFs associated to biotic response, their target genes, gene regulatory networks and protein-protein interaction during defense response.

2. STRUCTURE OF PATHOGEN STRESS-RELATED TRANSCRIPTIONAL FACTORS

Transcription factors are central components of plant innate immune system and basal defense. After induction by pathogen attack, TFs can activate PR (pathogen related) genes or promote HR response, or both, whereas HR is char-

Table 1. Main databases for plant transcription factor (TF) families.

Number or name of plant species	Number of TF families	Database
Glycine max *Lotus japonicus* *Medicago truncatula*	61	LegumeTFDB: http://legumetfdb.psc.riken.jp/
Glycine max	64	SoyDB: http://casp.met.missouri.edu/soydb
Nicotiana tabacum	64	TOBFAC: http://compsysbio.achs.virginia.edu/tobfac/
Oryza sativa ssp. *indica* *O. sativa* ssp. *japonica*	63	DRTF: http://drtf.cbi.pku.edu.cn/
Populus trichocarpa	64	DPTF: http://dptf.cbi.pku.edu.cn/
Zea mays *Sorghum bicolor* *Saccharum* spp. *O. sativa*	59	GRASSIUS: http://grassius.org/grasstfdb.html
Arabidopsis thaliana	50	AGRIS: http://arabidopsis.med.ohio-state.edu/AtTFDB/
19 plant species	84	PlnTFDB 3.0: http://plntfdb.bio.uni-potsdam.de/v3.0/
83 plant species	58	Plant TFDB v3.0: http://planttfdb.cbi.pku,edu.cn/

acterized by tissue necrosis, frequently accompanied by the induction of systemic acquired resistance (SAR). Families of defense-related transcription factors include basic leucine zipper (bZIP), the apetala2-ethylene-responsive element binding factors (AP2/ERF), NAM/ATAF1/CUC also termed NAC family, MYC (myelocytomatosis related proteins), MYB, DOF, Whirly and WRKY gene families [21, 32], among others. Some examples are provided in Fig. **2** based on cowpea (*Vigna unguiculata*) NAC, WRKY, and ERF gene products.

This section describes structural and functional aspects of important TFs families, which have been shown to play a functional role in plant defense against to pathogen.

2.1. WRKY

Since the identification of the first WRKY protein in sweet potato [35], multiple members of this TFs class have been experimentally identified in important crops, including maize (*Zea mays*), barley (*Hordeum vulgare*), coffee (*Coffea arabica*), pepper (*Capsicum annuum*), cucumber (*Cucumis sativus*), castor bean (*Ricinus communis*), cotton (*Gossypium hirsutum*), tomato (*Solanum lycopersicum*), tobacco (*Nicotiana tabacum*), soybean (*Glycine max*) and grapevine (*Vitis vinifera*) [36-48].

The WRKY family is defined by the presence of highly conserved WRKY-DBD sequence of 60 amino acids in length, which contains the almost invariant WRKYGQK sequence motif at the N-terminal and a zinc-binding motif with features of C-C-H-H (C-X_{4-5}-C-X_{22-23}-H-X-H) or C-C-H-C (C-X_7-C-X_{23}-H-X-C) at the C-terminal region [49]. Recently, variations in amino sequences of WRKYGQK motif have been described in various plant species, whereas WRKYGKK and WRKYGEK are the most common variants, but WRKYGMK and WQKYGQK were also detected [37, 43].

WRKY protein family is classified into three major groups (I, II and III) based on phylogenetic relationships, the number of WRKY domains and the type of zinc finger motif. Two WRKY domains are present in members of the group I, while members of group II or III possess only one WRKY domain. The difference between group II and III can be observed in amino acid sequences of the zinc-binding motif. Generally, proteins of the groups I and II share the same C-C-H-H zinc finger motif, while group III contains a C-C-H-C motif [49]. The N-terminal region of some group I WRKY proteins, conserved pro-directed Ser residues (SP cluster) and/or a D domain motif that can be activated by phosphorylation of MAPK (mitogen-activated protein kinase), suggesting a post-translation regulation of WRKY [50].

WRKY DBD acts in the recognition process of the W-box element with the core sequence TTGAC*Y* (where *Y* = C or T) in promoter regions of pathogen or PAMP responsive genes (like those encoding PR proteins) positively modulating the expression of early defense-related genes against various phytopathogens or, still, negatively affecting them [25, 50, 51]. Besides, some studies indicated that WRKY proteins can bind to non-W-box sequences, such as the interaction of barley WRKY protein SUSIBA2 with a sugar responsive *cis*-element (SURE) [52]. Several WRKY showed

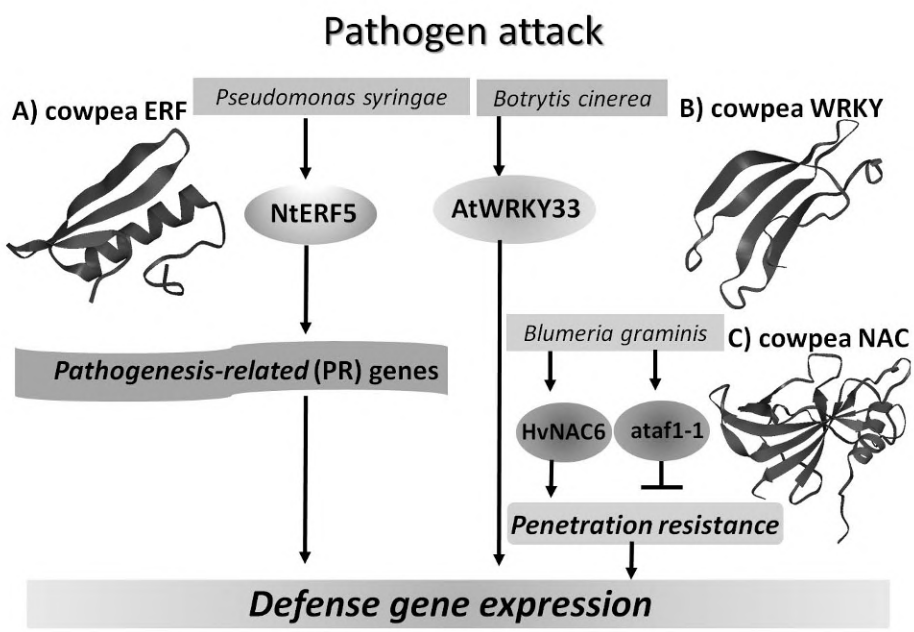

Fig. (2). Schematic representation of some known members of the ERF, NAC and WRKY transcription factors involved in biotic stress response integrating both positive (arrows) and negative (bars) regulatory mechanisms. Key to transcription factors: *Nicotiana tabacum* NtERF5; NAC types HvNAC6/ataf-1-1; *Arabidopsis thaliana* AtWRKY33. TF structures were generated using cowpea (*Vigna unguiculata*) sequences from NordEST database. Schematic representation in (A) ERF; (B) NAC and (C) WRKY regard available cowpea sequence expressed tags (EST). Comparative modelling (A, B, C) was based on known *A. thaliana* models (obtained by magnetic resonance or X-ray methods [33]) built from templates 3GCC (ERF/AP2), 3SWP (NAC) and 2AYD (WRKY) with 2.00, 4.11 and 1.6 Å of resolution, available in PDB (Protein Data Bank) using MODELLER 9v9 [34] and NOC 3.01 programs.

enrichment of W-boxes in their promoters, also acting on the promoters of other WRKY genes in a cotransfection process [53, 54].

2.2. bZIP

bZIP proteins include a bZIP domain, characterized by 60 to 80 amino acids in length, also exhibiting a basic region (BR) and a leucine zipper (LZ) that is functionally distinct [55]. The basic region shares a conserved region of 16 amino acid residues with an invariant N-x7-R/K motif responsible for nuclear localization and DNA binding. The leucine zipper is less conserved and is responsible for the dimerization of bZIP proteins, consisting of several heptad leucine repeats or other hydrophobic amino acids (phenylalanine, valine, or methionine) with conserved position at nine amino acids towards the C-terminus [56]. While a larger number of bZIP proteins can form homodimers, bZIPs members classified in different groups can be combined through heterodimerization to form bZIP pairs with different functionalities [57].

Recent analyses based on RNA-seq, expressed sequence tags (ESTs) and microarray analysis, revealed different numbers of bZIP representatives in plants, with 49 members in castor bean [58], 55 in grapevine [59], 64 in cucumber [60], 89 in rice [61], and 125 in maize [22]. Like WRKY, the bZIP family is classified into different groups, but in contrast to the three WRKY groups, the bZIP family is divided into ten groups (A, B, C, D, E, F, G, H, I and S) in the model plant *Arabidopsis* on the basis of amino acid sequence similarities of bZIP domains and protein structure [62]. It has been proposed that members of groups C and D in *Arabidopsis* play crucial roles in plant innate immunity, particularly the TGA proteins of the bZIP group D [63]. In maize members of group D have been proposed to participate in defense responses, with increased expression after infection by the fungus *Ustilago maydis* [22]. In other plants, members of the C class form heterodimers with the closely related S1 bZIP after biotic stimuli [32]. Plant bZIP proteins often bind to DNA sequences with the core sequence ACGT, like G-box (CACGTG), C-box (GACGTC) and A-box (TACGTA) [64, 65]. The bZIP monomers form long α-helices before binding to a DNA sequence. When it binds to specific sequences the N-terminal half binds in the major groove of double-stranded DNA and C-terminal half mediates dimerization to form superimposed coiled-coil [56].

2.3. ERF

Ethylene response factors (ERFs) belong to the AP2/ERF superfamily, one of the major group of plant TFs, characterized by the presence of a typical AP2 DNA-binding domain [66]. The AP2/ERF domain consists of approximately 60 to 70 amino acids that confer a typical helix-turn-helix structure responsible for sequence-specific DNA binding to modulate the target gene expression [67].

The ERF family is generally classified into two major subfamilies, dehydration-responsive element-binding (DREB) and ERF, based on DNA binding domain protein sequence [67]. Both ERFs and DREB subfamilies contain a single AP2/ERF domain with a conserved specific WLG motif, classified into I to X groups [68]. The ERF domain is composed by a three-strand anti-parallel β-sheet that recog-

nizes a target sequence at the N-terminal and a C-terminal α-helix, which is packed parallel to the second beta-strand [69]. Differences in amino acid sequences of both subfamilies are highly correlated to DNA affinity and specificity. Usually ERF subfamily recognizes the conserved nucleotide consensus sequence of the GCC-box (AGCCGCC) where G2, G5, and C7 are essential for binding to the promoter regions of PR genes (such as PR1 to PR5), modulating their expression in disease resistance signaling pathways [70]. Conversely, DREB subfamily interacts with a CCGAC core sequence in the promoter region of dehydration, low-temperature, high salinity stress-inducible genes and plant hormones such as ET, JA, SA and ABA [71].

3. TRANSCRIPTION FACTOR REGULATION AND FUNCTIONAL INTERACTION WITH OTHER PROTEINS IN DEFENSE RESPONSE

3.1. WRKY

WRKY TFs are the major regulators of immune responses and signaling involving PTI and ETI [51]. The PTI signaling cascades often lead to a series of early and late responses. Early response includes MAPK activation, deposition of callose and inhibition of seedling growth, while PAMP-induced resistance is considered to be a later response [72]. Transgenic approaches have been important for the understanding WRKY function and transcriptional regulatory network [73]. In rice a group II WRKY named *Os*WRKY62 was proposed to act as a negative regulator of both PTI and ETI. Therefore, *Os*WRKY62 overexpression compromised the activation of rice *Xa21*-mediated immunity signaling in response to infection by bacterial pathogen *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) [74, 75]. When ectopically expressed *Os*WRKY28 (a PAMP-responsive gene) decreased the rice resistance to biotrophic blast fungus *Magnaporthe oryzae*, also denoting a negative role of *Os*WRKY28 in PTI [76]. Similarly, *Ca*WRKY1 from chili pepper acted as a negative regulator of defense, as a virus-induced gene silencing (VIGS) factor, leading to decrease in growth of *Xanthomonas axonopodis* pv. *vesicatoria* race 1 [77]. Further, *Ca*WRKY1 overexpression in transgenic plants was associated with heightened hypersensitive cell death in response to *Pseudomonas syringae* pv. *tabaci* [77]. Additional studies have shown that plant mutants with HR and enhanced local cell death exhibited more resistance to biotrophic pathogens, but contributed to the high susceptibility to necrotrophic fungi [78, 79].

Overexpression or knock-out of WRKY members have also been associated to changes in resistance against pathogen attack [80-82]. For instance, *Os*WRKY89 overexpression in rice positively modulated pathogen defense response by elevated lignin accumulation and reduction of internode length, while the resistance was impaired after *Os*WRKY89 silencing [83]. Microarray analyses uncovered several induced WRKY genes by *M. oryzae* and chitin oligosaccharide elicitors, while their overexpression raised the resistance to blast infection [84]. *Os*WRKY45 overexpression, for example, involved two mechanism of resistance, a pre-invasive defense which prevented penetration of fungal hyphae into rice cells, and a post-invasive defense HR cell death [85]. *Os*WRKY53 overexpression was also associated with additional tolerance to *M. oryzae* in rice plant by upregulation of many defense-related genes [86, 87]. Similar to the function of rice WRKYs, the *At*WRKY33 expression was significantly induced in *Arabidopsis* treated with PAMPs or infected by *Botrytis cinerea* and *Alternaria brassicicola*. *Arabidopsis WRKY33* mutants were susceptible to both pathogens, indicating *At*WRKY33 as a key positive regulator of defense towards these necrotrophic fungi [88]. *Ca*WRKY27 from pepper also improved resistance against necrotrophic pathogen *Ralstonia solanacearum* [89]. Interestingly, many WRKY members of *Arabidopsis* represent dual roles in plant defense, either positive or negative, depending on the type of pathogen. For instance, *At*WRKY53 was positively regulated during plant response to biotrophic *P. syringae*, while the inactivation of *A*WRKY53 lead to a significant delay in defense response against *R. solanacearum*, revealing another dimension of the complex dynamic plant-pathogen interaction [90, 91]. *Arabidopsis* mutants also showed a positive role in plant resistance, as *AtWRKY*3 and *At*WRKY4 increased susceptibility to the necrotrophic fungus *B. cinerea* whereas overexpression of *At*WRKY4 enhanced susceptibility towards the biotrophic bacterium *P. syringae* [92]. During PTI, activation of MAPK cascade lead to the phosphorylation and activation of WRKY that in turn activated defense genes [51, 93]. For example, *At*WRKY33 was phosphorylated by MPK3/MPK6 which resulted in the expression of a camalexin, an antimicrobial agent of the phytoalexin group [94]. Effectors like bacterial flagellin flg22 and chitin also activated a MAPK cascade (MEKK1-MKK4/MKK5-MPK3/MPK6) in *Arabidopsis* that upregulated *At*WRKY29 and WRKY22, resulting in resistance against both bacterial (*B. cinerea*) and fungal pathogens (*P. syringae* pv. *Maculicola*). Additionaly, the overexpression of *At*WRKY29 in transiently transformed leaves activated by bacterial flagellin, lead to reduced chlorosis disease symptoms [95, 96]. Transcriptional regulation in immune response by the phosphorylation-dependent factor was also shown for tobacco *Nt*WRKY1.

Another example regards MAPK gene SPIK (salicylic acid-induced protein kinase) that mediated phosphorylation of *Nt*WRKY1 and increased DNA-binding activity to a W-box. In tobacco, *Nt*WRKY1 is involved in programed cell death, since its co-expression with SIPK in *Nicotiana benthamiana* resulted in more rapid local cell death than the expression of SIPK alone [97]. In *N. benthamiana*, *Nb*WRKY8 increased DNA-binding activity after phosphorylation of SIPK and other MAPKs, such as WIPK (wound-induced protein kinase) and NTF4, a tobacco mitogen-activated protein kinase associated to plant defense response. Besides, expression of phospho-mimicking *Nb*WRKY8 mutant induced the expression of defense genes, such as 3-hydroxy-3-methylglutuaryl CoA reductase 2 involved in biosynthesis of isoprenoid phytoalexins. On the other hand, silencing of *Nb*WRKY8 reduced the expression of genes involved in plant defense and enhanced disease susceptibility to the pathogens *Colletotrichum orbiculare* and *Phytophthora infestans*. The presented results supported the assumption that phosphorylation of *Nb*WRKY8 by MAPKs in tobacco plays a critical role by controlling response to pathogen attack [98].

WRKYs are frequently regulated by NPR1 (nonexpresser of pathogenesis-related), a transcription coactivator that regulates PR gene expression in the SA-dependent signaling pathway with NPR receptors, as NPR1 and its paralogues NPR3 and NPR4. They bind to SA with different affinities and activate PR gene expression and SAR [99, 100]. In *Arabidopsis* *At*WRKY38 and *At*WRKY62 were induced in a NPR1-dependent pathway associated with SA or by virulent *P. syringae*. Overexpression of *At*WRY38 and *At*WRKY62 reduced disease resistance and PR1 expression. Hence, *At*-WRKY38 and *At*WRKY62 function as negative regulators of plant basal defense. On the other hand, *Gh*WRKY15 from cotton can up-regulate the expression of NPR1 and several PR genes during infection by the fungus *Colletotrichum gossypii* [101]. In rice, overexpression of *Os*WRKY71 showed enhanced expression of *Os*NPR1 and *Os*PR1b and increased resistance to *X. oryzae* pv. *oryzae* [102]. Furthermore, WRKYs represent an important node of convergence between SA and JA signaling [103]. For instance, *Os*-WRKY13 positively regulated SA synthesis and genetic response but negatively controlled JA related genes [104]. Opposite to that, *At*WRKY18, *At*WRKY40, and *At*WRKY60 were proposed to function redundantly as negative regulators in SA-dependent pathways but played a positive role in JA-mediated pathways [105].

In *Arabidopsis*, many WRKY genes can be differentially regulated after treatment with SA [106]. For example, *At*-WRKY70 effectively acts as an integrator of cross-talk between SA- and JA-dependent pathways by promoting the activation of SA-dependent genes (such as PR2 and PR5) and suppressing JA-dependent defense response [107]. The study of *At*WRKY75 suggested positive regulation of the JA/ET signaling gene (PDF1.2) and negative regulation of the SA-dependent signaling (PR1), while *At*WRKY28 was involved in positive regulation of both JA/ET and SA-responsive pathways [73]. In banana, *Musa*WRKY71 transcripts were also up-regulated by SA [108]. Contrastingly, in cotton *Gh*WRKY40 overexpression induced by SA resulted in a reduction in transcription levels of downstream defense genes PR1a and PR2 after *R. solanacearum* infection [82]. Together, these examples illustrate how biotic stress-responsive WRKY TFs may represent convergence points between pathways with different functions, as summarized in Fig. **3**.

3.2. bZIP

Many of the well-studied TGA bZIP TFs are considered key regulators of signaling mediated by SA, playing a central role in defense against pathogen attack. Like WRKY, TGA factors interact with *NPR1* gene after recognition of a TGACGTCA motif found in NPR1. Under pathogen attack, the synthesis of SA modified the cellular redox status of NPR1 and resulted in the monomerization of NPR1 by activity of the thioredoxins H3 and H5 (TRX-H3/H5) [103]. Then, monomeric NRP1 accumulation in the nucleus formed a NPR1-TGA complex and subsequently induced the expression of defense related genes, including PR genes [109].

In *Arabidopsis* genome the TGA family comprises 10 members. Among these, members of group II (TGA2, TGA5, TGA6) and III (TGA3 and TGA7) have been studied in regard to their interaction with NPR1 [110, 111]. For example, the *Arabidopsis tga7* mutant showed enhanced susceptibility to *P. syringae* pv. *maculicola*, when compared to the wild-type, consistent with the idea that TGA7 acts as a transcription activator of PR genes [112]. Additionally, the physical interactions of NPR3 with both TGA2 and NPR1 suggested that the association to NPR3 acts as a negative regulator of defense response to *P. syringae* during early flower development [113]. In rice, *Os*TGA2.1 regulated SAR by interacting with *Os*NPR1 to alter PR gene expression. Transgenic rice suppressing *Os*TGA2.1 showed increased tolerance to *X. oryzae* pv. *oryzae* also altering PR gene expression [114]. Thus, it was suggested that wild-type *os*TGA2.1 had a negative impact on rice basal defense response to bacterial pathogens. On the other hand, *Arabidopsis* group-II TGA products (TGA2, TGA5, TGA6) were required for the establishment of the SA-dependent response (SAR), which was effective against *B. cinerea* [115]. At the same time, TGA2 was found to represses basal levels of PR-1 in the absence of SA [111, 116]. It is noteworthy that TGA genes can also function independently of NPR1 in disease resistance, as observed for TGA1 and TGA4, which comprise group I TGA factors, positively contributing to disease resistance to virulent strains of bacterial pathogen *P. syringae* [117, 118].

In another study with *Arabidopsis*, the bZIP10 gene was induced by ROS (reactive oxygen species), particularly during defense against the biotrophic fungus *Hyaloperonospora parasitica*, resulting in hypersensitive response [32]. An interesting example of bZIP linked to biotic stress is the *Os*TGAP1 gene of rice. Observation of knockout and overexpression mutants for *Os*TGAP1 indicated this gene as essential for the production of major diterpenoid phytoalexins involved in recognition of pathogen invasion in rice, by inducing momilactone and phytocassanes [119]. Another good example in rice regards the *Os*bZIP1 gene, whose expression was rapidly induced in leaves infected by *Magnaporthe grisea* or after treatment with SA, JA and ABA, suggesting that *Os*bZIP1 may play a positive role in defense against pathogens [120].

Functional genomics of crop species in response to infection by pathogens was carried out using microarray, qRT-PCR or RNA-seq, whereas up- or down-regulated genes were generally involved not only in cell protection from stress, but also in the regulation of regulatory genes, including bZIP TFs and signal transduction proteins activating the immune response. For example, two *Theobroma cacao* bZIP genes (RT42C09 and RT57A09) were discretely up-regulated in resistant genotypes 15 days after infection by the hemibiotrophic fungus *Moniliophthora perniciosa*, as revealed by macroarray data for bZIP-RT42C09 that uncovered a fold change (FC) of 2.96 after 72 h of pathogen infection and of 3.68 after 15 days. Similar expression intensities were observed using RT-qPCR, showing that bZIP expression increased in a small scale during the 15 days after infection (FCs: 0.93, 0.88, 0.81, 2.58 after 24, 48, 72 hours and 15 days of stress treatment, respectively) [121].

Transcriptional profiling of two contrasting ecotypes of the legume *Lotus japonicus* (Gifu B-129 and MG-20) during pathogenic interaction with *P. syringae* revealed that the

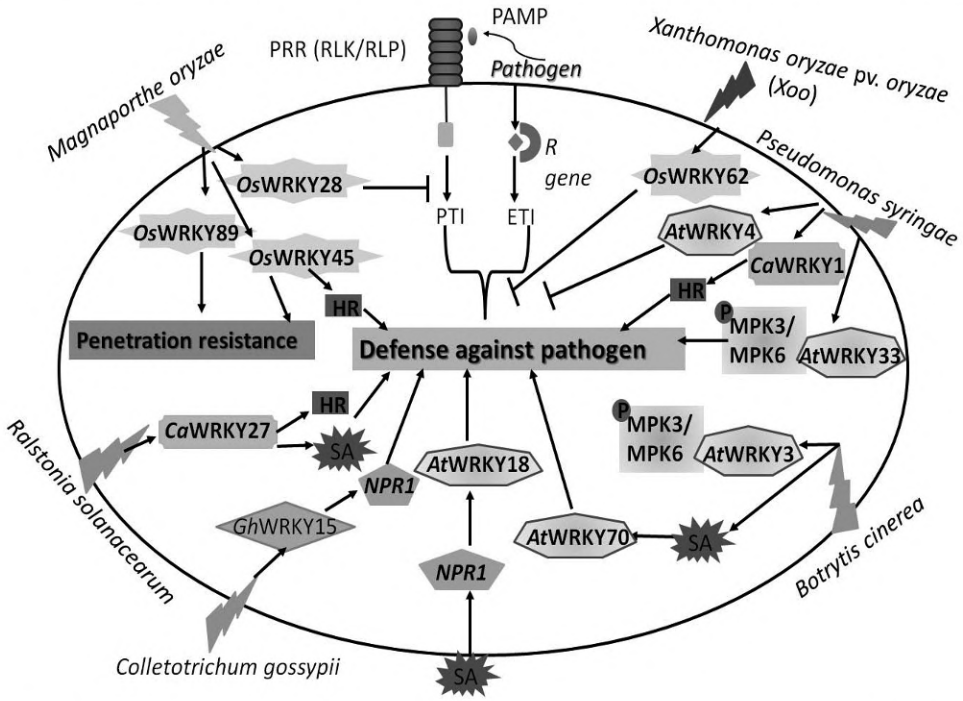

Fig. (3). Overview of WRKY interactions during stress response (pathogen defense) in crop plants integrating both positive (arrows) and negative (bars) regulatory mechanisms. Abbreviations: *At*WRKY, *Arabidopsis thaliana*; *Ca*WRKY, *Capsicum annum*; *Gh*WRKY15, *Gossypium hirsutum*; *Os*WRKY, *Oryza sativa*; HR, Hypersensitive Response; PAMP, Pathogen-Associated Molecular Patterns; PTI, PAMP-Triggered Immunity; ETI, Effector-Triggered Immunity; R gene, resistance gene; NPR1, Nonexpresser of Pathogenesis-Related genes 1; SA, Salicylic Acid.

expression of two TGA-bZIP genes were down-regulated in MG-20 while a distinct TGA-bZIP was up-regulated in Gifu B-129 [14]. Thus, additional studies of plant-pathogen interaction in legume species is of crucial importance to better understand the role of transcriptional factors in disease response within this group.

Another example was delineated by the study of Blanco-Ulate *et al*. [122] with tomato fruit transcriptome in response to infection by *B. cinerea*, which induced changes in relative expression of TGA6, suggesting that this factor probably serves as a control point to regulate SA signaling when fruit-pathogen interactions occur. A role of tomato *Si*TGA1.a in disease development caused by *B. cinerea* was previously implicated in association with a mechanism that uses SA-signaling pathway and also depends of NPR1 [123].

Recent studies have shown that up-regulation and activation of bZIP orthologs are common as part of plant defense response processes. A *N. benthamiana* orthologous of *At*bZIP60 (named *Nb*bZIP60) was significantly up-regulated in response to inoculation with soil bacterium *P. cichorii*, whereas it was unaffected by infection with the compatible pathogen *P. syringae* pv. *tabaci*. Furthermore, *Nb*ZIP60 silencing resulted in more susceptible plants to infection by *P. cichorri* compared to the control. These results indicated an involvement of this bZIP in plant innate immunity [124]. In tobacco, infection by *Potato virus x* (PVX) induced bZIP60 gene expression and was supposed to suppress host cell death response [125].

A possible role of bZIPs in mediating crosstalk response between abiotic and biotic stresses has also been reported [126]. The pepper bZIP *Ca*bZIP1 is a potential regulator in enhanced resistance to bacterial and fungi pathogens, and tolerance to environmental stresses. Notably, transgenic *Arabidopsis* overexpression *Ca*bZIP1 conferred enhanced resistance to *P. syringae* pv. *tomato* DC3000, accompanied by expression of the PR-gene *At*PR-4 and of a gene responsive to dehydration (*At*D29A) [127]. Similarly, in a recent study, a bZIP protein from tomato named SIAREB1 was induced by both drought and salinity, whereas its overexpression in tomato mutants up-regulated several PR-genes [128].

Due to the multiple functions of bZIP TFs in biotic stress response, these potential candidate genes have received far less attention for application in the improvement of pathogen resistance in crops. Such an approach would be interesting toward a better understanding of the network regulation associated to bZIP TFs. An overview of different studies currently available with BZIP TFs and examples of known interactions is represented in Fig. **4**.

3.3. ERF

The role of ERF proteins in plant defense against different pathogens has been widely studied and provides a foundation for applying these genes to enhance pathogen resistance in crops. For example, ERF transcription factor 1 (*At*ERF1) from *A. thaliana* mediated resistance to *Fusarium oxysporum* f.sp. *conglutinans* and *F. oxysporum* f.sp. *lycopersici*, and its expression in *Arabidopsis* is known to up-regulate defense genes, leading to enhanced resistance against the mentioned pathogens [129]. Furthermore, constitutive expression of *At*ERF1 activated plant defensin gene

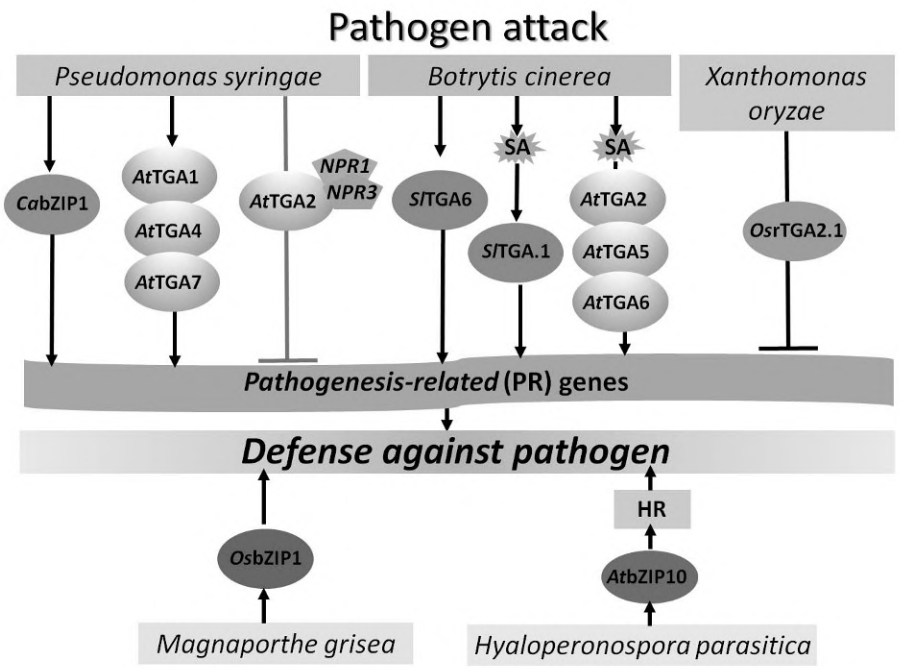

Fig. (4). Overview of bZIP interactions during biotic stress responses in crop plants, integrating both positive (arrows) and negative (bars) regulatory mechanisms. Key to transcriptional factors: *Capsicum annuum* bZIP1; *Arabidopsis thaliana At*TGA1, *At*TGA2, *At*TGA5, *At*TGA1, *At*TGA6, *At*TGA7; *Solanum lycopersicum Sl*TGA6 and *Sl*TGA.1; *Oryza sativa Os*rTGA2.1; *Oryza sativa Os*bZIP1; *A. thaliana At*bZIP10. Abbreviations: NPR1 and NPR3, Nonexpresser of Pathogenesis-Related genes 1 and 3; SA, salicylic acid; HR, Hypersensitive Response.

(PDF1.2) and other PR genes associated to resistance to the necrotrophic fungi *Botrytis cinerea* and *Plectosphaerella cucumerina* by integrating ET and JA defense responses [130]. In the medicinal plant *Artemisia annua*, ectopic expression of *Aa*ERF1 enhanced the expression level of the defense gene PDF1.2 and also of a basic chitinase (ChiB), increasing resistance against *B. cinerea* [131]. Conversely, ERF9 acted a negative regulator in plant defense against *B. cinerea* mediated by ET/JA signaling pathway [132]. Interestingly, the ERF *At*ORA59 implicated in JA and ET mediated defense and was required for PDF1.2a expression following infection by *B. cinerea* and *A. brassicicola*. However, plants silencing the *At*ORA59 gene showed increased susceptibility only to *B. cinerea*, presumably by impaired expression of the *At*ORA59-regulated defenses genes, while the level of basal resistance to *A. brassicicola* in *At*ORA59-silenced plants did not differ from wild-type [133].

A recent study on the ERF6 protein has shown that it was phosphorylated by MPK6, leading to defense gene expression, including PDF1.1 and PDF1.2, and enhancing resistance to *B. cinerea* [134]. These results were similar to the results reported by Moffat *et al.* [135] indicating that *At*ERF5 and *At*ERF6 played a positive role in plant defense against *B. cinerea* but had, in opposite, a negative role in resistance to *P. syringae* pv. *tomato*. Moreover, conflicting reports exist about the functions of ERF5 and ERF6. For example, Son *et al.* [136] observed that *At*ERF5 and *At*ERF6 positively regulated defense against bacterial *P. syringae* pv. *tomato*, whereas the same factors negatively regulated chitin-mediated defense response against the fungal pathogen *Alternaria brassicola*. These results suggested that several members of the ERF family may control the expression of defense genes both negatively and positively. Camehl *et al.* [137] discussed other examples of ERF negative regulatory role in defense gene expression, showing that ERF9 and ERF14 also inhibited the expression of PR-1 gene during colonization process by the endophytic fungus *Piriformospora indica*.

ERF genes may also mediate crosstalk between plant defense and ABA-related signaling. For instance, an ERF protein from tomato activated the expression of PR genes and positively regulated pathogen resistance in tomato and tobacco to the bacteria *R. solanacearum* as a result of ABA modulation. ABA enhanced the binding of TSRF1 isolated from tomato with the GCC box in tobacco, while fluridone, an inhibitor of ABA biosynthesis, decreased the binding of TSRF1 [138]. Therefore, overexpression of TSRF1 in tobacco and tomato constitutively activated the expression of PR genes. In opposition, pepper TF *Ca*ERF5 was induced by SA but no transcript accumulation was observed under ABA treatment. Overexpression of *Ca*ERF5 in tobacco upregulated defense-related genes and also enhanced resistance to *R. solanacearum* infection [139]. Recently, rice knockdown mutants of *Os*ERF922 (by means of RNAi) enhanced resistance to *M. oryzae* by increasing expression of PR and phytoalexin coding genes. Divergently, plants overexpressing *Os*ERF922 showed reduced expression of defense genes and enhanced susceptibility to *M. oryzae*. Thus, *Os*ERF922 negatively regulated resistance to *M. oryzae*. Furthermore, the ABA levels enhanced in the overexpressing lines and declined in the RNAi plants, indicating that *Os*ERF922 was integrated into the crosstalk between biotic and abiotic stress-signaling networks, possibly due to modulation of the ABA levels to suppress defense response [140].

ERF has been also considered to play a crucial role in the crosstalk between cold tolerance and pathogen resistance. For example, the ectopic expression of a pepper ERF gene named *Ca*FP1 improved tolerance to *P. syringae* pv. *tomato* and freezing stress in transgenic *Arabidopsis* [141]. Recently, the overexpression of *Ta*PIE1 from wheat (*Triticum aestivum*) exhibited significantly enhanced resistance to both necrotrophic fungus *Rhizoctonia cerealis* and freezing stress, while wheat plants underexpressing *Ta*PIE1 were more susceptible to both stresses relative to control plants [142]. Similar to the function of tomato *Ta*PIE1, ectopic expression of *Ti*ERF1, a gene from *Thinophyrum intermedium* (a wild wheat relative) enhanced resistance to fungus *Rhizoctonia cerealis* in both wheat and tobacco by activating PR genes primarily in an ET-dependent pathway [143]. ERF genes also played an important role in disease response in Chinese wild grapevine (*Vitis pseudoreticulata*) possibly via regulation of PR genes or still, directly involving abiotic stress responsive pathways. Overexpression of *Vp*ERF2 and *Vp*ERF3 in transgenic tobacco plants lead to enhanced resistance to both bacteria (*R. solanacearum*) and fungus (*Phytophtora parasitica* var. *nicotianae*). Importantly, *Vp*ERF2 was induced by drought, cold and heat treatments. Concurrently, *Vp*ERF3 was distinctly induced by SA and ET [144].

Distinct roles of ET-associated defense were identified for different plant species responding to the same pathogen. For example, overexpression of *Mt*ERF1-1 in roots of the legume *Medicago truncatula* (barrel medic) increased resistance to *R. solani* and also against the oomycete *Phytophthora medicaginis* [145]. However, previous studies on the related gene *At*ERF14, an important regulator of ET-dependent defense in *Arabidopsis*, indicated that its expression was not essential for resistance to *R. solani* but was required for resistance to *F. oxysporum* [146] while *M. truncatula* plants overexpressing *Mt*ERF1-1 and challenged by *F. oxysporum* exhibited no altered resistance. Another interesting example in legumes regarded *Gm*ERF3 from soybean. Overexpression of *Gm*ERF3 in transgenic tobacco plants induced the expression of some PR genes (such as PR1, PR2 and PR4) and enhanced resistance to infection by *R. solanacearum*, *A. alternata*, and tobacco mosaic virus, conferring tolerance to salinity and dehydration stresses [147]. Fig. **5** presents an overview of the effects of ERF considering some studies currently available.

4. FUNCTIONAL INTERACTIONS OF TFS WITH OTHER PROTEINS IN DEFENSE RESPONSES

In molecular biology, an interactome is the whole set of molecular interactions in a particular cell, tissue, developmental stage or organism. It includes interactions among molecules but also comprises indirect interactions among genes and their products [148]. A significant number of interacting patterns of plant TFs with roles in signaling, transcription, chromatin remodeling, and other cellular processes has been identified [149] but there are many interactions to be hypothesized, recognized and, even more, validated. Here we focus on some examples involving protein-protein interactions through analysis of the interactomes of TFs presented in section 3.

4.1 AtWRKY33 Interactome

In order to discern and exemplify the strong interaction between WRKY33 and other proteins, we used the database view of STRING (Fig. **6**). The output shows that *At*WRKY33 interacted with VG protein which contains a conserved FXXVQXLTG region, named VQ domain, like SIB1 (sigma factor-interactingg protein 1). Recent reports suggested a role of SIB1 in the disease resistance pathway of *Arabidopsis*. Mutations in SIB1 decreased the expression of defense-related PR genes triggered by necrotrophic fungus *B. cinerea,* while its overexpression increased resistance to this fungus [149, 150]. Also, phosphorylation of WRKY by MPKs could be an important mean to transduce the signal to the nucleous [151], also pointed by previous studies with MAPKs (MPK3, MPK4 and MPK6) that implicated in plant innate immunity [152]. Upon pathogen infection, *At*WRKY33 can be phosphorylated by two MAP kinases, MPK3 and MPK6, which resulted in an increase of camalexin biosynthesis [153].

A recent analysis found evidence that *At*WRKY33 was phosphorylated by MPK3 and by MPK6 *in vivo* in response to *B. cinerea* infection. Moreover, *At*WRKY33 was also capable of interacting with MPK4 and MSK1. During infection by *P. syringae*, the MPK4 was activated and phosphorylated MSK1, which released the *At*WRKY33 to bind to the promoter region of some defense genes, including genes involved with camalexin biosynthesis [154]. In addition, the MEKK-like class of MAPKKKs (MEKK1–MEKK4) also interacted with WRKY in plant innate immunity. Interestingly, previous studies have shown that MPK4, MEKK1, MKK1 and MKK2 act as negative regulator of plant immunity since these mutants constitutively expressed PR genes and also exhibited a severely dwarfed growth phenotype [155, 156].

Extensive interactions among TFs have been demonstrated in different plant species. In *Arabidopsis*, WRKY proteins (*At*WRKY18 and *At*WRKY40) interacted with themselves through the leucine zipper motifs present at the N-termini [105]. The interaction between *At*WRKY18 and *At*WRKY40 was suggested to play a role as negative regulator in PTI defense against *P. syringae* and powdery mildew fungus *Golovinomyces orontii* [105, 157, 158]. In the network generated, WRKY also interacted with zinc-finger CCCH. Interestingly, SZF1 protein also interacted with *At*WRKY33 in defense response (Fig. **6**). SZF1 and *At*WRKY33 are considered to play important roles in *Arabidopsis* tolerance also as a response to high concentration of NaCl [159, 160]. STZ protein exhibits also a repressor domain, effective in repressing the expression of other TFs, leading to increased salt stress tolerance [161]. This interaction represents an example of crosstalk between both biotic and abiotic stress. Another important interaction of *At*WRKY33 was observed in regard to CFZ1/ZFAR1, a zinc-finger protein, for which loss of function mutants increased local susceptibility to *Botryis* [162]. WRKY also interacted with AT5G61600, a member of ERF family (ERF104). Phosphorylation of ERF104 by MPK6 resulted in release of EFR104 from the complex, which was associated to pathogen perception presumably allowing ERF104 to bind to ET-

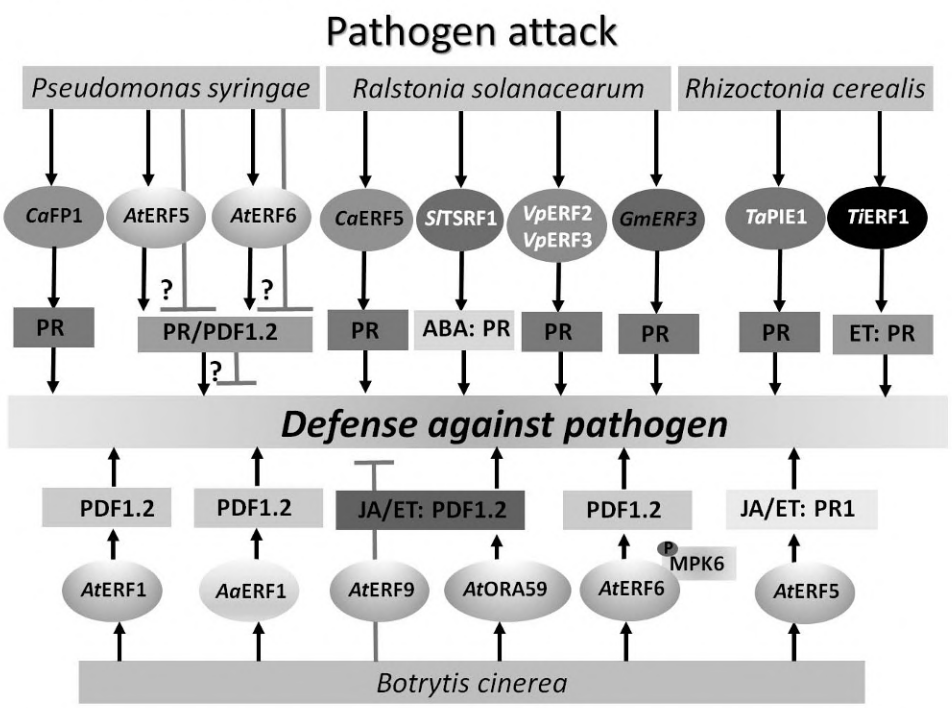

Fig. (5). Overview of ERF interactions during biotic stress responses in crops plants, integrating both positive (arrows) and negative (bars) regulatory mechanisms. Key to transcriptional factors:, *Capsicum annuum Ca*FP1, *Arabidopsis thaliana At*ERF1, *At*ERF5, *At*ERF6, *At*ERF9, *At*ORA59;, *Solanum lycopersicum Sl*TSRF1;, *Vitis pseudoreticulata Vp*ERF2 and *Vp*ERF3;, *Glycine max Gm*ERF3;, *Triticum aestivum Ta*PIE1;, *Thinophyrum intermedium Ti*ERF1. Abbreviations: PR, pathogenesis-related genes; PDF1.2, plant defensin gene 1.2; JA, jasmonic acid; ET, ethylene; ABA, abscisic acid.

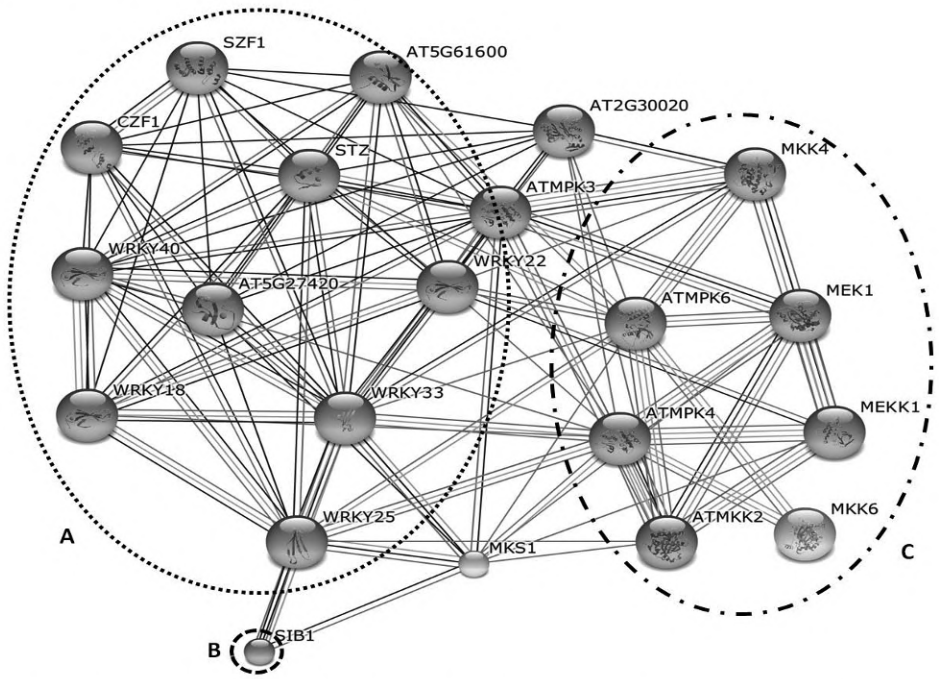

Fig. (6). Schematic representation of the interactions between WRKY33 and other proteins. STRING database program version 9.0 (Szklarczyk *et al.* [157]) was used for the bioinformatic prediction of protein-protein interactions. The MAP kinase (MPK) and MAP kinase kinase (MKK/MEKK) are confined within circle A, whereas SIB1 protein is within circle B, while circle C emcompasses interactions involving WRKY and other TFs.

responsive defense genes [163]. Additional interaction partners can be expected for *At*WRKY33 and other WRKY representatives regarding biotic stress situations in the future.

4.2. bZIP TGA1 Interactome

Many different roles have been attributed to protein interaction partners in the TGA1 interactome (Fig. **7**), and

some of these are regulators of the bZIP activity and expression level. Nonexpresser of Pathogenesis-Related proteins (NPR1 and NPR4) were identified as TGA1 interaction partners. NPR4 was recognized as negative regulator of plant defense, while NPR1 increased DNA activity of TGA1 [164]. Stronger associations were observed with genes essential for signaling defense response, including AT1G09740 (ET responsive protein), ATTPS10 (that encodes a trehalose phosphate synthase) and WNK4 (kinase protein). Another gene, ROXY1, has been classified as a NBS-LRR type R gene, also altering the expression of bZIP genes as shown by Zhou *et al*. [165] in a microarray experiment underlying the HR of rice to *Xanthomonas oryzae* pv. *oryzicola*. Another member of the network, AT1G31540, regarded an R gene of the TIR-NBS-LRR class. Similar to the observed in WRKY, bZIP genes also interact with other bZIP proteins.

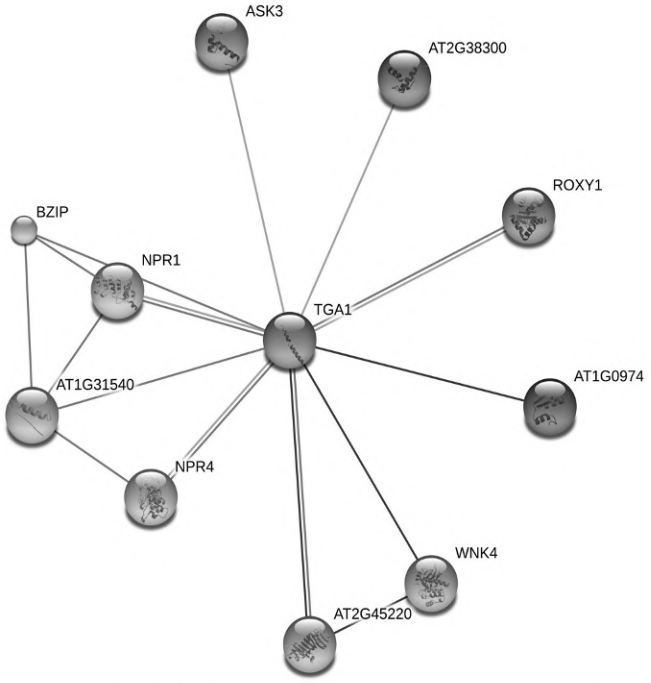

Fig. (7). Schematic representation of the TGA1 interaction with other proteins predicted in silico by STRING database program version 9.0 (Szklarczyk *et al.* [157]).

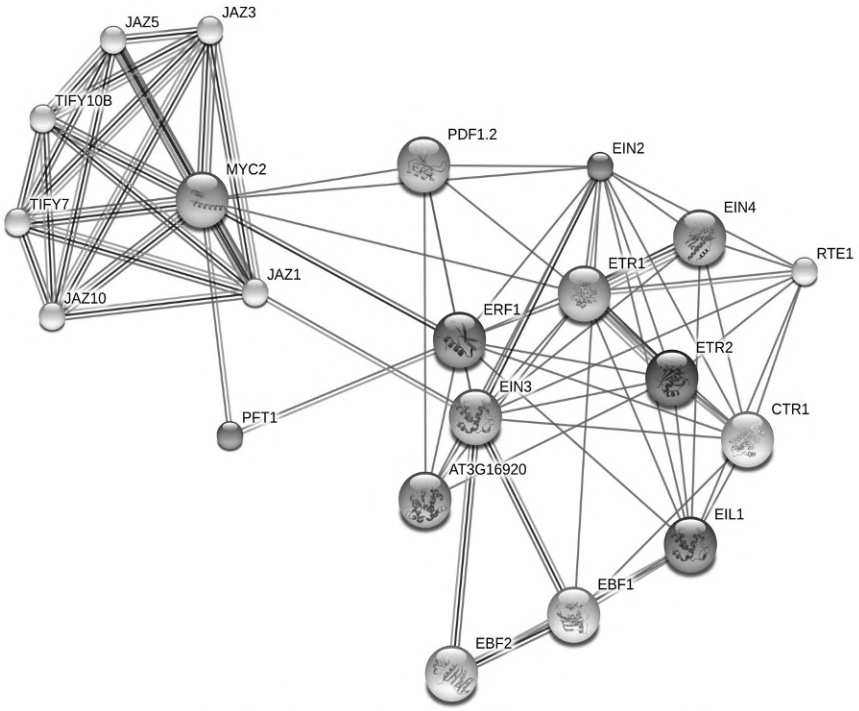

Fig. (8). Schematic representation of ERF1 with other proteins. STRING database program version 9.0 (Szklarczyk *et al.* [157]) was used for the bioinformatic prediction of protein-protein interactions.

4.3. ERF1 Interactome

ERF1 has a significant interactome (Fig. **8**) showing both positive and negative regulation of this major factor during biotic defense response, highlighting interaction with JAZ1 and ETI1. Upon necrotrophic fungi infections, plants can produce JA and subsequently induce the expression of downstream defense genes, including ERF1 and PDF1.2 [166]. Transcriptional factor EIN3 and EIL1 mediated ET signaling, and negatively regulated PTI immunity. Plants lacking EIN3 and EIL1 showed enhanced PAMP defenses and resistance to *P. syringae* [167]. In turn, EIN3 activation required JA signaling and directly regulated ERF1 gene expression by binding to a primary ethylene response element present in the promoter of ER1 [168].

ERF1 also presented interaction with *phytochrome and flowering time1* (*PFT1*), regulating JA-dependent defenses. Some studies showed that *pft1* mutant was unable to activate JA-dependent defense genes [169]. These interactions are considered to be conserved across plant species and further studies shall help to elucidate important biological processes modulated by ERF1 factors.

CONCLUDING REMARKS

In the past decade substantial efforts focused in improving high-throughput analytical technologies for investigating transcription factors. Nowadays, new breakthroughs in plant-pathogen interaction research rely on the development of novel omics approaches, including proteomics, metabolomics and interactomics that are important to uncover complex transcriptional factor networks. Next Generation Sequencing brought also benefits to the understanding of these factors, since many of them present discrete expression but are able to induce significant changes under stress. For many of the here mentioned TFs similar functions have been proposed in different plant species, indicating a crucial role in the induction of signal cascades, leading to cell reprogramming and stress response. Nevertheless, the discovery of post-transcriptional regulation of TFs is emerging as a crucial factor in the control of their activity, representing a new frontier to be unveiled. Several authors have already established the importance of TFs in the regulation of defense against pathogens in plants, sometimes also associated to resistance or tolerance to other types of stress. In face of their effects, these factors constitute promising candidates to improve resistance to pathogen in a variety of crops using biotechnological tools. Some results using crops have shown that resistance to fungal and bacterial pathogens requires ET, JA, SA and ABA signaling pathways through selectively interacting with TFs, once again highlighting the importance of the close relationships within all signaling pathways referred in this review.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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LIST OF ABBREVIATIONS

ABA	=	abscisic acid
AGRIS	=	*Arabidopsis* gene regulatory information server
AP2/ERF	=	ethylene-responsive element binding factors
ATAF1	=	*Arabidopsis* transcription activation factor
Avr	=	effector proteins
DOF	=	DNA-binding with one finger
BR	=	basic region
bZIP	=	the basic region-leucine zipper motif
ChiB	=	basic chitinase
CUC	=	cup-shaped cotyledon
DNA	=	deoxyribonucleic acid
DBD	=	DNA-binding domain
DOF	=	DNA-Binding with one zinc finger
DREB	=	dehydration-responsive element-binding
DRTF	=	database of rice transcription factors
DPTF	=	database of poplar transcription factors
EF-Tu	=	elongation factor-tu
ERF	=	ethylene response factors
EST	=	sequence expressed tag
ET		=ethylene
ETI	=	effector-triggered immunity
ETS	=	effector-triggered susceptibility
GRASSIUS	=	grass regulatory information server
HR	=	hypersensitive response
JA	=	jasmonic acid
LegumeTFDB	=	an integrative database of *Glycine max*, *Lotus japonicus*, *Medicago truncatula*
LZ	=	leucine zipper
MAMPs	=	microbial associated molecular patterns
MAPK or MEKs	=	mitogen-activated protein kinase
MTI	=	MAMPs Triggered Immunity
MYB	=	domain transcription factor family
MYC	=	myelocytomatosis related proteins
NAC	=	domain transcription factor family
NAM	=	no apical meristem

NPR1, NPR2, NPR3, NPR4 and NPR5	=	nonexpresser of pathogenesis-related genes 1, 2, 3, 4 and 5
PAMP	=	pathogen-associated molecular patterns
PCD	=	programmed cell death
PR	=	pathogenesis-related
PRRs	=	transmembrane pattern recognition receptors
PAMPs	=	pathogen-associated molecular patterns
PlanTFDB	=	plant transcription factor database
PDB	=	Protein Data Bank
PDF1.2	=	plant defensin gene
PFT1	=	phytochrome and flowering time1
PlnTFDB	=	the plant transcription factor database
PR	=	pathogenesis-related proteins
PTI	=	PAMP-triggered immunity
PVX	=	Potato virus x
RLKs	=	transmembrane receptor-like kinases
RLPs	=	transmembrane receptor-like proteins
RTq-PCR	=	real time reverse transcription PCR
R gene	=	disease resistance genes
RNAi	=	RNA interference
RNA-seq	=	high throughput sequencing of cDNA libraries
ROS	=	reactive oxygen species
SA	=	salicylic acid
SAR	=	systemic acquired resistance
SIB1	=	sigma factor-interactingg protein 1
SoyDB	=	database of soybean transcription factors
SP cluster	=	conserved pro-directed Ser residues
SPIK	=	salicylic acid-induced protein kinase
SZF1 protein	=	Salt-Inducible zinc finger 1
STZ	=	salt tolerance zinc finger
SURE	=	sugar responsive *cis*-element
TFs	=	transcription factors
TRX-H3/H5	=	thioredoxins H3 and H5
TIR-NBS-LRR	=	toll interleukin1 receptor-nucleotide binding site-leucine-rich repeat protein
TOBFAC	=	database of tobacco transcription factor
VIGS	=	virus-induced gene silencing factor
WIPK	=	wound-induced protein kinase
WRKY	=	domain transcription factor family

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