

WRKY transcription factors in plant responses to stresses^{FA}

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Invited Expert Review



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research have demonstrated the important biological functions of WRKY TFs in plant response to different kinds of biotic and abiotic stresses and working mechanisms. However, very little summarization has been done to review their research progress. Not just important TFs function in plant response to biotic and abiotic stresses, WRKY also participates in carbohydrate synthesis, senescence, development, and secondary metabolites synthesis. WRKY proteins can bind to W-box (TGACC (A/T)) in the promoter of its target genes and activate or repress the expression of downstream genes to regulate their stress response. Moreover, WRKY proteins can interact with other TFs to regulate plant defensive responses. In the present review, we focus on the structural characteristics of WRKY TFs and the research progress on their functions in plant responses to a variety of stresses.

Abstract The WRKY gene family is among the largest families of transcription factors (TFs) in higher plants. By regulating the plant hormone signal transduction pathway, these TFs play critical roles in some plant processes in response to biotic and abiotic stress. Various bodies of

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INTRODUCTION

Biotic and abiotic stresses influence all phenological stages of plant development. Biotic stresses include attacks from pathogenic bacteria, fungi, viruses and oomycetes. Abiotic stresses include drought, soil salinization, heavy metals, heat, cold, irradiation, and oxidative stress. Adaptation to these stresses and response to diverse environmental stresses are critical for survival and continuation of plants to the next generation. Many TFs families such as WRKY, AP2

(APETALA2)/ERF (ethylene-responsive factor) and NAC (NAM, ATAF1/2, CUC1/2) are plant-specific, and they play important and unique roles in the control of plant-specific regulation (Jiang et al. 2012a). The plant-specific WRKY TFs form one of the largest TF families and WRKY TFs are a class of DNA-binding proteins primarily found in plants and lower plants (with some exceptions) involved in diverse plant processes, involving growth, development and stress signaling through auto and cross regulation with different genes and TFs. The DNA-binding domain of these WRKY TFs is designated as the

WRKY domain with an invariant WRKYGQK sequence and a $CX_{4-5}CX_{22-23}HXH$ zinc binding motif (Bakshi et al. 2014). The first member of the WRKY superfamily – SPF1 was isolated from sweet potato (*Ipomoea batatas*) (Ishiguro and Nakamura 1994). Whole-genome sequencing of other plant species, especially model plants, enabled the identification of more WRKY genes in plants. There are 197, 100, and 74 WRKY superfamily members in *Glycine max*, *Oryza sativa*, *Arabidopsis*, *Brassica napus*, and *Fragaria vesca*, respectively (Rushton et al. 2010; Fan et al. 2015; He et al 2016; Wei et al. 2017). The expression of WRKY TFs is induced rapidly when the plants are exposed to a variety of stresses or defensive signals including salicylic acid (SA) or other molecules. Moreover, the expression of WRKY TFs is rapid, transient, and tissue-specific. So far, WRKY proteins have been implicated in plant defense against attack, plant growth, and development, metabolism, morphogenesis of trichome and embryos, senescence, biosynthesis and hormonal signal regulations (Song et al. 2010a; Zhou et al. 2011; Bakshi et al. 2014). Here we first summarized the structure characteristics and classification of WRKY TFs, and then reviewed the function of WRKY TFs in biotic and abiotic stresses, as well as the WRKY transcription factors regulatory network in response to the various stresses. In addition, WRKY TFs' involvement in plant hormones signal transduction and the MAPK signaling cascade were also analyzed. Moreover the special self-regulation of WRKY TFs was also described.

THE STRUCTURAL CHARACTERISTICS AND CLASSIFICATION OF WRKY TRANSCRIPTION FACTORS

WRKY TFs contain WRKY protein domain, which is a 60 amino acids long DNA binding domain (DBD) characterized by a highly conserved N-terminal core, WRKYGQK motif (Schmutz et al. 2010; Ishiguro and Nakamura 2011). WRKY TFs have a novel Zn-chelating DNA binding domain and are classified as a WRKY-GCM1 family. The DBDs of Mutator transposases or Mutator-like element (MULE) transposases also share the WRKY-GCM1 domain (Babu et al. 2006; Marquez et al. 2010). The GCM1 domain mainly comprises one or two N-terminal WRKY sequences and a C-terminal Zn-finger motif (Rushton et al. 2010), which are indispensable for WRKY

binding to W-box (C/T) TGAC (T/C) in the promoter. Yamasaki et al. (2005) determined that WRKY domain from the *A. thaliana* WRKY4 protein consists of a four-stranded β -sheet, with a zinc binding pocket formed by the Cys/His residues. Moreover, the Gly residue in the middle of the N-terminal β -strand enables hydrophobic interactions and contributes to the structural stability of the β -sheet. The β -strand containing the WRKYGQK motif makes contacts with an approximately 6-bp region, which is largely consistent with the length of the W-box (TTGACY). In a few WRKY proteins, the WRKY residues in WRKYGQK are replaced by WRRY, WSKY, WKRY, WVKY, or WKKY motifs (Xie et al. 2005). In rice, the WRKY family members have 19 variants of the WRKY domain where WRKYGEK and WRKYGKK are the two common variants shared by seven and five domains (Zhang et al. 2005). The other variants include WRICGQK, WRMCGQK, WKKYGQK, WIKYGQK, WKRYGQK, WSKYEQK, and WRKYSEK (Zhang et al. 2005). There are two main types of zinc-finger-like motifs: C_2-H_2 ($C-X_{4-5}-C-X_{22-23}-H-X-H$) and C_2-HC ($C-X_7-C-X_{23}-H-X-C$) (Li et al. 2010a).

WRKY proteins are classified into three groups based on the number of WRKY domains and the type of zinc finger-like motif. Those with two WRKY domains belong to Group I while those with one WRKY domain belong to group II or III. Group I and II members have the zinc-finger-like motif C_2-H_2 ($C-X_{4-5}-C-X_{22-23}-H-X_1-H$), where X can be any amino acid. Group III WRKY proteins contain a C_2-HC ($C-X_7-C-X_{23}-H-X-C$) zinc-finger-like motif (Li et al. 2010a). This classification method is solely based on protein structural characteristics and does not include the evolutionary origin and gene duplications among large families of WRKY genes. Based on phylogenetic analysis, conservation domains, and intron position of the WRKY domains, Zhang and Wang (2005) proposed another model, which classified the WRKY proteins into five groups: group I (I-N terminal and I-C terminal), group IIa + IIb, groups IIc, group II d + IIe, and group III. They classified WRKY TFs into two categories based on the insertion position of the intron (Zhang et al. 2005). The first category includes R-type intron WRKY (IIa and IIb subtypes) in which the splicing site is located between 2 Gs of arginine codon, AGG. The other category includes V-type intron WRKY, in which the splicing site is located in front of the valine codon. The

valine is located right after the 6th amino acid after the 2nd cysteine within the zinc-finger structure; and V-type intron WRKY proteins mainly belong to I, IIc, IIc, and III subtype WRKY TFs.

WRKY TFs can activate or inhibit transcription of a physiological process (Xie et al. 2005). In addition to WRKY domain and zinc-finger-like motif, most WRKY TFs also have nuclear localization signals (NLS), leucine zippers, serine/threonine-rich region, glutamine-rich region, proline-rich region, kinase domains, TIR-NBS-LRR, and other structures. These structures confer different transcriptional regulatory functions on WRKY TFs (Zhang et al. 2005).

THE FUNCTION OF WRKY TRANSCRIPTION FACTORS IN BIOTIC STRESS OF PLANTS

Biotic stress in plants activates SA, jasmonic acid (JA), and ethylene (EI) signaling pathways, which subsequently changes the transcription level of related genes and protein post-processing (Chen et al. 2012), thus response to different biotic stresses. WRKY transcription factors have been proven to play important roles in plant defence responses to attacks by several pathogens. CaWRKY27, a WRKY protein from pepper (*Capsicum annuum*) positively regulates the stress resistance response to *Ralstonia solanacearum* infection through modulation of SA-, JA- and ET-mediated signaling pathways in tobacco (*Nicotiana tabacum*) (Dang et al. 2014). Overexpression of the cotton (*Gossypium hirsutum*) genes GhWRKY39-1 and GhWRKY40 in tobacco regulates its resistance response to *R. solanacearum* (Shi et al. 2014). GhWRKY40 also regulates wounding-induced responses in tobacco (Wang et al. 2014c). The expression of at least 15 BdWRKY genes was upregulated in 2-week-old seedlings of *Brochypodium distachyon* sprayed with *Fusarium graminearum* and two strains of *Magnaporthe grisea*, and the expression of nine BdWRKY genes was upregulated including BdWRKY8/34/50/69/70 when the seedlings were sprayed with *F. graminearum* (Wen et al. 2014). In grape (*Vitis vinifera*), 57% (16 genes) of WRKY genes showed altered expression after biotic stress induced by a common fungal pathogen (*Coniothyrium diplodiella*) infection, which causes grape white rot (Zhang et al. 2014). Biological function investigation of *Arabidopsis* WRKY8 demonstrated that WRKY8 regulates the susceptibility of *Arabidopsis* to *Pseudomonas syringae* and *Botrytis cinerea* (Chen

et al. 2010). They further showed that WRKY8 regulates abscisic acid (ABA) and ethylene signaling pathways to mediate the crosstalk between ABA and ethylene signaling during the TMV-cg-*Arabidopsis* interaction to confer resistance against TMC-cg (Chen et al. 2013). WRKY22-knockout transgenic rice showed increased susceptibility to *Pyricularia oryzae* Cav. while overexpression of WRKY22 gene increased the resistance, which indicated that WRKY22 is a positive regulator of rice resistance responses to *Pyricularia oryzae* (Cheng et al. 2014). TaWRKY70 is positively involved in Wheat high-temperature seedling plant (HTSP) resistance to *Puccinia striiformis* f. sp. *tritici* (Pst), which induces stripe rust in wheat (*Triticum aestivum*), during which SA and ET signaling are probably activated (Wang et al. 2016). TaWRKY70's transcript was increased significantly when exposed to high temperatures (HTs) during the initial symptom expression stage of Pst infection and increased in plants treated with ethylene (ET), salicylic acid (SA) and cold (4 °C) stresses, but decreased in plants treated with methyl jasmonate (MeJA) and heat (40 °C) stresses. Silencing of TaWRKY70 led to greater susceptibility to Pst (Wang et al. 2016).

Most WRKY transcription factors with known function are negative regulators with only a few of those having a positive regulatory role (Kim et al. 2008; Xing et al. 2008). In *A. thaliana*, AtWRKY38 and AtWRKY62, encoding two structurally similar type group III WRKY transcription factors, negatively regulate the defense against pathogenic bacteria *P. syringae*. Disease resistance is enhanced in AtWRKY38 and AtWRKY62 single mutants and, primarily, in the double mutants (Kim et al. 2008). Overexpression of AtWRKY38 or AtWRKY62 reduces disease resistance (Kim et al. 2008). Transgenic AtWRKY48-overexpressing plants showed enhanced susceptibility while the loss-of-function AtWRKY48 mutants showed enhanced resistance to *P. syringae* (Xing et al. 2008). These results suggest that WRKY48 negatively regulates the basal resistance of *Arabidopsis* *P. syringae*.

The WRKY genes that positively regulate resistance against pathogens may activate the expression of resistance genes directly or indirectly. For example, WRKY DNA binding proteins recognize and bind specifically to the W-box sequences in the promoter region of *Arabidopsis* Natriuretic peptide receptor 1 (NPR1), and then activate defense gene expression

to induce disease resistance (Yu et al. 2001). WRKY TFs are also involved in mitogen-activated protein kinase (MAPK) signaling pathway, which is involved in stress-induced defensive responses (Tsuneaki et al. 2002). *Arabidopsis* AtWRKY22 and AtWRKY29 proteins are essential components of MAPK mediated plant defense responses against pathogens. Transient expression of AtWRKY29 in *Arabidopsis* enhanced its resistance to *P. syringe* (Tsuneaki et al. 2002). *Nicotiana attenuata* WRKY genes NaWRKY3 and NaWRKY6 are involved in response to wounding. NaWRKY3 transcripts accumulate in response to wounding, and the wound responses of NaWRKY6 are significantly amplified when fatty acid–amino acid conjugates in larval oral secretions are introduced into wounds during feeding (Skibbe et al. 2008). The knockdown of rice transcription factor OsWRKY45 reduces SA-induced resistance to fungal and bacterial pathogen while its overexpression induces strong resistance to both pathogens indicating its crucial role in SA-induced disease resistance (Akira et al. 2013).

THE FUNCTIONS OF WRKY TRANSCRIPTION FACTORS IN ABIOTIC STRESS OF PLANT

Abiotic stresses including heat stress, or temperature inversion, soil salinity, oxidative stress, drought, and nutritional deficiency adversely affect the physiological and biochemical processes of plants (Joshi et al. 2016). These stresses sometimes also co-occur and negatively affect plant growth. Such abiotic stresses also induce the WRKY TFs and trigger a network of signaling cascades to improve the stress tolerance in plants (Rushton et al. 2010, 2012; Schluttenhofer and Yuan 2015).

Heat stress

Temperature levels beyond an organism's optimal tolerance range are regarded as major abiotic stress. Extreme high or low temperatures cause extensive agricultural losses. Thus, devising strategies to protect plant cells from damages caused by drastic changes in temperature is necessary to boost agricultural production (Grover et al. 2013; Ohama et al. 2017). Various WRKY TFs respond to high-temperature and help plants to resist the temperature changes. High-temperature treatment represses the expression of AtWRKY33 and induces the expression of AtWRKY25 and AtWRKY26 in *A. thaliana* (Li et al. 2011). Constitutive overexpression

of AtWRKY25 and AtWRKY26 enhanced resistance to heat stress (Li et al. 2011). *A. thaliana* WRKY39 is a member of the group II WRKY proteins and responds to multiple stresses (Li et al. 2010b). Heat treatment induces AtWRKY39 transcripts while SA and JA signaling pathways positively co-regulate AtWRKY39 (Li et al. 2010b). Moreover, WRKY39 overexpressing plants exhibited enhanced thermotolerance (Li et al. 2010b). TaWRKY70 is not only positively involved in Wheat high-temperature seedling plant (HTSP) resistance to *Puccinia striiformis* f. sp. *tritici* (Pst), which induce stripe rust in wheat (*Triticum aestivum*), during which SA and ET signaling are probably activated (Wang et al. 2016). TaWRKY70's transcript was increased significantly when exposed to high temperatures (HTs) during the initial symptom expression stage of Pst infection and increased in plants treated with ethylene (ET), salicylic acid (SA) and cold (4 °C) stresses, but decreased in plants treated with methyl jasmonate (MeJA) and heat (40 °C) stresses. Silencing of TaWRKY70 led to greater susceptibility to Pst (Wang et al. 2016). In addition, TaWRKY33 transgenic lines exhibited enhanced tolerance to heat stress (He et al. 2016).

In chilling-sensitive plants, mature pollen is sensitive to cold stress. AtWRKY34 expression was upregulated upon cold treatment. AtWRKY34 expression is pollen-specific and negatively mediated cold sensitivity of mature *Arabidopsis* pollen (Zou et al. 2010). Pollen from an AtWRKY34 mutant showed higher viability than that from wide-type after 4 °C cold treatment (Zou et al. 2010). Moreover, overexpression of AtWRKY34 resulted in partial sterility even in a normal developmental environment (Zou et al. 2010). In addition, AtWRKY34 was also identified as a transcription factor in the sugar induction of mitochondria by interaction with a Nucleoside Diphosphate Kinase (NDPK), NDPK3a (Hammargren et al. 2008). However, whether the cold sensitivity of AtWRKY34 pollen was caused by mitochondria metabolism associated with some NDPK is not clear. Genomic and transcriptomic analysis determined VvWRKY24 from *Vitis vinifera* as a cold-specific responsive gene that is induced at all time points of the cold treatment, but not in response to drought or salt stresses that induce VvWRKY30 and VvWRKY52 (Wang et al. 2014b). Among the 287 WRKY genes *Brassica napus*, most of the genes were induced by low temperature, salinity and drought stress, and

BnaWRKY147, *BnaWRKY166* and *BnaWRKY210* were highly upregulated under drought stress, thus indicating their potential roles in low temperature, salinity, and drought stress, respectively (He et al 2016).

Salinity stress

Drought often leads to high salt conditions, which causes osmotic stress. *AtWRKY25* and *AtWRKY33* double mutants are susceptible to NaCl, and over-expression of either gene confers tolerance to NaCl-stress (Li et al. 2011). Likewise, the overexpression of *Dendranthema grandiflorum* WRKY genes, *DgWRKY1* or *DgWRKY3*, enhances their salt tolerance in tobacco. The accumulation of hydrogen peroxide (H_2O_2) and malondialdehyde induced by salt stress was reduced, accompanied by lower activities of antioxidant enzymes including superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), etc. in *DgWRKY1* or *DgWRKY3* overexpressing transgenic tobacco plants (Liu et al. 2013). Similarly, the transgenic rice plants overexpressing *OsWRKY45* and *OsWRKY72* displayed increased tolerance to drought and salt stress (Qiu and Yu 2009; Song et al. 2010b). When *OsWRKY11* cDNA was fused to the promoter of HSP101 of rice, the transgenic lines showed significant heat and drought tolerance, as indicated by the slower leaf-wilting and less-impaired survival rate of green parts of plants (Wu et al. 2009). When *TaWRKY10*, a WRKY gene from *Triticum aestivum*, was introduced into and overexpressed in tobacco, the drought and salt stress tolerances of tobacco were enhanced significantly. *TaWRKY10* is considered as a major regulator under drought and salt stresses by regulating the osmotic balance and transcription of stress related genes. When the transgenic lines were treated with drought and salt stress, the contents of proline and soluble sugar increased while the contents of MDA were maintained at a relatively low level (Wang et al. 2013). Constitutive overexpression of *BcWRKY46* (Pak-choy) and *HvWRKY38* (barley) in *A. thaliana* confer enhanced drought and salt stress tolerance to the resulting transgenic plants (Wang et al. 2012; Wang et al. 2013). In cotton, constitutive expression of *GhWRKY17* increases plant tolerance to drought and salt stress, but reduces the sensitivity to ABA transcript levels, ABA-inducible genes including ABA-responsive element binding; dehydration-responsive element binding (DREB), such as soybean *GmDREB2*, moss *PpDREB1*, and *Caragana korshinskii* *CkDREB* show different

response patterns under environmental stresses like drought, high-salt low-temperature and ABA treatment (Yan et al. 2014); nine-cis-epoxycarotenoid dioxygenase (NCED); early responsive to dehydration (ERD) and late-embryogenesis-abundant protein (LEA), etc. (Yan et al. 2014). Constitutive expression of *ZmWRKY23* (*Zea mays*) in *A. thaliana* also enhances its tolerance to salt stress (Jiang et al. 2009).

Oxidative stress

Oxidative stress is one of the most serious stresses caused by various other stresses (Sun et al. 2015). ROS-mediated signaling is controlled by a delicate balance between production and scavenging (Garg and Manchanda 2009). There are mainly four types of reactive oxygen species in plants: Singlet oxygen (O_2), hydroxyl radicals (OH), superoxide anion (O_2^-), and H_2O_2 . In *A. thaliana*, several WRKY TFs including *WRKY6*, *WRKY8*, *WRKY22*, *WRKY30*, *WRKY39*, *WRKY48*, *WRKY53*, and *WRKY75* are upregulated in response to H_2O_2 treatment. Davletova et al. (2005) showed that *A. thaliana* cytosolic H_2O_2 -scavenging enzyme ascorbate peroxidase 1 (APX1) plays a key role in protecting chloroplasts during light stress. Their study showed that knockout-Apx1 (KO-APX1) plants exposed to light stress exhibited upregulated transcription of mitogen-activated protein kinase 3 (MAPK3), *WRKY6*, *WRKY18*, *WRKY25*, *WRKY33*, *WRKY40*, *WRKY46*, *WRKY54*, *WRKY60*, *WRKY70*, and other transcription proteins implicating APX1 in the defense response against oxidative stress (Davletova et al. 2005). The correlation between H_2O_2 and the expression of the *Zat7*, *WRKY25*, and APX using *Zat12* knock-out *A. thaliana* plants was investigated, and the expression of *Zat7*, *WRKY25*, and APX was not induced upon H_2O_2 treatment indicating that *Zat12* is required in the oxidative stress response of the three genes (Rizhsky et al. 2004). *AtWRKY53* is an early factor in drought response (Sun et al. 2015). The expression of *WRKY53* can also be induced upon H_2O_2 treatment (Miao et al. 2004). A mitogen-activated protein kinase kinase kinase (MEKK1, a member of mitogen-activated protein kinase MAPK family) can interact with *WRKY53* directly to regulate the expression of proteins involved in antioxidant defense, such as *CAT1*, *CAT2*, and *CAT3* (Miao et al. 2007). *AtWRKY53* overexpression lines were also hypersensitive to drought stress. Activated expression of *AtWRKY53* inhibited stomatal closure via reduction of H_2O_2 content

and facilitated stomatal opening by promoting starch degradation in guard cells. AtWRKY53 can directly bind to the QQS promoter sequences, thus leading to increased starch metabolism (Sun et al. 2015). AtWRKY46 can regulate transcription by directly binding to the W-box in promoters of the antioxidant enzyme genes such as monodehydroascorbate reductase (MDHAR), glutathione S-transferase class Φ 14 (GSTF14), and thioredoxin H5 (TRX5) (Ding et al. 2014). AtWRKY8 induces resistance against *Phytophthora infestans* by interacting with downstream molecules of MAPKKK α -MEK2-WIPK signaling cascade; and thus, increasing the accumulation of H₂O₂ and ultimately inducing plant cells apoptosis (Zhang et al. 2012). The β -glucuronidase activity driven by the GhWRKY68 promoter was enhanced after exposure to drought, salt, abscisic acid (ABA) and H₂O₂ (Jia et al. 2015). GhWRKY68 may mediate salt and drought responses by modulating ABA content and enhancing the transcript levels of ABA-responsive genes. GhWRKY68-overexpressing plants exhibited reduced tolerance to oxidative stress after drought and salt stress treatments, which correlated with the accumulation of reactive oxygen species (ROS), reduced enzyme activities, elevated MDA content and altered ROS-related gene expression (Jia et al. 2015).

Drought stress

Drought is one of the most serious environmental factors limiting the productivity of agricultural crops worldwide. Drought can directly cause stomata closure to reduce transpiration and reduce the potential water content in plants. As a result, the photosynthesis is also weakened and some soluble matter accumulates, as well as the formation of ROS cleavage complexes like ascorbate, glutathione, and alpha-tocopherol in plants (Tripathi et al. 2014; He et al. 2016). WRKY TF has been reported frequently in drought resistance (Tripathi et al. 2014). Massively parallel signature sequencing (MPSS) technology for rice WRKY gene identified at least 17 rice WRKY genes induced by drought stress (Hattori et al. 2002). ABRs (ABA-responsive elements; ACGT-containing G-boxes in the promoter region) are an important homeopathic element in ABA-mediated signaling pathways. ABI signaling pathway is involved in the ABA signaling pathway through binding to the ABREs in the OsWRKY69 promoter region when the ABA signaling

pathway is activated, whereas the ABL1 gene can be inhibited by drought conditions (Yang et al. 2011).

BhWRKY1 transcription factor can bind to BhGolS1 to activate the regulation of BhGolS1 in response to drought stress (Wang et al. 2009). BhGolS1 (Galactinol synthase 1) gene is a kind of dehydrogenase and ABA-induced genes that can enhance the dehydration tolerance of plants in *Boea hygrometrica*. GmWRKY54 overexpressing plants in *A. thaliana* had a higher survival rate, indicating that GmWRKY54 could enhance the resistance to drought stress in *Arabidopsis* (Zhou et al. 2008). Overexpression of cotton GhWRKY25 reduces tolerance to drought and increases salt tolerance in *Arabidopsis* (Liu et al. 2016). Similarly, CsWRKY2 was found to be involved in drought stress in tea plants and the expression of CsWRKY2 was enhanced when exogenous ABA was used. The expression of CsWRKY2 was impaired when ABA synthesis inhibitors were used (Wang et al. 2016). Overexpressed GsWRKY20 transcription factor in *Arabidopsis* had reduced stomata density and reduced water loss efficiency, which improved the drought tolerance of transgenic plants (Luo et al. 2013). Photosynthesis and growth-related genes are inhibited under drought conditions, possibly because of the transcriptional recombination of these signal-aware factors such as NAC, NF-YA, MADS box, HSF, GRAS, and WRKY families members upregulates some (heat shock (HSP) proteins, early light-inducible (ELIP), late embryogenesis abundant (LEA). (Gechev et al. 2013).

The ethylene response factor family is one of the largest family of plant-specific transcription factors involved in plant development and stress response, and some plants can negatively regulate tolerance to drought by modulating ethylene response factors. ThWRKY2 in *Tamarix hispida* can initiate the expression of ThERF1 (ethylene-responsive factor) gene under drought stress, which encodes a novel ethylene response factor to negatively regulate abiotic stress including drought stress. Overexpression of ThERF1 in mustard increased the transpiration rate of the plant, resulting in more sensitivity to drought stress (Wang et al. 2016). TaWRKY44 may act as a positive regulator in drought/salt/osmotic stress responses by either efficient ROS elimination through direct or indirect activation of the cellular antioxidant systems or activation of stress-associated gene expression (Wang et al. 2015). The overexpression of GhWRKY68 in *N. benthamiana*

reduced resistance to drought and salt and affected several physiological indices (Jia et al. 2015).

Other stresses

In addition to the stresses discussed above, WRKY TFs are also involved in other stress responses such as nutrient stress, UV radiation, and dark treatment. AtWRKY75, AtWRKY6, and AtWRKY42 transcription factors modulate phosphate (Pi) acquisition in *Arabidopsis*. AtWRKY75 is induced strongly in the plant during Pi deficiency, while suppression of WRKY75 expression results in increased susceptibility to Pi stress and decreased Pi uptake in mutant plants (Devaiah et al. 2007). The overexpression of AtWRKY6 in *A. thaliana* results in plants that are sensitive to low Pi stress and have lower Pi contents. Moreover, AtWRKY6 modulates responses against low-Pi stress by directly binding to two W-boxes of the AtPHO1 promoter and repressing the PHO1 expression (Chen et al. 2009).

A rice OsWRKY74 was also involved in tolerance to phosphate (Pi) starvation and cold stress in rice by modulation of Pi homeostasis and potential crosstalk between P starvation and Fe starvation, (Dai et al. 2016). Overexpression of OsWRKY74 significantly enhanced tolerance to Pi starvation. Root and shoot biomass, and phosphorus (P) concentration in rice OsWRKY74-overexpressing plants were higher than those of wild-type plants in Pi-deficient hydroponic solution. In soil pot experiments, in tiller number, grain weight and P concentration were observed increased in rice OsWRKY74-overexpressing plants when grown in P-deficient medium (Dai et al. 2016). AtWRKY42 has been found to function synergistically with AtWRKY6 to bind to W-boxes of the PHO1 promoter and repress PHO1 expression (Chen et al. 2009). Furthermore, AtWRKY42 also regulated phosphate homeostasis in *Arabidopsis*. The WRKY42-overexpressing lines, similar to the *phosphate1* (*pho1*) mutant, were more sensitive to low-inorganic phosphate (Pi) stress and had lower shoot Pi content compared with wild-type plants. And AtWRKY42 modulated Pi homeostasis by regulating the expression of *PHO1* and *PHT1* to adapt to environmental changes in Pi availability (Su et al. 2015). Similar to AtWRKY42, AtWRKY45 is involved in *Arabidopsis* response to Pi starvation by direct upregulation of *PHT1*;1 expression. During Pi starvation, AtWRKY45 expression was markedly induced, typically in roots.

AtWRKY45 overexpression in *Arabidopsis* increased Pi content and uptake, while RNA interference suppression of AtWRKY45 decreased Pi content and uptake (Wang et al. 2014a). However, whether AtWRKY42 and AtWRKY45 work together or cross talk with each other is poorly understood.

Several WRKY TFs have been implicated as positive and negative regulators of senescence in different plants (Zentgraf et al. 2010). Transgenic rice plants overexpressing OSWRKY89 showed increased wax deposition on leaf surfaces and enhanced tolerance to UV-B irradiation (Wang et al. 2007). Zhao et al. (2010) determined a UV-B response cis-regulatory element to a 25 bp (AAGATCTAC-CATTGCTCTATAGCTT) region between -1,188 and -1,213 upstream of the translation start site of OsWRKY89 gene. WRKY TFs also regulate the leaf senescence process, for example, AtWRKY57 represses leaf senescence by interacting with JAZ4/JAZ8 (JASMONATE ZIM-DOMAIN4/8) and IAA29 (Indole Acetic Acid 29), which are the repressors of the JA and Auxin signaling pathways, respectively. JAZ4/8 and IAA29 interact with WRKY57 competitively, and exhibit different functions in JA-induced leaf senescence, which is consistent with the opposing functions of JA and auxin in leaf senescence (Jiang et al. 2014b). AtWRKY53 and AtWRKY70 were positive and negative regulators of senescence in *Arabidopsis*, respectively (Hu et al. 2012). AtWRKY54 and AtWRKY30 are two additional WRKY TFs involved in this process (2012). The structurally related AtWRKY54 and AtWRKY70 exhibit a similar expression pattern during leaf development and appear to have co-operative and partly redundant functions in senescence, as revealed by single and double mutant studies. These two negative senescence regulators and the positive regulator AtWRKY53 were shown to interact independently with AtWRKY30. AtWRKY30 was expressed during developmental leaf senescence and consequently it is hypothesized that the corresponding protein could participate in a senescence regulatory network with the other WRKYs. Expression in wild-type and salicylic acid-deficient mutants suggests a common but not exclusive role for SA in induction of AtWRKY30, 53, 54, and 70 during senescence. AtWRKY30 and AtWRKY53 but not AtWRKY54 and AtWRKY70 are also responsive to additional signals

such as reactive oxygen species. The results suggest that AtWRKY53, AtWRKY54, and AtWRKY70 may participate in a regulatory network that integrates internal and environmental cues to modulate the onset and the progression of leaf senescence, possibly through an interaction with AtWRKY30 (Besseau et al. 2012). Moreover, 13 TaWRKYs were confirmed as senescence-associated genes in wheat. TaWRKY7 is upregulated in the natural leaf senescence process. The ectopic overexpression of TaWRKY7 in *Arabidopsis* significantly promoted early leaf senescence under darkness treatment and prevented leaf moisture losses (Zhang et al. 2016a). We also summarized all of the abovementioned WRKY TFs into Table 1 for clearer and easier summarization.

WRKY TRANSCRIPTION FACTORS REGULATORY NETWORK IN RESPONSE TO STRESS

Many growth regulators are involved in the signal transduction network during a plant's growth and development or response to a variety of stresses. WRKY proteins are emerging players in such signaling networks. The interaction and cross-talk between WRKY proteins, their downstream targets, and upstream regulators constitute the complicated WRKY TF regulatory network, which is an emerging area of interest in the research community (Berri et al. 2009; Zentgraf et al. 2010; Banerjee et al. 2015).

Self-regulation of WRKY TFs

W-box exists in both target gene's promoter and WRKY TFs' promoter. The WRKY TFs regulate plant's defensive response to a variety of stresses by self-regulation its expression and the cross-talk between different WRKY TFs which is fulfilled by recognizing and binding to W-box in its target gene's, in its own, or in other WRKY TFs promoters (Zentgraf et al. 2010). CHIP assays demonstrated that PcWRKY1 (*Petroselinum crispum*) can bind to W-box in its promoter region and that in PcWRKY3 promoter (Turck et al. 2004). Structurally related AtWRKY18, AtWRKY40, and AtWRKY60 have physical and functional interaction because they all have a leucine-rich repeat in their N-terminus (Xu et al. 2006). ABA treatment induced AtWRKY60 expression in wild-type *A. thaliana* but not in AtWRKY18 and AtWRKY40 mutants, which indicated that WRKY60 might be a direct target gene of

WRKY18/WRKY40 in ABA signaling pathway (Chen et al. 2010). AtWRKY25, AtWRKY26, and AtWRKY33 were also involved in regulation of the heat-induced response (Li et al. 2011). AtWRKY25 interacts with AtWRKY26 and AtWRKY33 in the regulation of resistance to heat stress. Constitutive expression of AtWRKY33 enhanced resistance to heat stress by negative feedback to its own activity (Li et al. 2011).

WRKY TFs in the MAPK signaling cascade

Mitogen-activated protein kinase (MAPK) signaling cascade exists in all eukaryotic organisms and functions in downstream signaling of ABA-dependent defensive responses in the plant (de Zelicourt et al. 2016). It is also involved in the regulation of growth, development, and responses to a diversity of abiotic and biotic stresses (Pitzschke et al. 2009). MAPK signaling cascades link upstream receptors to downstream transcription factors via multiple phosphorylation events (Fiil et al. 2009; Ishihama et al. 2012). Group I WRKY TFs, which contain a conserved motif in the N-terminal region, are also activated by MAPK-dependent phosphorylation, underlining their importance in plant immunity (Ishihama et al. 2012). In *Arabidopsis*, the transcription factor WRKY33 forms a MAMP or PAMP complex with MAP kinase 4 (MPK4) in the absence of pathogen infection (Qiu et al. 2008). This complex depends on the MPK4 substrate MKS1, which is phosphorylated when the former is activated due to pathogen infection. Subsequently, the intranuclear complexes MPK4-MKS1-WRKY33 is disrupted, and MKS1 and AtWRKY33 are released. AtWRKY33 then activates the expression of PAD3 that encodes an enzyme required for the synthesis of antimicrobial complexes (Qiu et al. 2008) (Figure 1). Moreover, AtWRKY22 and AtWRKY29 are important components in MAPK mediated resistance to both bacterial and fungal pathogens. Transient expression of AtWRKY29 homologous gene in *Arabidopsis* leaves confers resistance to pathogens (Asai et al. 2002). The AtWRKY29 homolog AtWRKY22 can recognize and bind to the same promoters as AtWRKY29 and confer similar functions (Asai et al. 2002). Another example is OsWRKY30, which enhances the resistance against drought in rice via MAPK phosphorylation cascade (Danquah et al. 2014). Additionally, the MAPK-WRKY pathway also is required for AVR3a-effector-triggered immunity and INF1-pattern-triggered immunity reactive oxygen species bursts by activation

Table 1. List of WRKY TFs playing important role towards various stress tolerances

No.	Gene	Plant	Induced by factors	Function in stresses	References
1.	AtWRKY38/48/62	<i>Arabidopsis</i>	<i>Pseudomonas syringae</i>	Negatively regulate the defense	Xing et al. 2008; Kim et al. 2008
2.	AtWRKY22/29	<i>Arabidopsis</i>	<i>P. syringe</i>	Enhanced resistance by involved in MAPK signaling	Tsuneaki et al. 2002
3.	AtWRKY33	<i>Arabidopsis</i>	High-temperature	Represses its expression	Li et al. 2011
4.	AtWRKY25/26	<i>Arabidopsis</i>	High-temperature	Overexpression enhanced its resistance	Li et al. 2011
5.	AtWRKY39	<i>Arabidopsis</i>	High-temperature	Overexpression enhanced thermo tolerance and SA and JA signaling pathways positively co-regulate	Li et al. 2010a
6.	AtWRKY34	<i>Arabidopsis</i>	Low-temperature	Upregulated	Zou et al. 2010
7.	AtWRKY25/33	<i>Arabidopsis</i>	Salt	Overexpression of either gene confers tolerance	Li et al. 2011
8.	AtWRKY45	<i>Arabidopsis</i>	Pi starvation	Upregulation of PHT1-1 expression	Wang et al. 2014a
9.	AtWRKY6/8/22/30/39/48/53/75	<i>Arabidopsis</i>	H ₂ O ₂	Upregulated	Davletova et al. 2005
10.	AtWRKY75/6/42	<i>Arabidopsis</i>	Pi deficiency	AtWRKY75 is induced strongly while overexpression of AtWRKY6 results in sensitive to low Pi and AtWRKY42 functions synergistically with AtWRKY6	Chen et al. 2009
11.	AtWRKY57	<i>Arabidopsis</i>	Senescence	Repress leaf senescence	Jiang et al. 2014b
12.	AtWRKY53/54/70	<i>Arabidopsis</i>	Senescence	Through a regulatory network to response	Besseau et al. 2012
13.	BdWRKY8/34/50/69/70	<i>Brachypodium distachyon</i>	<i>F. graminearum</i>	Upregulated	Wen et al. 2014
14.	BhWRKY1	<i>Boea hygrometrica</i>	Drought	Bind to BhGolS1 to activate the regulation of BhGolS1	Wang et al. 2009
15.	BnaWRKY147/166/210	<i>Brassica napus</i>	Drought	Upregulated	He et al 2016
16.	CaWRKY27	Pepper	<i>R. Solanacearum</i>	Positive regulator in SA/JA/ET signaling	Dang et al. 2014
17.	CsWRKY2	Tea	Drought	Expression of CsWRKY2 was enhanced when ABA was used	Wang et al. 2016
18.	DgWRKY1/3	<i>Dendranthema grandiflorum</i>	Salt	Overexpression enhances salt tolerance	Liu et al. 2013
19.	GhWRKY25	Cotton	Drought	Overexpression plants reduces tolerance to drought	Liu et al. 2016
20.	GhWRKY39-1	Cotton	<i>R. solanacearum</i>	Overexpression regulates its resistance	Shi et al. 2014

(Continued)

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Table 1. (Continued)

No.	Gene	Plant	Induced by factors	Function in stresses	References
21.	GhWRKY40	Cotton	Wounding	Overexpression regulates its resistance	Shi et al. 2014
22.	GhWRKY68	Cotton	Salt and drought	Enhancing the transcript levels of ABA-responsive genes	Jia et al. 2015
23.	GhWRKY17	Cotton	Drought and salt	Constitutive expression increases plant tolerance	Yan et al. 2014
24.	GmWRKY54	Soybean	Drought	Overexpression plants in <i>Arabidopsis</i> had a higher survival rate	Zhou et al. 2008
25.	GsWRKY20	Glycine soja	Drought	Overexpressed GsWRKY20 reduced stomata density and reduced water loss efficiency	Luo et al. 2013
26.	NaWRKY3/6	<i>Nicotiana attenuate</i>	Wounding	Introduced by fatty acid–amino acid	Skibbe et al. 2008
27.	OsWRKY22	Rice	<i>Pyricularia oryzae</i> Cav.	Positive regulator	Cheng et al. 2014
28.	OsWRKY45	Rice	Fungal and bacterial pathogen	Overexpression induces strong resistance	Akira et al. 2013
29.	OsWRKY45/72	Rice	Drought and salt	Overexpression enhances salt tolerance	Qiu and Yu 2009; Song et al. 2010b
30.	OsWRKY11	Rice	Heat and drought	Transgenic lines showed significant heat and drought tolerance	Wu et al. 2009
31.	OsWRKY74	Rice	Pi starvation and cold	Overexpression significantly enhanced tolerance to Pi starvation	Dai et al. 2016
32.	OSWRKY89	Rice	UV-B irradiation	Overexpression increased wax deposition on leaf surfaces	Wang et al. 2007
33.	TaWRKY7	<i>Triticum aestivum</i>	Senescence	Upregulated	Zhang et al. 2016a
34.	TaWRKY10	<i>T. aestivum</i>	Drought and salt	Overexpression enhanced the drought and salt stress tolerances	Wang et al. 2013
35.	TaWRKY70	<i>T. aestivum</i>	high-temperature	Positively involved in resistance to Pst	Wang et al. 2016
36.	ThWRKY2	<i>Tamarix hispida</i>	Drought	Initiate the expression of ThEF1 gene	Wang et al. 2016
37.	VvWRKY24	<i>Vitis vinifera</i>	Low-temperature	Be induced at all-time points	Wang et al. 2014b
38.	ZmWRKY23	<i>Zea mays</i>	Salt	Enhance tolerance to salt stress	Jiang et al. 2009

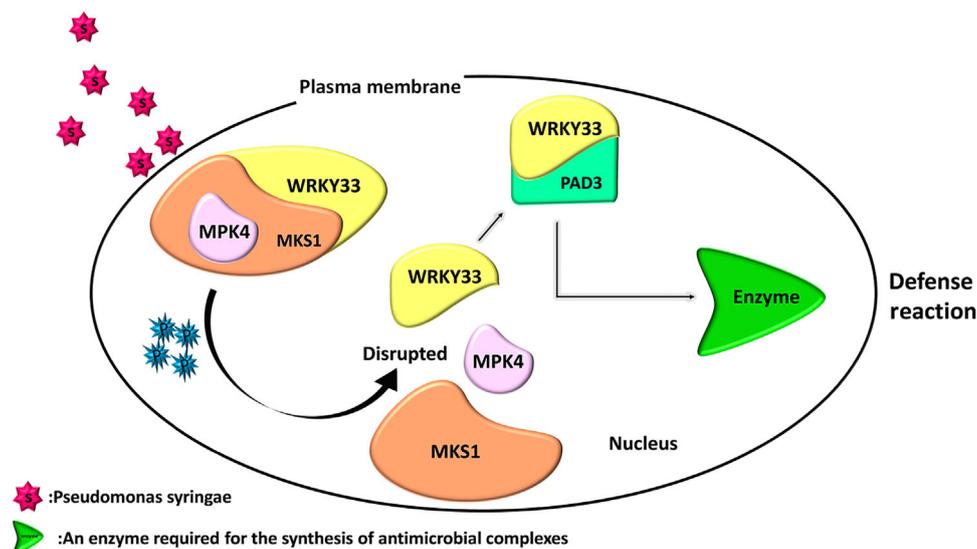


Figure 1. Hypothetical model of AtWRKY33 function with PAD3

The transcription factor AtWRKY33 forms a MAMP or PAMP complex with MAP kinase 4 (MPK4) in the absence of pathogen infection. This complex depends on the MPK4 substrate MKS1, which is phosphorylated when the former is activated due to pathogen infection. The complex MPK4-MKS1-WRKY33 is disrupted, and AtWRKY33 then activates the expression of PAD3, which encodes an enzyme required for the synthesis of antimicrobial complexes.

of RBOHB, a *Nicotiana benthamiana* NADPH oxidase (Adachi et al. 2015).

WRKY TFs are involved in plant hormones signal transduction

WRKY TFs play a key role in SA and ABA mediated signal pathways (Dong et al. 2003). AtWRKY39 is induced upon SA or methyl jasmonic acid (MeJA) treatment, and collaboratively participates in the regulation of SA and JA signaling pathways in responses to high-temperature stress (Li et al. 2010b). The overexpression of AtWRKY38 or AtWRKY62 decreases a plant's resistance to pathogens via inhibiting the SA-induced expression of defensive gene Pathogenesis-Related1 (AtPR1) (Kim et al. 2008). OsWRKY45 is pivotal in SA-mediated defensive responses; inhibition of its expression severely impairs the SA-mediated resistance against *Benzothiadiazole* while its overexpression significantly enhances blast resistance in rice (Shimono et al. 2007). The overexpression of SA-inducible PtrWRKY89 accelerates the expression of PR protein and improves resistance to *Marssonina brunnea* in poplar indicating its role in SA-dependent defensive signaling pathway (Jiang et al. 2014a).

Abscisic acid (ABA) is a phytohormone and plays a major role in integrating various stress signals and controlling downstream stress responses. Some WRKY

TFs are involved in ABA-mediated signaling pathways in responses to stress. *Larrea tridentata* thrives in vast arid areas. LtWRKY21 activates the promoter of an ABA-inducible gene HVA22 and upregulates its expression via synergistic interactions with ABA and transcriptional activators VP1 and ABI5 (Zou et al. 2004). A gain-of-function mutant, acquired drought tolerance (*adt*), showing improved drought tolerance was obtained by screening a pool of WRKY-associated T-DNA insertion mutants. *Adt* mutant accumulates higher levels of ABA than wild-type plants. T-DNA insertion in *adt* led to the activated expression of the WRKR57 protein. CHIP assays demonstrated that WRKY57 can directly bind the W-box of Responsive to Desiccation 29A (RD29A) and 9-cis-epoxycarotenoid dioxygenase 3 (NCED3) promoter and initiate the genes expression (Jiang et al. 2012b). AtWRKY40 binds to the W-box in promoters of multiple ABA-inducible genes, for example, AtABF4, AtABI4, AtABI5, AtDREB1A, AtMYB2, and AtRAB18, to inhibit their expression (Shang et al. 2010). In *Arabidopsis* ABA signaling pathway, WRKY18, WRKY40, and WRKY60 regulate downstream gene expression by interacting with ABI4 and ABI5. Among these, WRKY40 a central negative regulator, WRKY18 enhances the suppression of ABI4 and ABI5 transcription induced by WRKY40 while WRKY60 antagonize the effects of WRKY40 (Shang et al. 2010). A cucumber (*Cucumis*

sativus) group II WRKY gene, CsWRKY46, was upregulated in response to cold stress and exogenous abscisic acid treatment. CsWRKY46 was exclusively expressed in the nucleus and interact with the W-box in the promoter of ABI5. Transgenic *Arabidopsis* overexpressing CsWRKY46 had higher seedling survival rates upon freezing treatment, much higher proline accumulation, less electrolyte leakage and lower malondialdehyde (MDA) levels, hypersensitive to ABA during seed germination (Zhang et al. 2016b). CmWRKY1, a member of the group IIb WRKY family isolated from *Chrysanthemum morifolium*, plays an important role in the response to drought in chrysanthemum through an ABA-mediated pathway (Fan et al. 2016). Moreover, CmWRKY1-overexpressing transgenic lines exhibit enhanced dehydration tolerance in response to polyethylene glycol (PEG) treatment. The transgenic plants exhibit suppressed expression levels of genes negatively regulated by ABA, such as PP2C, ABI1 and ABI2, and activated expression levels of genes positively regulated by ABA (Fan et al. 2016).

Other regulatory networks

Arabidopsis group IId WRKY proteins contain a CAT binding domain (Chi et al. 2013) suggesting that group IId WRKY TFs may be regulated by CaM and Ga²⁺ (Park et al. 2005). Similar CAT binding domains are also present in over 10 WRKY TFs (belongs to all three groups of WRKY TFs) of *Arabidopsis*, which are also bound by CaM (Park et al. 2005). A group of highly conserved regulatory proteins—14-3-3—is present in all eukaryotic organisms, and regulates a variety of cellular physiological events through interactions with target proteins typically in a phosphorylation-dependent manner. *Arabidopsis* WRKY proteins (among other 300 proteins including BZR1 (a transcription factors of brassinosteroids), Repression of shoot growth (RSG), and Serine acetyltransferase (SAT) are the target proteins of 14-3-3 proteins (Ishida et al. 2004; Yin et al. 2005; Kumaran et al. 2009). The phosphorylation of the molecules in the stress-induced signaling cascade is required for interaction between *Arabidopsis* WRKY proteins and 14-3-3 proteins (Shen et al. 2003). Since, 14-3-3 proteins dimerize and each 14-3-3 dimer can bind to two protein ligands, both phosphorylated ligands, and other un-phosphorylated ligands are brought into proximity through mutual interactions with a 14-3-3 dimer. WRKY proteins with phosphorylated binding sites form complexes with other proteins indirectly and

consequently participate in many cellular events. For example, 14-3-3 WRKY client AtWRKY19 causes activation of defense response and hypersensitive cell death. AtWRKY6 is involved in the regulation of plant senescence and low-Pi stress response (Arulpragasam et al. 2012; Chi et al. 2013). The interaction of AtWRKY38 and AtWRKY62 with Histone deacetylase 19 (HDA19) may fine-tune plant basal defense responses against abiotic stress by maintaining the levels of acetyl groups on histone tails (Kim et al. 2008). In addition to WRKY TFs, there are other transcription factors that respond to stress in other ways, The plasma membrane-localized NTL6 protein can be translocated to the nucleus to regulate target genes such as COLD-REGULATED 15a (COR15a) and PR genes (Seo 2014).

CONCLUSIONS

WRKY transcription factors play critical roles in plant responses to biotic and abiotic stresses. The present review summarized information of WRKY based on their function in biotic and abiotic stresses, as well as their target genes and signaling pathways; however, the mode of WRKY TF self-regulation and the mechanisms of the cross-talk between the signaling pathways involving WRKY TFs are still poorly understood. Advances in genomic and transcriptomic studies help understand the whole genomics version of WRKY genes in different plants and help to reveal the mode of action of WRKY TFs in plant stress responses. In addition, the mechanisms of synergistic responses to combined stresses with WRKY TFs, their targets, as well as other TFs would be even more interesting when more and more information will be explored in the near future.

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