REVIEW

WRKY transcription factors and plant defense responses: latest discoveries and future prospects

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Abstract

Key message **WRKY transcription factors are among the largest families of transcriptional regulators. In this review, their pivotal role in modulating various signal transduction pathways during biotic and abiotic stresses is discussed.**

Abstract Transcription factors (TFs) are important constituents of plant signaling pathways that define plant responses against biotic and abiotic stimuli besides playing a role in response to internal signals which coordinate different interacting partners during developmental processes. WRKY TFs, deriving their nomenclature from their signature DNA-binding sequence, represent one of the largest families of transcriptional regulators found exclusively in plants. By modulating different signal transduction pathways, these TFs contribute to various plant processes including nutrient deprivation, embryogenesis, seed and trichome development, senescence as well as other developmental and hormone-regulated processes. A growing body of research suggests transcriptional regulation of WRKY TFs in adapting plant to a variety of stressed environments. WRKY TFs can regulate diverse biological functions from receptors for pathogen triggered immunity, modulator of chromatin for specific interaction and signal transfer through a complicated network of genes. Latest discoveries illustrate the interaction of WRKY proteins with other TFs to form an integral part of signaling webs that regulate several seemingly disparate processes and defense-related genes, thus establishing their significant contributions to plant immune response. The present review starts with a brief description on the structural characteristics of WRKY TFs followed by the sections that present recent evidence on their roles in diverse biological processes in plants. We provide a comprehensive overview on regulatory crosstalks involving WRKY TFs during multiple stress responses in plants and future prospects of WRKY TFs as promising molecular diagnostics for enhancing crop improvement.

Keywords Biotic stress · Abiotic stress · Functional domain · Crosstalk · Crop improvement

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Introduction

Environmental vagaries exert detrimental effects on plants including almost all phonological stages. Evolution of an intricate signaling system to sense and react to external stimuli is crucial for the survival and perpetuation of plants to the next generation (Takahashi and Shinozaki 2019). Signaling events encompass reception, interaction and reaction following a change in the environment, which remains under the control of regulatory molecules at the cellular and subcellular levels (Joshi et al. 2017). Transcription factors (TFs) are important constituents of plant signaling pathways that define plant responses against biotic and abiotic stimuli in addition to their response to internal signals which coordinate different interacting partners during developmental processes (Joshi et al. 2016). WRKY TFs are among the largest families of transcriptional regulators in plants (Bakshi and

Oelmüller 2014). In recent years, several WRKY superfamily members have been reported in different plant species including *Glycine max* (197), *Raphanus sativus* (126), *Oryza sativa* (109), *Populus* (104), *Pinus monticola* (80), *Arabidopsis thaliana* (75), *Sorghum bicolor* (68), *Citrullus lanatus* (63), *Carica papaya* (52), *Hordeum vulgare* (45), *Physcomitrella patens* (38), *Selaginella involucrate* (35) and *Ipomoea trifida* (83) (Mangelsen et al. 2008; Liu and Ekramoddoullah 2009; Song et al. 2010; Pan and Jiang 2014; Fan et al. 2015; Karanja et al. 2017; Yang et al. 2018; Li et al. 2019). Binding of WRKY TFs with the (T)TGAC(C/T), i.e., W-box *cis*-element in the promoter of target genes induces gene expression to achieve cellular homeostasis (Bakshi and Oelmüller 2014; Machens et al. 2014). WRKY DNA-binding domain (DBD) is characterized by an invariant heptad WRKYGQK amino acid motif at their N-terminus and a zinc-binding motif at their C-terminus (Jiang et al. 2017). Considerable diversity has been evident in the structure and function of WRKY TFs from a growing body of research. Variations have been found in the number of WRKY genes and proteins per genome, number of introns, nucleotide sequence, among and within different evolutionary levels of the plant kingdom. WRKYs have gained attention owing to their involvement in diverse plant processes including growth, development, biotic and abiotic stress responses and plant innate immunity including microbe- or pathogen-associated molecular pattern-triggered immunity (MTI or PTI) and effector-triggered immunity (ETI) (Rushton et al. 2010; Phukan et al. 2016; Jiang et al. 2017). WRKYs can act as activators or repressors, in various homo- and heterodimer combinations, and form a TF net that contributes to various cytoplasmic and nuclear processes including signaling events from organelles or the cytoplasm to the nucleus (Bakshi and Oelmüller 2014). In this review, we summarize recent advances in our understanding of the WRKY TF family, with an emphasis on the plant stress response. We then elaborate on the WRKY-mediated regulatory networks that impart innate immunity to plants.

Structural characteristics and classification of functional domains

Despite having a highly conserved W-box, the varying binding abilities of WRKY TFs could be credited to variable numbers of DBDs and zinc-finger-like motifs. Based on these features, WRKY proteins are classified into four groups: I (two WRKY DBDs), II (single DBD with different C2–H2 zinc finger), III (single DBD with C2–HC zinc finger) and IV (incomplete WRKY domain without zinc finger) (Xie et al. 2005). Unlike group I, II and IV, group II is not monophyletic and is further divided into IIa, IIb, IIc, IId, and IIe based on additional conserved structural motifs besides the WRKY domain (Chen et al. 2012; Phukan et al.

2016). In lower plants, such as algae (*Dunaliella bardawil*), four WRKY TFs have been identified and all of them contained WRKYGEK sequence of amino acids at N-terminal, a difference due to Zn-finger at C-terminal. For instance, DbWRKY1 contained CX4CX23HXH, DbWRKY2 contained CX4CX21HXH while DbWRKY3 and DbWRKY4 contained CX4CX22HXH. Investigations on WRKY structures suggest that pre-WRKY structures (Pro-WRKY) must have a single domain as an origin. This might have doubled to give group I members of WRKY TFs, while a loss of N-terminal WRKY domain gave rise to group IIc members. Group IIc might have branched prophylactically to give rise to other subgroups of group II, and group III is the youngest and less diverse compared to other two groups (Song and Gao 2014; Wu et al. 2017a). The proposition that group II and III WRKY members should have evolved from group I gathers strong support from sequence similarity that the WRKY domains of group II and III members share with the C-terminal WRKY domain of group I WRKY TFs (Chen et al. 2019).

Though WRKY domain is highly conserved, substitutions occur in amino acid sequence of WRKYGQK; for example, WRKYGKK in maize, banana, populus, mulberry and soybean (Eulgem et al. 2000; Zhou et al. 2008; Zhang et al. 2017), WRKYGRK in populus and banana, FWRKYGQK in populus, WRKYGEK in rice and banana. In banana, other variants are also reported, such as WRKYGNK and WRKYGHK. Several monocot crops have also been studied with regard to WRKY TFs. Distribution of WRKY genes across a genome is not uniform and varies even within chromosomes (Goel et al. 2016; Xu et al. 2016; Zhang et al. 2017; Chanwala et al. 2020). 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 and Wang 2005). The other variants include WRICGQK, WRMCGQK, WKKYGQK, WIKYGQK, WKRYGQK, WSKYEQK, and WRKYSEK (Zhang and Wang 2005). In a few WRKY proteins, the WRKY motifs are also replaced by WIKY, WRMC, WRIC, WKKY, WVKY, WKRY, WSKY patterns (Jiang et al. 2017). Further, in the primary WRKYGQK motif of DBD, the WRKY residues are replaced by WRRY, WSKY, WKRY, WVKY or WKKY (Jiang et al. 2017). In addition to the above, variants of metal-chelating zinc finger motifs, such as C–H$_{4-5}$–X$_{22-23}$–H–X–H and C–X$_{5-8}$–C–X$_{25-28}$–H–X$_{1-2}$–C, are characteristics of WRKY proteins (Zhang and Feng 2014). Besides, HARF motif (RTGHARFRR (A/G) P) of unknown function was also reported in sub-group IId in *Arabidopsis thaliana*, *Salvia miltiorrhiza* and *Phaseolus vulgaris* (Li et al. 2015a; Wang et al. 2016). A Calmodulin (CaM)-binding domain (DxxVxKFKxVISLLxxxR) was also reported in *Arabidopsis* Group IId WRKYs, such as *AtWRKY7* (Park et al. 2005).

WRKY TFs bind specifically through both the terminals of WRKY domains to W box-type *cis*-elements in target gene promoters and activate or inhibit their transcription (Kim et al. 2008; Yamasaki et al. 2013; Li et al. 2020a, b, c). W-box consists of a degenerated/core TGAC motif, a conserved GAC core which interacts with the WRKY proteins, and its flanking thymine and pyrimidine (C/T) residues are recognized by specific WRKY factors (Jiang et al. 2017; Chen et al. 2019). Further, functional W-box elements are mostly present in WRKY TFs that bind with their own promoters or other WRKY TFs for auto- or cross-regulation (Liu et al. 2021). WRKY-DBDs recognize the regulatory motif sequence and bind through an α-helix or a β-sheet with the major groove of hydrophobic W-box element allowing base-specific interaction between the protein and the DNA (Deeba et al. 2017). However, *NtWRKY12* having WRKYGKK sequence binds with WK-box (required for the *PR-1a* induction by salicylic acid (SA) and bacterial elicitors), not with W-box (van Verk et al. 2008). Mutation from GKK to GQK or GEK is reported to impair the DNA-binding activity of *NtWRKY12* (van Verk et al. 2008). Similarly, *SUSIBA2* (*HvWRKY46*) binds to W-box and SURE (Sun et al. 2003), *OsWRKY13* interacts with W-box and PRE4 (Xiao et al. 2013), *AtWRKY70* binds to W-box and WT-box (Machens et al. 2014) and *AtWRKY50* interacts with TGA2 and TGA5 TFs, and simultaneously bound to PR1 promoter (Hussain et al. 2018). Further, by swapping β4–β5 strands, *OsWRKY45*-DBD forms a homodimer which provides flexibility around strands (Cheng et al. 2019; Xu et al. 2018). The inhibitor and mutational analyses of WRKY domain structures demonstrate that Tyr, Trp and two Lys residues in the WRKYGQK sequence (Ciolkowski et al. 2008) and zinc finger structures (Cheng et al. 2019) are indispensable for DNA binding. Further, differences between amino acid heptad affect the structure of WRKY domain, thereby enabling the concerted and selective regulation of WRKY TF target genes (Chen et al. 2019).

The distribution of different groups of WRKY TFs is also reported to differ among different plant species, exemplified by the abundance of group I WRKY proteins in *A. thaliana* and *O. sativa* as compared to strawberry. Similarly, poplar genome consists of 50% of WRKY TFs that belong to group I. Group I members in mulberry family constitute only group Ia sub-group. Also, a distinct motif of GGDFDDNEPEAKRWKGE was found at C-terminal of all group Ia members and one member of the group IIb family (Baranwal et al. 2016). Tea also shows substitution, in residual protein sequence, of glutamine by lysine (Wu et al. 2016). Research on woody dicots like *Populus* has offered evidence for formation of WRKY III after duplication events that occurred during monocot-dicot divergence (Wang et al. 2015). The structural complexity of WRKY genes is also manifested in point of spliced domains with V-type or R-type introns, with a

low diversity between monocots and dicots than among lower plant groups (Liang et al. 2017). For example, both in strawberry and wheat, number and type of introns varied from zero to twenty and V-type introns were specific to IIa and IIb type groups (Zhou et al. 2016; Ning et al. 2017). In dicots like pepper, group IIa family contains members having leucine zipper structure, that serves as elicitors that mediate binding of WRKY TFs to W-box (Cormack et al. 2002). In tomato, a divergence in group IIe and group III members was observed at WRKY domain sequence, and also in group III members at Zn-finger motifs (Huang et al. 2012). In addition to this, WRKY TFs are reported to have undergone positive or neutral selection as well as gene duplication and loss (Tang et al. 2013; Zhou et al. 2016). Presence of a large number of duplicated blocks suggests occurrence of duplications during evolution and genome expansion within the WRKY family members (Xu et al. 2016; Zhang et al. 2017). In gymnosperms like pine, introns show synteny with the angiosperms as well as, among different WRKY families, group IId + IIe shows expansion with the highest number of members and WRKY3 family with the least representation (Liu and Ekramoddoullah 2009). This observation contrasts with angiosperms where WRKY members of all the families are present, though the number differs with different genomes. Therefore, binding affinity of various WRKY domains to W-box and others seems to be ambiguous, requiring deeper investigations on the domains outside the DBD.

WRKY TF and plant stress response

Role in biotic stresses

Plants have evolved mechanisms to respond to a range of biotic stresses, such as pathogen attacks, that they encounter in their life cycle (Sun et al. 2015; Jha et al. 2020). The role of WRKY TFs as key regulators in plant immune response to a variety of biotic stresses has been extensively investigated (Singh et al. 2017; Cui et al. 2019). WRKYs regulate expression of defense-related genes through binding to a consensus *cis*-element referred to the "W-box" (TTGACT/C) in the promoter regions of these genes. As reviewed in Peng et al. (2018), PAMP (pathogen-associated molecular patterns)-triggered immunity (PTI) and effector-triggered immunity (ETI) constitute the two lines of plant immune response, with former involving recognition of molecular patterns of the pathogen (PAMPs) with pattern-recognition receptors (PRR) in host cells; whereas toxins/effectors are detected by plant resistance (R) proteins in ETI that often involves a hypersensitive response (HR). Receptor-like kinases (RLKs), one of the largest gene families in plants, form the major class of pathogen recognition receptors.

WRKYs were reported to play pivotal roles in repressing or activating both kinds of plant defense responses through direct or indirect interaction with PAMPs/effector proteins or their regulation by mitogen-activated protein kinases (Phukan et al. 2016). Peng et al. (2008) demonstrated a role for a WRKY transcription factor *OsWRKY62* in both PTI (basal) and ETI (mediated by *Xa21*) in rice. Transgenic plants overexpressing *OsWRKY62.1* (one of the two splice variants) showed impairments in both PTI and ETI, with suppression of defense-related genes. This study established *OsWRKY62* as a negative regulator of innate defense response in rice against bacterial blight. By contrast, *OsWRKY67* acts as a positive regulator of PTI and ETI against two rice pathogens, *Magnaporthe oryzae* and *Xanthomonas oryzae* pv. *oryzae* (Xoo) (Vo et al. 2018).

In *A. thaliana*, Kim et al. (2008) described the action of *WRKY38* and *WRKY62* in reducing basal defense response to bacterial pathogen *Pseudomonas syringae* through transcriptional activation of some unknown regulatory players. Also, an antagonistic action of *Histone Deacetylase 19* (*HDA19*) against *WRKY38* and *WRKY62* confirmed *HAD19* as a positive regulator of defense response. An enhanced level of disease resistance was found in single (*wrky38* and *wrky62*) as well double mutant (Kim et al. 2008). In response to pathogen infection (*P. syringae*) in *Arabidopsis*, the association of MAP kinase 4 (*MPK4*) and *MKS1* with *WRKY33* in the nucleus is disrupted following the activation (*MPK4*) and phosphorylation (*MKS1*) events. The released *WRKY33* then represses *phytoalexin deficient3* (*PAD3*) gene, thus impairing the synthesis of antimicrobial compound camalexin (Qiu et al. 2008). Earlier, Zheng et al. (2006) showed greater susceptibility of Arabidopsis overexpressing *WRKY33* against necrotrophic fungal pathogens (*Botrytis cinerea* and *Alternaria brassicicola*). Previously in soybean, authors identified 174 WRKY genes from the genome sequence and overexpression of the three WRKYs *GmWRKY 13*6, *53* and *86* in the soybean cyst nematode (SCN)-susceptible cultivar Williams 82 enhanced SCN resistance level up to 55% (Yang et al. 2017). No significant increase was observed in these transgenic lines following SA application. In wheat, RNA-Seq associated differential expression of two *WRKY* genes (*TaWRKY49* and *TaWRKY62*) with high-temperature seedling-plant resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*). Gene silencing experiments further validated the RNA-Seq results, and *TaWRKY49*-silencing enhanced resistance while silencing of *TaWRKY62* reduced resistance. Authors suggested negative and positive regulatory roles of *TaWRKY49* and *TaWRKY62*, respectively, in *High-Temperature Seedling-plant resistance to Pst* (HTSP) through modulating SA, jasmonic acid (JA), ethylene and reactive oxygen species (ROS) pathways (Wang et al. 2016). Another example of negative regulation of plant immunity by WRKY includes *CaWRKY40b*, which regulates a set of

immunity associated genes in pepper under *Ralstonia solanacearum* infection. Virus-induced gene silencing (VIGS) of *CaWRKY40b* and overexpression of *CaWRKY40b-SRDX* caused up- and down-regulations of positive and negative regulators, respectively; whereas *CaWRKY40b*-overexpression exerted an opposite role (Khan et al. 2018). Further, enhanced transcript levels of *CaWRKY40* were reported to induce SA, JA and ethylene mediated pathways during *R. solanacearum* infection. Overexpression of *CaWRKY40* regulates hypersensitive response (HR)-associated and pathogenesis-related genes, thus providing resistance to *R. solanacearum* (Dang et al. 2013). *CaWRKY40b* thus acts as a negative regulator by directly modulating immunity associated gene *CaWRKY40*. Further, *CaWRKY6* positively regulates *R. solanacearum* resistance by activating *CaWRKY40* (Cai et al. 2015). Isolation of *SpWRKY1* from wild tomato (*Solanum pimpinellifolium*) following cloning and RT-PCR approaches, and its subsequent transformation into cultivated tomato (*Solanum lycopersicum*) caused an increase in resistance to *Phytophthora infestans* via mediating the regulation of abscisic acid (ABA) biosynthesis genes (Li et al. 2015b). In another attempt, tobacco plants transformed with *SpWRKY1* showed lower contents of malondialdehyde, relative electrolyte leakage and higher antioxidant enzymes peroxidase (POD) and superoxide dismutase (SOD) and phenylalanine ammonia-lyase (PAL) activities, indicating plant's resistance to *Phytophthora nicotianae* (Li et al. 2015c). Concomitantly, the expression of genes related to JA/SA and deference response also altered as a result of *SpWRKY1* overexpression.

Role in abiotic stress

A growing body of literature supports the involvement of WRKY transcription factors in the regulation of abiotic stress response in plants. Meeting the challenge of feeding nine billion by 2050 necessitates a sustainable increase in crop yields in an environment that is increasingly challenged by drought and salinity (Tester and Langridge 2010; Singh et al. 2015; Wani et al. 2018; Jha et al. 2019). A variety of biotic and abiotic factors have been reported to induce WRKY TFs, such as *OsWRKY45*, and *Arabidopsis* transformed with *OsWRKY45* had enhanced tolerance to drought via regulating stomatal closure and stress-related genes (Qiu and Yu 2009). An *acquired drought tolerance* (*adt*) mutant having improved drought tolerance was isolated in *Arabidopsis* after surveying 43 WRKY-associated T-DNA insertion lines. The insertion in *adt* caused an elevation in *WRKY57* expression level. The drought tolerance of *adt* could be credited to enhanced ABA levels. Further, the binding of *WRKY57* with stress-responsive genes (*RD29A*, *NCED3*) via the core W-box sequence was confirmed with chromatin immunoprecipitation (ChIP),

PCR and quantitative real-time (RT–PCR) analysis (Jiang et al. 2012). In wheat, overexpression of *TaWRKY146* having homology with the *AtWRKY46* showed hypersensitivity towards salt and drought stress in *Arabidopsis* (Ma et al. 2017). Significant up-regulation of *WRKY146* in wheat leaves and roots was found under osmotic stress. Further, transgenic *Arabidopsis* overexpressing *TaWRKY146* showed improved drought tolerance with elevated contents of proline and soluble sugar and lesser malondialdehyde (MDA) content, besides induced stomatal closure and reduced transpiration rate. Moreover, *Arabidopsis* plants overexpressing *WRKY46* from *Fagopyrum tataricum* (*FtWRKY46*) showed improved tolerance against salt stress by scavenging ROS (Lv et al. 2020). In contrast, overexpression of *AtWRKY46* in *Arabidopsis* (*OV46*) resulted in hypersensitivity to drought and salt stress, achieved by modulating the expression of *QUA-QUINE STARCH* (*QQS*) (Ding et al. 2014). Wan et al. (2018) identified a set of 53 *WRKY* genes from the transcriptome data in *Caragana intermedia*, and functional validation of the two WRKY genes *CiWRKY75–1* and *CiWRKY40–4* was evident with enhanced drought tolerance of transgenic *Arabidopsis*. Genome-wide analysis of 97 *WRKY* genes in *Pennisetum glaucum* demonstrated differential expression patterns in different tissues under drought and salinity stress conditions (Chanwala et al. 2020). Out of these *PgWRKY33, PgWRKY62* and *PgWRKY65* were found to be regulated under both dehydration and salinity stress responses. It was also shown earlier that transformation of tobacco with *SpWRKY1* increases tolerance against drought and salt stress (Li et al. 2015b). Given the highly up-regulated expression under drought stress, the transformation of *WRKY3* TF gene, isolated from horse gram (*Macrotyloma uniflorum)*, was performed in groundnut and consequently, improved drought tolerance of the transgenic lines was evident by less accumulation of MDA, more proline and higher antioxidant activities (Kiranmai et al. 2018). Other recent examples where overexpression of *WRKY* TF caused an improvement in drought tolerance of plants including wheat *WRKY1, WRKY2* and *WRKY33* into *Arabidopsis* (He et al. 2016; Gao et al. 2018) and *Malus baccata WRKY2* and *WRKY3* into tobacco (Han et al. 2018a, b).

Currently, salt-deteriorated soils form 20% of the irrigated land and 2% of the dry land, and half of the total arable land is likely to be impacted by salinity by 2050 (Kaashyap et al. 2017). Under osmotic/salt stress, an interplay between *WRKY46* and "ABA signaling" and "auxin homeostasis" was elucidated in the regulation of lateral root (LR) development in Arabidopsis (Ding et al. 2015; Li et al. 2020a, b, c). LR development was hampered in a mutant (*wrky46*) in contrast to *WRKY46* overexpressing lines that had enhanced LR. Exogenous application of the mutants with α-naphthaleneacetic acid (NAA)/ indole-3-acetic acid (IAA) rescued the LR phenotypes, whereas 2,3,5-triiodobenzoic acid (TIBA) inhibited the LR development in both WT and *OV46*. *WRKY46* was also shown to affect auxin conjugation in lateral roots. Also, the action of *WRKY46* on downstream *ABI4* was illustrated through the genetic analysis of the double mutants (*wrky46 abi4*). Recently, Wu and colleagues (2017b) found significant differences in expression levels of *PeWRKY83* in Moso bamboo (*Phyllostachys edulis*) during abiotic stresses (drought, salinity and ABA treatment). Further, authors defined the functional role of *PeWRKY83* by transforming it into *Arabidopsis*, and the transgenic *Arabidopsis* plants showed enhanced tolerance to salt stress, with higher germination rates, higher content of proline, less electrolyte leakage and lower MDA. Transgenic plants showed reduced sensitivity to exogenous ABA and *PeWRKY83* positively regulated ABA-related genes under salt stress. A new *WRKY* TF *DgWRKY5* was isolated recently from *Chrysanthemum* and the expression level of the TF showed up-regulation in response to various stresses (salt, ABA and H_2O_2) (Liang et al. 2017). Further, the transformation of *Chrysanthemum* with *DgWRKY5* elucidated improved salt tolerance of the transgenic plants consequent upon *DgWRKY5* overexpression, with contents of proline, soluble sugars and proteins accumulating proportionate to salt stress. Differential expression of *GmWRKY49* was obtained in salt-tolerant and salt-susceptible soybean genotypes and authors further performed functional characterization of *GmWRKY49* by overexpressing it into soybean seedlings and Arabidopsis (Xu et al. 2018). Enhanced tolerance to salt stress was evidenced in both soybean seedlings and transgenic *Arabidopsis*, with improvements in germination rate, survival rate, root length, in addition to proline content. Similar studies where overexpression of *WRKY* genes improved salt tolerance of plants include *Dendranthema grandiflorum DgWRKY2* and *DgWRKY4* into chrysanthemum (Wang et al. 2018; He et al. 2018) and so forth. In contrast, salt sensitivity was promoted following overexpression of *WRKY* genes like *CmWRKY17* (*Chrysanthemum*) and *PcWRKY33* (*Polygonum cuspidatum*) in *Arabidopsis*, resulting in down-regulation of stress-related genes and reduction in other parameters like antioxidant enzymatic activities, and proline content (Li et al. 2015c; Bao et al. 2018).

Heat stress is defined as an increase in air temperature above a threshold level (Teixeira et al. 2013). In tropical and subtropical areas, threshold levels of heat stress are above 32–35 °C (Bita and Gerats 2013), while in temperate crops, temperature above 25 °C is considered as heat stress (Wahid et al. 2007). Implications of heat stress on plant growth and function depend upon the intensity, duration of exposure, and the degree of the elevated temperature (Sita et al. 2017). In response to heat stress, a variety of *WRKY* genes enable plants to adapt temperature levels beyond "optimal tolerance range" (Jiang et al. 2017). In *Arabidopsis*, research groups have shown participation

of *WRKY 25*, *WRKY26*, *WRKY33*, and *WRKY39* in plant response to heat stress (Li et al. 2009, 2010, 2011). Previous study has shown the interaction of *B-cell lymphoma2* (*Bcl-2*)-*associated athanogene 7* (*BAG7*) and *WRKY29* is required for heat tolerance in *Arabidopsis* (Li et al. 2017a, b). It was reported that *CaWRKY40* is induced by heat shock and its overexpression enhanced heat shock tolerance in tobacco, while its silencing impaired thermotolerance in pepper (Dang et al. 2013). Further, it was observed that *CaWRKY6* binds and activates *CaWRKY40* promoter and thus acts as a positive regulator of heat stress tolerance (Cai et al. 2015). Other important plant WRKY TFs that confer combined tolerance to drought and heat include *TaWRKY1* and *TaWRKY33* from wheat (He et al. 2016), *OsWRKY11* from rice (Wu et al. 2009) etc. It was also shown earlier in *Arabidopsis* that *WRKY47* directly regulates *Xyloglucan Endo Transglucosylase Hydrolases17* (*XTH17*) and *Extensin-Like Protein* (*ELP*), thus regulating aluminium tolerance (Li et al. 2020a, b, c).

Signalling of WRKY TFs and regulation by plant hormones

As described in earlier sections, WRKY TFs play an essential role in the adaptation of crop plants to both biotic and abiotic stresses, and the adaptation results from an interplay between WRKYs and a variety of plant hormones. Empirical evidence suggests that exogenous application of different plant hormones altered expression of *WRKY* genes upon exposure to multiple abiotic stress including drought, salt and H_2O_2 (Yan et al. 2014). Under stressed conditions, WRKY TF may work independently or in coordination. Synergistic action of different *WRKY* TFs and enormous crosstalk with plant hormones and stress tolerance pathways demonstrates their differential expression. For instance, the synergistic interaction between ABA-inducible *OsWRKY51* and *OsWRKY71* genes inhibits gibberellic acid (GA) signalling in the aleurone cells of rice seeds (Xie et al. 2006; Hwang et al. 2016). Likewise, *AtWRKYs 18*, *40* and *60* are shown to participate in signaling pathways that are mediated by plant hormones SA, JA and ABA (Chen et al. 2010). One of the mechanisms of plant signaling involved receptor stimuli interaction and downstream signaling cascade that leads to expression of TFs and amplification of target genes and the corresponding response (Joshi et al. 2016). One of the major signalling pathways underlying both biotic and abiotic stresses is mediated through MAP kinase signaling cascade. It was demonstrated recently that ABA signalling repressor *OsWRKY29* suppresses expression of *OsABF1* and *OsVP1*, thus leading to a repressed seed dormancy (Zhou et al. 2020).

WRKY signalling in biotic stress

With regard to biotic stress, receptor *R* genes having NBS LRR domain activate downstream MAP kinase signaling cascades and *WRKY18/22/29/30/33/53* genes, thus serving against *P. syringe, Magnaporthe grisea,* and *B. cinerea* (Fig. 1) (Sheen et al, 2002; Chujo et al 2014). Upon infection to *B. cinerea*, MAPK3/6 phosphorylates *WRKY33* and phosphorylated *WRKY33,* in turn, activates *PAD3*, causing an increase in resistance through phytoalexin biosynthesis (Fig. 1) (Mao et al. 2007; 2011). In contrast, a decline was observed in resistance level as a result of overexpression of *WRKY38* and *WRKY62*. Both genes, induced in a *Non-expresser of Pathogenesis-Related genes 1* (*NPR1*)-dependent manner by SA or by virulent *P. syringae*, work additively as negative regulators of plant's basal defense (Kim et al. 2008). The NO signalling pathway mediated by *AtWRKY*27 improves defense against *R. solanacearum* (Mukhtar et al. 2008). Several defense-related genes and regulatory *NPR1* genes have statistically enriched *WRKY* TF binding sites (W box elements) in their promoter region, such as pathogen inducible *ICS1* gene, suggesting either autoregulation or cross-regulation by other WRKY proteins (Dong et al. 2003).

Out of 72 *WRKY* genes reported in *Arabidopsis*, 49 genes have been reported to be differentially regulated by *P. syringae* or SA treatment (Dong et al. 2003). Research suggests that TFs like *WRKY3*, *WRKY4* and *WRKY33* positively regulate the SA-mediated plant resistance pathways to necrotrophic fungal infection, such as *B. cinerea* (Zheng et al. 2006; Lai et al. 2008). Similarly, *WRKY33*, *WRKY46*, *WRKY53* and *WRKY70* positively regulate SA-mediated defense pathway against biotrophic bacterial pathogen, such as *P. syringae* (Zheng et al. 2006; Hu et al. 2012). Two alleles of *OSWRKY45*, both regulated by *WRKY13*, showed a contrasting response to Xoo (Qiu et al. 2007). *OsWRKY45-1* overexpressing plants showed increased susceptibility in contrast to *OsWRKY45-2*-overexpressing plants that had enhanced resistance to *Xoo* and *X. oryzae pv. oryzicola* (*Xoc*) (Tao et al. 2009). Further, *OsWRKY45-1* exhibited control to SA and JA levels, while *OsWRKY*45-2 only JA levels. Recently it was found that in rice, *VQ13* (JA-responsive valine-glutamine (VQ)-motif-containing protein) activates *MPK6* and *WRKY45*, and positively regulates JA-induced resistance to Xoo (Uji et al. 2019). *AtWRKY18* and *AtWRKY40* suppress *Jasmonate-Zim Domain* (*JAZ*) repressors which repress JA-signaling, causing suppression of several defense-related genes, such as *FMO1*, *PAD3*, and *CYP71A13*. All these eventually help *Trichoderma* root colonization (Brotman et al. 2013). As shown in Fig. 1, *CaWRKY27* acts as a positive regulator in tobacco resistance responses to *R.*
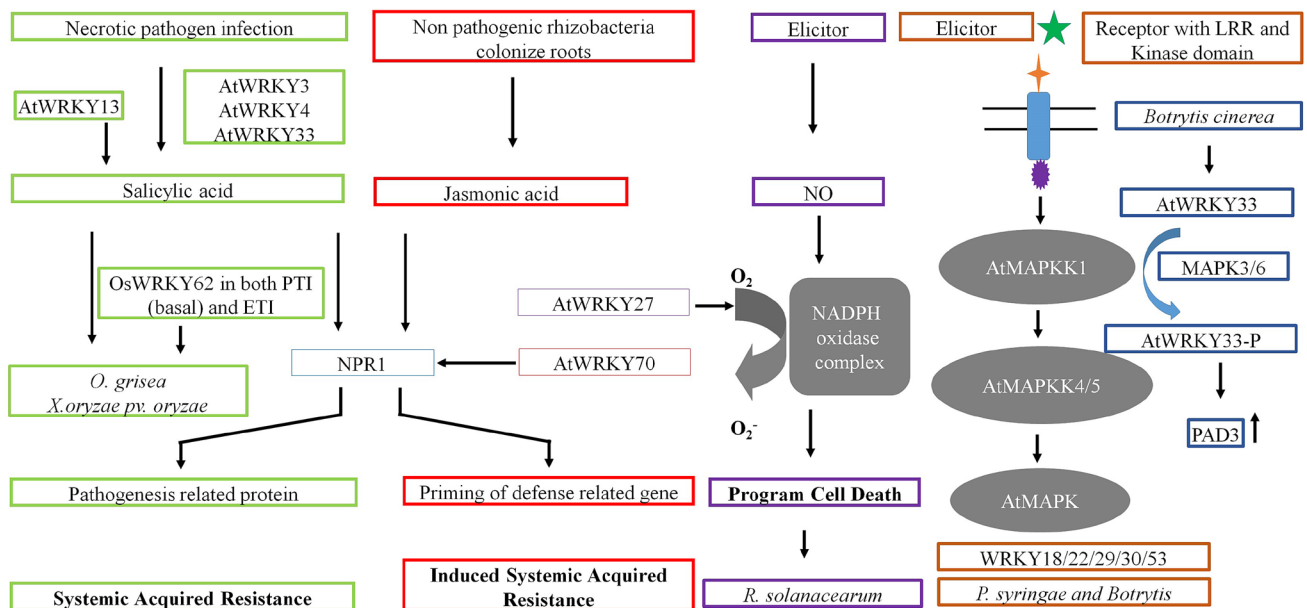
Fig. 1 Schematic diagram depicting the role of WRKY transcription factors under various biotic elicitors. WRKY TFs play an essential role in regulatory pathways of non pathogenic rhizobacteria and necrotic pathogens. During pathogen infection WRKY regulate downstream signalling pathways modulated by either salicylic acid dependent, or jasmonic acid dependent or nitric oxide dependent or by interacting with other WRKY genes. These WRKY regulated defense pathways has significant role in plant survival either by providing systemic acquired resistance or delaying senescence

solanacearum infection through modulation of SA, JA, ethylene, and NO-mediated signaling pathways (Dang et al. 2014). A recent study revealed that *HbWRKY83* is a positive regulator of JA-, ethylene-, and wound-responsive genes in the laticiferous cells of rubber tree (Kang et al. 2020).

Fu and Dong (2013) found that SA or benzothiadiazole (BTH)-induced systemic acquired resistance (SAR) can be achieved by transcriptional regulation of *NPR1* genes. Various WRKY TFs were identified as key regulators of *NPR1*-dependent or -independent SAR, such as *AtWRKY18, AtWRKY58*, and *AtWRKY70* (Wang et al. 2006), *OsWRKY03* and *OsWRKY71* (Liu et al. 2005, 2007) and *OsWRKY45* (Shimono et al. 2007). Recently, wheat transgenic lines overexpressing barley *HvWRKY6* and *HvWRKY70* showed improved resistance against *Puccinia striiformis* f. sp. tritici pathotype CYR32 and *Blumeria graminis* f. sp. tritici pathotype E20 (Li et al. 2020a, b, c).

WRKY signalling in abiotic stress

In plants, ABA is a key regulator of both biotic and abiotic stress responses and its biosynthesis and accumulation are also enhanced under stress (Xiong et al. 2002). Abiotic stress tolerance signaling works through both ABA-dependent and ABA-independent pathways. Different WRKY TFs function co-ordinately or independently to the ABA signaling pathway. Thus, overexpression of *AtWRKY21/33/40/57* and *AtWRKY70* improves osmotic stress tolerance in an ABA-dependent manner; while *AtWRKY25, ATWRKY45* and *TaWRKY93* work via ABA-independent pathways. *ATWRKY40* represses the expression of ABA-responsive genes (Rushton et al. 2012). Under abiotic-stressed scenario, ABA binds to PYR/PYL/RCAR protein phosphatase 2C-ABA complex and the chloroplast envelope located ABAR–ABA complex in the nucleus. These two complexes remove AtWRKY40 from the nucleus and depress ABA-responsive genes including *ABI4, ABI5, ABF4, MYB2, DREB1a, DREB2b, RAB18* and *AtWRKY60* (Fig. 2) (Rushton et al. 2012). Research in rice on the regulation of WKRY TFs under abiotic stress and plant hormone revealed that a set of *WRKY* genes is induced following abiotic stress whereas plant hormones act on another set of genes. Authors noted that majority of genes were regulated by both abiotic stress and plant hormones [ABA, IAA, GA3, Methyl jasmonate (MeJA) and SA] with extensive occurrence of crosstalks between both (Ramamoorthy et al. 2008). Analysis of *GsWRKY20*-overexpressing lines in *Arabidopsis* led authors to find an improved response to ABA, which reduced water loss and enhanced tolerance to drought stress via stomatal closure and reduced stomatal density (Luo et al. 2013). Further, multiple *WRKY* genes are deemed to be regulated by ABA-mediated responses (Fig. 2). ABA induces expression of different *WRKY* genes in rice, such as *OsWRKY11, OsWRKY71, OsWRKY72* and *OsWRKY77*, and it may reduce expression
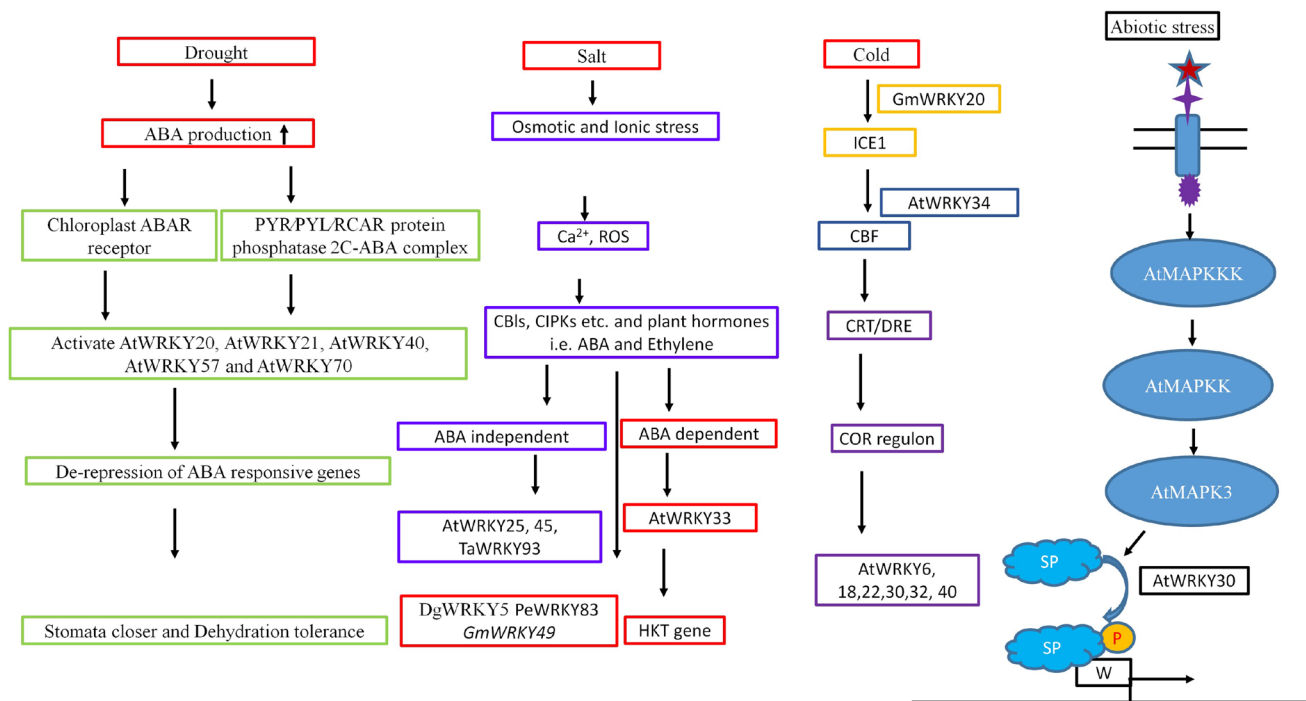
Fig. 2 Schematic diagram depicting the signalling of WRKY transcription factors under different abiotic stresses. Various WRKY members plays different roles in regulation of abiotic stress regulatory pathways in different plants and tissues indicates their essential role in plant stress tolerance. During abiotic stress regulation, response occurs by complex cross-talk between phytohormones, such as, ABA, SA, MeJA, and ETH, and individual pathway is regulated by specific WRKY genes further modulting different physiological and biological processes

or negatively regulate *OsWRKY24* and *OsWRKY45* genes. Further, *OsWRKY51* and *OsWRKY71* mediate the cross-talk between GA and ABA signaling. In rice, ABA-inducible nature of these genes is evident; however, these genes remain GA-repressible (Xie et al. 2006). *OsWRKY24*, *OsWRKY51* and *OsWRKY71* negatively regulate GA signaling pathway (Xie et al. 2005; Zhang et al. 2009). The transgenic lines overexpressing *OsWRKY45-1* and *OsWRKY45-2* registered their contrasting response to ABA. *OsWRKY45-2* overexpressing lines showed increased ABA sensitivity and reduced salt stress tolerance which is phenotypically contrasting to *OsWRKY45-2*-suppressing lines (Tao et al. 2011). Overexpression of different *WRKY* genes could lead to salt tolerance by following different tolerance mechanisms. The enhanced expression of *TaWRKY93* upon exogenous application of NaCl or abscisic acid improved salt tolerance via both ABA-dependent and -independent pathways and also by enhancing osmotic stress tolerance (Fig. 2) (Qin et al. 2015). Osmotic stress tolerance has been regulated by *AtWRKY70* and *AtWRKY54* with both working cooperatively and negatively regulating stomata closure (Li et al. 2013). The study established the role of both *WRKY* genes for improving drought tolerance in plants. Under salt stress, *AtWRKY25* and *AtWRKY33* have improved salt stress tolerance through SOS-pathway-independent manner. However, *AtWRKY33* showed salt tolerance through ABA-dependent signaling pathway (Jiang and Deyholos 2009). Recently, it was demonstrated that *Arabidopsis* plants overexpressing *IbWRKY2* (Zhu et al. 2020) and *HbWRKY83* (Kang et al. 2020) were tolerant against salinity and drought stress via improved ROS scavenging system. Under heat stress, *AtWRKY25* regulated expression of heat-inducible and oxidative stress-inducible genes containing W box at their promoter region, independent of the SA pathway. Overexpression of *WRKY25* increased the expression of *HsfA2*, *HsfB1*, *HsfB2a* and *Hsp101*, implying a role in *HsfB2a* and *HsfB1* pathway (Li et al. 2009). Cold stress tolerance is primarily regulated through *cold-responsive* (COR) regulon (Fig. 2). Overexpressing *WRKY46* in cucumber conferred cold tolerance by modulating cold signalling pathway in an ABA-dependent manner (Zhang et al. 2016). *AtWRKY34* regulates *CBF* and *GM20* regulates *ICE1* gene. Further, COR regulon regulates *AtWRKY6/187/22/30/32* and *AtWRKY40* genes (Banerjee and Roychoudhury 2015). Generally, abiotic stress signal activates or works through MAPK signaling pathways.

More recently, a global analysis of sesame (*Sesamum indicum* L.) WRKY TF identified 71 genes, of which 26 were drought-responsive while 33 genes responded to waterlogging (Li et al. 2017b). The gene *WRKY1* of *Poncirus*

trifoliate and *Citrus grandis* was analyzed under cold and drought stresses, and the results showed that both genes showed induced expression in response to drought while cold could evoke response only from *PtrWRKY1* (Şahin-Çevik and Moore 2013). Similarly, overexpression of various *WRKY* TFs led to tolerance to various abiotic stress, such as *OsWRKY89*-overexpressing lines in rice, showed enhanced tolerance to ultraviolet B irradiation (Wang et al. 2007), *OsWRKY11* under the control of the *heat shock protein 101* (*HSP101*) promoter enhanced heat and drought tolerance in rice (Wu et al. 2009). In summary, recent evidence in plant species supports multiple roles for *WRKY* genes against a variety of abiotic stresses.

WRKY-mediated crosstalk between abiotic and biotic stress responses

Recent evidence supports the involvement of WRKY TF in mediating response and adaptation to biotic and abiotic stresses. This crosstalk phenomenon is exemplified by the action of several WRKY TFs, such as *OsWRKY13*, in rice that alters plant response to both biotic (*Xoo* and *M. grisea*) and abiotic stresses (Qiu et al. 2007; 2008). *OsWRKY13* is possibly regulated by both *OsWRKY45-1* and *OsWRKY45-2*, the two alleles identified, respectively, from *japonica* and *indica* rice. Previous research has established *OsWRKY45* and *SlWRKY8* as the positive regulators of *PR* gene expression, resistance to *P. syringae* pv. *tomato* DC3000 (*PsPto*), tolerance to drought and salt stress and ABA sensitivity (Qiu and Yu 2009; Gao et al. 2020). Subsequent experiments elucidated that *OsWRKY45-1*, a negative regulator of ABA signaling, plays no role in salt tolerance in rice. In contrast, *OsWRKY45-2* is a positive regulator of ABA signaling, and a negative regulator of salt stress tolerance (Tao et al. 2011). Similarly, constitutive expression of grape *WRKY3* gene in *Arabidopsis* provided insights into its role in defining plant response to biotic (*Golovinomyces cichoracearum*, *B. cinerea*) and abiotic stresses (drought and salinity) (Guo et al. 2018). Research by Lee et al. (2018) established *OsWRKY11* as a positive regulator of rice–*Xoo* interaction and drought stress in rice through activating expressions of deference- (*Chitinase 2*) and drought-(*RAB21*) related genes. Improved resistance to *PsPto* and drought/salt stress in tomato was achieved by overexpression of *SlWRKY39* (Sun et al. 2015). The higher tolerance level of transgenic plants could be ascribed to the abundance of *PR* (*SlPR1*, *SlPR1a1*) and stress-related genes (*SlRD22*, *SlDREB2A*), and lower and higher contents of MDA and proline, respectively. Taken together, WRKY TFs participate in various cross regulatory networks related to defense response and their interaction provides insight into their coregulated functional dynamics of signaling response during different biological processes.

Other roles of WRKY TFs

In addition to stress response, WRKY TFs role in a range of important processes including plant development are well documented (Chen et al. 2017). The SPF1 (Sweet Potato Factor1), first identified *WRKY* protein, participated in tuberous root development in *Ipomoea batatas* (Ishiguro and Nakamura 1994). Further, WRKY proteins ABF1 and ABF2, isolated from *Avena fatua* were found to regulate seed germination (Rushton et al. 1995). Besides, *WRKY1*, *WRKY2*, and *WRKY3* were reported to regulate ribosomal protein gene expression in *Petroselinum crispum* (Rushton et al. 1996). *WRKY42, WRKY45, WRKY75, WRKY6* from *Arabidopsis* and *WRKY74, WRKY80* from rice were involved in plant nutrient (i.e., phosphorus, boron and iron) utilization (Chen et al. 2017). *AtWRKY6, AtWRKY53* and *OsWRKY45* regulate leaf senescense (Miao and Zentgraf 2010). Moreover, *AtWRKY12, AtWRKY13, AtWRKY71* and *OsWRKY11* were reported to be involved in floral development in angiosperms (Cai et al. 2014; Li et al. 2016; Yu et al. 2016). A recent study in *Arabidopsis* elucidated down-regulation of a set of genes associated with senescence (*SAG12, SAG13* and *SAG29*) and chlorophyll degradation genes *(PPH, PAO, NYE1/SGR1, NYC1, NOL)* resulting from the overexpression of *CiWRKY40–4* caused delayed leaf senescence in the transgenic plants (Wan et al. 2018).

WRKY's participation in plant reproductive development is evident from severe fertility defects resulting from a compromise in WRKY-mediated regulatory network. In *Arabidopsis*, gene expression patterns in mature pollen grains, inferred from publically available data, qRT-PCR assay and genetic analysis, led authors to assume that *WRKY2, WRKY34* and *VQ20*, suppress the expression of MYBs (*MYB97, MYB101* and *MYB120*) during male gametogenesis. Further, binding of the *WRKY2/WRKY34* with *MYB97* via the promoter containing W-box was confirmed (Lei et al. 2018). Prioritization of defense response overgrowth, as shown by *OsWRKY70* in mitigating insect herbivory in rice, can often yield unintended consequences (Li et al. 2015a). The authors highlighted the profound implications that these trade-offs may have, in breeding resistant plants.

Implications for future crop improvement

In recent years, a plethora of information has been generated in the wake of growing research interest on TFs, both in model and non-model crops. More comprehensive information is warranted on the activities of WRKY

Table 1 WRKY TF playing crucial roles in plant reproductive development

S. No	Name of the WRKY TF	Isolated from	Overexpressed in	Function	Reference
1	WRKY27	Arabidopsis	Arabidopsis	Pollen dehiscence	Mukhtar et al. (2008)
2	WRKY12/ WRKY13	Arabidopsis	Arabidopsis	Flowering time	Li et al. (2016)
3	WRKY75	Arabidopsis	Arabidopsis	Flowering time	Chen et al. (2017)
4	WRKY20	Soybean	Arabidopsis	Flowering time	Luo et al. (2013)
5	WRKY34/WRKY2	Arabidopsis	Arabidopsis	Pollen Development and germination, and pollen tube growth	Zou et al. (2010), Guan et al. (2014)
6	WRKY1	Potato (Solanum chacoense)	–	Embryogenesis	Lagace and Matton (2004)
7	RKY23	Arabidopsis	Arabidopsis	Embryo development	Grunewald et al. (2013)
8	WRKY2	Arabidopsis	Arabidopsis	Embryo development	Ueda et al. (2011)
9	WRKY75	Arabidopsis	Arabidopsis	Flowering	Zhang et al. (2017)
10	Dlf1(WRKY11)	Rice	Rice	Flowering time	Cai et al. 2014
11	MlWRKY12	Miscanthus lutarioriparius	Arabidopsis	Flowering time	Yu et al. (2016)

TFs in the plant genome, their communication with other biomolecules and sorting complexities of upstream elements that regulate them. It is further being traversed by modern tools of omics, analysis of complementarity with (*cis*-) promoter, systemics and several useful tools of bioinformatics. Different *WRKY* genes/TFs behave in a versatile manner even to an extent that homologs behave differently in different backgrounds (Cai et al. 2014). A set of WRKY TFs is known to regulate multiple genes with opposite effects (Liu et al. 2015) or could be induced and repressed depending on the external stimuli (Huang et al. 2016; Yan et al. 2016; Ding et al. 2013). In some cases, WRKY TFs upregulate both useful genes as well as unwelcomed genes (Wang et al. 2014). So, it is important to characterize them, elucidate their function and select the key TF translating gene for crop improvement. This deluge of information will be immensely useful when translated in crop improvement for the benefit the farmers and the mankind. However, practical implications of WRKY for crop improvement face a set of challenges.

Evidence suggests that WRKY TFs not only participate in plant growth and development, but also show complex regulatory mechanisms and networks involved in external abiotic stresses. A variety of roles of WRKYs have been elucidated on parts of the plant like root, leaf, etc.; however, evidence based on the whole plant is currently lacking. Considerable possibility exists that inferences gained from in vitro experiments might yield uncertain outcomes when applied for plant improvement in a different environment. Nothwithstanding this, there has been plenty of crop improvement illustrations recently based on transgenics and genomics-assisted breeding. Some of the recent examples are listed in Table 1. Growing body of literature on WRKY TFs advocates their usefulness for genetic characterization of a given crop population and

evolutionary studies at different levels as a function of WRKY TFs may vary as a consequence of environmental stress and in the process of adaptation (Yan et al. 2016). In conclusion, considerable scope exists for understanding WRKY TFs with respect to their functionality, evolution and intra/inter communication with other TFs in cooperative and antagonistic manner, noncoding RNAs and epigenetic modifications to find a common link in the complex signal pathways to facilitate improvement of agricultural crop yield and quality.

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Declarations

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