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Review and Progress **Open Access**

Research Progress of WRKY Transcription Factor Family in Plant Stress Resistance

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Abstract Transcription factors are a group of regulatory proteins that play significant roles in biological processes. They are the seventh largest family of transcription factors in higher plants, and are essential in plant growth, development, and response to biotic and abiotic stresses. This study provides a brief overview of the evolution of WRKY transcription factors in response to various abiotic stresses such as drought, high salt, temperature, inorganic elements, and oxidation, as well as biotic stresses such as infection by pathogenic bacteria and feeding by phytophagous insects. Furthermore, the research prospects and directions of WRKY transcription factors are envisioned.

Keywords WRKY; Transcription factor; Biotic stress; Abiotic stress

1 Introduction

Throughout their growth and development, plants are vulnerable to various stresses such as drought, flooding, high and low temperatures, salinity, oxidation, inorganic elements, as well as infestation by pathogenic bacteria and phytophagous insects. To maintain their normal life processes and adapt to the ever-changing external environment, plants have evolved a range of complex and effective defense mechanisms. One of the primary ways that plants deal with stress is through the transcription of specific genes, whereby transcription factors play a crucial role in regulating various developmental and physiological processes in plants by directly or indirectly binding to the cis-acting elements in genes that are involved in the stress signal transduction pathways.

WRKY is a unique and novel transcription factor specific to plants. Its members play a crucial role in enhancing plant stress tolerance. The WRKY protein comprises a 60-amino-acid conserved region known as the WRKY conserved region. The N-terminal of this region contains a core sequence of *WRKYGQK*, which is responsible for DNA binding and forms a positively charged concave surface. On the other hand, the C-terminal of the WRKY protein is a zinc-finger structure that can be linked to the W-box (C/TTGACT/C). This structure is responsible for DNA binding. The N-terminal region is positively charged and mainly responsible for DNA binding, while the C-terminal region is responsible for specific binding to DNA.

WRKY is induced by pathogens, mechanical damage, and the signaling molecule salicylic acid. Initially, the WRKY family was classified into three subfamilies based on the number of WRKY regions and zinc-finger structures, which are known as subfamily I, II, and III. Subfamily I contains two WRKY structural domains, family II contains one WRKY structural domain and one C2H2-type zinc-finger structure, and family III contains one WRKY structural domain and one C2HC-type zinc-finger structure.

Later, Zhang and Wang (2005) reclassified the family into five families based on the differences in the conserved structures and the positions of their introns. These are I, IIa+IIb, IIc, IId+IIe, and III, which are distinguished by the differences in the conserved structures and the positions of their introns.

In 1994, the first member of the WRKY transcription factors was discovered in sweet potato (*Ipomoea batatas*). Since then, researchers have identified numerous WRKY transcription factor members in many plants. Arabidopsis has over 100 WRKY members, each with one or two WRKY structural domains. Rice has 102 WRKY members, soybean has 197, cotton has 116, oilseed rape has 46, tomato has 81, poplar has 104, and rubber tree has 81 members. The WRKY structural domain is a sequence of 60 amino acids that includes a highly conserved amino acid sequence, *WRKYGQK*, at the N-terminus and a zinc finger domain. Most WRKY proteins bind to the W-box [TGAC(C/T)], which is present in the promoters of various genes related to plant defense responses. This binding helps in mediating transcriptional responses induced by pathogens. When the plant is infected with viruses, bacteria, or fungi, or treated with signaling agents like salicylic acid, mRNA and protein synthesis of WRKY transcription factors increases and enhances their DNA-binding activity (Dong et al., 2003). The W-box and WRKY transcription factors work together to regulate the expression of downstream gene products that provide protection and defense against pathogens.

2 Role of WRKY Transcription Factors in Abiotic Stresses

Abiotic stresses can affect normal physiological and biochemical processes in plants. Research has shown that WRKY transcription factors play a significant role in regulating plant responses to abiotic stresses. WRKY proteins are one of the largest families of transcription factors in higher plants, and they participate in complex signaling pathways and response mechanisms. Moreover, individual WRKY proteins can regulate multiple stress responses, and they may even play a role in both biotic and abiotic stresses.

WRKY transcription factors are involved in the response to abiotic stresses such as drought, high salt and temperature (Figure 1) (Wu et al., 2020). For example, transcriptome analysis showed that 41 *OsWRKY* genes in rice, 20 *AtWRKY* genes in Arabidopsis, and 74 *BnWRKY* genes in oilseed rape were involved in the response to abiotic stress (Ramamoorthy et al., 2008; Chen et al., 2012).

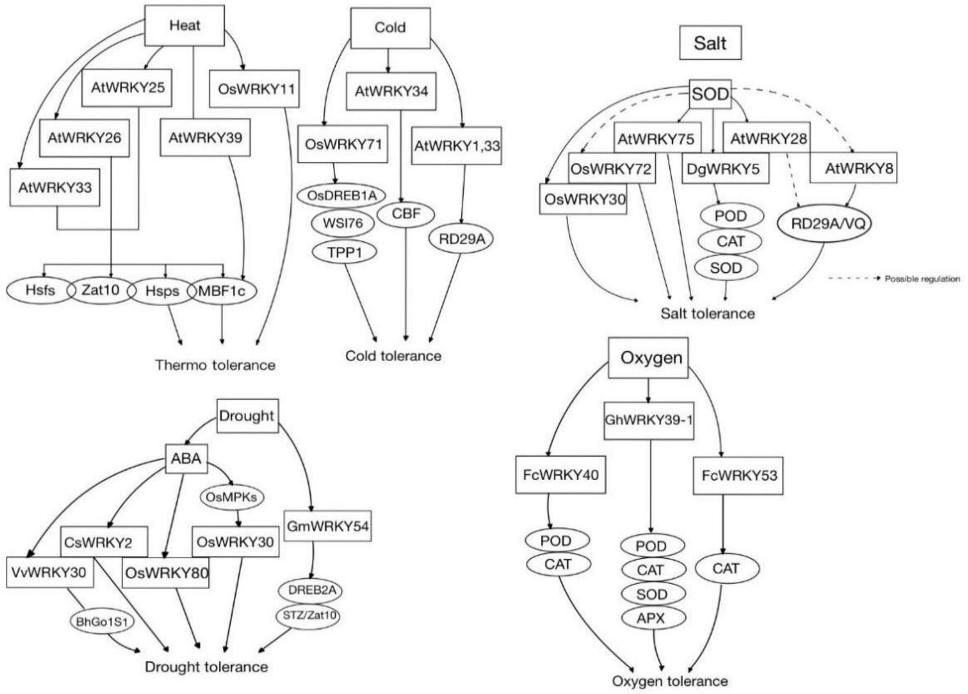

Figure 1 The function of WRKY in plant abiotic stress signaling network (Adopted from Wu et al., 2020)

2.1 Drought stress

Drought stress has been found to be the most detrimental abiotic stress on plant growth and development, according to studies. Drought causes stomatal closure and lowers plant water content, reducing transpiration and affecting photosynthesis and solute accumulation. The WRKY family of transcription factors is essential for plant drought tolerance.

The expression of some WRKY family transcription factors in the tomato genome can be induced by drought stress, including *SlWRKY1*, *SlWRKY25*, *SlWRKY31*, *SlWRKY32*, and *SlWRKY74.SlWRKY81* reduced proline synthesis and lowered drought tolerance in tomatoes, and the expression of *SlWRKY81* was up-regulated under drought conditions. The silencing of *SlWRKY81* accelerated the closure of tomato stomata under drought stress and significantly reduced drought-induced damage (Dong et al., 2023). It has been observed in a study that the overexpression of *CmWRKY10* in chrysanthemum leads to a significant increase in the expression of drought-related genes (Jaffar et al., 2016). Additionally, *CmWRKY1* has been reported to play a role in drought tolerance in chrysanthemums by down-regulating *PP2C*, *ABI1*, and *ABI2*, and up-regulating genes in the ABA signaling pathway such as *PYL2*, *SnRK2.2*, *ABF4*, *MYB2*, *RAB18*, and *DREB1A* (Fan et al., 2016).

Plants can regulate the expression of drought-related genes by controlling the accumulation of ROS (reactive oxygen species). In cotton, the *GhWRKY25* gene reduces drought tolerance by increasing MDA and ROS levels while decreasing the activities of SOD, POD, and CAT enzymes (Liu et al., 2016). On the other hand, overexpression of the *MbWRKY5* gene from Zingiber officinale in tobacco plants increases their chlorophyll, proline, glutathione, and ascorbic acid contents, as well as the activities of POD, SOD, and CAT enzymes, resulting in improved drought tolerance (Han et al., 2019). After being subjected to drought stress, WRKY-like transcription factors may have a negative impact on the expression of related genes. Some transgenic plants exhibited less resistance to drought stress, with lower leaf water content and higher levels of transpiration water loss, resulting in lower survival rates than wild-type plants. For instance, transgenic plants that had overexpressed *GhWRKY25* showed a decreased resistance to grey mould (Liu, 2015).

In addition, a single WRKY transcription factor can correspond to multiple physiological processes. For instance, in land cotton, the expression of the *WRKY4* gene is induced under both salt and drought stress, while *WRKY5* is induced only under drought stress.

2.2 High salt stress

In our country, plants not only suffer from drought stress, but also from high salt stress. This salt stress negatively affects the nutritional and reproductive growth of plants, causing primary and secondary salt damage. It destroys their normal morphological structure, and can even result in serious consequences such as plant death. Salt stress has become a major obstacle to the construction of a healthy ecological environment, as well as the sustainable development of agriculture in China, alongside drought stress.

First, WRKY transcription factors may be directly involved in regulating salt stress response to alleviate damage caused by high salt. For example, overexpression of the *SmWRKY28* gene in Arabidopsis thaliana enhances resistance to saline salts such as NaCl and $NaHCO_3$ and reduces oxidative toxicity (Wang, 2016); overexpression of *GsWRKY15* gene can significantly enhance alfalfa alkali tolerance (Zhu et al., 2017); Overexpression of *GmWRKY34* in *Arabidopsis thaliana* (Zhou et al., 2015), as well as overexpression of *GhWRKY41* (Chu et al., 2016) and *GhWRKY25* (Liu et al., 2016) in tobacco, can improve salt tolerance.

Plants have the ability to respond to salt stress by producing signaling molecules like ABA and H_2O_2. For instance, when *ZmWRKY17* is overexpressed, it can reduce the sensitivity of transgenic plants to ABA while increasing their sensitivity to salt stress. Additionally, with the addition of an ABA synthesis inhibitor, the seeds of transgenic lines can recover the phenotype of strongly inhibited germination under high salt stress (Cai, 2016). *OsWRKY50* in rice contains a *WRKY* structural domain and acts as a transcriptional repressor in the nucleus. *OsWRKY50* participates in the salt stress response of rice by regulating stress-responsive genes and decreasing the ABA sensitivity of the plant, and it plays a positive role in the regulation of salt stress in rice (Fan et al., 2023).

WRKY transcription factors are known to play a role in various abiotic stress responses. For instance, *TaWRKY44* expression in tobacco has been shown to enhance resistance to drought, salt stress, and osmotic stress (Han et al., 2015). In the case of ginseng, *PgWRKYs* transcript levels respond significantly to salt stress treatment (Xiu et al., 2016). Furthermore, the promoter sequence of *GhWRKY25* contains cis-acting elements that are associated with low temperature, drought, endosperm, and gibberellin elements, and are induced by high salinity and low temperature (4 °C), while being inhibited by polyethylene glycol (PEG) and mechanical damage. It is worth noting that the hormonal signaling molecules GA3, 6-BA, ABA and SA strongly induce gene expression in *GhWRKY25* (Liu, 2015).

The interaction of WRKY transcription factors with other proteins is very important in regulating salt tolerance responses in plants. For instance, in Arabidopsis, the transcription factor *WRKY8* interacts with VQ9, a member of the VQ protein family, to regulate salt tolerance responses in plants (Han et al., 2015). WRKY transcription factors can be induced by multiple stressors, including salt stress. For example, the overexpression of cotton *GHWRKY39-1* in tobacco increased the tolerance of the transgenic plants to salt stress (Shi et al., 2014). The overexpression of the tomato *SlWRKY39* gene in tomato plants also increased their proline content significantly, thereby improving their resistance to salt damage and drought caused by multiple stress factors such as PstDC3000, salt damage, and drought (Sun et al., 2015).

WRKY transcription factors are also negatively regulated by salt stress. For example, overexpression of *OsWRKY45-1* reduced rice tolerance to high salt (Tao et al., 2011); in transgenic *Arabidopsis thaliana* and chrysanthemum, chrysanthemum *GmWRKY17* negatively regulated its salt tolerance (Li et al., 2015).

2.3 Temperature stress

Temperature is a crucial factor that affects plant growth and development. High and low temperatures can cause stress on plants, which is referred to as abiotic stress. When plants are subjected to high or low temperatures, specific transcription factors known as WRKY transcription factors regulate the expression of related genes to reduce the damage caused by the temperature. For instance, the expression of transcription factors *WRKY5* and *WRKY24* in the highly cold-tolerant variety 'Dongnong Winter Wheat 1', varied significantly between different low-temperature treatments, indicating that this transcription factor plays a vital role in regulating the cold tolerance of plants. Furthermore, the chili *CaWRKY13* gene plays a crucial role in coping with abiotic stresses, including low and high temperatures (Wei et al., 2017).

The WRKY family of genes plays a crucial role in the response of plants to temperature-related stress by regulating the ABA signaling pathway. For instance, in the tea tree, 50 genes belonging to the WRKY family are identified, most of which are induced by cold stress. Among these genes, *CsWRKY2* is responsible for enhancing plant cold resistance by regulating the ABA signaling pathway (Wu et al., 2016). Overexpression of *VpWRKY1* and *VpWRKY2* in *Arabidopsis thaliana* has been found to increase the plant's response to cold stress, salt stress, and frost, thus aiding in better cold resistance in transgenic plants. In addition to this, *VpWRKY*2 also enhances plant resistance to downy mildew (Li et al., 2010a). Similarly, in oilseed rape, the *BcWRKY46* gene responds to strong induction of NaCl and drought and enhances cold resistance by regulating the ABA signaling pathway (Wang et al., 2012). The phytohormone JA, which is involved in the plant's response to various stressors, also reduces the damage caused by low temperatures in fruit. The *MaWRKY26* gene found in bananas is activated by low-temperature stress and MeJA. This activation helps to improve the cold resistance of banana fruits. Additionally, when combined with its promoter, *MaWRKY26* can also be reverse-activated to promote the synthesis of JA. This can reduce the damage caused by low temperatures on banana fruits. The transcription factors of the WRKY family, *HbWRKY2*, *HbWRKY3*, *HbWRKY4*, and *HbWRKY9*, respond to abiotic stresses such as PEG, high salinity, and low temperature. This response helps in improving the plant's resistance to these conditions (Xie, 2013; Zhao et al., 2015). Moreover, chili *CaWRKY40* is involved in plant response to high-temperature stress (Dang et al., 2013). In Arabidopsis, high temperature inhibited the expression of the *AtWRKY33* gene with a repressive effect, but induced the expression of the *AtWRKY25* and *AtWRKY26* genes. Among them, constitutive expression of *AtWRKY25* and *AtWRKY26* enhanced plant expression by activating *Hsfs* (Heat shock factors), *Hsps* (Heat shock proteins), *Zat10* (Transcription factor), and *MBF1c* (Multiprotein bridging factor 1) enhance plant resistance to heat stress (Ohama et al., 2017); heat treatment induces the expression of *AtWRKY39*, which positively regulates the signalling pathways involved in SA (salicylic acid) and JA (jasmonic acid) through the activation of MBF1c, thereby increasing plant heat tolerance (Li et al., 2010b; Ohama et al., 2017).

2.4 Inorganic element stress

During low phosphorus stress, *WRKY28* directly regulates phosphorus uptake and translocation from roots to crowns (Zhang, 2015). Similarly, *WRKY42* regulates the expression of PHO1 and PHT1;1, which are involved in the plant's response to low phosphorus stress (Su et al., 2015). Additionally, *AtWRKY6* (Xu et al., 2012) and *AtWRKY33* (Ding et al., 2013) are associated with low boron stress and aluminum ion stress in Arabidopsis, respectively.

It has been found that WRKY transcription factors play a negative role in regulating the expression of transcription factors related to elemental stress. This means that when plants are exposed to cadmium toxicity, their respiratory system is adversely affected. *AtWRKY18*, *AtWRKY40*, and *AtWRKY60* are known to negatively regulate the plant response to cadmium toxicity (Liu, 2015). Similarly, *WRKY6* and *WRKY42* genes are capable of directly binding to and negatively regulating the expression of the PH01 promoter, which makes the plant more sensitive to low phosphorus levels (Zhang, 2015).

2.5 Oxidative stress

Plants are exposed to various environmental stressors that cause the production and accumulation of reactive oxygen species (ROS) in their mitochondria. ROS is a highly oxidative molecule that can function as a signaling molecule and either positively or negatively regulate the plant's response to oxidative stress. In a study conducted on transgenic tobacco, it was found that the overexpression of *FcWRKY40* increased the plant's resistance to oxidative stress.

2.6 Other abiotic stresses

Apart from the five abiotic stresses mentioned earlier, there are several other abiotic stresses that plants have to endure such as light exposure, UV-B radiation, and sugar deprivation. For instance, WRKY proteins are responsible for regulating the reaction of most bamboo species to intense light (Zhao et al., 2016). Moreover, *GmWRKY30* can respond to various inducers in *Gentiana macrophylla*, including arachidonic acid, salicylic acid, and silver ions, in order to cope with abiotic stress (He et al., 2018).

3 WRKY Transcription Factors and Biotic Stresses

Plants face two main biological stresses - pathogenic bacteria infestation and feeding by phytophagous pests. When plants are exposed to these stresses, their metabolism and signal transduction processes change. Various signaling molecules, such as SA, JA, ET (ethylene), ABA, etc., get altered. This also affects the transcription levels of a large number of genes and proteins in the plant. All these lead to the plant's defense response to biotic stress.

3.1 WRKY transcription factors and pathogenic bacteria

Several studies conducted on Arabidopsis and other crops have identified multiple WRKY genes that play a vital role in regulating plant resistance to pathogenic bacteria. These genes include *WRKY3*, *WRKY33*, *WRKY40*, *WRKY46*, *WRKY18*, *WRKY53*, *WRKY70*, and *WRKY75*. Therefore, these genes can be seen as a valuable source for genetically enhancing crop resistance against bacterial infections.

Several studies have shown that overexpression of certain genes in Arabidopsis can enhance its resistance to various pathogens. For instance, Arabidopsis lines overexpressing *AtWRKY28* and *AtWRKY75* have been found to show enhanced resistance to Dictyostelium nucleatum (Chen et al., 2013). Similarly, overexpression of *AtWRKY33* in *Arabidopsis thaliana* has been found to confer resistance against the necrotrophic fungus Staphylococcus griseus (Sham et al., 2017). Late blight is caused by Phytophthora infestans, and transcription factors such as *StWRKY5* and *StWRKY59* have important regulatory roles in potato resistance to late blight. *StWRKY1* may mediate defense against infection of potato by Botrytis cinerea (Tian et al., 2023).

The *PsnWRKY70* gene in poplar may interact with specific members of the MAPK cascade to enhance resistance to leaf blight in poplar (Populussimonii × Populusnigra) (Zhao et al., 2017). It was shown that *VlWRKY3* could enhance resistance to leaf blight pathogen live nutrients by increasing the expression of *PR1* and *NPR1* genes associated with disease resistance while down-regulating the expression of PDF1.2 and LOX3 (Guo et al., 2018). Sequential expression of *CaWRKY40* in chickpea increased plant resistance to *Fusarium oxysporum* f. sp. ciceri Race1 (Foc1) (Chakraborty et al., 2019).

Upon being infected with pathogenic bacteria, plants and organisms respond by using signaling molecules such as SA, JA, ET, and ABA as well as modifying the signal transduction process. *TaWRKY70* may play a role in the resistance of high-temperature wheat nursery plants (HTSP) to striped stalk rust (Puccinia striiformis f. sp. tritici, Pst) infestation-induced stripe rust (Wang et al., 2017a). *TaWRKY70* showed a significant increase during the initial symptomatic stage of Pst infection and was induced by high temperature, ET, SA, and low-temperature stress (4 °C) treatments. However, its expression was down-regulated in plants treated with methyl jasmonate (MeJA) and heat stress (40 °C) (Wang et al., 2017a).

OsWRKY13 is involved in resistance to infection by rice blast fungus (Magnaporthe grisea) by activating the SA signaling pathway and repressing the JA signaling pathway, directly or indirectly regulating the expression of genes upstream and downstream of SA and JA (Schluttenhofer and Yuan, 2014). All these WRKY genes are involved in controlling the control of defense responses in plants through JA or SA-mediated signaling pathways.

3.2 WRKY transcription factors and phytophagous insects

There are few reports available on the association of WRKY transcription factors with phytophagous insects in plants.

Certain WRKY transcription factors have been shown to influence the feeding behavior of phytophagous insects (Ganbaatar et al., 2016). For instance, when H_2O_2 and ET levels were increased in *OsWRKY45* antisense repressor lines, the feeding and egg-laying preferences of *Nilaparvata lugens* (Stal) were diminished, leading to an anthelmintic effect. This indicates that WRKY transcription factors play a role in the plant's defense response to feeding by phytophagous insects (Huangfu, 2015). Additionally, *GhWRKY18* and *GhWRKY70* not only reduce cotton resistance to phytophagous insects, but also affect the fundamental growth and development of cotton (Chang, 2018).

Finally, some of the WRKY transcription factors related to phytophagous insects were summarized in this study (Table 1) (Wu et al., 2020).

Table 1 *WRKYs* involved in herbivoreinduced defense responses (Adopted from Wu et al., 2020)

Gene	Species	Research methods	Stress type
AtWRKY8	Arabidopsis	Mutation	Improve resistance to aphids
AtWRKY40	Arabidopsis	Expression analysis	Improve resistance to *Brevicoryne brassicae*
OsWRKY45	Rice	Expression analysis	Improve resistance to *Nilaparvata lugens*
OsWRKY53, *OsWRKY70*	Rice	Expression analysis	Induced by SSB larva

4 Conclusions

WRKY is a class of plant-specific transcription factors that play a crucial role in the life activities of plants. With the advancements in genomics, bioinformatics, and genetic engineering, research on WRKY has become increasingly extensive and thorough. It's now known that WRKY transcription factors not only impact plant growth and development but also have a sophisticated and effective regulatory mechanism for external stresses. The WRKY gene can regulate a variety of stresses through synergistic or antagonistic mechanisms. Moreover, the co-expression of WRKY produces a complex regulatory network to counteract stress via multiple expressions. The use of WRKY transcription factors to screen stress-resistant plant varieties and enhance plant stress tolerance holds enormous potential in terms of economic and scientific value.

Authors' Contributions

QJ, GD, XA, LZ, and CC conceived the idea; XA organized the data; QJ and GD conducted the formal analyses; XA obtained the funding. QJ, GD, and TL conducted the research; QJ, GD, and XL provided the methodology; XA and QJ, GD obtained the resources; XA and QJ and GD wrote the original manuscript, and XA wrote, reviewed, and edited the manuscript. All authors read and approved the final manuscript.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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