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Review

WRKY Transcription Factors (TFs) as Key Regulators of Plant Resilience to Environmental Stresses: Current Perspective

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Abstract: Plants encounter various stresses in their natural environments and can effectively respond to only one stress at a time. Through a complex gene network, transcription factors (TFs) such as WRKY TFs regulate a diverse array of stress responses. The clarification of the structural characteristics of WRKY proteins, along with recent advancements in molecular dynamics simulations, has shed light on the formation, stability, and interactions of DNA–protein complexes. This has provided a novel viewpoint regarding the control of WRKY TFs. The investigation of superfamilies, encompassing their historical development, diversity, and evolutionary patterns, has become feasible due to the transcriptome approach's capacity to provide extensive and comprehensive transcripts. The significance of WRKY TFs lies in their pivotal role within several signaling cascades and regulatory networks that influence plant defense responses. The present review summarizes the functional aspects of the high-volume sequence data of WRKY TFs from different species studied to date. Moreover, a comparative analysis approach was utilized to determine the functions of the identified WRKY TFs in response to both abiotic and biotic stresses, as revealed through numerous studies on different plant species. The results of this review will be pivotal in understanding evolutionary events and the significance of WRKY TFs in the context of climate change, incorporating new scientific evidence to propose an innovative viewpoint.

Keywords: WRKY TFs; growth and development in plants; regulatory mechanism; signaling pathways; biotic and abiotic stresses

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1. Introduction

TFs play a critical role in regulating gene expression throughout a range of cellular processes in plants and other living organisms. Furthermore, they hold a vital place in the field of molecular plant breeding, exerting significant influence on the agricultural domestication process [1]. To control the expression of the target gene, both temporally and spatially, TFs work along with other elements of the transcriptional machinery. Their mechanism of action involves binding to specific, short nucleotide motifs, or cis-regulatory elements, located in the regulatory regions of the genes they influence. Various cis-regulatory elements at target sites in the genome can be differentiated by the distinct DNA-binding domains of different TFs [2]. Numerous families of TFs have been identified and functionally characterized in relation to their roles in responding to biotic and abiotic stresses, including families such as WRKY, MYB, NAC, and bHLH. The WRKY family of TFs is considered to be one of the most important subgroups among plant transcriptional regulators. These plant-specific TFs provide a considerable contribution to the signaling network that governs a number of biological functions. The WRKY family's SWEET POTATO FACTOR1 (SPF1) gene was initially discovered in the *Impoea batatas* plant in 1994. Later research revealed that the ABF1 and ABF2 control seed germination in wild *Avena sativa*. Prior study demonstrated the cloning of WRKY1, WRKY2, and WRKY3 proteins from *Petroselinum crispum*, providing the first indication that WRKY proteins may play a role in controlling plant responses to pathogens [3,4].

WRKY transcription factors constitute a plant gene family that is essential for plant growth, development, and responses to abiotic stimuli such as salinity, drought, temperature variations, and environmental variables. Their abundance varies across species, and their importance in plant stress responses has been thoroughly investigated [5]. Numerous investigations have been conducted on WRKY TFs. For example, a recently investigated A WRKY TF from pearl millet, *PgWRKY44*, classified in Group IId, was categorized for its function in abiotic stress tolerance in transgenic *Arabidopsis* plants through ectopic expression. This expression positively influences ABA-mediated signaling pathways. Additionally, transgenic plants exhibited low levels of ROS and an upregulation of stress-associated genes, confirming their enhanced defense mechanisms in response to abiotic stress treatments [6]. The *mWRKY40* (*Solanum melongena* L.) belongs to WRKY TFs' group II subfamily and exhibits strong evolutionary connections to the *ScWRKY40* derived from *Solanum chilense*. Furthermore, the expression of *SmWRKY40* is crucial in modulating responses to ABA and salinity stress in *Arabidopsis* [7]. TF *TaWRKY31*, a member of the WRKY II family that is derived from wheat, increases *Arabidopsis* tolerance to drought by aiding in the removal of ROS, decreasing stomatal aperture, and increasing the expression of genes that respond to stress [8]. The WRKY gene family has been studied in Chinese rose (*Rosa chinensis*), revealing that *RcWRKY* gene expression is tissue-specific, with elevated levels noted under drought, heat, and salt stress [9]. In the genome of *Passiflora edulis*, 55 WRKY genes, referred to as *PeWRKYs*, were identified and classified into seven subgroups (I, IIa, IIb, IIc, IId, IIe, III), based on their homologs with *Arabidopsis thaliana*. Notably, under cold stress, the *PeWRKY48* gene from Group IIa was significantly upregulated, and its transgenic expression demonstrated enhanced resistance to drought, salt, and cold stress in both yeast and *Arabidopsis*. Additionally, metabolome and transcriptome co-expression analyses were conducted on two disease-resistant strains of *P. edulis*, revealing that *PeWRKY30* is a key transcription factor associated with flavonoid accumulation in yellow fruit *P. edulis*. This discovery could have important implications for responses to both biotic and abiotic stresses [10]. In *A. thaliana*, it has been confirmed that *MbWRKY53* genes can improve plant tolerance to cold and drought stress through various pathways, including the CBF pathway, SOS pathway, proline synthesis pathway, and ABA-dependent pathways [11]. However, this particular study has centered its attention on elucidating the biological roles of WRKY TFs in plants, examining their structural features and categorization, exploring the regulatory mechanism governing their activity, and discussing recent advancements in research progress.

2. The WRKY Domain's Structural Properties and Categorization

The complex and diverse organization of WRKY TFs significantly influences the regulation of plant gene expression. At the N-terminus lies the DNA-binding domain, which serves as the core of the WRKY structure. This domain is responsible for recognizing and binding to specific DNA sequences (Figure 1) [12]. The heptapeptides within this domain, e.g., WRKYGQK, WRKYGKK, WRKYGMK, WSKYGQK, WKRYGQK, WVKYGQK, and WKKYGQK, have undergone various modifications to enable a range of DNA-binding abilities [13]. Zinc finger motifs, which are necessary for DNA binding and protein–protein interactions, are present at the C-terminus of the WRKY structure. In addition to other zinc-finger structures like CX27HXH and CX7CX24HXC, these zinc-finger motifs also comprise the C2H2 and C2HC types. The diversity of zinc-finger configurations improves the ability of WRKY TFs to identify and engage with various DNA sequences. WRKY TFs are categorized into groups I, II, and III, based on the number of WRKY domains and their zinc-finger motifs. Group II and III types contain a single WRKY domain, while Group I examples contain two WRKY domains and one C2H2 zinc-finger motif, and Group II types have a C2H2 zinc-finger structure [14–16]. Leucine zipper structures, glutamate-rich domains, proline-rich domains, zinc-finger domains, and DNA-binding domains are the structural characteristics of WRKY proteins that enhance the functional variety and adaptability of WRKY transcription factors to diverse environmental stimuli. The intricate composition of the WRKY structure is suggestive of its essential role in modulating responses to biotic and abiotic stresses and its involvement in the developmental processes in plants. The wide range of structural components seen in WRKY TFs highlights their importance in the complex regulatory systems that control plant biology [17,18].

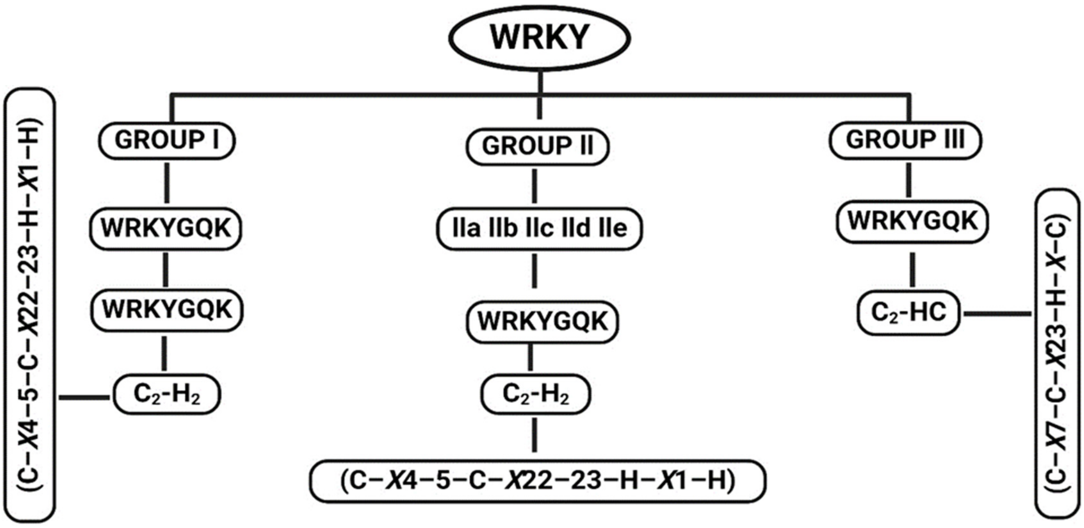

Figure 1. Structure and groups of WRKY TFs [12].

3. Major Research Tools for WRKY TFs Advancement

With the continuous advancements in molecular biology and bioinformatics, work regarding WRKY TFs is increasingly adopting innovative experimental techniques and utilizing new databases [19]. The WRKY TF gene was first cloned using Southwestern blotting technology, and this technique is still in use today. In the *Arabidopsis,* 143 WRKY genes were recognized in mustard; similarly, 83 WRKY genes were identified in rice using the BLAST similarity comparison tool, the method for finding genes in the plant genome database [20,21]. In comparison to BLAST or other computational bioinformatics techniques, due to the development of the database, retrieving *WRKY gene* sequences using HMM is now easier [22]. The Plant TF Database (TFDB) contains TF families from 165 species, including 14,549 WRKY genes [20].

A valuable tool for learning about the development and role of WRKY TFs is the phylogenetic tree reconstruction tool MEGA, the multiple sequence alignment tool widely used for WRKY gene, which assesses the degree of association and evolutionary distance between species sequences. The WRKY gene's nucleic acid sequence and gene structure schematic diagrams may both be submitted via the Gene Structure Display Server (GSDS), the NCBI nucleic acid sequence number, or the gene exon position information so as to obtain the corresponding gene structure diagram [23]. The Barley Gene Family Database (BGFD) is a free, user-friendly multi-omics platform that offers information on 5593 genes across 77 gene families. It includes intuitive visualizations, extensive multi-omics datasets, and useful toolkits with search and BLAST functionalities [24]. The study of quantitative expression of TFs is crucial for analyzing gene expression levels in plant samples and is also an important evaluator for obtaining research goal indicators.

4. The Transcriptome-Level (RNA-Seq) Investigations of WRKY TFs

Essential for a variety of plant developmental processes and defense mechanisms, examining the transcriptome-level expression patterns of WRKY TFs may offer significant insights into their regulatory mechanisms. Scientists can objectively and thoroughly measure the expression levels of WRKY TFs across the whole genome with the use of high-throughput sequencing techniques such as RNA-Seq. For instance RNA-Seq analysis of the resistant pepper line *CM334* and the susceptible pepper line *EC01* showed that the WRKY family was significantly enriched in both lines when challenged with *Phytophthora capsici* [25]. Using RNA-Seq, genes in tomato fruits that perceive chitin oligomers from *A. alternata* were identified, involving pattern recognition receptors with high similarity to those of *Arabidopsis* (*AtCERK1* and *LYK4*) and tomato (*SlLYK1*) plants [26]. Certain WRKY TFs have been identified by researchers through transcriptome analyses. Gene expression of these WRKY TFs varies in response to different stresses such as pathogen infection, drought, and salt. The data facilitates a comprehensive understanding of the regulatory networks associated with plant defense and stress responses, particularly focusing on WRKY TFs and their corresponding genes. For instance, phylogenetic and synteny analyses of the cucumber genome identified 61 WRKY genes [27]. Certain genes exhibited organ-specific expression and were categorized into three primary categories. Their significance for the growth and development of cucumber plants is supported by tissue expression profiles that revealed both constitutive and organ-specific expression. Various genes exhibited distinct expression patterns after stress treatment, and in response to salt and temperature stressors, and powdery mildew infections. It has been suggested that *CsWRKY* genes are implicated in enhancing resistance to biotic and abiotic stresses in cucumber [27]. A study has identified 78 WRKY TFs in *T. grandis*, categorized into three clades. *TgWRKY25* is a key gene involved in seed development, potentially affecting protein digestion and starch and sucrose metabolism. These findings highlight the critical role of WRKY genes in seed formation and suggest innovative breeding strategies. The study identified 18 candidates in plant hormone signal transduction in arginine and proline metabolism, form which 35 candidates responds to salt stress [28]. *Arachis* plants are valuable sources of oil, protein, and forage. The binding sites of WRKY TFs in homologous downstream genes show asymmetric evolution, indicating that WRKY TFs collaborate with other TFs to regulate the flowering process across the four *Arachis* species [29].

The upregulation of *RsWRKY40* in *Arabidopsis* resulted in enhanced seed germination, root length, and survival rate when the plants were exposed to salt, thereby indicating a possible function for this gene in enhancing the salt resistance of *Rhododendron* [30]. The upregulation of defense-related genes such as *AtWRKY33* in *Arabidopsis thaliana*, which plays a vital role in coordinating defense responses against pathogen attacks, has been investigated [31]. Furthermore, transcriptome analysis has uncovered the differential expression of WRKY TFs, such as *OsWRKY45* in rice, which are known for their role in regulating stress-responsive genes and enhancing drought tolerance [32]. Studies have shown that the WRKY33 gene regulates *B. cinerea* in non-heading Chinese cabbage plants, enhancing the plant's defense resistance. Overexpressing *BcWRKY33A* results in milder impairments compared to those in wild-type plants, while silencing it leads to more severe effects. Additionally, *BcMYB51*s exhibit similar patterns to *BcWRKY33A* during *B. cinerea* infection via directly activating expression of the biosynthetic genes [33].

As major transcriptional regulators in the central signaling pathways of plants that detect both internal and external stress biology, *WRKY genes* have evolved and expanded in correlation with global climate change [34]. The ancestors of current terrestrial plants are charophytes, or green algae that existed on land between 430 and 470 million years ago [35]. The WRKY domain, from *Incertae sedis fungi*, is the oldest in evolution, with structural divergence leading to the development of various groups and sub-groups [14]. According to research on its design in all taxa, the WRKY superfamily strongly responds to complexity and change over time. Primitive proteins with a single WRKY domain are found in early amoeba species and green algae, such as *Dictyostelium purpureum* and

Ostreococcus lucimarinus, which subsequently underwent gene duplication to produce two WRKY domain proteins [36].

Moreover, only the two WRKY domain proteins exhibited signs of positive selection as cellular complexity increased, as observed in *Chlamydomonas reinhardtii*. This suggests that one WRKY domain may have co-evolved with the green plant lineage prior to its transition to terrestrial habitats [37]. Throughout evolution, the WRKY gene family has expanded considerably, increasing from 2 genes in *Klebsormidium flaccidum* to 35 genes in *Selaginella moellendorffii* and 200 genes in *Glycine max*. This expansion provides substantial evidence of its importance in plant adaptation and diversification [38–40]. The term "transcriptome" (RNA-Seq) refers to all the transcripts present in a cell at any given time. This comprehensive approach to data analysis incorporates all areas of functional genomics and reveals the properties of a certain biological system operating in an organism [41]. For instance, it gives a thorough picture of the ways in which genes are expressed, managed, and channelized in diverse tissues under varied conditions. For the high-throughput identification of non-model plant genes associated with the synthesis of bioactive compounds, secondary metabolites, various stress tolerance, and genetic diversity, the transcriptomics-based perspective has emerged as the most illuminating method. This has helped to unravel the complete picture related to the regulation mechanism [42].

The evolutionary dynamics of WRKY transcription factors are critical for understanding their diversity and functional adaptability in response to biotic and abiotic stressors across plant species [14]. Positive selection has a crucial influence on the development of WRKY genes, as proven by research in Zea mays, *Arabidopsis thaliana*, *Glycine max*, and *Brassica oleracea* [43,44]. WRKY42, for example, has experienced positive selection, increasing its involvement in defending against infections and environmental stresses [4]. WRKY22 modulates responses to salt stress, suggesting its adaptive importance in saline settings [45]. WRKY33 improves resistance to Phytophthora sojae in soybeans, showing its crucial function in plant–pathogen interactions [46]. *Brassica oleracea* also identified WRKY11 as a critical element in plant response to abiotic stress, with indications of adaptive evolution connected to its expression patterns under drought circumstances [47].

Genetic engineering can be used to develop stress-tolerant plants by introducing genes involved in stress response and putative tolerance [48]. Advances in breeding methodologies and precise phenotyping have revealed candidate genes and metabolic pathways underlying drought tolerance in crops [49]. Transgenic plants have shown that certain WRKY TFs significantly contribute to abiotic stress tolerance [5]. Rice plants genetically modified to overexpress maize WRKY gene *ZmWRKY58* exhibit enhanced drought and salinity stress tolerance [50]. Arabidopsis WRKY46 regulates auxin levels, facilitating lateral root growth under osmotic and salt stress [51]. Overexpression of *GmWRKY12* enhances drought and salt stress tolerance [52]. *TaWRKY44* modulates responses to drought, salt, and osmotic stress by reducing ROS through antioxidant systems or the expression of stress-related genes [53]. The overexpression of *AcWRKY31* in pineapple and *Arabidopsis* diminishes tolerance to salt and drought stress, while augmenting resilience to pests and diseases [54].

WRKY TFs vary from other TFs by regulating the expression of co-expressed WRKY target genes, hence affecting physiological processes in response to diverse situations. They achieve this by interacting with cis-regulatory elements in the gene's 5′upstream region, thereby modulating gene expression. Both the promoter regions of the structural genes and the WRKY genes themselves contain multiple W-boxes. These TFs can interact with other WRKY proteins, initiating a cascade of events through cis/trans associations that facilitate self- and cross-regulation [55]. Furthermore, they may cooperate with other trans-elements to create dynamic protein complexes that facilitate transcription. In *Glycine max*, the interaction between the gene products *GmWRKY27* and *GmMYB174* may downregulate the expression of another transcription factor, *GmNAC29*, hence enhancing the host plant's resilience to salt and drought, similar to the way in which *CaWRKY6* activates *CaWRKY40* in *Capsicum frutescens*, which results in high-temperature resistivity. A few residues in the

"WRKYGQK" and zinc finger motif, specifically Tyr, Trp, and Lys, are essential for DNA binding, according to a mutational investigation on the WRKY signature domain [56,57]. The WRKY tetrapeptide physically interacts with the core "GAC" sequence of the W-box, whereas the nucleotides on each side are recognized by several WRKY TFs. This study reinforces previous findings that alterations in the core groove binding motif reduce DNA-binding activity, while changes in the heptapeptide WRKY sequence affect the protein's three-dimensional structure and its interaction network [58].

The most significant finding was that altering "GKK" to "GQK" improved the TF's capacity to bind to the W-box. *OsWRKY7*, which contains the WRKYGKK signature motif rather than the WRKYGQK, was the subject of the mutation-based investigation. These studies have shown the significance of sequence architecture across time for understanding the link between sequence modification and gene function, which results in adaptation to a changing or diverse environment. This relationship is not only important for defining phylogenies of organisms, but the plant's new environmental circumstances have caused the WRKY gene superfamily to expand and change throughout time. At the transcriptome (RNA-Seq) level, distinct WRKY TFs have been discovered in diverse plant species (Table 1).

Table 1. Examples of WRKY TFs identified at the genome level in various plant species.

Plant Species	WRKY Gene	Number	References
Camellia sinensis	*CsWRKYs*	78	[59]
Casuarina equisetifolia	*CeqWRKYs*	64	[60]
Miscanthus sinensis	*MsWRKYs*	179	[61]
Pisum sativum	*PsWRKYs*	89	[62]
Zanthoxylum bungeanum	*ZbWRKYs*	38	[63]
Suaeda australis	*SaWRKYs*	47	[64]
Glycyrrhiza uralensis Fish	*GuWRKYs*	52	[65]
Phoebe bournei	*PbWRKYs*	60	[66]
Platycodon grandiflorus	*PgWRKYs*	27	[67]
Citrus sinensis	*CsWRKYs*	52	[68]
Ginkgo biloba	*GbWRKYs*	37	[69]
Poncirus trifoliata	*PtrWRKYs*	51	[68]
Neolamarckia cadamba	*NcWRKYs*	85	[70]
Caragana korshinskii	*CkWRKYs*	86	[71]
Citrus reticulata	*CrWRKYs*	46	[72]
Camellia oleifera Abel	*CoWRKYs*	89	[73]
Crocus sativus	*CsWRKY*	40	[74]
Triticum aestivum	*TaWRKYs*	13	[75]
Glycyrrhiza uralensis	*GuWRKYs*	72	[76]
Bletilla striata	*BsWRKY*	29	[77]
Litsea cubeba	*LcWRKYs*	64	[78]
Litchi chinensis Sonn	*LcWRKYs*	50	[79]
Panax notoginseng	*PnWRKYs*	74	[80]
Oryza sativa and Arabidopsis	*OsWRKYs and AtWRKYs*	101 and 71	[81]
Panax notoginseng	*PnWRKYs*	27	[82]
Lonicera macranthoides	*LmWRKYs*	61	[83]

Table 1. *Cont.*

Plant Species	WRKY Gene	Number	References
Cymbidium sinense	*CsWRKYs*	64	[84]
Pinus massoniana Lamb	*PmWRKYs*	25	[85]
Camellia japonica	*CjWRKYs*	48	[86]
Rehmannia glutinosa	*RgWRKYs*	37	[87]
Malus sievesii	*MsWRKYs*	112	[88]
Helianthus annuus	*HaWRKYs*	90	[89]
Medicago sativa	*MsWRKYs*	107	[90]
Camellia japonica	*CjWRKYs*	48	[86]
Camelina sativa	*CsWRKYs*	242	[91]
Cucumis sativus	*CsWRKYs*	61	[27]
Corchorus capsularis	*CcWRKYs*	43	[92]
Sorghum bicolor	*SbWRKYs*	94	[93]
Pinus massoniana Lamb	*PmWRKYs*	31	[94]
Arachis hypogaea	*AhWRKYs*	174	[95]
Aquilaria sinensis	*AsWRKYs*	70	[96]
Pennisetum glaucum	*PgWRKYs*	97	[97]

5. WRKY TFs Regulatory Mechanism in Plants

TFs are critical elements of the transcriptional apparatus, regulating gene expression at designated times and locations. They bind to cis-regulatory elements in the genes they regulate and possess unique DNA-binding domains. WRKY TFs, a varied assemblage of DNA-binding proteins, are ubiquitous in all plant species and establish a particular regulatory network via their interaction with downstream target genes. To collectively respond to various environmental signals, proteins such as WRKY TFs and other regulatory proteins work together at the molecular level (Figure 2) [36,98]. The regulation of WRKY TFs involves both structural genes and other WRKY TFs at the transcript and protein levels. Their functional mechanism is based on their ability to bind to specific DNA regions known as W-boxes. WRKY TFs are composed of two primary components, i.e., the N-terminal domain responsible for DNA binding and the C-terminal region featuring zinc finger motifs, which derive from the heptapeptide WRKYGQK [99]. WRKY TFs can activate or repress target genes by binding to W-boxes located in their promoter regions. The specificity of this binding is influenced by the structure of the WRKY domain and the adjacent nucleotides. These TFs play a key function in regulating plant growth and development processes, such as gamete formation, seed germination, stem elongation, and leaf senescence. Their importance in modulating gene expression during plant stress responses underscores their role as essential molecular regulators.

WRKY TFs are critical to plant responses to environmental stressors, as they selectively inhibit non-essential gene pathways [100]. In *Arabidopsis*, WRKY33 adversely controls defense-related genes during pathogen invasion, prioritizing resource allocation to critical stress responses [101]. WRKY46 and WRKY70 inhibit genes associated with SA signaling, hence regulating the plant's immunological response [102]. WRKY11 play a role as a negative regulator in response to drought stress in rice via inhibiting genes associated with drought resistance [103]. WRKY15 adversely modulates genes associated with oxidative stress responses in soybeans, regulating reactive oxygen species under abiotic stress [17]. The association of WRKY factors with W-boxes may obstruct transcriptional machinery, thus averting the activation of superfluous growth and development genes under stress situations [104]. A multitude of WRKY proteins possess a C-terminal extension that engages with co-repressor proteins, increasing their capacity to assemble repression complexes that inhibit target gene expression. Structural changes, including changes to phosphorylation sites, may alter activity, enabling dynamic control in response to particular stressors [105].

Additionally gaining insight into the mechanism by which WRKY TFs operate is crucial in order to effectively utilize their capabilities in regards to crop improvement and genetic manipulation aimed at enhancing stress resilience. Through the manipulation of WRKY TFs, scientists have the potential to augment the plants' capacity to react to abiotic challenges and enhance their overall growth and productivity. WRKY TFs regulate stress-responsive genes and are involved in various plant growth and development processes [14,106]. They influence fertility, seed germination, stem elongation, and leaf senescence. For instance, *GmWRKY45* improves salt tolerance and fertility in transgenic *Arabidopsis* plants [107]. Additionally, *MsWRKY* genes in alfalfa are responsible for regulating seed vigor and aging, as highlighted in a study that conducted a genome-wide analysis [108]. *Paeonia lactiflora PlWRKY41a* improved stem strength by positively influencing the thickness of the secondary cell wall [109]. WRKY TFs were investigated in multiple plant species, and they exhibited variability in their abundance among different species. Researchers are currently investigating the prospective uses of WRKY TFs in the fields of crop breeding and genetic engineering, with the aim of cultivating stress-tolerant crops [110]. Several examples of WRKY TFs that have been identified are *AtWRKY29*, *AtWRKY38*, and *AtWRKY62*. These particular TFs have been found to confer resistance against pathogen attacks [111]. The *OsWRKY89* protein helps shield plants from UV radiation, while various WRKY proteins enhance tolerance to drought and salt stress [112]. For instance, *AcWRKY117* and *AcWRKY29* confer tolerance to waterlogging [113], whereas *GbWRKY1* assists plants in managing phosphate deficiency [17]. The *SlWRKY3* has been recognized as a key player in thermotolerance in tomatoes via binding to the promoters of the *Solanum lycopersicum Glutaredoxin S1* (*SlGRXS1*) gene cluster. This interaction promotes their expression and improves the scavenging of ROS [114].

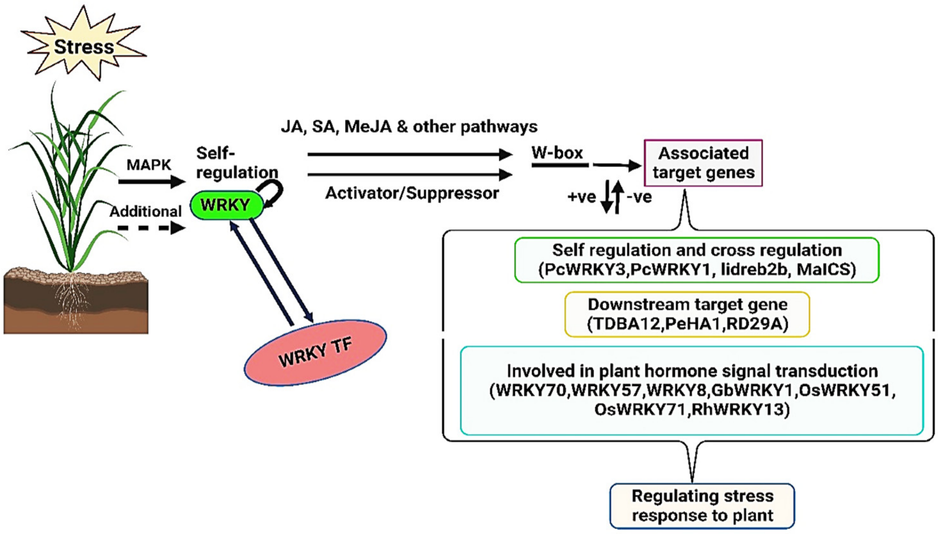

Figure 2. The regulatory mechanism of WRKY TFs in plants [115].

6. Self-Regulation Mechanism of WRKY TFs

WRKY TFs play a crucial role in physiological processes such as senescence, development, and plant defense responses. They regulate gene expression through complex interactions and self-regulatory feedback loops. LlWRKY22, identified in lilies, can regulate transcription by binding to specific sequences in its promoter region, activating it under elevated temperatures and improving thermotolerance. In both yeast and plant cells, *LlWRKY22* is transactivation active and is found in the nucleus. The overexpression of *LlWRKY22* stimulates the *LlDREB2B* gene, further enhancing thermotolerance [116]. It has been determined that the VQ motif-containing protein *AtVQ25* acts as a cooperator of *AtWRKY53*. Together, *AtVQ25* and *AtWRKY53* inhibit *AtWRKY53* from binding to the W-box elements on its own promoter, thereby counteracting its self-repression. Additionally, *AtVQ25* directly mitigates the self-repression of *AtWRKY53* during the onset of leaf senescence [117]. The study demonstrates that the autoregulation of WRKY TFs enables optimal expression in response to both internal and external signals. It also indicates that utilizing the wild tomato rootstock enhances cold resistance in seedlings. *SlWRKY50*, a TF involved in jasmonic acid production, improves tomato's resistance to chilling, which results in increased *Fv/Fm*, higher levels of antioxidative enzymes, elevated *SlAOS* expression, and greater JA accumulation. Additionally, diethyldithiocarbamate acid reduces cold tolerance, while *SlMYC2* regulates the expression *of SlWRKY50* [118]. In the case of *Arabidopsis thaliana*, for instance, the *AtWRKY33* enhances its transcription in response to stressors such as pathogen infection by binding to a W-box motif in its promoter region, thereby positively regulating its own expression [119]. WRKY TFs manage their activity and gene expression through the formation of homodimers and heterodimers. WRKY62 positively regulates genes related to hypoxia, helping to balance defense and hypoxia responses. By interacting with other WRKY TFs or co-regulatory proteins, WRKY TFs can alter their DNA binding affinity, resulting in the activation or repression of target genes [120]. Rice WRKY45 TFs generate a homodimer that regulates the expression of its target gene *OsWRKY13* by binding to its promoter during leaf senescence [120].

The self-regulation system plays a crucial role in the transcriptional reprogramming that occurs during plant stress reactions [98]. WRKY TFs are essential for plant development, growth, and stress responses, as they interact with various genes. Research has demonstrated that WRKY proteins provide protection against biotic stresses, including viral, fungal, and bacterial pathogens. *NbWRKY1* acts as a positive regulator in the defense against *TYLCV* infection, whereas *NbWhy1* negatively affects the plant's response to *TYLCCNV/TYLCCNB* infection [121]. *Citrus chlorotic dwarf-associated virus* (*CCDaV*), belonging to the *Citlodavirus* species, triggers a hypersensitive response resembling cell death in *Nicotiana benthamiana*, which is associated with the production of H_2O_2 and ion leakage. *NbWRKY1* positively regulates cell death induced via *CCDaV-RepA* in *N. benthamiana* [122]. Overexpressing *GmWRKY136*, 53, and 86 in soybeans enhances their resistance to soybean cyst nematodes [123]. WRKY TFs, which are activated by abiotic stimuli, play a key role in regulating plant tolerance to abiotic challenges. The overexpression of *PtWRKY2* in transgenic *Arabidopsis* enhances heat tolerance, resulting in higher seed germination and survival rates, reduced accumulation of reactive oxygen species, and increased catalase, superoxide dismutase, and peroxidase activities [124]. Likewise, in cotton (*Gossypium* spp.), *GhWRKY31* positively regulates salinity, as well as drought tolerance [125]. Numerous W-box motifs in the promoter region of *PcWRKY1* aid in the binding of WRKY TFs. The *PcWRKY1* has the capacity to connect to the W-box located in the promoter region of the *PcWRKY3*, in addition to the W-box present in its own promoter [126]. *PeWRKY1* regulates the expression of *P. euphratica* via binding to the W-boxes in the promoter regions of *PeHA1* and *PeMAX2*, thereby enhancing ion homeostasis through two different mechanisms. When *MaWRKY21* directly interacts with the *Malus domestica Isochorismate Synthase* (*MaICS*) promoter W-box, it negatively controls transcription and lowers the amount of enzyme activity in the *Musa acuminata* [20,127]. WRKY TFs, through their WRKY domains, interact with the W-boxes of downstream target genes, like the tobacco chitinase gene (*TDBA12*), in response to disease stress [128]. *AtWRKY8* boosts the ability of *Arabidopsis thaliana* to fight against *Phytophthora infestans* through engaging with genes downstream of the *MAPKKK-MEK2-WIPK* signaling cascade, resulting in H_2O_2 accumulation and subsequent plant cell death [129]. The *PeWRKY1* protein in *P. euphratica* enhances transcription by interacting with the W-box element of the *PeHA1* promoter, which encodes the plasma membrane (*H+-ATPase*), and it is also capable of binding to the *PcWRKY3* promoter [17,130].

WRKY TFs have the ability to not only govern their own expression, but also to engage in intercommunication with additional regulatory pathways, including those associated with plant hormone signaling. This enables the integration of various stress signals and the initiation of suitable gene expression responses. In general, the self-regulation of WRKY TFs constitutes a crucial process that facilitates the ability of the plants to effectively respond and adapt to challenging environmental conditions.

7. WRKY TFs Regulatory Function in the MAPK Signaling Pathway

All eukaryotes have a signaling cascade called the MAPK; it is comprised of the downstream signaling of the plant defense responses that depend on ABA. Additionally, it controls the responses to diverse abiotic and biotic stresses, as well as growth and development [131]. The MAP kinase signaling chain, upstream receptors, and downstream TFs are connected by many phosphorylation processes [132]. MAPK-dependent phosphorylation also activates Group I WRKYs with conserved patterns in the N-terminal region of the TFs, highlighting their significance in plant immunity [133]. In *Arabidopsis*, the *MAMP* or *PAMP* complex is produced by the interaction of the TF WRKY33 with the MAP kinase in the absence of MAP kinase 4 (*MPK4*) [134]. The infection by the pathogen activates and phosphorylates the former, while the latter relies on the *MPK4* substrate *MKS1*, leading to the disruption of the nuclear complex *MPK4-MKS1-WRKY33* and the subsequent release of *MKS1* and *AtWRKY33*, which activate the synthesis of enzymes encoded by *PAD3* that produce an antimicrobial complex [134,135]. *AtWRKY22* and *AtWRKY29* play a crucial role in MAPK-mediated resistance against bacterial and fungal infections. Transient expression of *AtWRKY29* homologs in *Arabidopsis* leaves boosts resistance to pathogens [136,137].

Additionally, *OsWRKY30* increases rice's tolerance to drought through a cascade of phosphorylated MAPKs [138]. Additionally, the MAPK–WRKY pathway activates *RBOHB*, an *NADPH oxidase* which results in ROS bursts that are driven by both the *AVR3a* effector and the *INF1* pattern [134]. HAMK, the first heat shock-activated MAPK found in plants, can be influenced by temperature fluctuations in rice, affecting the expression of *OsMRSMK2* [139,140]. The high-temperature shock causes tomato cells to activate MAPK, which is capable of phosphorylating *HsFA3*, a heat-shock TF. Stress caused by high temperatures in potatoes results in an increased *StMPK1* transcription [141]. In *Arabidopsis*, *flagellin* (*flg22*) can trigger the *MEKK1-MKK4/5-MAPK3/6* cascade by activating the expression of the downstream WRKY22 and WRKY29 genes [142]. *Bimolecular fluorescence interaction* (*BiFC*) may allow *CaMAPK1* and *CaWKRY40* to interact and contribute to the reaction of pepper plants to high-temperature stress [140].

WRKY TFs have been identified as potential targets of MAPKs, crucial for MAPK signaling cascades that regulate plant immunity and stress adaptation in pathogen-associated molecular PTI and ETI [143]. The phosphorylation of *WRKY33*, a protein kinase, is catalyzed by *CPK5/CPK6* and *MPK3/MPK6* in *Arabidopsis*. This phosphorylation event serves as an initiation signal for camalexin manufacturing, which in turn provides protection against infection caused by *B. cinerea* [4,144]. The interaction between *MPK3/MPK6* and *WRKY18* has been observed to have an impact on the expression of *protein phosphatase 2C5* (*PP2C5*), which subsequently leads to the formation of a module that effectively mitigates the infection caused by *Pseudomonas syringae* in *Arabidopsis* [143]. The research conducted revealed that the phosphorylation and ubiquitination processes of *OsWRKY31* resulted in the activation of a defense response in rice, mediated by *OsMKK10-2*. This response was specifically induced by the presence of *Magnaporthe oryzae* [145]. The regulatory module consisting of *GhMAP3K15*, *GhMKK4*, *GhMPK6*, *GhWRKY59*, and *GhDREB2* is implicated in a comprehensive MAPK cascade, which leads to the phosphorylation and activation of *GhWRKY59*, hence playing a role in the response of *Gossypium hirsutums* to drought conditions [146]. In *Arabidopsis* plants, elevated glutathione levels enhance the binding of WRKY40 to the *MPK3* promoter, which activates *MPK3* and initiates stress defense mechanisms [147]. This process results in the greater susceptibility of *Malus domestica* plants to infection by *Colletotrichum fructicola*. Additionally, the gene module comprising the apple genes *MKK4*, *MPK3*, and WRKY17 has been associated with this susceptibility [148].

Recent research has emphasized the important role of WRKY components in different plant stress responses and adaptive processes [5]. WRKY33 in *Arabidopsis thaliana* interacts with the *MPK3/MPK6* MAPK cascade, hence augmenting the expression of defense-related genes after pathogen infection [149]. For instance, exposure of strawberries to SA induces reactive oxygen species and calcium ion signaling, which elevates WRKY33 expression and promotes the synthesis of *PR10* and *camalexin* [150]. *BnMED16* boosts resistance to *S. sclerotiorum* in *B. napus* by enhancing *BnMED25*-mediated defense mechanisms and activating defensive signals through *BnWRKY33* [151]. Trypsin diminishes *CsWRKY33* expression, hence enhancing the production of antioxidant and antibacterial chemicals, which elevates fruit disease resistance and postpones senescence and decay [152]. WRKY40 modulates drought stress responses in soybeans by influencing stress-responsive genes via a MAPK-dependent mechanism, highlighting its significance in abiotic stress adaptation [153]. *DcWRKY33* promotes petal senescence via inducing genes associated with ethylene and ABA production, as well as the buildup of ROS in carnations [154]. WRKY46 is involved in JA signaling pathways, exerting a negative regulation on JA-responsive genes during herbivory, therefore balancing defense and growth [4]. Inhibition of *RcWRKY40* resulted in a reduction in *R12-26* leaf cell wall constituents and compromised the antioxidant system, eliciting an allergic reaction as a defensive strategy against black spot disease. WRKY15 interacts with ethylene signaling pathways, augmenting plant's response to stress situations [155]. The inhibition of *RcWRKY40* resulted in a reduction in *R12-26* leaf cell wall constituents and compromised the antioxidant system, eliciting an allergic reaction as a defensive strategy against black spot disease [156]. WRKY11 in *Brassica napus* is a crucial controller of ABA signaling, connecting it to drought tolerance processes by enhancing the expression of ABA-responsive genes [157]. Studies revealed that *SAPK10* interacts with WRKY87, therefore augmenting drought and salt tolerance in rice via the autophosphorylation of WRKY87 at the 177th serine, as shown by a yeast two-hybrid experiment [158]. These examples underscore the many functions of the WRKY factors in coordinating the MAPK and hormone signaling pathways.

The MAPK cascade serves as the main switch for regulating high-temperature stress in plants by activating a network of defense mechanisms, ultimately leading to the expression of WRKY transcription factors and stress-related genes. Thus, WRKY TFs may set up a regulatory structure, similar to a network, in response to different stresses.

8. Regulatory Function of WRKY TFs in Plant Hormone Signaling

Plant hormones, including WRKY TFs, are essential for regulating plant growth and development. Studies have shown that WRKY TFs modulate signal transduction pathways associated with hormones like jasmonic acid, ethylene, salicylic acid, and abscisic acid, particularly in response to elevated temperature stress. For instance, *AtWRKY39* is activated by treatment with SA or methyl jasmonate, engaging in cooperative interactions with other WRKY TFs [159]. In order to assist *P. notoginseng* in the fight against *F. solani*, *PnWRKY15* stimulates the JA/SA signaling pathways and promotes the expression of the resistance-related gene *PnOLP1* [160]. In *Nelumbo nucifera* roots, WRKY expression was influenced by jasmonic acid (JA) and salicylic acid (SA) signaling, particularly for *NnWRKY40a* and *NnWRKY40b*, which exhibited significant upregulation after JA treatment [161]. After being subjected to drought stress, *Elaeis guineensis* WRKY gene expression increases in response to various amounts of ABA, MeJA, SA, and H_2O_2 [162]. Notably, after a pathogen infection, the essential hormones JA and SA are crucial for signal transduction. The SA signaling pathway typically regulates the defensive responses to biotrophic infections, while the JA signaling pathway generally oversees the defense mechanisms against herbivores and necrotic diseases [163,164]. Recent years have witnessed significant progress in the study of WRKY transcription factors and their interactions with hormones, with the three WRKY genes *OsWRKY24/53/70*, known to negatively affect the transcription of ABA and GA signaling, sharing characteristics with common WRKY TFs [165,166].

Additionally, the gene's expression is supported by the synergistic interactions between several WRKY TFs and the significant interaction with pathways for plant hormones and stress tolerance. For instance, GA signaling is decreased in the aleurone cells of rice seeds by the synergistic interaction between the genes *OsWRKY51* and *OsWRKY71* [167]. Additionally, studies have revealed that the *wrky75* mutant slows down, and subsequently speeds up flowering in *Arabidopsis* when overexpressed. This demonstrates that WRKY TF is a helpful blooming regulator. Transgenic plants exhibited shorter blooming durations and more branches on their inflorescences as a result of *SlWRKY23* hypersensitivity to auxin, ET, and JA-mediated root development [168]. Similar research indicates that *AtWRKY18*, 40, and 60 are components of signaling pathways that are mediated by the plant hormones SA, JA, and ABA. The interaction between receptor stimuli and a subsequent signaling cascade, which results in the creation of TFs and the amplification of target genes, as well as the associated response, is one of the techniques of plant signaling [169,170]. Recent research has demonstrated that the ABA signaling repressor *OsWRKY29* decreases the expression of *OsABF1* and *OsVP1*, leading to reduced seed dormancy in rice [171].

WRKY transcription factors play a vital role in regulating genes involved in the production of SA and it signaling pathway. For example, they promote the activation of isochorismate synthase 1 (ICS1) expression in *Arabidopsis* by directly binding to the promoter region of the *ICS1* gene [172]. It has been determined that a novel WRKY TF, *BnaWSR1ca,* exhibits direct binding affinity towards the promoter regions of *ICS1*. This interaction subsequently leads to the promotion of SA production, hence exerting regulatory control over processes such as cell death and leaf senescence [173]. WRKY transcription factors activate *NPR1/3*, *TGA*, and *PR1*, which are essential for inducing SA-mediated defense responses in both biotic and abiotic stimuli [174]. The *NPR1-Cullin 3 E3 ligase* complex is responsible for facilitating plant SA-mediated cell survival by ubiquitinating substrates localized in *SINC*, such as *WRKY54* and *WRKY70*. This complex is produced when *NPR1* undergoes a transition into condensates [175]. The activation of the *PR1/2/10* genes enhances resistance to *Puccinia horiana* infection, requiring the interaction between *Chrysanthemum morifolium CmWRKY15-1* and *CmNPR1* [176]. *GhWRKY70* in cotton plants regulates defense mechanisms against *Verticillium dahliae* by upregulating the signaling pathways associated with SA [177]. SA also facilitates WRKY22's participation in freezing stress by stimulating the expression of genes like *TGA1*, *PR1*, and *NPR1* [178,179].

The *jasmonate ZIM domain* (JAZ) and WRKYs are crucial in regulating secondary metabolite production, which occurs when JA is conjugated with isoleucine under the supervision of the JAR enzyme [180]. The interaction between the *GmWRKY40* and *JAZ2* proteins activates the defense response against *Phytophthora sojae*, regulated by H_2O_2 buildup and the JA signaling cascade [181]. *PnWRKY9*, associated with resistance to *Fusarium solani* and responsive to JA, activates defense priming in *Panax notoginseng*. When *Arabidopsis* plants sustain damage, the *JAV1-JAZ8-WRKY51* complex is phosphorylated, resulting in the production of *JA. Calmodulins* (*CaMs*) are proteins that sense calcium ions and control this process [80]. *Calmodulins* (*CaMs*) are responsible for the detection of calcium ion Ca^{2+} and play a crucial role in regulating the phosphorylation of the *JAV1-JAZ8-WRKY51* complex, which aids in the production of JA in *Arabidopsis* plants in response to injury [182]. *Musa acuminata* demonstrates defensive priming in response to cold stress, initiating JA signaling via the interaction of *MaWRKY26* and *MaVQ5*, and trans-activating the genes associated with the JA system [183]. The activation of *SIMYC2* by JA initiates the expression of *SIWRKY37*, which then induces the activation of the *SIWRKY53* and *SISGR1* genes. This regulatory process ultimately governs the senescence of leaves triggered by darkness [184]. In rice and *Solanum lycopersicum*, the *OsWRKY72* and *SlWRKY45* genes have a role in regulating the synthesis of JA and conferring resistance to *Xanthomonas oryzae* infection and *Meloidogyne incognita* infestation, respectively [185,186].

Plant cells employ Ca^{2+} channels and pattern recognition receptors (*PRRs*) to initiate a Ca^{2+} spike, detect pathogen-associated molecular patterns (*PAMPs*), and elicit pattern-triggered immunity (PTI) within the cytoplasm [187]. The upregulation of *PsnWRKY70* in Populus species confers increased resistance against *Alternaria alternata* through the activation of genes involved in the MAPK and *CDPK* signaling cascades [188]. The module consisting of *CaCDPK29* and *CaWRKY27b* in *Capsicum annuum* has been found to augment the defense responses mediated by *CaWRKY40* against infection by *Ralstonia solanacearum* and the stress of high temperatures and humidity [189]. *GmWRKY54* enhances soybean plant drought tolerance by binding to the ABA receptor and kinase gene promoters, activating specific genes involved in the ABA and Ca^{2+} signaling pathways [190].

Furthermore, during stress, alterations in the ROS concentrations within different cellular compartments, as well as the coordination of other signaling mechanisms, including Ca^{2+} channels, MAPK cascades, and hormone pathways, trigger the activation of related stress-response networks downstream [191]. WRKY TFs are essential for activating genes related to the respiratory burst oxidase homologs (*RBOHs*) and antioxidant pathways. One notable regulatory module, known as *CsWRKY25-RbohB-RbohD-PR10*, has been shown to contribute to the enhancement of citrus fruit resistance against *Penicillium digitatum*. This regulatory module functions by maintaining the balance of ROS within the fruit, hence promoting ROS homeostasis [192]. Stripe rust infection in wheat plants is more likely to occur when *TaWRKY19* and the W-box motif in the *TaN-OX10* promoter region combine to disrupt the equilibrium of the ROS [193]. The transgenic variant of *Myrothamnus flabellifolia* exhibits an overexpression of *MfWRKY70*, resulting in an augmentation of its ability to withstand drought, as well as salt stress. This enhanced tolerance is achieved through the regulation of hydrogen peroxide (H_2O_2) levels, antioxidants, metabolic processes, and the transcription of genes associated with stress response [194]. The inhibition of drought tolerance in tomato plants via *SlWRKY81* is attributed to its ability to hinder the closure of stomata, a process that is regulated by H_2O_2 and guard cells [195]. The disruption of ROS equilibrium was observed in *Catalpa bungei* trees by the overexpression of *CbWRKY27*. This resulted in a decrease in antioxidant levels and an increase in H_2O_2 production, ultimately affecting salt tolerance and highlighting the crucial role of WRKYs in defense responses [196].

9. Noncoding RNAs

Next-generation and high-throughput sequencing have made it easier to identify long non-coding RNAs (lncRNAs), which are crucial for controlling plant defenses against stress, growth, development, immunity, and responses to environmental stressors [197]. Genome sequencing technologies have revealed a variety of non-coding RNAs in tomatoes, including microRNAs and long non-coding RNAs, which are increasingly recognized for their roles in plant responses to both biotic and abiotic stresses [198]. TFs are crucial in defense responses, and miRNAs play a key function in controlling stress-responsive TFs [199]. MiRNAs like MYB, NAC, WRKY, ERF, ARF, and bHLH regulate TFs, controlling secondary metabolites [200]. *MiR164* in wheat negatively interacts with *NAC21/22*, increasing its susceptibility to stripe rust [201]. *Md-miRNA395* and *Md-miRNA156ab* target *MdWRKY26* and *MdWRKYN1* in response to the leaf spot fungus *Alternaria alternata* [202]. In tomato plants, *Sly-miR1127* regulates *slyWRKY75* during *Botrytis cinerea* infection [203]. In rice, *M. oryzae* triggers the expression of *miR5819* and *miR5075*, which target *OsbZIP38* and *OsbZIP27* [204]. The study explored the competitive endogenous RNA mechanism in rice under low-temperature conditions. It focused on the peroxidase-related module, which includes WRKY TFs, a key gene in the abscisic acid signaling pathway, and a receptor-like kinase. These elements were selected and enriched to form important competitive endogenous RNA networks. The findings revealed that OsWRKY61 plays a negative regulatory role in the mutant, with its gene modules showing the strongest correlation with vital antioxidant enzymes such as superoxide dismutase and peroxidase [205].

Moreover, *PvAP2-ERF* genes in *Phaseolus vulgaris* L. are affected by *miRNAs* from other plant species, while *miR160* and *miR164* influence *ARF* and *NAC* during rhizobial infection [206]. The *miR156/SPL* module improves salt tolerance in apples by upregulating *MdWRKY100* [207]. However, the overexpression of *MIR156a* in apples leads to the suppression of *MdSPL13*, which subsequently reduces the transcription levels of *MdWRKY100* and results in lower salt resistance [208]. The MAPK signaling pathway is responsible for upregulating genes that encode *PHO1-3*, *WRKY2*, *CML29*, and *MAPK*, while also downregulating TFs *EAT1-LIKE* [209]. Under NaCl stress, ATP synthase subunits are upregulated in the photosynthesis pathway [210]. Significantly more abundant in the roots are the ribosome pathway and the plant hormone signal transduction pathway [211]. Genes encoding WRKY TFs 14, *60S ribosomal protein L3 isoform X1*, *acid phosphatase 1-like*, and *cytochrome c biogenesis FN* were downregulated, whereas genes encoding *MAPK NPK1-like isoform X1*, *ICE1*, and *X1* were upregulated [209].

10. Regulation of Biotic and Abiotic Stresses by WRKY TFs

WRKY TFs are essential for agricultural plants to adjust to environmental changes, as was described in prior sections. Crop plants are able to resist various challenges because of this interaction between WRKYs and different plant hormones. All phenological plant development phases are impacted by biotic and abiotic stressors. Examples of biotic stressors include attacks by pathogenic bacterial, fungal, viral, and oomycetic organisms. Oxidative stress, heavy metal toxicity, heat, cold, and soil salinization are examples of abiotic stressors. For plants to survive and reproduce in the future, they must be able to adapt to these and other environmental stressors [212].

10.1. Regulation of Biotic Stresses by WRKY TFs

WRKY TFs have been shown to be essential for plants to react defensively to multiple pathogen assaults (Table 2). A WRKY protein from *Capsicum annuum*, known as *CaWRKY27*, positively influences the stress resistance response to *Ralstonia solanacearum* infection in *Nicotiana tabacum* by modulating the SA-, JA-, and ET-mediated signaling pathways [213]. In response to biotic stress, the WRKY18/22/29/30/33/53 genes and the downstream MAP kinase signaling cascades are activated, which protects against the impact of *P. syringe*, *Magnaporthe grisea*, and *B. cinerea* [214,215]. Upon infection by *B. cinerea*, MAPK3/6 phosphorylates WRKY33, which then becomes activated and subsequently activates *PAD3*, enhancing resistance by promoting phytoalexin production (Figure 3) [216]. However, the levels of resistance decreased upon overexpression of the WRKY38 and WRKY62 genes, which are both additively negative regulators of the plants' basal defense and are triggered by SA or pathogenic *P. syringae*. The *AtWRKY27*-mediated nitric oxide (NO) signaling pathway improves protection against *R. solanacearum* [217,218]. Another study investigated role of WRKYs in the defense of wild tomato *LA1777* against the *O. neolycopersici strain lz.27*, and differentially expressed genes were identified, among them *ShWRKY41* being the most significant. The study found that *ShWRKY41* expression increased after inoculation or ACC treatment, and gene silencing reduced resistance. The research suggests that *ShWRKY41* plays a positive role in defense activation and host resistance.

Arabidopsis contains 72 WRKY genes, and studies have shown that treatment with SA *P. syringae* differentially regulates 49 of these genes. TFs such as WRKY3, WRKY4, and WRKY33 appear to positively impact the SA-mediated plant resistance pathways against necrotrophic fungal infections, including *B. cinerea* [17,219]. When facing biotrophic bacterial pathogens like *P. syringae*, the SA-mediated defense system exhibits similar positive regulation of WRKY33, 46, 53, and 70 [220]. When the cotton genes *GhWRKY39-1* and *GhWRKY40* are overexpressed in tobacco, the tobacco plant's response to *R. solanacearum* is controlled. It has been discovered that the cotton plant's *GhWRKY70* gene controls tolerance to *V. dahliae* in at least two ways, i.e., via the upregulation of genes associated with SA and the downregulation of genes associated with JA [178,221]. It has been found that the sweet orange's transcriptional response to *P. digitatum* infection was regulated by the *CsWRKY2* and *CsWRKY14* genes [222]. Recently, it was discovered that tobacco displaying increased CoWRKY78 expression was more susceptible to anthracnose. The transgenic tobacco plants showed less active defense-related enzymes and exhibited higher ROS levels than the WT tobacco plants. Stress-related genes linked to ROS homeostasis were also expressed less often in the *CoWRKY78* overexpressing plants. These observations expand our knowledge of the *C. oleifera* WRKYs and provide more evidence in favor of future studies into the processes behind *C. oleifera* anthracnose resistance [223].

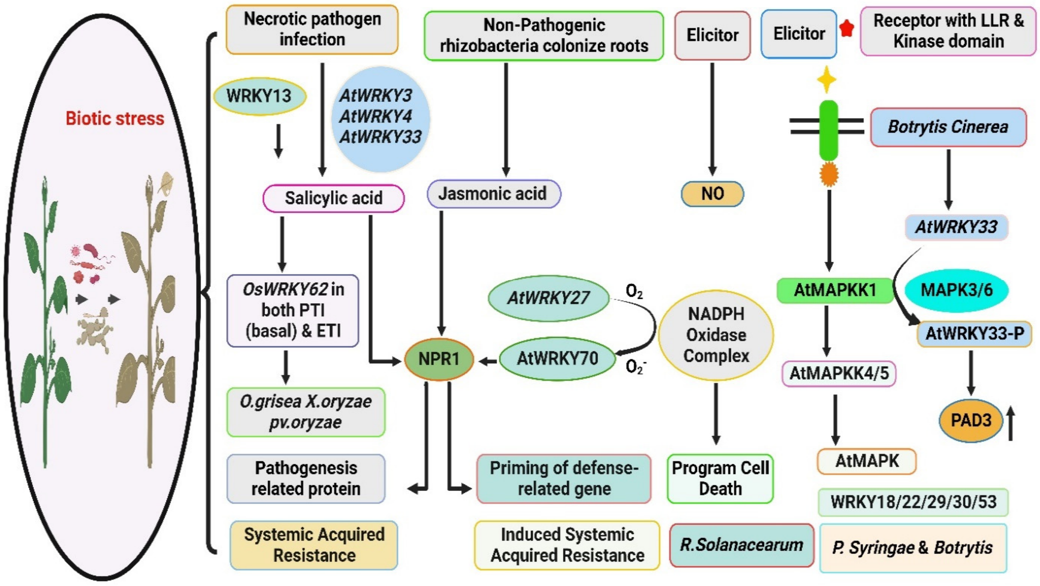

Figure 3. The WRKY TFs respond to different biotic elicitors. WRKY TFs are crucial in the regulation processes of necrotic pathogens and non-pathogenic rhizobacteria. WRKY controls signaling pathways that depend on SA, JA, nitric oxide, or interactions with other WRKY genes when a pathogen is in the body. These WRKY-regulated defense mechanisms are crucial for plant longevity because they either provide systemic acquired resistance or postpone senescence [4].

Table 2. Examples of regulatory role of WRKY TFs in biotic stress responses in plants.

WRKY Gene	Plant Specie	Factors	Function	Reference
GmWRKY164	Soybean	*Soybean mosaic virus*	Enhances resistance to SMV infection by regulating the expression of *GmGSL7c*, leading to callose deposition and the suppression of viral movement in soybeans.	[224]
CaWRKY01-10 and *CaWRKY08-4*	Pepper	*P. capsici*	Resistance to *P. capsici* infection in peppers is achieved by directly activating a cluster of defense-related genes, including one PR1, two PR4, and one pathogen-related gene, which could aid in genetic enhancement.	[225]
VviWRKY10/30	Grapevine	Powdery mildew	Regulates the activation of controlled and balanced defense responses to powdery mildew in grapevines, positively influencing ethylene production and ethylene-dependent defense mechanisms.	[226]
CsWRKY2/14	Sweet orange	*P. digitatum*	Associated with stress responses throughout plant growth and development and engaged in defense against *P. digitatum* and other diseases.	[222]
AktWRKY12	Three-Leaf Akebia	Pathogen	Controls the expression of crucial enzyme genes for lignin production during pathogen infection, which has a detrimental effect on how *A. trifoliata* reacts to biotic stress.	[227]

Table 2. *Cont.*

WRKY Gene	Plant Specie	Factors	Function	Reference
GhWRKY41	Cotton	*Verticillium dahliae*	Immediately and uniformly reacts to *V. dahliae*, directly activating GPP genes involved in the manufacture of monolignols and flavonoids, while also encouraging the buildup of lignin and a variety of flavonoids, increasing cotton resistance to *V. dahliae*.	[228]
CoWRKY78	Tobacco	*Anthracnose*	The overexpression of *CoWRKY78* in tobacco alters stress-related genes connected to pathogen challenge, defense, and ROS homeostasis, leading to increased cell death, elevated malonaldehyde concentration, and ROS.	[223]
GhWRKY53	Cotton	*Verticillium dahliae*	May change the expression of genes related to the SA and JA pathways, which would change the vulnerabilty of upland cotton to *V. dahliae*.	[229]
PnWRKY15	Chinese ginseng	*Fusarium solani*	Increased expression of the PnOLP1 gene, which is linked to resistance, and activation of the JA/SA signaling pathways, providing resistance to *F. solani*.	[160]
LrWRKY11	Regal lily	*Fusarium oxysporum*	Positively controls *L. regale* resistance to *F. oxysporum* by interacting with the salicylic/jasmonate signaling pathways and controlling the expression of *LrDIR1* and accumulation of lignin and lignans.	[230]
SlWRKY30/81	Tomato	*Ralstonia solanacearum*	Improves resistance to *RSI* using genetic alterations while simultaneously regulating tomato *SlPR-STH2a/b/c/d* expression to control *RSI* resistance.	[231]
CaWRKY50	Pepper	*Colletotrichum scovillei*	Has a detrimental impact on the antioxidant defense system, as well as the SA-mediated signaling pathway in *C. scovillei* resistance.	[232]
OsWRKY10	Rice	*Magnaporthe oryzae*	Plays a significant regulatory role, with broad transcriptional regulatory effects on the genes that produce rice diterpenoid phytoalexins, revealing information about the control of chemical defenses to enhance disease resistance in rice.	[233]
CsWRKY23	Citrus fruit	*Penicillium digitatum*	Contributes to the process of SA production, the buildup of reactive ROS, the strengthening of cell walls, and the development of a potential regulatory network for disease resistance.	[234]
PmWRYK31	Masson pine	*Dendrolimus punctatus*	*PmWRYK31* and *PmLp8* interact to enhance *P. massoniana's* insect resistance against *D. punctatus* by regulating hormone signaling pathways, thereby enhancing the expression of terpenoid synthase genes.	[235]
PtrWRKY18/35/89	Black cottonwood	*Melampsora medusae*	The resistance of *Melampsora medusae* has been improved through the activation of salicylic acid. (SA) pathway.	[236]
MdWRKY100	Apple	*Colletotrichum*	A potential positive regulator in enhancing resistance against *Colletotrichum gloeosporioides* in apples.	[237]
PyWRKY26	Red-skinned pears	*Aspergillus niger*	The interaction between *PyWRKY26* and *PybHLH3* was found to potentially co-target the *PyMYB114* promoter, resulting in the accumulation of anthocyanin in red-skinned pears.	[238]

10.2. WRKY TFs Regulatory Function under Abiotic Stress

Plants respond to stress by activating the proper signaling, which is subsequently sent to the cell's interior. ROS and Ca^{2+} ions are often exchanged in order to carry messages throughout the cell [239]. The plant stress response results from the subsequent activation of protein kinases like MPKs to control the activities of associated TFs [240]. Numerous WRKY TFs can be quickly expressed in a variety of ways in response to abiotic stressors, enhancing signal transduction and controlling the expression of associated genes. To determine how WRKYs are expressed and what functions they perform, most research employs transcriptome analysis, gene chip analysis, real-time quantitative PCR with fluorescence, and genetic engineering. For instance, a total of 78 WRKY TFs were identified in tea plants using transcriptome and genomic data, with *CsWRKY70-2* TF shown to positively regulate drought stress tolerance [59]. In *Platycodon grandiflorus*, *PgWRKY26* plays a key function in responding to temperature and drought stresses [241]. In transgenic *C. equisetifolia* plants display overexpression, *CeqWRKY11* exhibited reduced electrolyte leakage, increased chlorophyll content, and improved tolerance to NaCl and $NaHCO_3$. This was associated with the elevated expression of genes associated with abiotic stress, particularly *CeqHKT1* and *CeqPOD7* [60]. Research has shown that under salt, drought, and cold stress treatments, *CsWRKY20* and *CsWRKY28* function as positive regulatory factors in the cannabinoid biosynthesis pathway, which produces essential metabolites in *Cannabis sativa* [242]. A pearl millet gene, *PgWRKY44*, was identified as a positive regulator of abiotic stress tolerance in transgenic *Arabidopsis* plants. This regulation occurs through ABA-mediated signaling, involving the coordinated expression of Calmodulin-HSFs alongside *PgWRKY44* [6]. SmWRKY40 from eggplant regulates the responses to ABA and salt stress in *Arabidopsis thaliana* [7]. Therefore, the bulk of abiotic stress reactions or tolerances in a range of plants may be effectively regulated by WRKY genes (Table 3) [32].

The mechanisms of ABA-independent abiotic stress tolerance signaling are integrated within the ABA signaling cascade, where several WRKYTFs can function independently or collaboratively [243]. Thus, the overexpression of *AtWRKY21/33/40/57,70*, and *TaWRKY93* increases the tolerance to osmotic stress in an ABA-dependent manner, while *AtWRKY25*, *AtWRKY45*, and *TaWRKY93* work in ways that are not ABA-dependent. Abiotic stress leads ABA to bind to the *PYR-PYL-RCAR* protein phosphatase *2C-ABA* complex and the ABAR-ABA complex in the chloroplast envelope, while *AtWRKY40* suppresses the expression of ABA-sensitive genes. These complexes inhibit the activation of ABA-responsive genes such as *ABI4*, *ABI5*, *ABF4*, *MYB2*, *DREB1a*, *DREB2b*, *RAB18*, and *AtWRKY60* as *AtWRKY40* is withdrawn from the nucleus [244] (Figure 4).

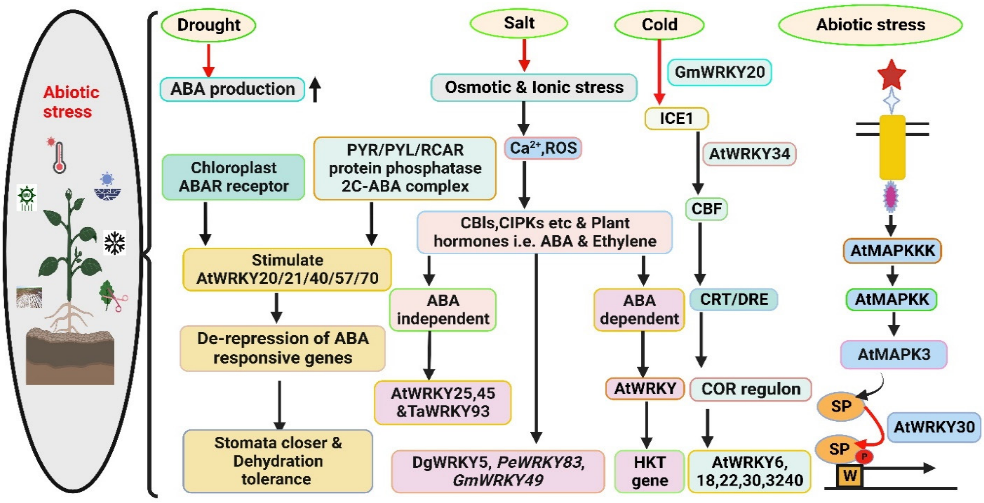

Figure 4. WRKY TFs control abiotic stress. During a response to abiotic stresses, certain WRKY genes change how physiological and biological processes work [245].

Drought-resistant genes can be directly regulated by WRKY proteins; for example, *SbWRKY30* in sorghum interacts with the W-box regions of the *SbRD19* promoter to control the drought stress response genes, enhancing ROS scavenging abilities and increasing drought tolerance [246]. The wheat protein *TaWRKY2* regulates the positive expression of the gene *RD29B*, which provides drought resistance, by binding to *STZ* and the downstream promoter of this gene. *TaWRKY19* binds to the *DREB2A* promoter in transgenic *Arabidopsis* plants, regulating the *RD29A*, *RD29B*, and *Cor6.6* genes related to dehydration stress through *DREB2A* [247,248].

Additionally, WRKY TFs control plant tolerance via signaling pathways involving ABA and ROS. Currently, it has been found that *RcNAC091* favorably affects ABA signaling and drought responses via activating *RcWRKY71* transcriptionally [249]. Drought stress caused the ABA levels in plants to rise, and the leaf stomata close to reduce transpiration, managing the water balance in plants. Cells are able to recognize and respond to their surroundings, thanks to the accumulation of ABA inside of them, as well as to a number of stress signals [250]. *Arabidopsis AtWRKY63* affects the drought response by changing how ABA causes the stomata to close and the way in which other signal transduction pathways work. *GhWRKY21* controls cotton ABA-mediated drought tolerance via enhancing *GhHAB* expression. The elevated expression of *BdWRKY36* in tobacco decreases ROS accumulation; activates *NtLEA5*, *NtNCED1*, and *NtDREB3* within the ABA biosynthesis pathway; and greatly improves the plant's drought tolerance. By limiting the buildup of H_2O_2, *SlWRKY81*, which has a negative regulatory function on stomatal closure in *Solanum lycopersicum*, increases plant tolerance to drought [195,251,252].

The ability of WRKY TFs to respond favorably to a plant's ability to resist high temperatures has been shown in several studies. In pepper plants, *CaWRKY40*, for example, affects how the plant reacts to high-temperature stress, whereas *CaWRKY40* overexpression reduces tobacco susceptibility to high-temperature treatment while improving its tolerance. Similar outcomes were discovered for the upland cotton genes *CaWRKY40* and *GhWRKY39* [5,253,254]. Additionally, the upstream stress response-related genes were activated to control resistance to high temperatures, i.e., wheat *TaWRKY1* and *TaWRKY33* are overexpressed in *Arabidopsis*. High temperature resistance is greatly influenced by *AtWRKY25*, *AtWRKY26*, and *AtWRKY33* [255,256]. Salt stress significantly impacts agricultural productivity in dry and semi-arid regions, with WRKY TFs playing a crucial role in regulating this response. *FcWRKY70* makes plants better able to handle salt by causing the heterologously expressed *arginine decarboxylase* (*ADC*) in tobacco to upregulate its expression and produce much more lemon putrescine. The *IbWRKY47* gene significantly enhances *Ipomoea batatas* salt tolerance and favorably regulates stress resistance-related genes [257,258]. By regulating ion homeostasis and interacting with the upstream promoters of *SOS1* and *HKT1*, *SbWRKY50* from Sorghum bicolor may contribute to the plant salt response [259]. Additionally, as negative regulators, several WRKY genes contribute to salt stress tolerance. WRKY53 *RPD3* of the *Arabidopsis* plant controls DNA binding and transcriptional activity, and similar to the results for *HDA9*, this plant's ability to withstand salt stress is decreased [207].

Abiotic stressors like UV radiation, mechanical damage, and oxidative stress are also mediated by WRKY TFs. By overexpressing *FcWRKY40*, it is possible to significantly boost the tolerance of transgenic tobacco to oxidative stress [260]. ROS significantly boosts the expression of *AtWRKY30*, *AtWRKY40*, *AtWRKY75*, *AtWRKY6*, *AtWRKY26*, and *AtWRKY45* in *Arabidopsis*, whereas mechanical damage affects the expression levels of *AtWRKY11*, *AtWRKY15*, *AtWRKY22*, *AtWRKY33*, *AtWRKY40*, and *AtWRKY53* [98]. Similar to *NaWRKY3*, which is abundantly expressed in tobacco, when *NaWRKY3* is knocked out, transgenic plants exhibit higher sensitivity [112]. In two prior studies, exposure to UV-B radiation resulted in the induction of the *OsWRKY89* gene in rice and three WRKY genes in *Arabidopsis*. As a result of these modifications, the leaf surface developed a thick waxy covering and showed a greater heat tolerance [261]. A single WRKY TF can engage in multiple stress responses through various signaling pathways and regulatory networks.

Pennisetum glaucum PgWRKY62 and *PgWRKY33* respond to both salt and drought at the same time, although tobacco *TaWRKY44* expression can increase resistance to osmotic, salt, and drought stress [261,262]. Regarding the ability to withstand low temperatures and drought, *BhWRKY1* interacts with the promoter of *BhGolS1* [195]. Interactions between *IbVQ4* and *IbWRKY2* have been observed, and salt and drought stress promote *IbVQ4* expression [263]. The overexpression of *MdWRKY30* in transgenic apple callus enhances tolerance to salt and osmotic stress by transcriptionally regulating stress-related genes, increasing resistance to both stressors [264]. When subjected to salt and osmotic stress, *PagWRKY75* actively controls the rate of leaf water loss in 84 *Populus alba* × *P. glandulosa*, via reducing ROS scavenging capacity and proline accumulation [265].

Table 3. Examples of regulatory function of WRKY TFs in regards to abiotic stress in plants.

WRKY Gene	Plant Species	Stress Factor	Function Role	Reference
CpWRKY16/51/80	Zucchini	Cold and drought	Several cis-regulatory elements were identified in the promoter region, such as *ABRE*, *MeJARE*, *LTR*, *MBS*, *ARE*, and *GRE*, indicating that these proteins likely regulate zucchini growth, development, and stress responses.	[266]
AcWRKY117/29	Kiwifruit calli	Waterlogging	They enhance the expression of hypoxia-related *AcADH* and *AcPDC* genes in response to waterlogging.	[113]
VhWRKY44	*Arabidopsis*	Salt and cold	The tolerance of plants to cold and salt is improved by enhancing the expression of downstream genes, including *KIN1*, *CBF1*, *CBF2*, *CBF3*, *COR47*, and *RAB18*.	[267]
PgWRKY74	*Arabidopsis*	Mannitol and salt	They negatively regulate plant responses to mannitol and NaCl stresses, likely by reducing ABA levels or sensitivity.	[268]
GhWRKY31	Cotton	Salt and drought	Silencing *GhWRKY31* in cotton resulted in lower levels of ABA, proline, POD, and SOD, along with decreased expression of stress-responsive genes.	[269]
MdWRKY56	Apple	Drought	Plays a vital part in regulating the capacity to withstand drought stress.	[270]
IlWRKY22	*Nicotiana tabacum* L.	Salt and drought	Transgenic *N. tabacum* overexpressing *IlWRKY22* exhibited significantly enhances resistance to salt and drought compared to that of the control plants.	[271]
WRKY48	*Arabidopsis*	Heat and salt	Crucial for plant acclimation to high heat and salt stress by acting as a negative regulator of *Arabidopsis's* transcriptomic response to HL + HS.	[272]
BnWRKY49	Arabidopsis	Salt and drought	The overexpression of *BnWRKY49* in *Arabidopsis* seedlings results in improved drought tolerance by influencing root elongation under conditions of drought and salt stress.	[273]
SbWRKY45	*Arabid Nicotiana tabacum* L. *opsis*	Drought	Improves germination rates and promotes root development in drought-stressed transgenic *Arabidopsis*.	[274]
TrWRKY	White clover	Cold	Participates in a number of gene regulatory pathways in response to cold stress.	[22]
TaWRKY1-2D	Wheat	Drought	Favorable potential gene for enhancing wheat breeding to produce drought tolerance.	[275]

Table 3. *Cont.*

WRKY Gene	Plant Species	Stress Factor	Function Role	Reference
MbWRKY46	*Arabidopsis*	Cold and drought	Contributes to the upregulation of expression in cold and water-stressed conditions in *Arabidopsis*.	[276]
MdWRKY115	Apple	Osmotic and drought	Plays a crucial role in regulating tolerance to osmotic and drought stress.	[277]
RsWRKY26	Radish	Heat	Promoting thermotolerance with the novel *RsVQ4-RsWRKY26-RsHSP70-20* module will simplify the analysis of the molecular regulatory network governing *RsWRKY* mediated thermal morphogenesis.	[278]
OsWRKY28	Rice	Salt	Increases the transcriptional activity of the *OsDREB1B* promoter and hence, provides salt tolerance. Additionally, it prevents abscisic acid's damage to rice seedling establishment.	[279]
GbWRKY	Ginkgo biloba	UV-B, drought, heat, and salt	Plays a critical part in controlling various stress tolerances.	[69]
FtWRKY29	*A. thaliana*	Low-P	Transgenic *Arabidopsis thaliana* plants exhibit improved tolerance to low-phosphorus stress, contributing to a better understanding of the regulatory mechanisms in Tartary buckwheat.	[280]
McWRKY57-like	*Arabidopsis*	Drought	Provides protection via controlling plant development, osmolyte buildup, antioxidant enzyme activity, and the expression of these genes associated with stress.	[281]
GmWRKY172	Soybean	Cd	Protects plants by effectively modulating many pathways associated with stress.	[282]
MsWRKY33	Alfalfa	Salt	Protection is achieved by directly connecting to the promoter of *MsERF5* to activate its transcription and upregulate downstream ROS-scavenging genes. This is accomplished by interacting with the functional fragment *MsCaMBP25*, likely inhibiting Ca^{2+} signal transduction in the cell.	[283]
MfWRKY40	Drought and salt tolerance	*Arabidopsis*	Protection is achieved by encouraging primary root elongation and improving water uptake and retention ability, osmotic adjustment, and antioxidation system, either directly or indirectly.	[284]
Bna.A07. WRKY70	*Brassica napus*	Leaf senescence	Prospective target for innovative stay-green material creation and genetic manipulation of leaf senescence to increase rapeseed output.	[285]
SbWRKY50	Sorghum	Leaf senescence	The regulator downstream of ET and *SbWRKY50* is responsive to various phytohormones, thus playing a crucial role in regulating senescence.	[286]
ClWRKY48	*Arabidopsis*	Phosphate	The upregulation of phosphate transporter genes results in an increase in gene expression levels, leading to greater phosphate uptake. Additionally, this upregulation causes a delay in the transition from the vegetative stage to the reproductive phase in *Arabidopsis* plants.	[287]
GmWRKY21	Soybean	Aluminum	Improves resistance to aluminum stress by controlling the expression of genes that are sensitive to abiotic and acidic stress.	[288]

11. Interaction of WRKY TFs with Other TFs

Plants have established a network of interconnected systems to prevent species extinction; these systems operate through a molecular cascade of events that enable rapid responses and adaptations to unfavorable conditions [289]. Stress responses involve the perception of signals, signal transduction, and the expression of stress-responsive genes [290]. Initially, plant cells detect stress through sensors or receptors located in the cell wall or membrane [291]. Second messengers, e.g., reactive ROS, calcium ions, and lipid-derived signaling molecules, convert the primary external signals into intracellular signals [292]. Phytohormones, including auxin, cytokinin, gibberellic acid, ABA, JA, ethylene, and salicylic acid, also serve as crucial second messengers that help coordinate signal transduction pathways during stress responses [293]. TFs such as WRKY, MYB, bHLH, and bZIP are essential for regulating gene expression in plants. In potato genomes, their roles are being investigated under heat, salinity, and drought stress conditions, focusing on expression patterns, co-expression relationships, and differentially expressed genes (DEGs) [294].

The bZIP proteins in *Arabidopsis*, particularly the TGA proteins, are vital for regulating their activity [295], subcellular localization, and function during defense responses against pathogens, serving as key regulators of SA-mediated signaling [296]. Research indicates that 17 CC-type glutaredoxins interact with *TGA2*, which may contribute to pathogen defense and plant development [297]. Additionally, WRKY proteins also engage with TGA proteins; in tobacco, the *NtWRKY12* protein has been shown to interact with TGA proteins both in vitro and in vivo [39,298]. MYB transcription factors, including WRKY70, are crucial in the antagonistic interaction between pathogens and JA [299]. WRKY70 activation or suppression is essential for developing an effective defense response against pathogen attack [300]. *AtMYB44* plays a role in establishing appropriate plant defense responses by directly regulating WRKY70 expression in the cross-talk between pathogens and JA [301]. *GmWRKY27* expression increases in response to abiotic stresses, which boosts salt and drought tolerance in transgenic soybean hairy roots. It achieves this by binding to the promoter region of *GmNAC29*, thereby inhibiting its expression and enhancing stress tolerance. Additionally, *GmWRKY27* interacts with *GmMYB174*, further suppressing *GmNAC29* expression and improving drought resilience [302]. *VvWRKY26* promotes the expression of target genes activated by *VvMYB5a/b*, which include those involved in vacuolar hyper-acidification, trafficking, and flavonoid biosynthesis. *MfWRKY70* overexpression in Arabidopsis significantly improved abiotic stress tolerance, positively regulating stress-associated genes like *P5CS*, *NCED3*, and *RD29A*, suggesting that *MfWRKY70* likely plays a positive role in abiotic stress responses [194]. *VvMYB5a* recruits *VvWRKY26*, indicating a functional diversification between them. The expression of *MBWW* complexes in leaves suggests that vacuolar hyper-acidification plays a role in repelling herbivores and in developmental processes [303].

bZIPs are conserved transcription factors in eukaryotic organisms, crucial for plant growth, development, photomorphogenesis, signal transduction, resistance to pathogens, stress, and secondary metabolism [304]. bZIP factors need to form heterodimers for DNA binding and transcription regulation, allowing them to establish more protein interactions compared to those created by WRKYs. While WRKYs regulate transcription within a transcriptional network, the function of bZIPs is heavily dependent on extensive heterodimerization [305]. The *L. indica* transcriptome database contains 85 *LibZIPs* and 61 *LiWRKYs*, which play a vital role in flower color development. Phylogenetic analysis indicates that nine *LibZIPs* and four *LiWRKYs* exhibit higher expression levels in colored samples, highlighting their significance in the flower color formation of *L. indica* [306]. Under salt and drought stress conditions, *GmbZIP15* transcript levels were reduced, resulting in hypersensitivity in soybean plants compared to wild-type plants. The overexpression of *GmbZIP15* led to decreased transcript levels of stress-responsive genes, impaired regulation of stomatal aperture, and lower antioxidant enzyme activities. Conversely, plants with functional repressor forms exhibited resistance to drought stress. *GmbZIP15* positively regulates the expression of *GmSAHH1*, while negatively regulating *GmWRKY12* and *GmABF1* in response to abiotic stress [307].

12. Conclusions and Future Prospects

Our understanding of the molecular processes underlying the actions of WRKY TFs in plants has advanced significantly over the past 20 years. Genetic, molecular, and computational biology research has identified the regulatory roles of the WRKY gene family in numerous plant stress and hormone responses, developmental processes, and the evolution of the gene family itself. A limited number of target genes that are regulated by these WRKY factors, as well as particular proteins that interact with a small subset of these WRKY factors, have both been identified through numerous investigations. The mechanistic viewpoint offered in this essay underlines the recent development and promising future of this fascinating topic. We believe that continuing research in this field will result in novel findings and uses that will advance agriculture and human society. Numerous questions are still unsolved, despite tremendous advancements in our understanding of the molecular processes that control WRKY genes and their roles in plants.

Future research needs to be primarily focused on the relationships that exist between WRKY TFs and other TFs that control gene expression, along with potential improvements to crops which could be achieved by WRKY TFs. It will be possible to design novel crop improvement methods and gain a greater knowledge of how WRKY TFs regulate plant growth by finding the answers to these questions. Furthermore, there is an increasing possibility to effectively capture, isolate, and analyze the remarkably dynamic transcriptional complexes associated with WRKY proteins at specific promoter locations after signaling events mediated by well-defined pathways. It is anticipated that this research will establish the biochemical foundation for investigating the resolution of synergistic and antagonistic signals at a specific promoter, therefore contributing to the understanding of how WRKY-dependent crosstalk is accomplished.

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