Review

WRKY Transcription Factor Responses and Tolerance to Abiotic Stresses in Plants

Ziming Ma * and Lanjuan Hu *

Posted Date: 3 June 2024

doi: 10.20944/preprints202406.0031.v1

Keywords: WRKY transcription factor; abiotic stress response and tolerance; target gene; plant growth and development

Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 3 June 2024 doi:10.20944/preprints202406.0031.v1

Review

WRKY Transcription Factor Responses and Tolerance to Abiotic Stresses in Plants

Ziming Ma [1,2,3,*] **and Lanjuan Hu**[1,*]

[1] Jilin Provincial Engineering Laboratory of Plant Genetic Improvement, College of Plant Science, Jilin University, Changchun, 130062, China
[2] Max-Planck-Institute of Molecular Plant Physiology, Am Muehlenberg 1, Potsdam-Golm 14476, Germany
[3] Plant Genetics, TUM School of Life Sciences, Technical University of Munich (TUM), Emil Ramann Str. 4, Freising 85354, Germany
* Correspondence: ma@mpimp-golm.mpg.de (Z.M.); hulj@jlu.edu.cn (L.H.)

Abstract: Plants are subjected to abiotic stresses throughout their developmental period. Abiotic stresses include drought, salt, heat, cold, heavy metals, nutritional element and oxidative stresses. Improving plant response to various environmental stresses is critical for plant survival and perpetuation. The WRKY transcription factors have special structure (WRKY structural domains), which enable WRKY transcription factors to have different transcriptional regulatory functions. The WRKY transcription factors can not only regulate abiotic stresses response and plant growth and development by regulating phytohormone signalling pathways, but also promote or suppress the expression of downstream genes by binding to the W-box [TGACCA/TGACCT] in the promoters of their target genes. In addition, WRKY transcription factors not only interact with other families of transcription factors to regulate plant defence responses in abiotic stresses, but also self-regulate by recognizing and binding to W-boxes in their own target genes to regulate their defence responses to abiotic stresses. However, in recent years, research reviews on the regulatory roles of WRKY transcription factors in higher plants are scarce and shallow. In this review, we focus on the structure and classification of WRKY transcription factors, as well as the identification of their downstream target genes and molecular mechanisms involved in the response to abiotic stresses, which can improve the tolerance ability of plants in abiotic stress and we also look forward to their future research directions, with a view to providing theoretical support for the genetic improvement of crop abiotic stresses tolerance.

Keywords: WRKY transcription factor; abiotic stress response and tolerance; target gene; plant growth and development

1. Introduction

Food is an indispensable and important resource in human life, and it carries people's survival and development. From planting to harvesting, from processing to consumption, food accompanies the historical process of mankind and profoundly affects the way of life and social structure of mankind. Food is the basic guarantee for human survival [1]. As one of the most important sources of food for human beings, grain provides the nutrition and energy needed by the human body and maintains its normal physiological functioning. Whether it is rice, wheat, corn or other grains, they are all important foods indispensable to human survival, providing humans with a wealth of carbohydrates, proteins and a variety of vitamins [2]. Finally, the food industry is also an important pillar of employment and economic development for human society. The production, processing and distribution of food involves a large number of practitioners and related industrial chains, creating enormous employment opportunities and economic benefits for society. The healthy development of the food industry is directly related to the prosperity and stability of national and regional economies [3]. In short, guaranteeing the stability of food production and supply, promoting the inheritance and innovation of food culture, and developing the food industry are all important guarantees for the sustained and stable development of human society [4].

Plants are subjected to a variety of stresses during growth and development, such as drought, temperature extremes, pests and diseases, etc., of which abiotic stresses are the major threats affecting the growth of food crops [5–8]. Currently, numerous studies have been conducted on the response of plants to abiotic stresses, for example, the response to cold temperature stress, drought stress, salt stress, heavy metal stress, etc [9–12]. The studies have been deepened to the level of molecular mechanisms, and the WRKY transcription factors, which are one of the largest families of transcription factors in plants, have gained great attention. Nowadays, a large number of WRKY transcription factor genes have been identified, and they are widely involved in the regulation of plant secondary metabolism, abiotic stress, growth and development [13–15]. Su et al. identified a WRKY group IIc transcription factor MdWRKY75, it is located in the nucleus. Overexpression of *MdWRKY75* promoted anthocyanin accumulation in apple (*Malus Domestica L.*) 'Orin' callus. Anthocyanins play an important role in plant secondary metabolism, and MdWRKY75 stimulates anthocyanin accumulation mainly by binding to the promoter of the MYB transcription factor *MdMYB1* [16]. Gentiana macrophylla is one of Chinese herbal medicines in which loganic acid and gentiopicroside, and kinds of iridoids or secoiridoids have been identified as major medicinal secondary metabolites. A total of 12 GmWRKYs were identified to be involved in the biosynthesis of secoiridoid, of which 8 genes *GmWRKY1*, *GmWRKY6*, *GmWRKY12*, *GmWRKY17*, *GmWRKY33*, *GmWRKY34*, *GmWRKY38*, and *GmWRKY39* were found to regulate the synthesis of gentiopicroside and 4 genes were found to be involved *GmWRKY7*, *GmWRKY14*, *GmWRKY26* and *GmWRKY41* regulate strychnic acid synthesis [17]. Zhang et al. identified a WRKY transcription factor OsWRKY63 negatively regulates cold tolerance in *Oryza sativa*. Overexpression of *OsWRKY63* lines were more sensitive to cold stress, and the knockout mutant line showed higher cold tolerance. OsWRKY63 was able to repress the expression of *OsWRKY76*, and the OsWRKY76-knockout mutant lines showed significantly lower cold tolerance and suppressed cold-induced expression of the five *OsDREB1* genes [18]. Ma et al. found that the tomato WRKY transcription factor SlWRKY57 acts as a negative regulator in salt stress response by directly attenuating the transcription of salt-responsive genes (*SlRD29B* and *SlDREB2*) and an ion homeostasis genes (*SlSOS1*) [19]. Devaiah et al. found WRKY75 was located in the nucleus and was differentially induced in plants during phosphate (P_i) deficiency. When WRKY75 expression was inhibited, the expression of several genes involved in the P_i starvation response decreased, and lateral root length and number as well as the number of root hairs increased significantly [20]. Because of the important role of WRKY transcription factors in the regulation of abiotic stress and plant growth and development, it has become a popular gene family for plant stress breeding research.

This paper reviews the structural domains and classification of WRKY transcription factors, that transcriptional regulation downstream genes are involved in the response to abiotic stress. In the future, we can focus on studying WRKY transcription factors as a signal regulatory gene network in response to abiotic stress, and we also look forward to their future research directions, with a view to providing theoretical support for the genetic improvement of crop abiotic stresses tolerance.

1.1. Structural Domains and Classification of WRKY Transcription Factors

WRKY is a family of transcription factors unique to plants and defined as WRKY transcription factors because of their protein sequences contain a DNA binding domain with the highly conserved amino acid sequence WRKYGQK at the N-terminus of the domain [21]. However, in a few WRKY proteins, there are different types of mutations in the WRKYGQK amino acid sequence, mainly WRKYGEK, WRKYGMK, WRKYGKK, WSKYEQK or WIKYGEN (Figure 1). The WRKY transcription factors proteins are usually composed of 60 amino acids, and this sequence recognises the W-box [TGACCA/TGACCT] and some similar W-boxes containing the TGAC core structure in the homeopathic element, and specifically binds to them to regulate the downstream target genes [22,23]. The neighbouring sequences of the TGAC core structure determine the priority of WRKY transcription factor binding sites [24]. A large number of previous studies have shown that most of the promoters of genes related to abiotic stresses contain more than one W-box sequence, which explains the ability of the WRKY family of transcription factors to be widely involved in the regulation of the expression of many plant abiotic stress-related genes [25] (Table 2).

Typically, WRKY transcription factors contain at least one WRKY structural domain at the N-terminal end and an atypical zinc finger structure at the C-terminal end [26]. Based on the number of

WRKY-binding domains and the characteristics of the zinc finger-like motifs, they can be classified into three groups: Group I contains two WRKY-binding domains with C_2-H_2 motifs (C-X_{4-5}-CX_{22-23}-H-X_1-H); Group II contains one WRKY-binding domain with C_2-H_2 motifs. Group II can be generally divided into five subgroups (II a, II b, II c, II d and II e). Group III contains a WRKY-binding domain and a different zinc finger-like motif, C_2-H-C (C-X_7-C-X_{23}-H-X_1-C). Analyses based on phylogenetic data indicate that WRKY families in higher plants are more accurately classified into groups I, II a+II b, II c, II d+II e, and III, whereas [27,28] (Figure 2).

Table 1. The *WRKYs* genes total numbers in different plants.

Gene name	Species	Total number	Reference
AtWRKYs	*Arabidopsis thaliana*	74	[29]
OsWRKYs	*Oryza sativa*	100+	[30]
GmWRKYs	*Glycine max*	197	[31]
HvWRKYs	*Hordeum vulgare*	45	[32]
CsWRKYs	*Cucumis sativus*	55	[33]
SlWRKYs	*Solanum lycopersicum*	81	[34]
PgWRKYs	*Panax ginseng*	118	[35]
VuWRKYs	*Vigna unguiculata*	92	[36]
HvWRKYs	*Hordeum vulgare*	86	[37]
IbWRKYs	*Ipomoea batatas*	84	[38]
PhWRKYs	*Petunia hybrida*	79	[39]
TkWRKYs	*Taraxacum kok-saghyz*	72	[40]
SbWRKYs	*Scutellaria baicalensis*	72	[41]
HuWRKYs	*Hylocereus undulatus*	70	[42]
DcWRKYs	*Daucus carota*	67	[43]
XsWRKYs	*Xanthoceras sorbifolium*	65	[44]
KoWRKYs	*Kandelia obovata*	64	[45]

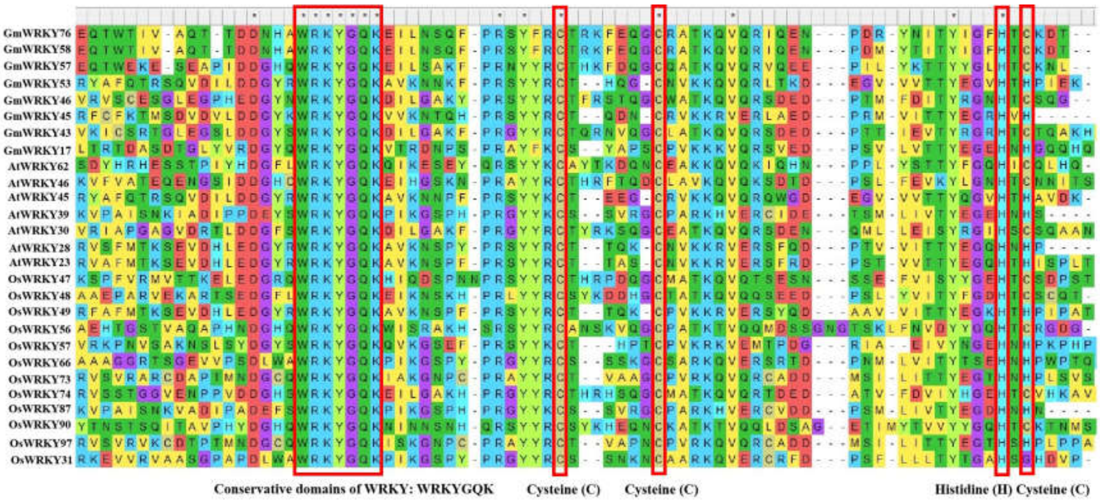

Figure 1. Conserved domains of WRKY family transcription factors in *Glycine max*, *Arabidopsis thaliana* and *Oryza sativa.* These asterisks "*"and red frame above the maps indicate the domain of conservative cysteine (C), cysteine (C), histidine (H) and cysteine (C), respectively.

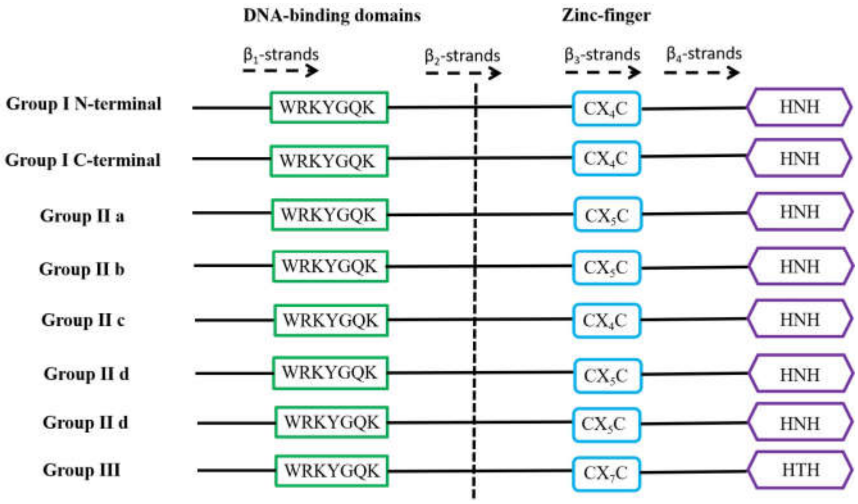

Figure 2. Domain structure of different WRKY subfamilies in higher plants. The WRKY motif, the cysteines, and histidines that form the zinc finger are shown in boxes. The 4 β-strands are shown with dashed arrows.

1.2. W-Box cis-Element in the Promoter Region of WRKY Downstream Genes

It has been shown that WRKY transcription factors can specifically bind to DNA through the cis-acting element W-box (5'-[TGACCA/TGACCT]-3') in the promoters of target genes to regulate the expression of related genes and affect plant in abiotic stresses, plant growth and development. The core sequence of the W-box is "TGAC", so the W-box can be used for the prediction of the target genes of WRKY transcription factors [21]. Different WRKY transcription factors bind different sequences near the W-box, which affects the selectivity and strength of WRKY transcription factor binding [46]. Mutations in the conserved sequence WRKYGQK in the WRKY structural domain or change any nucleotide in the W-box reduce the binding activity of WRKY transcription factor to DNA, whereas substitution of conserved cysteine (Cys) and histidine (His) residues in the C-terminal zinc finger structure removes their DNA-binding activity [47].

2. Response and Tolerance of WRKY Transcription Factor Family to Abiotic Stresses in Plant

Plants may encounter the effects of a wide range of abiotic stresses during growth and development, including drought, temperature extremes (high temperature and low temperature), salinity, heavy metal stresses and nutrient deficiencies. With climate change and increasing weather extremes, the impact of abiotic stresses on crops production is increasing, leading to growth retardation, quality deterioration and yield reduction [48,49]. Under abiotic stresses conditions, the WRKY transcription factors activate or suppress the transcription of downstream genes to regulate the expression of abiotic stress responsive genes or direct regulation of abiotic stress response gene expression, activate the defence mechanism against abiotic stresses in crops, and improve crops resilience to ensure grain yield under abiotic stresses [50,51].

2.1. Molecular Mechanisms of WRKY Transcription Factors Associated with Dought Stress

Drought is one of the major environmental factors affecting plant growth and development and crop yield (Figure 3). Many WRKY transcription factors genes have been identified to regulate drought tolerance in plants, and overexpression line or knockdown line of these WRKY genes has improved drought tolerance and even seed yield in *Arabidopsis thaliana*, *Nicotiana tabacum*, *Glycine max*, *Oryza sativa*, *Triticum*, *Cotton* [48–50]. It has been shown that WRKYs can improve plant tolerance to drought stress by reducing H_2O_2 content through the *Reactive oxygen species* (ROS) scavenging system. For example, overexpression of *MdWRKY70L* in *Nicotiana tabacum* reduced H_2O_2 and O_2^- accumulation and enhanced drought tolerance in transgenic plants [52]. Overexpression of the *GmWRKY17* enhances drought tolerance in soybean, and it positively regulates drought tolerance in soybean by activating the expression of the drought-inducible gene *GmDREB1D* and the abscisic acid

(ABA)-associated gene *GmABA2* through combining their promoters [53]. Duan et al. found transcript abundance of *MdWRKY56* was up-regulated under drought stress. *MdWRKY56* overexpressed line exhibited lower electrolyte leakage, malondialdehyde (MDA) content and ROS accumulation, proline content and antioxidant enzyme activities [54]. Zhang et al. found ChaWRKY40 may enhance hazelnuts drought tolerance by positively regulating *ChaP5CS* gene expression to increase proline content. In the wild type, the expression of *ChaWRKY40* and *ChaP5CS* increased with the increase of PEG-6000 concentration in the leaves and the gradual decrease of the relative water content of the leaves [55]. Wang et al. found the WRKY transcription factor *EjWRKY17* was identified in *Eriobotrya japonicaloqua*, which was significantly up-regulated in leaves by melatonin treatment during drought stress. Overexpression of *EjWRKY17* line was able to increase drought tolerance in plants, which had low water loss, limited electrolyte leakage, and lower levels of ROS and MDA compared to the wild type [56]. Huang et al. found *MfWRKY40* promoted primordial root length elongation, increased water uptake, and reduced water loss under stress, and the antioxidant capacity of the overexpression lines was also significantly enhanced, as evidenced by higher chlorophyll content and antioxidant enzyme activities, and less malondialdehyde and ROS accumulation [57].

Drought is one of the major abiotic stresses that limit plant growth and development and reduce crop yield. Many members of the WRKY transcription factor family have been found to be able to respond to drought stress by binding downstream to the W-box element in the promoter region of drought stress-related genes and regulating the expression of the genes, which ultimately improves the ability of plants to cope with drought stress.

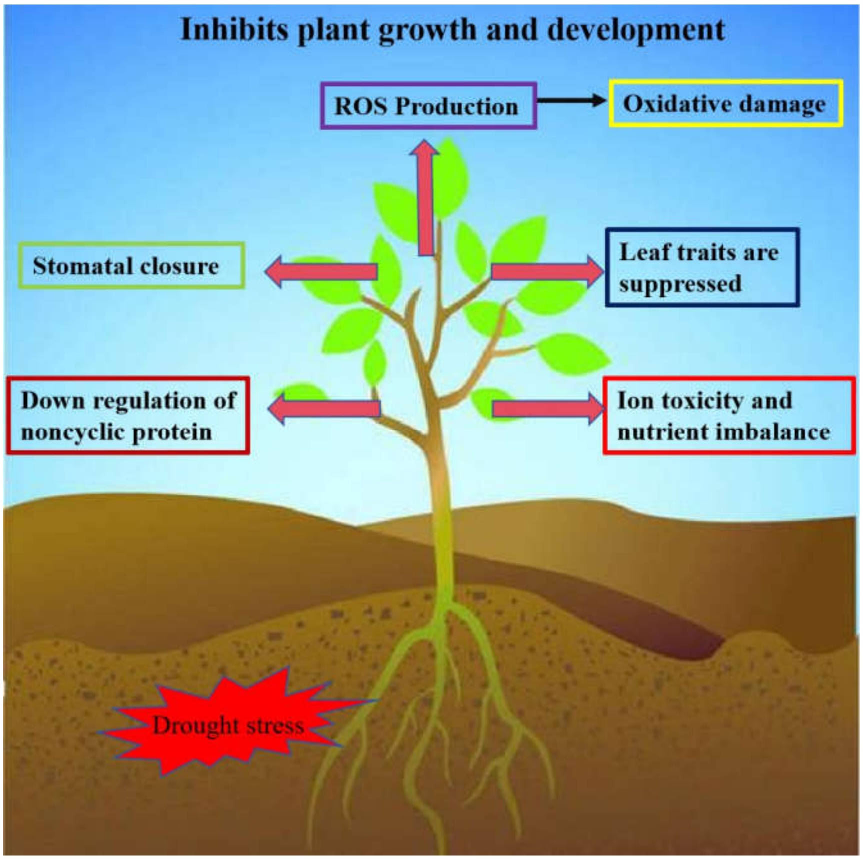

Figure 3. Impacts of drought stress in plants. Overexpression of WRKY transcription factor genes in plants can can reduce a ROS production, stomatal closure, down regulation of noncyclic protein, leaf traits are suppressed and ion toxicity and nutrient imbalance. This allows plants to improve their water retention capacity to cope with plant survival rate under drought stress.

2.2. WRKY Transcription Factors Involved in Response to Temperature Stress

Temperature is considered the major abiotic stress for plants. Extreme high or low temperatures can lead to severe effects on plants, resulting in plant mortality and extensive agricultural economic losses. It is therefore important to increase the tolerance of plant cells to drastic changes in temperature and is necessary to protect food production. WRKY transcription factors help plants to resist temperature changes by regulating the expression of genes involved in temperature stress, and they also respond to extreme temperatures by regulating the expression of genes involved in ABA response [58–60].

2.2.1. WRKY Transcription Factors and High Temperature Stress

When the temperature exceeds the maximum upper limit of the temperature to which the plant can adapt, it has an injurious effect on the plant and stunts its growth and development. High can also weaken photosynthesis and enhance respiration, causing plants to over-consume their own energy and causing them to die from long-term starvation. High temperatures can also disrupt the water balance of plants, leading to the accumulation of harmful metabolites in the body. Therefore, high temperature is very important for the normal growth and development of plants. Nowadays, more and more researchers are focusing on high temperature stress in the their study [61,62]. He et al. found the WRKY transcription factor TaWRKY1 and TaWRKY33 was identified in *Triticum aestivum L*. Overexpression of *TaWRKY33* lines showed enhanced heat stress tolerance. *TaWRKY1* was slightly up-regulated by high temperature and ABA and down-regulated by low temperature. TaWRKY33 was involved in the response to high and low temperatures. Overexpression of *TaWRKY1* and *TaWRKY33* activated several stress-related downstream genes and promoted root growth in *Arabidopsis* under various stresses [63]. Wang et al. identified a WRKY family transcription factor *SlWRKY3* that was induced and up-regulated under heat stress, whereas a knockout strain of *wrky3* resulted in reduced heat stress tolerance. Overexpression of *SlWRKY3* accumulated less ROS, whereas *wrky3* knockout lines accumulated more ROS under heat stress. They concluded that *SlWRKY3* activated the expression of a range of abiotic stress-responsive genes involved in ROS scavenging [64]. Wu et al. performed transcriptome analysis of lily (*Lilium longiflorum*) and identified the a WRKY family transcription factor gene *LlWRKY22*, which was activated for expression at high temperatures, and overexpression of *LlWRKY22* in *Lilium longiflorum* increased heat tolerance and activated the expression of heat-related *LlDREB2B* genes, which play a positive role in the regulation of heat tolerance [65]. Balfagón et al. found that the WRKY family transcription factor *AtWRKY48* was able to negatively control *Arabidopsis* acclimation to a combination of high light and heat stress, and that *AtWRKY48* gene expression was declined by jasmonic acid (JA) under this condition [66].

2.2.1. WRKY Transcription Factors and Low Temperature Stress

Temperature is one of the main environmental factors affecting the normal growth of plants and is necessary to ensure normal growth of plants, too low a temperature can cause stress to plants, affecting the growth and development of plants. With the change of global climate, low temperature has become one of the agrometeorological disasters, when the temperature drops to the lowest limit that plants can tolerate, it will cause crop growth obstacles, damage to the fruiting organs, and ultimately lead to the inability of normal growth and fruiting, which will result in a substantial reduction in crop yields. Therefore, the study of the molecular mechanism of plant response to low temperature stress is of great scientific significance to improve the cold tolerance of crops [67,68]. Mi et al. identified a WRKY family transcription factor CsWRKY21 in tea tree, which *CsWRKY21* was induced by low temperatures and expressed 6 times more compared to the control [69]. Yu et al. identified 42 *PgWRKY* genes of seven subclasses in the genome of *Platycodon grandiflorus*. Among them, the expression of *PgWRKY26* increased significantly after 6 h of cold stress [70]. Wang et al. identified a cold-inducible WRKY gene, *PmWRKY57* was cloned in *P. mume*. Overexpressing *PmWRKY57* line increased cold tolerance in *Arabidopsis*. Under cold treatment, the transgenic lines had significantly lower malondialdehyde content and significantly higher superoxide dismutase activity, peroxidase activity, and proline content in leaves than wild-type plants. The expression levels of cold-responsive genes such as *AtCOR6.6*, *AtCOR47*, *AtKIN1*, and *AtRCI2A* were up-regulated in transgenic *Arabidopsis thaliana* leaves compared with the wild type [71]. Liu et al. isolated an uncharacterized WRKY family transcription factor VvWRKY28, in Beichun (*V. vinifera x V.amurensis*). Cold treatments can induce high expression of *VvWRKY28*. Overexpression of *VvWRKY28* lines improved tolerance to low temperature in *Arabidopsis*. Among them, MDA content decreased, chlorophyll and proline content increased, and superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities increased in overexpression of *VvWRKY28* lines. In addition, WRKY28 can be associated with the regulation of the expression of downstream genes associated under cold stress (*RAB18*, *COR15A*, *ERD10*, *PIF4*, *COR47* and *ICS1*) [72]. Wang et al. identified a new WRKY family transcription factor SlWRKY50 in *Solanum lycopersicum.* SlWRKY50 responds to cold stimuli and plays a key role in JA biosynthesis. Overexpression of *SlWRKY50* lines increased cold resistance in tomato, and leading to higher levels of Fv/Fm, antioxidative enzymes, allene oxide synthase expression, and JA accumulation [73].

2.3. WRKY Transcription Factors in Response to Salt Stress

When the salt concentration in the soil is too high, it leads to dehydration of plant cells, affecting and nutrient absorption, thus inhibiting normal root growth. Salt is also capable of causing ionic toxicity in plants, leading to an ionic imbalance in the plant, affecting the osmotic pressure balance inside and outside the root cells, leading to cell swelling or shrinkage, and in severe cases, cell death. Salt therefore plays an important role in plant growth and development [74–76]. Huang et al. isolated a WRKY family transcription factor OsWRKY50, overexpression *OsWRKY50* lines enhanced salt stress tolerance in plants. *OsWRKY50* transcription was repressed under salt stress conditions but activated after ABA treatment. OsWRKY50 was able to bind to the promoter of *OsNCED5* and repress its transcription [77]. Huang et al. identified a new WRKY family transcription factor OsWRKY54. Salt stress resulted in rapid induction of *OsWRKY54* expression in roots. The *wrky54* mutant led to greater sodium accumulation in shoots and enhanced the sensitivity of rice plants to salt stress. OsWRKY54 regulates the expression of *OsHKT1;5*, this is an essential gene related to salt tolerance, OsWRKY54 regulates the expression of *OsHKT1;5* by directly binding to the W-box motif in its promoter [78]. Fang et al. found a new transcription factor gene *ZmWRKY86* in *Zea mays L.*, whose expression was up-regulated by salt stress. The *wrky86* mutant enhanced plant tolerance to salt stress, with higher viability, catalase activity, and K^+ content, and lower malondialdehyde accumulation and Na^+ content under salt stress conditions [79]. Ma et al. found *WRKY57* is able to negatively regulate plant salt stress response in tomato by directly attenuating the transcription of salt-responsive genes *SlRD29B* and *SlDREB2* and ion homeostasis gene *SlSOS1* [80]. Yu et al. found *TaWRKY17* expression was up-regulated by salt, drought, hydrogen peroxide (H_2O_2), and ABA treatments in wheat. Overexpression of *TaWRKY17* in *Arabidopsis thaliana* and wheat resulted in a significant increase in plant salt stress tolerance. Among the overexpression *TaWRKY17* plants, SOD, POD and CAT activities were elevated, whereas H_2O_2 and MDA accumulation were reduced [81].

2.4. Role of WRKY Transcription Factors in Plant Response to Heavy Metals Stress

Heavy metal levels in plants that exceed thresholds can affect produce quality and food safety. Heavy metals can also inhibit the growth of plants, resulting in short plants, loss of green leaves, poor root development and other phenomena. Heavy metals can interfere with the normal physiological and metabolic processes of plants, affecting photosynthesis and respiration, leading to poor nutrient uptake and ultimately causing the death of plants and affecting plants yields. If heavy metals accumulate excessively in food crops, human consumption of such excess crops will cause great harm to human health. Therefore, heavy metals are essential for human food security [82–85]. Gu et al. identified that the WRKY transcription factor gene *ZmWRKY64* is enhanced in maize roots and leaves under cadmium stress, and that knocking down the expression of *ZmWRKY64* leads to excessive cadmium accumulation in leaf and root cells, resulting in a cadmium-sensitive phenotype. *ZmSRG7* is a key gene that regulates ROS homeostasis under abiotic stress, and ZmWRKY64 directly enhances the transcription of this gene, thereby regulating maize tolerance in response to cadmium stress [86]. Jia et al. identified a WRKY transcription factor TaWRKY70, that regulates tolerance to the heavy metal cadmium in wheat. Cadmium accumulated in overexpressing *TaWRKY70 Arabidopsis* roots but not in leaf tissues. When *TaWRKY70* was expressed, the net influx of Cd^{2+} into *Arabidopsis* roots was reduced. Overexpression of *TaWRKY70* showed lower electrolyte leakage in *Arabidopsis thaliana*, malondialdehyde, and hydrogen peroxide contents than the wild type, and higher antioxidant enzyme activities than the wild type. TaWRKY70 directly binds to and regulates the expression of *TaCAT5* promoter, which in turn regulates the tolerance of plants to cadmium stress [87]. Xian et al. identified a WRKY transcription factor gene *GmWRKY172* expression was significantly up-regulated under cadmium stress, overexpressing *GmWRKY172* lines exhibited enhanced cadmium tolerance and reduced cadmium content in shoots. Under cadmium stress, transgenic soybean accumulated less MDA and H_2O_2, had higher flavonoids, lignin content and POD activity than wild type [88]. Under cadmium stress, the overexpression *StWRKY6* strain had significantly higher soil and plant analyzer development values and reactive oxygen scavenging enzyme content than the wild type. The ability of cadmium to induce StWRKY6 transcription factors up-regulated the expression of a number of potential genes, including those involved in cadmium chelation *APR2*, *DFRA*, plant defences *VSP2*, *PDF1.4*, toxic substance efflux *ABCG1*, light morphology development *BBX20* and auxin signal *SAUR64/67*. He et al. demonstrated that these genes coordinate the regulation of cadmium tolerance in *StWRKY6* overexpressing lines [89]. A new WRKY transcription factor GmWRKY142 positively regulating cadmium stress was identified by cai et al. *GmWRKY142* was highly expressed in roots and the expression of the gene was significantly up-regulated under cadmium stress, and overexpression of *GmWRKY142* in Arabidopsis and soybean hairy roots significantly enhanced cadmium tolerance. *ATCDT1*, *GmCDT1-1*, and *GmCDT1-2*, encoding cadmium tolerance 1, were induced in the overexpression *GmWRKY142* lines [90].

2.5. WRKY Transcription Factors Involved in Plant Response to Nutritional Element Stress

Nitrogen (N) is one of the most important nutrients in the growth and development of plants, and is a component of organic compounds such as proteins, chlorophyll, nucleic acids and various biological enzymes. Plants mainly obtain inorganic nitrogen nutrients in the form of nitrate nitrogen (NO_3^-) and ammonium nitrogen (NH_4^+) in the soil through the root system. The inorganic nitrogen in the soil that can be used directly by plants is very little, and inorganic nitrogen is easy to leach and volatilise, but also be fixed by the organic matter in the soil, so the effective nitrogen in the soil is far from enough for the normal growth of plants [91–93]. Javed et al. found four genes *ShWRKY13-2, ShWRKY*39-1, *ShWRKY*49-3 and *ShWRKY*125-3 exhibited significant up-regulation in resistance to leaf scald LCP85-384 in two *Saccharum spp* varieties triggered by Xanthomonas albilineans (Xa). In particular, *ShWRKY22-1*, *ShWRKY49-3* and *ShWRKY52-1* acted as negative regulators in both *Saccharum spp* varieties in response to a range of N injection doses [94]. To assess whether nitrogen form affects the synthesis of the high-value terpene metabolite steviol glycosides (SGs) in stevia (*Stevia rebaudiana*), Sun et al. utilised stevia plants to the same nitrogen level with NO_3^- or NH_4^+ and they found that nitrogen form had no significant effect on stevia leaf biomass or total nitrogen content, but that NO_3^- increased the leaf SGs content. Combined transcriptome analysis identified 397 genes that were differentially expressed (DEGs) between NO_3^- and NH_4^+ treatments. It was concluded that NO_3^- could promote leaf SG synthesis through the NO_3^--MYB/WRKY-GGPPS/CPS module [95]. Betalain is a water-soluble nitrogenous pigment, Zhang et al. identified a novel WRKY transcription factor HmoWRKY40 in *Hylocereus monacanthus*. Betalain content and *HmoWRKY40* expression increased rapidly during dragon fruit colouring, and silencing of the *HmoWRKY40* gene led to significant reductions in betacyanin content. HmoWRKY40 binds to the promoter of *HmoCYP76AD1* and activates its expression, thereby regulating betalain biosynthesis in *Hylocereus monacanthus* fruit [96].

Phosphorus (P) is one of the essential nutrients for plant growth and development, and phosphorus deficiency will lead to morphological and physiological changes in plants. Phosphorus deficiency has an effect on photosynthesis, respiration and biosynthetic processes in plants. Phosphorus is also an integral part of plant cells and is closely linked to all plant life activities, playing a vital role in plant growth and development [97–100]. Wang et al. identified a WRKY family of transcription factors OsWRKY108 and OsWRKY21 in rice, and overexpression of these two genes resulted in up-regulation of P_i transporter protein genes, thereby enhancing P_i accumulation [101]. Wang et al. identified the FtWRKY29 transcription factor in *Fagopyrum tataricum Gaertn*, FtWRKY29 regulates the ability to tolerate phosphorus deficiency. Overexpression of *FtWRKY29* in *Arabidopsis* produced transgenic lines that increased phosphorus uptake and regulated anthocyanin accumulation and were less sensitive to low phosphorus-induced stress. Low-phosphorus-responsive genes *PHT1;1*, *PHT1;4*, and *PHO1* were significantly up-regulated in these lines [102]. Liu et al. found that the *GmWRKY46* gene is involved in the regulation of phosphorus deficiency tolerance in soybean. The expression of *GmWRKY46* was significantly higher in low phosphorus-sensitive than in phosphorus-tolerant soybean varieties, and the gene was strongly induced by phosphorus deficiency. The expression patterns of many P-responsive genes, for example *GmPht1;1*, *GmPht1;4*, *GmPTF1*, *GmACP1*, *GmPAP21*, and *GmExpansin-A7* were altered in overexpression of the *GmWRKY46* lines and in *GmWRKY46*-silenced lines [103]. Zhang et al. found overexpression of *OsWRKY21* or *OsWRKY108* caused an increase in Pi accumulation due to elevated expression of phytophosphate transporter protein 1 (*PHT1*). *Oswrky21* and *Oswrky108* double mutants showed decreased P_i accumulation and *OsPHT1;1* expression in a Pi-dependent manner. Their results demonstrate that rice WRKY transcription factors function redundantly to promote P_i uptake by activating *OsPHT1;1* expression under Pi-sufficient conditions [104]. Knockdown of *OsWRKY10* results in increased P_i uptake and accumulation under conditions of P_i sufficiency. OsPHT1;2 results in increased P_i accumulation in *oswrky10*. OsWRKY10 is a transcriptional repressor, induced by Pi transcription, and it is up-regulated by a subset of the PHT1 gene upon its mutation. During P_i starvation, OsWRKY10 protein is degraded via the 26S proteasome. Their results demonstrate that the OsWRKY10-OsPHT1;2 module inhibits P_i uptake only in the presence of P_i sufficient [105].

2.6. WRKY Transcription Factors and Oxidative Stress

Oxidative stress is one of the most severe stresses caused by various other stresses. There are 4 main types of reactive oxygen species in plants: singlet oxygen ($^1O_2$), superoxide (O_2^-), hydroxyl radical (OH) and hydrogen peroxide H_2O_2 . Induction of ROS accumulation in Arabidopsis with salt stress or by treating plants with H_2O_2 or methyl viologen (MV) induces the expression of multiple genes encoding WRKY family transcription factors [106–109]. Jia et al. identified a WRKY family of transcription factors GhWRKY68 promoter-driven β-glucuronidase activity is enhanced after exposure to drought, salt, ABA and H_2O_2. *GhWRKY68* overexpression lines showed reduced resistance to drought and salt, and reduced tolerance to oxidative stress, which was associated with accumulation of ROS, reduced enzyme activity, increased MDA content and altered expression of ROS-related genes [110]. Sun et al. found *AtWRKY53* overexpression lines were highly sensitive to drought stress compared to Col-0 plants. Activated expression of *AtWRKY53* inhibited stomatal closure by reducing the H_2O_2 content of guard cells. AtWRKY53 could bind directly to the qua-quine starch (*QQS*, AT3G30720) gene promoter sequence and leading to enhanced starch metabolism [111].

3. Conclusion and Prospects

Due to the continuous changes in the global climate environment, plants often suffer from different forms of biotic and abiotic stress during their growth and development. In order to cope with these adverse conditions, plants have developed a complete coping system in the process of evolution. Plant adversities are dealt with through protein regulation of the expression level of downstream genes or interactions between proteins. Because transcription factors contain different gene binding sites, they can often regulate the expression of multiple downstream genes. Therefore, focusing on the functions of transcription factors has become a major issue in crops. As a large class of important transcription factors in plants, WRKY transcription factors genes play a key role throughout a plant's life cycle. With the continuous development of gene editing and third-generation sequencing technology, many researchers have verified the functions of WRKY family members in different types of plants, and found and proved that WRKY genes play a key role in plant growth and development, biotic and abiotic stresses [112–116]. In order to investigate the phylogeny and evolutionary relationships of WRKY family genes in different species, we constructed phylogenetic trees of the amino acid sequences of some WRKY family transcription factors in *Glycine max*, *Arabidopsis thaliana* and *Oryza sativa* using MEGA 11.0 software [117]. Among them, we found that GmWRKY58 and GmWRKY76 were highly related, GmWRKY46 and GmWRKY43 were highly related, AtWRKY39 and OsGmWRKY87 were highly related, and OsWRKY73 and OsGmWRKY97 were highly related, which indicated that the WRKY family of transcription factors were highly related in various species have close affinities between them, and it is possible that WRKY family transcription factors have similar functions in different species (Figure 4).

Future research on WRKY transcription factors can start from the following aspects, such as the use of CRISPR/Cas9 technology to knock out the WRKY family transcription factor genes and overexpression of genes and other technologies, to cultivate new varieties of resilient and excellent crops, and to promote the sustainable development of agriculture. To further investigate the upstream and downstream regulators and target genes of WRKY family transcription factor genes by using existing technologies, to analyse their regulatory networks in response to adversity stress, and to elucidate the molecular mechanisms of WRKY and plant response to abiotic stresses.

Nowadays, scientists mainly focus on the response of WRKY transcription factors to common abiotic stresses such as drought, cold, salt, heavy metals (Table 2). While the molecular mechanisms of WRKY transcription factors in response to chemical agent stresses are less reported. In today's increasingly developed industry, chemical pollutants such as car exhaust, haze and pesticides are extremely harmful to crops. The main component of automobile exhaust and haze is sulfide, and SO_2 in the atmosphere generates SO_3 under the action of sunlight, water vapour and drifting dust and so on. Firstly, while SO_3 falls to the ground in the form of rainfall and drenches the plants, damaging the waxy protective layer of the epidermis of the plant leaves and impairing the normal transpiration and gas exchange process. Secondly, acid rain also destroys a class of alkaline nutrients such as potassium, calcium and phosphorus in the soil, leading to withering and death of plants that cannot absorb nutrients in soils with insufficient fertility. Excessive use of pesticides will inhibit the growth and development of plants, resulting in short plants, small leaf area and yellowing of leaf colour. The toxicity of pesticides can also lead to cell membrane rupture, cytoplasmic leakage and ultimately affect the normal growth and development of plants. Today, people are more and more concerned about crop security, if we pay more attention to focus on the molecular mechanism of WRKY transcription factors and chemical reagents in the future, this will provide a guarantee for crop security.

In summary, the WRKY family of transcription factors is critical for plant growth and development as well as regulation in plant response to abiotic stresses. In the future, we will pay more attention to the mechanism by which WRKY transcription factors can regulate downstream target genes in response to abiotic stresses, which can provide more theoretical basis for the improvement of food production and safety.

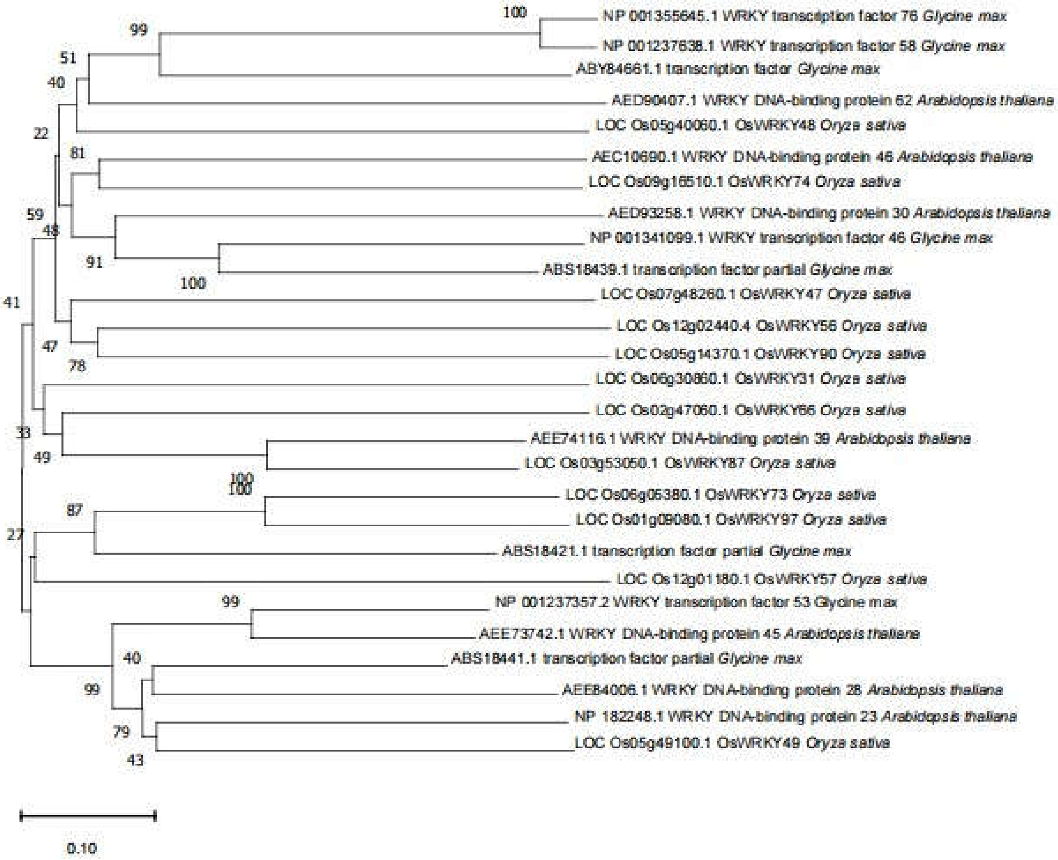

Figure 4. Phylogenetic tree WRKYs family genes in *Glycine max*, *Arabidopsis thaliana* and *Oryza sativa*. Phylogenetic tree of WRKY transcription factors proteins in selected angiosperms. The WRKY family gene sequences of *Glycine max*, *Arabidopsis thaliana* and *Oryza sativa* were retrieved using the China National Rice Data Center (https://www.ricedata.cn/) and NCBI (https://www.ncbi.nlm.nih.gov/). The phylogenetic tree was constructed using MEGA version 11.0 with the bootstrap method based on full amino acid sequences. Numbers next to the branches show the percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates).

Table 2. Abiotic stress responsive the WRKY transcription factors in plants.

Abiotic Stress Type	WRKY transcription factors	Species	Expression pattern	Reference
Heat	AtWRKY39	*Arabidopsis thaliana L.*	Increase	[118]
Boron	AtWRKY47	*Arabidopsis thaliana L.*	Decrease	[119]
Cadmium	AtWRKY13	*Arabidopsis thaliana L.*	Increase	[120]
Salt	AtWRKY28	*Arabidopsis thaliana L.*	Increase	[121]
Salt	AtWRKY33	*Arabidopsis thaliana L.*	Increase	[122]
Salt	AtWRKY46	*Arabidopsis thaliana L.*	Increase	[123]
Salt, drought	GmWRKY12	*Glycine max L.*	Increase	[124]
Salt, drought	GmWRKY16	*Glycine max L.*	Increase	[125]
Salt	GmWRKY20	*Glycine max L.*	Increase	[126]
Salt, drought	GmWRKY27	*Glycine max L.*	Increase	[127]
Salt, drought	GmWRKY54	*Glycine max L.*	Increase	[128]
Salt	GmWRKY144, 165	*Glycine max L.*	Increase	[129]
Salt	ZmWRKY17	*Zea mays L.*	Decrease	[130]
Salt	ZmWRKY86	*Zea mays L.*	Decrease	[79]
Drought	ZmWRKY104	*Zea mays L.*	Increase	[131]
Salt	OsWRKY50	*Oryza sativa*	Increase	[77]
Cold	OsWRKY63	*Oryza sativa*	Decrease	[18]
Cold	OsWRKY76	*Oryza sativa*	Increase	[132]

Salt	OsWRKY42	*Oryza sativa*	Increase	[133]
Drought	OsWRKY55	*Oryza sativa*	Decrease	[134]
Drought	OsWRKY5	*Oryza sativa*	Decrease	[135]
Drought	OsWRKY97	*Oryza sativa*	Increase	[136]
Aluminum	OsWRKY22	*Oryza sativa*	Decrease	[137]
Salt, drought	OsWRKY87	*Oryza sativa*	Increase	[138]

Author ContriAuthor Contributions: All the authors contributed to the present form of the manuscript. Z.M. collected the data and drafted the manuscript; Z.M., L.H., and W.J. edited the manuscript; Z.M. and L.H. created the figures and tables; Z.M. and W.J. supervised; Z.M. and L.H. and W.J. finalised and approved the final version of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Natural Science Foundation of China (Grant No. 32201695). Open Access funding provided by the Max Planck Society.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no competing interests.

References

1. Bailey-Serres, J.; Parker, J.E.; Ainsworth, E.A.; Oldroyd, G.E.D.; Schroeder, J.I. Genetic strategies for improving crop yields. *Nature*. **2019**, 575, 109-118.
2. Xiao, J.; Liu, B.; Yao, Y.; Guo, Z.; Jia, H.; Kong, L.; Zhang, A.; Ma, W.; Ni, Z.; Xu, S.; Lu, F.; Jiao, Y.; Yang, W.; Lin, X.; Sun, S.; Lu, Z.; Gao, L.; Zhao, G.; Cao, S.; Chen, Q.; Zhang, K.; Wang, M.; Wang, M.; Hu, Z.; Guo, W.; Li, G.; Ma, X.; Li, J.; Han, F.; Fu, X.; Ma, Z.; Wang, D.; Zhang, X.; Ling, H.Q.; Xia, G.; Tong, Y.; Liu, Z.; He, Z.; Jia, J.; Chong, K. Wheat genomic study for genetic improvement of traits in China. *Sci China Life Sci*. **2022**, 65, 1718-1775.
3. Valliyodan, B.; Ye, H.; Song, L.; Murphy, M.; Shannon, J.G.; Nguyen, H.T. Genetic diversity and genomic strategies for improving drought and waterlogging tolerance in soybeans. *J Exp Bot*. **2017**, 68, 1835-1849.
4. Thudi, M.; Palakurthi, R.; Schnable, J.C.; Chitikineni, A.; Dreisigacker, S.; Mace, E.; Srivastava, R.K.; Satyavathi, C.T.; Odeny, D.; Tiwari, V.K.; Lam, H.M.; Hong, Y.B.; Singh, V.K.; Li, G.; Xu, Y.; Chen, X.; Kaila, S.; Nguyen, H.; Sivasankar, S.; Jackson, S.A.; Close, T.J.; Shubo, W.; Varshney, R.K. Genomic resources in plant breeding for sustainable agriculture. *J Plant Physiol*. **2021**, 257, 153351.
5. Ma, Z.; Jin, Y.M.; Wu, T.; Hu, L.; Zhang, Y.; Jiang, W.; Du, X. OsDREB2B, an AP2/ERF transcription factor, negatively regulates plant height by conferring GA metabolism in rice. *Front Plant Sci*. **2022**, 13, 1007811.
6. Zhang, H.; Zhu, J.; Gong, Z.; Zhu, J.K. Abiotic stress responses in plants. *Nat Rev Genet*. **2022**, 23, 104-119.
7. Ma, Z.; Wu, T.; Huang, K.; Jin, Y.M.; Li, Z.; Chen, M.; Yun, S.; Zhang, H.; Yang, X.; Chen, H.; Bai, H.; Du, L.; Ju, S.; Guo, L.; Bian, M.; Hu, L.; Du, X.; Jiang, W. A Novel AP2/ERF Transcription Factor, OsRPH1, Negatively Regulates Plant Height in Rice. *Front Plant Sci*. **2020**, 11, 709.
8. Zhang, H.; Zhao, Y.; Zhu, J.K. Thriving under Stress: How Plants Balance Growth and the Stress Response. *Dev Cell*. **2020**, 55, 529-543.
9. Huang, S.; Ma, Z.; Hu, L.; Huang, K.; Zhang, M.; Zhang, S.; Jiang, W.; Wu, T.; Du, X. Involvement of rice transcription factor OsERF19 in response to ABA and salt stress responses. *Plant Physiol Biochem*. **2021**, 167, 22-30.
10. Ma, Z.; Hu, L. MicroRNA: A Dynamic Player from Signalling to Abiotic Tolerance in Plants. *Int J Mol Sci*. **2023**, 24, 11364.
11. Gupta, A.; Rico-Medina, A.; Caño-Delgado, A.I. The physiology of plant responses to drought. *Science*. **2020**, 368, 266-269.
12. Ma, Z.; Hu, L.; Jiang, W. Understanding AP2/ERF Transcription Factor Responses and Tolerance to Various Abiotic Stresses in Plants: A Comprehensive Review. *Int J Mol Sci*. **2024**, 25, 893.
13. Yamada, Y.; Sato, F. Transcription factors in alkaloid biosynthesis. *Int Rev Cell Mol Biol*. **2013**, 305, 339-82.
14. Wang, H.; Chen, W.; Xu, Z.; Chen, M.; Yu, D. Functions of WRKYs in plant growth and development. *Trends Plant Sci*. **2023**, 28, 630-645.
15. Guo, X.; Ullah, A.; Siuta, D.; Kukfisz, B.; Iqbal, S. Role of WRKY Transcription Factors in Regulation of Abiotic Stress Responses in Cotton. *Life (Basel)*. **2022**, 12, 1410.
16. Su, M.; Zuo, W.; Wang, Y.; Liu, W.; Zhang, Z.; Wang, N.; Chen, X. The WKRY transcription factor MdWRKY75 regulates anthocyanins accumulation in apples (Malus domestica). *Funct Plant Biol*. **2022**, 49, 799-809.

17. Yin, Y.; Fu, H.; Mi, F.; Yang, Y.; Wang, Y.; Li, Z.; He, Y.; Yue, Z. Genomic characterization of WRKY transcription factors related to secoiridoid biosynthesis in Gentiana macrophylla. *BMC Plant Biol*. **2024**, 24, 66.
18. Zhang, M.; Zhao, R.; Huang, K.; Huang, S.; Wang, H.; Wei, Z.; Li, Z.; Bian, M.; Jiang, W.; Wu, T.; Du, X. The OsWRKY63-OsWRKY76-OsDREB1B module regulates chilling tolerance in rice. *Plant J*. **2022**, 112, 383-398.
19. Ma, J.; Li, C.; Sun, L.; Ma, X.; Qiao, H.; Zhao, W.; Yang, R.; Song, S.; Wang, S.; Huang, H. The SlWRKY57-SlVQ21/SlVQ16 module regulates salt stress in tomato. *J Integr Plant Biol*. **2023**, 65, 2437-2455.
20. Devaiah, B.N.; Karthikeyan, A.S.; Raghothama, K.G. WRKY75 transcription factor is a modulator of phosphate acquisition and root development in Arabidopsis. *Plant Physiol*. **2007**, 143, 1789-801.
21. Eulgem, T.; Rushton, P.J.; Robatzek, S.; Somssich, I.E. The WRKY superfamily of plant transcription factors. *Trends Plant Sci*. **2000**, 5, 199-206.
22. Ishihama, N.; Yoshioka, H. Post-translational regulation of WRKY transcription factors in plant immunity. *Curr Opin Plant Biol*. **2012**, 15, 431-7.
23. Lee, S.W.; Han, S.W.; Sririyanum, M.; Park, C.J.; Seo, Y.S.; Ronald, P.C. A type I-secreted, sulfated peptide triggers XA21-mediated innate immunity. *Science*. **2009**, 326, 850-3.
24. Chen, L.; Song, Y.; Li, S.; Zhang, L.; Zou, C.; Yu, D. The role of WRKY transcription factors in plant abiotic stresses. *Biochim Biophys Acta*. **2012**, 1819, 120-8.
25. Grzechowiak, M.; Ruszkowska, A.; Sliwiak, J.; Urbanowicz, A.; Jaskolski, M.; Ruszkowski, M. New aspects of DNA recognition by group II WRKY transcription factor revealed by structural and functional study of AtWRKY18 DNA binding domain. *Int J Biol Macromol*. **2022**, 213, 589-601.
26. Rushton, P.J.; Somssich, I.E.; Ringler, P.; Shen, Q.J. WRKY transcription factors. *Trends Plant Sci*. **2010**, 15, 247-58.
27. Wani, S.H.; Anand, S.; Singh, B.; Bohra, A.; Joshi, R. WRKY transcription factors and plant defense responses: latest discoveries and future prospects. *Plant Cell Rep*. **2021**, 40, 1071-1085.
28. Li, W.; Pang, S.; Lu, Z.; Jin, B. Function and Mechanism of WRKY Transcription Factors in Abiotic Stress Responses of Plants. *Plants (Basel)*. **2020**, 9, 1515.
29. Ulker, B.; Somssich, I.E. WRKY transcription factors: from DNA binding towards biological function. *Curr Opin Plant Biol*. **2004**, 7, 491-8.
30. Wu, K.L.; Guo, Z.J.; Wang, H.H.; Li, J. The WRKY family of transcription factors in rice and Arabidopsis and their origins. *DNA Res*. **2005**, 12, 9-26.
31. Schmutz, J.; Cannon, S.B.; Schlueter, J.; Ma, J.; Mitros, T.; Nelson, W.; Hyten, D.L.; Song, Q.; Thelen, J.J.; Cheng, J.; Xu, D.; Hellsten, U.; May, G.D.; Yu, Y.; Sakurai, T.; Umezawa, T.; Bhattacharyya, M.K.; Sandhu, D.; Valliyodan, B.; Lindquist, E.; Peto, M.; Grant, D.; Shu, S.; Goodstein, D.; Barry, K.; Futrell-Griggs, M.; Abernathy, B.; Du, J.; Tian, Z.; Zhu, L.; Gill, N.; Joshi, T.; Libault, M.; Sethuraman, A.; Zhang, X.C.; Shinozaki, K.; Nguyen, H.T.; Wing, R.A.; Cregan, P.; Specht, J.; Grimwood, J.; Rokhsar, D.; Stacey, G.; Shoemaker, R.C.; Jackson, S.A. Genome sequence of the palaeopolyploid soybean. *Nature*. **2010**, 463, 178-83.
32. Mangelsen, E.; Kilian, J.; Berendzen, K.W.; Kolukisaoglu, U.H.; Harter, K.; Jansson, C.; Wanke, D. Phylogenetic and comparative gene expression analysis of barley (Hordeum vulgare) WRKY transcription factor family reveals putatively retained functions between monocots and dicots. *BMC Genomics*. **2008**, 9, 194.
33. Ling, J.; Jiang, W.; Zhang, Y.; Yu, H.; Mao, Z.; Gu, X.; Huang, S.; Xie, B. Genome-wide analysis of WRKY gene family in Cucumis sativus. *BMC Genomics*. **2011**, 12, 471.
34. Huang, S.; Gao, Y.; Liu, J.; Peng, X.; Niu, X.; Fei, Z.; Cao, S.; Liu, Y. Genome-wide analysis of WRKY transcription factors in Solanum lycopersicum. *Mol Genet Genomics*. **2012**, 287, 495-513.
35. Liu, T.; Yu, E.; Hou, L.; Hua, P.; Zhao, M.; Wang, Y.; Hu, J.; Zhang, M.; Wang, K.; Wang, Y. Transcriptome-Based Identification, Characterization, Evolutionary Analysis, and Expression Pattern Analysis of the WRKY Gene Family and Salt Stress Response in Panax ginseng. *Horticulturae.* **2022**, 8, 756.
36. Matos, M.K.D.S.; Benko-Iseppon, A.M.; Bezerra-Neto, J.P.; Ferreira-Neto, J.R.C.; Wang, Y.; Liu, H.; Pandolfi, V.; Amorim, L.L.B.; Willadino, L.; do, Vale, Amorim T.C.; Kido, E.A.; Vianello, R.P.; Timko, M.P.; Brasileiro-Vidal, A.C. The WRKY transcription factor family in cowpea: Genomic characterization and transcriptomic profiling under root dehydration. *Gene.* **2022**, 823, 146377.
37. Zheng, J.; Zhang, Z.; Tong, T.; Fang, Y.; Zhang, X.; Niu, C.; Li, J.; Wu, Y.; Xue, D.; Zhang, X. Genome-Wide Identification of WRKY Gene Family and Expression Analysis under Abiotic Stress in Barley. *Agronomy.* **2021**, 11, 521.
38. Liu, S.; Zhang, C.; Guo, F.; Sun, Q.; Yu, J.; Dong, T.; Wang, X.; Song, W.; Li, Z.; Meng, X.; Zhu, M. A systematical genome-wide analysis and screening of WRKY transcription factor family engaged in abiotic stress response in sweetpotato. *BMC Plant Biol*. **2022**, 22, 616.
39. Yao, H.; Yang, T.; Qian, J.; Deng, X.; Dong, L. Genome-Wide Analysis and Exploration of WRKY Transcription Factor Family Involved in the Regulation of Shoot Branching in Petunia. *Genes (Basel)*. **2022**, 13, 855.

40. Cheng, Y.; Luo, J.; Li, H.; Wei, F.; Zhang, Y.; Jiang, H.; Peng, X. Identification of the WRKY Gene Family and Characterization of Stress-Responsive Genes in Taraxacum kok-saghyz Rodin. *Int J Mol Sci*. **2022**, 23, 10270.
41. Zhang, C.; Wang, W.; Wang, D.; Hu, S.; Zhang, Q.; Wang, Z.; Cui, L. Genome-Wide Identification and Characterization of the WRKY Gene Family in Scutellaria baicalensis Georgi under Diverse Abiotic Stress. *Int J Mol Sci*. **2022**, 23, 4225.
42. Chen, C.; Xie, F.; Shah, K.; Hua, Q.; Chen, J.; Zhang, Z.; Zhao, J.; Hu, G.; Qin, Y. Genome-Wide Identification of WRKY Gene Family in Pitaya Reveals the Involvement of HmoWRKY42 in Betalain Biosynthesis. *Int J Mol Sci*. **2022**, 23, 10568.
43. Nan, H.; Gao, L.Z. Genome-Wide Analysis of WRKY Genes and Their Response to Hormone and Mechanic Stresses in Carrot. *Front Genet*. **2019**, 10, 363.
44. Liu, Z., Saiyinduleng.; Chang, Q.; Cheng, C.; Zheng, Z.; Yu, S. Identification of yellowhorn (Xanthoceras sorbifolium) WRKY transcription factor family and analysis of abiotic stress response model. *Journal of Forestry Research*. **2021**, 32, 987-1004.
45. Du, Z.; You, S.; Zhao, X.; Xiong, L.; Li, J. Genome-Wide Identification of WRKY Genes and Their Responses to Chilling Stress in Kandelia obovata. *Front Genet*. **2022**, 13, 875316.
46. Ciolkowski, I.; Wanke, D.; Birkenbihl, R.P.; Somssich, I.E. Studies on DNA-binding selectivity of WRKY transcription factors lend structural clues into WRKY-domain function. *Plant Mol Biol*. **2008** 68, 81-92.
47. Maeo, K.; Hayashi, S.; Kojima-Suzuki, H.; Morikami, A.; Nakamura, K. Role of conserved residues of the WRKY domain in the DNA-binding of tobacco WRKY family proteins. *Biosci Biotechnol Biochem*. **2001**, 65, 2428-36.
48. Hrmova, M.; Hussain, S.S. Plant Transcription Factors Involved in Drought and Associated Stresses. *Int J Mol Sci*. **2021**, 22, 5662.
49. Khoso, M.A.; Hussain, A.; Ritonga, F.N.; Ali, Q.; Channa, M.M.; Alshegaihi, R.M.; Meng, Q.; Ali, M.; Zaman, W.; Brohi, R.D.; Liu, F.; Manghwar, H. WRKY transcription factors (TFs): Molecular switches to regulate drought, temperature, and salinity stresses in plants. *Front Plant Sci*. **2022**, 13, 1039329.
50. Wang, H.; Cheng, X.; Yin, D.; Chen, D.; Luo, C.; Liu, H.; Huang, C. Advances in the Research on Plant WRKY Transcription Factors Responsive to External Stresses. *Curr Issues Mol Biol*. **2023**, 45, 2861-2880.
51. Krupinska, K.; Desel, C.; Frank, S.; Hensel, G. WHIRLIES Are Multifunctional DNA-Binding Proteins With Impact on Plant Development and Stress Resistance. *Front Plant Sci*. **2022**, 13, 880423.
52. Qin, Y.; Yu, H.; Cheng, S.; Liu, Z.; Yu, C.; Zhang, X.; Su, X.; Huang, J.; Shi, S.; Zou, Y.; Ma, F.; Gong, X. Genome-Wide Analysis of the WRKY Gene Family in Malus domestica and the Role of MdWRKY70L in Response to Drought and Salt Stresses. *Genes (Basel)*. **2022**, 13, 1068.
53. Liu, Y.; Cao, Y. GmWRKY17-mediated transcriptional regulation of GmDREB1D and GmABA2 controls drought tolerance in soybean. *Plant Mol Biol*. **2023**, 113, 157-170.
54. Duan, D.; Yi, R.; Ma, Y.; Dong, Q.; Mao, K.; Ma, F. Apple WRKY transcription factor MdWRKY56 positively modulates drought stress tolerance. *Environ. Exp. Bot*. **2023**, 212, 105400.
55. Zhang, P.; Chao, R.; Qiu, L.; Ge, W.; Liang, J.; Wen, P. ChaWRKY40 Enhances Drought Tolerance of 'Dawei' Hazelnuts by Positively Regulating Proline Synthesis. *Forests*. **2024**, 15, 407.
56. Wang, D.; Chen, Q.; Chen, W.; Liu, X.; Xia, Y.; Guo, Q.; Jing, D.; Liang, G. A WRKY Transcription Factor, EjWRKY17, from Eriobotrya japonica Enhances Drought Tolerance in Transgenic Arabidopsis. *Int J Mol Sci*. **2021**, 22, 5593.
57. Huang, Z.; Wang, J.; Li, Y.; Song, L.; Chen, D.; Liu, L.; Jiang, C.Z. A WRKY Protein, MfWRKY40, of Resurrection Plant Myrothamnus flabellifolia Plays a Positive Role in Regulating Tolerance to Drought and Salinity Stresses of Arabidopsis. *Int J Mol Sci*. **2022**, 23, 8145.
58. Hussain, A.; Noman, A.; Khan, M.I.; Zaynab, M.; Aqeel, M.; Anwar, M.; Ashraf, M.F.; Liu, Z.; Raza, A.; Mahpara, S.; Bakhsh, A.; He, S. Molecular regulation of pepper innate immunity and stress tolerance: An overview of WRKY TFs. *Microb Pathog*. **2019**, 135, 103610.
59. Cheng, Z.; Luan, Y.; Meng, J.; Sun, J.; Tao, J.; Zhao, D. WRKY Transcription Factor Response to High-Temperature Stress. *Plants (Basel)*. **2021**, 10, 2211.
60. Yoon, Y.; Seo, D.H.; Shin, H.; Kim, H.J.; Kim, C.M.; Jang, G. The Role of Stress-Responsive Transcription Factors in Modulating Abiotic Stress Tolerance in Plants. *Agronomy*. **2020**, 10, 788.
61. Li, S.; Khoso, M. A.; Wu, J.; Yu, B.; Wagan, S.; Liu, L. Exploring the Mechanisms of WRKY transcription factors and Regulated Pathways in Response to Abiotic Stress. *Plant Stress*. **2024**, 100429.
62. Manna, M.; Thakur, T.; Chirom, O.; Mandlik, R.; Deshmukh, R.; Salvi, P. Transcription factors as key molecular target to strengthen the drought stress tolerance in plants. *Physiol Plant*. **2021**, 172, 847-868.
63. He, G.H.; Xu J.Y.; Wang, Y.X.; Liu, J.M.; Li, P.S.; Chen, M.; Ma, Y.Z.; Xu, Z.S. Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in Arabidopsis. *BMC Plant Biol*. **2016**, 16, 116.
64. Wang, Y.; Gai, W.; Yuan, L.; Shang, L.; Li, F.; Gong, Z.; Ge, P.F.; Wang, Y.R.; Tao, J.B.; Zhang, X.Y.; Dong, H.Q.; Zhang, Y.Y. Heat-inducible SlWRKY3 confers thermotolerance by activating the SlGRXS1 gene cluster in tomato. *Hortic. Plant J*. **2023.**

65. Wu, Z.; Li, T.; Cao, X.; Zhang, D.; Teng, N. Lily WRKY factor LlWRKY22 promotes thermotolerance through autoactivation and activation of LlDREB2B. *Hortic Res*. **2022**, 9, 186.
66. Balfagón, D.; Pascual, L.S.; Sengupta, S.; Halliday, K.J.; Gómez-Cadenas, A.; Peláez-Vico, MÁ.; Sinha, R.; Mittler, R.; Zandalinas, S.I. WRKY48 negatively regulates plant acclimation to a combination of high light and heat stress. *Plant J*. **2024**, 117, 1642-1655.
67. Ritonga, F.N.; Ngatia, J.N.; Wang, Y.; Khoso, M.A.; Farooq, U.; Chen, S. AP2/ERF, an important cold stress-related transcription factor family in plants: A review. *Physiol Mol Biol Plants*. **2021**, 27, 1953-1968.
68. Xu, G.; Li, L.; Zhou, J.; Lyu, D.; Zhao, D.; Qin, S. Comparison of transcriptome and metabolome analysis revealed differences in cold resistant metabolic pathways in different apple cultivars under low temperature stress. *Hortic. Plant J*. **2023**, 9, 183-198.
69. Mi, X.; Tang, M.; Zhu, J.; Shu, M.; Wen, H.; Zhu, J.; Wei, C. Alternative splicing of CsWRKY21 positively regulates cold response in tea plant. *Plant Physiol Biochem*. **2024**, 208, 108473.
70. Yu, H.; Li, J.; Chang, X.; Dong, N.; Chen, B.; Wang, J.; Zha, L.; Gui, S. Genome-wide identification and expression profiling of the WRKY gene family reveals abiotic stress response mechanisms in Platycodon grandiflorus. *Int J Biol Macromol*. **2024**, 257, 128617.
71. Wang, Y.; Dong, B.; Wang, N.; Zheng, Z.; Yang, L.; Zhong, S.; Fang, Q.; Xiao, Z.; Zhao, H. A WRKY Transcription Factor PmWRKY57 from Prunus mume Improves Cold Tolerance in Arabidopsis thaliana. *Mol Biotechnol*. **2023**, 65, 1359-1368.
72. Liu, W.; Liang, X.; Cai, W.; Wang, H.; Liu, X.; Cheng, L.; Song, P.; Luo, G.; Han, D. Isolation and Functional Analysis of VvWRKY28, a Vitis vinifera WRKY Transcription Factor Gene, with Functions in Tolerance to Cold and Salt Stress in Transgenic Arabidopsis thaliana. *Int J Mol Sci*. **2022**, 23, 13418.
73. Wang, L.; Chen, H.; Chen, G.; Luo, G.; Shen, X.; Ouyang, B.; Bie, Z. Transcription factor SlWRKY50 enhances cold tolerance in tomato by activating the jasmonic acid signaling. *Plant Physiol*. **2024**, 194, 1075-1090.
74. Zhao, S.; Zhang, Q.; Liu, M.; Zhou, H.; Ma, C.; Wang, P. Regulation of Plant Responses to Salt Stress. *Int J Mol Sci*. **2021**, 22, 4609.
75. Van, Zelm E.; Zhang, Y.; Testerink, C. Salt Tolerance Mechanisms of Plants. *Annu Rev Plant Biol*. **2020**, 71, 403-433.
76. Gupta, A.; Mishra, R.; Rai, S.; Bano, A.; Pathak, N.; Fujita, M.; Kumar, M.; Hasanuzzaman, M. Mechanistic Insights of Plant Growth Promoting Bacteria Mediated Drought and Salt Stress Tolerance in Plants for Sustainable Agriculture. *Int J Mol Sci*. **2022**, 23, 3741.
77. Huang, S.; Hu, L.; Zhang, S.; Zhang, M.; Jiang, W.; Wu, T.; Du, X. Rice OsWRKY50 Mediates ABA-Dependent Seed Germination and Seedling Growth, and ABA-Independent Salt Stress Tolerance. *Int J Mol Sci*. **2021**, 22, 8625.
78. Huang, J.; Liu, F.; Chao, D.; Xin, B.; Liu, K.; Cao, S.; Chen, X.; Peng, L.; Zhang, B.; Fu, S.; Xia, J. The WRKY Transcription Factor OsWRKY54 Is Involved in Salt Tolerance in Rice. *Int J Mol Sci*. **2022**, 23, 11999.
79. Fang, X.; Li, W.; Yuan, H.; Chen, H.; Bo, C.; Ma, Q.; Cai, R. Mutation of ZmWRKY86 confers enhanced salt stress tolerance in maize. *Plant Physiol Biochem*. **2021**, 167, 840-850.
80. Ma J.; Li C.; Sun L.; Ma X.; Qiao H.; Zhao W.; Yang R.; Song S.; Wang S.; Huang H. The SlWRKY57-SlVQ21/SlVQ16 module regulates salt stress in tomato. J Integr Plant Biol. 2023 Nov;65(11):2437-2455.
81. Yu, Y.; Wu, Y.; He, L. A wheat WRKY transcription factor TaWRKY17 enhances tolerance to salt stress in transgenic Arabidopsis and wheat plant. *Plant Mol Biol*. **2023**, 113, 171-191.
82. Mirza, Z.; Haque, M.M.; Gupta, M. WRKY transcription factors: a promising way to deal with arsenic stress in rice. *Mol Biol Rep*. **2022**, 49, 10895-10904.
83. Khan, I.; Asaf, S.; Jan, R.; Bilal, S.; Lubna.; Khan, A.L.; Kim, K.M.; Al-Harrasi, A. Genome-wide annotation and expression analysis of WRKY and bHLH transcriptional factor families reveal their involvement under cadmium stress in tomato (Solanum lycopersicum L.). *Front Plant Sci*. **2023**, 14, 1100895.
84. Abdullah.; Wani, K.I.; Naeem, M.; Jha, P.K.; Jha, U.C.; Aftab, T.; Prasad, P.V.V. Systems biology of chromium-plant interaction: insights from omics approaches. *Front Plant Sci*. **2024**, 14, 1305179.
85. Shen, C.; Yang, Y.M.; Sun, Y.F.; Zhang, M.; Chen, X.J.; Huang, Y.Y. The regulatory role of abscisic acid on cadmium uptake, accumulation and translocation in plants. *Front Plant Sci*. **2022**, 13, 953717.
86. Gu, L.; Hou, Y.; Sun, Y.; Chen, X.; Wang, G.; Wang, H.; Zhu, B.; Du, X. The maize WRKY transcription factor ZmWRKY64 confers cadmium tolerance in Arabidopsis and maize (Zea mays L.). *Plant Cell Rep*. **2024**, 43, 44.
87. Jia, Z.; Li, M.; Wang, H.; Zhu, B.; Gu, L.; Du, X.; Ren, M. TaWRKY70 Positively Regulates TaCAT5 Enhanced Cd Tolerance in Transgenic Arabidopsis. *Environ. Exp. Bot*. **2021**, 190, 104591.
88. Xian, P.; Yang, Y.; Xiong, C.; Guo, Z.; Alam, I.; He, Z.; Zhang, Y.; Cai, Z.; Nian, H. Overexpression of GmWRKY172 enhances cadmium tolerance in plants and reduces cadmium accumulation in soybean seeds. *Front Plant Sci*. **2023**, 14, 1133892.
89. He, G.; Saleem, M.; Deng, T.; Zhong, Z.; He, T.; Wu, J. Unraveling the Mechanism of StWRKY6 in Potato (Solanum tuberosum)'s Cadmium Tolerance for Ensuring Food Safety. *Foods*. **2023**, 12, 2303.

90. Cai, Z.; Xian, P.; Wang, H.; Lin, R.; Lian, T.; Cheng, Y.; Ma, Q.; Nian, H. Transcription Factor GmWRKY142 Confers Cadmium Resistance by Up-Regulating the Cadmium Tolerance 1-Like Genes. *Front Plant Sci*. **2020**, 11, 724.
91. Chen, Y.; Kong, X.; Yang, L.; Fu, M.; Zhang, S. Genome-Wide Identification of WRKY Family Genes and the Expression Profiles in Response to Nitrogen Deficiency in Poplar. *Genes (Basel)*. **2022**, Dec 10;13(12):2324.
92. Zhang, T.; Zhang, C.; Zhang, X.; Liang, Z.; Xia, P. Multi-algorithm cooperation research of WRKY genes under nitrogen stress in Panax notoginseng. *Protoplasma*. **2023**, 260, 1081-1096.
93. Poll, A.A.; Lee, J.; Sanderson, R.A.; Byrne, E.; Gatehouse, J.A.; Sadanandom, A.; Gatehouse, A.M.R.; Edwards, M.G. Septoria Leaf Blotch and Reduced Nitrogen Availability Alter WRKY Transcription Factor Expression in a Codependent Manner. *Int J Mol Sci*. **2020**, 21, 4165.
94. Javed, T.; Zhou, J.R.; Li, J.; Hu, Z.T.; Wang, Q.N.; Gao, S.J. Identification and Expression Profiling of WRKY Family Genes in Sugarcane in Response to Bacterial Pathogen Infection and Nitrogen Implantation Dosage. *Front Plant Sci*. **2022**, 13, 917953.
95. Sun, Y.; Zhang, T.; Xu, X.; Yang, Y.; Tong, H.; Mur, L.A.J.; Yuan, H. Transcriptomic Characterization of Nitrate-Enhanced Stevioside Glycoside Synthesis in Stevia (Stevia rebaudiana) Bertoni. *Int J Mol Sci*. **2021**, 22, 8549.
96. Zhang, L.; Chen, C.; Xie, F.; Hua, Q.; Zhang, Z.; Zhang, R.; Chen, J.; Zhao, J.; Hu, G.; Qin, Y. A Novel WRKY Transcription Factor HmoWRKY40 Associated with Betalain Biosynthesis in Pitaya (Hylocereus monacanthus) through Regulating HmoCYP76AD1. *Int J Mol Sci*. **2021**, 22, 2171.
97. Tang, W.; Wang, F.; Chu, H.; You, M.; Lv, Q.; Ji, W.; Deng, X.; Zhou, B.; Peng, D. WRKY transcription factors regulate phosphate uptake in plants. *Environ. Exp. Bot*. **2023**, 208, 105241.
98. Zhang, Y.; Chen, H.; Liang, Y.; Lu, T.; Liu, Z.; Jin, X.; Hou, L.; Xu, J.; Zhao, H.; Shi, Y.; Ahammed, G.J. Comparative transcriptomic and metabolomic analyses reveal the protective effects of silicon against low phosphorus stress in tomato plants. *Plant Physiol Biochem*. **2021**, 166, 78-87.
99. Nilsson, L.; Müller, R.; Nielsen, T.H. Dissecting the plant transcriptome and the regulatory responses to phosphate deprivation. *Physiol Plant*. **2010**, 139, 129-43.
100. Shukla, D.; Waigel, S.; Rouchka, E. C.; Sandhu, G.; Trivedi, P. K.; Sahi, S. V. Genome-wide expression analysis reveals contrasting regulation of phosphate starvation response (PSR) in root and shoot of Arabidopsis and its association with biotic stress. *Environmental and Experimental Botany*. **2021**, 188, 104483.
101. Wang, S.; Zhang, J.; Gu, M.; Xu, G. OsWRKY108 is an integrative regulator of phosphorus homeostasis and leaf inclination in rice. *Plant Signal Behav*. **2021**, 16, 1976545.
102. Wang, S.; Lv, B.; Wang, A.; Hu, J.; Wu, Q.; Li, C. Cloning and functional characterization of FtWRKY29, a low phosphorus stress-inducible transcription factor in Tartary buckwheat. *Plant Physiol Biochem*. **2023**, 203, 107997.
103. Liu, X.; Yang, Y.; Wang, R.; Cui, R.; Xu, H.; Sun, C.; Wang, J.; Zhang, H.; Chen, H.; Zhang, D. GmWRKY46, a WRKY transcription factor, negatively regulates phosphorus tolerance primarily through modifying root morphology in soybean. *Plant Sci*. **2022**, 315, 111148.
104. Zhang, J.; Gu, M.; Liang, R.; Shi, X.; Chen, L.; Hu, X.; Wang, S.; Dai, X.; Qu, H.; Li, H.; Xu, G. OsWRKY21 and OsWRKY108 function redundantly to promote phosphate accumulation through maintaining the constitutive expression of OsPHT1;1 under phosphate-replete conditions. *New Phytol*. **2021**, 229, 1598-1614.
105. Wang, S.; Xu, T.; Chen, M.; Geng, L.; Huang, Z.; Dai, X.; Qu, H.; Zhang, J.; Li, H.; Gu, M.; Xu, G. The transcription factor OsWRKY10 inhibits phosphate uptake via suppressing OsPHT1;2 expression under phosphate-replete conditions in rice. *J Exp Bot*. **2023**, 74, 1074-1089.
106. León, J.; Gayubas, B.; Castillo, M.C. Valine-Glutamine Proteins in Plant Responses to Oxygen and Nitric Oxide. *Front Plant Sci*. **2021**, 11, 632678.
107. Tolosa, L.N.; Zhang, Z. The Role of Major Transcription Factors in Solanaceous Food Crops under Different Stress Conditions: Current and Future Perspectives. *Plants (Basel)*. **2020**, 9, 56.
108. Rai, G.K.; Mishra, S.; Chouhan, R.; Mushtaq, M.; Chowdhary, A.A.; Rai, P.K.; Kumar, R.R.; Kumar, P.; Perez-Alfocea, F.; Colla, G.; Cardarelli, M.; Srivastava, V.; Gandhi, S.G. Plant salinity stress, sensing, and its mitigation through WRKY. *Front Plant Sci*. **2023**, 14, 1238507.
109. Khedia, J.; Agarwal, P.; Agarwal, P.K. Deciphering hydrogen peroxide-induced signalling towards stress tolerance in plants. *3 Biotech*. **2019**, 9, 395.
110. Jia, H.; Wang, C.; Wang, F.; Liu, S.; Li, G.; Guo, X. GhWRKY68 reduces resistance to salt and drought in transgenic Nicotiana benthamiana. *PLoS One*. **2015**, 10, e0120646.
111. Sun, Y.; Yu, D. Activated expression of AtWRKY53 negatively regulates drought tolerance by mediating stomatal movement. *Plant Cell Rep*. **2015**, 34, 1295-306.
112. Song, H.; Cao, Y.; Zhao, L.; Zhang, J.; Li, S. Review: WRKY transcription factors: Understanding the functional divergence. *Plant Sci*. **2023**, 334, 111770.
113. Bai, Y.; Sunarti, S.; Kissoudis, C.; Visser, R.G.F.; van der Linden CG. The Role of Tomato WRKY Genes in Plant Responses to Combined Abiotic and Biotic Stresses. *Front Plant Sci*. **2018**, 9, 801.

114. Schluttenhofer, C.; Yuan, L. Regulation of specialized metabolism by WRKY transcription factors. *Plant Physiol*. **2015**, 167, 295-306.
115. Jiang, J.; Ma, S.; Ye, N.; Jiang, M.; Cao, J.; Zhang, J. WRKY transcription factors in plant responses to stresses. *J Integr Plant Biol*. **2017**, 59, 86-101.
116. Samad, A.F.A.; Sajad, M.; Nazaruddin, N.; Fauzi, I.A.; Murad, A.M.A.; Zainal, Z.; Ismail, I. MicroRNA and Transcription Factor: Key Players in Plant Regulatory Network. *Front Plant Sci*. **2017**, 8, 565.
117. Tamura, K.; Stecher, G.; Kumar, S. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Mol Biol Evol*. **2021**, 38, 3022-3027.
118. Finatto, T.; Viana, V.E.; Woyann, L.G.; Busanello, C.; Maia, L.C.D.; Oliveira, A.C. Can WRKY transcription factors help plants to overcome environmental challenges? *Genet Mol Biol*. **2018**, 41, 533-544.
119. Feng, Y.; Cui, R.; Huang, Y.; Shi, L.; Wang, S.; Xu, F. Repression of transcription factor AtWRKY47 confers tolerance to boron toxicity in Arabidopsis thaliana. *Ecotoxicol Environ Saf*. **2021**, 220, 112406.
120. Sheng, Y.; Yan, X.; Huang, Y.; Han, Y.; Zhang, C.; Ren, Y.; Fan, T.; Xiao, F.; Liu, Y.; Cao, S. The WRKY transcription factor, WRKY13, activates PDR8 expression to positively regulate cadmium tolerance in Arabidopsis. *Plant Cell Environ*. **2019**, 42, 891-903.
121. Babitha, K.C.; Ramu, S.V.; Pruthvi, V.; Mahesh, P.; Nataraja, K.N.; Udayakumar, M. Co-expression of AtbHLH17 and AtWRKY28 confers resistance to abiotic stress in Arabidopsis. *Transgenic Res*. **2013**, 22, 327-41.
122. Krishnamurthy, P.; Vishal, B.; Ho, W.J.; Lok, F.C.J.; Lee, F.S.M.; Kumar, P.P. Regulation of a Cytochrome P450 Gene CYP94B1 by WRKY33 Transcription Factor Controls Apoplastic Barrier Formation in Roots to Confer Salt Tolerance. *Plant Physiol*. **2020**, 184, 2199-2215.
123. Ding, Z.J.; Yan, J.Y.; Li, C.X.; Li, G.X.; Wu, Y.R.; Zheng, S.J. Transcription factor WRKY46 modulates the development of Arabidopsis lateral roots in osmotic/salt stress conditions via regulation of ABA signaling and auxin homeostasis. *Plant J*. **2015**, 84, 56-69.
124. Shi, W.Y.; Du, Y.T.; Ma, J.; Min, D.H.; Jin, L.G.; Chen, J.; Chen, M.; Zhou, Y.B.; Ma, Y.Z.; Xu, Z.S.; Zhang, X.H. The WRKY Transcription Factor GmWRKY12 Confers Drought and Salt Tolerance in Soybean. *Int J Mol Sci*. **2018**, 19, 4087.
125. Ma, Q.; Xia, Z.; Cai, Z.; Li, L.; Cheng, Y.; Liu, J.; Nian, H. GmWRKY16 Enhances Drought and Salt Tolerance Through an ABA-Mediated Pathway in Arabidopsis thaliana. *Front Plant Sci*. **2019**, 9, 1979.
126. Luo, X.; Bai, X.; Sun, X.; Zhu, D.; Liu, B.; Ji, W.; Cai, H.; Cao, L.; Wu, J.; Hu, M.; Liu, X.; Tang, L.; Zhu, Y. Expression of wild soybean WRKY20 in Arabidopsis enhances drought tolerance and regulates ABA signalling. *J Exp Bot*. **2013**, 64, 2155-69.
127. Wang, F.; Chen, H.W.; Li, Q.T.; Wei, W.; Li, W.; Zhang, W.K.; Ma, B.; Bi, Y.D.; Lai, Y.C.; Liu, X.L.; Man, W.Q.; Zhang, J.S.; Chen, S.Y. GmWRKY27 interacts with GmMYB174 to reduce expression of GmNAC29 for stress tolerance in soybean plants. *Plant J*. **2015**, 83, 224-36.
128. Wei, W.; Liang, D.W.; Bian, X.H.; Shen, M.; Xiao, J.H.; Zhang, W.K.; Ma, B.; Lin, Q.; Lv, J.; Chen, X.; Chen, S.Y.; Zhang, J.S. GmWRKY54 improves drought tolerance through activating genes in abscisic acid and Ca2+ signaling pathways in transgenic soybean. *Plant J*. **2019**, 100, 384-398.
129. Song, H.; Wang, P.; Hou, L.; Zhao, S.; Zhao, C.; Xia, H.; Li, P.; Zhang, Y.; Bian, X.; Wang, X. Global Analysis of WRKY Genes and Their Response to Dehydration and Salt Stress in Soybean. *Front Plant Sci*. **2016**, 7, 9.
130. Cai, R.; Dai, W.; Zhang, C.; Wang, Y.; Wu, M.; Zhao, Y.; Ma, Q.; Xiang, Y.; Cheng, B. The maize WRKY transcription factor ZmWRKY17 negatively regulates salt stress tolerance in transgenic Arabidopsis plants. *Planta*. **2017**, 246, 1215-1231.
131. Zhao, L.; Yan, J.; Xiang, Y.; Sun, Y.; Zhang, A. ZmWRKY104 Transcription Factor Phosphorylated by ZmMPK6 Functioning in ABA-Induced Antioxidant Defense and Enhance Drought Tolerance in Maize. *Biology (Basel)*. **2021**, 10, 893.
132. Yokotani, N.; Sato, Y.; Tanabe, S.; Chujo, T.; Shimizu, T.; Okada, K.; Yamane, H.; Shimono, M.; Sugano, S.; Takatsuji, H.; Kaku, H.; Minami, E.; Nishizawa, Y. WRKY76 is a rice transcriptional repressor playing opposite roles in blast disease resistance and cold stress tolerance. *J Exp Bot*. **2013**, 64, 5085-97.
133. Pillai, S.E.; Kumar, C.; Patel, H.K.; Sonti, R.V. Overexpression of a cell wall damage induced transcription factor, OsWRKY42, leads to enhanced callose deposition and tolerance to salt stress but does not enhance tolerance to bacterial infection. *BMC Plant Biol*. **2018**, 18, 177.
134. Huang, K.; Wu, T.; Ma, Z.; Li, Z.; Chen, H.; Zhang, M.; Bian, M.; Bai, H.; Jiang, W.; Du, X. Rice Transcription Factor OsWRKY55 Is Involved in the Drought Response and Regulation of Plant Growth. *Int J Mol Sci*. **2021**, 22, 4337.
135. Lim, C.; Kang, K.; Shim, Y.; Yoo, S.C.; Paek, N.C. Inactivating transcription factor OsWRKY5 enhances drought tolerance through abscisic acid signaling pathways. *Plant Physiol*. **2022**, 188, 1900-1916.
136. Lv, M.; Hou, D.; Wan, J.; Ye, T.; Zhang, L.; Fan, J.; Li, C.; Dong, Y.; Chen, W.; Rong, S.; Sun, Y.; Xu, J.; Cai, L.; Gao, X.; Zhu, J.; Huang, Z.; Xu, Z.; Li, L. OsWRKY97, an Abiotic Stress-Induced Gene of Rice, Plays a Key Role in Drought Tolerance. *Plants (Basel)*. **2023**, 12, 3338.

137. Li, G.Z.; Wang, Z.Q.; Yokosho, K.; Ding, B.; Fan, W.; Gong, Q.Q.; Li, G.X.; Wu, Y.R.; Yang, J.L.; Ma, J.F.; Zheng, S.J. Transcription factor WRKY22 promotes aluminum tolerance via activation of OsFRDL4 expression and enhancement of citrate secretion in rice (Oryza sativa). *New Phytol.* **2018**, 219, 149-162.
138. Yan, L.; Baoxiang, W.; Jingfang, L.; Zhiguang, S.; Ming, C.; Yungao, X.; Bo, X.; Bo, Y.; Jian, L.; Jinbo, L.; et al. A novel SAPK10-WRKY87-ABF1 biological pathway synergistically enhance abiotic stress tolerance in transgenic rice (Oryza sativa). *Plant Physiol.Biochem*. **2021**, 168, 252–262.