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REVIEW

# WRKY Transcription Factors in Rice: Key Regulators Orchestrating Development and Stress Resilience

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## ABSTRACT

Rice (*Oryza Sativa L.*) productivity is critical for global food security, but it is increasingly vulnerable to environmental fluctuation and emerging pathogens and insects. WRKY is one of the largest plant transcription factors families, governing plant growth and stress adaptation as versatile regulators. However, a comprehensive review on rice WRKYs, especially incorporating recent findings, is still lacking. Here, we integrate current advances in the multifaceted roles of OsWRKYs, including regulating seed germination, vegetative growth, reproduction, and leaf senescence, as well as coordinating adaptive responses to various abiotic stresses (temperature, drought, salinity, heavy metals, nutrient imbalance) and biotic challenges (pathogens and insect herbivory). We detail how OsWRKY transcriptionally modulates target genes by binding to W-box elements involved in signaling of phytohormones (abscisic acid, gibberellin, salicylic acid, jasmonic acid and ethylene), reactive oxygen species homeostasis, and defense responses, thereby fine-tuning the trade-off between growth and defense. Additionally, we propose future research directions on how OsWRKYs prioritize responses under combined stresses and how their activity is regulated across multiple levels. The insights into these regulatory mechanisms lay a foundation for rational genetic engineering and genome editing of OsWRKYs to facilitate the development of rice varieties with enhanced yield and stress resilience.

## 1 | Introduction

Plants are constantly exposed to various biotic and abiotic stresses that impede their growth and development. During their evolution, plants have developed sophisticated mechanisms at the morphological, physiological, and molecular levels to adapt to these adverse conditions (G. Chen et al. 2024; Khalid et al. 2022; Peng et al. 2022; Xue et al. 2017). A core strategy in plant defense involves in reprogramming gene expression, primarily mediated by diverse families of transcription factors (TFs). Also known as trans-acting factors, TFs are proteins that specifically bind to cis-elements in gene promoters, thereby modulating gene expression to fine-tune plant growth and stress resilience (Strader et al. 2022).

The WRKY TFs are vital regulators of a wide range of biological processes and are one of the most extensively studied and widely distributed in plants (Goyal et al. 2022; Yang et al. 2025). Ishiguro and Nakamura (1994) cloned the first *WRKY* gene *Sweet-Potato Factor 1* (*SPF1*) from sweet potato (*Ipomoea batatas*) (Ishiguro and

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Nakamura 1994). Subsequently, the studies of WRKYs have expanded rapidly, leading to the identification of numerous members throughout diverse species, such as Arabidopsis (*Arabidopsis thaliana*), rice (*Oryza sativa*), tobacco (*Nicotiana tabacum*), soybean (*Glycine max*) and tomato (*Solanum lycopersicum*) (Javed and Gao 2023). The WRKY family was named after its most defining feature, the WRKY domain, a sequence of approximately 60 amino acids containing a conserved WRKYGQK at the N-terminus and an atypical zinc-finger structure ($C_2H_2$ or $C_2HC$) at the C-terminus (Eulgem et al. 2000). In some proteins, the WRKY sequence may be replaced by WSKY, WKKY, WIKY, WVKY, WRRY, or WKRY, while the GQK sequence can be substituted with EQK, GKK, GEK, or SEK, resulting in different variants (Xie et al. 2005). The WRKYGQK signature specifically recognizes the W-box elements (TTGACC/T) in the promoter region of target genes, with the invariant TGAC core being essential for WRKY motif binding and function (Ülker and Somssich 2004). Mutations in the WRKYGQK sequence impair the ability of WRKY TFs to bind W-box elements (Duan et al. 2007). Moreover, W-box sequences are highly prevalent in the promoter regions of stress-responsive genes, including those encoding pathogenesis-related (PR) proteins and regulators of abiotic stresses (Dhatterwal et al. 2019; Rushton et al. 1996).

Rice is a ubiquitous staple crop worldwide with critical economic and nutritional roles in supporting the growing world population. However, its productivity is highly susceptible to diverse abiotic and biotic stresses. For instance, with ongoing climate change, heat stress during the reproductive stage dramatically diminishes grain quality (Ali et al. 2019), while prolonged drought triggers leaf senescence and impairs carbon assimilation (Panda et al. 2021). Additionally, pathogens and insect pests significantly reduce rice yield by causing disease, disrupting nutrient uptake, damaging vital plant structures, and interfering with key developmental processes (Vo et al. 2021). To adapt to these adverse conditions, rice has developed intricate regulatory networks, in which WRKY TFs play crucial roles in coordinating growth, development, and stress responses. We summarize the current knowledge of OsWRKY family members in rice growth and development (e.g., seed dormancy and germination, morphogenesis, sexual reproduction and senescence) as well as in abiotic and biotic stress responses. Therefore, these insights offer valuable perspectives for the potential applications of OsWRKYs in molecular breeding and sustainable production of rice.

## 2 | Classification of OsWRKYS in Rice

WRKY TFs are usually classified into three groups (I–III) based on two defining characteristics: the number of WRKY domains (two in Group I, and one in both Group II and Group III), and the type of zinc finger structures ($C_2H_2$ pattern [$\underline{C}x_{4\text{-}5}\underline{C}x_{22\text{-}23}\underline{H}x\underline{H}$] for both Group I and II, and $C_2$-HC pattern [$\underline{C}x_7\underline{C}x_{23}\underline{H}x\underline{C}$] for Group III). Group II WRKY TFs can be further categorized into five subgroups (IIa, IIb, IIc, IId, and IIe), primarily based on differences of their amino acid sequences (Rushton et al. 2010).

A total of 88 OsWRKY proteins were retrieved from PlantTFDB v5.0 (https://planttfdb.gao-lab.org/) with removal of uncharacterized isoforms, and annotated according to the nomenclature established by the RGAP. The phylogenetic tree of OsWRKYs (Figure 1) revealed their classification into three major groups (I–III), comprising 10, 46 and 32 members, respectively. Group II is further divided into five subgroups IIa (4), IIb (8), IIc (17), IId (9) and IIe (8) based on their amino acid sequence similarity. While Group I was previously subdivided into Ia and Ib subgroups based on the presence of dual WRKY domains and divergence in zinc finger motifs (Xie et al. 2005), comparative phylogenomic studies across *indica* and *japonica* subspecies suggest that Ib exhibits more evolutionary convergence with Group II clade (Jimmy and Babu 2019).

To better understand the evolution of WRKYs, we conducted a phylogenetic analysis of WRKY TFs across a broad range of green plant lineages. We selected representative species: the angiosperm eudicot model species *Arabidopsis thaliana*, monocots *Oryza sativa* and barley (*Hordeum vulgare*), gymnosperm *Pinus lambertiana*, the basal angiosperm *Nymphaea colorata*, two ferns *Azolla filiculoides* and *Ceratopteris richardii*, a lycophyte *Selaginella moellendorffii*, the model moss *Physcomitrella patens*, a hornwort *Anthoceros agrestis*, a streptophyte alga *Klebsormidium nitens* and a green alga *Volvox carteri* (Figure 2). The resulting phylogenetic tree also resolved WRKY proteins into three major groups: Group I, Group II (with subgroups IIa–IIe), and Group III, consistent with previous reports in *Arabidopsis* and *Oryza sativa* (Eulgem et al. 2000; Ross et al. 2007). We demonstrate that WRKYs may have two independent evolutionary origins. Group III WRKYs are likely originated from the very ancient green alga *Volvox carteri* and subsequently evolved in hornworts and seed plants (gymnosperms and angiosperms) without presence in moss and ferns. In contrast, Groups I and II appear to have emerged from the sister lineage of land plants, the Streptophyte alga *Klebsormidium nitens*, and further diversified in hornworts, mosses, lycophytes, ferns, and seed plants, supporting a stepwise evolutionary trajectory from green algae to bryophytes and ultimately to vascular plants. The phylogenetic tree clearly reveals a marked expansion of the WRKY family beginning from the moss *Physcomitrella patens*, reflecting a rapid diversification during the early stages of land plant evolution and the importance of WRKY gene family in plant evolution and adaptation.

To further investigate the structural diversity of WRKY proteins, we employed AlphaFold3 to predict the protein structures of representative WRKYs from each group (Supporting Information S1: Figure 1). Within Group II, subgroup IIb was selected for structural modeling due to its presence across multiple lineages and the occurrence of homologous gene copies, providing valuable insights into the structural and evolutionary diversification of this subgroup (Supporting Information S1: Figure 1B). Moreover, structural modeling across subgroup representatives consistently revealed a highly conserved WRKY domain (characterized by β-sheet structures in blue) accompanied by more variable α-helices and flexible loop regions (colored yellow to red), underscoring evolutionary conservation of key DNA-binding domains and the potential for lineage-specific functional adaptation (e.g., subfunctionalization, neofunctionalization) in different WRKYs.

Expression profiles of *OsWRKY*s reveal that they are ubiquitously expressed across various rice organs yet exhibit distinct tissue-specificity (Supporting Information S1: Figure 2). Generally, most *OsWRKY*s are preferentially expressed in root, with



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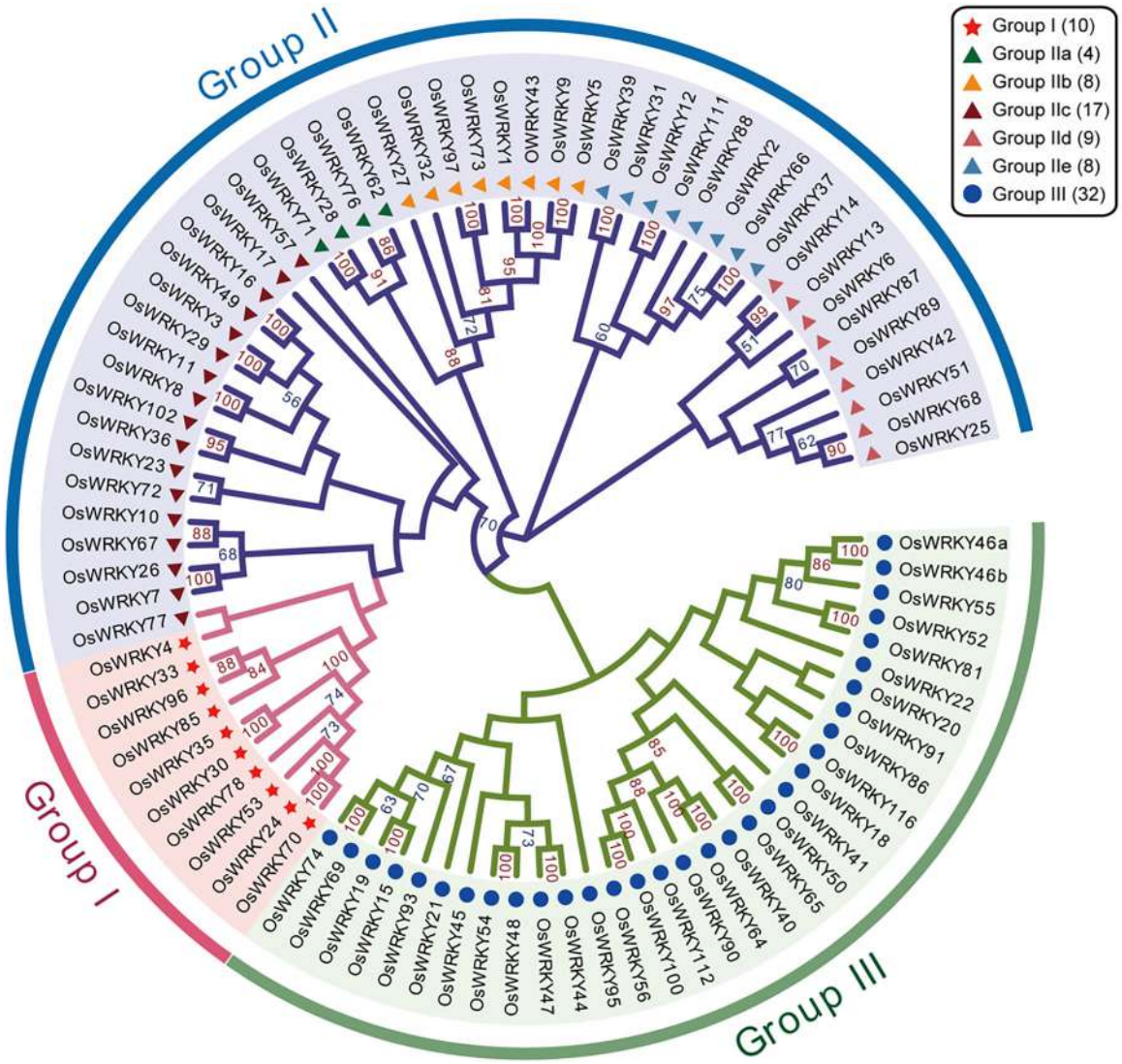


**FIGURE 1** | Phylogenetic analysis of WRKY proteins in rice. The phylogenetic tree of 88 OsWRKY proteins was performed in MEGA11 using the neighbor-joining method with 1000 bootstrap replicates. Group I (10 members) is marked with red pentagrams; Group II comprises five subgroups: IIa (4), IIb (8), IIc (17), IId (9) and IIe (8), each with distinct color-coded triangles; Group III (32 members) is indicated with blue circles. [Color figure can be viewed at wileyonlinelibrary.com]

clade IIa members *OsWRKY28, OsWRKY76* and *OsWRKY62* showing strong root expression, indicating their potential involvements in root development and function. Some genes, such as *OsWRKY6* shows higher expression in vegetative tissues (root, stem and leaf), while others, like *OsWRKY37* shows more prominent expression in reproductive tissues (inflorescence, anther and embryo). These expression patterns suggest that OsWRKYs may contribute to distinct functional processes during rice growth and development with unique spatial and temporal expression patterns. Therefore, some new technologies, such as spatiotemporal transcriptomics and proteomics, are essential for future investigations of OsWRKY functions.

## 3 | OsWRKYS Regulate Rice Growth and Development

Recent findings have increasingly highlighted the crucial roles of WRKYs in rice growth and development, including seed dormancy and germination, morphogenesis, reproduction and senescence (Figure 3 and Supporting Information S1: Table 1). Understanding how WRKYs coordinate these developmental processes is essential for unravelling the mechanisms to maintain growth and productivity, particularly under challenging stress conditions in rice.

### 3.1 | Seed Dormancy and Germination

Seed dormancy and germination are critical agronomic traits that directly influence rice yield and quality (do Nascimento et al. 2022). Premature germination results in preharvest sprouting, while excessive dormancy hampers germination and disrupts uniform seedling establishment during sowing. Some of the OsWRKYs are vital in balancing dormancy and germination, primarily via modulating the metabolism and signaling of abscisic acid (ABA) and gibberellic acid (GA) (Xie et al. 2006).



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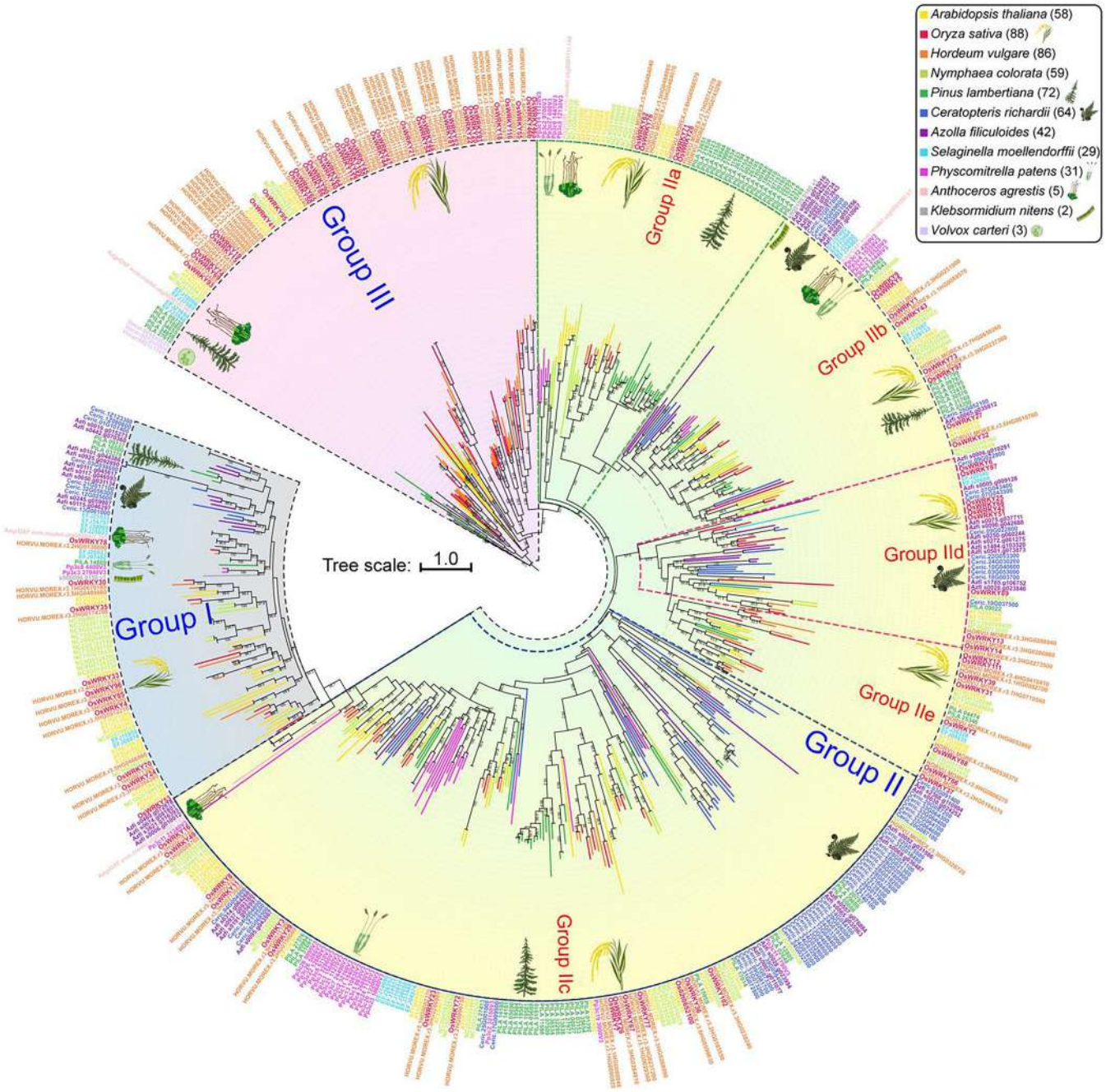


**FIGURE 2** | Phylogenetic analysis of WRKY proteins across plant lineages. The maximum likelihood phylogenetic tree of the WRKYs protein family was constructed using IQ-TREE (v2.4.0) (Minh et al. 2020) based on protein sequences containing the conserved WRKY domain (PF03106.17) from 12 representative plant species spanning major evolutionary lineages, from green algae to angiosperms. Each species is represented by a distinct color, with the number of WRKY proteins per species indicated in the corresponding color legend. The best-fit substitution model (JTT + R8) was selected automatically, and branch support was assessed with 1000 ultrafast bootstrap replicates. The tree was rooted and visualized using iTOL (https://itol.embl.de/login.cgi) (Letunic and Bork 2021). WRKYs group classification was assigned based on previously reported subgroup definitions in *Arabidopsis thaliana* and *Oryza sativa*. [Color figure can be viewed at wileyonlinelibrary.com]

ABA acts as the principal dormancy hormone by inhibiting germination-related processes. OsWRKY29 negatively regulates seed dormancy by repressing ABA-responsive genes *OsVP1* and *OsABF1*, while ABA inhibits *OsWRKY29* expression to reinforce dormancy (Zhou et al. 2020). Also, OsWRKY53 negatively modulates seed germination by directly suppressing the transcription of ABA catabolic genes, *OsABA8ox1* and *OsABA8ox2*, which increases endogenous ABA level and thus inhibits seed germination (Xie et al. 2022). On the contrary, OsWRKY50 enhances seed germination through reducing both ABA biosynthesis and response (S. Huang et al. 2021). OsWRKY50 binds to the promoter of *OsNCED5* (*9-cis-epoxycarotenoid dioxygenase*) to repress ABA accumulation, and overexpression of *OsWRKY50* exhibits higher germination rates under exogenous ABA, demonstrating lower ABA sensitivity compared to wild type (S. Huang et al. 2021). On the other hand, GA is a key phytohormone that promotes seed germination. OsWRKY72



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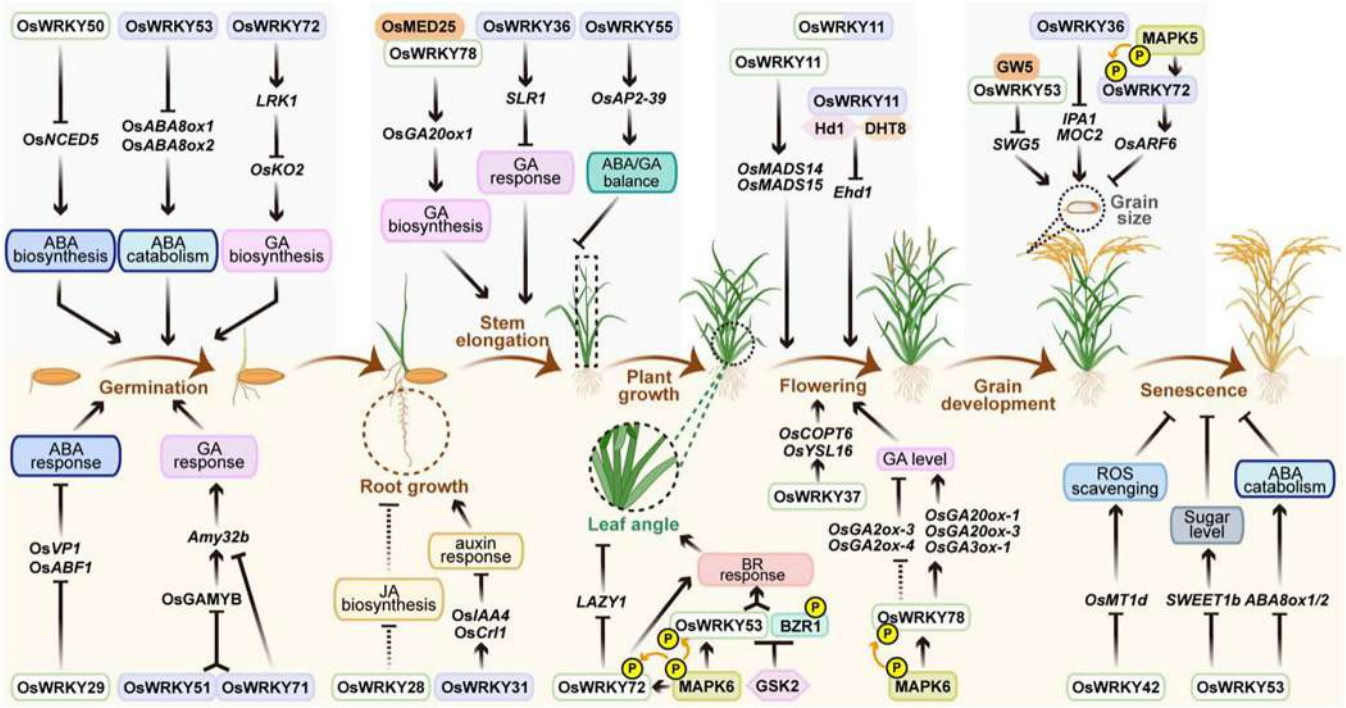


**FIGURE 3** | Regulatory functions of OsWRKY transcription factors in rice growth and development. This diagram illustrates the regulation of OsWRKYs in rice developmental processes, including seed germination, root growth, stem elongation, leaf angle, flowering, grain development, and senescence. OsWRKYs in green-bordered white boxes function as positive regulators, while those in purple boxes are negative regulators. Solid arrows and T bars represent direct activation and repression, respectively, while dashed lines denote indirect effects. The templates were obtained from Biorender (https://www.biorender.com). [Color figure can be viewed at wileyonlinelibrary.com]

directly activates *LRK1* (a leucine-rich repeat receptor-like kinase), which subsequently suppresses *ent-kaurene oxidase* (*OsKO2*), reducing endogenous GA accumulation and thereby inhibiting rice seed germination (Huimei et al. 2021).

WRKYs are also involved in the crosstalk of ABA and GA signaling to modulate seed germination. *OsWRKY51* and *OsWRKY71* are both induced by ABA and repressed by GA in rice embryos and aleurone cells (He et al. 2021; Xie et al. 2006). They synergistically suppress GA-induced *a-amylase* (*OsAmy32b*) expression by antagonizing the function of OsGAMYB (a GA-induced transcriptional activator of *Amy32b*), thereby reducing starch hydrolysis and inhibiting seed germination (He et al. 2021; Xie et al. 2006). Furthermore, physical interaction of OsWRKY51 and OsWRKY71 forms a repressor complex that enhances the binding affinity of OsWRKY71 to the W-box in the *OsAmy32b* promoter, further attenuating the GA response (Xie et al. 2006).

In summary, OsWRKYs primarily fine-tune the ABA-GA pathways to balance the seed dormancy and germination, providing novel genetic targets for optimizing seed performance in rice production.

## 3.2 | Morphological Development

WRKYs orchestrate rice morphogenesis by regulating root architecture, stem elongation, and leaf development via modulating plant hormone signaling networks, reactive oxygen species (ROS) homeostasis, and other growth-related genes (Tian et al. 2021; Tian et al. 2017; Xu et al. 2017).

### 3.2.1 | Root Architecture

Rice root architecture is critical for water and nutrient absorption, structural support and adaption to environmental stresses. OsWRKY62 and OsWRKY76 have been reported as SA-induced transcriptional repressors, which suppress the expression of redox and ROS scavenging-related genes to maintain ROS levels to promote the root meristem activity (Xu et al. 2017). The *oswrky28* mutant exhibits shorter root length and fewer lateral root tips, with upregulation of jasmonic acid (JA) biosynthesis genes revealed by RNA-sequencing (RNA-seq), implying that OsWRKY28 regulates root development via JA homeostasis (P. Wang et al. 2018). In contrast, overexpression of *OsWRKY31* dramatically reduces lateral root formation and elongation, accompanied by constitutive expression of early auxin-response genes, *Indole-3-Acetic Acid Inducible 4* (*OsIAA4*) and *Crown Rootless 1* (*OsCRl1*), and decreased sensitivity to high concentrations of exogenous auxins, implying that OsWRKY31 negatively modulates root development potentially by blocking auxin response pathway (Zhang et al. 2007). Notably, OsWRKY31 modulates the growth-defense trade-off by activating pathogen-resistant genes while disrupting root development, thereby prioritizing immunity over plant growth (Zhang et al. 2007).

### 3.2.2 | Stem Elongation

OsWRKY78, highly expressed in elongated stems, positively regulates rice plant height by stimulating GA biosynthesis. Disruption of *OsWRKY78* function results in shorter cell length



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and a semi-dwarf phenotype (Zhang et al. 2011). Further analysis showed that OsWRKY78 recruits OsMED25 as a coactivator to induce the transcription of a key GA biosynthesis gene *OsGA20ox1*, thereby elevating GA levels to promote rice stem elongation (Miao et al. 2025). OsWRKY55 inhibits plant height by reducing cell expansion, and directly binds to and activates the transcription of *OsAP2-39*, an APETALA2-like TF known to negatively regulate plant growth (K. Huang et al. 2021). OsAP2-39 has been reported to regulate plant growth by modulating ABA/GA balance, upregulating the ABA synthesis gene *OsNCED1* and the GA deactivating gene *Elongation of Upper Internode* (*OsEUI*) (Copenhaver et al. 2010). Thus, OsWRKY55 affects internode elongation via phytohormones modulation. OsWRKY36 restricts rice stem elongation by directly stabilizing the DELLA-like *OsSLR1* expression (Lan et al. 2020), and inhibits cell wall lignification in conjunction with OsWRKY102 to modulate rice culm morphology (Miyamoto et al. 2020).

#### 3.2.3 | Leaf Angle

Leaf morphology is an essential component in rice breeding, with leaf angle functioning as a crucial agronomic trait that influences light interception efficiency, plant density, and grain yield. Leaf angle is determined as the inclination degree between leaf blade and the stem at the ligule region (Huang et al. 2023). OsWRKY53 integrates brassinosteroid (BR) signaling and the mitogen-activated protein kinase (MAPK) cascade to positively regulate rice leaf angle (Tian et al. 2021; Tian et al. 2017). Phosphorylation by glycogen synthase kinase-2 (OsGSK2) destabilizes OsWRKY53 and suppresses BR responses. BR-mediated inhibition of OsGSK2 stabilizes OsWRKY53, which synergizes with Brassinazole-resistant1 (OsBZR1) to enhance BR responses and activate cell expansion-related genes. Simultaneously, OsWRKY53 is also a downstream substrate of the MAPKKK10-MAPKK4-MAPK6, where its activity is enhanced by MAPK6-phosphorylation to enlarge leaf angle (Tian et al. 2021; Tian et al. 2017). Os*WRKY72* is highly expressed in the leaf sheath and lamina joint to positively regulate rice leaf angle by directly binding to the promoter of BR receptor kinase gene *OsBRI1* to activate BR signaling, with its activity further enhanced by OsMAPK6-mediated phosphorylation (Wang et al. 2025). In addition, OsWRKY72 promotes leaf angle enlargement by directly suppressing the transcription of *LAZY1*, a key negative regulator of shoot-gravitropism (Liu et al. 2024).

In summary, OWRKYs orchestrate rice morphological development mainly through the integration of various phytohormone signaling (e.g., JA, IAA, GA, SA, ABA and BR), and future studies are needed to dissect their spatiotemporal dynamics and interactions to optimize architecture for enhanced productivity and resilience in rice.

### 3.3 | Sexual Reproduction

Flowering is an important physiological process that marks the transition from vegetative growth to reproduction of plants. In rice, key stages such as heading time, panicle exsertion, and grain development directly influence productivity, with OsWRKYs are of pivotal importance in regulating these essential reproductive processes (Abbas et al. 2024; Mei et al. 2024; Zhao et al. 2024).

#### 3.3.1 | Flower Development and Heading

Flower development and heading are crucial for subsequent effective fertilization in rice. OsWRKY37 promotes pollen development under copper (Cu) deficiency by directly activating *Copper Transporter 6* (*OsCOPT6*) and *Yellow Stripe-like Protein 6* (*OsYSL16*), enhancing the copper uptake and translocation to the stamens to ensure proper formation of pollen structures (baculae and tectum) and maintain pollen vitality (Ji et al. 2024). OsWRKY11 exerts dual effects to fine-tune rice heading time in a concentration-dependent manner (Zhao et al. 2024). Under normal conditions, OsWRKY11 promotes flowering by directly activating two MADS-box TFs *OsMADS14* and *OsMADS15*, with *oswrky11* mutant showing delayed heading (Zhao et al. 2024). However, overexpression of *OsWRKY11* promotes its formation of a ternary complex with Heading date 1 (OsHd1) and Days To Heading 8 (OsDTH8), inhibiting the expression of flowering-related gene *Ehd1* and resulting in delayed heading date in *OsWRKY11-OE* lines (Zhao et al. 2024). Heterologous expression of *OsWRKY72* in *Arabidopsis* resulted in early flowering, with the transcription of auxin-related genes [e.g., *AUXIN influx transporter* (*AUX1*), *AUXIN1 RESISTANT 1* (*AXR1*), and *BUSHY AND DWARF1* (*BUD1*)] and ABA-related genes [e.g., *ABA DEFICIENT 2* (*ABA2*), and *ABA INSENSITIVE 4* (*ABI4*)] significantly altered. It was thus suggested that OsWRKY72 may regulate rice heading by interfering with auxin transport and ABA signaling pathways (Song et al. 2010). In addition, panicle exsertion, the emergence of inflorescence from the flag leaf sheath, is critical for successful pollination and grain yield in rice. OsWRKY78 directly activates GA biosynthesis genes [*OsGA20ox-1* (*GIBBERELLIN 20-OXIDASE 1*), *OsGA20ox-3* and *OsGA3ox-1*] and indirectly suppresses GA metabolism genes (*OsGA2ox-3* and *OsGA2ox-4*), with disruption of its function leading to panicle enclosure due to decreased bioactive GA levels. In addition, OsWRKY78 is phosphorylated by OsMPK6, which enhances protein stability of OsWRKY78, essential for its biological functions in regulating panicle exsertion (Mei et al. 2024).

#### 3.3.2 | Grain Development

Rice grain development is a complex molecular physiological process that is regulated by genetic and hormonal networks. OsWRKY53 promotes grain size by enhancing cell expansion through integration of BR signaling and MAPKKK10-MAPKK4-MAPK6 cascade (Tian et al. 2021). Additionally, OsWRKY53 is involved in Quantitative Trait Locus (QTL)-based regulation by forming a transcriptional repressor complex with GW5, a master negative QTL of grain size. This complex binds to the W-box in the promoter of *Suppressor of gw5* (*SGW5*), a QTL that positively regulates grain width by enhancing cell division and



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expansion in spikelet hulls (Abbas et al. 2024). A natural T/G variation in the W-box of *SGW5* affects OsWRKY53 binding affinity, creating differential *SGW5* expression and grain size diversity across rice varieties (Abbas et al. 2024). Furthermore, OsWRKY24, a close homolog of OsWRKY53, functions redundantly with OsWRKY53 in regulating grain size, while another unique homolog OsWRKY70 plays a distinct role, with both overexpression and knockout of *OsWRKY70* leading to longer grains (Tang et al. 2022). Interestingly, heterologous overexpression of Os*WRKY24* in *Arabidopsis* shortens seeds, contrary to its positive regulation of grain size in rice, suggesting their plant species-specific roles (Jang and Li 2018). *OsWRKY78* knockdown by RNAi or T-DNA insertion reduces seed size by affecting cell length and slightly altering endosperm starch structure to promote rice seed development (Zhang et al. 2011). In contrast, OsWRKY72 negatively regulates grain length and weight, with its function stabilized through phosphorylation by OsMPK5, leading to the activation of a downstream target *OsARF6* to restrict grain size (Wang et al. 2024). A most recent study demonstrated OsWRKY36 as a negative regulator of the number of grains per panicle and tiller number by depressing the expression of the *Ideal Plant Architecture 1* (*IPA1*) and *MONOCULM 2* (*MOC2*) (Liu et al. 2025).

In short, OsWRKYs coordinate rice reproductive development by mediating hormonal and genetic regulations in rice. The combination of multi-omics and gene-editing approaches on OsWRKYs will advance the breeding programs of rice varieties with improved yield and quality.

### 3.4 | Leaf Senescence

Leaf senescence is a spontaneously initiated process of programmed cell death that facilitates the reallocation of nutrients and metabolites from vegetative to reproductive tissues, significantly affecting rice yield and quality (Woo et al. 2019). OsWRKY42 accelerates leaf senescence by directly binding to the W-box of the *Metallothionein 1d* (*OsMT1d*) promoter, repressing OsMT1d-mediated ROS scavenging to promote leaf senescence in rice (Han et al. 2014). OsWRKY53 functions as a transcriptional repressor of both glucose/galactose transporter *OsSWEET1b* and ABA catabolic genes *OsABA8ox1/2*, leading to cytosolic sugar starvation and elevated ABA accumulation, which coordinately promotes rice leaf senescence (D. Chen et al. 2024). OsWRKY5 is a positive regulator of leaf senescence by upregulating senescence-associated *NAC* TFs (*OsNAP2* and *OsNAC2*), ABA biosynthesis genes *OsNCED*s (*9-cis-epoxycarotenoid dioxygenase*) and chlorophyll degradation gene (Kim et al. 2019). RNA-seq analysis identified *OsWRKY93* as a senescence-associated gene in rice flag leaves (Li et al. 2021). Enhanced *OsWRKY93* expression delays dark-induced leaf senescence, while the knockout lines exhibit accelerated yellowing in rice (Li et al. 2021).

Thus, OsWRKYs regulate leaf senescence mainly by mediating ABA accumulation, sugar metabolism, chlorophyll degradation, and senescence-related gene expression, providing genetic targets to extend the duration of photosynthesis and promote nutrient remobilization towards enhanced rice grain yield.

## 4 | Regulatory Roles of OsWRKYS in Abiotic Stress Responses

Abiotic stresses such as temperature, drought, salinity, light, nutrient deficiencies and metal toxicity, significantly reduce rice productivity. OsWRKY TFs play crucial roles in rice abiotic stress responses, with many *OsWRKY*s rapidly upregulated under specific environmental challenges (Qiu 2004). They function by activating or repressing stress-responsive genes, thereby enhancing rice resilience (Figure 4 and Supporting Information S1: Table 2). Notably, some OsWRKYs often respond to multiple stressors, highlighting their functional versatility in the adaptation to abiotic stresses (Qiu and Yu 2009).

### 4.1 | Temperature Stress

Rice is very susceptible to temperature fluctuations. Both heat and cold stresses significantly reduce rice yield through multiple mechanisms, including protein misfolding, increased ROS accumulation, disruption of cell membrane fluidity and integrity, as well as reproductive defects such as reduced pollen viability, spikelet sterility, and impaired grain filling (Kan and Lin 2021). WRKYs are crucial regulators of rice temperature adaptation, coordinating intricate networks to modulate the expression of stress-responsive genes, hormonal signaling, and ROS homeostasis (Yang et al. 2025).

#### 4.1.1 | Cold Stress

As a crop native to subtropical and tropical regions, rice is highly sensitive to low temperature. Some OsWRKYs play a crucial role in regulating rice cold tolerance. Overexpression of Os*WRKY71* significantly improves rice chilling acclimation by upregulating downstream cold-responsive genes, including two *DREB* (*Dehydration-responsive element binding protein*) homologs *OsTGFR* and *WSI76* (Kim et al. 2016). Cold stress reduces GA levels in anthers, severely impairing pollen fertility. Cold-inducible OsWRKY53 regulates cold tolerance at the booting stage of rice by directly repressing the transcription of GA biosynthesis genes (*GA20ox1, GA20ox3* and *GA3ox1*). In the *wrky53* mutant, these GA biosynthesis genes maintain expression during cold stress, preserving anther GA levels to promote the degradation of OsSLR1 (a DELLA protein), thereby releasing Undeveloped Tapetum1 (OsUDT1) and Tapetum Degeneration Retardation (OsTDR) to activate tapetum development genes for pollen viability (Tang et al. 2022). Notably, knocking out *OsWRKY53* in some rice varieties enhances cold tolerance without compromising yield, making it a promising target for breeding cold-tolerant rice cultivars. OsWRKY63 also functions as a negative regulator of rice chilling tolerance by directly binding to and repressing both ROS scavenging-related genes and *OsWRKY76* expression. In contrast, OsWRKY76 acts as a positive regulator by interacting with the basic helix-loop-helix TF OsbHLH148, thereby synergistically activating *OsDREB1B* expression and enhancing rice cold tolerance (Zhang et al. 2022). This interaction reveals the crucial OsWRKY63-OsWRKY76-OsDREB1B transcriptional regulatory cascade in rice cold response (Zhang et al. 2022). OsWRKY70 enhances rice cold acclimation by upregulating key cold-responsive



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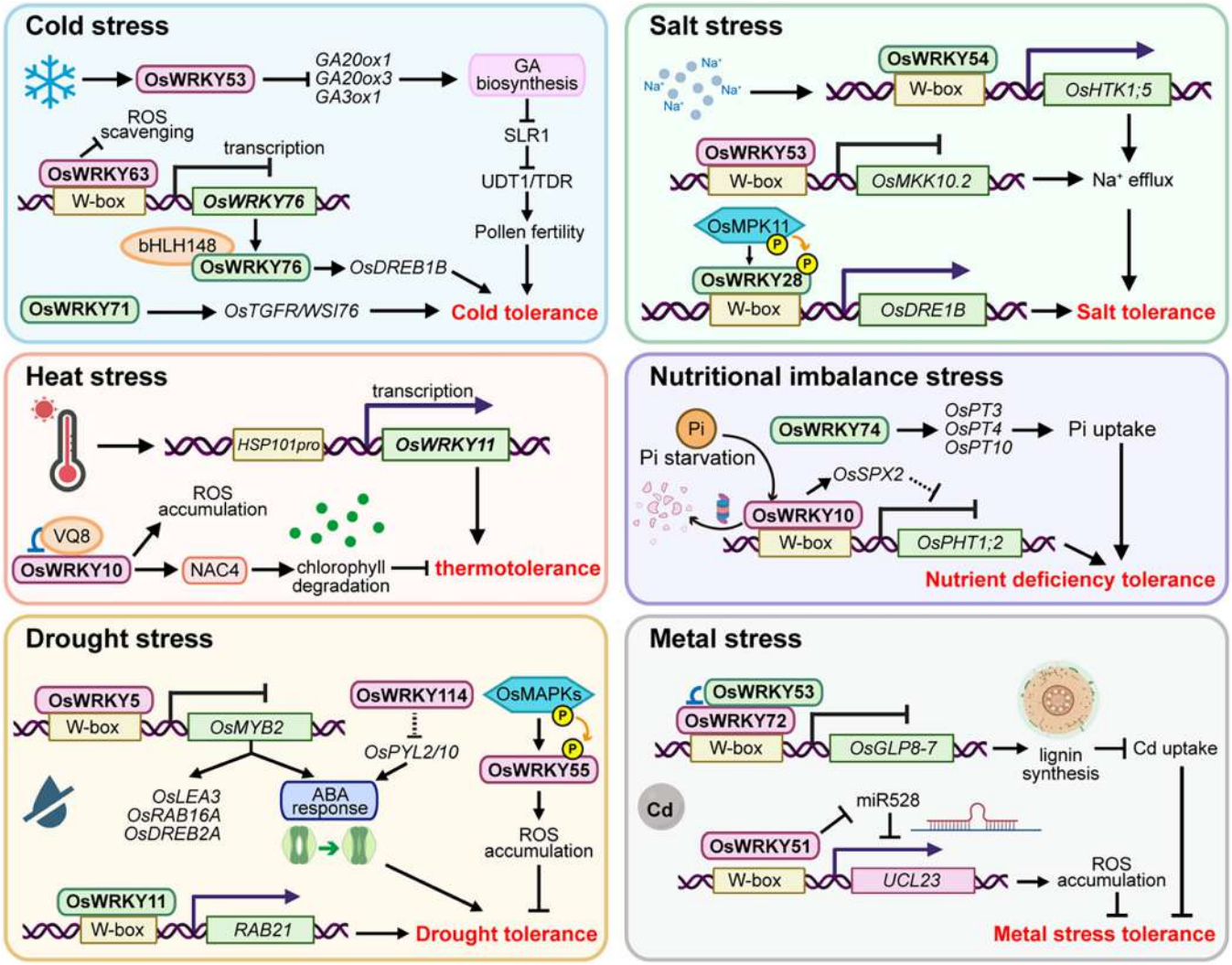


**FIGURE 4** | Functional roles of OsWRKYs in regulating rice responses to various abiotic stresses. The schematic diagrams illustrate representative regulation of OsWRKYs in rice responses to cold, heat, drought, salinity, nutritional imbalance, and heavy metal stresses. OsWRKYs in green boxes serves as positive regulators, while those in red boxes are negative regulators. Solid arrows and T bars represent direct activation and repression, respectively, while dashed lines denote indirect effects. The templates were obtained from Biorender (https://www.biorender.com). [Color figure can be viewed at wileyonlinelibrary.com]

genes, *Low Temperature Induced Protein 6b* (*OsLti6b*) and *Inducer of CBF Expression 1* (*OsICE1*). The increased activities of catalase and peroxidase mitigate cold-induced oxidative damage and maintain membrane integrity during chilling conditions (Li et al. 2024). Additionally, OsWRKY94 serves as a regulatory hub that prioritizes cold defense over growth under chilling conditions (Chen et al. 2018). It can be directly targeted and conversely regulated by two TFs, OsMADS57 (activator) and Teosinte Branched1 (OsTB1, repressor), which switch from organogenesis to cold adaption in rice (Chen et al. 2018).

### 4.1.2 | Heat Stress

High temperature also presents a major challenge to rice, causing substantial damage to growth and yield. OsWRKY10 negatively regulates thermotolerance by increasing ROS accumulation, activating NAC4-mediated cell death and accelerating chlorophyll degradation. VQ8 (VQ motif-containing protein 8) interacts with OsWRKY10 to function antagonistically by inhibiting its transcriptional activity, thereby positively regulating thermotolerance (Chen et al. 2022). Therefore, the OsWRKY10-VQ8 module effectively balances destructive and protective responses under heat stress. Additionally, *OsVQ30* was identified as a candidate gene for heat stress tolerance by genome-wide association study (GWAS) and RNA-seq analysis. *OsWRKY36* showed a similar expression pattern to *OsVQ30* under heat stress, suggesting they may interact as a WRKY-VQ regulatory module in rice heat stress response (Li et al. 2023). Os*WRKY11* is induced by heat stresses in rice seedlings, and its overexpression under the *heat shock protein 101* (*HSP101*) promoter can enhance rice heat tolerance, as characterized by slower leaf wilting and higher survival rates after heat treatment (Wu et al. 2008).

In summary, these findings highlight the pivotal functions of OsWRKYs in modulating rice responses to temperature extremes via hormone signaling, ROS scavenging and defense



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gene regulation. Future research could explore their complex interactions and regulatory networks to simultaneously enhance tolerance to both heat and cold stresses.

### 4.2 | Drought Stress

With global warming, drought stress has become a major constraint for rice growth and productivity, causing reduced photosynthesis due to stomatal closure, stunted root and shoot growth, disrupted water balance, and leaf wilting and desiccation (G. Chen et al. 2024; Raza et al. 2022; Xue et al. 2017; Zhao et al. 2019). OsWRKY11 can enhance rice drought tolerance by directly binding to the promoter of drought-responsive gene *Responsive to ABA 21* (*RAB21*) and activating its transcription (Lee et al. 2018). In contrast, other OsWRKYs have been shown to negatively regulate rice drought responses. OsWRKY5 can directly bind to and suppress the transcription of *OsMYB2*, a key TF that activates drought-responsive genes [including *Late Embryogenesis Abundant 3* (*OsLEA3*), *Responsive to Abscisic Acid 16a* (*OsRAB16A*) and *Dehydration-Responsive Element Binding Protein 2A* (*OsDREB2A*)]. Loss of function of *OsWRKY5* leads to increased *OsMYB2* expression and ABA-dependent stomatal closure, which consequently improves drought tolerance in rice (Lim et al. 2022). Overexpression of Os*WRKY55* in rice exhibited reduced drought tolerance, as evidenced by accelerated water loss and elevated ROS accumulation. Yeast two-hybrid (Y2H) and transactivation assays revealed that OsWRKY55 interacts with four drought-induced MAPKs (OsMPK7, OsMPK9, OsMPK20-1, and OsMPK20-4), which enhance its transcription activity, suggesting that MAPK-mediated activation of OsWRKY55 may contribute to drought sensitivity (K. Huang et al. 2021). OsWRKY114 also negatively regulates drought stress response. *OsWRKY114-OE* plants showed restricted stomatal closure, which is associated with reduced expression of ABA receptor genes *OsPYL2* and *OsPYL10* (Song et al. 2022).

In short, OsWRKYs regulate rice drought tolerance primarily by influencing ABA signaling, ROS homeostasis, and stomatal performance. Further efforts can be on the investigation of molecular strategies to optimize stomatal closure for improved drought resilience while preserving photosynthetic efficiency in rice.

### 4.3 | Salinity Stress

Salinity stress is often closely linked with drought conditions, perturbing cellular stability through osmotic imbalance, ionic toxicity, and oxidative stress, inhibiting water and nutrients uptake in rice (Chen et al. 2021; Liu et al. 2020; Munns et al. 2019). OsWRKY28 positively regulates salt tolerance in rice by directly binding to and activating the expression of *OsDREB1B*, a key salt-responsive gene (Zhang et al. 2022). Furthermore, OsMAPK11 physically phosphorylates OsWRKY28 to regulate its transcriptional activity, which may contribute to the salt stress tolerance (Zhang et al. 2022). OsWRKY50 enhances rice salt resilience by upregulating the expression of several stress-related genes, including *OsLEA3* (*Late embryogenesis abundant 3*), *OsRAB21* (*Response to ABA 21*), *OsHKT1;5* (*High affinity K+ transporter 1;5*) and *OsP5CS1* (*Pyrroline-5-carboxylate synthase 1*) (S. Huang et al. 2021). Interestingly, both OsWRKY28 and OsWRKY50 negatively regulate ABA signaling, suggesting their involvement in modulating salt tolerance via an ABA-independent pathway (S. Huang et al. 2021; Zhang et al. 2022). OsWRKY54 is rapidly induced in rice roots upon salt exposure. Loss of OsWRKY54 function disrupts $Na^+$/$K^+$ homeostasis, resulting in excessive accumulation of $Na^+$ in shoots and increased sensitivity to salinity. Further evidence indicated that OsWRKY54 can directly activate the expression of a key $Na^+$ transporter, *OsHKT1;5*, which regulates $Na^+$ translocation and distribution in rice to improve salt tolerance (Huang et al. 2022). Similarly, OsWRKY18 also enhances salt stress tolerance in rice by directly binding to the promoter of *OsHKT1;5* (Peng et al. 2025).

OsWRKY53, a negative regulator of salt stress was identified through GWAS. It directly binds to the promoters of two important salt tolerance-related genes, *OsMKK10.2* and *OsHKT1.5*. The OsWRKY53-mediated transcriptional repression of *OsMKK10.2* and *OsHTK1.5* contributes to the enhanced salt sensitivity observed in *OsWRKY53-OE* lines, with OsWRKY53-OsMKK10.2 module playing a more prominent role due to the biological significance of OsMKK10.2 in controlling $Na^+$ efflux (Yu et al. 2023). Interestingly, OsWRKY45 exhibited allelic difference in salt stress adaption, with *japonica* rice OsWRKY45-1 showing insensitive to salinity, while *indica* rice OsWRKY45-2 negatively regulating salt stress tolerance. This difference may be attributed to their distinct regulation of downstream genes expression [*Responsive to Dehydration 22* (*RD22*), *Rab16D* and *Rab21*], indicating the adaptive evolutionary divergence among rice cultivars to saline environment (Tao et al. 2011).

In short, OsWRKYs regulate rice salt tolerance by balancing $Na^+$ translocation, osmotic stability and stress-adaptive gene expression, showing high potential for the development of rice varieties with enhanced salt tolerance.

### 4.4 | Heavy Metal and Metalloid Stress

Heavy metal and metalloid contamination of soils, primarily caused by human activities, has emerged as pressing global environmental challenges to rice growth and productivity. Exposure to heavy metals and metalloids leads to toxicity that compete with essential mineral nutrients for binding sites, disrupt enzyme conformation, and interfere with normal cellular physiological and metabolic processes, ultimately altering root system architecture (RSA), reducing plant biomass and even causing death, while posing risks to food safety (Deng et al. 2021; Hassan et al. 2005).

Arsenic (As) is a common metalloid stressor that exists in two inorganic forms, Arsenate ($As^V$) and Arsenite ($As^{III}$). $As^V$, a phosphate analog, competes with phosphates for uptake through phosphate transporters (e.g., OsPT8 in rice), thereby impairing production of ATP in cells (Mawia et al. 2021). $As^{III}$ clings to sulfhydryl groups and disrupts the functions of sulfhydryl group-containing enzymes, and also blocks the efficient uptake of silicon (Mawia et al. 2021; Mirza et al. 2022).



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*OsWRKY28* expression is highly responsive to $As^{V}$ treatment, and its loss of function decreases $As^{V}$ accumulation and translocation to the shoot, possibly by enhancing endogenous JA levels to alleviate the oxidative stress caused by heavy metal exposure (P. Wang et al. 2018). As stress causes multiple adverse effects on rice root system, while iron (Fe) can function as a crucial factor in mitigating As-induced toxicity. *OsWRKY71* expression is suppressed under $As^{III}$ stress but significantly upregulated by $Fe^{II}$ supplementation, correlating with improved root morphology and anatomy (Mirza and Gupta 2024). Furthermore, the *OsWRKY71* promoter contains multiple gibberellin-responsive cis-regulatory elements and is predicted to interact with a DELLA protein SLR1. This suggests that OsWRKY71 may mediate rice responses to $As^{III}$ via integrating Fe and GA pathway (Mirza and Gupta 2024). Additionally, a substantial portion of OsWRKYs is significantly upregulated under both $As^{V}$ and $As^{III}$ stresses, indicating their potential involvements in rice's response to As stress (Huang et al. 2012; Norton et al. 2008; Yu et al. 2012). However, further research is required to unravel the detailed mechanisms by which OsWRKYs regulate tolerance to As stress, including their roles in As uptake and translocation, ROS scavenging, or modulation of hormone signaling pathway.

Cadmium (Cd) is a typical heavy metal pollutants which lead to toxicity and reduced crop yield. In rice roots, OsWRKY72 is significantly induced by Cd stresses at both the transcriptional and protein levels, which negatively regulates rice tolerance by promoting the Cd absorption and accumulation. Rice Germin-Like Protein 8-7 (OsGLP8-7), which is responsive to Cd, mediates lignin synthesis to retain heavy metals in the cell wall without entering the cytoplasm. In addition, OsWRKY53 interacts with OsWRKY72, alleviating the transcription repression of OsGLP8-7 by OsWRKY72 (Shangguan et al. 2024). In addition to the OsWRKY72-mediated cell barrier mechanism regulating Cd uptake, OsWRKY51 negatively regulates Cd tolerance by exerting a dual regulatory effect on Uclacyanin23 (UCL23), that reduces Cd tolerance by enhancing ROS levels (Tan et al. 2025). Specifically, OsWRKY51 increases *UCL23* transcripts by directly interacting with its promoter, and indirectly de-repressing *UCL23* by inhibiting miR528, a posttranscriptional suppressor of *UCL23* (Tan et al. 2025).

Aluminum (Al) is another major toxic metal ion limiting plant growth in acidic soils. OsWRKY22 can enhance rice Al tolerance by directly binding to and activating *OsFRDL4* (*Ferric Reductase-Like 4*) expression, which facilitates citrate secretion out of root cells to chelate $Al^{3+}$ in the rhizosphere, thus mitigating Al-induced damage to rice root system (Li et al. 2018). In addition, OsWRKY22 collaborates with *Aluminum Resistance Transcription Factor 1* (*ART1*) to synergistically regulates the expression of *OsFRDL4* expression (Li et al. 2018).

In short, OsWRKYs regulate rice metal stress by regulating the metal uptake, sequestration, ROS homeostasis, and hormone signaling. More exploration of interaction with other stress-responsive pathways could inform strategies to enhance rice tolerance to environmental pollution of heavy metals and metalloids.

### 4.5 | Nutritional Imbalance Stress: Deficiency and Excesses

Rice requires many essential macronutrients and micronutrients for optimal growth and development. Both nutrient deficiencies and excesses can severely impair plant health, stress resilience and yield (Shrestha et al. 2020). OsWRKYs play vital roles in balancing nutrient management in rice cultivation.

Phosphorus (P), as one of essential macronutrient, primarily absorbed by plants as inorganic phosphate (Pi). OsWRKY74 functions as a positive regulator of rice in response to Pi starvation. Overexpression of *OsWRKY74* confers greater tolerance to low Pi stress by activating Pi-starvation inducible genes [*Purple acid phosphatase 10a* (*OsPAP10a*) and *Sulfoquinovose synthase* (*OsSQD*)], Pi transporter genes (*OsPT3*, *OsPT4* and *OsPT10*), and developing larger RSA with longer primary root and adventitious root to increase Pi acquisition (Dai et al. 2016). In addition, OsWRKY74 is also involved in the response to Fe deficiencies in rice (Dai et al. 2016). Under Pi-sufficient conditions, OsWRKY21 interacts with OsWRKY108 in the nucleus and both bind to the W-box cis-elements in the promoter of the key Pi transporter *OsPHT1;1* to maintain its constitutive expression, thereby promoting Pi update in phosphate-replete rice (Zhang et al. 2020). Moreover, OsWRKY10 restricts Pi uptake under Pi-sufficient conditions by directly binding to and repressing the transcription of *OsPHT1;2*. Furthermore, OsWRKY10 is required for sustaining the constitutive expression of *OsSPX2*, which in turn indirectly inhibits *OsPHT1;2* by abolishing Phosphate Starvation Response 2 (OsPHR2) activity. Under Pi deficiency, OsWRKY10 is degraded via the 26S proteasome pathway, which alleviates its suppressive effects on *OsPHT1;2*. Collectively, the OsWRKY10-OsPHT1;2 module regulates Pi homeostasis in rice (Wang et al. 2023b).

Nitrogen (N) is another vital macronutrient, and its efficient absorption and utilization are essential for optimal rice productivity while minimizing environmental impacts from excessive fertilizer application. OsWRKY23 acts as a negative regulator for nitrate uptake and nitrogen use efficiency by directly binding to the promoter of an aminotransferase gene *Dull Nitrogen Response 1* (*DNR1*) and activating its expression (Zhang et al. 2025). *DNR1* reduces IAA levels and consequently attenuates auxin response required for nitrate transport and assimilation (Zhang et al. 2025).

Iron (Fe) is a typical micronutrient crucial for numerous metabolic processes, but its excessive accumulation can also result in physiological stress and toxicity in rice. The expression of *OsWRKY55-like*, Os*WRKY46, OsWRKY64*, and Os*WRKY113* was significantly upregulated in iron-sensitive genotype (BR IRGA 409), while showing unaltered patterns in iron-resistant genotypes (Epagri 108 and Nipponbare) under Fe excessive conditions. Further analysis indicated that OsWRKY46 and OsWRKY113 may act to repress root elongation to restrict iron uptake, while they may also promote the leaf development under Fe-excessive (Viana et al. 2017). Specific OsWRKYs are involved in regulating Copper ($Cu^{2+}$) homeostasis in rice. OsWRKY37 is activated under Cu deficiency and promotes uptake by directly activating *OsCOPT6* and *OsYSL16* (Ji et al. 2024). In contrast, OsWRKY72 alleviates Cu-induced toxicity under excessive copper conditions by modulating lignin synthesis (Shangguan et al. 2024).



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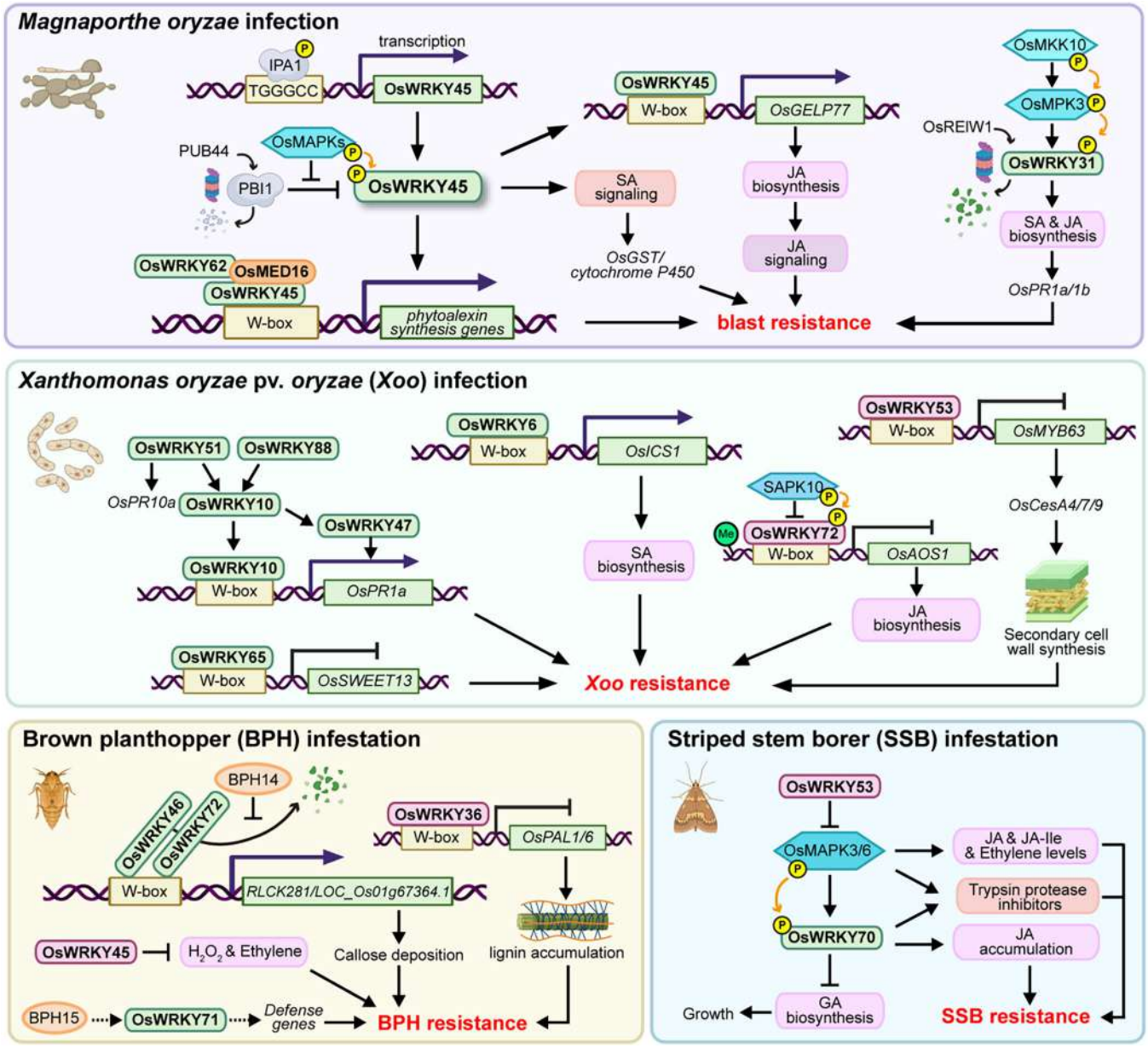


**FIGURE 5** | Functional roles of OsWRKYs in regulating rice defense against pathogens and insects. The combined schematic illustrates representative OsWRKY-mediated modulation of immunity against *M. oryzae* and *Xoo* infections, as well as resistance to brown planthopper (BPH) and striped stem borer (SSB) infestations. OsWRKYs in green boxes act as positive regulators of pathogen/insect resistance, while those in red boxes are negative regulators. Solid arrows and T bars represent direct activation and repression, respectively, while dashed lines denote indirect effects. The templates were obtained from Biorender (https://www.biorender.com). [Color figure can be viewed at wileyonlinelibrary.com]

In short, OsWRKYs are involved in the response of rice to nutrient imbalance mainly by regulating genes related to nutrient transport, uptake, and metabolism. Further research can expand into the investigations of OsWRKY functions in other micronutrient homeostasis, such as Zn and Mg, for a more comprehensive understanding of nutrient management for rice production.

## 5 | Regulatory Roles of OsWRKYS in Biotic Stress Responses

Rice is confronted with numerous biotic challenges, including fungal, bacterial, and viral diseases as well as insect herbivory, which severely impact global rice production. OsWRKYs have been extensively documented for their predominant roles in response to biotic stresses. Upon pathogen infection or insect infestation, OsWRKYs orchestrate complex signaling network involving SA, JA, and MAPK cascade pathways to activate the defense mechanisms (Figure 5 and Supporting Information S1: Table 3). Several OsWRKY members, such as OsWRKY45 and OsWRKY53, have been characterized as central regulators in rice defense against both pathogens and insects (Hu et al. 2015; Shimono et al. 2007). The functional versatility of OsWRKYs in mediating biotic stresses makes them as valuable genetic targets for developing board-spectrum disease and pest-resistant rice varieties.



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### 5.1 | Rice Blast

Rice blast, caused by fungus *Magnaporthe oryzae* (*M. oryzae*), is one of the most devasting disease that severely limits rice yield and grain quality. OsWRKY45 serves as a master regulator to enhance rice blast resistance through multiple mechanisms. It positively regulates benzothiadiazole (BHT)-induced blast resistance by transcriptionally activating defense genes including *glutathione S-transferase* (*GST*) and *cytochrome P450* via SA signaling (Shimono et al. 2007). OsWRKY45 also directly activates the *GDSL-type lipase* (*OsGELP77*) that modulates lipid metabolism to increase JA accumulation, which in turn triggers JA-dependent immunity (Zhang et al. 2023). Furthermore, OsWRKY45 interacts with the Mediator Complex Subunit 16 (OsMED16) and cooperates with OsWRKY62 to form a trimeric complex that synergistically activates several phytoalexin synthesis-related genes, thereby enhancing rice resistance to *M. oryzae* (Wu et al. 2024). As a pivotal regulator of blast resistance, OsWRKY45 is subject to precise regulation to optimally balance the defense response with growth requirements in rice. Ideal Plant Architecture 1 (IPA1) regulates OsWRKY45 via a phosphorylation-dependent switch. Under normal growth conditions, IPA1 primarily drives growth-related genes, but upon blast infection, phosphorylation redirects IPA1 to preferentially bind to the TGGGCC motif in the Os*WRKY45* promoter to activate its expression. This fine-tunes the trade-off between growth and immunity in rice (Liu et al. 2019; J. Wang et al. 2018). Additionally, OsWRKY45 is activated during pathogen perception through two coordinated mechanisms: U-box ubiquitin ligase PUB44-mediated degradation of PUB44-Interacting Protein 1(PBI1, an OsWRKY45 suppressor), and MAPK-dependent phosphorylation of OsWRKY45 to weaken PBI1-OsWRKY45 binding affinity (Ichimaru et al. 2022).

Moreover, OsWRKY31, OsWRKY67 and OsWRKY62 are also positive regulators of resistance to *M. oryzae*. OsWRKY31 functions as a critical component in the OsMKK10-OsMPK3-OsWRKY31 cascade activated upon *M. oryzae* infection (Wang et al. 2023a). Under normal conditions, OsWRKY31 is maintained at low levels through targeted degradation by a RING-finger E3 ubiquitin ligase interacting with OsWRKY1 (OsRElW1), thereby attenuating OsWRKY31-mediated suppression of IAA level and promoting rice growth. Upon infection, phosphorylated OsWRKY31 exhibits enhanced binding to W-box of defense-related genes (*OsPR1b*) and increased protein stability via reducing OsRElW1-mediated ubiquitination (Wang et al. 2023a). Moreover, OsWRKY31 activation elevates SA and JA levels to induce defense response genes (*OsPR1a* and *OsPR1b*) while decreasing IAA to inhibit growth, shifting rice from growth towards defense (Wang et al. 2023a). OsWRKY67 also positively regulates rice blast resistance and is strongly activated by both leaf and panicle blast infection (Liu et al. 2018). It acts through the SA-dependent defense pathway by inducing SA biosynthesis genes [*Isochorismate Synthase 1* (*ICS1*) and *Phenylalanine Ammonia-Lyase 1* (*PAL1*)], signaling genes [*Phytoalexin Deficient 4* (*PAD4*) and *NPR1 Homolog 1* (*NH1*)], and increasing SA accumulation. OsWRKY67 also directly activates *PR1a* and *PR10* by binding to W-box in their promoters (Liu et al. 2018). The immune function of OsWRKY62 remains controversial. OsWRKY62 plays contrasting roles in blast resistance depending on the presence of the blast-resistant protein Pi9 (Shi et al. 2023). In non-Pi9 background rice (Nipponbare), OsWRKY62 is induced upon infection and positively contributes to basal defense. However, in Pi9-harboring cultivar, it acts as a negative regulator. Normally, OsWRKY62 is degraded by a ubiquitin-like structural domain protein, ANIP1 (AVRPI9- Interacting Protein 1), but in Pi9 backgrounds, it becomes stabilized and forms a complex with ANIP1 and Pi9 that maintains Pi9 in an inactive state, thereby suppressing Pi9-mediated immunity and reducing blast disease resistance (Shi et al. 2023). In wild-type ZH17, overexpression of the full-length *OsWRKY62* transcript (*OsWRKY62.1*) increases susceptibility to rice blast, demonstrating its role as a negative regulator (Liu et al. 2016). Notably, an alternative splicing variant, OsWRKY62.2 identified in ZH17, lacking the N-terminal regions essential for W-box binding and transcriptional repression, exhibits reduced repressor activity and may interfere with OsWRKY62.1's function through interaction (Liu et al. 2016).

Therefore, OsWRKYs regulate rice blast resistance by activating defense genes, modulating JA and SA pathways, and balancing growth and immunity, which offers potential targets for improving blast resistance through genetic manipulation.

### 5.2 | Bacterial Blight

Bacterial blight, caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), is a major bacterial disease that affects rice cultivation worldwide. OsWRKY IIa subfamily members act as both positive and negative regulator of defense against *Xoo*. Overexpression of *OsWRKY71* induces the expression of defense-related genes and improves the immunity to *Xoo* (Liu et al. 2007). Interestingly, attempting to silence all four OsWRKY IIa members (OsWRKY62, OsWRKY71, OsWRKY28 and OsWRKY76) unexpectedly triggers their super-overexpression and enhances *Xoo* resistance, suggesting functional interactions among these members in synergistically modulating rice bacterial blight immunity (Peng et al. 2010). Rapidly induced by *Xoo* infection and SA treatment, OsWRKY6 positively confers rice immunity by directly binding to the W-box-like element 1 (WLE1) in the promoter of key defense gene *OsPR10a* (Choi et al. 2015; Hwang et al. 2011). In addition, OsWRKY6 reduces rice susceptibility to *Xoo* through SA-dependent pathway by directly binding to the promoter of *OsICS1* to increase SA level (Choi et al. 2015). Similarly, OsWRKY51 is also a positive transcriptional regulator in defense response to *Xoo* by directly binding to *OsPR10a* promoter (Hwang et al. 2016). Two transcriptional regulatory cascades, OsWRKY51-OsWRKY10-OsWRKY47 and OsWRKY88-OsWRKY10-OsWRKY47 were reported to be crucial in both basal defense and Xa1-meidated resistance against *Xoo*. OsWRKY10 functions as a central hub for both the cascades, and directly binds to the defense gene promoter *OsPR1a* and simultaneously activating *OsWRKY47* (Choi et al. 2020). OsWRKY7 enhances the defense against *Xoo* at both transcriptional and posttranscriptional levels. OsWRKY7 undergoes alternative translational initiation, with the unstable full-length protein degraded by proteasome-mediated pathway and the more stable shorter protein form translated from the downstream in-frame start codon. Both isoforms retain transcriptional activity



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for enhanced resistance to bacterial blight (Zheng et al. 2023). OsWRKY65 functions as a transcriptional repressor by directly binding to the W-box motif in the promoter of *OsSWEET13*, a major susceptibility gene for *Xoo*, thereby repressing its expression and restricting bacterial proliferation. Additionally, OsWRKY65 enhances by inducting the defense-related genes (*OsPR1a* and *OsPR10a*), while simultaneously reducing other susceptibility gene like *OsSWEET14* and *OsImpa1a* (Son et al. 2024).

In contrast, OsWRKY62 negatively regulates innate immunity, as overexpression its splice variant *OsWRKY62.1* reduces resistance to *Xoo* (Peng et al. 2008). OsWRKY53 negatively regulates the resistance to *Xoo* by transcriptionally repressing *OsMYB63*, a key TF that activates secondary cell wall-related cellulose synthase genes (*OsCesA4*, *OsCesA7* and *OsCesA9*), resulting in thinner sclerenchyma cell walls to weaken the physical barrier against *Xoo* invasion (Xie et al. 2021). The nonspecific serine/threonine protein kinase10 (SAPK10)-OsWRKY72-AOS1(allene oxide synthase) module is involved in *Xoo* resistance by integrating hormone-crosstalk, epigenetic regulation and posttranslational modifications. Specifically, OsWRKY72 suppresses the JA biosynthesis gene *AOS1* via promoter binding and DNA-hypermethylation, whereas its phosphorylation by ABA-induced kinase SAPK10 alleviates this repression (Hou et al. 2019). Interestingly, OsWRKY45 has two allelic variants, OsWRKY45-1 (from Nipponbare) and OsWRKY45-2 (from Minghui 63), which differ by 10 amino acids difference and play opposite roles in resistance to *Xoo*. Overexpression of *OsWRKY45-1* increases the *Xoo* susceptibility by suppressing the expression of defense-responsive genes and modulating the balance between SA and JA signaling pathways (Tao et al. 2009).

In short, OsWRKYs regulate rice blight resistance by controlling defense and susceptibility genes, JA and SA pathways, and cell wall reinforcement. Future research work could examine the intricate functional interplay and posttranslational modifications of OsWRKYs to precisely control their regulatory networks for durable blight resistance.

### 5.3 | Other Pathogens

Sheath Blight (ShB) is a serious disease caused by *Rhizoctonia solani* (*R. solani*) that significantly reduces rice yield. Like its negative regulatory role in resistance to *Xoo*, OsWRKY53 also negatively regulates rice defense responses to *R. solani*. It activates BR signaling by upregulating the BR receptor *OsBRI1*, which subsequently suppresses rice defense against *R. solani* (Peng Yuan et al. 2020). Additionally, OsWRKY53 enhances rice susceptibility to *R. solani* by forming a transcriptional complex with the fungal effector AOS2 and the rice TF Grassy tiller 1 (GT1). This activates *OsSWEET2a* and *OsSWEET3a* to promote sugar efflux into the apoplast and facilitates pathogen growth (Yang et al. 2023). Rice false smut caused by grain-infecting pathogen *Ustilaginoidea virens* (*U. virens*) threatens both rice production and health of human and animals through producing cyclopeptide mycotoxins. UvSec. 117, a key virulence effector secreted by *U. virens*, directly interacts with OsWRKY31 in the nucleus, and disrupts the OsWRKY31's DNA-binding activity on JA biosynthesis gene *Allene Oxide Cyclase* (*OsAOC*). This interaction inhibits OsWRKY31-mediated activation of JA accumulation, thereby suppressing JA-mediated immunity in rice (Duan et al. 2024).

### 5.4 | Beneficial Microbes

The interaction between rice and beneficial microbes (e.g., rhizobacteria, endophytes, and arbuscular mycorrhizal fungi (AMF)) can improve stress resilience, nutrition uptake, and rice yield, supporting sustainable cultivation under environmental challenges (Domingo and San Segundo 2023). For instance, the plant growth-promoting rhizobacterium (PGPR) *Bacillus megaterium* enhances rice growth and drought tolerance, with OsWRKY47 significantly upregulated in the PGPR-treated rice, indicating its potential involvement in these processes (Lee et al. 2024). The endophyte *Harpophora oryzae* induces rice systemic resistance to blast by triggering the OsWRKY45-dependent SA signaling pathway, suggesting OsWRKY45 as a crucial regulator in rice-endophyte mutualistic interaction (Su et al. 2013). Colonization by AMF can mitigate symptoms caused by *Xoo* infection in rice, accompanied by a significant increase in *OsWRKY30* expression, implying its role in contributing to the mycorrhiza-induced resistance (Guigard et al. 2023). However, studies on the regulatory roles of OsWRKYs in rice-beneficial microbe interactions remain limited, and further experiments are needed to elucidate the underlying molecular mechanisms.

### 5.5 | Phytophagous Insects

Rice is attacked by various phytophagous insects throughout its life cycle, resulting in substantial yield loss. For instance, the brown planthopper (BPH, *Nilaparvata lugens* Stål), a piercing-sucking herbivore, is particularly destructive due to its directly phloem feeding and transmission of viral diseases to rice (Xu et al. 2021). OsWRKY45 plays vital but contrasting roles in rice defense against pathogens and herbivores. Different from its positive regulation in rice blast resistance, OsWRKY45 conversely acts as a negative modulator in rice resistance to BPH. Silencing of *OsWRKY45* with antisense (*as-wrky*) significantly reduces feeding preference, lowers egg-hatching rate and decreases nymph survival by eliciting the BPH-induced ethylene and $H_2O_2$, while not affecting JA and SA biosynthesis (Huangfu et al. 2016). Under normal growth conditions, OsWRKY46 and OsWRKY72 undergo ubiquitin-mediated degradation. Upon BPH infestation, the first-isolated planthopper resistance CC-NB-LRR protein Brown Planthopper Resistance 14 (BPH14) directly interacts with these TFs to prevent their degradation. The stabilized OsWRKY46 and OsWRKY72 effectively bind to W-box elements to transcriptionally activate the expression of *RLCK281* (a receptor-like kinase gene) and *GSL* (a callose synthase gene), leading to enhanced defense responses and callose deposition to block BPH feeding (Hu et al. 2017). The *Bph15* gene, derived from wide rice *Oryza officinalis*, is another major BPH resistance locus that have been widely utilized in rice breeding (Yang et al. 2004). OsWRKY71 is essential for Bph15-mediated BPH resistance, with its disruption significantly compromising Bph15-conferred resistance by



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altering key defense genes expression (including sesquiterpene synthase *OsSTPS2*, EXO70 family gene *OsEXO70J1* and disease resistance gene *RGA2*). In contrast, overexpression of *OsWRKY71* did not enhance rice BPH resistance (X. Li et al. 2023). OsWRKY36 is a transcriptional suppressor of the key genes involved in phenylpropanoid pathway and lignin accumulation, including *OsPAL6* and *OsPAL1*. Knockout of *OsWRKY36* derepresses the transcription of these *OsPAL*s, promoting the formation of sclerenchyma and lignin deposition to strengthen the physical barrier against BPH penetration (Liu et al. 2025).

The striped stem borer (SSB, *Chilo suppressalis*) is a major chewing herbivore causing severe damage to rice crops. Its larvae bore into stems, leading to stunted growth, reduced tillering, and significant yield losses. OsWRKY53 suppresses SSB-induced defense by physically interacting with and inhibiting OsMPK3/OsMPK6 activity, leading to reduced induction of defense-related phytohormones such as JA, JA-Ile, and ethylene, as well as decreased defense compound trypsin protease inhibitors (TrypPIs), ultimately compromising the resistance to SSB (Hu et al. 2015). In contrast, OsWRKY70 positively regulates rice resistance against SSB via direct interacting with and activating by OsMPK3/OsMPK6, thereby enhancing the JA accumulation and TyrPIs activity. In addition, OsWRKY70 negatively regulates GA biosynthesis to prioritize defense over growth in rice plants (Li et al. 2015).

In summary, OsWRKYs regulate insect resistance primarily through hormonal signaling (JA, SA, GA and ethylene), ROS homeostasis, resistance-protein stabilization, callose/lignin-based physical barrier, defense compounds (TyrPIs) accumulation, providing genetic strategies to fine-tune these pathways for enhanced multiple herbivore resistance while balancing growth and yield in rice.

## 6 | THE Roles ofOsWRKYS in Plant Hormones Regulation

Plant hormones are pivotal regulators of rice growth, development and stress responses. As discussed above, OsWRKYs modulate these processes primarily by direct binding to promoter of critical genes or interacting with proteins involved in phytohormone biosynthesis, catabolism and signaling.

OsWRKYs finely tune hormone levels by controlling the relevant biosynthetic and catabolism genes. For instance, OsWRKY53 promotes ABA accumulation by repressing ABA catabolic genes (*OsABA8ox1/2*), whereas OsWRKY50 reduces ABA levels by inhibiting ABA biosynthetic gens (*OsNECD5*) (S. Huang et al. 2021; Xie et al. 2022). OsWRKY78 interacts with OsMED25 to co-activate the GA biosynthetic gene (*OsGA20ox1*), thereby increasing GA levels (Miao et al. 2025). Additionally, OsWRKY45 and OsWRKY6 enhance JA and SA production by directly inducing *OsGELP77* and *OsICS1*, respectively (Choi et al. 2015; Zhang et al. 2023). OsWRKYs regulate downstream response genes to mediate hormone signaling. OsWRKY29 blocks ABA signaling by inhibiting ABA-responsive gene *OsABF1* (Zhou et al. 2020), while OsWRKY36 suppresses GA signaling by stabilizing DELLA-protein OsSLR1 (Lan et al. 2020). OsWRKY45 is a well-established central modulator of SA signaling pathway in rice immunity (Shimono et al. 2007; Tao et al. 2009). OsWRKY53 is involved in the BR signaling pathway by serving as an OsGSK2 substrate and synergizing with OsBZR1 to enhance BR responses (Tian et al. 2021; Tian et al. 2017). OsWRKYs also function as regulators involved in plant hormone crosstalk. For example, OsWRKY51 and OsWRKY71 coordinate the balance between GA and ABA pathways to regulate seed germination (He et al. 2021; Xie et al. 2006). In contrast, OsWRKY70 mediates JA-GA interplay during insect infestation by promoting JA accumulation and repressing GA biosynthesis to prioritize defense over growth (Li et al. 2015).

In summary, OsWRKYs regulate rice development and stress resilience by tightly controlling hormone homeostasis, signaling, and crosstalk, coordinating the trade-off between growth and defense.

## 7 | Conclusions and Perspectives

Here, we comprehensively summarize the evolution and functional versatility of OsWRKYs in rice growth, development and stress resilience, underscoring their integration into dynamic regulatory networks. By binding to the W-box motifs and partnering with some co-regulators, OsWRKYs are transcriptional activators or repressors to fine-tune target gene expression, coordinating phytohormone crosstalk, secondary metabolism, and stress-adaptive mechanisms to enhance agronomic performance in rice.

OsWRKYs are involved in multiple abiotic and biotic stress responses. Some OsWRKYs confer board-spectrum tolerance (e.g., OsWRKY11 enhances both heat and drought tolerance), whereas others show stress-dependent antagonism (e.g., OsWRKY45 promotes pathogen defense but inhibits BPH resistance). In natural environments, rice is often exposed to various stresses simultaneously. A critical challenge is to decipher how these OsWRKYs reconfigure their regulatory networks under combined stresses and prioritize responses to these competing threats. Leveraging single-cell transcriptomics, spatially-resolved transcriptomics and other omics can map stress-specific OsWRKY spatiotemporal activity at the cellular level, providing insights into how rice decides among conflicting defense strategies (Figure 6A). Moreover, OsWRKYs are under precise regulation, with current studies primarily focused on phosphorylation and ubiquitination. In addition, the expression levels of specific *OsWRKYs* correlate with differential methylation patterns and histone acetylation/deacetylation processes, although the detailed regulatory mechanisms are not elucidated (Viana et al. 2018). Other posttranslational modifications (e.g., SUMOylation, S-nitrosylation, and glycosylation) and epigenetic plasticity (including DNA methylation or histone acetylation) remain largely unexplored in the regulation of OsWRKYs. Therefore, these can be further revealed by adopting techniques such as LC-MS/MS and CRISPR-dCas9-based epigenome editing (Figure 6B).

In addition, emerging evidence indicates that biomolecular condensates such as stress granules and processing bodies,



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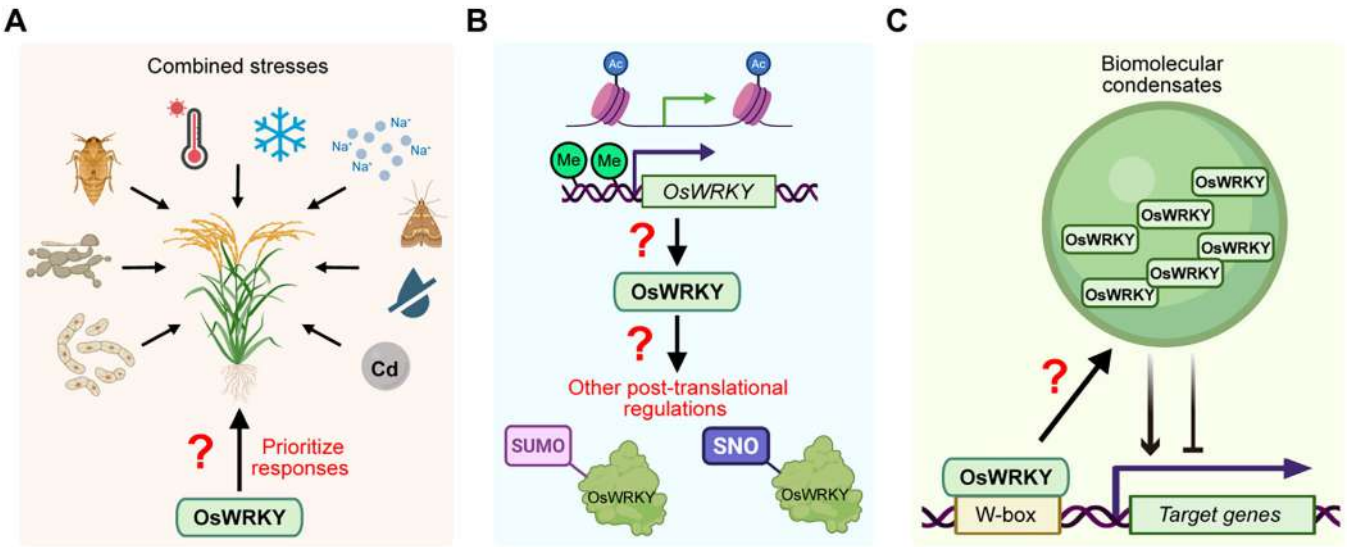


**FIGURE 6** | Future perspectives for the analysis of OsWRKYs in rice. The red question markers indicate areas for further investigations: (A) how OsWRKYs prioritize responses to combined stresses; (B) more regulatory mechanisms controlling OsWRKYs at multiple levels; and (C) their potential involvement in the biomolecular condensation. The templates were obtained from Biorender (https://www.biorender.com). [Color figure can be viewed at wileyonlinelibrary.com]

formed via liquid–liquid phase separation (LLPS), play central roles in the developmental processes and responses to environmental cues in plants (Solis-Miranda et al. 2023). Many TFs have been reported to undergo LLPS. For example, members of Auxin Response Factor (ARF) family were observed to form cytoplasmic condensates that sequesters ARFs to prevent their nuclear entry (Powers et al. 2019). Given the pivotal role of OsWRKYs in rice growth and stress resilience, as well as the presence of predicted prion-like domains and intrinsically disordered regions in several members (with representative examples shown in Supplementary Figure 3), it is important to investigate whether they could contribute to the assembly of stress-induced condensates as scaffolds or clients (Figure 6C). This may occur potentially through interactions with RNA-binding proteins or translational regulators, thereby influencing their transcriptional regulation of downstream target genes in rice (Figure 6C).

Collectively, deciphering the functional mechanisms of OsWRKY TFs across physiological, cellular and genetic levels reveals the intricate networks underpinning rice development and stress resilience. These will provide valuable insights for the molecular breeding strategies to develop high-yielding rice varieties with enhanced stress-tolerance.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.
3-Supplementary material 07.



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