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REVIEW

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Transcription factor WRKY complexes in plant signaling pathways

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Abstract

WRKY transcription factors (TFs) have evolved as a plant-specific gene family. Growing evidences indicate that WRKY TFs play crucial roles in plant growth, development, and responses to environmental stimuli. These TFs primarily recognize W-box *cis*-elements and to a less extent, WT-box. The binding affinity of WRKY TFs to these *cis*-elements is modulated by protein folding, post-translational modifications, and the nucleotide sequence adjacent to the core motif, including its methylation status. The interaction of WRKY proteins with receptors or as components of receptor complexes offers a potential shortcut signaling pathway for prompt and appropriate responses. Recent studies demonstrated that WRKY TFs can be targeted by effectors from pathogens and insects, leading to shared signaling events between these distinct invaders. Modifications of WRKY TFs by kinases or other regulators can alter their DNA-binding and/or transactivation abilities, thereby impacting the expression of target genes. Additionally, the formation of complexes involving WRKY TFs with other WRKY proteins or components provides valuable insights into the regulatory networks governed by this TF family. This review highlights recent advancements in understanding the interactions between WRKY TFs and other proteins or *cis*-elements, as well as their roles in responses to biotic and abiotic stresses, metabolism, growth, and development.

Keywords Abiotic stress, *cis*-element binding, Growth and development, Metabolism, Plant immunity, Protein interaction, WRKY transcription factor

Background

WRKY transcription factors (TFs) are predominantly found in plants and are characterized with the presence of a WRKY domain (WD), which has approximately 60 amino acid residues in length. This domain contains a highly conserved heptad WRKYGQK motif, followed by various zinc finger structures which confer potential DNA binding ability. WRKY TFs typically bind W-box *cis*-elements (TTGACY, with a core sequence TGAC). The expansion of *WRKY* gene numbers has been particularly noticed in certain flowering plants, especially in polyploid genomes, such as rapeseed (*Brassica napus*), sugarcane (*Saccharum spontaneum*), *Glycyrrhiza glabra*, and *Tritipyrum*, due to whole-genome, segmental, or tandem duplications (Chen et al. 2019, 2022a; Goyal et al. 2020, 2023; Li et al. 2020a, 2022). Phylogenetically, WRKY proteins are classified into three groups, and each group has various subgroups (Eulgem et al. 2000; Wu et al. 2005; Goyal et al. 2020; Li et al. 2020a). However, following the increasing amount of available genome sequence data, inconsistencies have emerged beyond classification roles, likely due to polymorphisms in key amino acids, variations in zinc finger length, or deletions of the entire or partial WD (Yang et al. 2017; Chen et al. 2019; Goyal et al. 2023; Javed and Gao 2023).

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Changes in the WD, potentially involving alterations to the entire *WRKY* gene, serve as mechanisms for gain or lost functions to adapt to the demands of whole-genome evolution.

Since the initial identification of the *WRKY* gene in sweet potato (Ishiguro and Nakamura 1994), *WRKY* genes have been recognized for their crucial roles in various biological processes, including plant growth, development, metabolism, and responses to biotic and abiotic stresses (recent reviews, Goyal et al. 2023; Javed and Gao 2023; Wang et al. 2023a; Zhang et al. 2023a; Saha et al. 2024). Dynamic protein–protein interactions and the capability to bind *cis*-elements are fundamental for WRKY TFs to execute their biological functions. In our previous review (Chen et al. 2019), we summarized WRKY structure and evolution, the binding elements, interaction with diverse kinases and receptor complexes, as well as the role in regulating metabolites. Nevertheless, comprehensive genome-wide investigations of the interacting partners of WRKY proteins including the targeted protein and DNA components has held immense promises in unraveling WRKY-mediated signaling cascades and transcriptional regulatory networks. This review focuses on recent achievement in understanding WRKY TF interactions with other proteins and DNA elements as well as their biological functions, updating our understanding to the previous review (Chen et al. 2019).

WRKY binding elements

WRKY proteins primarily bind W-box or W-box-like sequences, demonstrated by electrophoretic mobility shift assays (EMSAs) and crystal structure prediction. Some WRKY TFs have the capability to bind to DNA sequences distant from W-boxes (Chen et al. 2019). The conserved heptad WRKYGQK motif within a β-strand, directly interacts with DNA bases, confirming that W, Y, and two K residues in the WRKYGQK motif are indispensable for binding DNA. The Q amino acid residue in the heptad also influences the DNA-binding activity. For instance, mutation from WRKYGQK to WRKYGKK in Arabidopsis AtWRKY50 and to WRKYGEK in rice OsWRKY31 remain DNA-binding activity, while the WRKYGMK mutation in pepper CaWRKY27b does not (Hussain et al. 2018; Yang et al. 2022; Wang et al. 2023a). Meanwhile, WRKY proteins often form homo- and hetero-complexes, with the WDs being significant contributors of the association (Xu et al. 2006; Liu et al. 2016; Cheng et al. 2019; Grzechowiak et al. 2022). For example, the AtWRKY18-WD exhibits a preference for binding to probes containing tandem W-box repeats due to WD dimer formation, which facilitates the interaction with adjacent W-boxes (Grzechowiak et al. 2022). The OsWRKY45-WD dimer with two identical DNA-binding domains engages with the major groove of the W-box element (Cheng et al. 2019). Additionally, WD binding to W-boxes induces deformation of the B-type DNA helix and alters the major and minor groove widths, revealing that DNA sequence flexibility influences specific recognition by WRKY TFs (Grzechowiak et al. 2022).

The N-terminal WDs (NTWDs) of AtWRKY TFs form crystal complexes with DNA sequences containing W-boxes, where the distances between amino acids of AtWRKY1-NTWD and the DNA bases are shorter compared to AtWRKY4-CTWD (C-terminal WD), resulting in higher DNA binding affinity for AtWRKY1-NTWD (Xu et al. 2020). Recombinant proteins of partial AtWRKY1 containing both WDs can interact simultaneously with two W-boxes with appropriate protein-to-DNA ratios. The identification of NTWD-DNA complexes is particularly intriguing, as NTWDs were previously thought to have been lost during evolution and could not bind DNA, at least in the in vitro experiments (Eulgen et al. 1999; Wu et al. 2005; Yang et al. 2017). Additionally, a new subgroup IIf of WRKY TFs in *Glycyrrhiza glabra* and *Oryza nivara* exhibits similar zinc finger pattern as NTWD (Xu et al. 2016; Goyal et al. 2020). In rice, OsWRKY63 has been demonstrated to bind to the W-box sequence in *OsWRKY76* promoter (Zhang et al. 2022a). The two WDs in OsWRKY63 are phylogenetically closer to subgroup IIIa WRKYs than group I, with NTWDs (N-terminal WDs) containing the heptad WSKYEQK followed by a C-X_8-C-X_{23}-HXC zinc finger motif, which is different from the general C-X_4-C-X_{22}-HXH, while CTWD (C-terminal WD) has a C-X_4-C-X_{22}-HXC that is different from the conserved C-X_4-C-X_{23}-HXH (Wu et al. 2005, named as OsWRKY93 there). Identifying which OsWRKY63-WD is responsible for DNA binding is necessary. Notably, NTWD-DNA interactions primarily target G'T'C' on the Crick strand (or GAC on the Watson strand), indicating that there is more extensive DNA interaction than CTWD (Xu et al. 2020). AtWRKY50 and AtWRKY70 bind not only to the classic W-box (TGAC core sequence) but also to the WT-box (GACTTT core sequence), with the GAC sequence being the preferred binding motif for NTWD (Machens et al. 2014; Hussain et al. 2018; Xu et al. 2020). Furthermore, methylation of the 5-position of cytosine (5mC) at the core W-box (TGAC) severely reduces AtWRKY40's binding ability, as 5mC modification causes steric hindrance and prevents tight binding of AtWRKY40 to the modified W-box element (Charvin et al. 2023). These findings may explain why flanking sequences of W-boxes are involved in the molecular recognition of WRKY TFs (Ciolkowski et al. 2008; Machens et al. 2014; Cheng et al. 2019; Grzechowiak et al. 2022; Hsin et al. 2022).

Chromatin immunoprecipitation (ChIP)- and DNA affinity purification (DAP)-sequencing methods have successfully identified TF binding sites on a genome-wide scale (O'Malley et al. 2016). Comparison of AtWRKY18, AtWRKY40, and AtWRKY33 binding sites, determined by ChIP-seq after treatment with a 22-amino-acid epitope from flagellin (flg22), reveals that these WRKYs predominantly bind to W-box elements, offering valuable insights into the transcriptional regulatory network involved in early pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) (Birkenbihl et al. 2017). However, some binding fragments enriched by these three WRKY TFs do not contain W-boxes. Reanalysis of the data indicates the presence of WT-boxes within the 500 bp promoter region, suggesting that WT-boxes, although they are not part of the classic W-box, are also WRKY binding sites *in planta* (Arndt et al. 2022). Additionally, AtWRKY33 also binds the TC-box (TCTCT) identified from ChIP-seq data of *AtWRKY33*-overexpressing plants under submergence treatment (Zhang et al. 2021a).

Post-translational protein modifications, protein–protein interactions, and protein conformation are also key factors in WRKY-DNA interactions. For instance, the WD of AtWRKY50 binds WT-box and WT-box-like elements, but full-length AtWRKY50 inhibits DNA binding activity in vitro (Hussain et al. 2018). *In planta*, full-length AtWRKY50 regulates the promoter activities of target genes, suggesting that there are possible changes in protein folding, modification, or interaction with other components (Arndt et al. 2022). The UV RESISTANCE LOCUS 8 (UVR8) protein, an ultraviolet-B radiation photoreceptor, interacts with AtWRKY36 in the nucleus to release its binding to the W-box in the *ELONGATED HYPOCOTYL 5* (*HY5*) promoter for transcriptional repression (Yang et al. 2018). The bacterial effector PopP2 secreted from the plant pathogen *Ralstonia solanacearum* can acetylate Lys residues in the WRKYGQK region of certain WRKY TFs, inhibiting their DNA binding activities (Le Roux et al. 2015; Sarris et al. 2015). Conversely, PopP2 and the bacterial effector AvrRps4 from *Pseudomonas syringae* pv. *pisi* also interact with the integrated WD of RRS1-R (resistance to *R. solanacearum* 1), diminishing its DNA-binding capability (Zhang et al. 2017; Mukhi et al. 2021). Persulfidation of tomato SlWRKY71 facilitates its binding to the promoter of the cyanoalanine synthase gene and enhances the protein stability, augmenting transcriptional repression, and delaying tomato ripening (Sun et al. 2023). Phosphomimetic OsWRKY31 and OsWRKY53 markedly elevate their binding activity to W-box elements (Tian et al. 2017; Wang et al. 2023a). Phosphorylation of AtWRKY70 alters its association with different *cis*-elements. Phosphomimetic AtWRKY70 can still bind to WT-box, but has reduced affinity for the W-box element (Liu et al. 2021a). Although phosphorylation sites of WRKY TFs are located outside the WDs, changes in phosphorylation status may alter protein charges, conformation, and homocomplex formation, leading to variations in DNA-binding activity. The availability of crystal structures of full-length WRKY proteins and their DNA complexes will aid in elucidating the intricate protein-DNA interactions.

WRKY in receptor complexes

WRKY proteins often integrate to receptor complexes to expedite transcriptional reprogramming to bolster plant immunity and growth. OsWRKY62, a member of subgroup IIa WRKYs, interacts with XA21 (*Xanthomonas* resistance 21), an immune receptor that recognizes RaxX (required for activation of XA21 mediated immunity X), a sulfated peptide secreted by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) (Park and Ronald 2012; Ercoli et al. 2022) (Fig. 1a). The intracellular kinase domain of XA21 is cleaved and translocated to the nucleus, leading to XA21-mediated resistance to *Xoo* through a de-repression mechanism. Moreover, OsWRKY62 interacts with the resistance protein Pi9 and its cognate effector AvrPi9 in rice and *Magnaporthe oryzae* interaction (Shi et al. 2023). AvrPi9 regulates OsWRKY62 abundance via ANIP1 (AVRPI9-INTERACTING PROTEIN 1), a ubiquitin-like domain-containing protein, facilitating OsWRKY62 accumulation in the presence of Pi9 but promoting its degradation in the absence of Pi9. Notably, OsWRKY62 plays a dual role against the rice blast fungus *M. oryzae* either positively or negatively, depending on the presence of *Pi9* (Shi et al. 2023). Although OsWRKY62 is predominantly located in the cytosol, it translocates to the nucleus upon binding with other proteins (Liu et al. 2016; Xu et al. 2022). It may act as an activator when associates with mighty activators, such as OsWRKY45; however, the OsWRKY62 homocomplex functions as a repressor of defense responses (Fukushima et al. 2016; Wu et al. 2024).

OsWRKY45 interacts with PANICLE BLAST 1 (Pb1), a coiled-coil nucleotide binding/leucine-rich repeat (CNL) protein that confers broad-spectrum resistance to *M. oryzae* (Inoue et al. 2013). PUB44, a U-box type ubiquitin ligase, positively regulates rice immunity and is targeted by the *Xoo* effector XopP (Ishikawa et al. 2014). PUB44 interacts with PUB44-INTERACTING PROTEIN 1 (PBI1) and inhibits the transcriptional activity of OsWRKY45 through their association (Ichmaru et al. 2022). Unlike the stabilization of OsWRKY45 by Pb1, the abundance of OsWRKY45 protein is negatively regulated by PBI1, although OsWRKY45 is unlikely a

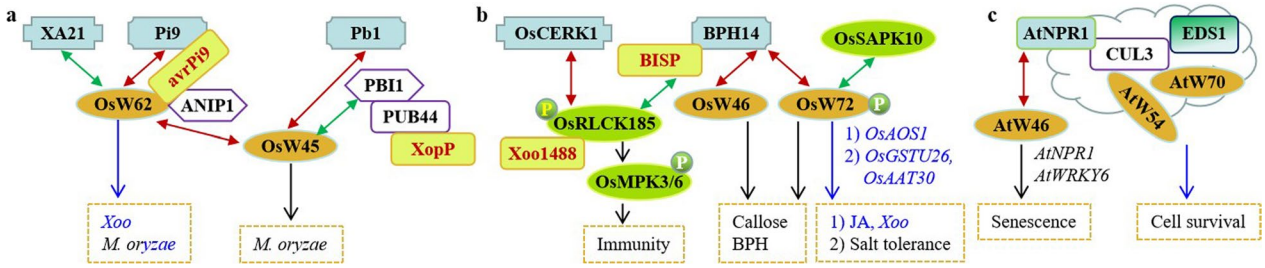

Fig. 1 WRKY transcription factors in receptor complexes. **a** Rice OsWRKY62 (OsW62) interacts with XA21 (*Xanthomonas* resistance 21) and the rice blast resistance gene product Pi9 as well as its cognate avirulence effector avrPi9, leading to the resistance to *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) and *Magnaporthe oryzae* (*M. oryzae*). OsW62 acts as an either negative or positive regulator in disease resistance, depending on its interaction component. OsWRKY45 (OsW45) forms a complex with the receptor Pb1 (PANICLE BLAST 1), positively regulating rice resistance to *M. oryzae*; however, PBI1 (PUB44-INTERACTING PROTEIN 1) destabilizes OsW45 protein. **b** OsWRKY46 (OsW46) and OsWRKY72 (OsW72) interact with the receptor BPH14 (BROWN PLANTHOPPER RESISTANCE 14) and positively regulate callose biosynthesis and resistance against the brown planthopper (BPH). The insect effector BISP (BPH salivary protein) targets the receptor-like cytoplasmic kinase OsRLCK185, which is a critical signaling component at downstream of OsCERK1 (chitin elicitor receptor kinase 1). OsW72 negatively regulates jasmonic acid (JA) biosynthesis via inhibiting of *OsAOS1* (*allene oxide synthase 1*) expression and the resistance to *Xoo* infection. Phosphorylation of OsW72 by an abscisic acid-inducible SnRK2 type kinase OsSAPK10 compromises the repression. OsW72 suppresses the expression of the glutathione transferase gene *OsGSTU26* and the amino acid transporter gene *OsAAT30*, conferring salt tolerance. **c** Arabidopsis AtWRKY54 (AtW54) and AtWRKY70 (AtW70) are in the AtNPR1 (NON-EXPRESSER OF PATHOGENESIS-RELATED GENES 1) condensate. Degradation of AtW54 and AtW70 by the CUL3 (Cullin 3 E3 ligase) complex promotes cell survival during effector-triggered immunity. Interaction of AtWRKY46 (AtW46) with AtNPR1 facilitates the expression of *AtNPR1* and *AtWRKY6*, leading to leaf senescence. Protein names are in bold, and protein–protein interaction are indicated by adjacent or double arrowheads in green for weakening, red for enhancing their functions. Arrows and words are in blue for negative, black for positive, and in mixed colors for both negative and positive regulations. Words are in red for pathogen or insect effector. "P" next to the protein indicates phosphorylation. Number preceding the gene are linked to the consequences described in the box. ANIP1, AVRPI9-INTEACTING PROTEIN 1; EDS1, ENHANCED DISEASE SUSCEPTIBILITY 1; PUB44, U-box protein 44; Xoo1488 and XopP, *Xathomonas* effectors

direct target of PUB44 (Ichmaru et al. 2022). Knockout of *PBI1* increases the levels of OsWRKY45 and resistance to *Xoo* but not to the compatible race of *M. oryzae*. A gain-of-function mutant of the *RESISTANCE TO P. SYRINGAE PV MACULICOLA1* (*RPM1*)-like resistance gene (*OsRLR1*) exhibits a hypersensitive response lesion with strong retardation in growth and resistance to both *M. oryzae* and *Xoo* (Du et al. 2021). OsRLR1 positively regulates disease resistance through interaction with OsWRKY19. Additionally, wheat PM2b, a CNL resistance protein against the powdery mildew pathogen, interacts with TaWRKY76-D, a negative regulator of the disease (Jin et al. 2022).

BROWN PLANTHOPPER RESISTANCE 14 (*BPH14*), encoding a CNL protein, confers resistance to BPH infestation and activates the salicylic acid (SA) signaling pathway (Hu et al. 2017) (Fig. 1b). Transgenic plants expressing *BPH14* or its domain fragments exhibit enhanced resistance to both BPH and the bacterial pathogen *Xoo*. OsWRKY46 and OsWRKY72 interact with BPH14 in the nuclei of rice protoplasts, thereby increasing the transactivation activity and protein levels of OsWRKY46 and OsWRKY72, which in turn upregulates the expression of callose synthase genes. Moreover, OsWRKY72 negatively regulates jasmonic acid (JA) biosynthesis and resistance to *Xoo* infection (Hou et al. 2019). OsSAPK10, an abscisic acid (ABA)-inducible SnRK2 type kinase, interacts with OsWRKY72 and phosphorylates it, compromising its suppression of the JA biosynthesis gene *OsAOS1* (*allene oxide synthase 1*), which underlines the cross-talk between ABA and JA in defense signaling. OsWRKY72 also participates in the regulation of reactive oxygen species (ROS) scavenging under salinity stress by suppressing the expression of the glutathione transferase gene *OsGSTU26* and the amino acid transporter gene *OsAAT30* (Liu et al. 2024a). Allelic variations of OsWRKY72 result in different levels of repression of *OsGSTU26* and *OsAAT30*, which contributes to salt tolerance in hybrid rice. Furthermore, the insect-secreted effector BPH salivary protein (BISP) binds with BPH14 and the receptor-like cytoplasmic kinase OsRLCK185 (Guo et al. 2023) (Fig. 1b), and the perception of BISP triggers BPH14-mediated resistance, whereas BISP attenuates OsRLCK185 autophosphorylation, leading to susceptibility to BPH. OsRLCK185 is also a target of the *Xoo* effector Xoo1488 (Yamaguchi et al. 2013). Phosphorylation of OsRLCK185 by OsCERK1 (chitin elicitor receptor kinase 1) upon chitin perception activates the mitogen-activated protein kinase (MPK) cascade, leading to the enhanced disease resistance through involvement of WRKY and other TFs (Yamaguchi et al. 2013; Wang et al. 2017; Yamada et al. 2017) (Figs. 1b, 2b). These results revealed that WRKY

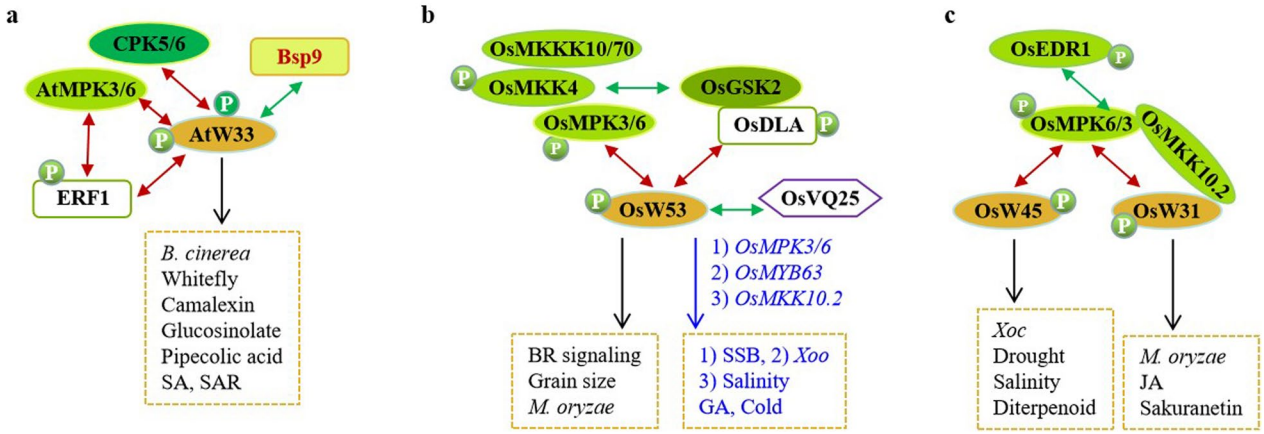

Fig. 2 WRKY transcription factors are targets of kinases. **a** Phosphorylation of AtWRKY33 (AtW33) by AtMPK3/6 (mitogen-activated protein kinase 3/6) and CPK5/6 (calcium-dependent protein kinase 5/6) regulates metabolite biosynthesis and disease resistance to *Botrytis cinerea*. AtW33 is targeted by the whitefly effector Bsp9. AtW33 and ERF1 (ethylene response factor 1) form transcriptional complexes and cooperatively promote camalexin biosynthesis. **b** OsWRKY53 (OsW53) functions at downstream of OsMKKK10/70-OsMKK4-OsMPK3/6 cascades, positively regulating brassinosteroid (BR) signaling, grain size, and disease resistance to *M. oryzae*; while, OsDLA (DECREASED LEAF ANGLE) increases OsWRKY53 stability and OsVQ25 dampens OsWRKY53 transactivation activity. Conversely, OsWRKY53 negatively regulates diverse stress responses; for instance, attenuating resistance to striped stem borer (SSB) infestation by suppressing *OsMPK3/6* expression, decreasing resistance agianst *Xoo* through inhibition of *OsMYB63* expression, reducing tolerance to salinity stress by suppression of *OsMKK10.2*, and cold tolerance through repression of gibberellin (GA) biosynthetic genes. **c** OsWRKY31 (OsW31) and OsWRKY45 (OsW45) can be phosphorylated by OsMPK3/6, promoting rice disease resistance, stress tolerance, and metabolite biosynthesis. OsMPK6 destabilizes OsEDR1 (Raf-like MKKK) via phosphorylation. OsWRKY31, OsMPK3, and OsMKK10.2 form a ternary complex. Drawing descriptions are the same as in Fig. 1. OsGSK2, glycogen synthase kinase-2; SA, salicylic acid; SAR, systemic acquired resistance; *Xoc*, *Xanthomonas oryzae oryzicola*

TFs are involved in the overlapping pathways for host defense against pathogens and insects.

The head-to-head RRS1-R and RPS4 (resistance to *P. syringae* 4) pair, both nucleotide-binding/leucine-rich repeat receptors (NLRs), confer resistance to various bacterial pathogens. The WD of RRS1-R functions as an integrated decoy that intercepts effectors targeting WRKY TFs while retaining DNA binding capability, suggesting that RRS1-R operates in a shortcut signaling pathway for rapid immune responses against invading pathogens (Le Roux et al. 2015; Sarris et al. 2015; Ma et al. 2018). AtWRKY19 also functions as part of an NLR pair and together they co-regulate Arabidopsis susceptibility to the root-knot nematode *Meloidogyne incognita* (Warmerdam et al. 2020). *YrU1*, a stripe rust resistance gene from wheat *Triticum urartu*, encodes an NLR with an N-terminal ankyrin-repeat and a C-terminal WD (Wang et al. 2020). It is intriguing to consider whether the WD in YrU1 serves a similar role as that in RRS1-R. A similar *NLR-WD* chimeric gene has been annotated in the rice genome, albeit with mutations in the conserved heptad WRKYGQK (Wu et al. 2005), suggesting that chimeric proteins of NLR-WD likely have existed before the divergence of monocots and dicots and have adapted to the changes of invading pathogens.

Arabidopsis NON-EXPRESSER OF PATHOGENESIS-RELATED GENES 1 (AtNPR1), an SA receptor, is integrated into cell death or survival decisions in plant immunity (Zavaliev et al. 2020) (Fig. 1c). In response to SA signaling, the AtNPR1-Cullin 3 E3 ligase complex ubiquitinates substrates localized in the AtNPR1-condensate, such as EDS1 (ENHANCED DISEASE SUSCEPTIBILITY 1), AtWRKY54, and AtWRKY70, and promotes cell survival during effector-triggered immunity (ETI). AtWRKY46, a close homolog of AtWRKY54 and AtWRKY70, forms a complex with AtNPR1 in the nucleus and cooperatively regulates leaf senescence-related genes including *AtWRKY6* and *AtNPR1* (Zhang et al. 2021b). Overall, some WRKY proteins could act as the components of receptor complexes to enable rapid integration in transcriptional reprogramming for efficient defense responses and contribute beneficially on plant growth and development.

Interactions of WRKY with protein kinases

The intricate interplay between WRKY proteins and receptor complexes underscores their role as key signaling hubs, while their extensive interactions with protein kinases further highlights the dynamic regulation of WRKY activity through phosphorylation to fine-tune plant responses.

MPK cascades play crucial roles in plant growth and responses to environmental cues (Zhang and Zhang 2022). AtWRKY33, OsWRKY53, and NbWRKY8 are

phylogenetic homologues, containing a serine/threonine-proline residue (S/TP) cluster in their N-terminal, serving as potential phosphorylation sites for MPKs, which are essential for their functions (Ishihama et al. 2011; Mao et al. 2011; Tian et al. 2017; Chen et al. 2019). Phosphomimetic mutants of WRKY TFs often alter their DNA binding and/or transactivation activities. In Arabidopsis, AtMPK3 and AtMPK6 phosphorylate AtWRKY33, thereby regulating the biosynthesis of phytoalexin camalexin and the production of pipecolic acid (Pip), a systemic acquired resistance (SAR) signal molecule (Wang et al. 2018a; Zhou et al. 2020) (Fig. 2a). Phosphorylation of AtWRKY33 by AtMPK3 and AtMPK6 enhances its transactivation activity without affecting DNA binding affinity (Zhou et al. 2020). Additionally, CPK5 (calcium-dependent protein kinase 5) and CPK6 phosphorylate Thr-229 of AtWRKY33, augmenting its W-box binding ability but not its transactivation activity. AtWRKY3/AtMPK6 and CPK5/CPK6 coordinately regulate indole glucosinolates and camalexin biosynthesis, and influence the disease resistance to *Botrytis cinerea* via differential phospho-regulation of AtWRKY33 (Yang et al. 2020; Zhou et al. 2020). The whitefly effector Bsp9 targets AtWRKY33, suppressing the immune signaling by disrupting its interaction with AtMPK6, promoting whitefly preference, performance, and virus transmission (Wang et al. 2019).

OsWRKY53 is primarily phosphorylated at the N-terminal SP cluster by OsMPK3/OsMPK6 (Chujo et al. 2014; Hu et al. 2015; Tian et al. 2017). Phosphorylated OsWRKY53 or its phosphomimetic mutant enhances the transactivation activity (Chujo et al. 2014), W-box binding ability (Tian et al. 2017), and resistance to the fungal pathogen *M. oryzae* (Chujo et al. 2014) (Fig. 2b). Interaction with OsVQ25 suppresses the transactivation activity of OsWRKY53, compromising rice resistance against *M. oryzae* and *Xoo* (Hao et al. 2022). Conversely, OsWRKY53 negatively regulates OsMPK3/OsMPK6 activity and their expression upon striped stem borer (SSB, *Chilo suppressalis*) infestation (Hu et al. 2015). Ethylene and jasmonate accumulation are reduced in *OsWRKY53*-overexpressing plants in response to SSB attack, leading to attenuated resistance to SSB larvae (Hu et al. 2015). Knockout of *OsWRKY53* enhances resistance to *Xoo* by thickening sclerenchyma cell walls in vascular bundles (Xie et al. 2021). Acting as a transcriptional repressor, OsWRKY53 inhibits OsMYB63 as a positive regulator of cellulose biosynthesis and resistance against *Xoo*, providing evidence for enhanced disease resistance through the reinforcement of physical barriers (Xie et al. 2021).

OsWRKY53 is downstream of the MKKK10/MKKK70-MKK4-MPK6 cascades in regulating plant architecture and grain size (Tian et al. 2017, 2021; Liu et al. 2021b) (Fig. 2b). Overexpression of phosphomimetic *OsWRKY53* results in robust phenotype changes, including dwarfism, enlarged leaf angles, and increased grain size. Conversely, knockout of *OsWRKY53* leads to brassinosteroids (BRs)-deficient phenotypes and reduced BR response, indicating a positive role of OsWRKY53 in rice BR signaling (Tian et al. 2017). OsWRKY53 interacts with glycogen synthase kinase-2 (OsGSK2), a key component in rice BR signaling, which phosphorylates and destabilizes OsWRKY53, and OsWRKY53 acts at downstream of OsGSK2 and OsMPK6 in regulating seed size (Tian et al. 2021). Moreover, OsGSK2 negatively regulates OsMPK6 activity by inactivating OsMKK4 via phosphorylation. OsGSK2 also phosphorylates OsDLA (DECREASED LEAF ANGLE), a member of the GRAS (GAI-RGA-and-SCR) family, positively regulating BR signaling and defense against rice blast fungus (Meng et al. 2024a). Interestingly, the interaction with OsDLA enhances OsWRKY53 stability, counteracting the destabilizing effect of phosphorylation caused by OsGSK2 (Tian et al. 2021; Meng et al. 2024a). Recently, OsWRKY53 and OsMKK10.2 have emerged as important regulators under salinity stress by modulating Na^+ homeostasis in rice root (Yu et al. 2023). OsWRKY53 negatively regulates rice salt tolerance by transcriptionally suppressing *OsHKT1;5* (*high-affinity* K^+ *transporter 1;5*) and *OsMKK10.2*. Similar to SSB infestation, OsWRKY53 negatively modulates the phosphorylation level of OsMPK6 under salt treatment (Hu et al. 2015; Yu et al. 2023). Furthermore, OsWRKY53 negatively regulates cold tolerance at the booting stage by suppressing the expression of gibberellin (GA) biosynthesis genes in rice (Tang et al. 2022a). Conversely, OsWRKY78, a close homolog of OsWRKY53, plays a positive role in the regulation of GA biosynthesis and panicle exsertion (Mei et al. 2024).

The OsMKK10.2-OsMPK3/OsMPK6-OsWRKY31/OsWRKY45 cascades positively regulate disease resistance and confer tolerance to salinity and drought stress in rice (Ueno et al. 2015; Ma et al. 2017, 2021; Wang et al. 2023a) (Fig. 2c). OsMKK10.2 activates OsMPK3/OsMPK6, which phosphorylate OsWRKY TFs, such as OsWRKY31 and OsWRKY45. Additionally, activated OsMPK6 phosphorylates OsEDR1, a Raf-like MKKK, destabilizing OsEDR1 (Ma et al. 2021). OsEDR1 is a negative player in resistance to the bacterial leaf streak pathogen *X. o. oryzicola* (*Xoc*) by inhibiting OsMKK10.2 activation. Phosphorylation of OsMKK10.2 at Ser-304 is induced by *Xoc* infection and is crucial for OsMPK6 activation and *OsWRKY45* expression (Ma et al. 2021). OsWRKY31 directly interacts with OsMKK10.2, forming a ternary complex with OsMPK3, allowing prior phosphorylation opportunities (Wang et al. 2023a). Phosphomimetic OsWRKY31 exhibits elevated stability and

DNA-binding activity, conferring enhanced resistance to *M. oryzae*. Additionally, barley SnRK1 (sucrose non-fermenting-related kinase 1) phosphorylates WRKY3, destabilizing the repressor and increasing resistance to powdery mildew (Han et al. 2020). These data underscore WRKY TFs as substrates for diverse kinases, in which the phosphorylation could potentially alter DNA-binding affinity, transactivation, or protein–protein interaction. Additionally, WRKY proteins may exert feedback regulation on kinase expression.

WRKY in jasmonate signaling pathways

Notably, the role of WRKYs in jasmonate signaling pathways, particularly through their interactions with jasmonate ZIM-domain (JAZ) and VQ proteins (a group of proteins characterized by the conserved FxxxVQxLTG motif), was further exemplified for their pivotal function in orchestrating plant responses to environmental stimuli. Numerous WRKY proteins from diverse plants have the ability to interact with VQ proteins, thereby influencing DNA binding, transactivation, and stability of the associated TFs (Yuan et al. 2021; Tian et al. 2024). In Arabidopsis, AtWRKY51, AtWRKY75, and AtWRKY57 belong to this type of TFs. AtJAV1 (jasmonate-associated VQ domain protein 1) forms a complex with AtJAZ8 (JASMONATE-ZIM-DOMAIN PROTEIN 8) and AtWRKY51, which restrains JA at low basal level to ensure normal plant growth. However, injury-induced calmodulin-dependent phosphorylation of AtJAV1 disrupts this complex, leading to JA biosynthesis for defense against herbivory (Yan et al. 2018) (Fig. 3a). Recently, AtWRKY51 has been implicated in balancing growth and disease resistance during pathogen infection by suppressing *RPW8.1* (*RESISTANCE TO POWDERY MILDEW 8.1*) expression (Yang et al. 2024). AtWRKY75 participates in diverse biological processes, positively regulating both SA- and JA-biosynthesis and signaling pathways (Guo et al. 2017; Chen et al. 2019, 2021a). AtJAZ8 interacts with AtWRKY75 to repress its transcription, thereby attenuating resistance to necrotrophic pathogens (Chen et al. 2021a).

Conversely, AtWRKY57 negatively regulates Arabidopsis resistance against *B. cinerea* via JA signaling pathway (Jiang and Yu 2016) (Fig. 3a). AtWRKY57 binds to the promoters of *AtJAZ1* and *AtJAZ5* and induce their expression. SIGMA FACTOR BINDING PROTEIN1 (SIB1) and SIB2, two VQ-containing proteins, interact with repressor AtWRKY57 and activator AtWRKY33, fine-tuning the regulation of *AtJAZ1* and *AtJAZ5* expression and the resistance to *B. cinerea* (Jiang and Yu 2016). Acting as a positive regulator, AtWRKY57 is identified as one of the WRKY TFs that could bind the promoter of *INFLORESCENCE DEFICIENT IN ABSCISSION* (*IDA*) gene, involved in floral organ abscission (Galindo-Trigo et al. 2024). The WRKY binding sites in the *IDA* promoter are also required for flg22 and chitin induced promoter activity, suggesting its potential role in basal immunity. Similarly, tomato SlWRKY17 stimulates *IDA-Like 6* (*SlIDL6*) expression in low light-induced tomato flower abscission (Li et al. 2021).

In tomato, SlWRKY45 interacts with several SlJAZ proteins, and represses the expression of *SlAOC* (*ALLENE OXIDE CYCLASE*) gene, resulting in reduced resistance against the root-knot nematode *M. incognita* (Huang et al. 2022a) (Fig. 3b). SlWRKY31, along with its interaction partner SlVQ15, positively regulates disease resistance to *B. cinerea*, while SlJAZ11 disrupts the interaction and promotes SlWRKY31 transactivation activity (Huang et al. 2022b). SlWRKY57 interacts with SlVQ16 to positively regulate salt tolerance, but interacts with SlVQ2 to negatively regulate salt tolerance (Ma et al. 2023). SlVQ16 and SlVQ21 antagonistically modulate the repression activity of SlWRKY57. In addition, SlJAZ2 also interacts with these proteins, implying that JA

(See figure on next page.)

Fig. 3 WRKY transcription factors in jasmonate signaling pathways. **a** The ternary complex of AtWRKY51 (AtW51), AtJAV1 (jasmonate-associated VQ domain protein 1), and AtJAZ8 (JASMONATE-ZIM-DOMAIN PROTEIN 8) is disrupted when AtJAV1 is phosphorylated, therefore activating jasmonic acid (JA) biosynthesis for defense against herbivory. AtW51 represses *RPW8.1* (*RESISTANCE TO POWDERY MILDEW 8.1*) expression to balance growth and disease resistance during pathogen infection. Formation of the AtWRKY75 (AtW75) and AtJAZ8 complex attenuates AtW75-mediated resistance against necrotrophic pathogens. SIB1 (SIGMA FACTOR BINDING PROTEIN 1) and SIB2 interact with repressor AtW57 and activator AtWRKY33 (AtW33), promoting their fine-tuning regulation of *AtJAZ1* and *AtJAZ5* expression and the resistance to *B. cinerea*. However, AtW57 acts as a positive regulator of floral organ abscission by stimulating the expression of the *INFLORESCENCE DEFICIENT IN ABSCISSION* (*IDA*) gene. **b** Tomato SlWRKY45 (SlW45) enables interaction with several SlJAZs and inhibits *SlAOC* (*ALLEENE OXIDE CYCLASE*) expression, leading to susceptibility to root-knot nematodes. The SlWRKY31 (SlW31) and SlVQ15 complex positively regulates the resistance to *B. cinerea*, but SlJAZ11 interferes with its transcriptional activity. Tomato SlWRKY57 (SlW57) acts as a negative regulator of salt tolerance. SlVQ16 and SlVQ21 antagonistically modulate SlW57 repression activity. Meanwhile, SlJAZ2 can interact with SlW57, SlVQ16, and SlVQ21. The complex of SlWRKY37 (SlW37) and SlVQ7 activates *SlWRKY53* expression and accelerates leaf senescence. **c** Apple MdWRKY75 (MdW75) interacts with MdVQ10 to positively regulate leaf senescence, whereas MdCML15 (calmodulin-like 15) and MdJAZs associate with MdVQ10 to increase and weaken the interactions between MdW75 and MdVQ10, respectively. Grape *VvWRKY5* positively regulates JA accumulation and disease resistance to grape white rot, whereas VvJAZ2 interacts with VvWRKY5 (VvW5) to stimulate the repression of *VvJAZ2* and activation of *VvMYC2*. Drawing descriptions are the same as in Fig. 1

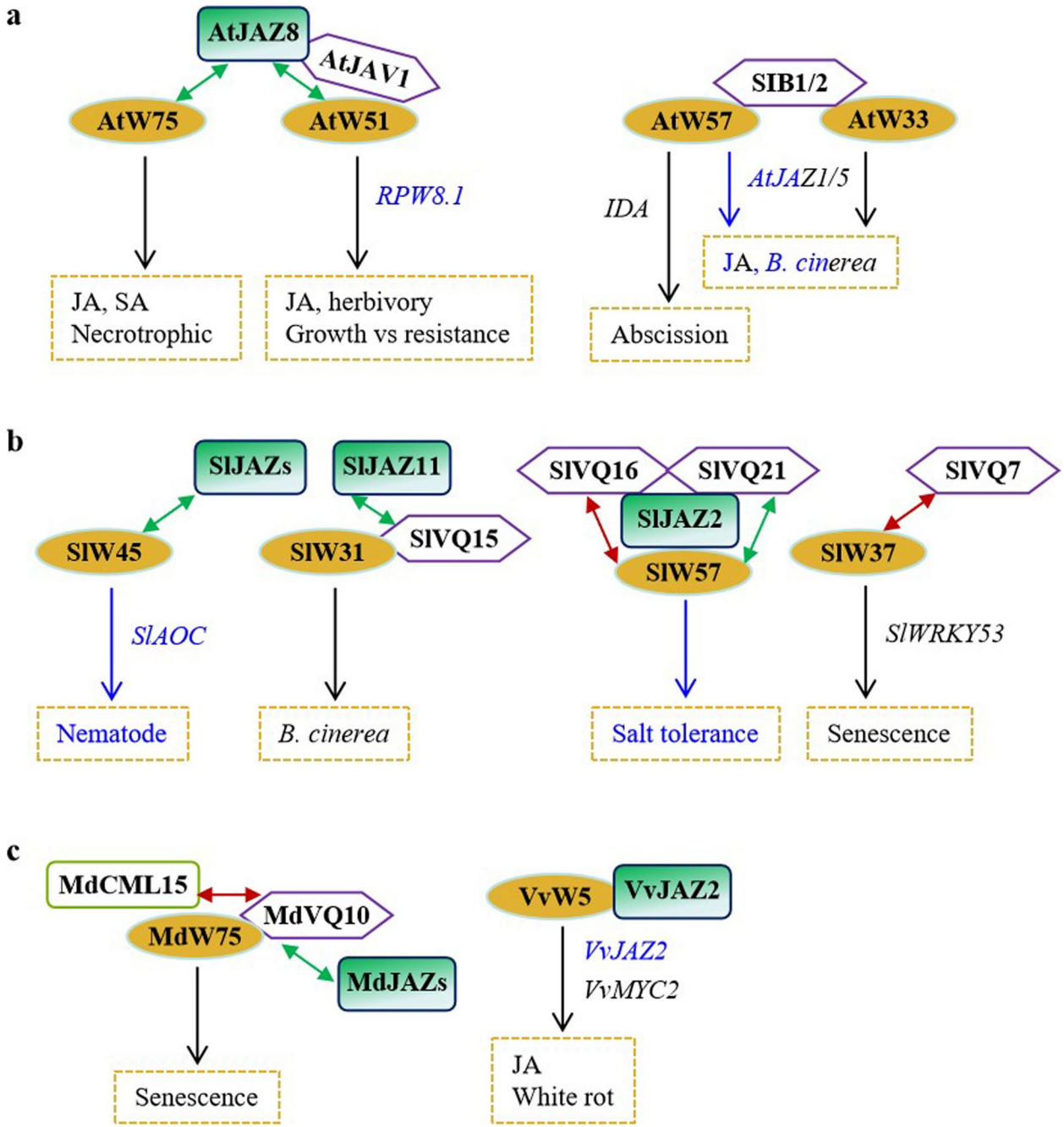

Fig. 3 (See legend on previous page.)

signaling regulates tomato tolerance to salinity stress (Ma et al. 2023). Tomato SlWRKY37 forms a complex with SlVQ7, increasing its stability and transactivation activity to target genes, such as *SlWRKY53*, thereby accelerating leaf senescence induced by JA and darkness (Wang et al. 2022a).

In apple, MdWRKY75 and MdVQ10 act as positive regulators of wounding-triggered leaf senescence, and their interaction enhances the transactivation and DNA-binding activity of MdWRKY75 (Zhang et al. 2023b) (Fig. 3c). MdVQ10 also associates with calmodulin-like protein MdCML15 and MdJAZs, where MdCML15 stimulates but MdJAZs weakens the interaction of MdWRKY75 with MdVQ10. Overexpression of grape *VvWRKY5*, a subgroup IIe member, increases JA accumulation and resistance to grape white rot caused

by *Coniella diplodiella* (Zhang et al. 2023c) (Fig. 3c). VvJAZ2 interacts with VvWRKY5 to stimulate the repression of *VvJAZ2* and activation of *VvMYC2* promoter activities, respectively. Collectively, WRKY TFs can form complexes with VQ and JAZ proteins, altering the biochemical properties of the TFs and modulating jasmonate-related signaling pathways.

WRKY in regulating of metabolite biosynthesis

Beyond the hormonal signaling, WRKYs are also involved in dynamic regulation of metabolic networks in diverse plants. Plants produce phytoalexins, such as diterpenoids, sakuranetin, and phenolamides with antimicrobial activities during pathogen infections (Cho and Lee 2015; Chen et al. 2019). In rice, for example, knocking down of both *OsWRKY62* and *OsWRKY76* (dsOW62/76) leads to metabolic reprogramming, resulting in a remarkable increase in diterpenoids, sakuranetin, serotonin, and phenolamides and a decrease in flavonoids (Liang et al. 2017). Levels of the phytohormones SA and JA/Ile-JA are also elevated in dsOW62/76 and individual *OsWRKY62* and *OsWRKY76* knockout lines (Liu et al. 2016; Liang et al. 2017) (Fig. 4a). Conversely, OsWRKY45 primes diterpenoid phytoalexin biosynthesis and OsWRKY31 positively regulates sakuranetin biosynthesis, which is strongly associated with jasmonate accumulation (Akagi et al. 2014; Miyamoto et al. 2016; Wang et al. 2023a) (Fig. 2c). Sakuranetin and its precursor naringenin are effective antibacterial and antifungal agents (Murata et al. 2020). Moreover, sakuranetin can act as an inhibitor of clathrin-mediated endocytosis, attenuating *M. oryzae* effectors' uptake into rice cells (Jiang et al. 2024). Notably, sakuranetin and serotonin biosynthesis are induced by insect invasion in rice (Liu et al. 2023; Lu et al. 2018).

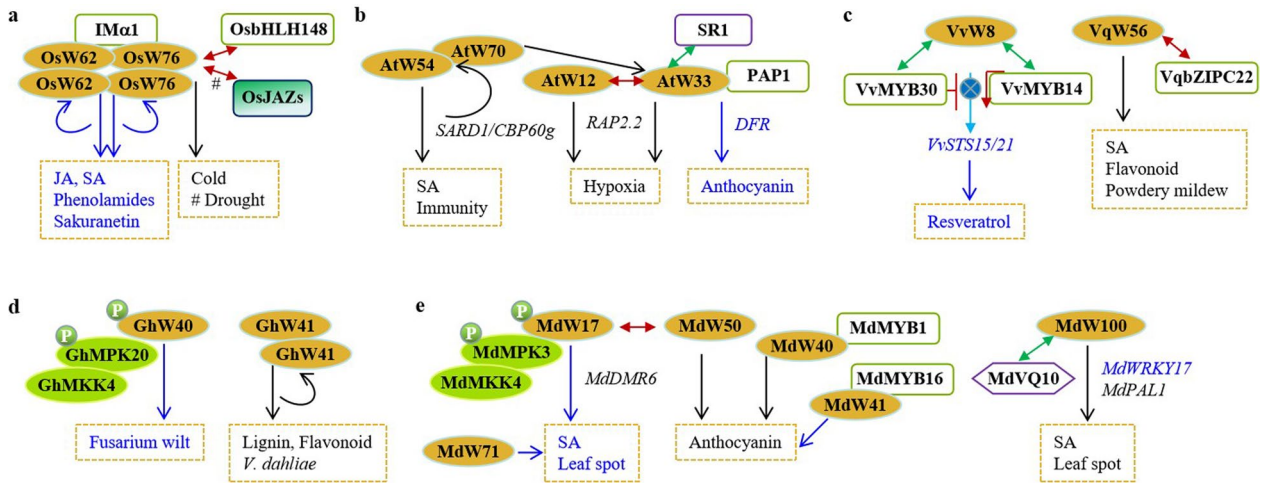

Fig. 4 WRKY transcription factors in metabolism. **a** OsWRKY62 (OsW62) and OsWRKY76 (OsW76) enable the formation of homo- and hetero-complexes and negatively regulate the biosynthesis of jasmonic acid (JA), salicylic acid (SA), and secondary metabolites. OsW62 and OsW76 can also interact with importinα1 (IMα1) for nuclear translocation. OsW76 enhances chilling tolerance via interacting with OsbHLH148, and drought tolerance through interaction with OsJAZs. **b** The AtWRKY54 (AtW54) and AtWRKY70 (AtW70) complex activates SA accumulation and immunity through upregulating of *SAR-DEFICIENT 1* (*SARD1*) and CALMODULIN-BINDING PROTEIN 60-LIKE G (*CBP60g*) expression. SARD1 and CBP60g transcription factors show positive feedback regulation of *AtW54* and *AtW70*. AtWRKY33 (AtW33) reduces anthocyanin biosynthesis via suppressing of dihydroflavonol 4-reductase (*DFR*) transcription, and interacts with PAP1 (production of anthocyanin pigments 1) to interfere with its complex formation. AtW33 is a positive regulator and functions at downstream of Submergence Resistance1 (SR1), a RING-type E3 ligase. AtW33 and AtWRKY12 (AtW12) complexes stimulate the expression of *RAP2.2* (*RELATED TO AP2 2*) and hypoxia tolerance. Additionally, AtW70 promotes the expression of *AtW33*. **c** Grapevine VvWRKY8 (VvW8) indirectly represses the expression of stilbene synthase genes (*VvSTS15/21*), leading to the reduced accumulation of resveratrol. The complex formed by VvW8 and activator VvMYB14 competes with the repressor VvMYB30-VvW8 complex to bind to the same MYB binding sites in *VvSTS15/21* promoters. Wild grape VqWRKY56 (VqW56) interacts with VqbZIPC22 and cooperatively increases SA and flavonoid contents, enhancing resistance to the powdery mildew pathogen. **d** Cotton GhWRKY40 (GhW40) can be phosphorylated by the GhMKK4-GhMPK20 module and negatively regulates resistance to Fusarium wilt pathogen in cotton plants. GhWRKY41 forms a homodimer to positively regulate by feedback mean and stimulate the accumulation of lignin and flavonoids, leading to the enhanced resistance to *Verticillium dahliae*. **e** Apple MdWRKY17 (MdW17) can be phosphorylated by the MdMKK4-MdMPK3 module and induces the expression of *MdDMR6* (*DOWNY MILDEW RESISTANT 6*), leading to the reduced SA accumulation and enhanced susceptibility to the Glomerella leaf spot pathogen. MdWRKY71 (MdW71) functions similarly to MdW17. Conversely, MdWRKY100 (MdW100) positively regulates SA accumulation and resistance to Glomerella leaf spot pathogen via inhibiting *MdW17* and increasing *MdPAL1* expression; while, MdVQ37 suppresses the transcriptional activity of MdW100. MdW17-MdW50 and MdW40-MdMYB1 complexes positively regulate anthocyanin biosynthesis, whereas the MdW41-MdMYB16 complex reduces anthocyanin accumulation. Arc arrow for feedback regulation. Other drawing descriptions are the same as in Fig. 1

Serotonin plays a negative role in resistance to rice BPH and striped stem borer, whereas sakuranetin protects rice from BPH infestation by inhibiting its beneficial endosymbionts. Recently, methylglyoxal, a highly reactive sugar metabolite, was identified as a negative regulator of rice resistance to *Xoo*, with OsWRKY62.1 induced to suppress *OsGLY II* (*glyxoxalase II*) expression, resulting in methylglyoxal accumulation (Fu et al. 2024). Therefore, methylglyoxal modifies OsCDR1 (CONSTITUTIVE DISEASE RESISTANCE 1) to inhibit its aspartic protease activity, which is required for plant immunity. Additionally, HvWRKY23, a likely member of subgroup IIa WRKYs in barley, positively regulates flavonoid and hydroxycinnamic acid amide biosynthesis, reinforcing cell walls to constraining the Fusarium head blight pathogen within the initial infection site (Karre et al. 2019).

In Arabidopsis, WRKY TFs mediate the biosynthesis of SA and NHP (N-hydroxypicolic acid), essential for SAR (Huang et al. 2020). AtWRKY54 and AtWRKY70 in the same phylogenetic clade function redundantly at downstream of suppressor of *npr1-1*, constitutive 2 (SNC2), to stimulate the expression of the TFs *SAR-DEFICIENT 1* (*SARD1*) and CALMODULIN-BINDING PROTEIN 60-LIKE G (*CBP60g*) (Chen et al. 2021b) (Fig. 4b). Phosphorylation of AtWRKY70 is important for the induction of *SARD1* expression (Liu et al. 2021a). In contrast, SARD1 and CBP60g also positively regulate *AtWRKY70* transcription, suggesting that AtWRKY54/AtWRKY70 and SARD1/CBP60g form a positive feedback loop to promote each other's expression (Chen et al. 2021b). Interestingly, the basal level of SA is higher in *atwrky70* and *atwrky54 atwrky70* mutants than that in wild type plants, suggesting that AtWRKY54 and AtWRKY70 negatively regulate SA accumulation (Wang et al. 2006). Moreover, AtWRKY46, AtWRKY54, and AtWRKY70 are also individually or cooperatively integrated into the BR signaling pathway, leaf senescence, root development, iron translocation, disease resistance, and drought tolerance (Chen et al. 2019). Recently, AtWRKY46 association with AtMYC2 together participated in E-2-hexenal-induced accumulation of ROS and flavonoids, which eventually modulated plant tolerance to insects (Hao et al. 2023). AtWRKY33 is a master positive regulator in responses to various stresses, where it facilitates the biosynthesis of many metabolites, such as SA, NHP, glucosinolates, and camalexin (Chen et al. 2019; Yang et al. 2020; Zhou et al. 2020). AtWRKY33 forms a transcriptional complex with ERF1, synergistically stimulating camalexin biosynthesis (Zhou et al. 2022) (Fig. 2a). Additionally, AtWRKY33 acts as a negative regulator of anthocyanin biosynthesis during acclimation to Pi deficiency. (Tao et al. 2024) (Fig. 4b). AtWRKY33 binds to the promoter of dihydroflavonol 4-reductase gene (*DFR*), a rate-limiting enzyme of anthocyanin biosynthesis, and also associates with PAP1 (production of anthocyanin pigments1) to interfere with the formation of the ternary MBW regulatory complex that comprises of R2R3-type MYB, bHLH, and WD40 domain proteins.

Stilbenes are polyphenolic secondary metabolites and play important roles in plant defense against pathogens and adaptation to abiotic stress (Valletta et al. 2021). In grapevine (*Vitis vinifera*), overexpression of *VvWRKY8* suppresses the expression of the stilbene synthase genes *VvSTS15/21* and *VvMYB14*, leading to reduced resveratrol accumulation (Jiang et al. 2019) (Fig. 4c). Although VvWRKY8 does not directly bind the promoters of *VvSTS15/21* and *VvMYB14*, its interaction with the activator VvMYB14 prevents the latter from binding to the *VvSTS15/21* promoter. Similarly, VvWRKY8 associates with the repressor VvMYB30, forming a complex without DNA-binding activity. Notably, VvMYB14 and VvMYB30 compete for the same binding sites in *VvSTS15/21* promoter, suggesting that VvWRKY8 bridges fine-tune regulation of metabolism in response to environmental stress (Mu et al. 2023). Overexpression of *VqWRKY56*, a gene from wild grape (*Vitis quinquangularis*), increases the accumulation of proanthocyanidins and SA in grapevine, leading to enhanced resistance to the powdery mildew pathogen *Erysiphe necator* (Wang et al. 2023b) (Fig. 4c). VqWRKY56 interacts with VqbZIPC22 and synergistically up-regulates the expression of flavonoid biosynthetic genes.

In cotton, subgroup IIc WRKYs have been shown to positively regulate resistance against the Fusarium wilt pathogen (*Fusarium oxysporum* f. sp. *vasinfectum*) by increasing *GhMKK2* transcription, which activates GhMYC2 to promote flavonoid biosynthesis and accumulation, thereby enhancing defense against pathogen invasion (Wang et al. 2022b). In an earlier study, Wang et al. (2018b) demonstrated that the GhMKK4-GhMPK20-GhWRKY40 cascade negatively regulates cotton resistance to the Fusarium wilt pathogen (Fig. 4d). Overexpression of cotton *GhWRKY41* increases the contents of lignin and several flavonoids, conferring resistance to *Verticillium dahliae* (Xiao et al. 2023). GhWRKY41, forming a homodimer, shows positive feedback regulation of itself and stimulates the expression of genes involved in the phenylpropanoid biosynthesis pathway.

In apple, MdWRKY17 has been characterized to promote SA degradation via increased expression of *MdDMR6* (*DOWNY MILDEW RESISTANT 6*), a SA hydroxylase gene, and acts as a negative regulator to Glomerella leaf spot caused by *Colletotrichum fructicola* (Shan et al. 2021a) (Fig. 4e). Phosphorylation of MdWRKY17 by the MdMKK4-MdMPK3 module

elevates its DNA-binding and transactivation activities, which are critical for its regulation. Moreover, MdWRKY17 forms a complex with MdWRKY50 to promote MdWRKY50 activity in regulation of anthocyanin biosynthesis under drought stress (Bai et al. 2024). Additionally, MdWRKY71 negatively regulates Glomerella leaf spot through the regulation of the *MdDMR6* homologous gene *MdDLO1* (*MDR6-like oxygenase 1*) (Pei et al. 2024). Conversely, MdWRKY100 acts as a positive regulator of Glomerella leaf spot through inhibiting *MdWRKY17* and increasing *MdPAL1* and *MdRPM1* expression, resulting in elevated SA accumulation in *MdWRKY100*-overexpressing plants (Dong et al. 2024). MdVQ37 interacts with MdWRKY100 and suppresses its transcriptional activity. The results suggest that SA is a key factor in resistance to the Glomerella leaf spot pathogen, and WRKY TFs are intricately involved in the process. MdWRKY11 in red-fleshed apple and PyWRKY26 in pear are positive regulators of anthocyanin biosynthesis (Liu et al. 2019; Li et al. 2020b). MdWRKY40, together with its interaction component MdMYB1, promotes wounding-induced anthocyanin production (An et al. 2019). Conversely, the MdWRKY41-MdMYB16 complex represses the expression of anthocyanin biosynthesis genes and negatively regulates the accumulation of anthocyanin and proanthocyanidin in red-fleshed apple (Mao et al. 2021). These findings indicate that WRKY TFs are widely involved in the regulation of primary and secondary metabolite biosynthesis, including phytohormones and important signal molecules. Moreover, the changes in metabolites offer new adaptive properties in response to environmental challenges.

WRKY in environmental stress

WRKY transcription factors play crucial roles in orchestrating plant responses to both biotic and abiotic stresses, balancing plant immunity and growth. Members of the WRKY family exhibit diverse regulatory functions, acting either positively or negatively in regulatory cross-talks. For instance, in Arabidopsis, AtWRKY18, AtWRKY40, and AtWRKY60, members of subgroup IIa WRKYs, form homo- or hetero-complexes via leucine zipper motifs, exhibiting additive, cooperative, and antagonistic effects on functional interactions in response to various stresses (Chen et al. 2019). Analysis of these WRKYs and their homologous alleles reveals distinct protein–protein and/or protein-DNA interactions, which is essential for the defense in allotetraploids (Abeysinghe et al. 2019). AtWRKY18 is mediated in rhizobacterium *Bacillus cereus* NJ01-induced disease resistance (Wang et al. 2024) (Fig. 5a). The interaction with EDS1 enhances its DNA binding capability stimulates the expression of SA and ABA biosynthesis genes, and thereby modulates the induced resistance. Moreover, AtWRKY18 can be phosphorylated by AtMPK3/AtMPK6 and together with AtWRKY40 and AtWRKY60, it positively regulates the expression of phosphatase genes *AtPP2C1* and *AtPP2C5*, integral in PTI-mediated ETI suppression and maintenance of plant fitness during ETI (Wang et al. 2023c) (Fig. 5a). In banana, transcriptomic analysis shows that MaWRKY TFs are highly involved in the transcriptional regulation of banana peel browning at low temperatures (Zhu et al. 2023). The authors demonstrated that MaWRKY18, MaWRKY40, and MaWRKY60, the orthologs of Arabidopsis subgroup IIa WRKYs, interact with each other to promote the expression of browning-related genes.

In Arabidopsis, subgroup IId members, including AtWRKY7, AtWRKY11, and AtWRKY17, are identified as the negative regulators of basal resistance (Journot-Catalino et al. 2006). Upon flg22 treatment, the triple mutant *atwrky7/11/17* exhibits induced expression of endoplasmic reticulum (ER) stress genes and *bZIP28*, a key component of the unfolded protein response, indicating that these WRKYs are involved in the ER stress response (Arrano-Salinas et al. 2018). In addition, quintuple mutants *atwrky11/15/17/21/39* and *atwrky7/11/17/21/39* exhibit retarded growth and constitutive induction of defense responsive genes (Du et al. 2023). The AtWRKYs in subgroup IId redundantly form complexes with OBERON proteins, which coordinately suppresses the basal transcription of stress-responsive genes and balances plant growth and stress tolerance during pathogen infection (Du et al. 2023). Moreover, these AtWRKYs can interact with calmodulin, suggesting a potential role of calmodulin as a co-regulator of IId WRKYs (Park et al. 2005). Through activation tagging screening, AtWRKY14/ABT1 (ABNORMAL THERMOMORPHOGENESIS 1) was identified as a repressor of plant thermomorphogenesis (Qin et al. 2022). Overexpression of *AtWRKY14* or its close homologs confers insensitivity to high temperatures, while the quadruple mutant *atwrky14/35/65/69* is more sensitive to high temperatures than wild type plants. AtWRKY14 interacts with TCP5 (TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL FACTOR 5) and disrupts the TCP5–PIF4 (PHYTOCHROME INTERACTING FACTOR 4) complex formation to attenuate transcriptional activation activity.

AtWRKY33 acts as a positive regulator at downstream of Submergence Resistance1 (SR1), a RING type E3 ligase (Liu et al. 2021c) (Fig. 4b). Phosphorylation of AtWRKY33 during submergence accelerates its degradation mediated by SR1. AtWRKY12 and AtWRKY33 form a complex that activates the expression of *RAP2.2* (*RELATED TO AP2 2*), a gene encoding an ERF TF and

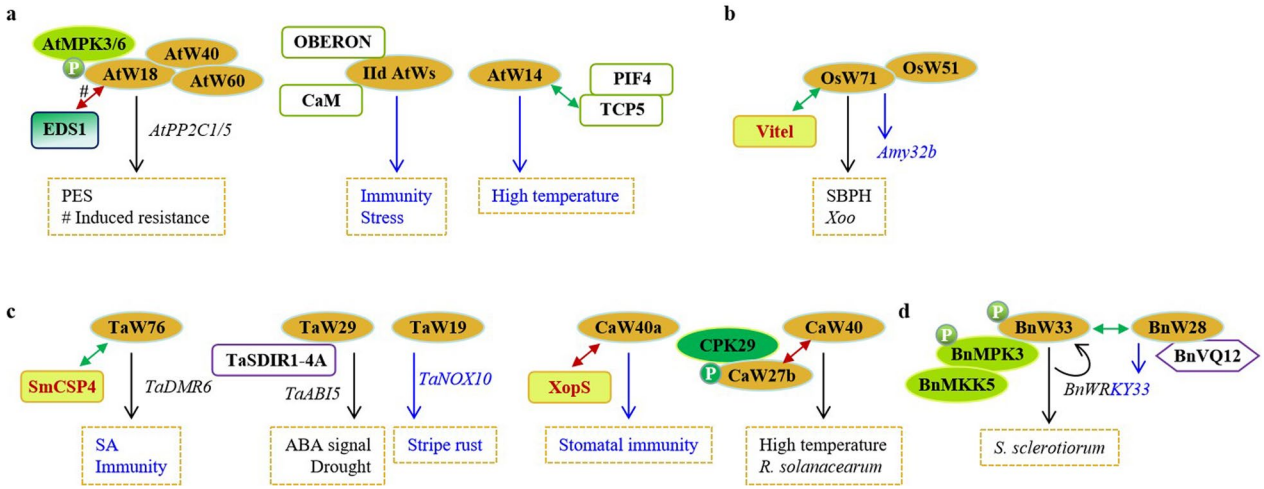

Fig. 5 WRKY transcription factors in environmental stresses. **a** AtWRKY18 (AtW18), AtWRKY40 (AtW40), and AtWRKY60 (AtW60) form homo- and hetero-complexes. AtWRKY18 participates in rhizobacterium-induced disease resistance. EDS1 (ENHANCED DISEASE SUSCEPTIBILITY 1) interacts with AtWRKY18 to enhance its activity. AtWRKY18 can be phosphorylated by AtMPK3/AtMPK6 and together with AtWRKY40 and AtWRKY60, positively regulates the expression of phosphatase *AtPP2C1/5* genes and pre-PTI-mediated ETI suppression (PES). Many subgroup IId AtWRKYs (IId AtWs) interact with OBERON and calmodulin (CaM) proteins and negatively regulate basal resistance and stress tolerance redundantly. AtWRKY14 (AtW14) acts as a negative regulator of thermomorphogenesis. AtW14 interacts with TCP5 (TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL FACTOR 5) and disrupts TCP5-PIF4 (PHYTOCHROME INTERACTING FACTOR 4) complex formation. **b** OsWRKY71 (OsW71) is targeted by the effector vitellogenin (Vitel), secreted by the small brown planthopper (SBPH), attenuating resistance to SBPH. OsW71, forming a complex with OsWRKY51 (OsW51), cooperatively represses the promoter activity of the alpha-amylase gene *Amy32b*. **c** The effector SmCSP4 from the aphid *Sitobion miscanthi* can activate SA-mediated host defense response by associating with wheat TaWRKY76 (TaW76), which acts as a transcriptional activator to regulate *TaDMR6* expression, leading to low SA levels and the compromised basal immunity. TaWRKY19 (TaW19) functions as a negative regulator of *TaNOX10* (NADPH oxidase 10) and resistance to wheat stripe rust fungus. TaWRKY29 (TaW29) is activated by TaSDIR1-4A (SALT- AND DROUGHT-INDUCED REALLY INTERESTING NEW GENE FINGER1) and is translocated from the membrane to the nucleus to stimulate *TaABI5* (*ABA INSENSITIVE 5*) transcription. Pepper CaWRKY40a (CaW40a) is stabilized by interacting with XopS (*Xanthomonas* outer protein S) and suppresses stomatal immunity. CaWRKY27b (CaW27b) is phosphorylated by CaCDPK29 (CPK29), translocating from the cytoplasm to the nucleus afterwards. CaWRKY40 (CaW40), forming a complex with CaW27b, promotes DNA-binding activity, high temperature tolerance, and *Ralstonia solanacearum* resistance. **d** Phosphorylation of oilseed rape BnWRKY33 (BnW33) by BnMKK5-BnMPK3 enhances its transcriptional activity and resistance against *Sclerotinia sclerotiorum* infection. The complex comprising BnWRKY28 (BnW28) and BnVQ12 competes with BnW33 to bind to the *BnW33* promoter and suppresses its expression. Drawing descriptions are the same as in Fig. 1

playing a positive role in hypoxia tolerance (Tang et al. 2021). Genome-wide association studies reveal that a variation in the WT-box in the *AtWRKY33* promoter correlates with different responses to submergence (Liu et al. 2024b). AtWRKY70 binds both the WT-box in the promoter and a conserved WT-box within the first intron of *AtWRKY33*, activating *AtWRKY33* transcription. Histone deacetylase HDA9 interacts with AtWRKY53, reducing its lysine acetylation status, and repressing its transcription and DNA-binding activity (Zheng et al. 2020). On the contrary, AtWRKY53 inhibits HDA9 histone deacetylase activity. AtWRKY53 and HDA9 function as the positive and negative regulators under salt stress, respectively, implying that there is a reciprocal negative regulation between them in response to stress tolerance.

In rice, there are four members of subgroup IIa WRKYs, the OsWRKY28, OsWRKY62, OsWRKY71, and OsWRKY76. OsWRKY62 and OsWRKY76 form homo- and hetero-complexes, negatively regulating rice defense responses against *M. oryzae* and *Xoo* pathogens (Yokotani et al. 2013; Liu et al. 2016) (Fig. 4a). *OsWRKY62* and *OsWRKY76* exhibit a negative feedback regulatory loop and an alternative splicing upon pathogen infection (Liu et al. 2016). Nuclear localization of OsWRKY62.1 depends on its own transportation signals as well as interactions with other proteins, such as importin α1 and OsWRKY76 (Liu et al. 2016; Xu et al. 2022). OsWRKY76 functions at downstream of *OsWRKY63* as a positive regulator of chilling tolerance via interacting with OsbHLH148, and drought tolerance through interaction with OsJAZs (Zhang et al. 2022a, 2023d). OsWRKY28 acts as a repressor, negatively regulating resistance against *M. oryzae,* and as a transactivator of the *OsDREB1B* promoter, promoting salinity tolerance (Chujo et al. 2013; Zhang et al. 2023e). Overexpression of *OsWRKY71* increases the expression of *OsNPR1* and *OsPR1b* and enhances resistance against *Xoo* (Liu et al. 2007). Meanwhile, OsWRKY71 is targeted by a novel effector, vitellogenin, secreted by

small brown planthopper (SBPH, *Laodelphax striatellus*), which suppresses OsWRKY71-mediated H_2O_2 accumulation and related host defense responses (Ji et al. 2021) (Fig. 5b). OsWRKY71 also inhibits the promoter activity of the alpha-amylase gene *Amy32b* by binding to its W-boxes. The DNA-binding affinity of OsWRKY71 is enhanced by its interaction with OsWRKY51, indicating a synergistic suppression of *Amy32b* (Xie et al. 2006). Both *OsWRKY51* and *OsWRKY71* are ABA-inducible, and may mediate ABA and GA signaling cross-talk. OsWRKY7 positively regulates resistance to *M. oryzae* and *Xoo* (Tun et al. 2023; Zheng et al. 2024). Interestingly, OsWRKY7 was alternatively translated with the smaller protein being more resistant to degradation by the ubiquitin–proteasome system than the larger protein, although there is no lysine residue in its N-terminal degradation domain (Zheng et al. 2024).

In wheat, subgroup IIa TaWRKY76 is targeted by SmCSP4, a chemosensory protein from the aphid *Sitobion miscanthi*, activating SA-mediated host defense response (Zhang et al. 2023f) (Fig. 5c). Interestingly, TaWRKY76 acts as a transcriptional activator to regulate *TaDMR6* expression, which is dampened by SmCSP4.

In pepper, CaWRKY40a, a close homolog of subgroup IIa AtWRKY40, is targeted by *Xanthomonas* outer protein S (XopS) secreted by *X. campestris* pv. *vesicatoria* (*Xcv*) (Raffeiner et al. 2022). Stabilization of CaWRKY40a by XopS perpetuates its repressor activity, which further suppresses the expression of both SA- and JA-responsive genes. Although CaWRKY27b lacks W-box binding activity, its complex formation with CaWRKY40, another AtWRKY40 homolog, enhances DNA-binding activity, tolerance to high temperature, and disease resistance against *R. solanacearum* (Yang et al. 2022). Moreover, phosphorylation of CaWRKY27b by CaCDPK29 is required for its translocation from the cytoplasm to the nucleus.

In maize, the *ZmWRKY20* mutant accumulates much less ROS but exhibits higher salt-tolerance than wild type plants (Bo et al. 2022). ZmWRKY20 associates with ZmWRKY115, synergistically repressing *ZmbZIP111* transcription through direct binding to its promoter. In wheat, TaWRKY19 is a transcriptional repressor of *TaNOX10*, which encode an NADPH oxidase; knockout of *TaWRKY19* enhances wheat resistance to virulent stripe rust fungus (Wang et al. 2022c) (Fig. 5c). TaWRKY29 is a substrate of TaSDIR1-4A (SALT- AND DROUGHT-INDUCED REALLY INTERESTING NEW GENE FINGER1, on wheat chromosome 4A), a RING finger E3 ligase, positively regulating ABA signaling and drought tolerance (Meng et al. 2024b). TaWRKY29 is cleaved after interaction with TaSDIR1-4A, moving from the membrane to the nucleus to activate *TaABI5* (*ABA INSENSITIVE 5*) transcription. Oilseed rape BnWRKY33, an ortholog of AtWRKY33, is phosphorylated by the BnMKK5-BnMPK3 module in the early *Sclerotinia sclerotiorum* infection, stimulating its transcriptional activity (Zhang et al. 2022b) (Fig. 5d). The BnWRKY28 and BnVQ12 complex competes with BnWRKY33 to bind to the *BnWRKY33* promoter, repressing its expression, which suggest that the two BnWRKYs fine-tune the defense response to *Sclerotinia*.

Furthermore, WRKY transcriptional regulatory cascades, such as OsWRKY51-OsWRKY10-OsWRKY47 and OsWRKY88-OsWRKY10/OsWRKY6-OsWRKY47, participate in Xa1-mediated resistance and basal resistance against the bacterium pathogen *Xoo* in rice (Choi et al. 2020: Im et al. 2022), while OsWRKY45-2-OsWRKY13-OsWRKY42 cascade is linked to resistance against the fungal pathogen *M. oryzae* (Cheng et al. 2015). OsWRKY10, OsWRKY45-2, OsWRKY47, OsWRKY51, and OsWRKY88 positively regulate disease resistance against *M. oryzae* and/or *Xoo*, while OsWRKY13 and OsWRKY42 act as transcriptional repressors to regulate JA signaling-related gene expression and disease resistance to *M. oryzae* (Cheng et al. 2015). OsWRKY10 also functions in thermotolerance as a negative regulator (Chen et al. 2022b). OsVQ8, a positive regulator of thermotolerance, interacts with OsWRKY10, inhibiting its transactivation activity and W-box binding affinity.

Taken together, numerous WRKY proteins participate in responses to both biotic and abiotic stresses and act as positive and/or negative regulators. Their variant regulatory roles in multiple signaling pathways are characterized by associating with different proteins, thereby affecting the balance of phytohormones.

WRKY in plant growth and development

WRKYs have evolved to fight off pathogens, insects, as well as abiotic stresses; however, unraveling the intricate networks that regulate the balance between growth, development, stress tolerance, and disease resistance is essential to optimize plant performance in facing the ever-changing environmental conditions.

From modulating grain size and lignification to orchestrating leaf senescence and flowering time, WRKYs exhibit a remarkable versatility in plant growth and development. A gain-of-function mutant of *OsWRKY36*, resulting from a T-DNA insertion in its 5'-UTR, displays small grain and semi-dwarf phenotypes (Lan et al. 2020) (Fig. 6a). OsWRKY36 promotes the expression of *SLENDER RICE1* (*SLR1*) and protects SLR1 from GA-mediated degradation, thus acting as GA signaling repressor. Moreover, OsWRKY36 and OsWRKY102 are implicated in the inhibition of rice lignification (Miyamoto et al. 2020). Previously, the gain-of-function

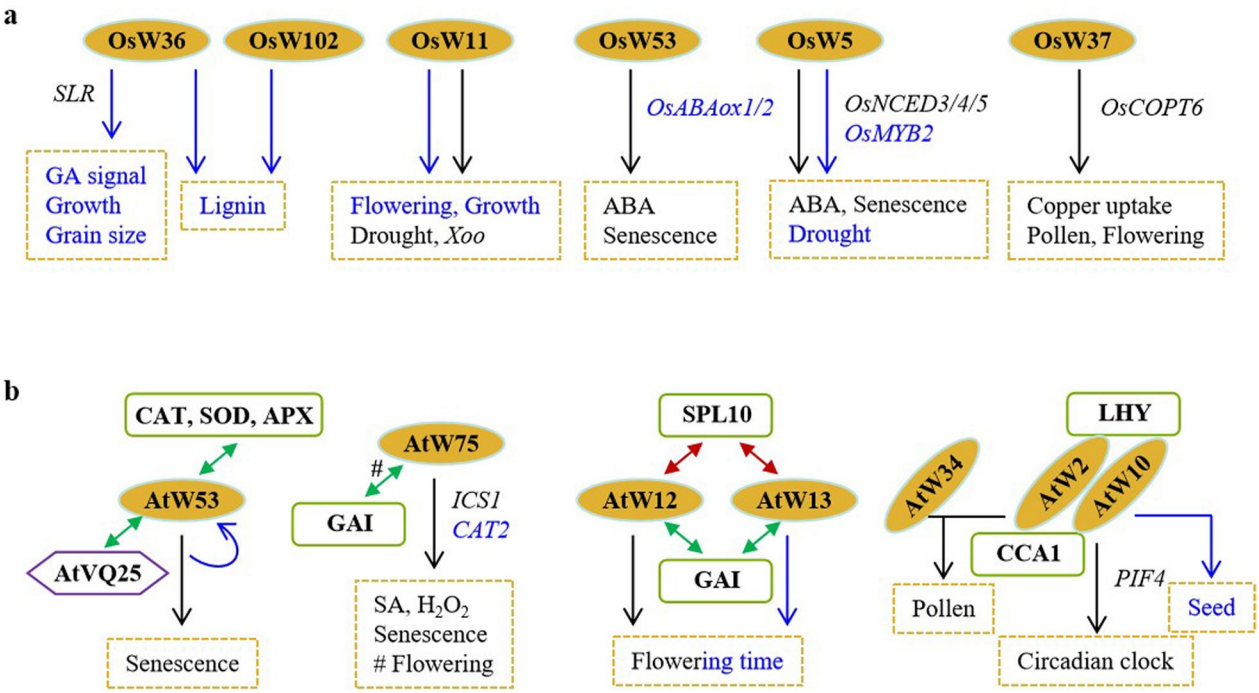

Fig. 6 WRKY transcription factors in growth and development. **a** OsWRKY36 (OsW36) increases *SLR1* (*SLENDER RICE1*) expression and acts as a repressor of gibberellin (GA) signaling, leading to growth retardation and small grain size. Moreover, OsW36 and OsWRKY102 (OsW102) act coordinately to inhibit lignification. OsWRKY11 (OsW11) negatively regulates growth and flowering time, but positively regulates resistance to *Xoo* (*X. o. oryzae*) and drought tolerance. OsWRKY53 (OsW53) suppresses the expression of *OsABA8ox1* and *OsABA8ox2*, leading to the accumulation of abscisic acid (ABA) and early leaf senescence. OsWRKY5 (OsW5) elevates ABA content via increased expression of *OsNCED3/4/5* (9′-*cis*-epoxycarotenoid dioxygenase 3/4/5) genes, leading to the precocious leaf yellowing. OsW5 negatively regulates drought tolerance by repressing *OsMYB2* expression. OsWRKY37 (OsW37) promotes copper uptake through upregulating of the copper transporter *OsCOPT6* and positively regulates rice pollen development and flowering time under copper deficient conditions. **b** AtWRKY53 (AtW53) interacts with different catalases (CATs), superoxide dismutases (SODs), and ascorbate peroxidases (APXs) to inhibit these enzyme activities and, conversely, the transcriptional activity of AtW53. AtVQ25 associates with AtW53 to attenuate *AtW53* self-repression during leaf senescence. AtWRKY75 (AtW75) increases the expression of *ICS1* (*isochorismate synthase 1*) and suppresses the expression of *CAT2*, facilitating the accumulation of salicylic acid (SA) and H_2O_2 and promoting leaf senescence. AtW75 interacting with DELLA repressors, such as GAI (GIBBERELLIN INSENSITIVE), compromises transcriptional regulation activity and accelerates flowering in Arabidopsis. AtWRKY12 (AtW12) and AtWRKY13 (AtW13), two close homologs, are positive and negative regulators of flowering time, respectively. Both AtW12 and AtW13 interact with GAI compromising their transcriptional activity. AtW12 and AtW13 forms a complex with SQUAMOSA PROMOTER BINDING-LIKE 10 (SPL10) to cooperatively regulate *miR172b* expression, which targets *SPL10* to control flowering time. AtWRKY2 (AtW2) and AtWRKY10 (AtW10) forms a heterodimer to promote *PIF4* expression. Both AtW2 and AtW10 can interact with CCA1 (CIRCADIAN CLOCK ASSOCIATED 1) and LHY (LATE ELONGATED HYPOCOTYL) to enhance their regulation of *PIF4* expression in a circadian pattern. In addition, AtW10 negatively regulates seed development, whereas AtW2 and AtWRKY34 (AtW34) act redundantly in pollen development. Drawing descriptions are the same as in Fig. 1

mutant *dlf1* of *OsWRKY11*, with a similar T-DNA insertion as *OsWRKY36* mutant, shows semi-dwarf and late-flowering phenotypes (Cai et al. 2014). Overexpression of the normal *OsWRKY11* transcript inhibits plant growth but promotes resistance to *Xoo* and drought tolerance (Cai et al. 2014; Lee et al. 2018). OsWRKY24, OsWRKY53, and OsWRKY70 are closely related homologs, with OsWRKY53 positively regulating grain size (Tian et al. 2017). Using single, double, and triple mutants of *OsWRKY24*, *OsWRKY53*, and *OsWRKY70*, Tang et al. (2022b) found that *OsWRKY24* participates in grain size regulation redundantly with *OsWRKY53*, while *OsWRKY70* is a negative regulator of grain size independent of *OsWRKY53*. Furthermore, overexpression of *OsWRKY53* increases the levels of ABA by suppressing the expression of ABA catabolic genes, such as *OsABA8ox1* and *OsABA8ox2*, leading to early leaf senescence (Xie et al. 2022). The gain-of-function mutant of *OsWRKY5* displays precocious leaf yellowing due to elevated ABA accumulation through increased expression of its biosynthesis genes *OsNCED3/4/5* (9′-*cis*-epoxycarotenoid dioxygenase 3/4/5) (Kim et al. 2019). OsWRKY5 negatively regulates drought tolerance by directly inhibiting the expression of *OsMYB2*; therefore, genome editing of OsWRKY5 improves grain yield under drought conditions (Lim et al. 2022). OsWRKY37 positively regulates

pollen development, flower time, and grain yield in rice under copper deficient conditions, which stimulates copper uptake via upregulating the expression of the copper transporter *OsCOPT6* (Ji et al. 2024) (Fig. 6a).

WRKY TFs are largely involved in leaf senescence, an integral aspect of plant development (Zentgraf and Doll 2019). Among these, AtWRKY53 has been extensively studied. Recently, AtWRKY53 is characterized to interact with different antioxidative enzymes, including catalases (CATs), superoxide dismutases, and ascorbate peroxidases, resulting in the repression of the enzyme activities and, reciprocally, the transcriptional activity of AtWRKY53 (Andrade Galan et al 2024) (Fig. 6b). Tan et al. (2024) found that AtVQ25 interacts with AtWRKY53 to attenuate self-repression during the onset of leaf senescence. Both *AtWRKY53* and *AtWRKY75* act as positive regulators of senescence and are responsive to SA and ROS treatments (Guo et al. 2017; Zentgraf and Doll 2019). AtWRKY75 increases the expression of *SALICYLIC ACID INDUCTION DEFICIENT 2A* (*SID2*)/*ICS1* (*ISOCHORISMATE SYNTHASE 1*), while suppressing *CAT2* transcription, facilitating SA and H_2O_2 accumulation, and inducing leaf senescence through a tripartite positive feedback loop (Guo et al. 2017) (Fig. 6b). A complicated regulatory network likely exists for AtWRKY53, as feedback regulation loops between AtWRKY53 and CATs occur not only at the transcriptional level but also at translation or even post-translation levels (Andrade Galan et al. 2024). Overexpression of *AtWRKY75* accelerates flowering via GA-mediated flowering time control (Zhang et al. 2018). DELLA repressors, such as RGA (REPRESSOR OF GA1-3), RGL1 (RGA-LIKE1), and GAI (GIBBERELLIN INSENSITIVE), interact with AtWRKY75 to inhibit its transcriptional regulatory activity.

AtWRKY12 and AtWRKY13 are two closely related homologs, but they regulate flowering time in an opposite way under short-day conditions (Li et al. 2016). They interact with GAI and RGL1, compromising the transcriptional activity of both AtWRKY12 and AtWRKY13. Furthermore, they interact with SQUAMOSA PROMOTER BINDING-LIKE 10 (SPL10), a target gene of *miR156* that controls phase transition and flowering (Ma et al. 2020) (Fig. 6b). The AtWRKY12-SPL10 and AtWRKY13-SPL10 complexes respectively promote and repress SPL10 transcriptional activity, together regulating *miR172b* expression. Additionally, AtWRKY63 mediates the vernalization-induced flowering by promoting the expression of *FLOWERING LOCUS C* (*FLC*) and two long noncoding RNAs, *COOLAIR* (*COLD INDUCED LONG ANTISENSE INTRAGENIC RNA*) and *COLDAIR* (*COLD ASSISTED INTRONIC NONCODING RNA*), which are derived from the 3′ end and the first intron of *FLC*, respectively (Hung et al. 2022). AtWRKY2 and AtWRKY10 form a heterodimer that binds to the promoter of the bHLH gene *PIF4* near the MYB element associated with MYB TFs CCA1 (CIRCADIAN CLOCK ASSOCIATED 1) and LHY (LATE ELONGATED HYPOCOTYL) (Wang et al. 2022d). Furthermore, AtWRKY2 and AtWRKY10 interact with CCA1 and LHY, enhancing their regulation of *PIF4* and maintaining an optimal circadian pattern of *PIF4* expression. Additionally, AtWRKY10, also known as MINISEED3, regulates seed development (Luo et al. 2005), while AtWRKY2 and AtWRKY34 function redundantly in pollen development (Guan et al. 2014) (Fig. 6b).

AtWRKY23 operates at downstream of AUXIN RESPONSE FACTOR (ARF) 7 and ARF19, mediating in regulation of flavonol synthesis, auxin-induced pluripotent callus formation, and response to nematode invasion (Grunewald et al. 2012; Xu et al. 2024). The activator AtWRKY23 and repressor bHLH041 act synergistically to confer shoot-regenerating capability of callus cells (Xu et al. 2024). In poplar, PdeWRKY75 is involved in the development of adventitious roots, lateral buds, and callus by positively regulating the NADPH oxidase gene *PdeRBOHB* to control H_2O_2 generation (Zhang et al. 2022c). Furthermore, PdeWRKY75 recruits PdeERF114 to stimulate the expression of *PdeRBOHB* and expansin *PdeEXPB2*, although PdeERF114 is not a direct regulator of these target genes (Zhang et al. 2024). Several PtrWRKYs interact with PtrMYB074, a specific TF in woody dicots involved in wood formation in *Populus trichocarpa* (Liu et al. 2022). PtrWRKY19, together with PtrMYB074, promotes *PtrbHLH186* transcription, which is involved in lignification and vessel cell development. In herbaceous peony, PlWRKY41a positively modulates secondary cell wall thickness by binding and activating the promoter of *PlXTH4* (*xyloglucan endotransglucosylase/hydrolase 4*) in *Paeonia lactiflora* (Tang et al. 2023). Furthermore, PlWRKY41a forms a complex with PlMYB43 to increase the transactivation activity of the *PlXTH4* promoter.

Collectively, WRKY TFs are involved in numerous processes of plant growth, development, stress tolerance, and disease resistance. However, trade-offs between growth and disease resistance or stress tolerance exist extensively. Understanding the molecular mechanisms and mitigating these trade-offs are crucial for molecular engineering of plants to achieve a balance between resistance and growth.

Conclusion and future prospects

As sessile organisms, plants have evolved complex mechanisms to adapt to diverse environmental challenges. *WRKY* genes, which are expanded in higher plants,

undergo divergence and significantly impact the evolution of plants. Accumulating evidences highlight the critical roles of WRKY TFs in various processes of growth, development, and stress responses in plants. The orthologous *WRKYs* in different species often exhibit similar functions, suggesting that the knowledge on model plants can provide valuable insights into *WRKY* functions in other species. However, caution is warranted as homologous *WRKYs* may display not only redundant but also divergent and even antagonistic functions. Additionally, species-specific *WRKYs* may play distinct roles in species development and responses to biotic stresses.

The interactions of WRKY TFs with *cis*-elements are dynamic and depend on the conformation of WRKY proteins as well as the *cis*-elements per se. Furthermore, the DNA-binding affinity is influenced by various modifications of WRKY proteins and DNA, the interactions with other components, or dosage input. Although identifying a WRKY binding element in a gene promoter is relatively straightforward, elucidating the interaction in planta under in vivo circumstances requires considerable efforts. Techniques for genome-wide analysis of DNA binding, combined with temporal and spatial expression patterns of *WRKYs,* are promising to dissect the regulatory specificity and diversity of each WRKY gene.

As executors in transcriptional regulatory networks, the regulation targets and efficiency of WRKY TFs may be influenced by their interacting partners and the downstream consequences. Activation or strengthening of WRKY TFs is often associated with their phosphorylation status, linked to specific kinases and integrated signaling pathways that determine phosphorylation timing and sites. WRKY TFs within the receptor perception complexes can expedite signaling pathways, facilitating rapid responses to environmental stresses. Understanding how the receptor-WRKY complex recruits new members to enhance or dampen processes is vital. Discovering of overlapping signaling pathways between pathogen and insect invasion in rice provides a platform to dissect the mechanisms of the responses to different invaders, and offers the opportunities to improve rice resistance against both pathogens and insects by gene editing.

Interactions among WRKY TFs or with other TFs provide insights into uncovering the dynamic regulation of target genes coordinately or antagonistically. The auto- and cross-regulation properties of WRKY TFs, particularly in the phytohormone biosynthesis, have uncovered many complicated regulatory mechanisms. However, deciphering these mechanisms is essential for establishing a comprehensive WRKY signaling and transcriptional regulatory network. Moreover, it is challenging but of great importance to clarify that under what circumstances a WRKY TF functions negatively or positively in transcriptional regulation. The switch of a WRKY TF from an activator to a repressor is likely influenced by the properties of its interacting partners. Genome-wide analyses of WRKY protein interacting components, including proteins and DNAs, will undoubtedly contribute to unraveling their versatile and complex functions.

Abbreviations

ABA	Abscisic acid
ABI5	ABA INSENSITIVE 5
ABT1	ABNORMAL THERMOMORPHOGENESIS 1
ANIP1	AVRPI9-INTERACTING PROTEIN 1
AOC	ALLENE OXIDE CYCLASE
AOS1	Allene oxide synthase 1
ARF	AUXIN RESPONSE FACTOR
BISP	BPH salivary protein
BPH14	BROWN PLANTHOPPER RESISTANCE 14
BRs	Brassinosteroids
CATs	Catalases
CBP60g	CALMODULIN-BINDING PROTEIN 60-LIKE G
CCA1	CIRCADIAN CLOCK ASSOCIATED 1
CDR1	CONSTITUTIVE DISEASE RESISTANCE 1
CERK1	Chitin elicitor receptor kinase 1
ChIP	Chromatin immunoprecipitation
CNL	Coiled-coil nucleotide binding/leucine-rich repeat
COLDAIR	COLD ASSISTED INTRONIC NONCODING RNA
COOLAIR	COLD INDUCED LONG ANTISENSE INTRAGENIC RNA
CPK	Calcium-dependent protein kinase
CTWD	C-terminal WD
DAP	DNA affinity purification
DFR	Dihydroflavonol 4-reductase
DMR6	DOWNY MILDEW RESISTANT 6
DLA	DECREASED LEAF ANGLE
DLO1	MDR6-like oxygenase 1
EDS1	ENHANCED DISEASE SUSCEPTIBILITY 1
EMSAs	Electrophoretic mobility shift assays
ER	Endoplasmic reticulum
ETI	Effector-triggered immunity
FLC	FLOWERING LOCUS C
flg22	22-Amino-acid epitope from flagellin
GAI	GIBBERELLIN INSENSITIVE
GRAS	GAI-RGA-and-SCR
GSK2	Glycogen synthase kinase-2
HKT	High-affinity K^+ transporter
HY5	ELONGATED HYPOCOTYL 5
ICS1	ISOCHORISMATE SYNTHASE 1
IDA	INFLORESCENCE DEFICIENT IN ABSCISSION
IDL6	IDA-Like 6
JA	Jasmonic acid
JAV1	Jasmonate-associated VQ domain protein 1
JAZ8	JASMONATE-ZIM-DOMAIN PROTEIN 8
LHY	LATE ELONGATED HYPOCOTYL
MPK	The mitogen-activated protein kinase
NCED	9′-*cis*-Epoxycarotenoid dioxygenase
NHP	N-hydroxypicolic acid
NLRs	Nucleotide-binding/leucine-rich repeat receptors
NPR1	NON-EXPRESSER OF PATHOGENESIS-RELATED GENES 1
NTWDs	The N-terminal WDs
PAMP	Pathogen-associated molecular pattern
PAP1	Production of anthocyanin pigments1
Pb1	PANICLE BLAST 1
PBI1	PUB44-INTERACTING PROTEIN 1
PIF4	PHYTOCHROME INTERACTING FACTOR 4
Pip	Pipecolic acid
PTI	Pathogen-associated molecular pattern-triggered immunity
RAP2.2	RELATED TO AP2 2
RaxX	Required for activation of XA21 mediated immunity X
RGA	REPRESSOR OF GA1-3
RGL1	RGA-LIKE1

ROS	Reactive oxygen species
RPM1	RESISTANCE TO *P. SYRINGAE* PV *MACULICOLA1*
RPS4	Resistance to *P. syringae* 4
RPW8.1	RESISTANCE TO POWDERY MILDEW 8.1
RRS1-R	Resistance to *R. solanacearum* 1
SA	Salicylic acid
SAR	Systemic acquired resistance
SARD1	SAR-DEFICIENT 1
SBPH	Small brown planthopper
SDIR1-4A	SALT- AND DROUGHT-INDUCED REALLY INTERESTING NEW GENE FINGER1, on wheat chromosome 4A
SIB1	SIGMA FACTOR BINDING PROTEIN1
SID2	SALICYLIC ACID INDUCTION DEFICIENT 2A
SLR1	SLENDER RICE1
SNC2	Suppressor of *npr1-1*, constitutive 2
SnRK1	Sucrose non-fermenting-related kinase 1
SPL10	SQUAMOSA PROMOTER BINDING-LIKE 10
SR1	Submergence Resistance1
SSB	Striped stem borer
TCP5	TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL FACTOR 5
TFs	Transcription factors
UVR8	UV RESISTANCE LOCUS 8
WD	WRKY domain
XA21	*Xanthomonas* resistance 21
XopS	*Xanthomonas* outer protein S
XTH4	Xyloglucan endotransglucosylase/hydrolase 4

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XC and ZG wrote the manuscript. TZ, HW, and WZ drew the figures. All authors read and approved the manuscript.

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