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Roles of auxin response factors in rice development and stress responses

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Abstract

Auxin signalling plays a key role in various developmental processes ranging from embryogenesis to senescence in plants. Auxin response factor (ARF), a key component of auxin signalling, functions by binding to auxin response element within promoter of auxin response genes, activating or repressing the target genes. Increasing evidences show that ARFs are crucial for plant response to stresses. This review summarises the recent advance on the functions and their regulatory pathways of rice ARFs in development and responding to stresses. The importance of OsARFs is demonstrated by their roles in triggering various physiological, biochemical and molecular reactions to resist adverse environmental conditions. We also describe the transcriptional and post-transcriptional regulation of *OsARFs*, and discuss the major challenges in this area.

KEYWORDS
development, OsARFs, rice, stress

1 | INTRODUCTION

Auxin plays a central role in almost every facet of plant development from cellular to whole-plant levels, including cell expansion, cell differentiation, organogenesis, vascular tissue differentiation, root initiation and so on (Mockaitis & Estelle, 2008; Mueller-Roeber & Balazadeh, 2014; Vanneste & Friml, 2009). In the past decades, core components that translate auxin sensing to transcription responses of auxin signalling pathway have been reported in *Arabidopsis thaliana* (Weijers & Wagner, 2016). A coreceptor comprising a TRANSPORT INHIBITOR RESISTANT 1/AUXIN SIGNALLING F-BOX (TIR1/AFB) F-box protein and an AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) transcriptional coregulator senses auxin molecules. Auxin promotes the interaction between TIR1/AFB and Aux/IAA, thereby triggering ubiquitin-mediated degradation of the Aux/IAA proteins via the proteasome (Gray et al., 1999; Ruegger et al., 1997). Auxin response factors (ARFs) are a family of transcription factors that can be negatively regulated by Aux/IAAs (Guilfoyle & Hagen, 2007). Aux/IAA inhibits ARFs bound at their target loci by recruiting corepressor complexes (Ulmasov et al., 1997). An increase in auxin levels results

in the degradation of Aux/IAA proteins and eviction of related repressive complex from activating ARF target sites, which plays important roles in auxin-mediated growth and development.

Most ARF proteins are composed of a plant-specific and N-terminal B3-type DNA binding domain (DBD), a middle region (MR) that functions as an activation domain (AD) or repression domain (RD), and a carboxy-terminal dimerisation domain (CTD) (Ulmasov et al., 1999). The AD is enriched in glutamine (Q), serine (S) and leucine (L) residues, and the RD is enriched in S, proline (P), L and glycine (G) residues (Ulmasov et al., 1999). ARFs are categorised as transcriptional activators and repressors based upon the amino acid composition of the non-conserved MR located between the DBD and CTD (Ulmasov et al., 1999). The DBD of an ARF binds specifically to TGTCTC auxin response elements (AuxREs) found in promoters of primary/early auxin response genes to transcriptionally activate or repress the expression of auxin responsive genes (Liu et al., 1994). Variations in the two last nucleotides of AuxREs can fine-tune the transcriptional response profile of downstream genes by affecting the interaction between ARFs and AuxREs (Freire-Rios et al., 2020; Lieberman-Lazarovich et al., 2019).

Monocotyledonous (e.g., rice, *Oryza sativa*) and dicotyledonous plants (e.g., *Arabidopsis*) are two major taxonomic groups within Angiosperms (flowering plants). In comparison with intensive studies of auxin signalling implemented in *Arabidopsis*, less is known in rice about the functions of ARFs. Due to the tremendous variation of anatomical, morphological, and developmental features within the two-type plants, the roles of auxin in regulating their responses to environmental cues are greatly diverse. Rice genome contains 25 OsARF members, among which 9 OsARFs (OsARF5, 6, 11, 12, 16, 17, 19, 21 and 25) are predicted to be transcriptional activators and the other 16 OsARFs as repressors based on the amino acid sequence of MR (Shen et al., 2010).

There is increasing evidence on the post-transcriptional regulation of *OsARF* transcript abundance by microRNAs (miRNAs) and trans-acting small interfering RNAs (tasiRNAs) (Jodder, 2020). These small RNAs are short RNA molecules (18–24 nucleotides) directing cleavage of complementary messenger RNA (mRNA) targets and target sites are widely conserved in dicots and monocots, and which control gene expression as key negative regulators at the post-transcriptional level. Target genes are identified for not only tasiR-ARFs but also non-tasiR-ARF siRNAs by analyzing rice Parallel Analysis of RNA Ends datasets, since that *TAS3* siRNA-mediated target cleavage, in particular tasiR-ARFs targeting *OsARF2/3/14/15*, might be important for plants to adapt to their environment (Luo et al., 2022). In rice, two miRNAs, miR160 and miR167, are proved to target *OsARF8/10/18/22* and *OsARF6/12/17/25* respectively to regulate the expression of their downstream genes to control different developmental pathways and stress responses (Huang et al., 2016; Liu et al., 2012).

Here we briefly summarise the recent advances on the function and their regulatory pathways of rice ARFs in responding to abiotic and biotic stresses and describe how plants regulate growth and development depended on OsARFs to cope with adverse environmental factors.

2 | ROLES OF OsARFs IN RICE GROWTH AND DEVELOPMENT

The *OsARF* genes are represented by a large multigene family in rice, and these OsARFs play essential functions in different tissues of the plant. The roles that individual OsARFs control distinct developmental processes have been characterised upon the phenotypes of their loss-of-function mutants (Figure 1). *OsARF1/23* (LOC_Os11g32110) is the first reported as an early auxin-responsive gene (Waller et al., 2002). OsIAA1 plays a key role in mediating auxin and BR signalling pathway by interacting with OsARF1. Both *osarf1* mutant and *OsIAA1* overexpression plants show hyper-sensitivity to BR (Song et al., 2009).
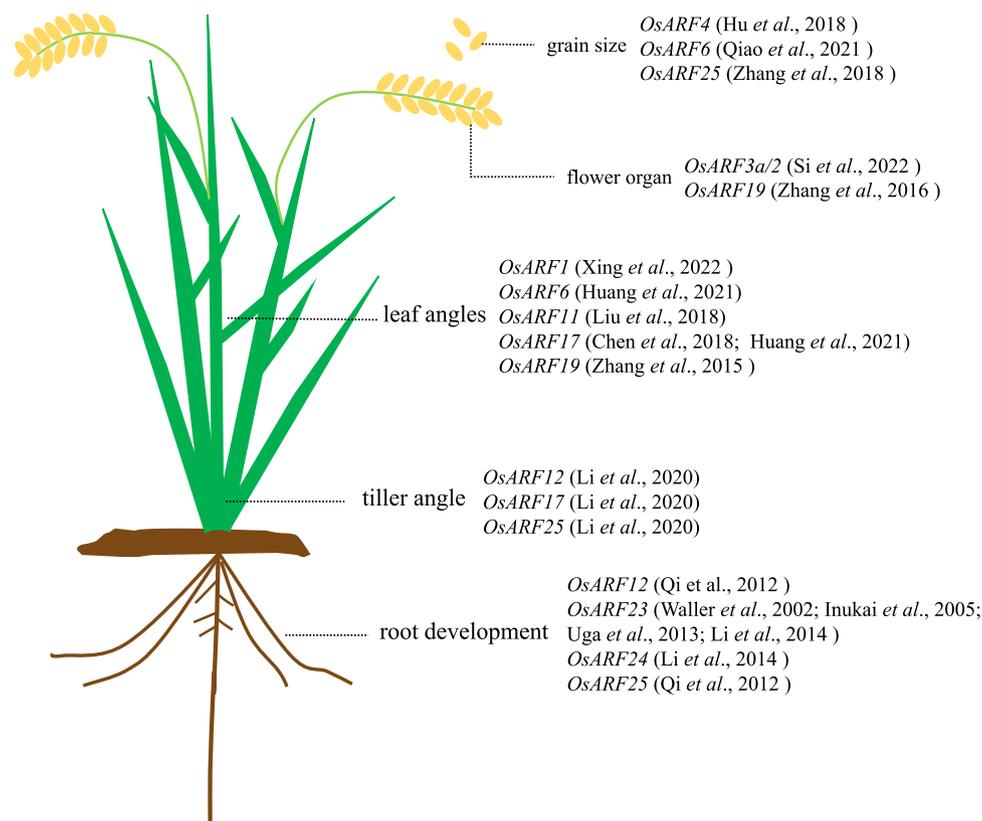
FIGURE 1 Physiological functions of OsARFs in rice. OsARFs are shown with their roles in controlling root development (OsARF12, 23, 24, 25), tiller angle (OsARF12, 17, 25), leaf angles (OsARF1, 6, 11, 17, 19), flower organ (OsARF3a/2, 19), grain size (OsARF4, 6, 25). ARF, auxin response factor

The *antisense* (*AS*)-*OsARF1* plants show pleiotropic defects including extremely dwarfism, poor vigor, short curled leaves and tillered but are sterile, suggesting that OsARF1 is of paramount importance for the growth of vegetative organs and seed development (Attia et al., 2009).

OsARFs function critical roles in modulating optimal architecture of root system (RSA) essential for normal growth and development. OsARF23 binds to the promoter and directly regulates the expression of *CROWN ROOTLESS1* (*CRL1*), which encodes a member of the plant-specific ASYMMETRIC LEAVES2 (AS2)/LATERAL ORGAN BOUNDARIES (LOB) protein family and acts a positive regulator in crown and lateral root (LR) formation (Inukai et al., 2005). *DEEPER ROOTING 1* (*DRO1*) is an early-auxin-response gene that might be directly repressed by OsARF23 in the auxin signalling pathway to control root growth angle in response to drought conditions (Uga et al., 2013). Moreover, the expression of *RICE MORPHOLOGY DETERMINANT* (*RMD*) encoding the type II formin FH5 is directly regulated by OsARF23 and OsARF24 in modulating the orientation of F-actin arrays that control root cell elongation (Li et al., 2014). Knockout mutants of *OsARF12* exhibit decreased primary root length (Qi et al., 2012). The auxin concentrations in the elongation zones of *osarf12* and *osarf12/25* mutants are lower than WT roots, possibly as a result of decreased expression of auxin synthesis genes *OsYUCCAs* (*OsYUCs*) and auxin efflux carriers *OsPINs* and *OsPGPs* (Qi et al., 2012). The crosstalk between auxin and cytokinin signalling plays important roles in root growth regulation. OsNAC2 can directly bind to the promoters of *OsARF25* and *CYTOKININ OXIDASE/DEHYDROGENASE4* (*OsCKX4*) functioned as an upstream integrator of auxin and cytokinin signals to regulate primary root length and the number of crown roots (Mao et al., 2020).

Flower organ development is fundamentally important in plant cycle. Mutation in *OsARF19* increases the expression level of *OsYUCCA* (*OsYUC*) and *OsPIN* family members and decreases the transcription of *OsGHs* (Zhang et al., 2016). Furthermore, *OsMADS29* and *OsMADS22*, two key flower organ regulators, are significantly induced by high auxin performance which may explain the abnormal small flowers and enlarged plant architecture observed in *osarf19* mutant (Zhang et al., 2016). As a MYB-like transcription factor, OsKANADI1 can bind and positively regulate the transcriptional level of *OsARF3a*/*OsARF2* (LOC_Os01g48060), which is required for establishing the abaxial–adaxial polarity of lemma in rice (Si et al., 2022). Besides, *OsARF3a/2* is negatively regulated by tasiR-ARFs at post-transcriptional level to contribute to rice lemma development (Si et al., 2022). In addition, OsETTIN2/OsARF2 promotes awn development in rice (Toriba & Hirano, 2014).

Grain size and weight are two of important agronomic traits determining rice yield. OsARF4 interacts with and is phosphorylated by OsSK41 (also known as OsGSK5), a member of the GLYCOGEN SYNTHASE KINASE 3/SHAGGY-like family. Loss-of-function mutation in either *OsARF4* or *OsSK41* results in larger rice grains possibly by upregulating a common set of downstream genes during rice grain development (Hu et al., 2018). As a direct target that is post-transcriptionally regulated by miR167a, OsARF6 binds directly to the AuxREs of the *OsAUX3* promoter, and thereby negatively controls grain length and grain weight by altering the longitudinal expansion and auxin distribution/content of glume cells (Qiao et al., 2021). Moreover, OsARF25 directly activates the expression of *SMALL ORGAN SIZE1* (*OsERF142/SMOS1*) and which plays a positive regulator of grain length (Zhang et al., 2018).

Leaf angle impacts the photosynthetic capacity of densely grown plants and is thus an important agronomic breeding trait for crop architecture and yield. OsARF6 and OsARF17 directly bind to the *Increased Leaf Angle1* (*ILA1*) promoter and activate its expression to control flag leaf angle in response to auxin (Huang et al., 2021). Consistently, transgenic plants of overexpression of *OsIAA12* or deficiency of *OsARF17* which interacts with OsIAA12 display enlarged leaf angle (Chen et al., 2018). Moreover, brassinosteroid (BR) promotes cell elongation and propagation at the adaxial side of the lamina joint, and is a positive regulator in leaf angle (Bai et al., 2007; Tian et al., 2019). OsARF11 interacts with EMF1-like protein 1 (DS1/OsEMF1) to upregulate the expression of *Brassinosteroid Insensitive 1* (*OsBRI1*) in controlling plant height and leaf angle (Liu et al., 2018; Sakamoto et al., 2013). OsARF19 positively controls rice leaf angles owing to the increase of the adaxial cell division relied on directly activating the expression of *OsGH3-5* and *Brassinosteroid Insensitive 1* (*OsBRI1*) in rice (Zhang et al., 2015). In addition, recent study reports that the module of OsIAA6-OsARF1 negatively regulates leaf angle via suppressing auxin signalling (Xing et al., 2022).

Rice tiller angle is among the key factors influencing planting density and thus contributes production. At the heading stage, *osarf12* and *osarf17* show tiny increased tiller angle, and *osarf25* shows obviously increased tiller angle compared to WT. The double mutants of *osarf12/osarf17* and *osarf12/osarf25* display larger tiller angle phenotype (Li et al., 2020). OsARF12, OsARF17 and OsARF25 seem to function redundantly to modulate tiller angle (Li et al., 2020). miRNAs play crucial roles in the negative regulation of gene expression by cleaving target mRNAs and/or repressing translation at post-transcriptional level. OsmiR167 is demonstrated to repress the expression level of *OsARF12*, *OsARF17* and *OsARF25* as in the overexpression plants of OsmiR167a, the expression of *OsARF12*, *OsARF17* and *OsARF25* are severely reduced and the transgenic plants show a larger tillering angle, indicating that OsmiR167a-OsARF12/17/25 module controls the tillering angle of rice (Li et al., 2020). OsmiR167a-OsARFs fashion functions as a key regulator in the regulation of tiller angle.

Increasing crop yields on limited arable land to feed the growing world population is an urgent problem to be solved (Tilman et al., 2011). Dense planting can improve productivity, but it will cause competition among plants for water, nutrients and light. Rice plant architecture determined by smaller leaf angle and tiller angle, raised number of grains per panicle, and increased grain size and weight is considered to be one of the main agronomic traits that contribute to grain yield upon dense planting (Khush, 2003). To optimise growth and productivity under adverse environmental conditions caused by climate change and human factors, plants have developed complex mechanisms to sense and respond to external pressures (Zhu, 2016). Plants resist adverse environmental conditions by triggering various
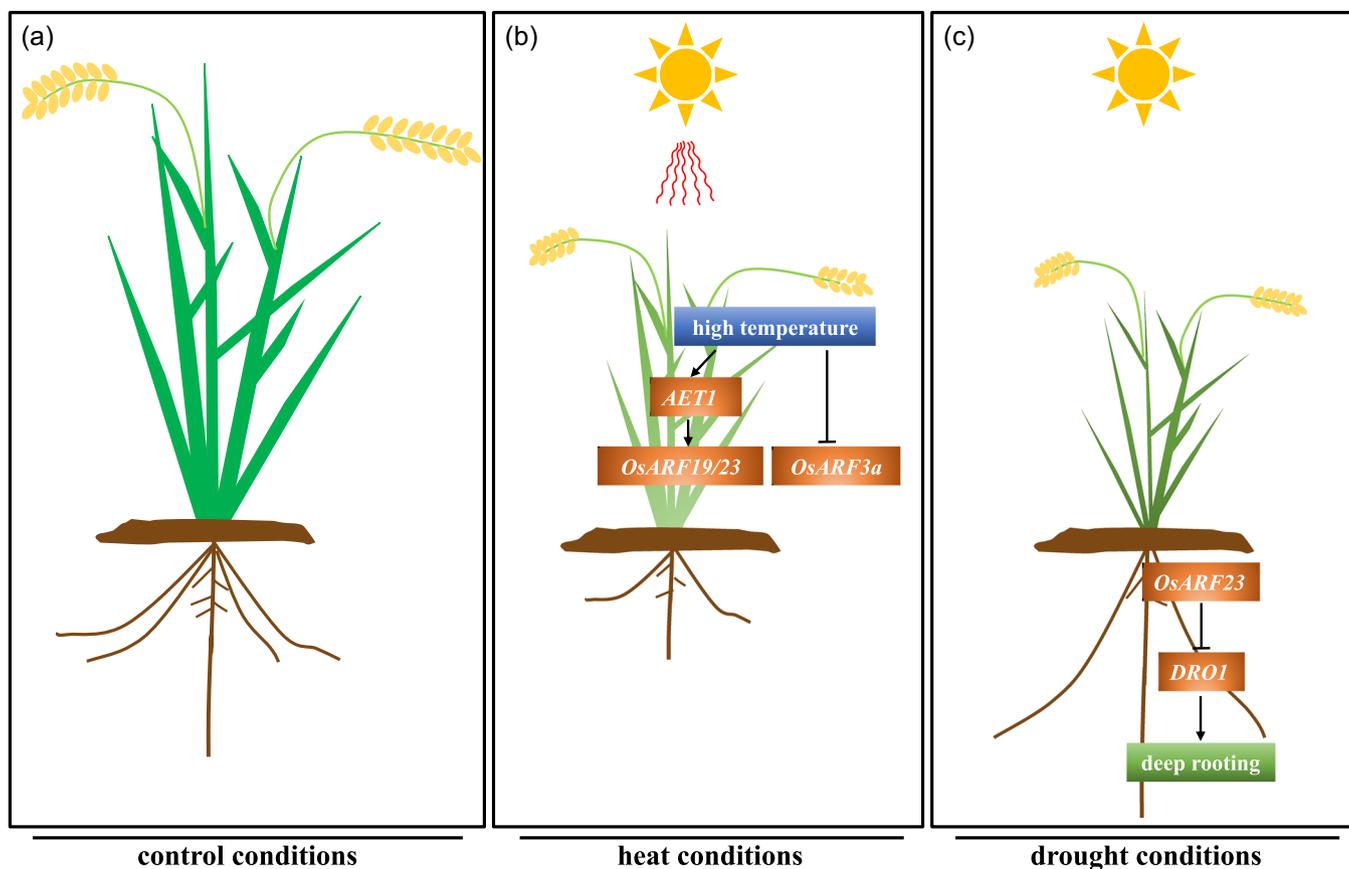
FIGURE 2 Simplified model of the OsARFs-dependent resistance to environment stress signals. (a) Representative cartoon of a rice architecture at control conditions. (b) Physiological phenotype and molecular changes in rice at heat conditions. AET1 is required for normal growth under high-temperature conditions in rice and it can directly bind to and regulate translational efficiency of mRNA of *OsARF19* and *OsARF23*. *OsARF3a* transcript level is significantly decreased at drought conditions. (c) Physiological phenotype and molecular changes in rice at high temperature conditions. DRO1 contribute to increase the root growth angle, resulting in deeper rooting under drought condition and *DRO1* might be directly repressed by OsARF23. ARF, auxin response factor; mRNA, messenger RNA

physiological, biochemical and molecular reactions resulting from changes of gene expression. A series of OsARFs-mediated signal-pathways against abiotic stress have been established through molecular genetics research (Figure 2). Among the 25 *OsARF* genes, most are suppressed by drought, cold and/or heat stresses, while several *OsARF* genes (*OsARF4*, *OsARF11*, *OsARF13*, *OsARF14*, *OsARF16*, *OsARF18* and *OsARF19*) are induced by at least one of the stresses (Du et al., 2013).

3 | ROLES OF OsARFs IN RESPONSE TO ABIOTIC STRESSES

3.1 | Heat stress

At present, global warming poses a serious challenge to improve crop yield. To survive, plants have evolved various internal heat-resistant mechanisms to adapt to environmental changes (Cortijo et al., 2017). As a tRNA^{His} guanylyltransferase, AET1 (adaptation to environmental

temperature 1) can directly bind to and regulate translational efficiency of mRNA of *OsARF19* and *OsARF23*, so as to participate in auxin signalling responding to high temperature (Chen et al., 2019) (Figure 2b). *OsARF3a/2* transcript level is significantly decreased at high temperature conditions, suggesting that OsARF3a/2 plays an important role in temperature responses in rice (Si et al., 2022) (Figure 2b).

3.2 | Drought stress

RSA is recognised as an important trait that could be improved to allow plants to adapt to deficiencies of water (Uga et al., 2013). Generally, a deep RSA facilitates to enhance drought avoidance (Lynch & Brown, 2001). OsARFs function critical roles in modulating optimal RSA essential for normal growth and development. OsARF23 binds to the promoter and directly regulates the expression of *CRL1*, which contributes to the gravitropic response in rice (Inukai et al., 2005). Furthermore, OsARF23 also plays an important role in plant

morphological response to drought. *DRO1* might be directly repressed by OsARF23 in the auxin signalling pathway (Uga et al., 2013). Enhancement of functional DRO1 accumulation can increase the root growth angle, resulting in deeper rooting to maintain high yield performance under drought condition (Uga et al., 2013) (Figure 2c).

3.3 | Flood stress

The capacity of roots to obtain water is essential for the survival of terrestrial plants. While, excessive water caused by floods, causing a drop in the rate of oxygen diffusion, which will severely restrict the growth of plants (Garcianovo & Crawford, 1973). Shallower adventitious roots (ARs) are formed to survive flooding (Visser, 2003). Auxin signalling is crucial for flooding-induced ARs formation, as the auxin coreceptor TIR1/AFB F-box protein AFB2 has revealed to play a role for ARs formation in *Arabidopsis* (da Costa et al., 2020). However, the roles of ARFs in *Arabidopsis* and rice for the formation of flooding induced ARs are not well understood.

3.4 | Salt stress

Salt stress causes ionic toxicity and reduces water availability by changing osmotic pressure (Munns & Tester, 2008). Soil salinization has a profound negative impact on global agriculture. Decreased auxin response inhibits salt induced root growth (Wang et al., 2009). The cascade of calmodulin-mediated phosphorylation plays a critical role in recruiting auxin signalling in rice roots under salt stress (Yang et al., 2021). But the roles of OsARFs under salt stress is largely unknown. Further studies are necessary to dissect interplay between OsARFs and these abiotic stress.

3.5 | Nutrient stresses

It has long been proposed that there is an interaction between nutrient and auxin signalling (Figure 3). Nitrogen (N) and phosphorus (P) are two of the most important mineral nutrients determining plants' growth and productivity. Iron (Fe) is an essential micronutrient for plant. The uneven distribution of nutrients in the soil often causes the root system to be in the situation of nutrient deficiency, which leads to the specific signal transmission and development adaptation in plants.

3.5.1 | OsARFs are involved in nitrogen signal

Nitrate (NO_3^-) is the main form of soluble N, which is prone to leach into deeper soil layers with water (Meisinger & Delgado, 2002). To access N from deeper soil layers, rooting depth and root branching length are increased to maximise N foraging under N-limited

conditions in rice (Kiba & Krapp, 2016). Recent genetic studies provide compelling evidence that auxin is involved in acquisition and use efficiency of N. DULL NITROGEN RESPONSE1 (qDNR1) might contribute the differences of NO_3^- uptake activity between *indica* and *japonica* rice varieties by modulating auxin homeostasis (Zhang et al., 2021). Seven *OsARF* members (*OsARF1*, *OsARF5*, *OsARF6*, OsARF17, *OsARF19*, *OsARF24* and *OsARF25*) are upregulated in *dnr1* but downregulated in *pAct:DNR1-Flag* overexpression plants compared to WT, meanwhile these OsARFs promote nitrogen use efficiency (NUE) and grain yield by trans-activating the expression of genes related to NO_3^- metabolism (Zhang et al., 2021) (Figure 3b).

3.5.2 | OsARFs respond to external phosphate

RSA is also recognised as an important trait upon encountering the deficiencies of P and a shallow RSA is beneficial for the acquisition of P in P-deficient soils (Lynch & Brown, 2001). Cross-talk between auxin and P-starvation (-P) response has been well investigated in *Arabidopsis*, but still less reported in rice (Huang et al., 2018b; Pérez-Torres et al., 2008; Zhou et al., 2008) (Figure 3c). OsARF16 is the first reported ARF that plays a critical role in phosphate starvation response in rice. The knockout mutant of *OsARF16* results in decreased sensitivity of primary root, LR and root hair to auxin and -P. These data reveal that the biological function of OsARF16 in linking auxin and -P responses (Shen et al., 2013). Furthermore, OsARF16 is also required for the cytokinin response and is involved in the cytokinin-mediated inhibition of P uptake and signalling in rice (Shen et al., 2014). OsARF12, a negative regulator of P absorption and transport, has a significant role on P utilisation efficiency of rice (Wang et al., 2014). Knockout-of-*OsARF12* mutant improves the absorption and translocation of P, and OsARF12 is involved in the P response possibly dependent on OsPHR2-mediated P pathway (Wang et al., 2014). Moreover, the expression of *RMD* encoding the type II formin FH5 is directly regulated by OsARF23 and OsARF24 in modulating the orientation of F-actin arrays that control root cell elongation (Li et al., 2014). And adaptive changes to root angle in response to external P availability are RMD dependent (Huang et al., 2018a). Therefore, whether OsARF23 and OsARF24 perform roles in P response needs to be studied in the future.

3.5.3 | The roles of OsARFs in iron acquisition

Iron (Fe) is an essential micronutrient for plant growth and development. The capacity of plants coping with Fe deficiency is required for their survive in Fe-limited soils (Figure 3d). Fe deprivation induces the expression of *OsARF16* in roots and shoots to upregulate the expression of Fe-deficiency response genes. Therefore, in *osarf16* mutant, most Fe-deficiency symptoms have been partially restored, including dwarfing, decreased photosynthesis, reduced iron content and the regulation of RSA
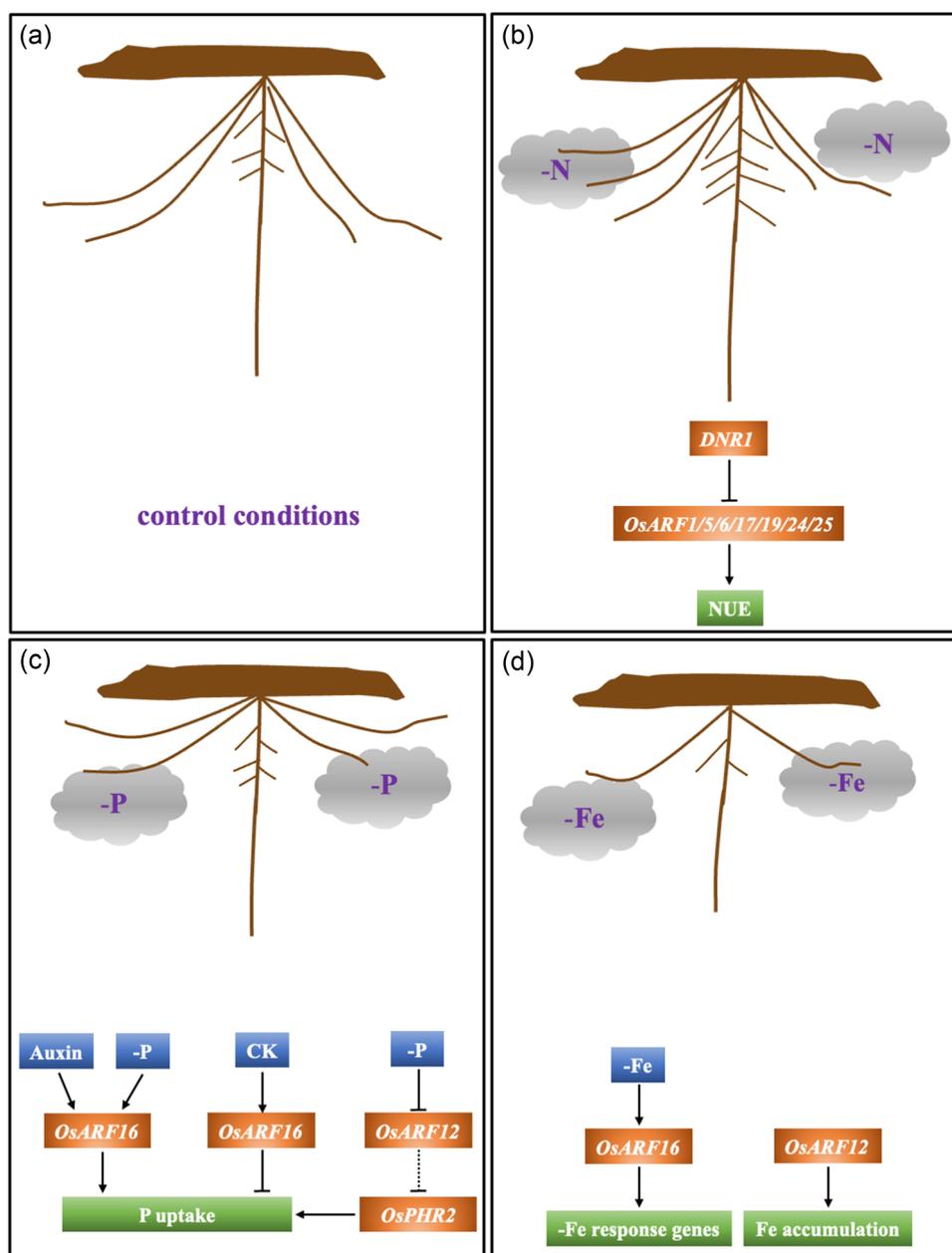
FIGURE 3 Simplified model of the OsARFs-dependent resistance to nutrient stress signals. (a) Representative cartoon of a rice root architecture at control conditions. (b) Physiological phenotype and molecular changes in rice root under -N (low nitrogen) conditions. DNR1 might contribute the activity of NO_3^- uptake. Seven *OsARF* members (*OsARF1, OsARF5, OsARF6, OsARF17, OsARF19, OsARF24* and *OsARF25*) are negatively regulated by DNR1. (c) Physiological phenotype and molecular changes in rice root under -P (low phosphate) conditions. OsARF16 plays a critical role in -P response by linking auxin and -P responses in rice. OsARF16 is also involved in the cytokinin-mediated inhibition of P uptake and signalling in rice. OsARF12 is a negative regulator of P absorption and transport dependent on OsPHR2-mediated P pathway. (d) Physiological phenotype and molecular changes in rice root under -Fe (low iron) conditions. Fe deprivation induces the expression of *OsARF16* to upregulate the expression of Fe-deficiency response genes. OsARF12 contribute the accumulation of Fe in rice roots. ARF, auxin response factor

(Shen et al., 2015). The knockout mutant of *OsARF12* exhibits short primary root length and changes the abundance of mitochondrial iron-regulated (OsMIR), iron-regulated transporter 1 (OsIRT1) and short postembryonic root 1 (OsSPR1) in rice roots, resulting in a decrease in Fe content (Qi et al., 2012). *OsARF12* transcription is inhibited by miRNA167d when co-transient expressed in tobacco and

rice callus (Qi et al., 2012). At the same time, the auxin concentrations in the elongation zones of *osarf12* and *osarf12/25* mutants are lower than WT roots, possibly as a result of decreased expression of auxin synthesis genes *OsYUCs* and auxin efflux carriers *OsPINs* and *OsPGPs*, suggesting the inseparable relationship between auxin response and Fe acquisition (Qi et al., 2012).

4 | OsARFs IS INVOLVED IN REGULATING BIOTIC STRESS RESPONSE

Virus infection often causes abnormal host plant development, resulting in the stunting of plants and leaves (Zhou et al., 2013). Plants have evolved a variety of defence mechanisms against the persistent threat of virus infection (Mandadi & Scholthof, 2013). Increasing reports have showed that auxin plays an important role in plant defence against various pathogens (Spaepen & Vanderleyden, 2011). Auxin signalling increases the susceptibility of *Arabidopsis* to the fungus *Fusarium oxysporum* (Kidd et al., 2011). RDV (rice dwarf virus) P2 protein interacts with OsIAA10 to arrest the interaction of OsIAA10 with OsTIR1, thereby interfering with the host plant's auxin signalling by preventing the degradation of OsIAA10 in rice (Jin et al., 2016).

OsARFs also play crucial roles in host antiviral immune defence (Figure 4). OsARF17 plays a key role in plant defence against different types of plant viruses (Zhang et al., 2020b) (Figure 4b). Proteins of different viruses bind to OsARF17 in different ways, thereby repressing its transcriptional activation or inhibiting its DNA binding activity, which makes plants more susceptible to virus infection (Zhang et al., 2020b). Genetic data shows that OsARF11, OsARF12 and OsARF16 have different regulatory effects on rice antiviral defence (Qin et al., 2020). Functional loss mutant of either *osarf12* or *osarf16* shows reduced resistance to RDV, in contrast *osarf11* or *osarf5* shows increased resistance to RDV (Qin et al., 2020). Real-time quantitative PCR analysis demonstrates a modest increase in the *OsARF8* transcript levels in RGDV (rice gall dwarf virus)-S11 transgenic rice plants compared with non-transgenic rice plants (Shen et al., 2012). These findings significantly deepen our understanding of auxin-signalling' roles in virus-host interactions and provide novel targets of molecular breeding rice cultivars against plant viruses.

5 | ARFs IN *ARABIDOPSIS* AND RICE

ARF genes exist in the form of family in plants, and the *ARF* genes of each family have certain homology among species. To date, the explanation of *ARF* genes function mainly comes from the study of *Arabidopsis*. Due to the functional redundancy between *ARF* genes, not all *ARF* genes functions can be well investigated, and the *ARF* genes in dicotyledonous plant *Arabidopsis* cannot fully represent the functions of *ARF* genes in all plants, such as monocotyledonous plant rice. Therefore, the study of *ARF* genes in different species will help to deeply understand the comprehensive roles of *ARFs* in plant development and signal transduction.

The comparison of ARF families among a large number of species shows that there is homology not only among ARF members of the same species, but also within different species. All 48 members of ARF gene families in *Arabidopsis* and rice fall into a total of 13 sister pairs, including 9 OsARF-OsARF, 2 AtARF-AtARF and
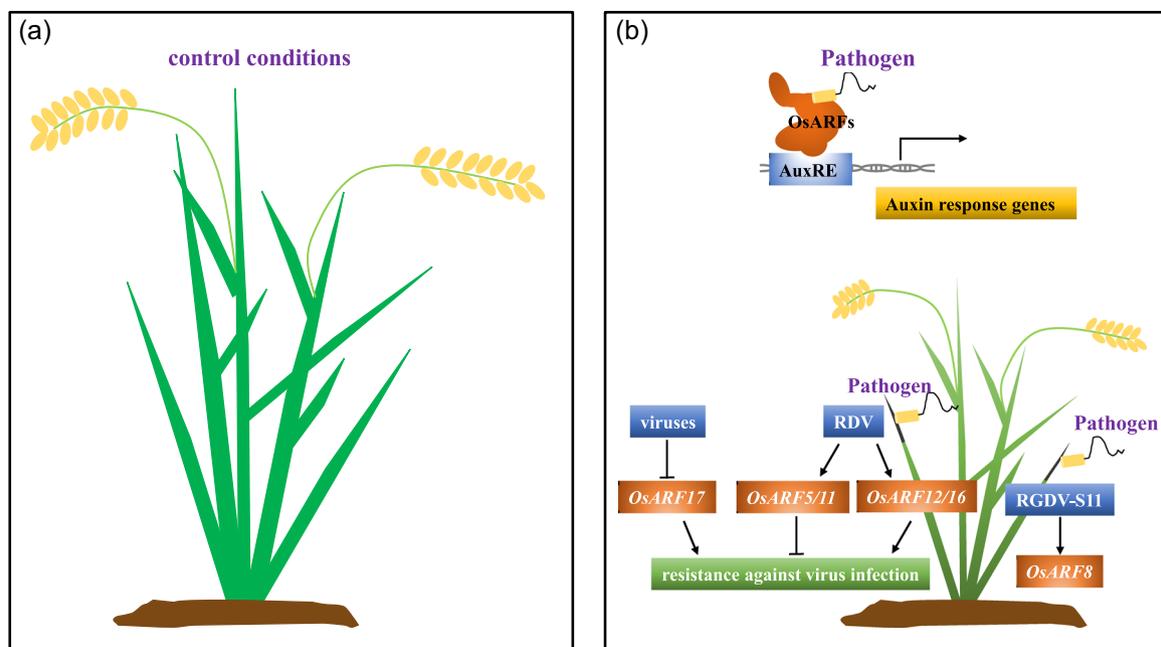
FIGURE 4 Simplified model of the OsARFs-dependent resistance to biotic stress signals. (a) Representative cartoon of a rice shoot architecture at control conditions. (b) Physiological phenotype and molecular changes in rice shoot under biotic stress. OsARF17 plays positive roles in host antiviral immune defence. Proteins of different viruses can bind to OsARF17 to repress its transcriptional activation or inhibiting its DNA binding activity, making plants more susceptible to virus infection. OsARF5/11 and OsARF12/16 have different regulatory effects on rice antiviral defence. *OsARF8* transcript level is upregulated by RGDV-S11. ARF, auxin response factor

2 AtARF-OsARF sister pairs are formed, showing different orthologous relationships between AtARFs and OsARFs. However, none of the nine sister pairs of OsARFs are genetically linked to each other matched with their corresponding chromosomal locations (Wang et al., 2007). At the same time, there seems to be no homologous genes in rice corresponding to ARF on *Arabidopsis* chromosome 1, suggesting that these genes may be lost from rice after monocots and dicots divergence (Guilfoyle & Hagen, 2007).

The first mutant of *atarf* gene identified in *Arabidopsis* is *monopteros* (*mp*) mutant, which is later proved to be *atarf5*, interfered with the formation of vascular strands at all stages and also with the initiation of the body axis for the early embryo (Hardtke, 1998). It shows that MONOPTEROS (MP, AtARF5) plays a determinant role in the establishment of embryo model and the normal formation of vascular tissue. In addition, OsARF11, the closet rice homolog of

Arabidopsis MP appears to play a central role in auxin-mediated growth of multiple organs and leaf veins (Sims et al., 2021). Compared to WT, *osarf11*, a transfer DNA insertion mutant produces fewer and shorter roots, shorter and less wide leaves with fewer veins and larger areoles, fewer branches per panicle, fewer grains per panicle and fewer filled seeds (Sims et al., 2021). OsARF18 decreases the transcription of downstream genes *PLT1* and *PLT2*, and inhibits callus formation of the mature embryo (Zhang et al., 2020a), this is opposite to the AtMP function reported in *Arabidopsis*.

ARF genes show specificity in the process of plant growth and development, however, there is a certain degree of redundancy among ARFs. For example, as transcriptional repressors, AtARF1 and AtARF2 co-regulate leaf senescence, and initiation and abscission of flowering (Ellis et al., 2005). AtARF6 and AtARF8 act redundantly in the maturation of flower organ (Finet et al., 2010). AtARF7 and

TABLE 1 Summary of the physiological functions and the target genes of OsARFs in rice

Gene name	IAA-ARF complex	Target gene(s)	Function	Reference
OsARF1/23			Vegetative organs growth and seed development	Attia et al. (2009)
	OsIAA1-OsARF1		Mediate auxin and BR signalling pathway	Song et al. (2009)
		DRO1	Negatively regulate the root growth angle	Uga et al. (2013)
		CRL1	Crown and lateral root formation	Inukai et al. (2005)
	OsIAA6-OsARF1		Negatively regulate leaf angle	Xing et al. (2022)
OsARF2			Awn development	Toriba & Hirano (2014)
OsARF4			Negatively regulate grain size and weight in rice	Hu et al. (2018)
OsARF6		*OsAUX3*	Negatively regulate grain length and weight in rice	Qiao et al. (2021)
OsARF6/OsARF17		*ILA1*	Control the flag leaf angle in rice	Huang et al. (2021)
OsARF17	OsIAA12-OsARF17		Regulate leaf inclination	Chen et al. (2018)
OsARF11		*OsBRI1*	Control the plant height, leaf width and flag leaf angle in rice	Liu et al. (2018); Sakamoto et al. (2013)
OsARF16			Iron deficiency response	Shen et al. (2015)
			Cytokinin-mediated inhibition of P uptake and P signalling in rice	Shen et al. (2014)
OsARF18			Dwarf stature, rolled leaves, and small seeds	Huang et al. (2016)
		PLT1 and *PLT2*	Inhibit callus formation of the mature embryo	Zhang et al. (2020a)
OsARF19		*OsGH3-5* and *OsBRI1*	Enlarge lamina inclination	Zhang et al. (2015)
			Regulate floral and vegetative organ development	Zhang et al. (2016)
	OsIAA13-OsARF19	*LBD1-8*	Regulate lateral roots formation	Yamauchi et al. (2019)
OsARF23/OsARF24		*RMD*	F-Actin organisation and cell growth	Li et al. (2014)
OsARF25		*OsERF142/SMOS1*	Positively regulate grain length	Zhang et al. (2018)

Abbreviation: ARF, auxin response factor.

AtARF19 function redundant roles within positively regulating LR formation through activation of the plant-specific transcriptional regulators *LOB Domain-Containing* (*LBD*) genes (Goh et al., 2012). For rice, OsARF12, OsARF17 and OsARF25 function redundantly to modulate tiller angle (Li et al., 2020). Moreover, the redundant roles are characterised in the regulation of flag leaf angle by OsARF6 and OsAR17 (Huang et al., 2021), and OsARF23-OsARF24 mediated primary root elongation (Li et al., 2014).

There are great differences in the features between the dicotyledonous and monocotyledonous plants. Hence, the roles of ARFs are at least some but not all different. For instance, LRs are the advantageous roots occupying most of the root system, and there is only one kind of LRs in *Arabidopsis*. While, rice can produce two types of LRs: one is S-type (short and thin) and the other one is L-type (long and thick), capable of further branching, which is conducive to increase total root length in response to drought stress (Kawai et al., 2022b). OsARFs play an important role in regulating root system development in rice, but their functions in the development of LRs are largely unknown. Auxin signalling can increase LR diameter by inducing the expression of a positive regulator of LR diameter, *OsWOX10*, and it is revealed as a potential target of OsARF19 (Kawai et al., 2022a; 2022b). OsARF19 is an interactor of IAA13 and targets *LBD1-8*, which has been showed to function in the initiation of LR formation in rice (Yamauchi et al., 2019). Whether OsARF19 plays a role in determining S- or L-type LRs remains to be further studied. Moreover, the initiation process of LRs in *Arabidopsis* is completely different from that of rice. In *Arabidopsis*, LRs start from pericycle cells adjacent to primary xylem, while rice LRs start from pericycle cells adjacent to primary phloem (De Smet et al., 2006). Although the existing reports show that the mechanism of auxin signalling in regulating LR development is relatively conservative in *Arabidopsis* and rice, there may be more diversities in LR development between rice and *Arabidopsis* due to the great differences in root tissue structure between the two species. However, because the research on LR in rice is not deep enough, more truth needs to be unrevealed.

6 | CONCLUSIONS AND CHALLENGE

This review highlights the roles of OsARFs in rice growth and development, and the mechanisms by OsARFs regulating target genes (Table 1) in response to external stress. We have also introduced the regulation of *OsARF* expression at both transcription and post-transcription levels. miRNAs- and tasiRNAs-mediated the regulation of *OsARF* expression is a complex process that is strictly controlled. The effective roles of miRNAs and tasiRNAs can maintain the balance of auxin concentration and signal, which are required for the normal growth and development of plants and resistance to biotic and abiotic stresses.

The development of plants is closely related to/determined by the environment. RSA is recognised as an important trait that could be improved to allow plants to adapt to a range of soil environments, such as those experiencing deficiencies of water or nutrients (Uga et al., 2013). Typically, a deep RSA facilitates to enhance drought avoidance, by contrast, a shallow RSA is beneficial for the acquisition of P in P-deficient soils (Lynch & Brown, 2001). Under low P condition, AtARF7 and AtARF19 directly co-activate the expression of *AtPHR1* to increase the number of LRs but decrease the primary root length for forming shallow RSA in *Arabidopsis* (Huang et al., 2018b). While, that is totally different in rice. Rice will shape shallow root system by increasing the growth angle of crown root to acquire more phosphate accumulated in the topsoil (Huang et al., 2018b). AtARF7-dependent asymmetric *LBD16* expression plays key roles in triggering the initiation of LR toward water side (Orosa-Puente et al., 2018). In rice, OsARF23 can directly bind to the promoters of *DRO1* to form deep RSA via controlling the growth angle of crown root in drought conditions (Inukai et al., 2005; Uga et al., 2013). Hence, it is a good strategy to study on the roles of OsARFs to uncover the mechanism when rice adopt to adapt to various environment cues.

The roles of rice ARFs are largely unclear in comparison to that of *Arabidopsis*. The auxin signalling transmission speed is very fast. In this process, how ARFs respond quickly and make regulatory actions merits more attention. Besides, there is a problem of functional redundancy due to the high homology between ARFs. However, the construction of multiple mutants is arduous, and the sterility brings a great challenge to research. OsARFs are the central components of auxin signalling playing key roles in the regulation of many important agronomic traits, such as (flag) leaf angle, root angle and length, tiller angle and number, and plant height. Furthermore, increasing studies demonstrate that OsARFs are required for plants' adaption/resistance to various stress conditions, including high temperature, water deficiency, N deprivation, P starvation and Fe limitation. Thus, genetic engineering of rice plants with better architecture and improved stress resistance is likely be achieved by the precise editing of *OsARF* genes.

ACCESSION NUMBERS

Sequence data from this article can be found in the Rice Genome Annotation Project (RGAP) under accession numbers: *OsARF1*, LOC_Os01g13520; *OsARF3a/2*, LOC_Os01g48060; *OsARF3*, LOC_Os01g54990; *OsARF4*, LOC_Os01g70270; *OsARF5*, LOC_Os02g04810; *OsARF6*, LOC_Os02g06910; *OsARF7*, LOC_Os02g35140; *OsARF8*, LOC_Os02g41800; *OsARF10*, LOC_Os04g43910; *OsARF11*, LOC_Os04g56850; *OsARF12*, LOC_Os04g57610; *OsARF13*, LOC_Os04g59430; *OsARF14*, LOC_Os05g43920; *OsARF16*, LOC_Os06g09660; *OsARF17*, LOC_Os06g46410; *OsARF18*, LOC_Os06g47150; *OsARF19*, LOC_Os06g48950; *OsARF22*, LOC_Os10g33940; *OsARF23*, LOC_Os11g32110; *OsARF24*, LOC_Os12g29520; *OsARF25*, LOC_Os12g41950.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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