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REVIEW

Towards a better understanding of auxin response factors for improving cereal crops

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Highlights

- Auxin response factor (ARF) gene families in the big three cereal crops are classified together to facilitate functional prediction.
- Nomenclatures for previously reported ARFs are revised to the family numbers to better summarize ARFs' functions.
- Regulatory models of ARF and other genes/miRNAs on agronomic and yield traits are introduced.

Abstract

The auxin response factor (ARF) is the key component of phytohormone auxin signal pathway and is crucial in regulating a plurality of functions throughout the plant life cycle. Although ARFs' structure and function have been well studied in *Arabidopsis*, such knowledge is far from being sufficient for cereal crops, especially wheat, rice, and maize. This review is based on a comprehensive retrospection into the studies on ARFs in the three cereal crops, consisting of four parts: (1) characterization of the domains of 23, 25, and 33 ARF family members in wheat, rice, and maize, respectively; (2) revision of nomenclatures for previously reported ARFs to the family numbers based on sequence alignment, and summary of ARFs' functions including the regulation of agronomic traits and response to biotic/abiotic stresses; (3) highlight of general regulatory models for fundamental physiological and reproductive traits from miRNA-*ARFs*, IAA-ARF-*LBD*, IAA-ARF-Auxin response gene, and IAA-ARF-*ERF* (4) prospects to promising future ARF research for anticipated agronomic traits. This review is expected to enhance understanding of ARF functions in the three cereal crops and promote their application in molecular breeding to achieve optimal plant architecture, higher yield, and wider adaptability.

Keywords: ARFs, nomenclature, domain, function, wheat–rice–maize

1. Introduction

The major natural phytohormone auxin, indole-3-acetic acid (IAA), is mainly synthesized in the shoot apexes, root tips, and other organs or tissues with vigorous growth and serves as a signaling molecule in plants (Dharmasiri *et al.* 2005) (Fig. 1-A). Throughout the plant life cycle, the perception of IAA and its binding to extra- or intra-cellular receptors triggers diverse growth, development, and reproduction processes, including cell elongation, gravitropism, leaf primordia initiation, lateral root formation, vascular tissue differentiation, and apical dominance (Jia *et al.* 2024; Sun *et al.* 2025). Auxin-binding protein 1 (ABP1) senses extracellular auxin, while the nuclear auxin pathway (NAP) transduces signals within the plant cell nucleus (Burian *et al.* 2022; Martin-Arevalillo *et al.* 2023; Yu *et al.* 2023; Kuhn *et al.* 2024) (Fig. 1-B).

The NAP consists of three basic components: the receptor TRANSPORT INHIBITOR RESPONSE 1 (TIR1)/AUXIN-SIGNALING F-BOX (AFB), the transcription factor AUXIN RESPONSE FACTOR (ARF), and the repressor AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA), along with co-repressor

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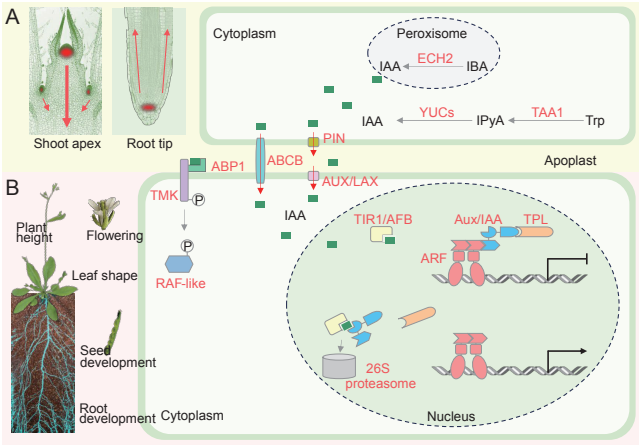


Fig. 1 Main metabolism pathways for auxin in *Arabidopsis*. A, biosynthesis and transportation of indole-3-acetic acid (IAA). The left profiles show the polar auxin transport in the shoot apex and root tip, and the right diagram displays the main intracellular pathway of IAA biosynthesis. IAA molecules are indicated as green rectangles. IAA-related metabolites are shown in black, and enzymes and IAA transporters are shown in red. The direction of the IAA movement is displayed by the red arrow. Metabolites, indole-3-butyric acid (IBA), L-tryptophan (Trp), and indole-3-pyruvic acid (IPyA); enzymes, ENOYL-COA HYDRATASE2 (ECH2), TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1), and YUCCA flavin-containing monooxygenases (YUC); transporters, PIN-FORMED (PIN), ATP-BINDING CASSETTE subfamily B (ABCB), and AUXIN1/LIKE-AUX1 (AUX/LAX). B, signal transduction pathways of IAA and the phenotypes regulated by their downstream genes. The left image shows the organ development regulated by the auxin signaling pathway in *Arabidopsis*, and the right diagram reveals two signal transduction pathways, including the rapid response pathway and the classic nuclear auxin pathway, triggered by extra- or intra-cellular IAA receptors, respectively. IAA molecules are indicated as green rectangles, and proteins are shown in red. Proteins, AUXIN-BINDINGPROTEIN 1 (ABP1), TRANSMEMBRANE KINASE (TMK), TRANSPORT INHIBITOR RESPONSE 1/AUXIN-SIGNALING FBOX (TIR1/AFB), AUXIN RESPONSE FACTOR (ARF), AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA), and TOPLESS (TPL).

component TOPLESS/TOPLESS-RELATED (TPL/TPR). When auxin is present, Aux/IAAs are degraded by TIR1/AFB-mediated ubiquitin-proteasome-dependent degradation to release ARF activators from inhibition (Israeli *et al.* 2020; Cancé *et al.* 2022; Ang and Østergaard 2023). When auxin is absent, Aux/IAAs inhibits ARF-induced transcription by forming heterodimers with ARF activators (Ulmasov *et al.* 1999b; Guilfoyle 2015) and by recruiting a TPL/TPR co-repressor (Szemenyei *et al.* 2008).

ARFs are the key components in auxin signaling (Chapman and Estelle 2009), which link NAP and transcriptional regulation of downstream genes. A typical ARF consists of an amino-terminal DNA-binding domain (DBD), a middle region (MR), and a carboxy-terminal Phox and Bem1 (PB1) dimerization domain. Monopteros (MP, later named ARF5) is the first ARF discovered from an *Arabidopsismp* mutant (Hardtke and Berleth 1998; Schlereth *et al.* 2010). Later, 23 *Arabidopsis* ARFs (AtARFs) were identified and categorized into three conserved classes A, B, and C (Finet *et al.* 2013; Li Y *et al.* 2023). ARFs in Class A (including AtARF5-8 and -19) act as transcriptional activators, and ARFs in Class B (including AtARF1–4, 9, 11–15, 18, and 20–23) as transcriptional repressors. Less is known about Class C (including AtARF10, 16, and 17) (Ulmasov *et al.* 1999a; Flores-Sandoval *et al.* 2018). It is generally perceived that the ARF family is rooted in a single proto-ARF gene in early charophyte algae (Finet *et al.* 2013). The proto-ARF diversified into two classes (A/B and C) in late-diverging charophytes after the first duplication event, and then split into three classes in the first terrestrial plant as a result of the division of class A/B into classes A and B. Each of the three classes is further duplicated to enlarge and diversify the ARF family (Qiao *et al.* 2017; Mutte *et al.* 2018; Cancé *et al.* 2022).

Human civilization is accompanied by the artificial modification of higher plants, and cereal crops lay the foundation for agriculture. It is estimated that the "trinity" of wheat (*Triticum aestivum*), rice (*Oryza sativa*), and maize (*Zea mays*) accounts for more than half of human calorie acquisition, thus significant for global food security (Tilman *et al.* 2011; Wakeman and Bennett 2023). During the past decade, multiple reviews have been published on the structure and function of ARFs in *Arabidopsis* (Tiwari *et al.* 2003; Guilfoyle and Hagen 2007; Cancé *et al.* 2022), but few are available for crops. This review summarizes the latest advances in wheat, rice, and maize, focusing on the regulatory mechanisms underlying growth, development, stress responses, and yield formation.

The nomenclatures of ARF genes vary across studies. For example, *TraesCS5B01G039800*, *TaARF6* (Liu *et al.* 2019), and *TaARF25* (Jia *et al.* 2021) are synonyms, so are *Os01g0670800*, *OsETT2* (Toriba and Hirano 2014), *OsARF2* (Zhao Z *et al.* 2022), and *OsARF3a* (Si *et al.* 2022) in rice, and *GRMZM2G034840*, *ZmARF4* (Ravazzolo *et al.* 2021; Li J *et al.* 2022), *ZmARF5* (Yang *et al.* 2022), and *ZmARF8* (Zhang *et al.* 2014) in maize. For the sake of consistency and convenience in research, this review performed protein sequence alignment for the reported ARFs and ARF family members in wheat (Qiao *et al.* 2018), rice (Wang *et al.* 2007), and maize (Galli *et al.* 2018), respectively, in which the E value of 0 and the sequence similarity of 100% were used to identity ARFs for nomenclature revision. The phylogenetic tree, the domains of ARF family (Fig. 2), and the key information of TaARFs, OsARFs, and ZmARFs are presented (Appendices A–C).

2. Classification and structure of ARFs in wheat, rice, and maize

The availability of crop whole genomes has enabled systematic identification of ARF family members. There are 23 *TaARF* genes in the genome of wheat variety Chinese Spring v1.0 (Qiao *et al.* 2018), 25 *OsARF* genes in the genome of rice variety Nipponbare (Wang *et al.* 2007), and 33 expressed *ZmARF* genes in the genome of maize inbred B73 (Galli *et al.* 2018). The phylogenetic tree revealed that the ARF family differentiated after the divergence of mono- and dicotyledons (~130 MYA) and that further specific differentiation occurred in *Arabidopsis*, wheat, rice, and maize (Fig. 2-A). High structural similarity is observed among

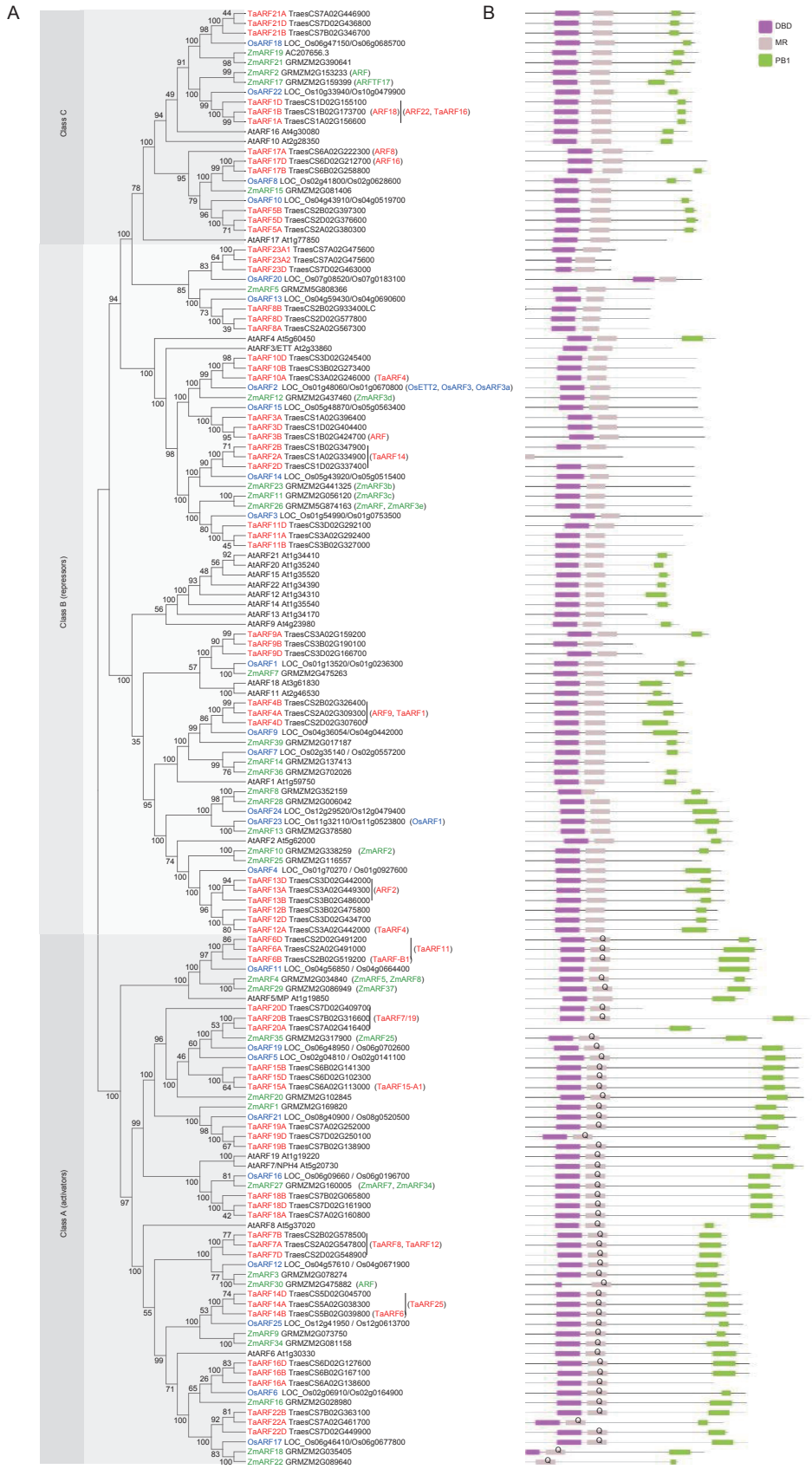


Fig. 2 Phylogenetic tree and domains of the AUXIN RESPONSE FACTOR (ARF) family. A, neighbor-joining phylogenetic tree of ARF protein sequences from wheat (red), rice (blue), maize (green), and *Arabidopsis* (black) with accession numbers. The previously reported gene names are in parentheses. B, conserved domains in ARF proteins identified with the Batch CD-search Tool (https://www.ncbi.nlm.nih.gov/Structure/bwrpsb/bwrpsb.cgi). Magenta box, DNA-binding domain (DBD); pink box, middle region (MR); lime box, carboxy-terminal Phox and Bem1 (PB1) dimerization domain; Q, poly Q region.

TaARF, OsARF, and ZmARFs, which fall into classes A, B, or C based on their sequence homology with AtARFs (Fig. 2-B).

2.1. Class A ARFs

The NAP is primarily triggered by ARF activators from Class A (Cancé *et al.* 2022). Class A consists of 9 TaARFs, 9 OsARFs, and 13 ZmARFs. For each ARF, its amino-terminal DBD binds to all three configurations of double auxin response elements (AuxREs) in genomic regions, including the inverted repeats (IR), direct repeats (DR), and everted repeats (ER), with wide spacing permission (Freire-Rios *et al.* 2020).

The MRs of Class A ARFs are usually highly disordered and contain high glutamine residues (Q), excluding TaARF20D in wheat, OsARF11 in rice, and AtARF5 in *Arabidopsis*. The Q-rich MR, a feature of Class A ARFs (Powers *et al.* 2019), interacts with proteins such as DELLA, BRASSINAZOLERESISTANT 1 TF (BZR1), and AUXIN RESPONSE FACTOR F-BOX1 (AFF1) for signaling cross-talk (Oh *et al.* 2014; Hu J *et al.* 2018; Jing *et al.* 2022).

The carboxy-terminal PB1 domain of Class A ARFs and the PB1 domain of Aux/IAA exhibit similar 3D structures, and they all lead to heterotypic interactions between the Aux/IAA-ARF. This is fundamental to auxin signaling, since the domains establish the connection between auxin and auxin-response genes. Such interactions of Class A ARFs have been described in a range of studies, e.g., the TaIAA21-TaARF14 in wheat (reported as TaARF25; Jia *et al.* 2021), OsIAA10-OsARF11/12/16 (Qin *et al.* 2020), OsIAA12-OsARF17 (Chen S H *et al.* 2018), OsIAA1/13-OsARF19 (Zhang *et al.* 2015; Yamauchi *et al.* 2019), and OsIAA3-OsARF25 (Zhang *et al.* 2018) in rice, and ZmIAA9-ZmARF1 (Yan *et al.* 2023), ZmIAA5-ZmARF4 (reported as ZmARF5, Yang *et al.* 2022), ZmIAA8-ZmARF20 (Zhang *et al.* 2024), ZmIAA29-ZmARF25 (Ma C *et al.* 2023), ZmRUM1-ZmARF35/27 (reported as ZmARF25/34, von Behrens *et al.* 2011; Zhang *et al.* 2014), and ZmIAA8-ZmARF27 (Ramos *et al.* 2020). In addition, certain PB1 domains of Class A ARFs in *Arabidopsis* mutually interact to form dimers (Kato *et al.* 2020) or even with proteins outside the NAP, e.g., AtARF7 with MYB (Shin *et al.* 2007) and AtARF8 with bHLH (Varaud *et al.* 2011). Interestingly, individual Class A ARFs (e.g., AtARF5) reportedly produce transcripts insensitive to Aux/IAA inhibition by alternative splicing without PB1, possibly a consequence of transforming activator into repressor (Cucinotta *et al.* 2021; Hu *et al.* 2023).

2.2. Classes B and C ARFs

It is known that Class B ARFs are mostly repressors (Tiwari *et al.* 2003), but Class C is functionally unclear (Kato *et al.* 2020). Class B consists of 10 TaARFs, 12 OsARFs, and 14 ZmARFs, and Class C includes 4 TaARFs, 4 OsARFs, and 5 ZmARFs. The DBDs of Class B ARFs commonly bind to IR sites with narrow spacing (Freire-Rios *et al.* 2020), and the AtARF10 DBD of Class C binds to IR sites with relaxed spacing specificity (Martin-Arevalillo *et al.* 2019).

Among ARFs in both Class B and C, the MRs are rich in serine (S), proline (P), and threonine (T) with a lower degree of disorder than those in Class A (Roosjen *et al.* 2018; Cancé *et al.* 2022). In *Arabidopsis*, most MR sequences of Class B ARFs contain the repression R/KLFG motif relevant to recruiting carboxy-terminal of TPL/TPR co-repressors (Choi *et al.* 2018), and certain MRs like AtARF2 contain the ETHYLENE-RESPONSIVE ELEMENT BINDING FACTOR-ASSOCIATED AMPHIPHILIC REPRESSION (EAR) motif (sequence LxLxLx) that allows for interaction with the amino-terminal of TPL/TPRs (Causier *et al.* 2012; Ke *et al.* 2015; Martin-Arevalillo *et al.* 2017). For the crops of this review, 20 Class B ARFs contain the R/KLFG motif, i.e., TaARF2, 4A/B, 9A, and 23D in wheat, OsARF1, 3, 7, 9, 14, and 23 in rice, and ZmARF7, 8, 11, 13, 14, 23, 26, 28, 36, and 35 in maize. Class B ARF MRs also interact with BRASSINOSTEROID INSENSITIVE 2 kinase (BIN2) or ETHYLENE INSENSITIVE3-like 1 (EIL1) (Vert *et al.* 2008; Zhang T *et al.* 2020). No report is available about the interaction of Class C ARF MRs with proteins, although certain Class C ARF MRs contain a similar repressor VLFG motif.

It was commonly believed that only the PB1 domain of Class A ARF activators interacts with Aux/IAAs. However, the PB1 of Class B was also found interacting with a few Aux/IAAs like OsIAA6-OsARF1 (Xing *et al.* 2022), OsIAA4-OsARF23 (reported as OsARF1, Kitomi *et al.* 2011), OsIAA10-OsARF4 (Ma M *et al.* 2023), and ZmIAA8-ZmARF12 (Wang *et al.* 2022). In addition, several ARFs such as 7 TaARFs (TaARF2, 3, 8, 9B/D, 10, 11, and 23), 6 OsARFs (OsARF2, 3, 13, 14, 15, and 20), and 7 ZmARFs (ZmARF5, 11, 12, 14, 23, 25, and 26) from Class B and TaARF17A/D and ZmARF15 from Class C all lack PB1 domain, for which the implications are yet known. Studies on OsARF2/18 and AtARF3 (ETTIN) have shown their noncanonical auxin mechanisms. Both OsARF2 from Class B and OsARF18 from Class C are without PB1; the former binds to the sugar-responsive elements (SuREs) in the promoter of *OsSUT1 via* its DBD to regulate *OsSUT1* expression, and the latter inhibits *OsSUT1*/*OsARF2* expression by binding to SuRE or AuxRE promoters (Zhao Z *et al.* 2022). The PB1-lacking AtARF3 from Class B does not interact with Aux/IAA but directly binds to auxin through its MR to further regulate certain co-repressors and several transcription factors, thus influencing diverse developmental processes (Simonini *et al.* 2017; Chung *et al.* 2019; Kuhn *et al.* 2020).

3. Functions of ARFs in wheat, rice, and maize

As an important transcriptional regulator in the auxin signaling pathway, ARFs are involved in the regulation of plant growth and development, including root system, flowering time, plant architecture, leaf senescence, and defense response by activating or inhibiting the expression of downstream genes, and these traits are also the main targets of crop agronomic character improvement. The biological/non-biological functions of ARFs in wheat, rice, and maize were reviewed according to the revised nomenclature of ARFs.

3.1. Functions of ARFs in wheat

TaARF1, also named *ARF22* (Ma *et al.* 2015) or *ARF18* (Liu H *et al.* 2017), is relevant to drought stress response.

TaARF1 serves as the target of *tae-miR160* in common wheat and shows upregulated expression in tolerant accessions after dehydration stress and a negative correlation to the downregulation of *tae-miR160* (Ma *et al.* 2015). Moreover, *TaARF1* is considered the target for conserved *miR160a* in durum wheat. In tolerant accessions, *TaARF1* is upregulated by water-deficit stress and negatively correlated to the expression of *miR160a* (Liu H *et al.* 2017).

TaARF2 may be relevant to tillering. The abnormal expression of *TaARF2* (reported as *TaARF14*) is one of the main causes for constrained of a *dwarf monoculm* (*dmc*) wheat mutant (Li *et al.* 2021).

TaARF4 was previously reported as *ARF9-like* (Liu H *et al.* 2017) and *TaARF1* (Chen D *et al.* 2018; Tuan *et al.* 2019). *TaARF4* is the target of *miR397b* and exhibits differential response expression patterns in water-deficit stress across durum varieties (Liu H *et al.* 2017). *TaARF4* is upregulated in *ROOT-EXPRESSED NAC* (*TaRNAC1*)-overexpressing plants with consequent root elongation, biomass gain, and drought resistance enhancement (Chen D *et al.* 2018). Moreover, endospermic *TaARF4* exhibits transcriptional repression in the mid-phase of seed maturation (Tuan *et al.* 2019).

TaARF6, previously reported as *TaARF11*, is the ortholog of AtARF5/MP and a potential regulator for wheat tillering (Li *et al.* 2021). Reduced *TaARF6* expression has been identified as a causative factor in reduced tiller number of the *dmc* mutant. Our study team observed that when *TaARF6B* (*TraesCS2B02G519200*) was repressed by the awn inhibitory protein B1, the expression of auxin downstream genes in young spikes was low (Qiao *et al.* 2025).

TaARF7, previously reported as *TaARF8* (Wang Y *et al.* 2019) and *TaARF12* (Li A *et al.* 2022; Kong *et al.* 2023), is relevant to flower and grain development as well as plant architecture (Fig. 3-A). *TaARF7* is mediated by *tae-miR167a* and controls pollen fertility in a photothermo-sensitive genic male sterile wheat line (Wang Y *et al.* 2019). *TaARF7* was found to pleiotropically regulate both plant height and grain weight in genome-wide association studies. The RNA

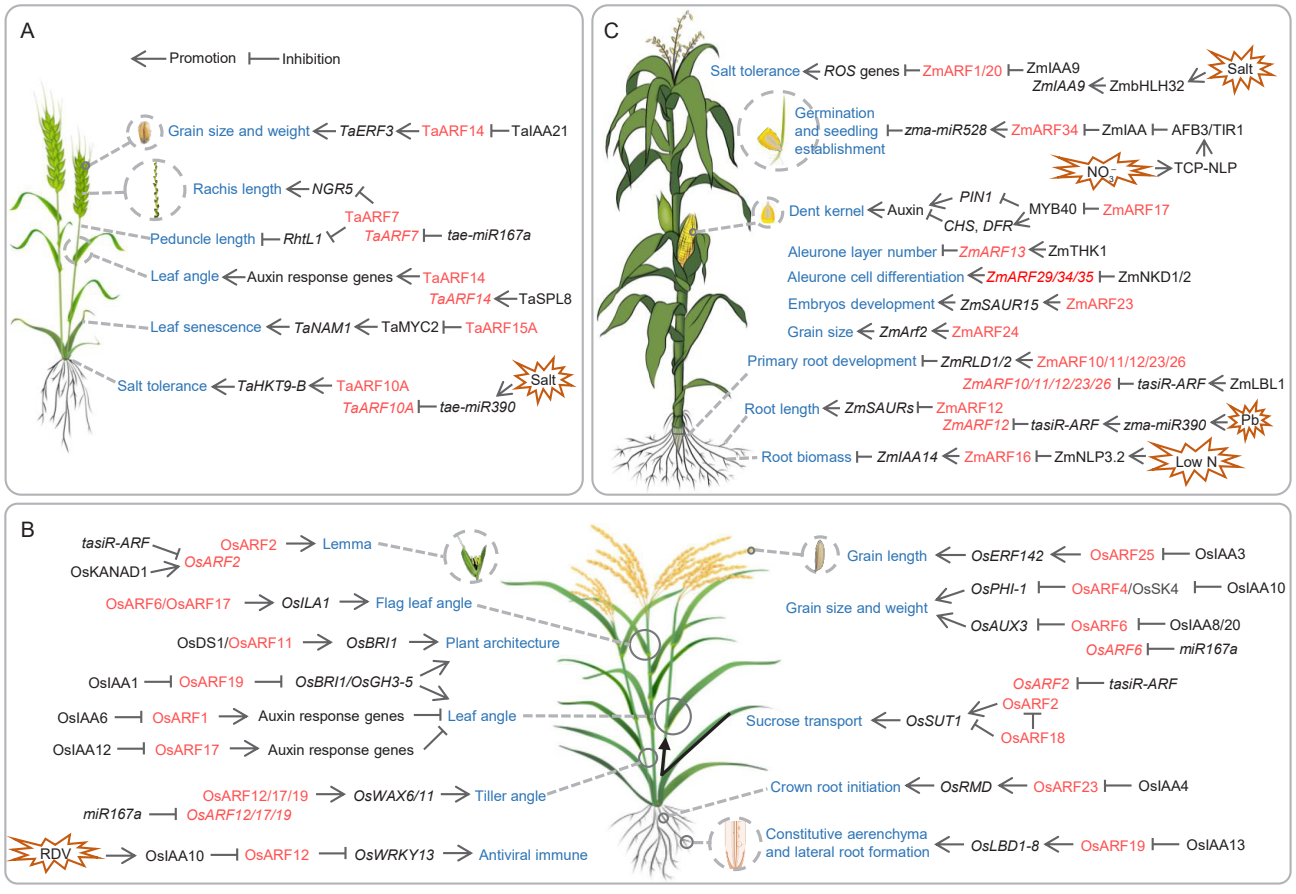


Fig. 3 Auxin response factors (ARF) regulatory models for development and stress response in wheat, rice, and maize. A, TaARFs and their regulated phenotypes are displayed in red and blue. *TaARF7* (*TraesCS2A03G1263300*, *TraesCS2B03G1444700*, and *TraesCS2D03G1217700*) was reported as *TaARF8* (Wang Y *et al.* 2019) and *TaARF12* (Li A *et al.* 2022; Kong *et al.* 2023). *TaARF10A* (*TraesCS3A02G246000*) was reported as *TaARF4* (Du *et al.* 2024). *TaARF14* (*TraesCS5A02G038300*, *TraesCS5B02G039800*, *TraesCS5D02G045700*) was reported as *TaARF6* (Liu *et al.* 2019) and *TaARF25* (Jia *et al.* 2021). B, the OsARFs and their regulated phenotypes are displayed in red and blue. *OsARF2* (*Os01g0670800*) was reported as *OsARF3a* (Si *et al.* 2022). C, the ZmARFs and their regulated phenotypes are displayed in red and blue. *ZmARF10* (*GRMZM2G338259*), *ZmARF11* (*GRMZM2G056120*), *ZmARF12* (*GRMZM2G437460*), *ZmARF23* (*GRMZM2G441325*), and *ZmARF26* (*GRMZM5G874163*) were each reported as *ZmARF2*, *ZmARF3e*, *ZmARF3d*, *ZmARF3b*, and *ZmARF3e* (Gautam *et al.* 2021). *ZmARF16* (*GRMZM2G028980*) was reported as *ZmARF19* (Wang R *et al.* 2024), *ZmARF27* (*GRMZM2G160005*) was reported as *ZmARF34* (Xu *et al.* 2015), *ZmARF35* (*GRMZM2G317900*) as *ZmARF25* (von Behrens *et al.* 2011).

interference (RNAi) of *TaARF7* renders reduced plant height and internode length, but enhanced spike elongation (Li A *et al.* 2022). Subsequent research demonstrates that *TaARF7* regulates peduncle and rachis development trajectories by inhibiting the transcription of downstream genes *REDUCED HEIGHT-LIKE 1* (*TaRhtL1*) and *NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5* (*TaNRG5*). The edited *TaARF7* renders reduced plant height, larger spikes, up to 14.7% more grains per spike, and 11.1% more yield in field trials (Kong *et al.* 2023).

TaARF10, reported as *TaARF4*, is targeted by *tae-miR390*/*TaTAS3* (Du *et al.* 2024). TaARF10 directly binds to the AuxRE in the promoter of *TaHKT9-B* for transcriptional activation of *TaHKT9-B*, subsequently attenuating shoot K^+ accumulation and salt tolerance (Du *et al.* 2024).

TaARF12, reported as *TaARF4*, is relevant to root and stem elongation in wheat (Wang J *et al.* 2019). The ectopic expression of *TaARF12-A* in *Arabidopsis* reduces primary root length and stem height. TaARF12-A represses the expression of *GRETCHEN HAGEN 3* (*GH3*) genes, which in turn upregulates the auxin concentration. The association analysis demonstrates that *TaARF12-B* strongly relates to PH and root depth at the tillering, jointing, and grain-filling stages.

TaARF13, reported as *ARF2* (Liu X *et al.* 2017), is upregulated in aluminum (Al) treatment in a concentration- and time-dependent manner. In this case, auxin serves as a key signaling molecule to regulate the responsive malic acid efflux to Al stress *via* TaARF13 activation in wheat.

TaARF14, reported as *TaARF6* (Liu *et al.* 2019) and *TaARF25* (Jia *et al.* 2021), controls leaf angle, grain size, and weight. The expression of *TaARF14* is activated by the SQUAMOSA PROMOTER BINDING-LIKE (SPL) protein TaSPL8 to regulate lamina joint development *via* the auxin signaling pathway and ultimately alters leaf angle (Liu *et al.* 2019). *TaARF14* mutation significantly reduces grain size and weight in tetraploid wheat by promoting *ETHYLENE RESPONSE FACTOR3* (*TaERF3*) transcription, which is inhibitable by TaIAA21 (Jia *et al.* 2021).

TaARF15 is upregulated by auxin treatment, and the ectopic expression of *TaARF15-A1* in *Arabidopsis* promotes root and leaf growth (Qiao *et al.* 2018). Subsequent research shows that *TaARF15-A1* acts as a negative regulator of senescence in wheat. TaARF15-A1 delays leaf senescence by negatively regulating senescence-promoting processes *via* interacting with TaMYC2 and positively modulating senescence-delaying genes such as the NAC gene *TaNAM-1*. The earlier-maturity-relevant haplotype of *TaARF15-A1* has undergone strong selection through wheat breeding in China (Li H *et al.* 2023).

TaARF17, reported as *ARF8* (Liu H *et al.* 2017) and *ARF16* (Mao *et al.* 2020), is relevant to drought stress response. *TaARF17* is targeted by *miR160a* and shows an upregulated expression pattern under water-deficit stress in tolerant durum wheat (Liu H *et al.* 2017). *TaARF17* is upregulated in NAC transcription *TaSNAC8-6A* transgenic lines, which exhibits enhanced drought tolerance. TaSNAC8-6A directly binds to the promoter of *TaARF17* in the presence of a NAC recognition core sequence (CACG) in the *TaARF17* promoter, demonstrating the participation of *TaARF17* in the TaSNAC8-6A-mediated regulatory networks in drought stress response (Mao *et al.* 2020).

TaARF20 was reported as *TaARF7/19* (Wang *et al.* 2018). Its expressions show a significant correlation to the number of laterals of primary root in diploid, allotetraploid, and natural allohexaploid wheat. *TaARF23-A1* and *TaARF23-A2* are a pair of tandem repeat genes on the *TaARF23A* site. They show high expression in spindle spikes relative to compacted spikes. Association analysis shows that *TaARF23-A1* and *TaARF23-A2* are significantly correlated with spikelet number in a recombinant inbred line derived from the cross of spindle spike-type wheat and compacted spike-type wheat under six field environmental conditions (Tan *et al.* 2024).

Moreover, a reported ARF member ARF5 (TraesCS6D02G100900) interacts with MORE ROOT (TaMOR) to induce the expression of the auxin transporter gene *PIN2* (*PIN-FORMED 2*) in the root base to regulate crown root initiation (Li C *et al.* 2022). It is notable that ARF5, with only the PB1 domain but not DBD and MR, is likely to be a member of the Aux/IAA family. It is referred that *ARF5* is the same as *TaIAA25D* (Qiao *et al.* 2015) since their genes show 100% sequence similarity.

In addition, the expression of anther-specific genes *TaARF8*, *TaARF9*, and *TaARF21* was found to be significantly altered by low temperature in thermosensitive genic male-sterile wheat (Xu *et al.* 2020), and *TaARF9* (XLOC_043700) is downregulated in TaD27-knockdown plants with more tillers (Zhao *et al.* 2020). The *TaARF* family is also evidently related to nitrogen-use efficiency (NUE). Under low nitrogen stress in the field, as few as 7 *TaARFs* were downregulated in spikes of the high-NUE-variety of Kenong 9204 at the jointing stage, and nearly all *TaARFs* were downregulated in the low-NUE-variety of Jing 411, suggesting that low nitrogen stress negatively affects wheat yield by reducing auxin concentration in spikes at the jointing stage, ultimately decreasing the number of grains per spike (Shi *et al.* 2022).

3.2. Functions of ARFs in rice

OsARF1 interacts with *OsIAA6* to suppress auxin signaling and promote cell elongation at the adaxial side of the lamina joint, leading to leaf inclination (Xing *et al.* 2022).

OsARF2, reported as *OsETT2* (Toriba and Hirano 2014) or *OsARF3* (Si *et al.* 2022), is relevant to source–sink carbohydrate partitioning and reproductive organ development (Fig. 3-B). The gene significantly downregulates in the lodicule of the rice *dao* mutant, which features closed spikelets, indehiscent anthers, and parthenocarpic seeds; it also stimulates the expression of *OsSUT1* to regulate sucrose accumulation in photosynthetic leaves and reproductive organs (particularly in lodicules, anthers, and ovaries) (Zhao Z *et al.* 2022). *OsARF2* regulates awn development via interaction with DROOPING LEAF (OsDL), and the awnless phenotype of *japonica* rice may lack *OsARF2* expression in awn primordia (Toriba and Hirano 2014). The expression of *OsARF2* was found to be positively regulated by OsKANADI1's binding to *OsARF2* intron (Si *et al.* 2022), rendering rice lemma morphogenesis.

OsARF4 negatively regulates rice grain size and grain weight. The loss or suppression of *OsARF4* function results in larger grain size and higher grain weight (Hu Z *et al.* 2018; Ma M *et al.* 2023). The gene also negatively controls grain development by interfering with longitudinal expansion and auxin distribution/concentration in glume cells.

In the *osarf6* mutant, the grain length and weight are significantly higher than in the wild type (WT), quite opposite to the *OsARF6*-overexpressing phenotypes (Qiao *et al.* 2021). *OsARF6* is also relevant to leaf angle. The *osarf6-osarf17* double mutant displays reduced secondary cell wall levels of lamina joint sclerenchymatous cells, leading to wider flag leaf angle and lower grain yield under dense planting conditions (Huang *et al.* 2021).

OsARF10 participates in the mechanism underlying H_2-triggered Al tolerance in plants. Under Al stress, the germinating rice seeds produce H_2, which increases *miR160a* transcription, decreases transcription of the target *OsARF10*, and alleviates Al-induced germination inhibition (Xu *et al.* 2017).

OsARF11 is the homolog of *AtARF5/MP*. It is relevant to plant development and immune response. The *osarf11* mutant exhibits typical auxin-deficient phenotypic features, including reductions in stem and root length, flag leaf angle and width, and grain size and weight (Sims *et al.* 2021; Uzair *et al.* 2021), but an increase in tillers (Uzair *et al.* 2021). *OsARF11* interacts with the EMF1-like protein DS1 to co-regulate auxin and brassinosteroid signaling pathways, thereby controlling plant height and leaf angle (Liu *et al.* 2018). In addition, the *osarf11* mutant displays enhanced resistance to rice dwarf virus (Qin *et al.* 2020).

OsARF12 plays a key role in regulating plant and root system architecture (RSA). The inhibited expression of *OsARF12* targeted by *miR167* renders increased tiller angle (Li *et al.* 2020). The expression of *OsARF12* is regulated by GROWTH-REGULATING FACTOR (OsGRF7) *via* binding to the ACRGDA motif in the promoter to control rice plant architecture (Chen *et al.* 2020). The *osarf12* single mutant shows a shorter stem height and aborted apical spikelets (Zhao Z X *et al.* 2022). The *osarf12* mutant shows higher Pi concentration and Pi-intoxicated symptoms (Wang *et al.* 2014), and reduced resistance to rice dwarf virus (Qin *et al.* 2020).

OsARF13 is upregulated in *OsMADS50*-overexpressing plants that produce fewer crown roots (Shao *et al.* 2019). The *OsARF16* is a necessary factor for either Pi starvation response or Fe-deficiency response. In the former case, the *PHOSPHATE STARVATION-INDUCED* genes (*OsPSIs*) are weakly induced in the *osarf16* mutant, exhibiting the loss of Pi-deficiency response (Shen *et al.* 2013), and in the latter case Fe-deficiency response genes are compromised in *osarf16*mutant relative to the WT Nipponbare (Shen *et al.* 2015). The single knockout lines of *osarf16* render short stems and narrow leaves but more tillers (Uzair *et al.* 2021), as well as reduced resistance to rice dwarf virus (Qin *et al.* 2020).

OsARF17 is relevant to the regulation of plant architecture and virus resistance. Either the *osarf17* mutant or the *osarf6-osarf17* double mutant displays wider flag leaf angles (Chen S H *et al.* 2018; Huang *et al.* 2021). *OsARF17* is targeted by *miR167* for repression, rendering reduced stature and tillers, and wider tiller angle by finely adjusting the asymmetric auxin distribution in buds (Li *et al.* 2020). It is also crucial to plant defense against viruses. *OsARF17* protein overexpression strengthens resistance to rice stripe virus in transgenic plants. However, it is noted that some viral proteins also interact with *OsARF17* to impair the *OsARF17*-mediated resistance (Zhang H *et al.* 2020).

OsARF18 is repressible by *OsmiR167* to produce pleiotropic defects that affect rice stature, leaves, and seed development (Huang *et al.* 2016). On the other hand, it represses *OsARF2* and *OsSUT1* expression via binding to AuxRE or SuRE in promoters to regulate source-sink carbohydrate partitioning and reproductive organ development (Zhao Z *et al.* 2022). The *OsARF19* regulates the growth and development of leaves, flowers, and roots in rice. Its overexpression renders shorter height and narrower leaves, as well as dramatically wider leaf angle due to adaxial cell over-division in lamina (Zhang *et al.* 2015). The *osarf19* null mutant or RNA interference lines display enlarged plant architecture and abnormal florets with expanded but degenerated palea, along with additional lemma (Zhang *et al.* 2016). It targets the LATERAL ORGAN BOUNDARY DOMAIN (LBD) gene *OsLBD1-8* to regulate the formation of constitutive aerenchyma and lateral roots (Yamauchi *et al.* 2019).

OsARF23, reported as *OsARF1*, is important to auxin-induced root formation (Li *et al.* 2014). The *osarf23* mutant displays disrupted cell growth, less sensitivity to auxin response, and altered auxin distribution. *OsARF23* and *OsARF24* form heterodimers that directly regulate the expression of *RICE MORPHOLOGY DETERMINANT* (*OsRMD*), thus affecting cell growth by altering auxin distribution gradient at the root tip (Li *et al.* 2014).

OsARF25 has, to some extent, functional redundancy with *OsARF6*, *OsARF12*, and *OsARF17*. Their expression is inhibited by *miR167*, altering plant height, tiller number and angle, stigma size, and flower opening (Li *et al.* 2020; Zhao Z X *et al.* 2022). *OsARF25* stimulates *OsCKX4* expression, which positively mediates crown root development by integrating the interaction of cytokinin to auxin (Gao *et al.* 2014), and promotes *OsERF142* expression to regulate grain length in rice positively (Zhang *et al.* 2018).

3.3. Functions of ARFs in maize

ZmARF1 is relevant to salt tolerance mediated by the ZmbHLH32-ZmIAA9-ZmARF1 module (Fig. 3-C). The gene represses the expression of ROS-scavenging genes. The *ZmIAA9* is induced by ZmbHLH32 and physically interacts with and inhibits *ZmARF1*, which upregulates ROS scavenging genes to enhance salt tolerance (Yan *et al.* 2023).

ZmARF2 is targeted and downregulated by *zma-miR160b* in kernels at various stages after pollination, suggesting that *ZmARF2* is relevant to kernel development (Ding *et al.* 2013).

ZmARF4, reported as *ZmARF8* and *ZmARF5*, is the ortholog of *AtARF5/MP* and controls root system development

and nutrient uptake. In the mutant of functionless Aux/IAA protein ZmRUM1 (ROOTLESS WITH UNDETECTABLE MERISTEMS 1), the *ZmARF4* expression is downregulated (Zhang *et al.* 2014). There is evidence that Aux/IAA proteins ZmLLG1 (Sun *et al.* 2023) and ZmIAA5 (Yang *et al.* 2022) interact with *ZmARF4*, each to regulate main root length and lateral root number. The *ZmARF4* transcription is inducible in response to nitrate (Ravazzolo *et al.* 2021) and its overexpression in *Arabidopsis* confers tolerance to Pi deficiency, salinity and osmotic stress, and better root phenotype than WT (Li J *et al.* 2022).

ZmARF7 interacts with ZmIAA29 to shorten time to flowering by regulating the key genes for signal transduction and flowering control (Ma C *et al.* 2023). The *ZmARF10*, reported as *ZmARF2*, is the potential target of *trans*-acting short interfering RNA (tasiRNA). The suppressed *tasiR-ARF* production leads to the upregulation of *ZmARF10* in a leafbladeless1-ragged seedling1 (*lbl1-rgd1*) mutant, significantly altering the root growth, anatomical patterning, number of lateral roots (LRs), monocot-specific crown roots (CRs), and seminal roots (SRs) (Gautam *et al.* 2021).

ZmARF11, reported as *ZmARF3c*, is also targeted by tasiRNA. Its expression is regulated by tasiRNA either in the *lbl1* mutant with radial and abaxialized leaves (Dotto *et al.* 2014) or in the *lbl1-rgd1* mutant with defective roots (Gautam *et al.* 2021).

ZmARF12, reported as *ZmARF3d*, is relevant to leaf and root development *via* the LBL1–*tasiR*-ARF3 module (Dotto *et al.* 2014; Gautam *et al.* 2021). The *ZMARF12* mutant exhibits a larger seed size and a higher grain weight, and transient knockdown of *ZmARF12* facilitates cell expansion and division, suggesting that the gene represses cell division and potentially controls seed size (Wang *et al.* 2022). Moreover, *ZmARF12* also regulated Pb tolerance *via* the *zma-miR390*–tasiARF–ZmARF12–*SAURs* pathway, which elevated indole acetic acid levels and thus reactive oxygen species-scavenging capacity in maize roots (Li *et al.* 2024).

ZmARF13 is relevant to maize aleurone production. Its transcription is downregulated in the *thick aleurone1* (*thk1*) mutant, featured with multiple cell layers of fully differentiated aleurone cells, and is activated by ZmTHK1 to regulate endosperm and aleurone development (Wu and Becraft 2021).

ZmARF16 regulates root biomass in response to nitrogen limitation *via* the ZmNLP3.2-ZmARF19-ZmIAA14 module in maize (Wang R *et al.* 2024).

ZmARF17 is highly expressed in the pericarp and controls the dent and flint kernel phenotypes. It inhibits ZmMYB40, which restrains *ZmPIN1* expression and flavonoid biosynthesis genes such as *ZmCHS* and *ZmDFR* to increase IAA content of seed pericarp and to enhance cell division and expansion, thus creating a dent kernel. Mutation of *ZmARF17* in a dent genetic background yields a flint-like kernel phenotype (Wang H *et al.* 2024).

ZmARF20 is relevant to abiotic stress tolerance. Its expression is upregulated by nitrate in roots (Ravazzolo *et al.* 2021), and the repression by ZmIAA9 triggers the upregulation of ROS scavenging genes for enhancing salt tolerance (Yan *et al.* 2023). Being the downstream responsive gene of the ZmCCT-ZmIAA8 module, *ZmARF20* is upregulated by ZmIAA8 under drought treatment. In comparison, this upregulation response is impaired in ZmCCT-deficient strains (Zhang *et al.* 2024).

ZmARF23, reported as *ZmARF3b*, is the target of tasiRNA for regulating RSA (Gautam *et al.* 2021). It shows that the intragenic variations of *ZmARF23* influence embryonic callus induction efficiency among various maize lines, and the gene binds to the promoter of the *SMALL AUXIN-UP RNA* gene *ZmSAUR15*, a known causal gene for embryonic callus induction, to regulate the expression level of *ZmSAUR15* positively (Liang *et al.* 2023).

ZmARF24 controls maize kernel size *via* the ARF24-ZmArf2 module. The ADP-ribosylation factor ZmArf2 positively regulates kernel size and ZmARF24 directly binds to ZmArf2 promoter and negatively regulates *ZmArf2* expression to influence kernel size (Gao *et al.* 2023). The *ZmARF25*-coded protein interacts with ZmIAA29 to regulate flowering time (Ma C *et al.* 2023). The *ZmARF26*, reported as *ZmARF3e*, is relevant to leaf and root development via the LBL1-tasiR-ARF3 module (Dotto *et al.* 2014; Gautam *et al.* 2021), and it exhibits a certain regularity in the auxin signaling pathway influenced by stimulated kernel development (Du *et al.* 2023).

ZmARF27, reported as *ZmARF7* and *ZmARF34*, is orthologous to *AtARF19* and mainly regulates root development. Loss of *ZmARF27* leads to short primary roots and scarce root hairs (Dash *et al.* 2023). The interaction of *ZmARF27* and Aux/IAA (such as ZmRUM1 or ZmLLG1) is required for initiating development of seminal roots and lateral roots (von Behrens *et al.* 2011; Zhang *et al.* 2014; Sun *et al.* 2023). *ZmARF27* binds to the promoters of two paralogous *LATERAL ORGAN BOUNDARIES DOMAIN* (*LBD*) genes, the *ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS* (*ZmRTCS*), and the *RTCS-LIKE* (*ZmRTCL*) and activates their expressions to regulate shoot-borne root formation (Xu *et al.* 2015). In addition, a ZmAFB2/3-ZmIAA-ZmARF27 module has been identified in the development of ear and tassel inflorescences (Ramos *et al.* 2020).

ZmARF28 is prominent in *Truffula* (*Trf*) mutant phenotypes, featured with reduced plant height, more leaves, and male tassel feminization. The gene is not differentially expressed in *Trf* and normal siblings; a single SNP in exon 8, which causes a Ser-to-Asn alternation in DBD, is *Trf*-specific in reference to other maize inbred strains. These suggest that the mutated phenotype is caused by altered protein activity or post-translational regulation of *ZmARF28* (Prigge *et al.* 2023).

ZmARF29, reported as *ZmARF37*, is a co-ortholog of *AtARF5/MP*. Its expression is downregulated in *rum1* mutant (Zhang *et al.* 2014) and its transcription is upregulated in the double mutants of *naked endosperm 1* and *naked endosperm 2* (*nkd1*,*2*), which exhibits multiple aleurone cell layers with disrupted aleurone cell differentiation. The gene contains a NKD1 *cis*-binding motif in promoter (Gontarek *et al.* 2016), and it is repressible by ZmNKD in regulating endosperm and aleurone development (Wu and Becraft 2021). The *ZmARF30* is downregulated by *zma-miR167a* in developing kernels after pollination (Ding *et al.* 2013).

The *ZmARF34* transcription is inhibitable by ZmNKD, rendering restricted auxin response in aleurone development (Wu and Becraft 2021). The gene also participates in auxin-mediated transcriptional regulation over *zmaMIR528a*. The mature *miR528* sharply accumulates throughout maize embryonic development, mildly increases seed imbibition, and declines at post-germinative stages (Luján-Soto *et al.* 2021). In this process, *ZmARF34* recognizes and binds to the AuxRE in the *zma-MIR528a* promoter to enhance its expression, followed by the increase of *miR528* to downregulate its mRNA targets (Lujan-Soto *et al.* 2021).

ZmARF35, reported as *ZmARF25*, is relevant to root and aleurone development. It interacts with ZmRUM1 or ZmLLG1 to regulate the initiation of embryonic seminal root and post-embryonic lateral root (von Behrens *et al.* 2011; Zhang *et al.* 2014; Sun *et al.* 2023). The ZmNKD binds to ZmNKD1 or ZmNKD2 motifs in the *ZmARF35* promoter (Gontarek *et al.* 2016), and this binding represses *ZmARF35*, regulating endosperm and aleurone development (Wu and Becraft 2021).

4. Common regulatory models

This part provides a summary of the common regulatory models based on recent advances in ARF research. The results were used to revise the nomenclatures of the ARF family in wheat, rice, and maize.

4.1. miRNA-ARF models

MicroRNAs are characterized by high conservatism and temporal and tissue specificity, and they participate in crucial processes in plant growth and development by regulating the transcription of targeted genes. The latest studies show that all *miRNA167* targets fall into Class A ARFs, including *AtARF6* and *8*, *TaARF7*, *OsARF6*, *12*, *17*, and *25*, and *ZmARF30*; all *miRNA390* targets fall into Class B ARFs, including *AtARF2*, *3*, and *4*, *TaARF10A*, *OsARF2*, and *ZmARF10*, *11*, *12*, *23*, and *26*; and all *miRNA160* targets fall into Class C ARFs, including *AtARF10*, *16*, and *17*, *TaARF1* and *17*, *OsARF18*, and *ZmARF2* (Table 1). In contrast, unlike *miRNA167* and *miRNA160*, *miRNA390* does not directly target *ARF* genes but generates various fragments by cleaving the target gene, *TRANS-ACTING SHORT INTERFERING RNA3* (*TAS3*), to form double-stranded RNA under the catalysis of RNA enzymes. These TAS-induced RNAs (tasiRNAs) further inhibit the expression of class B ARFs.

4.2. IAA-ARF-*LBD* model in root regulation

The root development in *Arabidopsis* and cereal crops differs in both general architecture and specific anatomical features. The *Arabidopsis* root system mainly comprises the embryonic roots from the primary root with lateral roots. In contrast, the root systems of cereal crops are dominated by post-embryonic shoot-borne roots like seminal, crown, and lateral roots (Hochholdinger *et al.* 2004). In terms of root development regulation, it is known that several Aux/IAAs-inhibitable ARFs promote the expression of downstream *LBD* genes such as the OsIAA13-OsARF19-*OsLBD1-8* (Yamauchi *et al.* 2019) and OsIAA4-OsARF23-*OsCRL1* (Kitomi *et al.* 2011) models in rice and the RUM1-ZmARF27-*RTCS* model (Xu *et al.* 2015) in maize.

Table 1 Summary of micro RNAs that regulate *AtARFs*, *TaARFs*, *OsARFs*, and *ZmARFs*

Micro RNA	Target *ARFs*	Class	Reference
miR167	*AtARF6*, *8*	A	Gutierrez *et al.* (2009)
	TaARF7	A	Wang Y *et al.* (2019)
	OsARF6, *12*, *17*, *25*	A	Wang *et al.* (2014); Li *et al.* (2020); Qiao *et al.* (2021)
	ZmARF30	A	Ding *et al.* (2013)
miR390-tasiR	*AtARF2*, *3*, *4*	B	Williams *et al.* (2005); Marin *et al.* (2010)
	TaARF10A	B	Du *et al.* (2024)
	OsARF2	B	Si *et al.* (2022)
	ZmARF10, *11*, *12*, *23*, *26*	B	Gautam *et al.* (2021); Dotto *et al.* (2014); Li *et al.* (2024)
miR160	*AtARF10*, *16*, *17*	C	Wang *et al.* (2005)
	TaARF1, *17*	C	Ma *et al.* (2015); Liu H *et al.* (2017)
	OsARF18	C	Huang *et al.* (2016)
	ZmARF2	C	Ding *et al.* (2013)

4.3. IAA-ARF-Auxin response gene model in the regulation of leaf angle

Leaf angle is significant for light interception and plant density, which makes it critical for crop productivity (Sinclair and Sheehy 1999). In wheat and rice, the leaf angles are reportedly regulated by the IAA-ARF-mediated auxin response genes. For example, *TaARF14* stimulates auxin-responsive families *Aux/IAA*, *SAUR*, and *GH3* to widen leaf angles in wheat (Liu *et al.* 2019), while the *OsIAA6-OsARF1* model promotes (Xing *et al.* 2022) and the *OsIAA12-OsARF17* model inhibits (Chen S H *et al.* 2018) downstream auxin-responsive genes to regulate leaf angles in rice.

4.4. IAA-ARF-*ERF* in the regulation of grain size

In cereal plants, the grain size plays a large role in determining grain weight and overall yield. It is known that the IAA-ARF-ERF model regulates the grain size. *TaARF14* is inhibited by *TaIAA21*, promotes *TaERF3* transcription to increase grain length, width, and weight (Jia *et al.* 2021). Studies have shown that *OsIAA3* represses the activity of *OsARF25*, and the latter facilitates the expression of *OsERF142* (also known as *REDUCED LEAF ANGLE 1*/*SMALL ORGAN SIZE 1*, *OsRLA1*/*SMOS1*) to positively regulate grain length in rice (Zhang *et al.* 2018).

5. Conclusion and prospect

This review summarizes the domain characteristics and modifies the classification of the ARF gene family in wheat, rice, and maize. A new nomenclature is proposed for *ARF* genes based on sequence alignment. It also summarizes the functions of *ARFs* in terms of regulations to phenotypic features, growth, development, and stress response, along with three common regulatory models.

Notably, there is a gap in the understanding of the ARFs in the three cereal crops. With morphological and histological

differences in monocots and dicots, the knowledge of *Arabidopsis* may not be fully relevant to cereal crops. For crops like wheat, rice, and maize, future studies should delve into the regulation mechanisms of ARFs, including miRNA- and tasiRNA-mediated *ARF* transcription and/or post-transcription, the ARF-targeted downstream genes, and the crosstalk with other hormone signaling pathways.

First, the functional redundancy and subtly varied phenotypic features present main challenges in examining ARF family members. One potential way is to use multi-order mutants to cope with the bottle-neck problem with the anticipation to shed light on this field. For highly redundant ARFs, the multi-gene CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) generates knockout lines and higher-order mutants containing more accurate phenotypic information than the overexpression and RNAi lines. Therefore, genome-edited mutants are very promising for ARF functional studies in cereal crops. The fluorescent auxin biosensors developed in rice have improved the characterization approaches for auxin genes (Yang *et al.* 2017), and the orthogonal convex-concave auxin-TIR1 pair (Torii *et al.* 2018) and synthetic auxin yeast systems (Pierre-Jerome *et al.* 2016) allow for studying the ARF family regardless of ARFs' functional redundancy. Meanwhile, the single-cell sequencing technology extracts genetic information from a single cell and is useful for revealing ARF's role in regulating plant cell development; a series of biochemical inhibitors is useful for testing auxin biosynthesis, transport, and signal transduction (Ma *et al.* 2018).

Second, ARFs are applicable in breeding based on our understanding of their regulatory mechanisms for agronomic phenotypes, immunity, and stress tolerance for higher yields and better adaptability. For example, RSA is an important phenotypic trait of crops for adaptation to diverse soil environments. Genetic improvement of crop root structure proves a feasible strategy for increasing yields (de Dorlodot *et al.* 2007), which is also regarded as a key breakthrough point in the "Second Green Revolution" (den Herder *et al.* 2010). Underwater-deficient condition *OsARF23* renders more developed RSA by controlling crown root growth direction for absorbing moisture in deep soil, thereby enhancing drought resistance and increasing rice yield (Uga *et al.* 2013). In comparison, in nutrient-deficient soil, a prosperous shallow RSA is favorable for the acquisition of soil elements to lessen demand for fertilizers (Lynch and Brown 2001). Leaf angle is also important in cereal crop architecture. By appropriately reducing the leaf angle through the regulatory effect of *ARF* genes like *TaARF14*, *OsARF1*, *OsARF17*, and/or *OsARF19* erect leaves with a higher leaf area index and increased photosynthetic efficiency can be obtained (Sakamoto *et al.* 2006; Tian *et al.* 2019), beneficial for dense wheat and rice planting for higher yields. Additionally, the manipulation of ARFs directly regulating grain development would significantly increase yield in staple crops.

The study of one crop may provide useful information to other crops. This is specifically true for wheat in reference to rice and maize. Wheat is a hetero-hexaploid with a large genome, and its genome draft sequencing and post-omics research are used to lag behind those of diploid rice and maize. The common dosage compensation effect in three sub-genomic copies of wheat gene affects plant traits (He *et al.* 2022), posing a huge challenge to map-based cloning and affecting the expected phenotypes in over-expressed or knocked-out strains. As cereal plants exhibit parallel evolution in post-domestication adaptation (Woodhouse and Hufford 2019), genes with known functions in rice or maize provide guidance to the functional research of their homologs in wheat. For instance, rice gene *GRAIN WIDTH2* (*OsGW2*) plays a key role in regulating grain development (Song *et al.* 2007). Its homologous gene in wheat, *TaGW2*, proves to have increased grain size and weight along with abundant allelic variation in wheat germplasm (Su *et al.* 2011; Qin *et al.* 2014). Similar examples include wheat spikelet development genes *WFZP* and *WAPO1* (Dobrovolskaya *et al.* 2015; Kuzay *et al.* 2022), each homologous to the rice genes *FRIZY PANICLE* (*OsFZP*) and *ABERRANT PANICLE ORGANIZATION 1* (*OsAPO1*) (Komatsu *et al.* 2003; Ikeda *et al.* 2007).

The ARF family extensively regulates agronomic traits and tolerance to abiotic and biotic stresses on crops, making it an ideal selection target in breeding and cereal improvement. At present, a plurality of publications on ARF functions in rice and maize are available, including those of plant architecture, RSA, grain development, and stress resistance (Fig. 4). Several studies demonstrate similar functions among certain wheat ARFs, e.g., the orthologous *TaARF14* and *OsARF25*, both of which regulate grain size via the IAA-ARF-ERF model (Fig. 3) (Zhang *et al.* 2018; Jia *et al.* 2021). In improving wheat plant architecture, the *TaARF* genes are potentially promising, as evidenced by their homolog to rice *ARF* genes controlling tiller and/or leaf angle. The candidates include *TaARF6*-*OsARF11*, *TaARF7*-*OsARF12*, *TaARF9*-*OsARF1*, *TaARF16*-*OsARF6*, *TaARF21*-*OsARF19*, and *TaARF22*-*OsARF17*. Among them, *TaARF6* and *TaARF9* have shown possible correlation to wheat plant tillering (Zhao *et al.* 2020; Li *et al.* 2021). Similarly, the *TaARF* genes homologous to *OsARF19*, *23* and *ZmARF10*, *11*, *12*, *23*, *26*, *27* are potentially relevant to regulating RSA. Also, both *OsARF*s and *ZmARF*s are known molecular mechanisms of grain development and response to pathogen infection and salt stress, suggesting an equivalent wheat ARF function and its usefulness in molecular breeding to develop varieties with optimal plant architecture, high yield, and broad adaptability.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

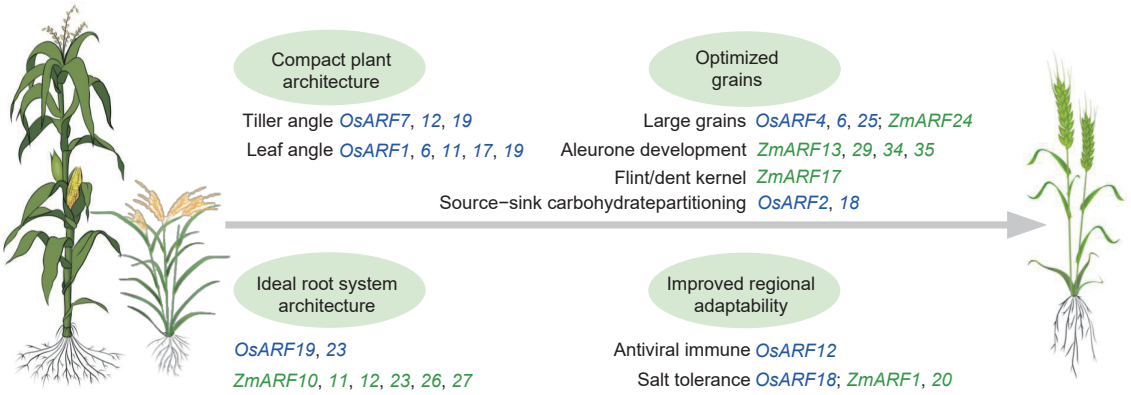


Fig. 4 ***ARF*** **genes with known functions in rice and maize with implications for wheat study.**

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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