Auxin Response Factors

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Auxin response factors (ARFs) are an important family of transcription factors in the auxin signaling pathway that are involved in the exertion of auxin in plants and play a key role in regulating plant growth and development.

IAA auxin plant hormone transcription factor

1. Introduction

Auxin is the first discovered plant hormone, one that regulates plant growth and development extensively. The function of auxin depends on a signal transduction pathway involving a variety of transcription factors, one of the most important of which is auxin response factor (ARF). Since the ARF was discovered in Arabidopsis in 1997, ARF has been found in Arabidopsis (*Arabidopsis thaliana*), rice (*Oryza sativa*), maize (*Zea mays* L.), tomato (*Solanum lycopersicum*), grapes (*Vitis vinifera*), and other plants. The numbers of ARF genes that have been reported in various species are summarized in **Table 1**. ARFs were identified as large gene families and showed high homology in the same species. As a key factor in plant auxin signaling, ARFs can specifically bind to the auxin response element (AuxRE) in the promoter region of the auxin response genes and activate or repress the expression of auxin response gene, which in turn triggers many auxin-mediated physiological effects.

Table 1. Summary of the number of ARF genes in species that have been reported.

Species	Gene No.
Agave americana	32
Ananas comosus	20
Arabidopsis thaliana	23
Aquilegia caerulea	12
Banana	47
Beta vulgaris	16
Boehmeria nivea	14
Brachypodium distachyon	24
Brassica rapa	31

Species	Gene No.
Capsicum annuum	22
Carica papaya	15
Cicer arietinum	28
Citrus clementina	17
Citrus sinensis	22
Cucumis melo	17
Cucumis sativus	15
Dendrobium officinale	14
Dimocarpus longan	17
Eucalyptus grandis	17
Fagopyrum tataricum	20
Fragaria vesca	17
Glycine max	55
Gossypium raimondii	35
Hordeum vulgare	20
Jatropha curcas	17
Litchi chinensis	39
Malus domestica	33
Manihot esculenta	18
Marchantia polymorpha	3
Medicago truncatula	24
Mimulus guttatus	19
Mulberry	17
Oryza sativa	25
Osmanthus fragrans	50

Species	Gene No.
Phaseolus vulgaris	25
Phyllostachys edulis	24
Physcomitrella patens	12
Populus trichocarpa	39
Prunus mume	17
Prunus persica	17
Prunus sibirica	14
Rafflesia cantleyi	9
Ricinus communis	17
Selaginella moellendorffii	7
Setaria italica	23
Solanum lycopersicum	22
Solanum tuberosum	20
Sorghum bicolor	25
Tamarix chinensis	12
Theobroma cacao	19
Triticum aestivum	27
Vitis vinifera	19
Zea mays	36
Ziziphus jujuba	16

ARFs are structurally similar, with most members containing three regions: DBD (DNA-binding domain), MR (middle region), and PB1 (Phox and Bem 1). As shown in **Figure 1**, DBD is a DNA-binding domain directly involved in binding to AuxRE elements, while the MR region is responsible for activation or repression of target genes. It is believed that the amino acid composition and sequence length of MR region determine whether activation or inhibition. If this region is rich in proline, serine, and threonine it is able to produce inhibition, while activator-class ARFs often have glutamine-rich and leucine-rich MR regions. The PB1 domain can bind to Aux/IAA proteins to form heterodimers ^{[1][2]}. Some reports show that Aux/IAA and ARFs can form not only dimers but also larger complexes (oligomers), noting that oligomerization of Aux/IAA proteins may be essential for the inhibition of ARF proteins and

only sufficient amounts of Aux/IAA proteins can exert the inhibitory effect of ARF proteins. The PB1 domain contributes to the oligomerization of ARFs and is important for Aux/IAA-ARF-mediated gene regulation ^{[3][4]}. The mode of action of ARF in auxin signaling is shown in **Figure 1**: When the cellular auxin concentration is low, Aux/IAA, encoded by the auxin early response gene family, binds to ARF and inhibits the activity of ARFs. When the auxin concentration is increased to a certain level, ubiquitinated Aux/IAA proteins are rapidly hydrolyzed. Aux/IAA protein's inhibition of ARF transcription factors is relieved, and ARFs then promote or repress the expression of downstream genes.



Figure 1. Model of ARF involvement in auxin response. The process of auxin signaling is coordinated by the auxin receptor TIR1/AFB, as well as the signal response factors AUX/IAA and ARF, which together mediate the auxin signaling response. Auxin acts as a "molecular glue" and facilitates the interaction between SCF-TIR1/AFB and Aux/IAA proteins. At low concentrations of auxin, the AUX/IAA repressor binds to the ARF transcription factor and forms a dimer that recruits the co-repressor TPL (TOPLESS) to inhibit the ARF activity and the expression of auxin responsive genes. When the concentration of auxin is increased, Aux/IAA binds to the SCF TIR1/AFB complex and is ubiquitinated and then degraded by 26S protease, and then ARF transcription factors are released to activate the transcription of downstream genes. DBD, DNA-binding domain; MR, middle region; PB1, Phox and Bem 1.

ARF is commonly expressed in all periods of plant growth and development and in different parts of the plant, which also determines its comprehensive influence on plant life activities. In addition, Estrada-Johnson et al. ^[5] found the gene family of strawberry (*Fragaria ananassa*) auxin response factors (FaARFs) were differentially expressed in the receptacle at four developmental stages by RNAseq. A large number of studies have shown that ARF is involved in the regulation of a variety of plant life activities, including leaf, flower, root development, and fruit ripening, senescence, and shedding. ARF is also involved in stress response and anthocyanin metabolism in plants. In addition, ARFs are also involved in plant hormone crosstalk, and the relevant research results are valuable for us to fully understand the regulatory effects of plant hormones. In recent years, studies on the regulation of plant life through hormone signaling pathways have been carried out, and increasingly more genome-

wide identification and expression analyses of ARF gene families in plants have been reported, as shown in **Table 1**, which are of great significance for a more comprehensive understanding of the functions of ARF.

2. ARF Is Involved in Regulating Leaf Development

Most plants can perform photosynthesis by themselves, absorb carbon dioxide and release oxygen at the same time, and synthesize organic substances. This process is the prerequisite for all organisms on the earth to obtain energy. Leaves are the most important place for photosynthesis of plants. Important indicators such as the shape, size, and chlorophyll content of plant leaves usually determine whether photosynthesis can proceed normally and play a key role in the efficiency of photosynthesis [6]. In addition, in the leaves of plants, there are usually many other physiological activities, such as respiration. Generally speaking, there are stomata on the back of the leaves to support high-intensity respiration. Plants mainly maintain their own metabolic balance through these two activities on the leaves to maintain vitality. In addition, the transpiration also requires the participation of leaves.

At present, there have been a large number of reports showing the plant auxin plays a critical role in the life activity of leaves. A moderate increase in the concentration of auxin will stimulate the growth of leaves, while exceeding the optimal concentration will have an inhibitory effect. Auxin response factor (ARF), as a key regulator in the process of auxin signal transduction, directly participates in the regulation process of auxin on plant leaves in many links [7]8]. Arabidopsis thaliana is one of the first species to be used to study the regulation of ARF. In Arabidopsis, AtARF is already a well-studied member of the ARF family, and its regulatory role in leaves has been widely reported. AtARF2, AtARF3, AtARF4, and MONOPTEROS (MP)/ARF5 are involved in the regulation of auxinresponsive gene expression and leaf development. MP can promote the expression of WUSCHEL-RELATED HOMEOBOX1 (WOX1) and PRESSED FLOWER (PRS) directly, promoting leaf flattening. However, the expression of WOX1 and PRS can be repressed by several other members of the ARF family, AtARF2/3/4, as shown in **Figure 2**. These ARFs are all able to bind directly to the promoters of WOX1 and PRS ^[6]. Schuetz et al. ^[7] reported that ARF7 and ARF3 act synergistically with ARF5 in leaf formation, indicating a synergistic interaction, and these gene combinations work in parallel to maintain meristem organization and induce leaf formation. In addition, some studies have indicated that auxin induces leaf expansion by activating NPH4/ARF7 and ARF19 [8] (Figure 2). In tomato, Wu et al. ^[9] found that tomato leaf development was co-regulated by several members of the ARF family, including SIARF6A/8A/8B/24. In addition, SIARF6A/24 can influence the process of leaflet initiation by binding to the promoter of PIN-FORMED1 (SIPIN1), which affects the local accumulation of auxin. There are also reports that the chlorophyll content in leaves and fruit is significantly increased in tomato mutant lines of overexpressing SIARF6A. While downregulation of SIARF6A reduces the chlorophyll content ^[10]. ARF also plays a significant role in the leaves of some other species. In rice, OsARF19 controls rice leaf angles by binding to the promoters of the auxin early response gene OsGH3-5 and brassinosteroid (BR) response gene OsBRI1^[11].



Figure 2. A model of ARFs involved in leaf development and senescence in *Arabidopsis thaliana*. ARF2/3/4/5 regulates leaf flattening by targeting the promoters of WUSCHEL-RELATED HOMEOBOX1 (WOX1) and PRESSED FLOWER (PRS). ARF3/5/7 synergistically regulate the leaf formation process. ARF 7 and 19 affect leaf expansion. ARF1 and 2 promote leaf senescence.

Leaf senescence is a necessary process of plant metabolism, accompanied by physiological changes such as the decrease of ribonucleic acid content, the destruction of chloroplasts, and the decrease of photosynthesis capacity. ARF also plays a regulatory role in the process. The *AtARF1* and *AtARF2* genes in Arabidopsis are involved in regulating leaf senescence, which is independent of the ethylene and cytokinin pathways ^{[12][13]}. In tomato, overexpression of *SlARF2* accelerates leaf senescence ^[14]. In litchi, Zhang et al. ^[15] concluded that LcARF2 may be related to the senescence of litchi leaves.

3. ARF Is Involved in Regulating Root Development

Roots are the nutritional organs of plants, usually located below the ground surface, and are responsible for absorbing water and dissolving inorganic salts from the soil, as well as supporting, reproducing, and storing and synthesizing organic matter. Wang et al. ^[16] reported that microRNA160-targeted AtARF10/AtARF16 plays a crucial role in root cap formation. In rice, OsARF1 is also able to regulate crown roots ^[17]. Another ARF of rice species is OsARF12, which plays an active role in promoting root elongation ^[18].

The formation of lateral roots plays a key role in plant development, as well as the ability of plants to obtain nutrients depends on the degree of root branching. Numerous studies have suggested that auxin is a common signal for the formation of lateral roots. In Arabidopsis, AtARF5 is essential for lateral root formation ^[19]. In the root

tissue of seedlings, AtARF7 and AtARF19 are transcriptional activators of early auxin response genes and control the expression of most plant auxin response genes. They regulate lateral root formation through direct activation of LBD/ASLs, as well as AtARF7 and AtARF19 double mutations caused impaired hypocotyl and root development ^[20]. In tomato, SIARF2 regulates the formation of lateral roots, and high expression of SIARF2 promotes lateral root growth ^[14].

In addition to lateral roots, ARF genes also play an important role in adventitious root development. *AtARF6* and *AtARF8* genes regulate adventitious root formation with the involvement of micro160 and micro167, and AtARF6 has been shown to positively control the development of adventitious roots. It has also been shown that AtARF17 is involved in this process and negatively regulates adventitious roots in Arabidopsis ^[21]. In rice, crown rootless1 (*OsCRL1*) encodes a plant-specific protein, and OsARF1 binds directly to AuxRE in the OsCRL1 promoter, which plays an important role in adventitious root initiation ^[22]. In addition, Yang et al. ^[23] reported PeARFs may play diverse regulatory roles in adventitious root development of Populus.

4. ARF Is Involved in the Regulation of Floral Structure and Sexual Reproduction

A plant's flowers are essential for its own reproduction and are the organs of sexual reproduction for the vegetation. Over the course of evolution, the flower of a plant has developed into a more stable structure, generally consisting of a stalk, calyx, receptacle, corolla, pistil, and stamens. The stamens and pistils are composed of different parts, with the stamens consisting of the anthers and filaments and the pistils consisting of the style, stigma, and ovary. Flower development, maintenance, abscission process, and the normal formation of pistil and stamen are all crucial for plant growth and fruit formation. It has been extensively reported that auxin response factors play a key regulatory role in these processes.

Research on the regulatory role of ARF in plant flowers has been carried out mostly in Arabidopsis. Ellis et al. ^[12] reported that AtARF1 and AtARF2 in Arabidopsis affect flower initiation, stamen development, and flower senescence and abscission. arf2 mutant plants show delays in flowering and abscission of floral organs. arf1 mutations enhanced many arf2 phenotypes, indicating that ARF1 acts in a partially redundant manner with ARF2. AtARF3 regulates floral meristem determinacy by repressing cytokinin biosynthesis and signaling, and loss of AtARF3 leads to the development of pistil appearance defects ^[24]. There are many reports about the crucial roles of MONOPTEROS (MP)/ARF5 in the regulation of flower formation and other activities of shoot apical meristem. For example, Yamaguchi et al. ^[25] uncovered a molecular framework for flower initiation that includes AtARF5 and LEAFY, a master regulator of flower development, which reveals a mechanistic link between flower primordium initiation and subsequent steps in flower morphogenesis. AtARF6 and AtARF8 are thought to control stamen and pistil maturation, respectively, and the loss of a single gene in either ARF6 or ARF8 causes delayed stamen filament elongation and delayed anther dehiscence, resulting in reduced self-pollination.

5. ARF Is Involved in Regulating Fruit Development and Ripening

Research on fruit development and ripening has always been a hot topic. Human demand for high-quality fruits drives researchers to conduct in-depth research on the formation, development, and quality improvement of fruits, and its economic value is also huge. Plant fruits generally include two parts: pericarp and seed. Pericarp can be divided into exocarp, mesocarp, and endocarp, and seeds play a key role in the process of propagation and reproduction. The process of fruit development depends on cell division and cell expansion. After the completion of the pollination and ovary fertilization process, the carpel tissue around the ovary begins to expand rapidly ^[26]. The research on fruit includes the entire process from the occurrence of flowers to the later fruit preservation. For a long time, it has been believed that plant hormones play an important regulatory role in fruit growth and development, especially auxin, ethylene, and abscisic acid.

Some progress has been made in recent years regarding the role of ARF in the regulation of tomato fruit development and ripening. Figure 3 shows a model of ARFs regulating tomato fruit development and ripening. SIARF2 is an important part of tomato maturation regulatory network. Overexpression of SIARF2 enhances the expression of ethylene biosynthesis genes, increasing ethylene production and accelerating fruit ripening. However, downregulation or silencing of SIARF2 will lead to maturation defects and even inhibit maturity [27][28]. SIARF4 affects many physiological indicators of tomato fruits. For example, GOLDEN2-LIKE (GLK) transcription factors are required for the regulation of chloroplast and chlorophyll levels ^[29], and SIARF4 may control the accumulation of chlorophyll and the structure of the fruit cell wall through transcriptional inhibition of GLK1 expression in tomato fruits, as shown in Figure 3. Chlorophyll content is a key feature of immature fruit that affects the nutrient composition and flavor of mature fruit. Inhibition of SIARF4 expression can make tomato fruits show a dark green immature phenotype, and the resulting fruit is harder than the wild type. In addition, SIARF4 is also a major participant in mediating the control of auxin on sugar metabolism ^[30]. SIARF10 plays a similar role to SIARF4 and regulates chlorophyll and sugar accumulation during tomato fruit development through transcriptional activation of SIGLK1 [31]. SIARF10 is also involved in seed development and the regulation of fruit size and shape ^[32]. Another auxin response factor that has an effect on the chlorophyll content of tomato fruits is SIARF6A. The chlorophyll content in fruit was significantly increased in tomato mutant with overexpression of SIARF6A. In addition, ethylene production was inhibited, and fruit ripening rate decreased ^[10]. When pollination occurs, SIARF5 plays a role in fruit germination [33]. SIARF7 negatively regulates both fruit set and fruit development, slowing the plant auxin response during fruit growth [34][35]. In addition, SIARF8 and SIARF9 in tomato play a role in regulating fruit development and growth, and in negatively regulating cell division during early fruit development, respectively [<u>31][36</u>]



Figure 3. A model of ARFs regulating tomato fruit development and ripening. Several members of the auxin responsive factor family influenced the development and ripening of tomato fruits by regulating the expression of genes related to ethylene biosynthesis and chlorophyll accumulation. SIARF2 regulates ethylene synthesis and tomato ripening by regulating the expression of ethylene biosynthesis genes ACO1/ACS2/ACS4. GOLDEN2-LIKE transcription factor SIGLK1 plays an important role in chloroplast formation and chlorophyll accumulation. SIARF4 inhibits the expression of its encoding gene SIGLK1, while SIARF10 and SIARF6A promotes its expression. Moreover, SIARF6A also targets the promoters of CAB (genes encoding chlorophyll A/B binding) and RbcS (gene encoding ribulose bisphosphate carboxylase small chain), genes that affect chlorophyll accumulation, and positively regulates the expression of these genes. SIARF6A is also a negative regulator of SAMS1, which in turn negatively regulates ripening and ethylene biosynthesis in tomato fruit. EXPANSIN5 (EXP5) likely promotes cell expansion during fruit development. SIARF7 inhibits tomato fruit set and early development by directly regulating EXP5 and ACO4.

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