Horticulture Research

Horticulture Research, 2024, **11**: uhae209

https://doi.org/10.1093/hr/uhae209

Mini Review

Auxin response factors: important keys for understanding regulatory mechanisms of fleshy fruit development and ripening

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Abstract

Auxin response transcription factors (ARFs) form a large gene family, many of whose members operate at the final step of the auxin signaling pathway. ARFs participate directly in many aspects of plant growth and development. Here we summarize recent advances in understanding the roles of ARFs in regulating aspects of fleshy fruit development and ripening. ARFs play a crucial role in regulating fruit size, color, nutrients, texture, yield, and other properties that ultimately influence the ripening and quality of important crops such as tomato, apple, strawberry, and peach. ARFs impact these processes acting as positive, negative, or bidirectional regulators via phytohormone-dependent or -independent mechanisms. In the phytohormone-dependent pathway, ARFs act as a central hub linking interactions with multiple phytohormones generating diverse effects. The three domains within ARFs, namely the DNA-binding domain, the middle region, and the carboxy-terminal dimerization domain, exhibit distinct yet overlapping functions, contributing to a range of mechanisms mediated by ARFs. These findings not only provide a profound understanding of ARF functions, but also raise new questions. Further exploration can lead to a more comprehensive understanding of the regulatory mechanisms of fleshy fruit development and ripening mediated by ARFs.

Introduction

Fleshy fruits are popular worldwide and make important contributions to human health and the economy. Fruit development and ripening involve a series of complex physiological and biochemical processes that determine quality, yield, and nutritional value. Fruit development normally begins with fertilization, which stimulates the ovary and/or other floral parts to develop into a fleshy fruit, although fruit set and parthenocarpy can also occur naturally, or be induced by supplying phytohormones, without fertilization. During seed development, the fruit accumulates stored reserves and remains unattractive to eat. At maturity, the ripening process involves changes in color, flavor, texture, and aroma, which contribute to formation of quality attributes and impact attractiveness, nutritional value and storage life [1]. Hence, the regulatory mechanisms underlying the ripening processes are important research hotspots.

Auxin is an important phytohormone that participates in controlling fleshy fruit development and ripening via its signaling pathway [2]. Auxin signaling involves its direct binding to TIR1/AFB (TRANSPORT INHIBITOR RESISTANT 1/AUXIN SIGNALING F-BOX), which can recruit other components to form an SCF ubiquitin protein ligase, which causes the degradation of the inhibitory Aux/IAA (AUXIN/INDOLE-3-ACETIC ACID) protein by the ubiquitin-proteasome system [3, 4]. Subsequently, the ARFs (auxin response factors), previously constrained by Aux/IAA, are released and can function in the regulation of auxin-dependent gene expression [5]. Therefore, ARFs are regarded as an indispensable connecting link between the auxin signaling pathway and the various downstream response processes triggered by auxin [6].

It is well known that ARFs play a crucial role in various aspects of plant growth and development [7, 8], including fruit development and ripening. These key transcription factors usually possess three important domains, comprising a conserved B3-type DNA binding domain (DBD) at their N-terminus, a middle region (MR) following the DBD, and a carboxy-terminal dimerization domain (CTD: domain III/IV, also named PB1 or AUX/IAA) at the C-terminus [9]. The DBD domain can bind to the auxin response element (AuxRE, TGTCTC/GAGACA) in the promoter region of target genes to regulate their expression [10,

Received: 8 February 2024; **Accepted:** 18 July 2024; **Published:** 31 July 2024; **Corrected and Typeset:** 1 October 2024
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amino acid sequences involved in recognition of other interacting proteins? What are the functions of ARF–ARF dimerization? Further exploration of these questions will enhance our understanding of the various functions and multiple regulatory mechanisms of ARFs, leading to a more comprehensive understanding of the mechanisms and regulatory networks governing fleshy fruit development and ripening.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (U23A20215), the Guangxi Natural Science Foundation (2024GXNSFBA010399), the National Natural Science Foundation of China (32102345), the 111 Project (B17039), and the Fundamental Research Funds for the Central Universities (226-2024-00063).

Data availability statement

There are no new data associated with this article.

Conflict of interest

The authors declare no conflict of interest.

References

1. Gómez MD, Vera-Sirera F, Pérez-Amador MA. *Molecular programme of senescence in dry and fleshy fruits J Exp Bot*. 2014;**65**:4515–26
2. Fenn MA, Giovannoni JJ. Phytohormones in fruit development and maturation. *Plant J*. 2021;**105**:446–58
3. Gray WM, Kepinski S, Rouse D, *et al.* Auxin regulates SCF^{TIR1}-dependent degradation of AUX/IAA proteins *Nature* 2001;**414**:271–6
4. Zenser N, Ellsmore A, Leasure C. *et al.* Auxin modulates the degradation rate of aux/IAA proteins. *Proc Natl Acad Sci USA*. 2001;**98**:11795–800
5. Okushima Y, Overvoorde PJ, Arima K' *et al.* Functional genomic analysis of the *AUXIN RESPONSE FACTOR* gene family members in *Arabidopsis thaliana*: unique and overlapping functions of *ARF7* and *ARF19*. *Plant Cell* 2005;**17**:444–63
6. Roosjen M, Paque S, Weijers D. Auxin response factors: output control in auxin biology. *J Exp Bot*. 2018;**69**:179–88
7. Rienstra J, Hernández-García J, Weijers D. To bind or not to bind: how auxin response factors select their target genes. *J Exp Bot*. 2023;**74**:6922–32
8. Song X, Xiong Y, Kong X. *et al.* Roles of auxin response factors in rice development and stress responses. *Plant Cell Environ*. 2023;**46**:1075–86
9. Li SB, OuYang WZ, Hou XJ. *et al.* A review of auxin response factors (ARFs) in plants. *Front Plant Sci*. 2016;**46**:1075–86
10. Ulmasov T, Hagen G, Guilfoyle TJ. ARF1, a transcription factor that binds to auxin response elements. *Science*. 1997;**276**:1865–8
11. Boer DR, Freire-Rios A, van den Berg WA. *et al.* Structural basis for DNA binding specificity by the auxin-dependent ARF transcription factors. *Cell*. 2014;**156**:577–89
12. Ulmasov T, Hagen G, Guilfoyle TJ. Activation and repression of transcription by auxin-response factors. *Proc Natl Acad Sci USA*. 1999;**96**:5844–9
13. Tiwari SB, Hagen G, Guilfoyle T. The roles of auxin response factor domains in auxin-responsive transcription. *Plant Cell*. 2003;**15**:533–43
14. Ulmasov T, Murfett J, Hagen G. *et al.* Aux/IAA proteins repress expression of reporter genes containing natural and highly active synthetic auxin response elements. *Plant Cell*. 1997;**9**:1963–71
15. Li Y, Han S, Qi Y. Advances in structure and function of auxin response factor in plants. *J Integr Plant Biol*. 2022;**65**:617–32
16. Gillaspy G, Ben-David H, Gruissem W. Fruits: a developmental perspective. *Plant Cell*. 1993;**5**:1439–51
17. Tanksley SD. The genetic, developmental, and molecular bases of fruit size and shape variation in tomato. *Plant Cell*. 2004;**16 Suppl_1**:S181–9
18. de Jong M, Wolters-Arts M, Schimmel BC. *et al. Solanum lycopersicum* AUXIN RESPONSE FACTOR 9 regulates cell division activity during early tomato fruit development. *J Exp Bot*. 2015;**66**:3405–16
19. Liu S, Zhang Y, Feng Q. *et al.* AUXIN RESPONSE FACTOR 5 regulates fruit set and development via the mediation of auxin and gibberellin signaling. *Sci Rep*. 2018;**8**:2971
20. de Jong M, Wolters-Arts M, Feron R. *et al.* The *S. lycopersicum* auxin response factor 7 (SlARF7) regulates auxin signaling during tomato fruit set and development. *Plant J*. 2009;**57**:160–70
21. Hu J, Israeli A, Ori N. *et al.* The interaction between DELLA and ARF/IAA mediates crosstalk between gibberellin and auxin signaling to control fruit initiation in tomato. *Plant Cell*. 2018;**30**:1710–28
22. Hu J, Li X, Sun TP. Four class A AUXIN RESPONSE FACTORs promote tomato fruit growth despite suppressing fruit set. *Nat Plants*. 2023;**9**:706–19
23. Israeli A, Schubert R, Man N. *et al.* Modulating auxin response stabilizes tomato fruit set. *Plant Physiol*. 2023;**192**:2336–55
24. Liu K, Yuan C, Li H. *et al.* Genome-wide identification and characterization of *auxin response factor* (*ARF*) family genes related to flower and fruit development in papaya (*Carica papaya* L.). *BMC Genomics*. 2015;**16**:901
25. Yuan J, Xu X, Gong Z. *et al.* Auxin response factor 6A regulates photosynthesis, sugar accumulation, and fruit development in tomato. *Hortic Res*. 2019;**6**:85
26. Zhou J, Sittmann J, Guo L. *et al.* Gibberellin and auxin signaling genes RGA1 and ARF8 repress accessory fruit initiation in diploid strawberry. *Plant Physiol*. 2021;**185**:1059–75
27. Li BJ, Grierson D, Shi Y. *et al.* Roles of abscisic acid in regulating ripening and quality of strawberry, a model non-climacteric fruit. *Hortic Res* 2022;**9**:uhac089
28. Hao Y, Hu G, Breitel D. *et al.* Auxin response factor SlARF2 is an essential component of the regulatory mechanism controlling fruit ripening in tomato. *PLoS Genet*. 2015;**11**:e1005649
29. Breitel DA, Chappell-Maor L, Meir S. *et al.* AUXIN RESPONSE FACTOR 2 intersects hormonal signals in the regulation of tomato fruit ripening. *PLoS Genet*. 2016;**12**:e1005903
30. Jones B, Frasse P, Olmos E. *et al.* Down-regulation of DR12, an auxin-response-factor homolog, in the tomato results in a pleiotropic phenotype including dark green and blotchy ripening fruit. *Plant J*. 2002;**32**:603–13
31. Sagar M, Chervin C, Mila I. *et al.* SlARF4, an auxin response factor involved in the control of sugar metabolism during tomato fruit development. *Plant Physiol*. 2013;**161**:1362–74
32. Xu X, Zhang Q, Gao X. *et al.* Auxin and abscisic acid antagonistically regulate ascorbic acid production via the SlMAPK8–SlARF4–SlMYB11 module in tomato. *Plant Cell* 2022;**34**:4409–27
33. Yuan J, Mei L, Wu M. *et al.* SlARF10, an auxin response factor, is involved in chlorophyll and sugar accumulation during tomato fruit development. *J Exp Bot*. 2018;**69**:5507–18

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34. Zhang T, Li W, Xie R. *et al.* CpARF2 and CpEIL1 interact to mediate auxin–ethylene interaction and regulate fruit ripening in papaya. *Plant J*. 2020;**103**:1318–37
35. Yi SN, Mao JX, Zhang XY. *et al. FveARF2* negatively regulates fruit ripening and quality in strawberry. *Front Plant Sci*
36. Wang CK, Han PL, Zhao YW. *et al.* Genome-wide analysis of auxin response factor (ARF) genes and functional identification of *MdARF2* reveals the involvement in the regulation of anthocyanin accumulation in apple. *New Zeal J Crop Hortic Sci*. 2021;**49**: 78–91
37. Wang YC, Wang N, Xu HF. *et al.* Auxin regulates anthocyanin biosynthesis through the aux/IAA–ARF signaling pathway in apple. *Hortic Res*. 2018;**5**:59
38. Zhai Z, Xiao Y, Wang Y. *et al.* Abscisic acid-responsive transcription factors PavDof2/6/15 mediate fruit softening in sweet cherry. *Plant Physiol* 2022;**190**:2501–18
39. Yue P, Lu Q, Liu Z. *et al.* Auxin-activated MdARF5 induces the expression of ethylene biosynthetic genes to initiate apple fruit ripening. *New Phytol*. 2020;**226**:1781–95
40. Chen X, Liu Y, Zhang X. *et al.* PpARF6 acts as an integrator of auxin and ethylene signaling to promote fruit ripening in peach. *Hortic Res*. 2023;**10**:uhad158
41. Cancé C, Martin-Arevalillo R, Boubekeur K. *et al.* Auxin response factors are keys to the many auxin doors. *New Phytol*. 2022;**235**: 402–19

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