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The Role of Auxin Signal Transduction in the Differentiation of Fruit Tree Branches

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Abstract The phytohormone auxin plays a pivotal role in the differentiation and development of fruit tree branches. This study synthesizes recent advances in understanding the mechanisms of auxin signal transduction and its impact on branch differentiation. Auxin's influence on plant growth and development is mediated through complex signaling pathways involving auxin response factors (ARFs) and Aux/IAA proteins, which regulate gene expression and cellular responses. The interaction between auxin and other phytohormones, such as gibberellic acid (GA), further modulates fruit development and branch differentiation. This review highlights the molecular and genetic evidence supporting the role of auxin in these processes, emphasizing the importance of auxin signaling in the regulation of cell division, expansion, and differentiation in fruit trees. The findings underscore the complexity of auxin-mediated responses and the potential for manipulating auxin pathways to improve fruit tree growth and productivity.
Keywords Auxin; Signal transduction; Branch differentiation; Fruit trees; Phytohormones

1 Introduction

Auxin is one of the most crucial phytohormones in plant biology, playing a central role in regulating plant growth and development. It was one of the first phytohormones to be identified and has been extensively studied for over a century. Auxin influences various physiological processes, including cell division, elongation, and differentiation, by modulating gene expression through specific transcription factors and proteins (Gomes and Scortecci, 2021; Yu et al., 2022). The auxin signaling pathway involves complex mechanisms, including the perception of auxin by TRANSPORT INHIBITOR RESPONSE 1 and AUXIN SIGNALING F-boxes (TIR1/AFBs), which mediate both transcriptional and non-transcriptional responses (Gallei et al., 2019; Yu et al., 2022). Additionally, auxin's role extends to the regulation of secondary xylem development and wood formation in tree species, highlighting its importance in both primary and secondary growth processes (Xu et al., 2019).

Branch differentiation is a critical aspect of fruit tree development, influencing both the structural integrity and reproductive success of the plant. Proper branch differentiation ensures optimal light capture, nutrient distribution, and mechanical support, which are essential for the growth and yield of fruit trees. Auxin plays a pivotal role in this process by regulating the formation and differentiation of branches through its effects on cell division and elongation (Kato et al., 2019; Xu et al., 2019). The interaction between auxin and other phytohormones, such as gibberellins, further modulates branch development and fruit set, demonstrating the intricate hormonal crosstalk involved in these processes (Liu et al., 2018; He and Yamamuro, 2022).

By synthesizing recent advances in auxin research, this study provides a comprehensive understanding of the molecular mechanisms underlying auxin-mediated branch differentiation; covers the biosynthesis, transport, and signaling pathways of auxin, as well as its interaction with other phytohormones and environmental factors; explore the genetic and epigenetic regulation of auxin signaling and its implications for the growth and development of fruit trees. Through this analysis, this study aims to identify potential targets for genetic and biotechnological interventions to enhance fruit tree productivity and resilience.

2 Auxin Biosynthesis and Transport

2.1 Pathways of auxin biosynthesis

Auxin, primarily indole-3-acetic acid (IAA), is synthesized through multiple pathways, both tryptophan-dependent and tryptophan-independent. The tryptophan-dependent pathways involve several intermediate compounds such as indole-3-acetamide, indole-3-acetaldoxime, indole-3-pyruvic acid, and tryptamine. Key enzymes in these pathways include YUCCA (YUC) flavin monooxygenases and TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA) (Gomes and Scortecci, 2021; Liu et al., 2023). These enzymes catalyze the conversion of tryptophan to IAA through a series of biochemical reactions. The regulation of these biosynthetic pathways is crucial for maintaining appropriate auxin levels, which in turn influence various developmental processes in plants, including fruit tree branch differentiation.

2.2 Mechanisms of auxin transport within plant tissues

Auxin transport is a highly regulated process that involves both influx and efflux carrier proteins. The polar nature of auxin transport is mediated by the AUXIN1/LIKE-AUX1 (AUX1/LAX) family of influx carriers and the PIN-FORMED (PIN) family of efflux carriers, along with P-GLYCOPROTEIN/ATP-BINDING CASSETTE B (PGP/ABCB) transporters (Swarup and Bhosale, 2019; Hammes et al., 2021). These transporters facilitate the directional movement of auxin from the site of synthesis to target tissues, ensuring the formation of auxin gradients essential for plant development. The PIN proteins, in particular, are known for their role in establishing auxin maxima and minima, which are critical for processes such as embryogenesis, organogenesis, and vascular patterning (Swarup and Bhosale, 2019; Hammes et al., 2021).

2.3 Regulation of auxin distribution in fruit trees

The distribution of auxin within fruit trees is tightly regulated by both biosynthesis and transport mechanisms. Environmental cues such as light, temperature, and nutrient availability can influence auxin biosynthesis and transport, thereby affecting the overall growth and development of the plant (Mroue et al., 2018). For instance, the NRT1.1 nitrate transceptor in Arabidopsis has been shown to coordinate auxin biosynthesis and transport in response to nitrate availability, which in turn regulates root branching (Maghiaoui et al., 2020). Similarly, in fruit trees, the dynamic distribution of auxin is crucial for branch differentiation and fruit development. The interplay between auxin and other phytohormones, such as gibberellic acid (GA), further modulates these processes, highlighting the complexity of hormonal regulation in plant development (He and Yamamuro, 2022).

3 Auxin Signal Transduction Pathway

Auxin, a key phytohormone, plays a crucial role in regulating plant growth and development through a complex signal transduction pathway. This pathway involves multiple components, including receptors, transcription factors, and downstream signaling cascades, which together modulate gene expression and interact with other hormonal signaling pathways.

3.1 Components of the auxin signaling pathway

The auxin signaling pathway is primarily mediated by the interaction between auxin response factors (ARFs) and auxin/indole-3-acetic acid (Aux/IAA) proteins. ARFs are transcription factors that bind to auxin response elements in the promoters of auxin-responsive genes, while Aux/IAA proteins act as repressors of ARF activity. The pathway also involves the F-box proteins TIR1/AFBs, which function as auxin receptors and facilitate the degradation of Aux/IAA proteins, thereby releasing ARFs to activate gene expression (Gomes and Scortecci, 2021; Li et al., 2022).

3.2 The role of auxin receptors in signal perception

Auxin perception is primarily mediated by the TIR1/AFB family of F-box proteins, which function as auxin receptors. These receptors form part of the SCF (SKP1-CUL1-F-box) ubiquitin ligase complex, which targets Aux/IAA proteins for ubiquitination and subsequent degradation. The binding of auxin to TIR1/AFB enhances the interaction between TIR1/AFB and Aux/IAA proteins, leading to the degradation of Aux/IAA and the activation of ARFs. This process is crucial for the regulation of gene expression in response to auxin (Figure 1) (Gomes and Scortecci, 2021; Yu et al., 2022).

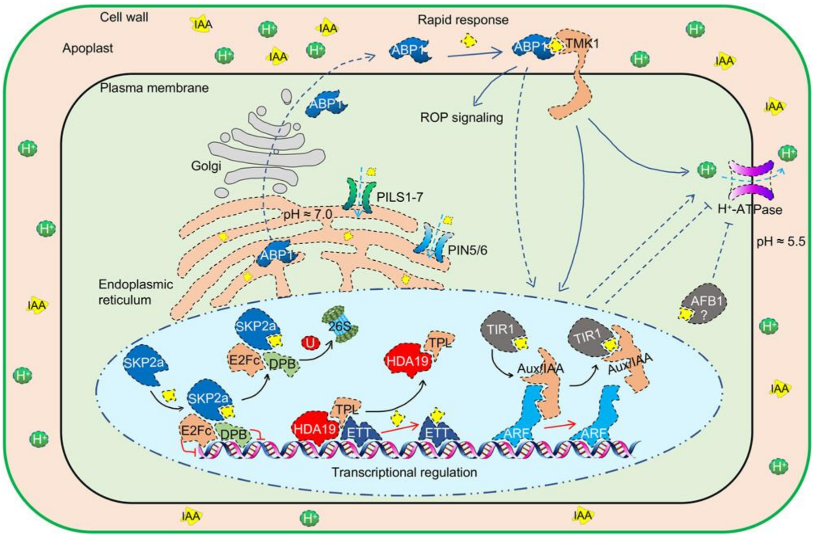

Figure 1 Subcellular localization and activity patterns of candidate auxin receptors (Adopted from Yu et al., 2022)

Image caption: During auxin-driven cell cycle progression, the nuclear S-PHASE KINASE-ASSOCIATED PROTEIN 2a (SKP2a) binds to indole-3-acetic acid (IAA) to enhance its interaction with G1-to-S checkpoint regulators, E2FC, and its dimerization partner DPB, leading to their degradation via the 26S proteasome and accelerating cell division. ETT/ARF3 (AUXIN RESPONSE FACTOR 3), which lacks the Phox/Bem1 (PB1) domain necessary for interaction with Aux/IAAs, follows a distinct auxin signaling pathway: in low auxin conditions, ETT/ARF3 represses auxin-responsive genes by recruiting TOPLESS (TPL)/TPL-RELATED PROTEINs (TPRs) and HISTONE DEACETYLASE 19 (HDA19). Elevated auxin levels disrupt this complex, enabling transcription. Auxin also serves as a "molecular glue" in canonical signaling, facilitating the interaction between TRANSPORT INHIBITOR RESPONSE 1 (TIR1) and AUXIN SIGNALING F-boxes (AFBs) with Aux/IAAs, leading to their degradation and subsequent activation of ARF transcription factors. The role of AUXIN BINDING PROTEIN 1 (ABP1) in auxin signaling, potentially involving its secretion and interaction with TRANSMEMBRANE KINASE 1 (TMK1), remains speculative (Adapted from Yu et al., 2022)

3.3 Downstream signaling cascades and gene expression

Upon the degradation of Aux/IAA proteins, ARFs are released to bind to auxin response elements in the promoters of target genes, thereby modulating their expression. This regulation of gene expression is essential for various developmental processes, including cell division, elongation, and differentiation. Recent studies have also highlighted the role of microRNAs in fine-tuning the auxin signaling pathway, adding another layer of complexity to the regulation of gene expression (Gallei et al., 2019; Gomes and Scortecci, 2021).

3.4 Crosstalk with other hormonal signaling pathways

Auxin signaling does not operate in isolation but interacts with other hormonal pathways, such as gibberellins (GA), to coordinate plant growth and development. For instance, the interaction between ARF and DELLA proteins mediates crosstalk between auxin and GA signaling pathways, which is crucial for processes like fruit initiation and development. This crosstalk ensures that the hormonal signals are integrated to produce a coherent response to environmental and developmental cues (Zhou et al., 2020; He and Yamamuro, 2022; Li et al., 2022).

4 Auxin and Branch Differentiation in Fruit Trees

4.1 Mechanisms of auxin-induced branching

Auxin plays a pivotal role in the regulation of branch differentiation in fruit trees by influencing various hormonal and genetic pathways. The hormone auxin, primarily synthesized in the shoot apex, is transported basipetally and regulates the growth and development of lateral buds. This transport mechanism is crucial for maintaining apical dominance, where the main shoot apex suppresses the growth of lateral buds (Holalu et al., 2020). Additionally, auxin interacts with other hormones such as cytokinins (CKs) and strigolactones (SLs) to modulate bud outgrowth. For instance, auxin depletion after decapitation can lead to an increase in CK levels, promoting bud growth, while SLs can inhibit this process (Cao et al., 2023). Furthermore, auxin's role in bud outgrowth is also influenced by sugars, which act in concert with CKs but antagonistically to SLs, highlighting a complex network of hormonal interactions (Kotov et al., 2021).

4.2 Influence of auxin on apical dominance and lateral bud formation

Apical dominance is a well-documented phenomenon where the presence of an active shoot apex inhibits the growth of lateral buds. This process is largely mediated by auxin, which is produced in the shoot apex and transported down the stem, suppressing lateral bud growth (Holalu et al., 2020). The suppression of bud growth is not solely due to auxin levels but also involves the enhanced expression of auxin-induced genes, which increase the sensitivity of buds to auxin (Holalu et al., 2020). Additionally, auxin's interaction with other hormones such as CKs and SLs plays a significant role in this process. For example, SLs have been shown to suppress branching after decapitation, although their effect is less pronounced when CKs or sugars are abundant (Cao et al., 2023). This intricate balance between auxin and other hormones ensures the proper regulation of apical dominance and lateral bud formation.

4.3 Role of auxin in the timing and patterning of branching

The timing and patterning of branching in fruit trees are tightly regulated by auxin through its influence on gene expression and hormonal interactions. Auxin's role in branch patterning is evident in its ability to coordinate the transcriptional reprogramming of auxin-responsive genes, which are crucial for branch initiation and outgrowth (Thelander et al., 2022). In pear trees, for instance, early defoliation leads to auxin redistribution, promoting paradormancy release and out-of-season blooming, which negatively affects fruit production (Figure 2) (Wei et al., 2022). This redistribution of auxin involves changes in auxin metabolism, transport, and signal transduction pathways, highlighting the hormone's role in the precise timing and patterning of branching (Wei et al., 2022). Moreover, auxin's interaction with other hormones such as gibberellins (GAs) further influences the timing of bud release and sustained growth (Cao et al., 2023).

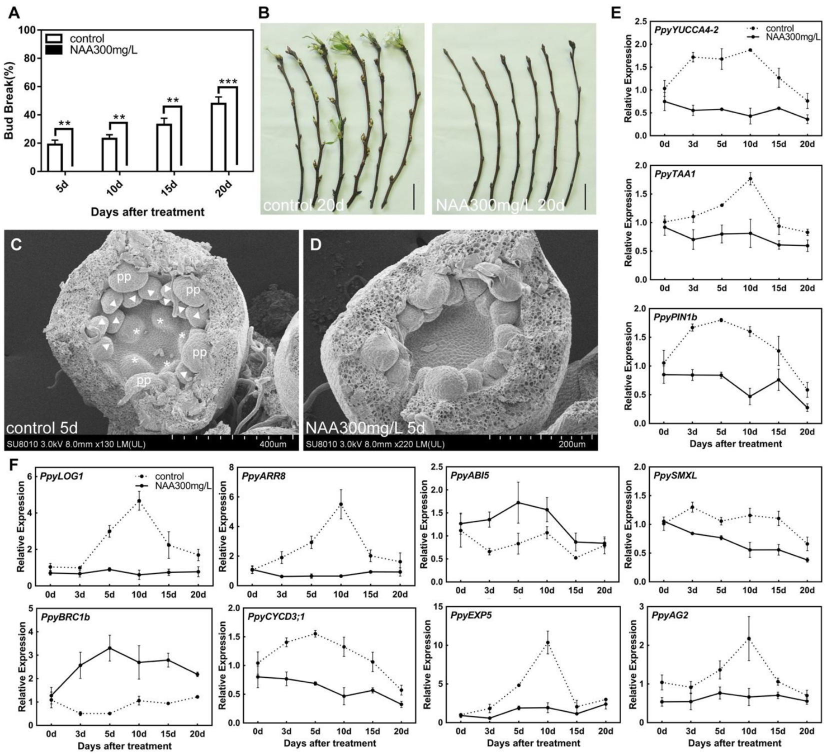

Figure 2 Inhibitory effects of a high auxin concentration on flower bud break after defoliation and expression patterns of hormone-related genes after an NAA treatment (Adopted from Wei et al., 2022)

Image caption: A, Bud break percentage of current-year long shoots after a 300 mg/L NAA treatment. B, Representative images of bud break on day 20 on defoliated (left) and NAA-treated current-year long shoots (right). Scale bars, 5 cm. C and D, Scanning electron micrographs of flower buds of current-year long shoots on day 5 in the control group (C) and the NAA-treated group (D). pp, petal primordium; triangles, stamen primordium; and asterisks, pistil primordium. E and F, Expression patterns of genes related to auxin (E) and other hormones (F) after the NAA treatment. Error bars indicate the SEs of three biological replicates and asterisks indicate significant differences between control (defoliated) and NAA-treated branches (Student's t test). $*P<0.05$, $**P<0.01$, $***P<0.001$ (Adopted from Wei et al., 2022)

Wei et al. (2022) investigates how high auxin concentrations influence flower bud break after defoliation. Using 1-naphthaleneacetic acid (NAA) treatment on mature shoots, the research found that high auxin levels significantly inhibit bud break, as evidenced by reduced bud development and suppressed flower bud primordia formation. The study also reveals that high auxin concentrations disrupt the expression of genes related to auxin metabolism, transport, and signaling, which are typically upregulated following defoliation. Notably, the inhibition of PpyPIN1b protein expression is identified as a key factor in preventing auxin efflux from buds, leading to the suppression of bud break. These findings underscore the role of auxin in regulating developmental processes and suggest that manipulating auxin levels could control flowering in horticultural practices.

4.4 Comparative analysis of auxin-mediated branching in different fruit tree species

Auxin-mediated branching mechanisms exhibit both conserved and species-specific features across different fruit tree species. In pear trees, early defoliation-induced auxin redistribution accelerates bud paradormancy release, whereas in longan, auxin signal transduction is crucial for the growth and maturity of autumn shoots, influencing floral bud induction (Liang et al., 2022; Wei et al., 2022). Additionally, in Chinese fir, auxin plays a key role in inhibiting bud outgrowth by modulating the biosynthesis of secondary messengers such as CKs, GAs, and abscisic acid (ABA), thereby inducing paradormancy of axillary buds (Yang et al., 2022). These examples illustrate the diverse yet interconnected roles of auxin in regulating branching across different fruit tree species, emphasizing the hormone's central role in plant architecture and development.

5 Environmental Factors Influencing Auxin-Mediated Branching

5.1 Light and photoperiod effects on auxin distribution

Light is a critical environmental factor that influences auxin distribution and, consequently, the branching patterns in fruit trees. Light-regulated auxin signaling plays a significant role in various developmental processes, including root and shoot development. Phytochromes (PHYs), cryptochromes (CRYs), phototropins (PHOTs), and phytochrome-interacting factors (PIFs) are some of the light-response components that regulate auxin-mediated growth. These components affect the primary root, lateral root, adventitious root, and root hair development through the auxin signaling transduction pathway (Yun et al., 2023). The interaction between light and auxin signaling is complex and varies among different plant species, such as barley and wheat, highlighting the importance of light in modulating auxin levels and distribution, which in turn affects branching patterns.

5.2 Impact of nutrient availability on auxin-induced branching

Nutrient availability is another crucial factor that influences auxin-induced branching in fruit trees. Auxin production and distribution are tightly regulated by the plant's nutritional status. Nutrients such as nitrogen, phosphorus, and potassium can affect auxin biosynthesis and transport, thereby influencing the plant's growth and branching patterns. The integration of nutrient signals with auxin signaling pathways ensures that the plant can adapt its growth and development to the availability of essential nutrients. This fine-tuning mechanism allows plants to optimize their branching architecture for better resource acquisition and overall fitness (Mroue et al., 2018).

5.3 The role of temperature and water stress on auxin signaling

Temperature and water stress are significant environmental factors that impact auxin signaling and, consequently, the branching of fruit trees. Plants have evolved complex signaling networks to integrate these environmental cues and modulate their growth and development accordingly. Auxin plays a pivotal role as an integrator of these signals, helping plants to adapt to varying temperature and water conditions. For instance, temperature fluctuations can affect auxin biosynthesis, metabolism, and transport, leading to changes in auxin gradients that influence branching patterns. Similarly, water stress can alter auxin distribution, affecting cell expansion, division, and tissue specification, which are critical for branch formation and growth (Mroue et al., 2018). Understanding the interplay between temperature, water stress, and auxin signaling is essential for developing strategies to improve the resilience and productivity of fruit trees under changing environmental conditions.

6 Case Study

6.1 Case study: auxin signal transduction in apple trees

Auxin, a pivotal phytohormone, plays a crucial role in the growth and development of apple trees (Malus domestica). The auxin signaling pathway involves various components, including auxin response factors (ARFs) and small auxin-up RNA (SAUR) genes, which regulate diverse physiological processes such as fruit ripening, cell division, and differentiation. Recent studies have highlighted the complexity and significance of auxin signal transduction in apple trees, providing insights into its molecular mechanisms and potential applications in horticulture (Figure 3) (Gallei et al., 2019; Wang et al., 2020; Yue et al., 2020).

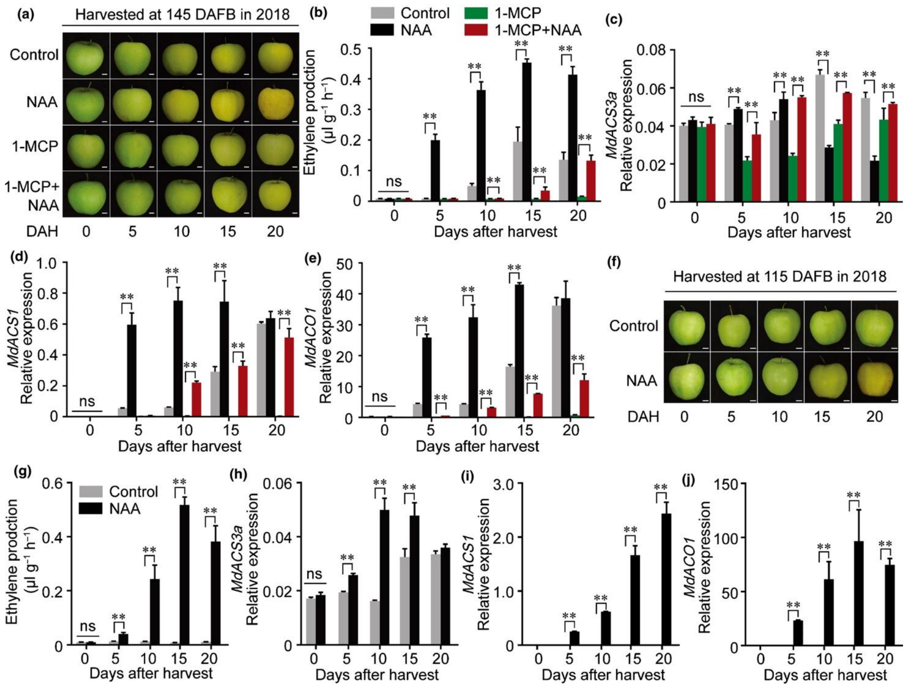

Figure 3 Auxin-induced ethylene production and expression of ethylene-related genes in apple (Adopted from Yue et al., 2020)

Image caption: (a–e) Apple fruits were harvested at 145 days after full bloom (DAFB) in 2018 and treated with naphthaleneacetic acid (NAA), 1-methylcyclopropene (1-MCP), or a combination of 1-MCP followed by NAA (1-MCP + NAA) (a). Fruits were stored at room temperature for 20 days and sampled every 5 days. Untreated fruits served as controls. Scale bars represent 1 cm. Ethylene production was measured (b), and the expression levels of ethylene-related genes MdACS3a (c), MdACS1 (d), and MdACO1 (e) were analyzed using quantitative reverse transcription PCR (qRT-PCR). (f–j) Apple fruits were harvested at 115 DAFB, treated with NAA (f), stored at room temperature for 20 days, and sampled every 5 days. Scale bars represent 1 cm. Ethylene production was measured (g), and the expression levels of MdACS3a (h), MdACS1 (i), and MdACO1 (j) were analyzed. Control fruits did not receive any treatment. Three independent biological experiments were conducted for each treatment group. Data are presented as means ± SE. Asterisks indicate significant differences determined by Student's t-test (**, $P < 0.01$); ns, not significant (Adapted from Yue et al., 2020)

Yue et al. (2020) examines the effect of auxin, specifically naphthaleneacetic acid (NAA), on ethylene production and the expression of ethylene-related genes in apple fruit. The research demonstrates that NAA treatment significantly enhances ethylene production and accelerates the expression of key ethylene biosynthesis genes (MdACS3a, MdACS1, and MdACO1) during apple ripening. This effect is observed even when fruit are treated with 1-methylcyclopropene (1-MCP), a compound known to inhibit ethylene production, indicating that auxin can override ethylene inhibition. The study highlights the critical role of auxin in regulating ethylene synthesis and suggests that manipulating auxin levels could be a potential strategy for controlling apple ripening and improving post-harvest fruit quality.

6.2 Study design

To investigate the role of auxin signal transduction in apple trees, a comprehensive study was conducted involving the identification and expression analysis of key auxin-responsive genes. The study focused on the small auxin-up

RNA (SAUR) gene family and the auxin response factor (ARF) transcription factors. Researchers employed quantitative real-time polymerase chain reaction (qRT-PCR) to analyze the expression levels of these genes in various tissues, including leaves, stems, and fruits, under different auxin treatments. Additionally, genetic transformation techniques were used to overexpress or silence specific auxin-responsive genes to observe their effects on apple fruit development and size (Wang et al., 2020; Yue et al., 2020; Iqbal et al., 2022).

6.3 Findings and analysis

The study identified 80 MdSAUR genes in apple, with several showing increased expression levels in response to exogenous auxin treatment. Notably, MdSAUR4, MdSAUR22, MdSAUR37, MdSAUR38, MdSAUR49, and MdSAUR54 were significantly up-regulated, indicating their potential roles in the auxin signaling pathway (Wang et al., 2020). Furthermore, the overexpression of MdARF5, an auxin response factor, was found to induce the expression of ethylene biosynthetic genes, thereby promoting ethylene production and fruit ripening in apple (Yue et al., 2020). Another key finding was the role of MdAux/IAA2, a transcriptional repressor, in regulating cell and fruit size. Overexpression of MdAux/IAA2 resulted in smaller fruit size and reduced cell size, while its silencing led to increased fruit weight and cell size (Iqbal et al., 2022).

These results underscore the intricate interplay between auxin and other phytohormones, such as ethylene, in regulating apple fruit development. The findings also highlight the importance of specific auxin-responsive genes in modulating key physiological processes, providing valuable insights into the molecular mechanisms underlying auxin signal transduction in apple trees (Wang et al., 2020; Yue et al., 2020; Iqbal et al., 2022).

6.4 Implications for practical applications in fruit tree cultivation

The insights gained from this study have significant implications for practical applications in fruit tree cultivation. Understanding the molecular mechanisms of auxin signal transduction can inform strategies to enhance fruit quality and yield in apple orchards. For instance, manipulating the expression of specific auxin-responsive genes, such as MdARF5 and MdAux/IAA2, could be used to control fruit ripening and size, thereby improving marketability and consumer preference (Yue et al., 2020; Iqbal et al., 2022). Moreover, the identification of key SAUR genes involved in auxin signaling provides potential targets for genetic engineering to optimize growth and development in apple trees. By fine-tuning the expression of these genes, it may be possible to achieve desired traits such as increased fruit size, enhanced ripening, and improved stress tolerance, ultimately contributing to more sustainable and productive apple cultivation practices (Wang et al., 2020; Yue et al., 2020; Iqbal et al., 2022).

7 Advances in Manipulating Auxin Signaling for Improved Branching

7.1 Genetic engineering approaches

Genetic engineering has emerged as a powerful tool to manipulate auxin signaling pathways for improved branching in fruit trees. By targeting key components of the auxin signal transduction pathway, researchers have been able to modulate plant architecture effectively. For instance, the manipulation of auxin response factors (ARFs) and auxin/indole-3-acetic acid (Aux/IAA) proteins, which are crucial regulators of auxin signaling, has shown promising results in altering plant growth patterns (Li et al., 2022). Advances in whole-genome sequencing have facilitated the identification of numerous ARF genes in various crops, including tomato, rice, and maize, providing a rich resource for genetic manipulation (Li et al., 2022). Additionally, the use of CRISPR/Cas9 technology to edit genes involved in auxin biosynthesis, transport, and signaling has opened new avenues for precise control over auxin-mediated processes (Wang et al., 2018). These genetic engineering approaches hold significant potential for enhancing branching and overall plant architecture, thereby improving fruit yield and quality.

7.2 Use of auxin analogues and inhibitors

The application of auxin analogues and inhibitors represents another strategy to manipulate auxin signaling for improved branching. Auxin analogues, such as synthetic auxins, can mimic the action of natural auxins and are used to regulate plant growth and development. For example, the use of auxin analogues has been shown to promote cell division and expansion, which are critical for branch formation (He and Yamamuro, 2022). On the other hand, auxin inhibitors can be employed to block specific steps in the auxin signaling pathway, thereby modulating plant growth. In grapevine, the application of an auxin inhibitor reduced cell number and mesocarp diameter, highlighting the potential of such compounds in controlling fruit development and branching (Gomes and Scortecci, 2021). These chemical approaches provide a flexible and non-genetic means to influence auxin signaling and can be integrated with genetic engineering techniques for more comprehensive control over plant architecture.

7.3 Potential for crop improvement and yield enhancement

Manipulating auxin signaling holds significant promise for crop improvement and yield enhancement. By optimizing branching patterns, it is possible to increase the number of fruit-bearing branches, thereby boosting overall fruit production. The interplay between auxin and other phytohormones, such as gibberellic acid (GA), further underscores the potential for integrated hormone management to enhance crop yields (He and Yamamuro, 2022). Recent studies have demonstrated that the interaction between ARF/IAA and DELLA proteins, which are involved in both auxin and GA signaling pathways, plays a crucial role in fruit development and can be targeted for crop improvement (He and Yamamuro, 2022). Moreover, the crosstalk between auxin and sugar signaling pathways has been shown to regulate various agriculturally important traits, suggesting that a holistic approach to hormone management could lead to significant advancements in crop productivity (Mishra et al., 2021). Overall, the strategic manipulation of auxin signaling, through both genetic and chemical means, offers a promising avenue for enhancing branching, improving fruit quality, and increasing crop yields.

8 Challenges and Future Directions

8.1 Limitations in current research on auxin signaling

Despite significant advancements in understanding auxin signaling, several limitations persist. One major challenge is the complexity of auxin signal transduction pathways, which involve multiple components and interactions that are not yet fully elucidated. For instance, while the canonical TIR1/AFB-mediated transcriptional pathway is well-studied, the non-canonical pathways, such as those mediated by TRANSMEMBRANE KINASEs (TMKs), require further exploration to understand their roles in plant growth and development (Gallei et al. 2019; Yu et al. 2022). Additionally, the feedback inhibition mechanisms that prevent the over-amplification of auxin signals are not completely understood, posing a challenge for manipulating these pathways for agricultural benefits (Yu et al. 2022).

Another limitation is the species-specific nature of auxin signaling components. For example, while ARF genes have been extensively studied in model plants like Arabidopsis, their roles in other species, including fruit trees, are less well-characterized (Li et al., 2022). This gap in knowledge hinders the application of findings from model plants to economically important fruit trees. Moreover, the interaction between auxin and other phytohormones, such as gibberellic acid (GA), in regulating fruit development is complex and not fully understood, necessitating further research (He and Yamamuro, 2022).

8.2 Emerging technologies and their potential impact

Emerging technologies offer promising avenues to overcome current limitations in auxin signaling research. Advanced genomic and transcriptomic techniques, such as whole-genome sequencing and RNA sequencing, have already facilitated the identification of numerous ARF genes across different species, including fruit trees (Li et al., 2022; Liang et al., 2022). These technologies enable a more comprehensive understanding of the genetic basis of auxin signaling and its role in plant development.

CRISPR/Cas9 genome editing technology holds significant potential for functional studies of auxin signaling components. By enabling precise modifications of specific genes, CRISPR/Cas9 can help elucidate the roles of less-studied auxin signaling components and their interactions with other phytohormones (Xu et al., 2019). Additionally, bioinformatics tools and integrative analyses, such as those used to study the regulatory networks in longan, can provide insights into the complex interactions between auxin signaling and other pathways (Liang et al., 2022).

High-throughput phenotyping platforms and advanced imaging techniques can also enhance our understanding of auxin-mediated processes. These technologies allow for the detailed observation of phenotypic changes in response to genetic modifications or environmental conditions, thereby linking molecular changes to physiological outcomes (Mroue et al., 2018).

8.3 Research gaps and proposed future studies

Several research gaps need to be addressed to advance our understanding of auxin signaling in fruit tree branch differentiation. First, there is a need for more studies on the non-canonical auxin signaling pathways and their interactions with the canonical pathways. Investigating the roles of TMKs and other non-canonical components in different species could provide new insights into the versatility and complexity of auxin signaling (Gallei et al. 2019; Yu et al. 2022).

Second, the interaction between auxin and other phytohormones, such as GA and ethylene, in regulating fruit development and branch differentiation requires further investigation. Studies focusing on the molecular mechanisms underlying these interactions could lead to the development of strategies for improving fruit yield and quality (He and Yamamuro, 2022; Iqbal et al. 2022).

Third, research should focus on the species-specific aspects of auxin signaling. Comparative studies across different fruit tree species can identify conserved and unique signaling components, facilitating the transfer of knowledge from model plants to economically important crops (Kato et al. 2018; He and Yamamuro, 2022).

Finally, the application of emerging technologies, such as CRISPR/Cas9 and advanced imaging techniques, should be expanded to study auxin signaling in fruit trees. These technologies can help identify key regulatory genes and pathways, providing targets for genetic improvement and breeding programs (Liang et al., 2022; Xu et al., 2019).

9 Concluding Remarks

The role of auxin in the differentiation of fruit tree branches is multifaceted, involving complex interactions with other phytohormones and environmental cues. Auxin, along with gibberellic acid (GA), is crucial for fruit development, promoting cell division and expansion, which are essential for fruit enlargement post-fertilization. The auxin signaling pathway, particularly the nuclear auxin pathway involving TIR1/AFB receptors, AUX/IAA co-repressors, and ARF transcription factors, plays a significant role in regulating cell differentiation and expansion. Additionally, auxin's role in cell wall expansion and modification further underscores its importance in plant growth and development. Recent studies have also highlighted the complexity of auxin signaling, revealing both nuclear and cell surface-based mechanisms that contribute to diverse cellular responses.

Understanding the role of auxin in fruit tree branch differentiation has significant implications for fruit tree breeding and cultivation. By manipulating auxin levels and signaling pathways, it is possible to influence fruit set, growth, and maturation, thereby improving fruit yield and quality. For instance, auxin treatments can mimic pollination effects, promoting fruit set in grapevines. Additionally, the interaction between auxin and other phytohormones, such as GA and abscisic acid (ABA), can be leveraged to optimize fruit development and ripening processes. This knowledge can be applied to develop new cultivars with desirable traits, such as increased fruit size, improved stress tolerance, and enhanced nutritional content.

The intricate role of auxin in fruit tree branch differentiation presents numerous opportunities for future research and practical applications. Further studies are needed to elucidate the molecular mechanisms underlying auxin signaling and its interactions with other phytohormones and environmental factors. Advances in genetic and molecular tools will enable more precise manipulation of auxin pathways, leading to innovative strategies for fruit tree breeding and cultivation. Additionally, exploring the role of auxin in different fruit tree species and under various environmental conditions will provide valuable insights into its broader applications in horticulture. Ultimately, a deeper understanding of auxin's role in plant development will contribute to sustainable and efficient agricultural practices, ensuring food security and environmental sustainability.

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Conflict of Interest Disclosure
The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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