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Metabolic Pathways in Kiwifruit: From Gene Expression to Metabolite Accumulation

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Abstract By combining metabolome and transcriptome data, we found several important regulatory pathways and transcription factors. These components are all related to the production and accumulation of flavor substances in kiwifruit during development and ripening. The L-galactose pathway is the main way to synthesize AsA (ascorbic acid), while the D-galacturonic acid pathway and AsA cycle pathway are secondary. MYB transcription factors affect the accumulation of chlorophyll and carotenoids, which is directly related to the color performance of the fruit. Key structural genes such as AaLDOX have also been found, which are involved in the synthesis of anthocyanins and form the red flesh of some kiwifruit varieties. These findings give us a clearer understanding of how flavor substances are synthesized and regulated in kiwifruit. These studies can be used in breeding in the future, such as improving the flavor, nutrition and appearance of kiwifruit to make the quality better.

Keywords Kiwifruit (*Actinidia* spp.); Metabolic pathway; Gene expression; Accumulation of metabolites; Ascorbic acid

1 Introduction

Kiwifruit (*Actinidia* spp.) is a popular fruit because of its unique taste, rich nutrition and high economic value. Kiwifruit is native to China and is rich in vitamin C, dietary fiber, and many active ingredients that are beneficial to health, so it is very popular in many countries around the world (Huang et al., 2013). At present, kiwifruit is grown in many parts of the world, with New Zealand, Italy and China as the main production areas. As the demand for kiwifruit is increasing, many researchers have begun to pay attention to its genetic, metabolic and physiological characteristics (Wang et al., 2021; Shu et al., 2023).

To improve the quality of kiwifruit, we must first understand its metabolic process. The flavor, taste and nutrition of kiwifruit are mainly determined by metabolic components such as sugar, organic acids, flavonoids and vitamins (Wang et al., 2021; Shu et al., 2023). Studying metabolic pathways can help us find out how these components are produced and which genes regulate them. For example, soluble sugars and organic acids are important for flavor, while flavonoids and carotenoids give the fruit its color and improve antioxidant capacity (Ampomah-Dwamena et al., 2018; Wang et al., 2021).

By analyzing metabolic pathways, we can also better understand how kiwifruit develops and ripens. At different growth stages, some transcription factors and enzymes control the synthesis of certain key components (Jia et al., 2022a; Shu et al., 2023). For example, studies have found transcription factors related to the synthesis of proanthocyanidins and vitamin C (Shu et al., 2023).

This study will systematically summarize the current research results on kiwifruit metabolic pathways, including the process from gene expression to the accumulation of metabolites. We will especially introduce recent research results on genes and transcription factors for the synthesis of some key metabolites (such as flavonoids, carotenoids and vitamins). At the same time, the application prospects of these research results in kiwifruit breeding and quality improvement will also be discussed. It is hoped that these contents can help improve the quality of kiwifruit and provide reference materials for people doing related research and breeding work.

2 Genetic Basis of Kiwi Metabolic Pathways

2.1 Overview of kiwi genomics

Kiwifruit (*Actinidia* spp.) is a respiratory climacteric fruit with a unique taste and rich nutrition. These characteristics are closely related to the complex metabolic processes in its body. In recent years, scientists have used high-precision metabolomics and transcriptomics technologies to conduct in-depth analysis of the metabolic changes of kiwifruit at different developmental stages (Wang et al., 2021; Shu et al., 2023). As the fruit develops, the types and quantities of metabolites in it will change a lot. These metabolites often work with some specific genes to form a complex network (Shu et al., 2023). Through these methods, researchers have found many gene modules related to metabolism, which also helps us to more comprehensively understand the metabolic changes of kiwifruit throughout its growth process.

2.2 Key genes involved in primary and secondary metabolism

Both the primary and secondary metabolism of kiwifruit are inseparable from the role of some important genes and regulatory factors. When synthesizing ascorbic acid (AsA), two enzymes, GalDH and GalLDH, are required, and MDHAR and DHAR are also required to participate in the regeneration process of AsA (Liao et al., 2021). In addition, MYB7 in the MYB transcription factor can activate the expression of genes related to chlorophyll and carotenoid synthesis, which is critical for the accumulation of pigments (Ampomah-Dwamena et al., 2018). There are also two transcription factors, MYBC1 and WRKY44, which can regulate the synthesis pathways of anthocyanins and proanthocyanidins and promote the synthesis of certain flavonoids (Peng et al., 2020).

2.3 Regulation of gene expression and its impact on metabolism

The expression of genes directly affects the metabolism in kiwifruit. The miR164-NAC pathway controls the fruit ripening process by regulating ethylene response-related genes (Wang et al., 2019) (Figure 1). MiR858 inhibits the expression of the AaMYBC1 gene, reduces the synthesis of anthocyanins, and affects the change of peel color (Li et al., 2020). By integrating proteomic and metabolomic data, some key enzymes play an important role in glycolysis, tricarboxylic acid cycle (TCA cycle) and ethylene synthesis, which are critical to the ripening and quality of fruits (Tian et al., 2021).

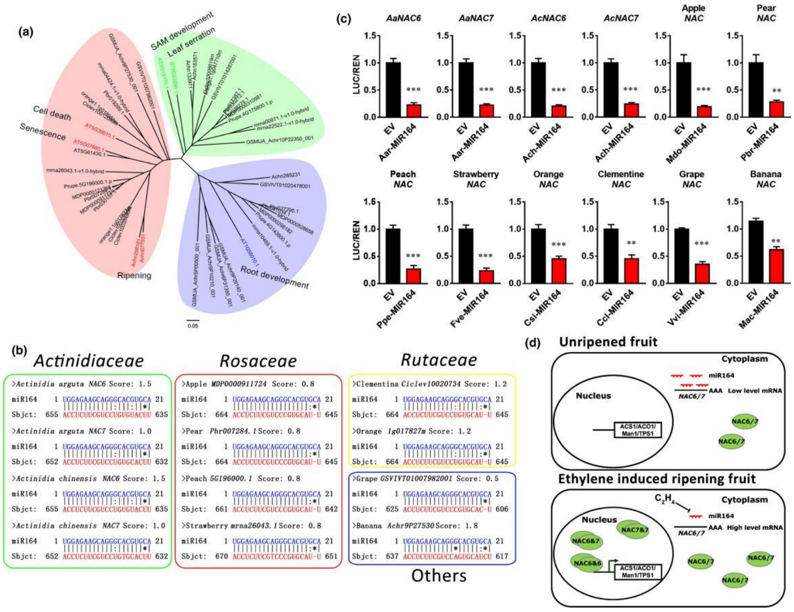

Figure 1 Analysis of miR164 regulation on NAC transcription factor in various fruit (Adopted from Wang et al., 2019)

Image caption: (a) Phylogenetic tree analysis of miR164 targeted NACs in different species. The labeled functions for partial members are cited from the literature. (b) Prediction of miR164 on NAC6/7 homologs in other fleshy fruit. (c) The effects of miR164 on the target sites of AdNAC6/7 homologs from different fleshy fruit. The ratio of luciferase: Renilla (LUC/REN) of the empty SK vector (EV) plus target site vector was set at 1. Error bars indicate SEs from five replicates (**, $P< 0.01$; ***, $P< 0.001$). (d) Proposed model of miR164-NAC pathway regulating fruit ripening. Ethylene downregulates miR164, which results in the accumulation of NAC6/7 in the nucleus and leads to activation of ripening-related genes

3 Primary Metabolism of Kiwifruit

3.1 Carbohydrate metabolism

3.1.1 Photosynthesis and sugar synthesis

Kiwifruit has some special features in carbohydrate metabolism. It can synthesize some uncommon sugars, such as inositol and phytose. Inositol is synthesized in the fruit and is mainly related to seed development, not used to synthesize phytose. Phytose is transported from the "source" tissue to the "storage" tissue through the phloem. Its amount is similar to sucrose, and sometimes even more. These soluble sugars can be effectively transported to the fruit (Boldingh et al., 2018).

Starch synthesis is also important. ADP-Glc pyrophosphorylase (AGPase) is a key enzyme that is very important for starch accumulation in kiwifruit. The activity of this enzyme is significantly higher in those high-starch kiwifruit varieties (Nardozza et al., 2013).

3.1.2 Sugar transportation and storage

How sugars are moved and stored in kiwifruit is actually quite complicated. When the fruit is developing, glucose will increase, which is related to an enzyme called "neutral invertase" (NI). However, as the fruit enters the stage of cell enlargement and starch accumulation, the activity of this enzyme will gradually decrease.

At this stage, the expression level of two other genes will increase, one is β-amylase 9 (BAM9) and the other is sucrose phosphate synthase (SPS). Together, they help sugars to circulate and convert, and starch is slowly formed in this process (Nardozza et al., 2013). The way plant sugars are transported in kiwifruit is also a bit special, which can help sugars be efficiently transported to the developing fruit (Boldingh et al., 2018).

3.2 Organic acid metabolism

3.2.1 Citric acid cycle and its role in kiwifruit

The citric acid cycle (also called TCA cycle) is a very important metabolic process in kiwifruit, which helps the ripening and quality regulation of the fruit. There are two key enzymes involved in this cycle, one is aconitase (ACO4) and the other is aspartate aminotransferase (ASP3). They are not only involved in the conversion of amino acids, but also related to the synthesis of ethylene, which is essential for fruit ripening (Tian et al., 2021). During the development of the fruit, the amount of organic acids changes, and this change is important for maintaining the balance between sugar accumulation and organic acids (Tian et al., 2021; Wang et al., 2021).

3.2.2 Accumulation and changes of organic acids

The organic acids in kiwifruit change with the development stage and variety. When the fruit first begins to develop, the content of organic acids and their derivatives is usually high, and as the fruit matures, these contents will slowly decrease (Xiong et al., 2020).

Quinic acid is an important organic acid in kiwifruit. It not only affects the flavor of the fruit, but is also related to the shikimic acid metabolic pathway, which is also involved in the synthesis of aromatic substances (Mittelstädt et al., 2013). The metabolism of organic acids is also related to the expression of certain genes that control the activity of key enzymes in the TCA cycle (Xiong et al., 2020; Tian et al., 2021; Wang et al., 2021).

4 Secondary Metabolism of Kiwifruit

4.1 Biosynthesis of flavonoids and phenolics

4.1.1 Key enzymes and regulatory genes

The synthesis of flavonoids and phenolics in kiwifruit is relatively complex and requires several important enzymes and related genes. Enzymes such as chalcone synthase (CHS), chalcone isomerase (CHI) and flavonol synthase (FLS) play a central role in the flavonoid biosynthesis pathway (Jia et al., 2022a). Some transcription factors, such as MYBC1 and WRKY44, regulate anthocyanin-related genes, such as F3'H and F3'5'H, which are important for anthocyanin accumulation (Peng et al., 2020). The expression of these genes and the activity of the enzymes will change with the development and maturity stages of the fruit, affecting the amount of phenolics (Liang et al., 2020).

4.1.2 Health benefits and impacts

Flavones and phenolics have strong antioxidant capacity and therefore have many benefits for health. They can remove free radicals in the body and reduce oxidative stress, thereby helping to reduce the risk of heart disease and certain cancers (Pott et al., 2019). Kiwifruit contains some particularly high levels of phenolics, such as epicatechin and some anthocyanins, which also makes kiwifruit more nutritious and a good choice for a healthy diet (Liang et al., 2020). By regulating the production process of these substances, the content of beneficial ingredients in kiwifruit can be further increased (Jia et al., 2022a). .

4.2 Synthesis of terpenes and volatile compounds

4.2.1 Pathways and their contribution to fruit aroma and flavor

Terpenes and various volatile compounds are the main sources of kiwifruit aroma and flavor. These substances are mainly synthesized through two pathways, one is the mevalonate (MVA) pathway and the other is the methylerythritol phosphate (MEP) pathway. These two pathways can produce a variety of volatile components such as monoterpenes and sesquiterpenes (Pott et al., 2019).

By combining metabolome and transcriptome data, scientists have found that these substances are affected by a complex regulatory network during the development and maturity of the fruit (Wang et al., 2021). Ripe kiwifruit can emit a soft fragrance because they contain hundreds of volatile components, which come from the basic metabolites in the fruit (Pott et al., 2019).

4.2.2 Genetic control of the production of volatile compounds

The aroma components in kiwifruit are actually controlled by genes. Some transcription factors and structural genes play a decisive role in the synthesis of these compounds. Scientists have found some key transcription factors that can regulate the expression of related genes such as terpene synthase, allowing kiwifruit to produce specific aromas and flavors (Wang et al., 2021). If we can figure out how these genes control the production of aroma substances, it is possible to breed kiwifruit varieties with better aroma (Shu et al., 2023).

5 Regulation of Metabolic Pathways by Hormones

5.1 Role of plant hormones in metabolism

Plant hormones play an important role in the metabolism of fruits. They affect the growth, development and ripening process of fruits. In kiwifruit, several hormones, including ethylene, abscisic acid (ABA), gibberellins (GA) and cytokinins, are involved in many metabolic reactions. Ethylene can promote fruit ripening by increasing the production of enzymes related to cell wall decomposition and sugar metabolism (Tian et al., 2021). Abscisic acid often works when plants are under stress, and it can also affect the accumulation of metabolites such as ascorbic acid (AsA) (Liao et al., 2021). Gibberellins and cytokinins can cause cells to divide and grow larger, affecting the volume and quality of fruits (Wu et al., 2021b).

5.2 Interaction between hormone signals and metabolic pathways

The relationship between plant hormone signals and metabolic processes is relatively complex, with many levels of regulation. Ethylene and methyl jasmonic acid (MeJA) affect each other. Together, they can activate some NAC genes, which in turn promote the production of enzymes that synthesize ethylene, such as ACS1 (Wu et al., 2020a). ABA helps kiwifruit enhance its cold resistance by activating genes related to reactive oxygen species (ROS) metabolism under low temperature conditions (Jin et al., 2021).

5.3 Case study of hormone regulation in kiwifruit

After using a synthetic cytokinin called Forchlorfenuron (CPPU), kiwifruit fruits became larger and heavier. This is because CPPU promotes cell division and expansion. It also promotes the synthesis of gibberellins and cytokinins, while inhibiting the effects of auxin and ABA. These changes allow the fruit to accumulate more sugar and vitamin C, and the fruit quality is better (Wu et al., 2021b). When certain MYB transcription factors controlled by hormone signals are overexpressed, they affect the accumulation of chlorophyll and carotenoids in kiwifruit (Ampomah-Dwamena et al., 2018) (Figure 2).

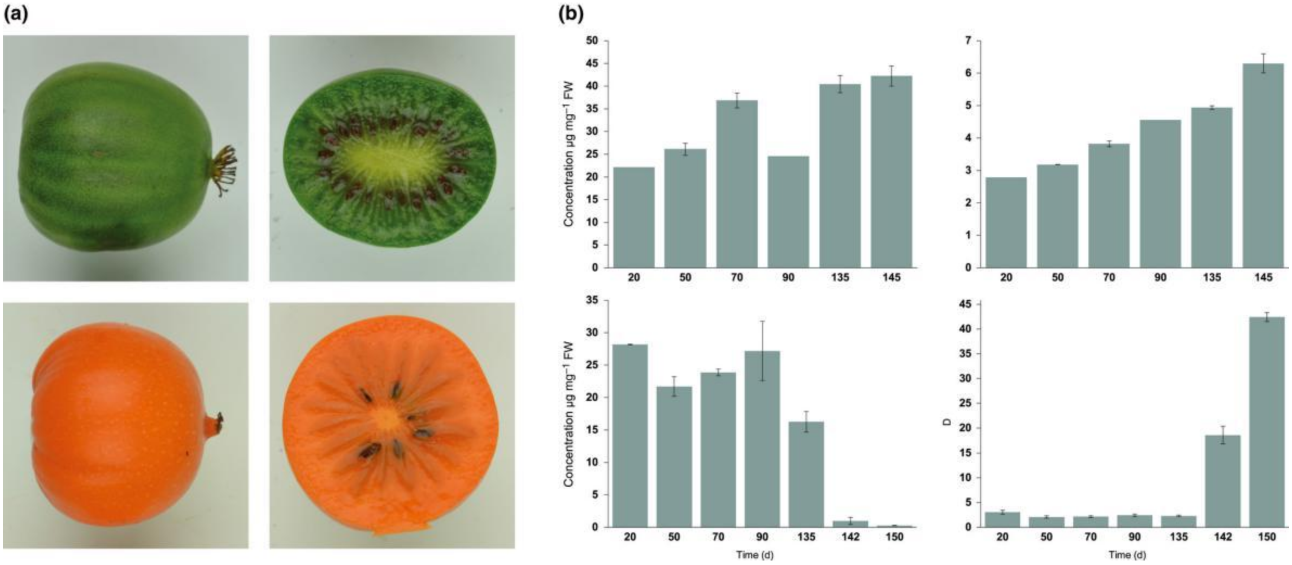

Figure 2 (a) Ripe fruit of *Actinidia arguta* (green) and *Actinidia macrosperma* (orange). (b) Total Chl (left) and total carotenoid concentration (right) in fruit of *A. arguta* (top panel) and *A. macrosperma* (bottom panel) during fruit development. Error bars indicate ± SE from three biological replicates (Adopted from Ampomah-Dwamena et al., 2018)

6 Environmental and Developmental Effects on Metabolic Pathways

6.1 Effects of environmental factors (temperature, light, water) on gene expression and metabolite accumulation

Environmental factors such as temperature, light, and moisture significantly affect the gene expression and metabolite accumulation of kiwifruit. Especially temperature, it has been proven to regulate the expression of genes involved in sugar metabolism. Lower temperatures increased the expression of β - amylase (BAM) genes associated with higher soluble sugar accumulation in kiwifruit. The ethylene response factor (ERF) gene exhibits differential expression in response to temperature changes, and there are complex interactions between environmental signals and metabolic pathways (Gunaseelan et al., 2019).

Light also plays an important role in the process of pigment synthesis. MYB transcription factors can activate genes involved in the synthesis of carotenoids and chlorophyll, which are important for the color and nutritional value of fruits (Ampomah-Dwamena et al., 2018). Although the effect of water on metabolite accumulation has been less studied, it may indirectly affect metabolite accumulation by affecting the stress response of plants.

6.2 Developmental stages and their metabolic characteristics

The metabolic characteristics of kiwifruit vary with developmental stages. In the early stages, the fruit is rich in organic acids, which gradually decrease as the fruit matures. The levels of soluble sugars and starch increase and reach their highest levels at the ripening stage. These changes are regulated by genes involved in sucrose and starch metabolism, and changes in metabolite levels are consistent with changes in the expression of these genes (Xiong et al., 2020).

The accumulation of ascorbic acid (AsA) follows certain rules and reaches its highest level at specific developmental stages. The synthesis of AsA is mainly completed through the L-galactose pathway, in which key enzymes such as GalDH and GalLDH play an important role (Liao et al., 2021).

6.3 Case studies of environmental and developmental regulation

The study revealed the complex relationship between environmental factors, developmental stages, and kiwifruit metabolic regulation. Studies on red-fleshed kiwifruit (*Actinidia chinensis*) found that gene expression and metabolite accumulation were strictly regulated at different developmental and ripening stages. Researchers have identified novel transcription factors that regulate the accumulation of important metabolites such as proanthocyanidins and vitamin C (Shu et al., 2023).

A study on the yellow-fleshed kiwifruit variety "Jinshi No. 1" used metabolomics and transcriptomics to analyze fruits at different developmental stages. Metabolites such as organic acids, lipids, and amino acids showed significant fluctuations in composition at different developmental stages (Xiong et al., 2020). During kiwifruit ripening, the ERF/AP2 gene family showed differential expression in response to temperature and ethylene treatment (Gunaseelan et al., 2019).

7 Metabolite Analysis and Analysis of Kiwifruit

7.1 Metabolite analysis techniques (GC-MS, LC-MS, NMR)

When studying kiwifruit, scientists use some tools to find the metabolites inside. These tools include gas chromatography-mass spectrometry (GC-MS), liquid chromatography-mass spectrometry (LC-MS), and nuclear magnetic resonance (NMR). GC-MS and LC-MS are very sensitive and can separate complex substances and then measure them. For example, some studies have used GC-MS and UPLC-MS/MS to analyze the sugars and organic acids of kiwifruit in the ripening stage after picking, with good results (Mao et al., 2023). NMR can analyze the types and contents of metabolites without destroying the samples, which is also very useful. These techniques are used together to clearly see the metabolic changes that occur in kiwifruit from growth to maturity.

7.2 Quantitative and qualitative analysis of kiwifruit metabolites

Through quantitative and qualitative analysis, scientists can figure out where the nutrition and flavor of kiwifruit come from. There are many metabolites in kiwifruit, such as sugars, organic acids, amino acids, and vitamins, and these substances change as the fruit grows. A study found 285 metabolites in yellow-fleshed kiwifruit, indicating that the content of organic acids, lipids, and amino acids will continue to change during the development of the fruit (Xiong et al., 2020). Another study specifically looked at kiwifruit as it ripened after being picked, and found 12 soluble sugars and 31 organic acids, and their content also changed significantly (Mao et al., 2023).

7.3 Progress in metabolomics in kiwifruit research

The progress of metabolomics has given us a clearer understanding of the metabolic process of kiwifruit. Researchers often analyze metabolomics and transcriptomics together, so that they can better see which genes and metabolites change together. A study integrated the data from these two aspects and found some genes that control the flavor of kiwifruit, which are related to sugars, organic acids, and flavor substances (Wang et al., 2021). Others have used high-resolution metabolomics technology to map the metabolic changes of kiwifruit at different growth stages (Shu et al., 2023).

8 Integration of Metabolic Pathways: A Systems Biology Approach

8.1 Network analysis of metabolic pathways

The metabolic pathways of kiwifruit have complex regulatory networks that control the accumulation of key metabolites. Researchers constructed these networks by integrating metabolomics and transcriptomics data from *Actinidia chinensis* cv. Hongyang at different developmental stages. These networks helped us identify key genes and transcription factors that regulate the metabolism of soluble sugars, organic acids, and important volatiles, which are important for the flavor of kiwifruit (Wang et al., 2021). Studies on red-fleshed kiwifruit revealed which transcriptomics and transcriptional regulatory networks play a key role in metabolic changes during kiwifruit growth, especially the role of some novel transcription factors in regulating the accumulation of proanthocyanidins, vitamin C, and other metabolites (Shu et al., 2023).

8.2 Integrated models of genomics, transcriptomics, and metabolomics

Integrating genomics, transcriptomics, and metabolomics data has provided great help in revealing the metabolic pathways of kiwifruit. Through high-resolution metabolomics and transcriptomics analysis, the researchers divided 515 metabolites and their co-expressed genes into different metabolic and gene modules. This approach provides a comprehensive view of metabolic changes and also identifies key regulatory networks involved in kiwifruit development and ripening (Shu et al., 2023). The combined analysis of proteomics and metabolomics provides a better understanding of the dynamic changes in kiwifruit ripening and helps identify key pathways related to fruit ripening, softening, and sugar and organic acid metabolic balance (Tian et al., 2021).

8.3 Case study of systems biology in kiwifruit metabolism

A study focused on the high ascorbic acid (AsA) content in kiwifruit (*Actinidia eriantha*). The accumulation of AsA is mainly controlled by the L-galactose pathway, while the D-galacturonic acid pathway and AsA cycle pathway also contribute to a certain extent. The study also identified key enzymes and genes related to AsA biosynthesis and regeneration, providing theoretical support for the genetic improvement of kiwifruit quality (Liao et al., 2021) (Figure 3). Another study on the yellow-fleshed kiwifruit variety "Jinshi No. 1" used metabolomics and transcriptomics methods to analyze the nutritional composition and gene expression levels of the fruit, revealing how the levels of nutritional metabolites change dynamically during fruit development and the relationships between these metabolites (Xiong et al., 2020).

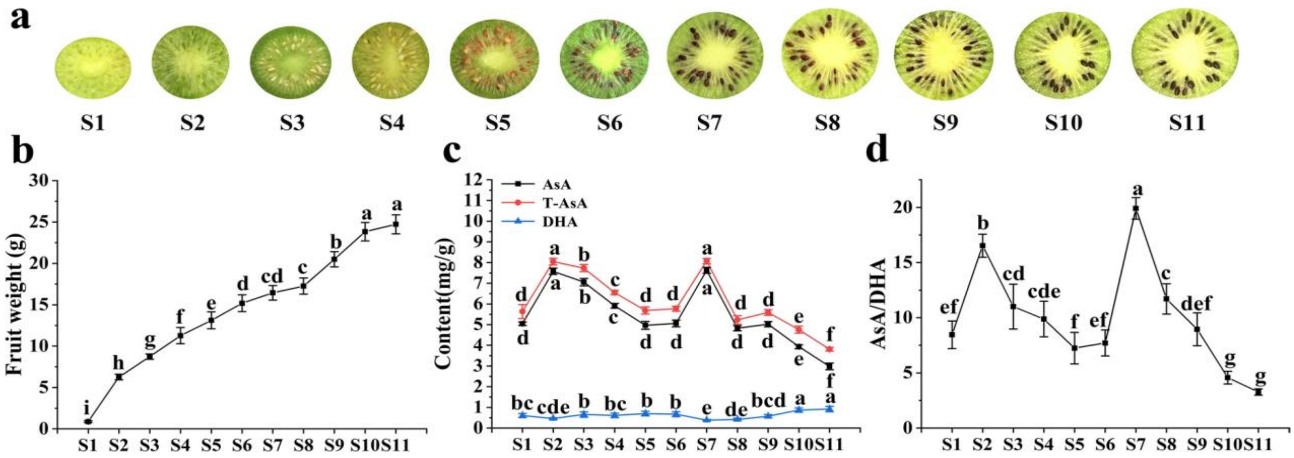

Figure 3 Fruit development of ‘Ganmi 6’ (Adopted from Liao et al., 2021)

Image caption: Fruit: 20 DAF (S1), 35 DAF (S2), 50 DAF (S3), 65 DAF (S4), 80 DAF (S5), 95 DAF (S6), 110 DAF (S7), 125 DAF (S8), 140 DAF (S9), 155 DAF (S10) and 170 DAF (S11). a The transverse of ‘Ganmi 6’ during the fruit development. b The fruit weight change of ‘Ganmi 6’ during the fruit development. c Changes of AsA, T-AsA and DHA content of ‘Ganmi 6’ during the fruit development. d Changes of AsA/DHA ratio during the fruit development. Duncan’s method was used to detect the differences between different development of fruit at $P \leq 0.05$. In the same index, there was no significant difference between stages with the same lowercase letter

9 Application and Impact of Metabolic Pathway Research

9.1 Improving fruit quality and nutritional value through metabolic engineering

Understanding the changes in nutrients and gene expression during fruit development can help researchers find key metabolites and genes that affect fruit quality. When studying the yellow-fleshed kiwifruit variety "Jinshi No. 1", it was found that the metabolism of important components such as sugars, organic acids and ascorbic acid (AsA) was strictly regulated during development. This provides a direction for improving fruit quality through metabolic engineering (Xiong et al., 2020). Studies have found that by regulating the accumulation of metabolites such as proanthocyanidins and vitamin C in red-fleshed kiwifruit, its nutritional content can be improved through genetic modification (Shu et al., 2023). The role of abscisic acid and indoleamine in kiwifruit development and ripening also provides additional targets for improving fruit quality (Commisso et al., 2019).

9.2 Breeding strategies to enhance metabolite profiles

The study of metabolic pathways can help breeding strategies, allowing the selection of kiwifruit varieties to focus more on the superiority of metabolite profiles. Studies comparing different kiwifruit varieties have shown that there are large differences in health-promoting phytochemicals and sugar accumulation, which can be used in breeding programs. Analysis of two cold-tolerant kiwifruit varieties revealed differences in their sugar metabolism and antioxidant capacity, providing breeding information to enhance these traits (Lin et al., 2022). Identification of key enzymes and genes involved in the synthesis of phenolic acids, flavonoids, and AsA can help select varieties with higher nutritional value. Combining metabolomics and transcriptomics data can identify candidate genes and metabolic pathways as breeding targets to help develop kiwifruit varieties with better quality and nutritional content (Jia et al., 2022b).

9.3 Commercial applications and future prospects

Understanding the regulatory networks that affect kiwifruit flavor can help us breed more attractive varieties. The identification of transcription factors and structural genes for flavor-related metabolites lays the foundation for improving fruit flavor using breeding and genetic engineering (Wang et al., 2021). Studying the metabolic pathways of pigment accumulation, such as those regulated by MYB transcription factors, can provide support for the development of kiwifruit varieties with ideal appearance and nutritional characteristics (Ampomah-Dwamena et al., 2018). By integrating metabolome and transcriptome data, establishing a comprehensive metabolic map and regulatory network not only provides valuable resources for improving kiwifruit quality, but also lays the foundation for innovation in future kiwifruit breeding and commercial production (Tian et al., 2021; Shu et al., 2023).

10 Conclusion

Kiwifruit metabolism studies have shown that gene expression and metabolite accumulation have a great impact on fruit development, ripening and quality. Several important enzymes were found in the study, which are involved in starch synthesis and decomposition, ethylene production and amino acid metabolism, and some key regulatory networks were revealed.

During the development and ripening of kiwifruit, researchers have drawn a "map" of metabolic changes and found many laws related to gene expression, such as some transcriptional regulation methods. Plant hormones, such as abscisic acid and indoleacetic acid, have also been shown to play an important role in fruit growth. Some long non-coding RNAs and splicing changes are also related to the synthesis of nutrients and ethylene signaling pathways. The high content of vitamin C in kiwifruit may be related to some synthesis and circulation pathways in its body.

Future research can continue to deepen, such as better understanding which transcription factors and non coding RNAs affect fruit quality, or how different hormones interact with each other. These studies can help us improve the taste and nutrition of fruits. Genomics and metabolomics methods can also be used to identify more genes and enzymes related to flavor and color. If biotechnology is used to manipulate these genes, it may be possible to cultivate new kiwifruit varieties with better nutrition and taste.

These research results are also helpful for horticultural cultivation and the food industry. We can use this information to breed new kiwifruit varieties that are better tasting, more nutritious, and can be preserved for longer. By identifying key genes and enzymes, we can also provide targets for genetic engineering or marker selection breeding. Understanding how environmental factors, such as temperature, affect the accumulation of metabolites, can also help us improve post-harvest handling and storage methods.

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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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