

Research Insights

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Unraveling the Genetic Basis of Fruit Quality in Kiwifruit: Insights from Genomic Studies

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Abstract Different kiwifruit germplasms have obvious genetic differences in fruit quality. To better understand the genetic basis of kiwifruit fruit quality, this study collated the achievements in genomics, transcriptomics and metabolomics in recent years. We focused on introducing the main quality traits such as sweetness, acidity, texture and aroma, and analyzed their genetic regulation methods and related metabolic pathways. The establishment of high-quality reference genomes, the application of high-throughput sequencing, and the acquisition of rich genomic resources have all promoted the discovery of important genes, transcription factors, and quantitative trait loci (QTL) related to quality traits. Through case studies on sweetness, acidity, texture and aroma, we demonstrated how molecular-level research results can be transformed into specific breeding goals. This study also explored the prospects of genomic selection (GS) and marker-assisted selection (MAS) in kiwifruit breeding, as well as the advantages and difficulties of integrating genomic data in breeding. This study provides valuable references for researchers and breeders in cultivating new kiwifruit varieties with better flavor, higher nutrition and stronger market competitiveness.

Keywords Kiwifruit; Fruit quality; Genomics; Breeding; Quantitative trait loci (QTL)

1 Introduction

Kiwifruit (*Actinidia* spp.), a berry crop of the Actinidiaceae family, has a soft texture and a sweet and sour taste. It is rich in essential vitamins (especially vitamin C) and other nutrients, and is known as the "crown of Vitamin C". It is a horticultural crop with significant nutritional and economic value and has been widely cultivated around the world, it is highly favored among consumers (Huang et al., 2013; Wu et al., 2019). Based on its unique flavor, high antioxidant content and potential health care functions, kiwifruit has become a common fruit in many diets (Jia et al., 2023a; Shu et al., 2023). In order to response to the growing global market demand for kiwifruit, extensive research has been conducted on the optimization of cultivation techniques, genetic improvement, and post-harvest quality management of fruits (Commisso et al., 2019; Lei et al., 2022)..

What makes kiwifruit good or bad? The quality of kiwifruit is depends on the following four key characteristics: soluble sugar content, organic acids, vitamins and flavor compounds. These characteristics do two important jobs: it not only determine the taste and nutritional value of the fruit (Wang et al., 2021; Shu et al., 2023), but also influenced consumers' fondness for it and the sales situation in the market. The biosynthesis and regulation of these compounds is a complex process, which is influenced by genetics and environmental factors of growth conditions. To cultivate better kiwifruit, scientists need to understand how these traits function at the molecular level (Wu et al., 2019; Jia et al., 2009). Recent studies have shown that metabolic pathways and gene regulation play significant roles in determining sweetness, acidity and aroma (Wang et al., 2021; Shu et al., 2023).

This study aims to outline the genetic basis of kiwifruit fruit quality and introduce the insights gained from recent genomic research. How we did it? We combined transcriptome, metabolome and genomic data to clarify the key genes and regulatory pathways that control fruit quality. We will also discuss the impact of current research findings on kiwifruit breeding and the potential they hold in developing new kiwifruit varieties with higher quality attributes. We hope this summary of current research, we can provide references for kiwifruit research and breeding work.

2 Genetic Determinants of Fruit Quality

2.1 Key quality traits in kiwifruit

The quality characteristics of kiwifruit are complex quantitative trait, mainly including the following four key features: sweetness, acidity, texture and aroma, which together constitute the flavor of the fruit. Among them, sweetness is the primary indicator for evaluating kiwifruit fruits, and its level is mainly influenced by the content of soluble sugar in the fruit. Studies have shown that there can be significant differences in sugar content among different kiwifruit varieties (Liao et al., 2019; Lee et al., 2020). Acidity determines the astringency of the fruit, and the level of acidity depends on the content of organic acids such as quinic acid and citric acid (Wang et al., 2021). The ratio of sour to sweet is the key to determining the best flavor and texture experience. Texture is influenced by fruit hardness and the balance of starch synthesis and degradation during ripening. Texture is an important characteristic of consumer preference (Tian et al., 2021). The texture characteristics of different varieties vary significantly. Aroma is determined by the composition and content of volatile compounds. Aroma affects the overall flavor characteristics (Wang et al., 2021).

2.2 Overview of genetic factors influencing these traits

The quality characteristics of kiwifruit are jointly regulated by multiple genes, and its genetic basis is rather complex, involving multiple regulatory networks. In terms of sweetness, some genes involved in carbohydrate metabolism play a key role, such as genes encoding enzymes like pyruvate kinase and hexokinase, which regulate the sweetness of kiwifruit (Jia et al., 2023a). The acidity of fruits is mainly influenced by genes related to organic acid metabolism, which are involved in metabolic processes such as the tricarboxylic acid (TCA) cycle. Studies have shown that texture is related to two types of genes, one type is AGPase, SS, SBE and BM5 that regulate starch degradation, and the other type is ACO4 and ACS9 that participate in ethylene synthesis (Tian et al., 2021). The formation of aroma is related to the synthesis of volatile substances. Therefore, the aroma characteristics are controlled by the gene network that regulates the biosynthesis of volatile compounds. Existing studies have demonstrated that some key transcription factors regulate the metabolism of soluble sugars, organic acids and volatile substances (Wang et al., 2021).

2.3 Importance of understanding genetic basis for breeding programs

The genetic research on the quality of kiwifruit fruits has significant theoretical guiding significance for subsequent variety improvement and breeding work. When we understand which genes control quality, we can make smarter breeding choices. The application of genomic selection (GS) technology can significantly shorten the breeding cycle and also improve the accuracy of selection. Through this technology, breeders use molecular markers to select parent plants, which are associated with superior traits. By analyzing traits such as sweetness, acidity, texture and aroma, GS can predict breeding values and help breeders screen out plants that may produce high-quality offspring (Cheng et al., 2019). Recent progress has also been of great help. Now, the research on high-quality genomic data and metabolic maps of kiwifruit has been successively released, which further prompts researchers to better study the genetic mechanism of quality traits and promotes the application of related genetic knowledge in breeding practice (Wu et al., 2019; Shu et al., 2023). Ultimately, these genetic discoveries will help cultivate new varieties of high-quality kiwifruit to meet consumers' preferences and market demands.

3 Advances in Kiwifruit Genomics

3.1 Recent genomic studies and their methodologies

Scientists have made big progress in understanding kiwifruit genes using modern techniques. Here are some key findings: Jia et al. (2023a) utilized PacBio single-molecule real-time (SMRT) sequencing technology to provide the first set of gene isoforms from the full-length transcriptome of *Actinidia arguta* cv. Qinzhiyu. They also provides insights into the molecular mechanisms of biosynthesis of soluble sugars, organic acids and anthocyanins. Shu et al. (2023) utilized high-resolution metabolomics and transcriptomics analysis to investigate the metabolic profiles of *A. chinensis* at different developmental and maturation stages. By integrating bioinformatics and functional genomics analysis, they revealed the key regulatory networks of major metabolic changes (Figure 1). Liao et al. (2019) used SSR markers to evaluate the genetic diversity of fruit quality traits in 145 wild kiwifruit (*A. eriantha*) samples and established the association between fruit quality traits and genotypes with specific allelic variations.

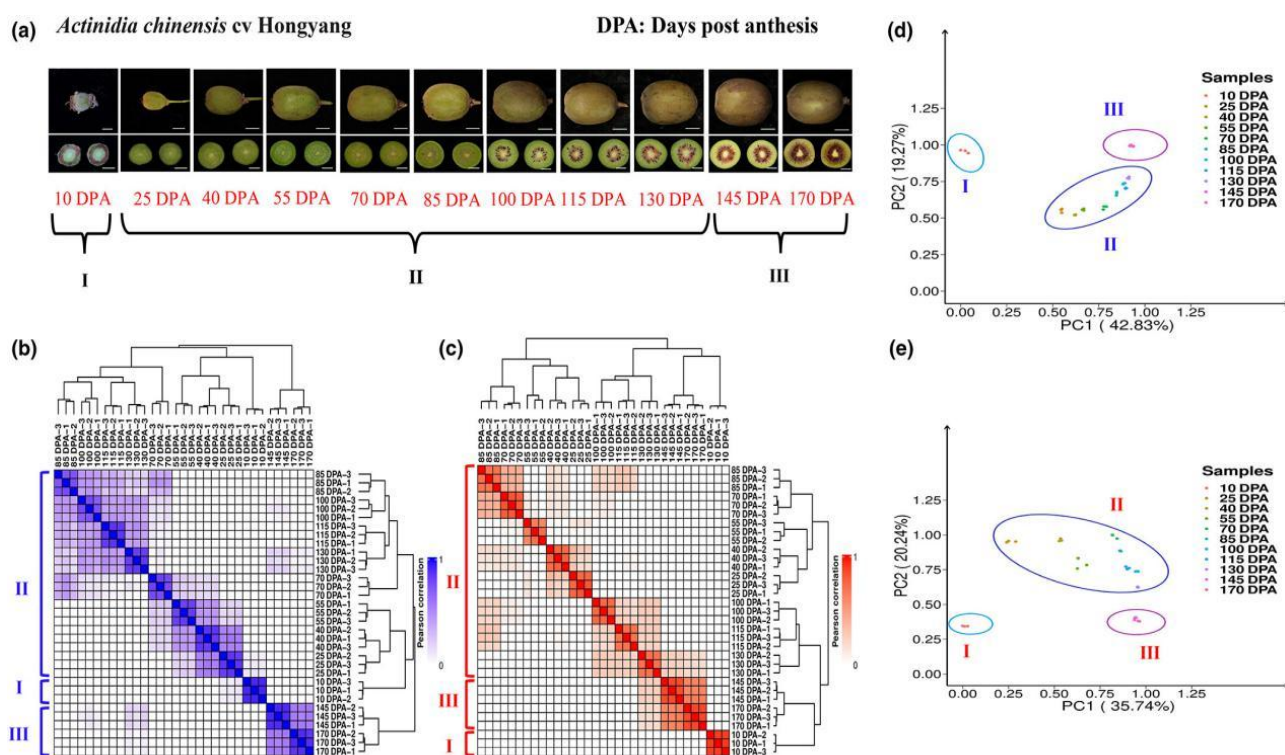


Figure 1 Summary of metabolome and transcriptome data sets (Adopted from Shu et al., 2023)

Image caption: (a) Phenotypic changes in kiwifruits (*Actinidia chinensis* cv Hongyang) at 11 different fruit developmental and ripening stages (FDRSs). Intact and sectioned kiwifruits were photographed at 10, 25, 40, 55, 70, 85, 100, 115, 130, 145, and 170 d postanthesis (DPA). Bar, 1 cm. (b, c) Cluster analysis for metabolomes (b) and transcriptomes (c). The color scales 0–1 represent Pearson correlation coefficient. (d, e) Principal component analysis for metabolomes (d) and transcriptomes (e). Kiwifruits at the 11 FDRSs can be categorized into three major Groups I, II, and III based on purple, green, or yellow phenotypes in pericarps (a), metabolomes (b, d), and transcriptomes (c, e) (Adopted from Shu et al., 2023)

3.2 High-throughput sequencing technologies and their impact on kiwifruit research

High-throughput sequencing technology, with its ability to generate high-quality genomic data, has significantly advanced research related to kiwifruit. Wu et al. (2019) constructed an improved chromosomal level reference genome (v3.0) of kiwifruit using PacBio long-read sequencing technology and Hi-C data. Compared with previous versions, improvements include: this reference genome has significant improvements in continuity, accuracy and gene annotation. Tilahun et al. (2020) sequenced the total mRNA of Gold 'Haegeum' kiwifruit using the Illumina high-throughput sequencing platform, identified the differentially expressed genes (DEGs) during the kiwifruit ripening process, and through in-depth analysis of the expression patterns of DEGs, further understood the impact of ethylene treatment on kiwifruit ripening and related changes at the genomic level. It provides valuable information for revealing the impact of ethylene treatment on fruit quality. The application of these technologies has greatly promoted the identification of key regulatory pathways and genes in the ripening, metabolism and quality improvement of kiwifruit.

3.3 Genomic resources available for kiwifruit

At present, significant progress has been made in the genetic research of kiwifruit. Researchers have established multiple genomic databases and reference genomes, providing fundamental resources for subsequent studies. Wu et al. (2019) completed the construction of a high-quality reference genome (v3.0) of *Actinidia chinensis*, which is an important resource, containing 40,464 annotated protein-coding genes. Through further genetic collinearity analysis, they found that the *Actinidia chinensis* genome underwent two genome-wide replication events (Wu et al., 2019). In addition, there have been relevant research results reported on transcriptome datasets generated based on multiple kiwifruit varieties. Such as the full-length transcriptome of *A. arguta* cv. Qinzhiyu (Jia et al., 2023a) and the transcriptome of Gold 'Haegeum' kiwifruit (Tilahun et al., 2020), these datasets can help researchers better understand gene expression and its regulatory mechanisms. These genomic and transcriptomic

resources are helpful for: studying the molecular characteristics of kiwifruit, supporting breeding efforts, and conducting evolutionary research. Researchers have made a major discovery using the most advanced genomic technology available today. By using high-throughput sequencing methods and a large amount of genomic data, they have made it clearer how the quality of kiwifruit is inherited. These achievements have also provided new ideas for improving the quality of kiwifruit.

4 Key Genes and QTLs Associated with Fruit Quality

4.1 Identification of major genes influencing fruit quality traits

In the study of kiwifruit (*Actinidia arguta* cv. Qinziyu), Jia et al. (2023a) discovered some key enzyme genes, which play important roles in carbohydrate and amino acid metabolism. Among them, the pyruvate kinase gene (PK), enolase gene (ENO), hexokinase gene (HK), and phosphoglycerate kinase gene (PGK) are particularly worthy of attention, as they may be involved in the regulation of kiwifruit quality. Meanwhile, Jia et al. (2023a) also identified and analyzed members of the bHLH gene family that regulate anthocyanin biosynthesis in *Actinidia arguta* cv. Qinziyu (Table 1). These members of the gene family are closely related to the presentation of fruit color and the formation of nutritional quality. In addition, Shu et al. (2023) conducted a study on *Actinidia chinensis*, revealing the parallel classification of 515 metabolites and their co-expressed genes, and also discovered new transcription factors that can regulate the accumulation of proanthocyanidins, vitamin C and other important metabolites.

4.2 Quantitative trait loci (QTL) mapping and its findings

QTL mapping, as an important molecular biology research method, has been widely applied to identify regions of the genome associated with fruit quality traits in various fruits, including kiwifruit. In melon (*Cucumis melo*), with the aid of QTL mapping technology, 33 stable QTLs involved in sugar and carotenoid content, fruit and seed morphology were identified. At the same time, the major loci controlling external color of immature fruit and mottled rind were also located (Pereira et al., 2018). In apricot (*Prunus armeniaca* L.), the significant QTLs were localized in LG4 linkage group, which is related to soluble solids content, and the QTL located in LG3 is related to the color of peel and pulp. Further analysis revealed that the relevant candidate genes involved in D-glucose and D-mannose binding and MYB genes linked to peel color (García-Gómez et al., 2019). In papaya study, 21 QTLs were identified for key fruit quality traits, including important indicators such as pulp sweetness, fruit weight, and firmness, with some QTLs could explain 19.8% of the phenotypic variance (Nantawan et al., 2019).

4.3 Functional validation of candidate genes through genetic and biochemical approaches

Functional validation of candidate genes is crucial to confirm their roles in fruit quality traits. In the research on apricot, some scholars used qPCR technology to analyze the expression of nine candidate genes associated with identified QTL. The results showed that there were different expression patterns throughout the fruit development stage and between the comparison genotypes, verifying the correlation between the genes and the associated QTL. Among them, the *MYB10* gene was verified and confirmed as a key candidate gene affecting the peel color (García-Gómez et al., 2019). In melon, the metabolic activity of the *CmThAT1* gene was validated in bacteria and *in vitro*, confirming this gene plays a role in producing S-methyl-thioacetate (a key aroma component) (Galpaz et al., 2018). In the research of kiwifruit, through the comprehensive application of proteomic and metabolomic analysis, some key enzymes (AGPase, SS, SBE, and BMY) were identified, which are crucial for starch synthesis and degradation. Additionally, ACO4 and ACS9 are essential for ethylene synthesis. These key enzymes all have significant influences on fruit ripening and quality (Tian et al., 2021).

We have integrated genomic, transcriptomic and metabolomic data. The above research results have provided a more comprehensive understanding of the genetic basis of fruit quality in kiwifruit and other fruits, laying a foundation for future research on marker-assisted breeding and genetic improvement of fruit quality traits.

Table 1 Details of candidate anthocyanin biosynthesis-related AabHLH gene family in *A. arguta* cv. Qinziyu (Adopted from Jia et al., 2023a)

Name	Transcript ID	Homologous Gene Name	Protein ID	Identity (%)	CDS Length (bp)	Protein Size (aa)	Molecular Weight (Da)	Isoelectric Points	Location
AabHLH15	dazi_transcript_50917	AcbHLH42 (<i>A. chinensis</i>)	QAT77714.1	93.68	2333	520	57 493.60	5.06	Nuclear
AabHLH10	dazi_transcript_36784	AtEGL3, AtGL3 (<i>A. thaliana</i>)	NP_001185302.1	53.85	1352	290	31 530.91	5.82	Nuclear
AabHLH39	dazi_transcript_65784	AtTT8 (<i>A. thaliana</i>)	NP_192720.2	53.33	3439	138	14 914.02	9.89	Nuclear
AabHLH8	dazi_transcript_66315	AtEGL3, AtGL3 (<i>A. thaliana</i>)	NP_001185302.1	52.00	2157	175	19 926.09	5.70	Nuclear
AabHLH9	dazi_transcript_54058	AtEGL3, AtGL3 (<i>A. thaliana</i>)	NP_001185302.1	51.92	1327	289	31 609.09	5.23	Nuclear
AabHLH7	dazi_transcript_27074	AtEGL3, AtTT8 (<i>A. thaliana</i>)	NP_001332706.1	50.00	1132	273	30 150.45	5.89	Nuclear
AabHLH4	dazi_transcript_70053	SlAH (<i>S. lycopersicum</i>)	ALC74034.1	50.94	1661	320	35 826.42	5.88	Nuclear
AabHLH13	dazi_transcript_71260	SlAH (<i>S. lycopersicum</i>)	ALC74034.1	50.00	1821	317	35 412.00	5.88	Nuclear
AabHLH25	dazi_transcript_56358	SlAH (<i>S. lycopersicum</i>)	ALC74034.1	56.25	1630	259	28 501.88	6.33	Nuclear
AabHLH31	dazi_transcript_47866	SlAH (<i>S. lycopersicum</i>)	ALC74034.1	56.25	1535	264	29 028.87	9.19	Nuclear

5 Case Studies

5.1 Detailed case study on the genetic control of sweetness in kiwifruit

5.1.1 Identification and functional analysis of key genes

The sweetness of kiwifruit is mainly influenced by the metabolism of soluble sugar. By comprehensively analyzing metabolome and genome-wide transcriptome data, researchers have identified some key genes and transcription factors involved in regulating the process of soluble sugar metabolism. Studies using the *Actinidia chinensis* cv. Hongyang as experimental materials have shown that the level of soluble sugar changes during fruit development and ripening, and these changes are jointly regulated by multiple genes related to sugar synthesis and decomposition. This is a complex regulatory network (Wang et al., 2021), which has a significant impact on the final sweetness of the fruit.

5.1.2 Impact on breeding for sweeter varieties

Identifying the key genes that regulate the synthesis and degradation of sugar is very helpful for the breeding work to improve the sweetness of kiwifruit. Breeders can precisely manipulate these key genes through selective breeding or genetic engineering methods, thereby influencing the metabolism of soluble sugar in fruits and enhancing their sweetness. Insights gained from the regulatory network also provide practical guidance, which can help breeders select parent plants with ideal traits, thereby optimizing the breeding mix. This not only helps to shorten the breeding cycle, but also accelerates the cultivation of new and sweeter kiwi cultivars (Wang et al., 2021).

5.2 Case study on the genetic basis of acidity

5.2.1 QTL mapping and candidate genes

Through the analysis of organic acid metabolism in kiwifruit, researchers have gained a certain understanding of the genetic basis of acidity. Studies have found that citric acid and malic acid play major roles in regulating the acid quality of kiwifruit and are the key substances that determine the acidity level. In the case of *Actinidia eriantha*, The concentration of citric acid in its body is relatively high, which is because the activity of citrate synthase (CS) has been enhanced. And the activities of some enzymes related to citric acid degradation [such as mitochondrial aconitase (Mit-ACO) and NAD-dependent isocitrate dehydrogenase (NAD-IDH)] have decreased. Similarly, the accumulation of malic acid is similar, and it is influenced by the activities of NAD-dependent malate dehydrogenase (NAD-MDH) and phosphoenolpyruvate carboxylase (PEPC) (Jia et al., 2023b).

5.2.2 Breeding implications

Using QTL mapping and by finding important genes like AeCS2 and AeMDH2 (Jia et al., 2023b), researchers have gained useful clues about how kiwifruit acidity is controlled by genes. With a better understanding of what these genes do, breeders may be able to adjust them using tools like gene editing. This could help create new types of kiwifruit with better acidity, which would improve their taste and make them more appealing to consumers.

5.3 Case study on texture and aroma

5.3.1 Genomic insights and key genetic players

The texture and aroma of kiwifruit are important quality indicators that will directly affect consumers' choices. In recent years, genomic research has helped us identify the key genetic factors that regulate these traits. Through a comprehensive analysis of metabolome and transcriptomic data, researchers have identified a variety of volatile substances that affect the aroma. These substances have specific regulatory networks that help form the unique aroma of kiwifruit. Wang et al. (2021) have revealed the role of some specific transcription factors in regulating the biosynthesis of these volatile substances (Figure 2). These findings provide important clues for understanding the formation mechanism of the aroma of kiwifruit.

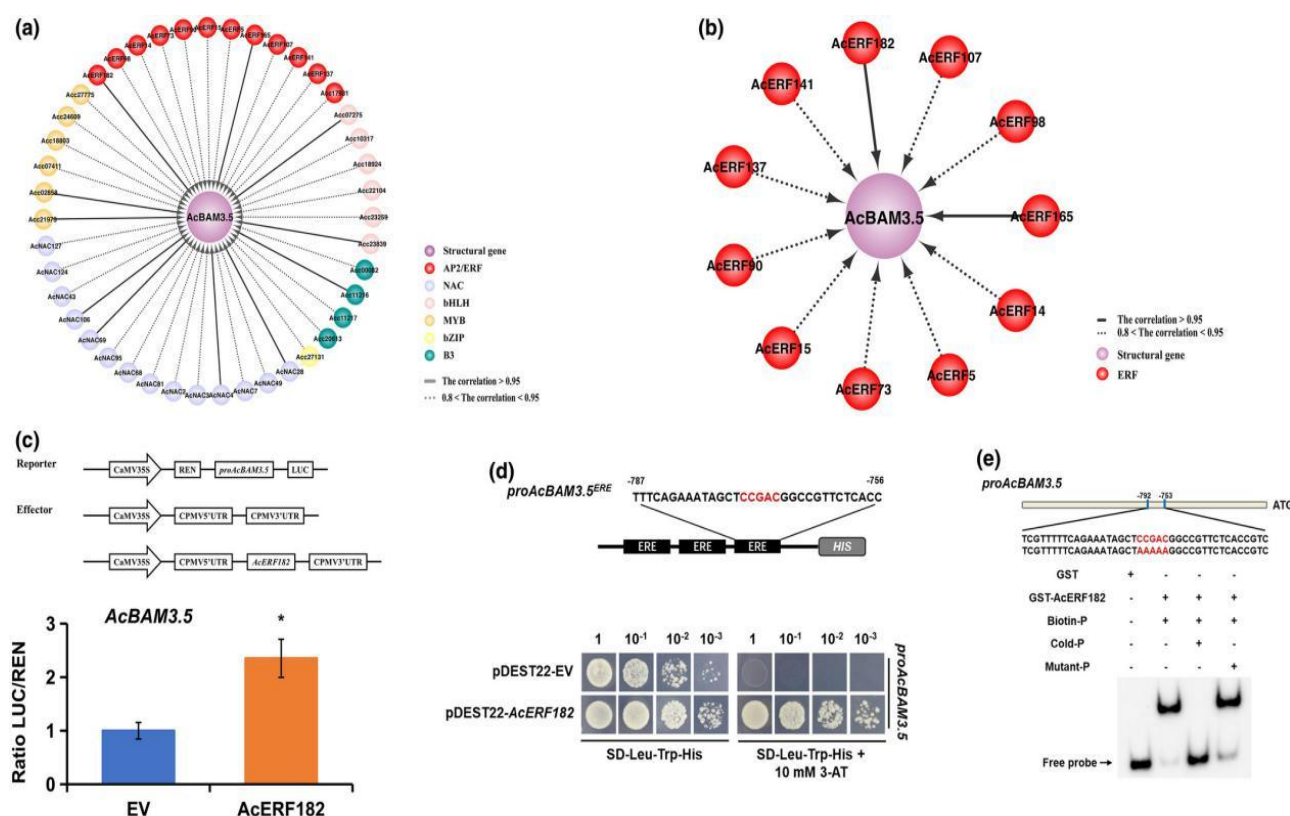


Figure 2 Identification of AcERF182 as a key transcription factor regulating AcBAM3.5 in kiwifruit (Adopt from Wang et al., 2021)

5.3.2 Practical applications in improving texture and aroma

These genomic studies have found many practical uses. Researchers can now better improve the quality of kiwifruit. Specifically, on the basis of understanding the genetics of texture and aroma, breeders can develop kiwifruit varieties with better sensory quality. For instance, regulating the expression of genes involved in the biosynthesis of volatile substances can make fruits more fragrant; regulating genes related to cell wall metabolism can improve fruit texture. Through these methods, kiwifruit that not only tastes better but also has a more attractive texture can be produced, thus better meeting consumers' demands (Xiong et al., 2020; Wang et al., 2021).

The combination of genomic and metabolomic data research has helped us better understand the formation mechanism of kiwifruit quality. In particular, there is a more comprehensive understanding of the genetic basis of important characteristics such as sweetness, acidity, texture and aroma. These research findings are very helpful for kiwifruit breeding work and can assist breeders in developing new varieties with better quality.

6 Integrating Genomic Data in Breeding Programs

6.1 Genomic selection and marker-assisted selection in kiwifruit breeding

Genomic selection (GS) and marker-assisted selection (MAS) are two commonly methods in current plant breeding. Both methods have their own characteristics: MAS has been traditionally used to select for traits controlled by a few major genes, making it effective for traits with large-effect quantitative trait loci (QTL) (Budhlakoti et al., 2022; Merrick et al., 2022). However, in kiwifruit breeding, the application of MAS is limited for complex traits controlled by multiple minor effect alleles, which are common in kiwifruit, such as yield, fruit quality, and disease resistance (Cheng et al., 2019; Budhlakoti et al., 2022).

As for GS, it assesses the breeding value of individuals through genome-wide marker analysis. This method can effectively integrate the cumulative effects of multiple micro-effect genes (Cheng et al., 2019; Budhlakoti et al., 2022). At present, GS has achieved remarkable results in crop breeding such as corn, sugarcane and apples, and researchers have also begun to gradually apply it to kiwifruit breeding (Cheng et al., 2019; Jung et al., 2020; Budhlakoti et al., 2022). The development of sequencing-based genotyping (GBS) and advanced statistical models

has promoted the application effect of GS in kiwifruit, significantly improving the prediction accuracy of breeding value (Cheng et al., 2019).

6.2 Benefits and challenges of using genomic information in breeding

There are many advantages to using genomic information in breeding. This method can use a large number of gene markers for seed selection, which can improve the accuracy of selection and has a better improvement effect (Cheng et al., 2019; Larkin et al., 2019; Budhlakoti et al., 2022). Especially for some complex traits, when the effect of traditional breeding methods is limited, this method becomes particularly effective. GS can also shorten the breeding cycle, eliminating the need for excessive phenotypic assays, and thus the demand for extensive phenotypic testing is reduced, making the entire breeding process more efficient and cost-effective (Larkin et al., 2019; Budhlakoti et al., 2022).

However, there are still several problems that need to be solved in the practical application of GS technology. This technology is very costly. It is necessary to purchase expensive genetic testing equipment and build a dedicated data management system (Nti-Addae et al., 2019; Sandhu et al., 2022). The prediction results may not be 100% accurate. It is influenced by multiple factors, including how many gene markers are used, the genetic characteristics of the traits themselves, the relationship between training data and validation data, etc. (Larkin et al., 2019; Robertsen et al., 2019). To make good use of GS technology, professional talents are also needed. Experts who understand statistical analysis and bioinformatics are needed to truly apply genetic data to breeding (Larkin et al., 2019; Budhlakoti et al., 2022).

6.3 Case examples of successful integration of genomic data in breeding programs

So far, multiple studies have demonstrated the practical application effects of genomic data in breeding. In apple breeding, Jung et al. (2020) proposed an apple REFPOP, which is a reference population of 534 genotypes, has been established to accelerate breeding through genomics-assisted selection. This population is suitable for the identification of marker-trait associations, and makes it possible to improve the predictive ability of key traits such as floral emergence and harvest date.

In sugarcane, Sandhu et al. (2022) proposed an integrated approach combining GS with high-throughput phenotyping, genotyping, and machine learning, which can fully leverage its potential, to enhance genetic gain and accelerate the breeding cycle. This approach leverages the breeder's equation to optimize selection intensity and accuracy (Sandhu et al., 2022).

Some practical progress has also been made in kiwifruit breeding research. Hale et al. (2018) developed molecular markers that can distinguish male and female plants, which are applicable to varieties such as *Actinidia arguta* and *A. kolomikta*. These markers can identify the gender of the plant at the seedling stage, which greatly facilitates breeding work. In addition, researchers also applied genotyping technology (GBS) and new statistical analysis methods. These techniques help breeders identify those genes with less effect, improving the accuracy of seed selection (Cheng et al., 2019). These examples clearly demonstrate the three major benefits that genomic data brings to breeding work: more accurate seed selection, faster breeding, and better improvement effects. These innovative methods are transforming the traditional breeding model.

7 Future Directions and Research Gaps

7.1 Emerging technologies and their potential impact on kiwifruit genomic research

New metabolomics and transcriptomics technologies have enabled us to have a clearer understanding of the metabolic process of kiwifruit. These new technologies and methods have helped scientists identify the key metabolites and their regulatory networks, thereby clearly depicting the changing patterns of metabolites during the growth and ripening of fruits (Shu et al., 2023). PacBio single-molecule real-time (SMRT) sequencing technology has also been used to construct full-length transcriptomes, enabling us to understand the formation process of fruit quality at the molecular level (Jia et al., 2023a). In the future, researchers can combine these tools and apply CRISPR/Cas9 gene editing and new bioinformatics methods to further explore more genes related to the quality traits of kiwifruit fruits.

7.2 Identification of research gaps and areas needing further investigation

Although significant progress has been made in the genomic research of kiwifruit, there are still some gaps. First of all, our understanding of the complex genetic networks that control the taste and ripening of fruits is still insufficient. Although existing studies have preliminarily revealed these networks by combining metabolomics data and whole-genome transcriptome data, the key genes and regulatory factors therein have not been fully clarified (Wang et al., 2021). Secondly, the utilization of wild kiwifruit resources is still very limited. Some studies on the correlation analysis of wild species diversity and SSR have found that there are significant differences in important quality traits among different germplasms (Liao et al., 2019). These valuable germplasm resources have important breeding value and remain to be developed. Future research needs to focus on: in-depth analysis of these genetic resources and making better use of them in breeding programs.

7.3 Future prospects for enhancing fruit quality through genomic approaches

The key to improving the quality of kiwifruit in the future lies in fully utilizing genomic technology to discover and regulate key functional genes. Existing studies have found that: Proteomics and metabolomics studies have shown that pathways such as starch synthesis and degradation, ethylene synthesis and amino acid metabolism directly affect fruit ripening and quality (Tian et al., 2021). Transcriptomic studies have shown that metabolic pathways such as the L-galactose pathway are also important for improving the nutritional value of fruits (Lei et al., 2022). Furthermore, researchers also discovered differentially expressed genes and long non-coding RNA (lncRNAs) related to maturation and softening, which may be new targets for genetic improvement (Tilahun et al., 2020; Chen et al., 2021). Combining these genomic discoveries with modern breeding techniques can cultivate new varieties of high-quality kiwifruit that have better taste, richer nutrition and better storage capacity.

In conclusion, integrating innovative technologies, overcoming research difficulties and applying genomic approaches offer great potential for improving the quality of kiwifruit. Through continuous exploration in these key areas, we can not only gain a deeper understanding of the genetic essence of kiwifruit quality traits, but also accelerate the cultivation of higher-quality new kiwifruit varieties, ultimately achieving a win-win situation for industrial upgrading and consumption upgrading.

8 Concluding Remarks

The latest genomic research has enabled us to have a better understanding of the genetic characteristics of kiwifruit quality. The completion of sequencing of the high-quality reference genome (v3.0) of *Actinidia chinensis* provides a comprehensive resource for identifying genes related to important traits. Metabolomics and transcriptomics analyses have revealed the dynamic changes in metabolites and gene expression during the growth, development and ripening of kiwifruit, and have also pointed out the key regulatory networks involved in the accumulation of carbohydrates, flavonoids and vitamins. Nowadays, breeders use genomic selection (GS) technology to predict the complex traits of fruits more accurately, making breeding plans more effective. The full-length transcriptome data further clarified the molecular mechanism of fruit quality formation.

These genomic discoveries will be very helpful for future research and breeding. Nowadays, with high-quality genomic data and genetic testing tools such as SNP chips, it has become simpler and more accurate to select superior traits during breeding. Scientists have identified some key genes and metabolic pathways that control traits such as sweetness, color and nutrition. These findings point the way for genetic engineering and marker-assisted selection. It is also very important to study the genetic diversity and population structure of kiwifruit, which can not only protect and utilize germplasm resources but also provide materials for long-term breeding. Looking to the future, research should: verify the functions of promising genes more, develop new biotechnological methods, so as to improve the quality of fruits.

Genomics can help us understand the complex genetic mechanisms that affect the fruit quality of kiwifruit. By integrating genomics, transcriptomics and metabolomics data, researchers have gained a broader understanding of the molecular processes behind fruit growth and quality traits. These advancements not only deepen our fundamental knowledge of kiwifruit biology, but also provide new methods for cultivating better varieties. With the continuous advancement of genomic technology, breeding work has become more efficient: on the one hand, it

can more accurately select and breed good varieties; on the other hand, it can also more conveniently apply genetic technology to improve fruit quality. This will make kiwifruit taste better, be more nutritious and more popular among consumers.

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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.

References

- Budhlakoti N., Kushwaha A., Rai A., Chaturvedi K., Kumar A., Pradhan A., Kumar U., Kumar R., Juliana P., Mishra D., and Kumar S., 2022, Genomic selection: a tool for accelerating the efficiency of molecular breeding for development of climate-resilient crops, *Frontiers in Genetics*, 13: 832153.
<https://doi.org/10.3389/fgene.2022.832153>
- Chen Y., Cheng C., Feng X., Lai R., Gao M., Chen W., and Wu R., 2021, Integrated analysis of lncRNA and mRNA transcriptomes reveals the potential regulatory role of lncRNA in kiwifruit ripening and softening, *Scientific Reports*, 11(1): 1671.
<https://doi.org/10.1038/s41598-021-81155-1>
- Cheng C., Datson P., Hilario E., Deng C., Manako K., McNeillage M., Bomert M., and Hoeata K., 2019, Genomic predictions in diploid *Actinidia chinensis* (kiwifruit), *European Journal of Horticultural Science*, 84(4): 213-217.
<https://doi.org/10.17660/eJHS.2019/84.4.3>
- Commisso M., Negri S., Bianconi M., Gambini S., Avesani S., Ceoldo S., Avesani L., and Guzzo F., 2019, Untargeted and Targeted Metabolomics and Tryptophan Decarboxylase In Vivo Characterization Provide Novel Insight on the Development of Kiwifruits (*Actinidia deliciosa*), *International Journal of Molecular Sciences*, 20(4): 897.
<https://doi.org/10.3390/ijms20040897>
- Galpaz N., Gonda I., Shem-Tov D., Barad O., Tzuri G., Lev S., Fei Z., Xu Y., Mao L., Jiao C., Harel-Beja R., Doron-Faigenboim A., Tzfadia O., Bar E., Meir A., Sa'ar U., Fait A., Halperin E., Kenigswald M., Fallik E., Lombardi N., Kol G., Ronen G., Burger Y., Gur A., Tadmor Y., Portnoy V., Schaffer A., Lewinsohn E., Giovannoni J., and Katzir N., 2018, Deciphering genetic factors that determine melon fruit-quality traits using RNA-Seq-based high-resolution QTL and eQTL mapping, *The Plant Journal*, 94: 169-191.
<https://doi.org/10.1111/tpj.13838>
- García-Gómez B., Salazar J., Dondini L., Martínez-Gómez P., and Ruiz D., 2019, Identification of QTLs linked to fruit quality traits in apricot (*Prunus armeniaca* L.) and biological validation through gene expression analysis using qPCR, *Molecular Breeding*, 39: 1-19.
<https://doi.org/10.1007/s11032-018-0926-7>
- Hale I., Melo A., and Gustafson H., 2018, Sex-linked molecular markers for two cold-hardy kiwifruit species, *Actinidia arguta* and *A. kolomikta*, *European Journal of Horticultural Science*, 83(4): 236-246.
<https://doi.org/10.17660/eJHS.2018/83.4.4>
- Huang S., Ding J., Deng D., Tang W., Sun H., Liu D., Zhang L., Niu X., Zhang X., Meng M., Yu J., Liu J., Han Y., Shi W., Zhang D., Cao S., Wei Z., Cui Y., Xia Y., Zeng H., Bao K., Lin L., Min Y., Zhang H., Miao M., Tang X., Zhu Y., Sui Y., Li G., Sun H., Yue J., Sun J., Liu F., Zhou L., Lei L., Zheng X., Liu M., Huang L., Song J., Xu C., Li J., Ye K., Zhong S., Lu B., He G., Xiao F., Wang H., Zheng H., Fei Z., and Liu Y., 2013, Draft genome of the kiwifruit *Actinidia chinensis*, *Nature Communications*, 4(1): 2640.
<https://doi.org/10.1038/ncomms3640>
- Jia D., Xu Z., Chen L., Huang Q., Huang C., Tao J., Qu X., and Xu X., 2023b, Analysis of organic acid metabolism reveals citric acid and malic acid play major roles in determining acid quality during the development of kiwifruit (*Actinidia eriantha*), *Journal of the Science of Food and Agriculture*, 103(12): 6055-6069.
<https://doi.org/10.1002/jsfa.12678>
- Jia Y., Zhang Y., Zhang L., Wang F., Yu G., Wang Y., Kang X., and Wu Y., 2023a, Characterization and Analysis of the Full-Length Transcriptome Provide Insights into Fruit Quality Formation in Kiwifruit Cultivar *Actinidia arguta* cv. Qinzhiyu, *Agronomy*, 13(1): 143.
<https://doi.org/10.3390/agronomy13010143>
- Jung M., Roth M., Aranzana M., Auwerkerken A., Bink M., Denancé C., Dujak C., Durel C., Forcada C., Cantín C., Guerra W., Howard N., Keller B., Lewandowski M., Ordidge M., Rymenants M., Sanin N., Studer B., Żurawicz E., Laurens F., Patocchi A., and Muranty H., 2020, The apple REFPOP-a reference population for genomics-assisted breeding in apple, *Horticulture Research*, 7: 189.
<https://doi.org/10.1038/s41438-020-00408-8>
- Larkin D., Lozada D., and Mason R., 2019, Genomic selection-considerations for successful implementation in wheat breeding programs, *Agronomy*, 9(9): 479.
<https://doi.org/10.3390/agronomy9090479>
- Lee M., Kim H., Rhee H., Kwack Y., Kumarihami H.M.P.C., and Kim J., 2020, Evaluation of the genetic resources of kiwifruit with multivariate analysis, *Korean Journal of Horticultural Science and Technology*, 38(4): 569-581.
<https://doi.org/10.7235/HORT.20200053>

- Lei D., Lin Y., Chen Q., Zhao B., Tang H., Zhang Y., Chen Q., Wang Y., Li M., He W., Luo Y., Wang X., Tang H., and Zhang Y., 2022, Transcriptomic analysis and the effect of maturity stage on fruit quality reveal the importance of the l-galactose pathway in the ascorbate biosynthesis of hardy kiwifruit (*Actinidia arguta*), *International Journal of Molecular Sciences*, 23(12): 6816.
<https://doi.org/10.3390/ijms23126816>
- Liao G., Li Z., Huang C., Zhong M., Tao J., Qu X., Chen L., and Xu X., 2019, Genetic diversity of inner quality and SSR association analysis of wild kiwifruit (*Actinidia eriantha*), *Scientia Horticulturae*, 248: 241-247.
<https://doi.org/10.1016/j.scienta.2019.01.021>
- Merrick L., Herr A., Sandhu K., Lozada D., and Carter A., 2022, Optimizing plant breeding programs for genomic selection, *Agronomy*, 12(3): 714.
<https://doi.org/10.3390/agronomy12030714>
- Nantawan U., Kanchana-udomkan C., Bar I., and Ford R., 2019, Linkage mapping and quantitative trait loci analysis of sweetness and other fruit quality traits in papaya, *BMC Plant Biology*, 19: 1-11.
<https://doi.org/10.1186/s12870-019-2043-0>
- Nti-Addae Y., Matthews D., Ulat V., Syed R., Sempéré G., Pétel A., Renner J., Larmande P., Guignon V., Jones E., and Robbins K., 2019, Benchmarking database systems for Genomic Selection implementation, *Database: The Journal of Biological Databases and Curation*, 2019: baz096.
<https://doi.org/10.1093/database/baz096>
- Pereira L., Ruggieri V., Pérez S., Alexiou K., Fernández M., Jahrman T., Pujol M., and Garcia-Mas J., 2018, QTL mapping of melon fruit quality traits using a high-density GBS-based genetic map, *BMC Plant Biology*, 18: 1-17.
<https://doi.org/10.1186/s12870-018-1537-5>
- Robertson C., Hjortshøj R., and Janss L., 2019, Genomic selection in cereal breeding, *Agronomy*, 9(2): 95.
<https://doi.org/10.3390/agronomy9020095>
- Sandhu K., Shiv A., Kaur G., Meena M., Raja A., Vengavasi K., Mall A., Kumar S., Singh P., Singh J., Hemaprabha G., Pathak A., Krishnappa G., and Kumar S., 2022, Integrated approach in genomic selection to accelerate genetic gain in sugarcane, *Plants*, 11(16): 2139.
<https://doi.org/10.3390/plants11162139>
- Shu P., Zhang Z., Wu Y., Chen Y., Li K., Deng H., Zhang J., Zhang X., Wang J., Liu Z., Xie Y., Du K., Li M., Bouzayen M., Hong Y., Zhang Y., and Liu M., 2023, A comprehensive metabolic map reveals major quality regulations in red flesh kiwifruit (*Actinidia chinensis*), *The New Phytologist*, 238(5): 2064-2079.
<https://doi.org/10.1111/nph.18840>
- Tian X., Zhu L., Yang N., Song J., Zhao H., Zhang J., Ma F., and Li M., 2021, Proteomics and metabolomics reveal the regulatory pathways of ripening and quality in post-harvest kiwifruits, *Journal of Agricultural and Food Chemistry*, 69(2): 824-835.
<https://doi.org/10.1021/acs.jafc.0c05492>
- Tilahun S., Choi H., Kwon H., Park S., Park D., and Jeong C., 2020, Transcriptome analysis of 'haegeum' gold kiwifruit following ethylene treatment to improve postharvest ripening quality, *Agronomy*, 10(4): 487.
<https://doi.org/10.3390/agronomy10040487>
- Wang R., Shu P., Zhang C., Zhang J., Chen Y., Zhang Y., Du K., Xie Y., Li M., Ma T., Zhang Y., Li Z., Grierson D., Pirrello J., Chen K., Bouzayen M., Zhang B., and Liu M., 2021, Integrative analyses of metabolome and genome-wide transcriptome reveal the regulatory network governing flavor formation in kiwifruit (*Actinidia chinensis*), *The New Phytologist*, 233(1): 373-389.
<https://doi.org/10.1111/nph.17618>
- Wu H., Ma T., Kang M., Ai F., Zhang J., Dong G., and Liu J., 2019, A high-quality *Actinidia chinensis* (kiwifruit) genome, *Horticulture Research*, 6: 117.
<https://doi.org/10.1038/s41438-019-0202-y>
- Xiong Y., Yan P., Du K., Li M., Xie Y., and Gao P., 2020, Nutritional component analyses of kiwifruit in different development stages by metabonomic and transcriptomic approaches, *Journal of the Science of Food and Agriculture*, 100(6): 2399-2409.
<https://doi.org/10.1002/jsfa.10251>

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