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Improving the Fruit Flavor of Golden Pitaya through Gene Editing: Applications of CRISPR/Cas9 in Metabolic Pathways

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Abstract This study analyzed the current status and application prospects of gene editing technology in improving the flavor of tropical fruit bird's nest fruit (golden pitaya, *Selenicereus megalanthus*). This study analyzed the flavor composition and metabolic pathways of bird's nest fruit, including the accumulation mechanism of key substances such as sugars, organic acids and aromatic volatiles, and discussed the key gene selection strategies that affect flavor, such as enzymes and inhibitors that regulate sugar accumulation, genes that control organic acid synthesis and transportation, and pathway enzymes involved in the biosynthesis of aromatic substances. The application strategies of CRISPR/Cas9 technology in flavor improvement are mainly introduced, including targeted gene knockout to increase sugar content and reduce acidity, metabolic pathway reprogramming to increase the content of aromatic substances, and multi-gene editing to achieve comprehensive improvement of flavor. At the same time, the latest progress in fruit flavor improvement at home and abroad is outlined, such as the simultaneous editing of multiple genes in tomatoes to significantly increase the soluble sugar content, the identification and functional verification of aroma regulatory genes in fruits such as strawberries, etc., and based on this, the feasibility and potential effect of flavor improvement of bird's nest fruit through gene editing are prospected. The targeted flavor improvement of bird's nest fruit provides new ideas and new ways for tropical fruit breeding and industrial upgrading.

Keywords Golden pitaya; Fruit flavor; Metabolic pathway; Gene editing; CRISPR/Cas9

1 Introduction

Flavor is one of the key factors in judging the quality and market value of fruits. The sweetness and sourness of fruits are mainly determined by the content of soluble sugars and organic acids, while the aroma depends on the complex composition of volatile organic compounds (Miao et al., 2024). As a tropical specialty fruit, bird's nest fruit (commonly known as golden pitaya, *Selenicereus megalanthus*) is favored by consumers for its unique sweet and sour flavor and aroma. Golden pitaya is native to the Andes Mountains in Central America and is currently cultivated in South America and Southeast Asia. It is a fruit crop with important economic value in the Cactaceae family (Chen et al., 2021). Compared with red or white pitaya (*Hylocereus undatus*, etc.), golden pitaya has golden flesh, smaller seeds, sweet taste and not watery and astringent taste, and has unique competitiveness in the international market (Valero et al., 2025). Recent studies have sequenced and annotated the genome of golden pitaya and assembled a high-quality reference genome (Chen et al., 2021). The acquisition of genomic information lays the foundation for analyzing the flavor formation mechanism of golden pitaya and exploring flavor-related genes.

Traditional breeding has been effective in improving fruit yield and disease resistance, but quality traits such as flavor are often neglected due to complex genetic mechanisms and breeding trade-offs, resulting in the phenomenon of “high yield but not delicious” (Kaur et al., 2023). For emerging fruits such as golden pitaya, how to balance yield and flavor in breeding and achieve targeted improvement of flavor is the key to improving their market competitiveness. The gene editing technology that has emerged in recent years, especially the genome fixed-point editing tools represented by CRISPR/Cas9, has provided a new way to accurately improve fruit flavor (Ma et al., 2023; Tiwari et al., 2023).

CRISPR/Cas9 has been widely used in plant functional gene research and crop breeding improvement due to its simplicity, high efficiency and strong specificity (Karkute et al., 2017; Ma et al., 2023). Since the first report of plant gene editing in 2013, many fruit trees and vegetable crops have successfully achieved knockout or precise mutation of target genes. In particular, CRISPR technology has shown great potential in improving fruit quality, including a series of breakthroughs such as increasing the sugar content of tomatoes, reducing the acidity of citrus, and optimizing the aroma substances of strawberries (Fan et al., 2022; Ma et al., 2023).

This study will focus on the formation mechanism and key metabolic pathways of the flavor of golden pitaya, explore genes that can be used as targets for flavor improvement, and summarize the strategies and research progress of CRISPR/Cas9 technology in improving fruit flavor. At the same time, the technical bottlenecks that may be encountered in carrying out gene editing in golden pitaya are analyzed and coping strategies are proposed, in order to provide a theoretical basis and technical support for the targeted improvement of tropical fruit quality, thereby achieving precise breeding of golden pitaya flavor and enhancing industrial value.

2 Analysis of Flavor Components and Metabolic Pathways of Golden Pitaya

2.1 Composition of flavor-related metabolites

The pitaya fruit is round or oval, and the peel color is red (*H. polyrhizus*, *H. undatus*), green (*H. stenopterus*) and yellow (*H. megalanthus, Selenicereus megalanthus*) (Figure 1) (Shah et al., 2023). Bird’s nest fruit is a golden pitaya, and its flavor components are mainly composed of sugars, organic acids and volatile aromatic substances. The soluble sugars in its pulp are mainly glucose and fructose, and the sweetness is more prominent than that of red or white pitaya. The soluble solids content (TSS) is generally 12~15 Brix, and some high-quality strains even reach 20 Brix (Valero et al., 2025). The sour taste of bird's nest fruit mainly comes from malic acid, citric acid and a more special citric maleic acid (Citramalic acid), the latter of which accounts for 7.56%~71.42% in different strains (Wu et al., 2020). During the fruit ripening process, sugar gradually accumulates and organic acid decreases, which increases the sugar-acid ratio and makes the flavor tend to be sweet and balanced.

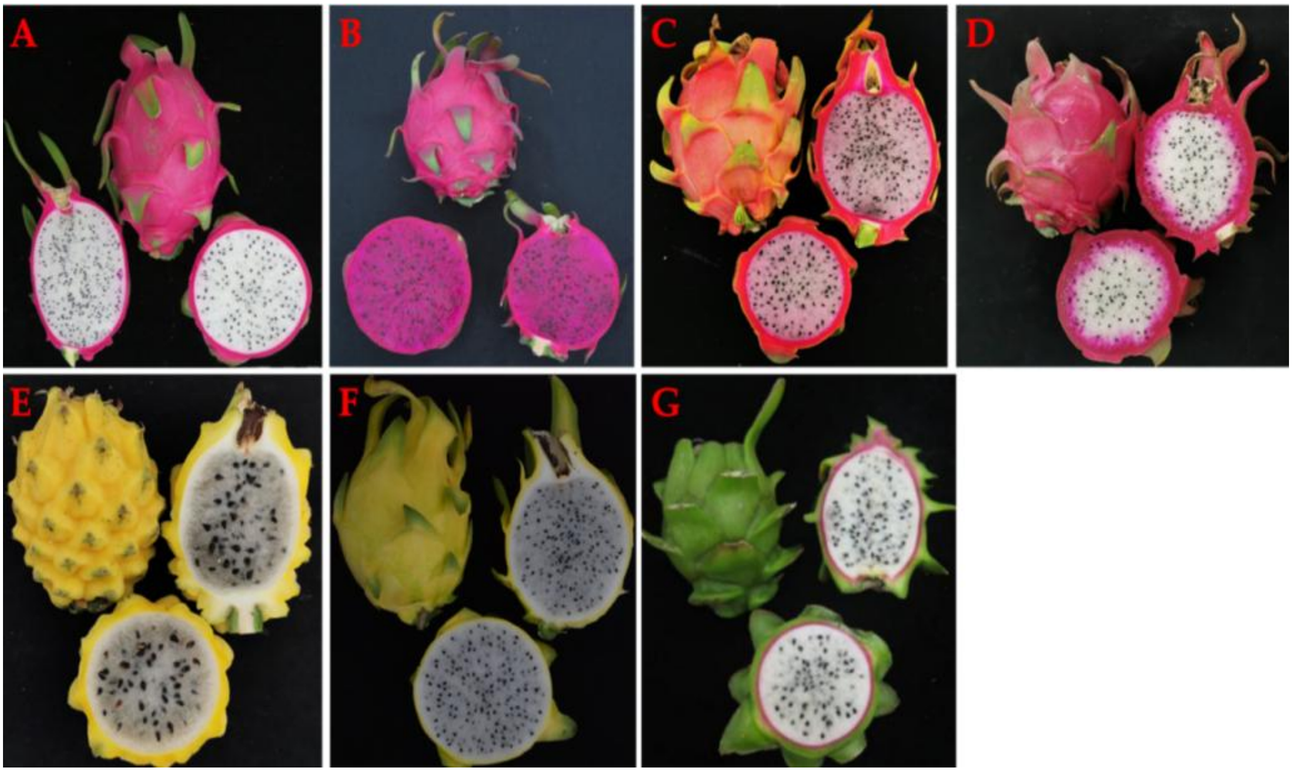

Figure 1 Fruit peel, pulp, and scale and areoles phenotype found in different Hylocereus species (Adopted from Shah et al., 2023)

Image caption: (A) *H. undatus*; (B) *H. polyrhizus*; (C, D) hybridization offspring of *H. polyrhizus* and *H. undatus*; (E) *H. megalanthus*; (F) Golden pitaya (yellow clone of *H. undatus*), (G) *H. stenopterus* (Adopted from Shah et al., 2023)

The aroma of golden pitaya is relatively light, mainly grassy, and its volatile organic compounds mainly include alcohols (such as 1-hexanol), aldehydes (such as hexanal) and esters (such as hexyl acetate). During the ripening process, the accumulation of C6 alcohols and aldehydes increases, especially hexanal and 1-hexanol with a grassy aroma, and their concentration plays a decisive role in the flavor differences of different strains (Wu et al., 2022).

2.2 Key metabolic pathways and regulatory genes

In terms of carbohydrate metabolism, the accumulation of sugar in golden pitaya involves sucrose synthase (SUSY) and cell wall invertase (CWIN), and efficient transport and distribution of fruit sugar is achieved through sugar transporters such as SWEETs and TSTs. Protein kinases such as CDPKs that regulate the activity of these enzymes are important negative regulators that affect the accumulation of fructose and glucose (Wang et al., 2021).

Organic acid synthesis is mainly through the tricarboxylic acid cycle (TCA), and citrate synthase (CS) and malate dehydrogenase (MDH) are the core enzyme systems that control the production of citric acid and malic acid. In addition, members of the ALMT (aluminum-activated membrane protein) family on the vacuole membrane participate in the transmembrane transport of organic acids such as malic acid and determine their accumulation level in the vacuole (Miao et al., 2024).

In terms of aromatic substances, the main aroma compounds are synthesized through the fatty acid cleavage pathway, involving key enzymes such as lipoxygenase (LOX), alcohol dehydrogenase (ADH) and alcohol acyltransferase (AAT). Among them, LOX catalyzes fatty acids to produce C6 aldehydes, ADH reduces them to C6 alcohols, and AAT further produces esters with fruity aroma (Wu et al., 2022). In addition, some aromatic components such as terpenes and phenylpropanoids are catalyzed by terpene synthase (TPS) and phenylalanine aminolyase, and also play a certain role in flavor expression (Fan et al., 2022).

2.3 Molecular regulatory mechanism of golden pitaya flavor formation

During the formation of golden pitaya flavor, there are significant interactions between metabolic pathways such as sugar, acid, and aroma. For example, sugar and organic acids share intermediates (such as PEP) in carbon metabolism, and the accumulation of the two is competitive (Miao et al., 2024). Volatile organic compounds (VOCs), such as esters, terpenes, aldehydes, alcohols, and ketones, are the main contributors to fruit aroma and flavor. These substances are produced through multiple biosynthetic pathways, especially terpenoids, phenylalanine, and fatty acid pathways (Xu et al., 2022; Lu et al., 2024).

Key enzyme-encoding genes and transcription factors (TFs) are essential for regulating the synthesis of flavor compounds. For example, NAC transcription factors (such as PpNAC1 and PpNAC5) activate genes involved in ester formation, sugar accumulation, and organic acid degradation, directly affecting aroma and taste. Epigenetic modifications (such as removal of repressive histone marks) and post-transcriptional mechanisms (such as alternative splicing and mRNA methylation) further fine-tune the expression of flavor-related genes during fruit ripening (Cao et al., 2021; Zhang et al., 2023). The expression levels of these regulatory factors and their interactions with target metabolic genes constitute a complex flavor metabolic regulatory network. By identifying and intervening in these core regulatory nodes, it is expected to achieve precise regulation and optimization of the flavor components of golden pitaya.

3 Target Gene Selection for Flavor Improvement of Golden Pitaya

3.1 Genes related to sugar metabolism

Increasing the sugar content of fruit is a direct way to enhance sweetness. The genes that affect the sugar content of fruit mainly include: enzymes and regulatory factors that control the decomposition and transport of sucrose, and source-sink signaling pathway genes that affect the distribution of photosynthetic products (Vimolmangkang et al., 2016; Fang et al., 2023). In tomatoes, several effective gene editing targets for increasing the sugar content of fruit have been identified. For example, the cell wall acid invertase inhibitor protein SlINVINH1 is a negative regulator that inhibits the decomposition of sucrose by cell wall invertase (CWIN). Wang et al. (2021) used CRISPR/Cas9 to knock out SlINVINH1, thereby increasing the activity of invertase and significantly increasing the accumulation of glucose and fructose in tomato fruit. These results show that relieving the inhibition of sucrose decomposition or reducing sugar consumption can effectively increase the sweetness of fruit. For golden pitaya, it is possible to consider identifying sucrose invertase inhibitor analogs in its genome and editing them to make them functionally deficient to enhance the sugar accumulation of the pulp.

Another important target gene is the gene related to sugar transport and signaling pathways. Source-sink allocation in plants is often regulated by sugar signals. For example, calcium-dependent protein kinases SlCDPK27 and SlCDPK26 in tomatoes were found to act as “sugar brakes”: they reduce the conversion of sucrose to hexose by phosphorylating sucrose synthase. After knocking out these two genes, the glucose and fructose content of tomato fruits increased by up to 30%, significantly improving sweetness without reducing yield (Zhang et al., 2024). This suggests that in golden pitaya, it is also possible to consider targeting signal factors that negatively regulate sugar accumulation, such as similar CDPKs or other kinases/transcription factors, to increase sugar content.

3.2 Genes related to organic acid metabolism

Moderately reducing organic acid content and increasing the sugar-acid ratio are another effective strategy to improve flavor. Especially for some fruits with excessive or unbalanced sourness, reducing acidity through gene editing can significantly improve edibility. Genetic factors that affect fruit acidity mainly include: enzymes that regulate organic acid synthesis, transporters that promote organic acid accumulation, and proton pumps that control vacuolar acidification. Recent studies have used CRISPR/Cas9 to mutate the CitPH4 gene (encoding a MYB-type transcription factor that regulates the vacuolar proton pump) of citrus, and found that the citric acid content decreased significantly and the sour taste of the fruit was greatly reduced (Miao et al., 2024). In golden pitaya, if there are similar key factors that regulate vacuolar pH (such as transcription factors such as PH4 or PH5), they can also be used as editing targets to reduce acidity.

In addition, enzyme-encoding genes directly involved in the synthesis and decomposition pathways of organic acids are also potential targets. For example, the production of citric acid involves citrate synthase, and the removal of malic acid involves malic enzyme and citrate lyase. In kiwifruit, researchers used CRISPR/Cas9 to knock out the *AcNAC1* gene encoding the vacuolar NAC transcription factor, which positively regulates the accumulation of organic acids. The citric acid content of the mutant kiwifruit dropped dramatically, and the sour taste was significantly reduced (Ling et al., 2024). This case shows that by targeting transcription factors that regulate organic acid metabolism, the acidity of the fruit can also be effectively changed. If there are similar transcription factors that promote acid accumulation (such as NAC and MYB) in golden pitaya, it can be considered to knock them out to reduce acidity and enhance sweet taste.

3.3 Genes related to aroma compound metabolism

Unlike sugar acid, most aromatic volatiles are secondary metabolites, and a few key steps are often controlled by specific genes. Therefore, there is a large space for regulation through gene editing. When selecting aroma improvement target genes, two ideas need to be considered: one is to remove bad odor components, and the other is to increase pleasant aroma components. The mutation of the TomLOXC gene in tomatoes leads to a reduction in some green volatiles and a prominent fruity aroma, which is considered to help improve flavor. There are also multiple LOX family genes in golden pitaya. Members that are highly expressed during the fruit ripening period can be selected as editing objects to reduce the grassy smell (Wu et al., 2022). In terms of increasing pleasant aroma components, key enzymes that limit related metabolism can be targeted. For example, the *FaFAD1* gene in strawberries controls the presence or absence of γ-decalactone (with a strong fruity aroma) (Oh et al., 2021).

Another category that deserves attention is the enzymes that degrade aromatic substances. The low content of aromatic substances in some fruits is not due to insufficient synthesis, but to excessive degradation. For example, the presence of esterases in strawberries will decompose ester aromas and weaken the aroma concentration. Recent studies have shown that inhibiting a carboxylesterase FanCXE1 in strawberry fruits can increase the retention of ester volatiles, thereby enhancing the fruity aroma (Martínez-Rivas et al., 2022). Inspired by this, if a significantly expressed volatile degrading enzyme gene is found in golden pitaya, it may be considered to make it functionally deficient or reduce its expression to increase the accumulation of aroma substances.

4 Application Strategies of CRISPR/Cas9 in Flavor Improvement of Golden Pitaya

4.1 Gene knockout and multi-gene stacking

Gene knockout (knock-out) is the most commonly used strategy of CRISPR/Cas9, which completely loses its function by inducing frameshift mutations or large fragment deletions in the target gene. For negatively regulated flavor genes, knockout often improves flavor (Wang et al., 2021). Tomato *SlINVINH1* and *SlVPE5* inhibitors can increase sugar content by using CRISPR single gene knockout. In golden pitaya, if the function of a gene is confirmed to inhibit sugar accumulation or promote acid formation, then knockout can produce an improvement effect.

For complex flavor traits, multi-gene regulatory networks are often involved, and knocking out a single gene alone has limited effect. In this case, a multi-gene stacking editing strategy can be used to knock out two or more related genes at the same time to achieve a synergistic effect. For example, Wang et al. (2021) hybridized the SlINVINH1 and SlVPE5 knockout lines to obtain a tomato line with further improved sugar content. In terms of improving sweetness, it is possible to consider editing several key sites in the golden pitaya at the same time (such as knocking out a sugar inhibitor and an acidity promoter at the same time) to achieve the dual effects of higher sugar and lower acid.

4.2 Base editing and site-directed mutagenesis

Base editing is a CRISPR-derived technology that does not produce DNA double-strand breaks. It catalyzes base changes at the target site through a fused deaminase to achieve precise point mutations (Miao et al., 2024). For example, the key site encoding the enzyme is mutated to a more active allele. Assuming that a certain aroma synthase in the golden pitaya has lower activity due to a difference in one amino acid, a guide RNA can be designed to target the codon and change it to the codon corresponding to the high-activity allele through base editing, thereby improving the aroma synthesis efficiency.

In addition to base editing, site-directed mutagenesis/insertion (also known as site-directed modification) can also be completed using traditional CRISPR in combination with homologous recombination templates. For example, in order to enhance the regulation of a certain transcription factor on a flavor gene, several cis-element sequences can be inserted into its promoter to increase expression. This requires providing a repair template so that the cell can integrate the new sequence into the target site through homologous recombination (Miao et al., 2024). However, the efficiency of homologous recombination in plant cells is generally low, especially in new varieties whose regeneration system is not yet sound. Therefore, gene knockout is still the main means of fruit flavor improvement. Base editing is expected to be gradually applied as an emerging technology, while site-specific insertion and more precise regulation and transformation are still in the exploratory stage.

4.3 Gene editing vector and strategy optimization

For the application of CRISPR/Cas9 in golden pitaya flavor improvement, it is necessary to comprehensively consider factors such as editing strategy (knockout vs. mutation), vector system (stable genetic transformation vs. transient RNP), and target number (single gene vs. multiple genes). Reasonable experimental design and technical optimization will significantly improve editing efficiency and breeding process. Domestic teams have carried out gene editing practices on fruits such as strawberries, such as using CRISPR to knock out pectinase genes to improve strawberry firmness and storage (López-Casado et al., 2023). These experiences can provide useful reference for the flavor editing of golden pitaya.

5 Research Progress and Case Analysis of Gene Editing Technology to Improve the Flavor of Golden Pitaya

5.1 Successful cases of gene editing of related fruit flavors

As a model fruit vegetable, the research on flavor gene editing of tomatoes is the most abundant. For example, in terms of improving sweetness, CDPK27/26 double knockout tomatoes were completed by the Chinese Academy of Agricultural Sciences and the University of Florida, which significantly increased the sugar content of the fruit without compromising yield (Zhang et al., 2024). In terms of acidity regulation, a study in 2022 reported that knocking out *SlALMT9* reduced the malic acid content of tomato fruit by about half, and tried to cultivate low-acid and sweeter tomato varieties. In terms of aroma, for example, the Klee and Tieman research group used multi-omics methods to identify dozens of candidate genes related to tomato flavor. Among them, the synthesis of cheese-flavored volatile esters is related to an acyltransferase, and mutation of this gene can reduce unpleasant odors (Miao et al., 2024).

Strawberry flavor is known for its aroma. Because strawberries are allo-octoploid and have a complex genome, direct gene editing applications are still limited, but the discovery of related genes is very active. In 2022, the Whitaker team at the University of Florida constructed a strawberry multi-omics analysis framework and identified important genes that control strawberry aroma, including the aforementioned FaOMT (controlling caramel aroma substance dimethoxyfuranone) and FanAAT (controlling jasmine aroma substance methyl mandelate) key allele variants (Fan et al., 2022). Recently, the U.S. Department of Agriculture and the University of Florida collaborated to significantly extend the shelf life of the fruit while maintaining the flavor by editing the strawberry softening enzyme gene (López-Casado et al., 2023). Therefore, by learning from the successful cases of model fruits such as tomatoes and strawberries, and combining the flavor metabolism characteristics of golden pitaya itself for gene editing design, it is expected to break through the bottleneck of traditional breeding and cultivate new varieties of golden pitaya with significantly improved flavor.

5.2 Prediction of potential successful cases of flavor improvement of golden pitaya

As far as golden pitaya is concerned, there is no public report on direct gene editing and improvement of it. However, China has made some progress in pitaya tissue culture and transgenic. For example, the team of South China Agricultural University has established an efficient tissue culture regeneration system and genetic transformation method for red dragon fruit. These methods are expected to be applied to golden pitaya.

It is expected that by knocking out the sugar repression gene and acid accumulation gene in golden pitaya at the same time, it is expected to cultivate a new strain that is sweeter and has moderate acidity, greatly improve the sugar-acid ratio, and have a better taste; by editing the key aromatic pathway genes, the aroma concentration and level of golden pitaya will also be enhanced, or it will be given a new charming aroma. For example, if the ability to synthesize γ-decalactone in strawberries can be introduced, or the grassy volatiles can be reduced, it is believed that the flavor of golden pitaya will be more perfect.

6 Technical Challenges and Solutions

6.1 The genetic transformation system is not yet perfect

Golden pitaya belongs to the cactus family. The stem is fleshy and juicy and contains unique mucilage. Studies have found that grafting technology can change the physical properties of golden pitaya (such as fruit weight, diameter and length) (Figure 2) (Sanmiguel et al., 2025), but traditional tissue culture and genetic transformation are difficult. In previous studies on pitaya plants, regeneration is often carried out by inducing adventitious buds from callus tissue, which is inefficient and has a long cycle. Therefore, how to establish a stable and efficient golden pitaya regeneration and transformation system is the first problem to be solved.

Figure 2 Color comparison of grafted *S. megalanthus* fruits at different maturity stages (Adopted from Sanmiguel et al., 2025)

Solutions include: optimizing the composition of the culture medium (adding appropriate hormones and balancing salts), selecting suitable explants (such as young stem nodes or inflorescence tissues), and improving resistance to stress bacteria to prevent contamination. In addition, new transformation technologies can be tried, such as the aforementioned virus-mediated in vivo editing method- directly inoculating plant viruses carrying editing elements into golden pitaya plants to induce gene editing mutations (Baumann et al., 2020).

6.2 Challenges of polyploidy and heterologous genomes

The genome of the bird's nest fruit has undergone a whole genome duplication (WGD) event (Chen et al., 2021). Although it is diploid, it may have some gene family redundancy or multi-copy homologous sequences. This will bring challenges to precise editing: when there are multiple homologous copies of the target gene, all copies need to be knocked out at the same time to show the phenotype, otherwise the unedited copies may compensate for the function. In this regard, a multi-sgRNA parallel editing strategy can be adopted to design multiple sgRNAs at one time to target each homologous sequence, thereby increasing the probability of mutation of each copy (Tiwari et al., 2023).

Another point is to prevent off-target effects caused by high sequence similarity between different copies. To this end, sgRNA design should avoid conservative sequence regions as much as possible, and select variant sites to guide editing to achieve differential editing. For example, the citrus *CitAN1* and *CitPH4* genes belong to the MYB family. When designing sgRNAs, their specific sequences can be targeted to avoid off-target effects (Miao et al., 2024).

6.3 Multi-gene regulation characteristics of flavor traits

The flavor metabolic network is complex, and multi-gene editing may bring unexpected metabolic effects. For example, reducing a certain organic acid may cause carbon flow to shift to other metabolites, causing changes other than flavor (De Carvalho et al., 2017; Holt et al., 2018). Solving such problems requires comprehensive analysis of the edited strains through metabolomics to detect abnormalities early. If negative effects occur, consider refining the editing strategy, such as using promoter editing (reducing expression rather than knocking out) to achieve mild regulation rather than completely shutting down the pathway. By comparing gradient mutation materials, find the best balance between flavor enhancement and growth performance.

7 Future Outlook

7.1 New model of multi-omics co-breeding

Gene editing breeding in the future will rely more on big data support. By integrating genome, transcriptome, metabolome and phenolic spectrum analysis, we will have a more comprehensive understanding of the complex network of golden pitaya flavor formation. By using machine learning and other means, we can dig out the key factors affecting flavor from massive data and improve the accuracy of target gene selection (Kaur et al., 2023). In particular, for the metabolism of aromatic substances, which is currently underrecognized, new regulatory genes are expected to be discovered with the help of multi-omics. For example, we may find enzymes that determine the unique floral fragrance of golden pitaya or transporters that affect aroma release. These new discoveries will continue to expand the editable target library, making flavor improvement more targeted and creative.

7.2 Coordination of flavor improvement with other traits

Excellent varieties need to have excellent comprehensive performance in flavor, yield, resistance and other aspects. In the future, gene editing is expected to improve multiple traits at the same time through "superimposed editing". For example, while improving the sweetness of golden pitaya, superimposing the editing of disease-resistant genes, we can cultivate varieties that are both delicious and disease-resistant. This requires sophisticated design and balance, but some successful cases have emerged: for example, flavor and storage-resistant genes were edited simultaneously in tomatoes, achieving the best of both worlds (Ortega-Salazar et al., 2024). With the development of multi-gene editing technology, scientists can tailor multi-trait optimization solutions for golden pitaya, so that flavor enhancement does not sacrifice agricultural traits, and truly achieve a “flavor-agronomy win-win”.

7.3 Consumer market and industry impact

In the long run, the launch of gene-edited golden pitaya is expected to increase consumers' awareness and preference for the fruit, and drive the upgrading of the planting industry. New varieties with better flavor will be more popular in the market, with higher prices and added value, and increased income for growers. At the same time, since gene editing does not produce exogenous proteins like genetic modification, consumer acceptance may be higher. Once the supervision is clear and public science is in place, gene-edited fruits are expected to gradually enter the mainstream market. As an emerging region for golden pitaya cultivation, China can take this opportunity to create a high-end specialty fruit brand and enhance its international competitiveness.

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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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