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RESEARCH ARTICLE

# Increasing fruit weight and altering flavour of pitaya by supplementing blue light during fruit growth

**Qingming Sun[1#], Juncheng Li[1], Satish Kumar[2], Ran Yao[3], Honghua Su[4#]**

[1] *Institute of Fruit Tree Research, Guangdong Academy of Agricultural Sciences/Key Laboratory of South Subtropical Fruit Biology and Genetic Resource Utilization, Ministry of Agriculture and Rural Affairs/Guangdong Provincial Key Laboratory of Science and Technology Research on Fruit Trees, Guangzhou 510640, China*
[2] *The New Zealand Institute for Plant & Food Research Limited, Private Bag 1401, Havelock North 4157, New Zealand*
[3] *Institute of Semiconductors, Chinese Academy of Sciences, Beijing 100083, China*
[4] *College of Plant Protection, Yangzhou University, Yangzhou 225009, China*

## Highlights

- Blue light increased the weight, firmness, and antioxidant activity of pitaya fruit.
- Blue light had minor effects on primary metabolites but more pronounced effects on volatile compounds.
- Supplemental blue light enriched bioactive compounds in the pitaya fruit peel.
- The accumulation of flavor-associated volatile compounds, such as organic acids, esters, and terpenes in the pulp, was significantly altered.

## Abstract

Supplemental light is often used in fruit production, but few studies have been conducted on pitaya. In this study, supplemental blue light was applied to pitaya for four hours each night in the field from flowering to fruit ripening to examine changes in peel and pulp physicochemical parameters and metabolites. Blue light treatment significantly increased fruit weight, improved fruit firmness by increasing pectin content and retarding hemicellulose degradation, and enhanced antioxidant enzyme activity. Blue light had minor effects on primary metabolites but more pronounced effects on volatiles. By affecting alanine, aspartate and glutamate metabolism, blue light treatment resulted in significant fruit growth, increased accumulation of bioactive ingredients in the peel, and significantly altered the accumulation of flavor-associated volatile compounds, such as organic acids, esters and terpenes in the pulp. Our results provide an important reference for improving the yield and quality of pitaya production using supplemental light in the field.

**Keywords:** pitaya, blue light supplementation, fruit weight, fruit quality, primary metabolites, volatiles

## 1. Introduction

Pitaya (*Selenicereus polyrhizus* and *Selenicereus undatus*), also known as dragon fruit, originated in Latin America (Fan *et al.* 2018). It is now widely cultivated in tropical and subtropical regions worldwide (Matan *et al.* 2015) due to its strong vitality, ability to withstand extreme environments, resistance to pathogens, convenient field management, and higher economic value (Mizrahi *et al.* 2002; Nobel and Barrera 2004). Consumers prefer pitaya not only because of its decorative appearance and striking colours, but also because the betacyanins extracted from pitaya have potential benefits in ameliorating high-fat diet-related diseases (Song *et al.* 2016), and due to its rich nutritional values, including antioxidants, dietary fibre, vitamins, betalains, minerals, polyphenols, flavonoids, sugars, organic acids, amino acids and phytalbumin (Wu *et al.* 2006; Suh *et al.* 2014; Hua *et al.* 2018).

In the northern hemisphere, such as in China and Vietnam, pitaya which blooms from May to October, has been shown to be a long-day plant (Nerd and Mizrahi 2010; Jiang *et al.* 2012). To harvest pitaya fruit of high economic value during the winter or early spring season, when short day conditions

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[#]Correspondence Qingming Sun, Tel: +86-20-38765789, E-mail: sunqingming@gdaas.cn; Honghua Su, Tel: +86-514-87979344, E-mail: susugj@126.com

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prevail, additional night lighting is required to induce flowering (Jiang *et al*. 2012). Therefore, supplemental lighting is a useful and proven technology for farmers to induce flowering and produce pitaya fruit during short day seasons (Xiong *et al*. 2020). In addition, light and temperature affect the color and betalain content of the pitaya peel (Cejudo-Bastante *et al*. 2016). Whether it is possible to regulate fruit weight and quality by light supplementation in the field is a question worthy of further investigation.

Light is not only an energy source for plants, but also an essential signal for plant growth and development (Terzaghi and Cashmore 1995; Nagy and Schäfer 2022). Light can activate various biological activities in plants when it is perceived and processed by complicated photoreceptors (Galvão and Fankhauser 2015), leading to significant changes in the contents of primary metabolites and volatile compounds, eventually influencing fruit maturation and resistance against biotic stresses (Escobar-Bravo *et al*. 2018). However, different light qualities play different roles in plants. For example, the red light promoted rind color development, β-cryptoxanthin concentration and gene expression pattern related to the accumulation of β-cryptoxanthin and lutein of citrus fruit (Ma *et al*. 2012, 2015; Yamaga *et al*. 2016). An artificial light source with UV-B was reported to increase the phenolic compounds and antioxidant activity in Pak choi (*Brassica rapa* ssp. chinensis) and Swiss chard (*Beta vulgaris* subsp. vulgaris) (Wessler *et al*. 2025). Supplemental greenhouse lighting strongly enhanced photosynthesis and plant growth while increasing water use efficiency in *Cannabis sativa* (Collado *et al*. 2024). In tomato and rice (*Oryza sativa*), blue light treatment showed greater induction and higher steady-state non-photochemical quenching (Hamdani *et al*. 2019; Zhang *et al*. 2019). Supplemental blue/red lighting accelerated fruit coloring and promoted lycopene synthesis in tomato, resulting in enhanced fruit coloring (Wang *et al*. 2021). Acclimation to supplemental blue light can improve light use efficiency and reduce photoinhibition under high solar light exposure, benefiting plant growth in cucumber (Kang *et al*. 2021). Supplemental blue light treatment improved flowering and ripening process and nutritional qualities of tomato fruits, and significantly enhanced lycopene content, total phenolic compounds, total flavonoids, vitamin C, and soluble sugar (He *et al*. 2022). The response to blue light could trigger the biosynthesis of primary metabolites, amino acids and secondary metabolites in tomato fruit (Xiao *et al*. 2022). Blue light treatment can also effectively delay the decay of many fruits during postharvest storage. The decay of pitaya fruit was significantly delayed by 300 lx blue light for 2 h, and changes in several physiological characteristics of pitaya fruit were also significantly reduced (Wu *et al*. 2020b)

Metabolites change significantly during fruit development and senescence (Li J *et al*. 2017; Hua *et al*. 2018). With the development of detection technologies, high-throughput methods now provide large datasets for detecting the accumulation and fluctuation of metabolites and nutrients (Ikeda *et al*. 2016; Feng *et al*. 2017). A previous study indicated that starch, organic acids and inositol decreased, while glucose, fructose, sucrose and sorbitol increased markedly during fruit ripening (Hua *et al*. 2018). In recent years, more valuable research focusing on pitaya metabolomics has been reported. The contents and changes in sugars, aldehydes, free amino acids and alkanes may influence pulp quality and the biotic resistance of dragon fruit (Wu Q *et al*. 2023). Essential fatty acids are abundant in pitaya seeds, and the seed oil extracts contain about 50% essential fatty acids (C18:2 and C18:3) (Ariffin *et al*. 2009). Aside from its nutritional properties, previous research has found that pitaya fruit is a valuable antioxidant due to its polyphenol content (Wu *et al*. 2006).

We have previously used different single wavelength LED light sources, including 730, 660, 590, 520 and 450 nm, to supplement light to pitaya for 4 hours per night in field production and found that blue 450 nm light was effective in significantly increasing single fruit weight and fruit firmness, and in extending post-harvest freshness (unpublished data). Therefore, this study aimed to investigate the effect of supplemental blue LED light during the fruit development period on physiological parameters, primary metabolites and volatile compounds in pitaya peel and pulp, and to provide a theoretical basis and method for efficient light supplementation in pitaya cultivation and fruit quality improvement.

## 2. Materials and methods

### 2.1. Plant materials and treatments

Three-year-old red flesh pitaya 'Dahong' (*Selenicereus polyrhizus*) plants from a commercial plantation in Guangzhou, central Guangdong Province, China (23°57´N, 113°55´E), were used in this study.

Blue light treatment was applied from the day of flowering until fruit ripening, which occurred from June 25 to July 30, 2022. The plants were provided with additional light for four hours per night from 18:30 to 22:30 using LED lights with a wavelength of 450 nm, at 15 W.

The lights were placed 50 cm above the plants at 1.0 m intervals and the plant canopy received 20 μmol $m^{-2}$ $s^{-1}$ PPFD. The control plants received no additional light.

At 25, 30 and 35 days after anthesis (DAA), 30 individual fruits were randomly selected at a distance of 50 to 60 centimetres from the canopy. Each sample was randomly divided into three replicates (10 fruits per replicate) for the subsequent experiments. After basic index measurements, peel and pulp samples were immediately collected in liquid nitrogen and stored at –80°C for further physiological parameter analysis and metabolomic analysis.

### 2.2. Determination of physiological indices in the pitaya peel

Fruit firmness was determined by using a penetrometer (GY-4, Beijing Jinke Lida Company, China) according to the manufacturer's instructions. The *a**, *b** and *L** values were measured directly in the middle of the light-facing side of the peel using a SP-60 colour meter (X-Rite Inc., Grand Rapids, MI, USA). Measurements were taken on 30 fruits and averaged for comparison purposes. The *a** value indicates the degree of reddish-yellow colour of the peel; the higher the *a** value, the redder the peel. The *b** value indicates the degree of yellow and blue in the peel; the higher the *b** value, the greater the degree of yellow bias in the peel. The $L^*$ value indicates the brightness of the peel; the higher the $L^*$ value, the brighter the peel.

Hemicellulose and total pectin contents were measured according to the manufacturer's instructions for the test kits (D799023-0100 and D799294-0100, Sangon Biotech Co., Ltd., Shanghai, China). Cellulose content was measured using the test kit (BC4285, Solarbio Science & Technology Co., Ltd., Beijing, China), following the manufacturer's instructions.

The content of betacyanin was measured as described by Hua *et al.* (2018). A total of 2 g of pulp or peel powder ground with liquid nitrogen, was weighed and made up to 20 mL with 80% methanol, extracted by ultrasound for 10 min, and then extracted by oscillation in the dark for 20 min. This was centrifuged at 5,000 r $\text{min}^{-1}$ for 10 min at room temperature, then 1 mL of the supernatant was diluted four times, and light absorbance at 538 nm was determined. The formula used was:

Betacyanin content (mg 100 $\text{g}^{-1}$ FW) $=(A_{538}\times MW\times V\times DF\times 100)/(E\times L\times m)$

where $A_{538}$ is the light absorption value of the diluent at 538 nm; $V$ is the volume of the extracted liquid (mL); $DF$ is the dilution ratio; $E$ is the molar absorption coefficient of betacyanin, which is 65,000 L $\text{mol}^{-1}$ $\text{cm}^{-1}$; $MW$ is the molecular weight of betacyanin, which is 550 g $\text{mol}^{-1}$; $L$ is the optical path length, which is 1.0 cm; and $m$ is the fresh weight of samples (g).

The activities of catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) were measured following the manufacturer's instructions for the test kits (D799592-0100, D799598-0100 and D799594-0100, Sangon Biotech Co., Ltd., Shanghai, China). The DPPH free radical scavenging ability, hydroxyl radical scavenging ability, and flavonoid content were measured as described in the manufacturer's instructions for the test kits (D799295-0100, D799276-0100 and D799280-0100, Sangon Biotech Co., Ltd., Shanghai, China). For all physiological index determinations of the pitaya peel, three replicates were measured.

## 2.3. Determination of physiological indices in the pitaya pulp

The total sugar content was measured as described in the manufacturer's instructions for the test kit (D799167-0100, Sangon Biotech Co., Ltd., Shanghai, China). The reducing sugar content was measured as described in the manufacturer's instructions for the test kit (D799394-0100, Sangon Biotech Co., Ltd., Shanghai, China). The amino acid content was measured as described in the manufacturer's instructions for the test kit (D799584-0100, Sangon Biotech Co., Ltd., Shanghai, China). Protein contents were measured according to the method described by Elfalleh *et al.* (2009). Three replicates were measured for all physiological index determinations of the pitaya pulp.

## 2.4. Profiling of primary metabolites

Primary metabolomic profiling was based on the method described by Zhu *et al.* (2015), with minor modifications. A 200 mg sample was added to 1,800 μL of methanol (–20°C) for extraction, and 200 μL of 0.2 mg $\text{mL}^{-1}$ ribitol in water was used as an internal standard for quantification. The extracts were incubated with ultrasound treatments at 4°C and heated at 70°C with a water bath for 15 min. After 0.5 h in a refrigerator at –20°C, the extracts were centrifuged at 5,000 g for 15 min at 4°C. Then 100 μL of the supernatant was collected for the derivatization reaction. The derivatization reaction was first incubated in 80 μL of 20 mg $\text{mL}^{-1}$ methoxyamine hydrochloride in pyridine for 1.5 h at 37°C, and then 80 μL of MSTFA [N-Methyl-N-(trimethylsilyl) trifluoroacetamide] was added at 37°C for 0.5 h.

A volume of 1 μL of the sample was used for analysis using a gas chromatography-mass spectrometry (GC-MS) system (GCMS-QP2010 Plus, Shimadzu Corporation, Kyoto, Japan) with the DB-5ms fused-silica capillary stationary phase column (30 m×0.25 mm ID, 0.25 μm, Agilent Technologies Inc., California, USA). The injector temperature was 250°C, and the carrier gas (99.999% helium) flow rate was 1.2 mL $\text{min}^{-1}$. The column temperature was initially held at 100°C for 1 min, then increased to 184°C at 3°C $\text{min}^{-1}$, further increased to 190°C at 0.5°C $\text{min}^{-1}$ and held for 1 min, and finally increased to 280°C at 15°C $\text{min}^{-1}$ for 5 min. The interface temperature was 250°C, and the ionization voltage of the MS was 70 eV. The spill ratio was 10:1, and the total ion current (TIC) spectra were scanned in the range of 45–600 m/z.

## 2.5. Volatile aroma analysis

Each fruit peel (4 g) was ground and homogenized with 4 mL of saturated sodium chloride solution. A total of 10 μL of 0.2 mg $\text{mL}^{-1}$ ribitol in water was used as an internal standard for quantification. The extracts were then placed at 40°C for 15 min before collecting the aromatic compounds. The aromatic compounds were collected for 45 min using the method described by Jing *et al.* (2015).

GC-MS analysis was carried out following the method described by Jing *et al.* (2015). A GC-2010 gas chromatograph (Shimadzu, Suzhou, China) equipped with a GCMS-QP2010 Plus mass spectrometer (Shimadzu, Suzhou, China) was used. Volatile separation was performed using a 30 m Rxi-5ms capillary column (0.25 mm ID) with a split/ splitless injector. Samples were loaded into the injector, and three replicates of each sample were analyzed. The amount of each volatile compound was determined based on the ratio of the peak area of the target compound to the peak area of the internal standard, which was cyclohexanone.

## 2.6. Gene expression

Total RNA was extracted from pitaya peel and pulp tissues using a Plant RNA Kit (R6827-01, Omega Biotek, USA) according to the manufacturer's instructions. RNA was treated with the PrimeScript RT Reagent Kit (RR037A, TaKaRa, Japan) for RNA reverse transcription. The primers were designed for the 28 target genes and one reference gene in Appendix A and quantitative RT-PCR, transcription normalization, and relative quantification were performed as previously described using three biological replicates with the

SYBR Premix Ex Taq Kit (RR420A, TaKaRa, Japan).

### 2.7. Statistical analysis

The experiments were designed as completely randomized, and the results were expressed as the mean values of three biological replicates. The mean±standard error (SE) was calculated for each set of biological replicates. Data analysis was performed using SPSS version 16.0. One-way analysis of variance (ANOVA) was performed, followed with Tukey significant difference test at an alpha level of 0.05.

Data analysis of primary metabolites and volatile aromas included PLS-DA and KEGG pathway analysis. Partial least squares-discriminant analyses (PLS-DA) were conducted using SIMCA version 13.0 to investigate variety-specific accumulation of metabolites. The thresholds for statistical significance were a p-value of 0.05 and a fold-change of 2.0, respectively. KEGG pathway analyses were conducted using MetaboAnalyst 5.0 (https://www.metaboanalyst.ca/).

## 3. Results

### 3.1. Effects of blue light treatment on pitaya fruit weight and firmness

The visual appearances of pitaya fruit from the control and blue light groups are shown in Fig. 1-A. Fruit weight and pulp weight showed an increasing trend during fruit growth and development (Fig. 1-B and C). The average fruit weight of the control group was slightly higher than that of the blue light treatment group at 25 DAA (214.33 g *vs*. 197.67 g), but the supplemental blue light treatment resulted in higher average fruit weight compared to the control at 30 (259.67 g *vs*. 263.33 g) and 35 DAA (301.67 g *vs*. 354.33 g) (Fig. 1-B; Appendix B) . The average peel weight gradually decreased with fruit development. At 25 and 30 DAA, the peel weight of the blue light treatment group was lower than that of the control group (Fig. 1-D). However, at 35 DAA, the peel weight of the blue light treatment group ((88.67±1.86) g) was slightly higher than that of the control group ((77.67±8.09) g). The firmness of the fruit under blue light treatment was significantly higher than the control group (Fig. 1-E). The *a** and *b** values of the peel in the control group were slightly higher than those in the blue light group (Fig. 1-F), indicating that the peel in the control group was more skewed towards red and yellow and more ripe. Therefore, blue light delayed fruit ripening.

Further analysis showed that the average fruit weight of the control group increased by 21% from 25 to 30 DAA, while a 19% increase was observed from 30 to 35 DAA. For the same periods, the average fruit weight increased by 33 and 34.56%, respectively, under the blue light treatment (Appendix B). The blue light treatment resulted in significantly higher fruit weight than the control during the later stages (i.e., 25 and 35 DAA) of the fruit development, suggesting that the main stage at which blue light promotes an increase in fruit weight is between 25 and 35 DAA.

Between 25 and 30 DAA, the average peel weight decreased by 21.26 and 20.85% in the control and blue light treatments, respectively, while the average pulp weight increased by 128.57 and 166.67%, respectively. Similarly, between 30 and 35 DAA, the peel weight decreased by 35.81 and 20.36% in the control and blue light treatments,

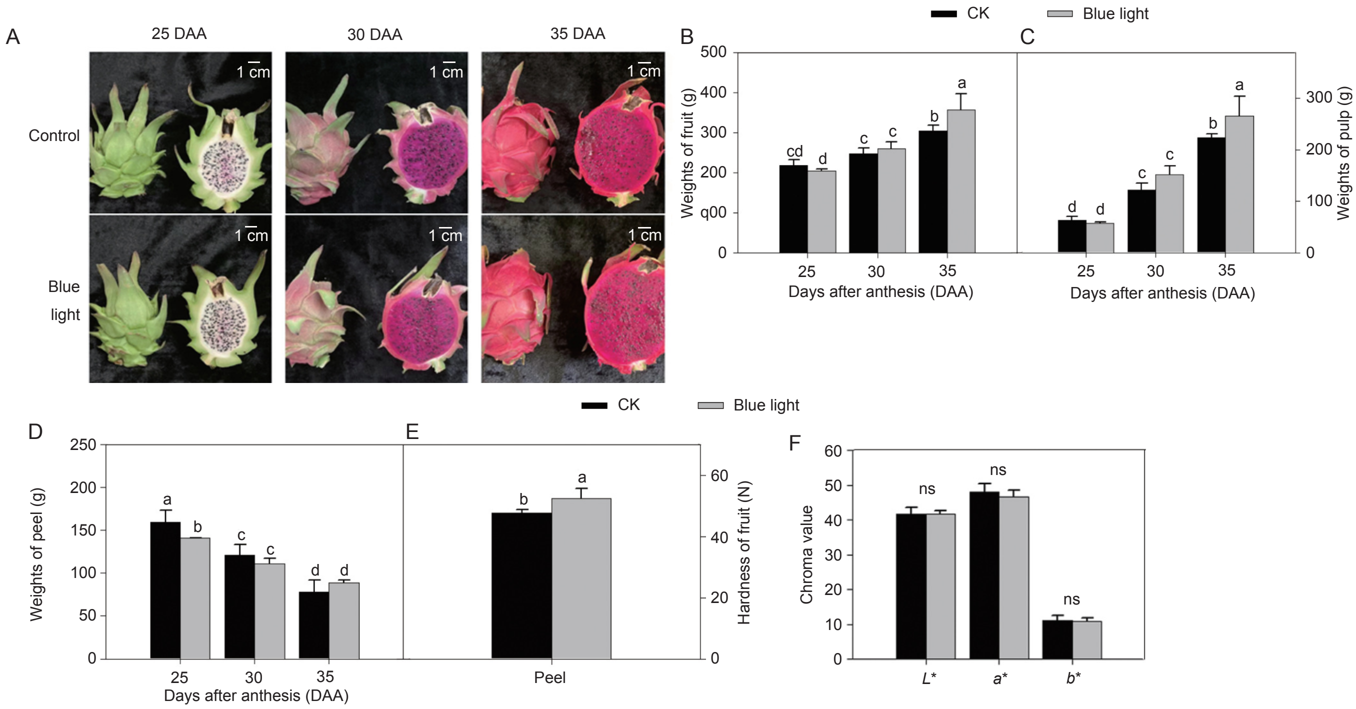

**Fig. 1 Physical and chemical indices of pitaya fruit after blue light treatment.** A, change in visual appearance of pitaya fruit. Scale bar=1 cm. B, the weights of fruit. C, the weights of pulp. D, the weights of peel. E, the hardness of fruit. F, the chroma value of peel. Data are presented as the mean±SE (*n*=3). Different letters indicate significant ($P<0.05$) differences between means by ANOVA combined with Duncan's multiple range test, and ns indicates non-significant difference ($P>0.05$).

respectively (Appendix B), while the average pulp weight increased by 61.54 and 74.78%, respectively. Therefore, in the later stages of fruit development (25 to 35 DAA), the blue light treatment helped increase pulp weight, leading to a significant increase in overall fruit weight.

### 3.2. Effect of blue light treatment on the physicochemical parameters of the pitaya peel

Compared to the control group, the blue light treatment resulted in higher levels of hemicellulose in the peel (Fig. 2-A). During the fruit development period from 25 to 35 DAA, hemicellulose content degraded more slowly in the blue light treatment compared to the control.

The peel pectin content was significantly different, especially at 35 DAA, between the blue light treatment ((71.05±7.63) μmol g$^{-1}$) and the control ((51.63±2.2) μmol g$^{-1}$) (Fig. 2-C). Compared with the control group, blue light treatment decreased cellulose content (Fig. 2-B). The primary plant cell wall is composed of a complex network of pectin, hemicellulose and cellulose. Blue light treatment retarded hemicellulose degradation, maintained high pectin levels, and slightly affected cellulose, thereby reducing cell wall degradation compared to the control group. There was no significant difference in pulp and peel betacyanin content between the two treatments (Fig. 2-D). These results showed that blue light treatment delayed fruit ripening and increased fruit firmness, mainly by decreasing the hemicellulose degradation rate and promoting the accumulation of pectin in the pericarp.

The activities of CAT (Fig. 2-E) increased gradually during fruit growth, but there was no significant difference between the blue light treatment and the control group at 35 DAA. The blue light treatment increased POD activity (Fig. 2-G), especially at 35 DAA; the POD activity of the blue light-treated group was significantly higher than that of the control group. Unlike the patterns of CAT and POD, SOD activities decreased gradually during fruit growth, but blue light treatment significantly enhanced SOD activities (Fig. 2-I) compared with the control group. During the fruit development period, flavonoid contents (Fig. 2-J) increased in both groups. Compared with the control group, blue light treatment significantly increased flavonoid content in the fruit peel, especially at 35 DAA, when the flavonoid contents in the control group and the blue light treatment group were 3.25 and 4.18 mg g$^{-1}$ FW, respectively. Due to significant changes in the activities of CAT, POD, SOD, and flavonoid contents under blue light treatment, free radical scavenging ability may have been enhanced. Compared with the control group, the hydroxyl radical scavenging ability (Fig. 2-H) increased after blue light treatment, with significant changes observed between 25 and 35 DAA, while DPPH free radical scavenging ability (Fig. 2-F) was similar at maturity.

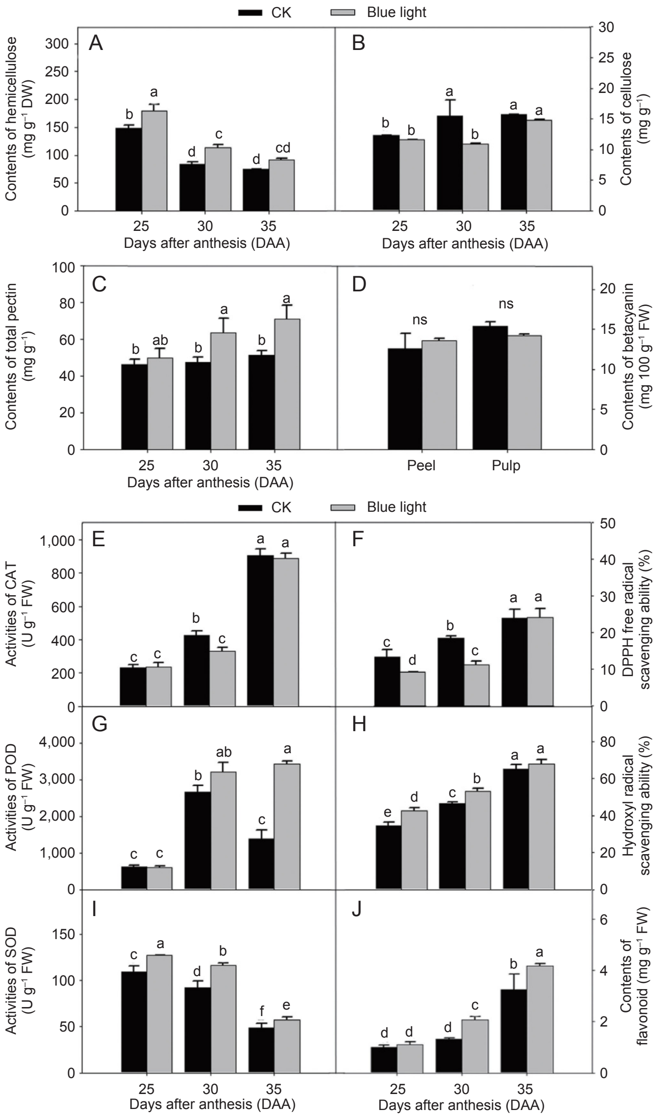

**Fig. 2 Physical and chemical indices of pitaya peel after blue light treatment.** A–D, contents of hemicellulose (A), cellulose (B), pectin (C), and betacyanin (D). E, G and I, activities of CAT (E), POD (G) and SOD (I). F, DPPH free radical scavenging ability. H, hydroxyl free radical scavenging ability. J, contents of flavonoid. Data are presented as the mean±SE (*n*=3). Different letters indicate significant ($P<0.05$) differences between means by ANOVA combined with Duncan's multiple range test.

### 3.3. Effect of blue light treatment on the physicochemical parameters of the pitaya pulp

Compared to the control, the blue light treatment increased the contents of total sugar and reducing sugar in the pulp at 25 and 30 DAA (Fig. 3-A and B). The content of total sugar in the blue light treatment group at 25 and 30 DAA was (83.01±6.29) and (82.35±2.88) mg g$^{-1}$, respectively (Fig. 3-A). Blue light treatment significantly increased the content of reducing sugar especially at 30 DAA, reaching (4.81±0.16) mg g$^{-1}$; both sugars increased gradually and reached the same level at 35 DAA. The content of total amino acids in the pulp decreased gradually from 25 to 35 DAA (Fig. 3-C), reaching (67.38±3.37) μmol g$^{-1}$ FW at 35 DAA in the blue light group, which was markedly greater than that in the control group (Fig. 3-C). These results suggest that blue light treatment can improve fruit quality and nutritional value of pitaya fruit. During the fruit development period, the contents of total protein (Fig. 3-D) in the blue light-treated group were higher

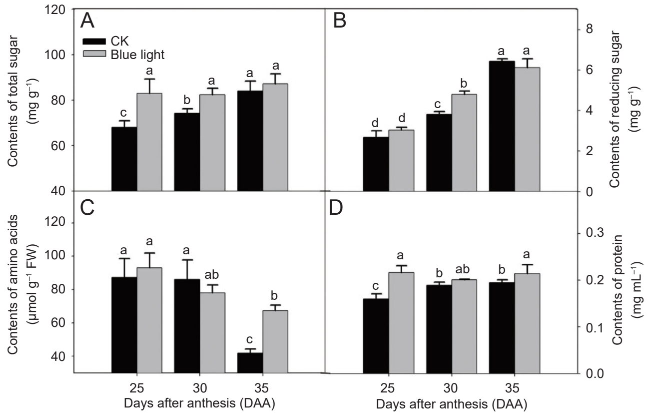

**Fig. 3 Physical and chemical indices of pitaya pulp after blue light treatment.** A–D, contents of total sugar (A), reducing sugar (B), amino acids (C), and protein (D). Data are presented as the mean±SE (*n*=3). Different letters indicate significant ($P<0.05$) differences between means by ANOVA combined with Duncan's multiple range test.

than that in the control group. It can be inferred that blue light treatment promoted the accumulation of sugars, amino acids and proteins in the pulp to a certain extent, thereby improving fruit quality.

## 3.4. Comparative analyses of primary metabolites in the peel and pulp of pitaya fruit

The primary metabolites and volatile components were analyzed from the peel and pulp of pitaya in the blue light treatment group and the control group. Based on the categories and total content of metabolites (Fig. 4-A and B), significant differences were found between the peel and pulp. A total of 272 primary metabolites were detected and divided into 7 different categories, including 63 acids, 15 alcohols, 29 amino acids, 23 esters, 26 sugar alcohols, 52 sugars and 64 others. Acids (52), sugars (40), sugar alcohols (24) and esters (22) were more abundant in the peel than in the pulp, where the numbers of compounds in these categories were 45, 31, 16 and 11, respectively.

The content of primary metabolites in the pulp was greater than that in the peel, except for ester compounds (Fig. 4-B). Blue light treatment had a minor effect on primary metabolites in the peel and pulp (Fig. 4-E and F).

## 3.5. Comparative analyses of volatile components in the peel and pulp of pitaya fruit

A total of 234 volatile components were detected. Details of the categories of volatile components and their relative concentrations are shown in Fig. 4-C and D. There were nine categories of volatile components, including acids, alcohols, aldehydes, alkanes, esters, heterocyclic compounds, ketones, terpenes and others. Except for acids, other volatile components were more frequently found in the peel than in the pulp. The peel was rich in alcohols, aldehydes, esters and ketones, while the pulp was rich in aldehydes, alcohols and acids.

Volatiles from the peel showed different trends during fruit development. As shown in the Fig. 4-G, from 25 to 35 DAA, the contents of alkanes and ketones increased; acids and aldehydes decreased; and alcohols, esters, heterocyclic compounds, and terpenes showed an increasing and then decreasing trend in both the control group and in the blue-light-treated group. Compared with the control group, under blue light treatment the levels of esters, alcohols, and ketones decreased, while the levels of acids, alkanes, and aldehydes increased. In the later stages of development (30 to 35 DAA), aldehydes and ketones increased significantly, and alcohols decreased rapidly.

During fruit development, volatiles from the pulp (Fig. 4-H) showed that acids, ketones, terpenes and esters increased; aldehyde content decreased; and ketones increased rapidly as the fruit color changed between 30 and 35 DAA. Supplemental blue light led to an increase in acid, ester and terpene content during fruit development, an increase in alcohol content, and a significant decrease in aldehydes at the ripening stage (30 to 35 DAA). This could be attributed to the changes in fruit flavor due to the accelerated conversion of aldehydes to acids, alkanes, esters, and terpenes caused by blue light, but there was no effect on ketone content at the final stage (35 DAA).

## 3.6. Differentially accumulated metabolites in the peel in response to the blue light treatment

PLS-DA analysis was carried out on the peel metabolomics data (Fig. 5-A). The blue-light-treated group was mainly distributed in the third quadrant, while the control group was discretely distributed in the first, second and fourth quadrants, indicating that the metabolites differed greatly between the control and blue light-treated groups during peel development.

A total of 22 differential metabolites (Fig. 5-C) were detected in the peel between the blue light treatment and the control. These included acids (10), sugar alcohols (5), alcohols (2), sugars (1), aldehydes (1), esters (1), and others (2).

With blue light treatment, the content of most differential metabolites in the peel (Fig. 5-C) increased significantly, except for (*E*)-2-hexen-1-ol. Compared with the control group, (*E*)-2-hexen-1-ol decreased markedly after blue light treatment from 25 to 35 DAA, while in the control group, it increased gradually. (*E*)-2-Octenal was a uniquely differentially accumulated aldehyde in this study. During fruit development, its levels tended to decrease in both the control and blue light treatment groups, however most of the other differential metabolites from the peel were gradually accumulated (Fig. 5-C). Between 25 and 30 DAA, the content of (*E*)-2-Octenal decreased significantly, and the rate of decline slowed from 30 to 35 DAA. However, supplemental blue light significantly increased the amount of (*E*)-2-octenal accumulated at various stages of peel development from 25 to 35 DAA. At day 30 of fruit development, the accumulation of eight metabolites was significantly promoted by blue light, including three acids: 2,3,5,6-tetrahydroxy-4-[3,4,5-trihydroxy-6-(hydroxymethyl) oxan-2-yl] oxyhexanoic acid, (+)-pantothenic acid and vanillic acid; one alcohol: 2,5,7,8-tetramethyl-2-(5,9,13-trimethyltetradecyl)-3,4-dihydro-

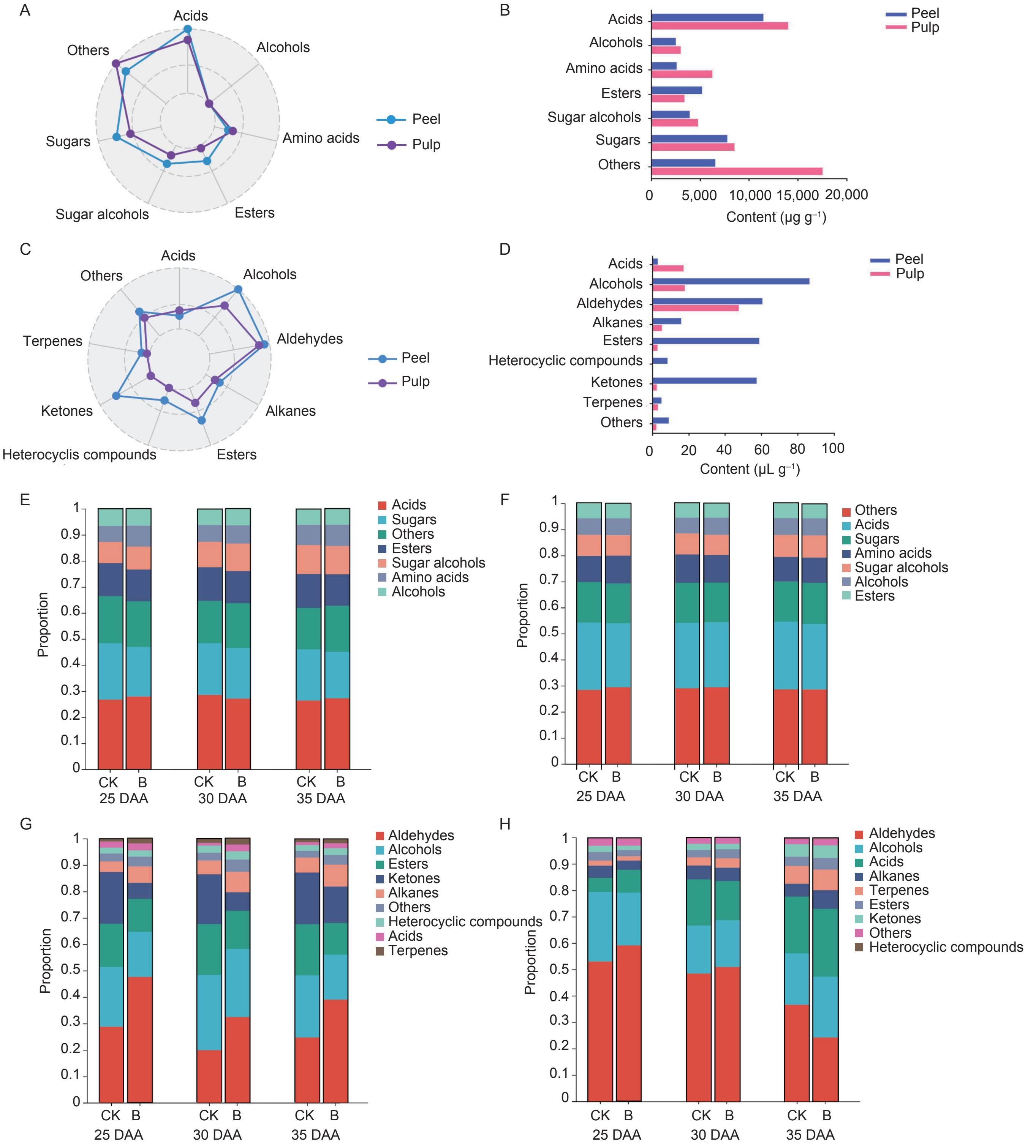

**Fig. 4 Data analyses of metabolomics of pitaya peel and pulp.** A, distribution of various primary metabolites in peel and pulp of pitaya fruit. B, total concentrations of different primary metabolites in peel and pulp of pitaya fruit. C, distribution of various volatile compounds in peel and pulp of pitaya fruit. D, total concentrations of different volatile compounds in peel and pulp of pitaya fruit. E, percentage of primary metabolities in peel from control (CK) and blue light (B) treatment. F, percentage of primary metabolities in pulp from CK and B. G, percentage of volatile compounds in peel from CK and B. H, percentage of volatile compounds in pulp from CK and B. DAA, days after anthesis.

2*H*-chromen-6-ol); one aldehyde (*E*)-2-octenal, one ester arachidonate, 1,5-anhydro-D-glucitol and alpha-D-mannose 1-phosphate. At 35 DAA, five important volatile compounds including three acids, (9*Z*,12*Z*,15*Z*)-octadecatrienoic acid, vanillic acid, and pipecolic acid, one aldehyde (*E*)-2-octenal; and one compound benzene-1,2,4-triol, were enhanced after blue light treatment.

The accumulation of bioactive ingredients in the peel was significantly promoted by blue light treatment. The contents of DL-tartaric acid, 2-oxoglutarate, nicotinic acid, 2-hydroxyglutaric acid, D-glucaric acid, gamma-tocopherol, 1,5-anhydrohexitol, beta-sitosterol, delta-tocopherol and coniferin were gradually stabilized at 30 and 35 DAA in both the control and blue-light-treated groups.

### 3.7. Differentially accumulated metabolites in the pulp in response to blue light treatment

The PLS-DA score plot of the pulp metabolites showed that each treatment group clustered and was distributed separately (Fig. 5-B), and the difference between groups was significant. Blue light treatment had a significant effect on metabolites in the pulp.

A totol of 26 differential metabolites (Fig. 5-D) were detected in the pulp between the control and blue-light-treated groups, belonging to eight categories: acids (9), aldehydes (6), alcohols (5), heterocyclic compounds (1), alkanes (1), ketones (1), terpenes (1), and others (2).

Six acids (palmitoleic acid, *cis*-7-hexadecenoic acid, *n*-decanoic acid, octanoic acid, pentanoic acid, and hippuric acid) gradually accumulated with fruit development (Fig. 5-D). Among them, the level of hippuric acid was significantly increased by blue light treatment at 35 DAA. In contrast, three acids (2-methylpropanoic acid, linolenic acid, and propanoic acid) decreased with fruit development, with linolenic acid being significantly down-regulated by blue light compared to the control. Except for *n*-tridecan-1-ol, alcohols and aldehydes decreased with fruit growth in both groups (Fig. 5-D). Compared to the control, the levels of 3-methyl-3-buten-1-ol and 2-ethyl-1-hexanol were slightly decreased by blue light. Except for 2-propenal, the contents of differential aldehydes (Fig. 5-D) increased significantly after blue light treatment, with the most notable change observed in benzeneacetaldehyde at 35 DAA, which was significantly greater in the blue-light-treatment group than in the control group. The same pattern was observed with 2-methylbutanal and 3-methylbutanal. In addition, blue light treatment promoted the accumulation of 3-methylfuran, 14-methyloxacyclotetradecan-2-one and longifolene at 30 DAA and significantly inhibited the production of lauroyl-L-carnitine in the pulp.

### 3.8. KEGG pathway analysis of the pitaya fruit response to blue light treatment

The results of KEGG pathway analysis showed that blue light supplementation significantly affected alanine, aspartate and

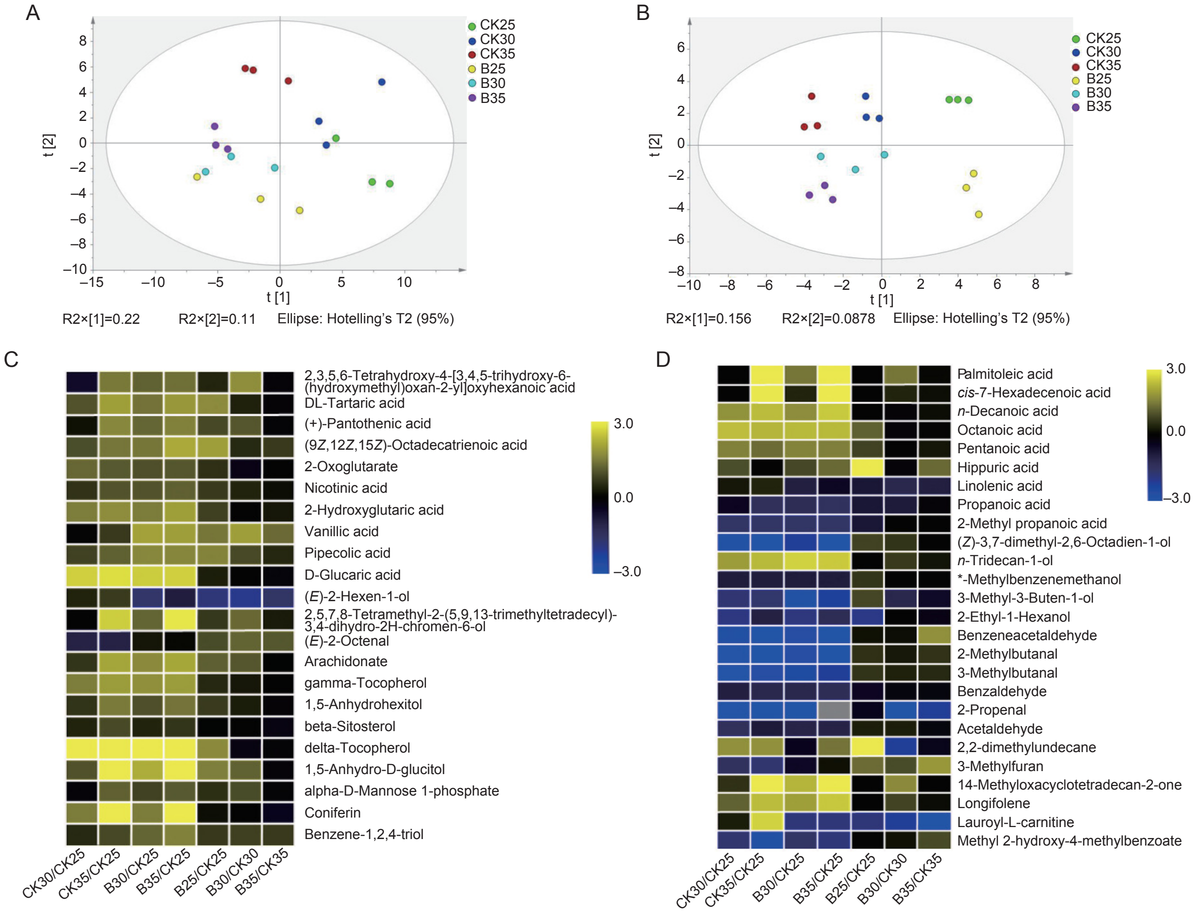

**Fig. 5 PLS-DA score plots and differential metabolites in pitaya peel and pulp after blue light treatment.** A and B, PLS-DA score plot of metabolomics of pitaya peel (A) and pitaya pulp (B). C and D, the differential metabolites in pitaya peel (C) and pitaya pulp (D). CK25, CK30, and CK35, samples from the control group collected at 25, 30, and 35 days after anthesis, respectively. B25, B30, and B35, samples from the blue light treatment group at the corresponding time points.

glutamate metabolism in pitaya fruit (Fig. 6-A). Therefore, quantitative RT-PCR on related genes in this pathway was conducted to clarify the mechanism of action (Fig. 6-B). *HuAGT2-1*, *HuAGT2-2*, *HuGAD5*, *HuGSs*, *HuALT2-2* and *HuALT2-3* were significantly up-regulated in the peel and showed varying degrees of up-regulation throughout the fruit development stage. *HuSSP2*, *HuAS2*, *HuGOGAT1-2/1-3*, *HuGADs*, and *HuGSs* were significantly upregulated at 25 DAA compared with the control group, and *HuAS2*, *HuGOGAT1-3* and *HuGAD1* were significantly upregulated during fruit development. The remaining genes were downregulated.

According to KEGG pathway analysis, a metabolic

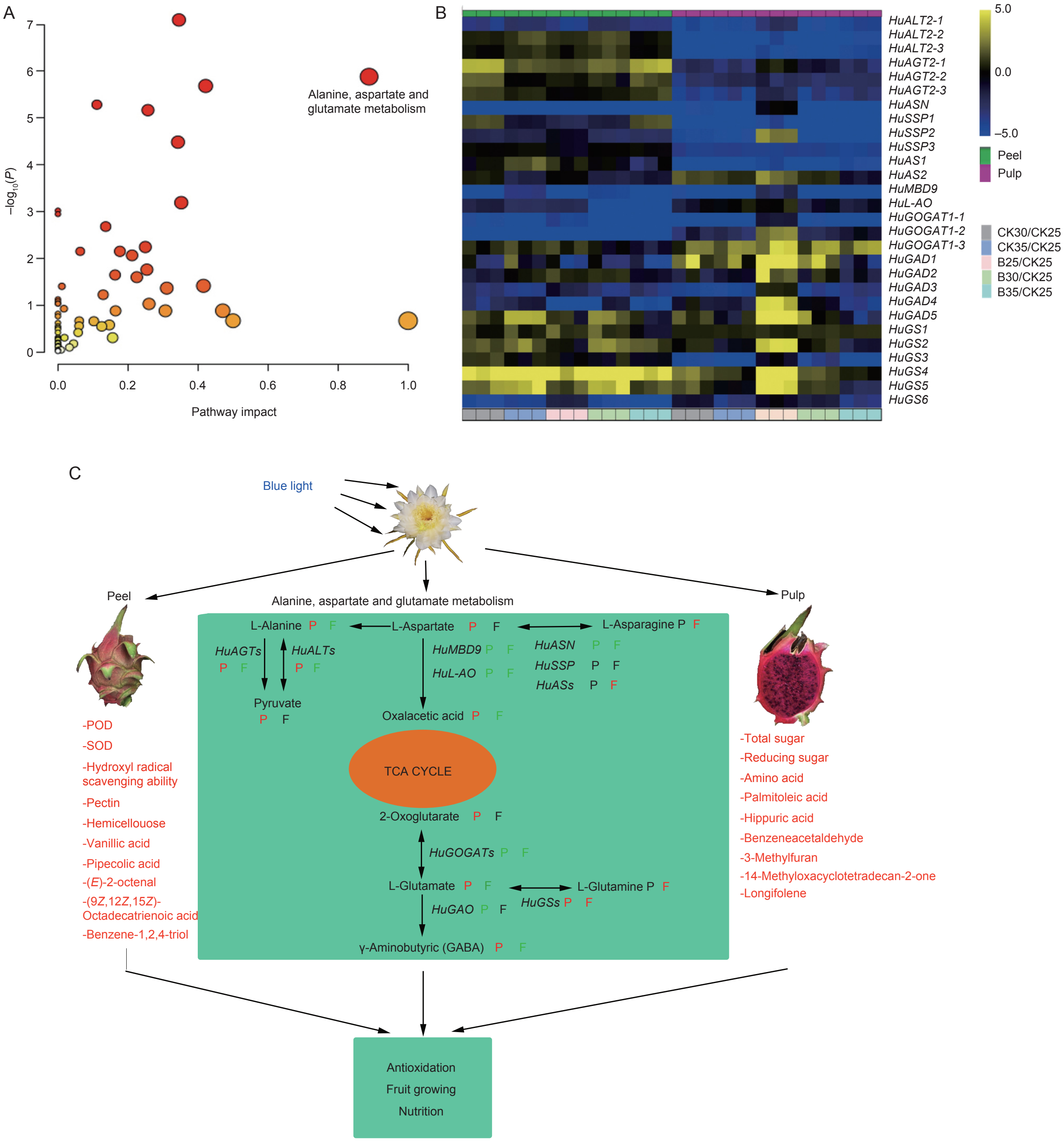

**Fig. 6 Significant KEGG pathway analysis and regulatory schematic of blue light on pitaya peel and pulp.** A, KEGG pathway analysis of pitaya peel and pulp metabolomics. The number of metabolites enriched in this pathway is indicated by the size of the bubbles in the graph. Bubble color represents significance: the redder the bubble, the more statistically significant the difference. CK25, CK30, and CK35, samples from the control group collected at 25, 30, and 35 days after anthesis, respectively. B25, B30, and B35, samples from the blue light treatment group at the corresponding time points. B, gene changing patterns in alanine, aspartate and glutamate metabolism which changed significantly after blue light treatment. Data are presented as the mean±SE ($n$=3). C, metabolic regulatory schematics of peel and pulp of pitaya treated with blue light. P and F represent the change patterns in the peel and pulp, respectively, while red and green indicate increase and decrease, respectively, and black denotes no significant change.

pathway diagram (Fig. 6-C) was drawn. After blue light treatment, the contents of L-alanine, pyruvate, L-aspartate, oxalacetic acid, 2-oxoglutarate, L-glutamate, and gamma-aminobutyric acid (GABA) were significantly increased, while L-glutamine and L-asparagine were not detected in the peel (Fig. 6-C). In the pulp, the contents of pyruvate, L-alanine, GABA and L-glutamate were significantly decreased, while L-glutamine and L-asparagine were significantly increased (Fig. 6-C). Thus, the blue light treatment significantly influenced the distribution of amino acids, such as L-alanine, L-aspartate, and L-glutamate in the peel and pulp, affecting fruit quality. Blue light treatment also increased the contents of pyruvate, oxalacetic acid and 2-oxoglutarate, which play roles in the TCA cycle (Fig. 6-C), and directly increased basic metabolism levels in the peel and pulp of pitaya fruit.

## 4. Discussion

### 4.1. Effects of blue light treatment on pitaya fruit yield

Many studies have demonstrated that fruit quality can be affected by environmental factors, such as light. Light plays a vital role in flowering, fruit development and ripening (He *et al.* 2022). Supplemental LED lighting has been shown to increase the size of tomatoes, and tomato fruit development was faster during the night for the plants receiving LED light (Paponov *et al.* 2020). In this study, the average fruit weight was increased by supplemental blue light. Although the control group had greater average fruit weight than the blue light treatment group at 25 DAA (Fig. 1-A), the average fruit weight in the blue light treatment group increased by 79.26% from 25 to 35 DAA, while the growth rate of the control group for the same time period only increased by 40.75%. This indicates that the main stage at which blue light significantly promotes an increase in individual fruit weight is from 25 to 35 DAA.

We further dissected the fruit weight increment by analysing the relative changes in the peel and pulp weight. During the key fruit development period from 25 to 35 DAA, the peel weight decreased by 49.46 and 36.97% in the control and blue light treatments, respectively (Appendix B), while the pulp weight increased by 269.23 and 366.08%, respectively. This indicates that at this stage the peel was beginning to be used as a resource to provide nutrients for pulp development. At the same time, the amount of increase in the pulp was much greater than the amount of decrease in the peel. Therefore, it can be concluded that the increase in pulp weight in the later stages of fruit development is the main contributor to the increase in individual fruit weight under blue light.

We found that blue light treatment increased the contents of total sugar and reducing sugar in the pulp (Fig. 3-A and B). Supplemental blue light treatment improved tomato fruit ripening and quality (He *et al.* 2022). Amino acids are essential food compounds and provide important nutritional value. We found that the content of total amino acids in the pulp (Fig. 3-C) decreased slowly, while the blue light treatment retarded the rate of decrease. Therefore, blue light treatment can improve fruit quality and nutritional value of pitaya fruit. It is reported that supplemental light treatment increases biomass accumulation for different plants (Muhammad *et al.* 2018; Wu B S *et al.* 2023). During the fruit growing period, the contents of total protein (Fig. 3-D) in the blue light treated group were higher than those in the control group. It can be inferred that blue light treatment promoted the accumulation of sugars, amino acids and proteins in the pulp to a certain extent and improved fruit quality.

It is worth noting that the late stage of fruit development, i.e., 25 to 35 DAA in pitaya, is particularly important for fruit weight increase. Therefore, when blue light or other technological measures are utilized to promote yield in pitaya, more attention should be paid to the late stage of fruit development. According to the research of Xiao *et al.* (2022), light quality affects plant growth and the functional component accumulation in fruit, and this study showed consistent experimental results.

Blue light treatment significantly increased individual fruit weight, fruit firmness, total sugar content and total amino acid content of the fruit pulp. It also suppressed the degradation of hemicellulose and increased pectin content in the peel. These improvements in nutritional parameters significantly enhanced both fruit quality and yield. In other fruits, it has also been reported that blue light treatment increased the accumulation of sucrose in mango pulp (Ni *et al.* 2022), and LED light played an important role in improving grape fruit quality (Zhang *et al.* 2021). Our results are consistent with those of Liu *et al.* (2025) that cell wall materials, cellulose, and hemicellulose show a declining trend during apple development, positively correlating with the reduction in fruit firmness.

### 4.2. Effects of blue light treatment on pitaya fruit anti-oxidative activities

CAT, POD and SOD are enzymes related to antioxidant activities (Ling and Zhang 2013; Zhang *et al*. 2024). The blue light treatment increased CAT (Fig. 2-E) and POD (Fig. 2-G) activity. Although SOD activity gradually decreased during fruit growth, the blue light treatment significantly enhanced SOD activity (Fig. 2-I) compared with the control group. Compared with the control group, the hydroxyl radical scavenging ability (Fig. 2-H) was increased after blue light treatment, with significant changes from 25 to 35 DAA. Flavonoids play an essential role in regulating oxidative stress and are an important source of daily intake of antioxidant supplements (Wang *et al.* 2022). Compared with the control group, the blue light treatment significantly increased the flavonoid content in the fruit peel, which could be a result of significant changes in free radical scavenging ability. In an earlier study, supplemental blue light treatment on tomato fruit significantly enhanced the contents of total flavonoids, vitamin C, as well as antioxidant activity (Aalifar *et al.* 2020; He *et al.* 2022; Zhang *et al.* 2022). Therefore, it can be hypothesized that blue light treatment improved the antioxidant capacity of the fruit, which may be mainly related to the changes in the activity of SOD, POD, and CAT, as well as the increase in flavonoid content, resulting in enhanced scavenging capacity of hydroxyl radicals.

### 4.3. Dynamic accumulated metabolites in pitaya fruit in response to blue light treatment

Light is one of the most important environmental factors that affects plant growth and development. It also influences plant morphogenesis, photosynthesis, metabolism and signal transduction (Yang *et al.* 2020). A total of 39 volatile compounds in red pitaya changed significantly after blue light treatment during storage (Wu *et al.* 2019). In a previous study, it was reported that middle-intensity blue light treatment was the most effective condition for developing an intense and persistent fruity and floral scent (He *et al.* 2025). In our study, blue light treatment accelerated the accumulation of key metabolites in peel and pulp, and there were some differences in the effects of blue light treatment between the peel and the pulp.

With blue light treatment in pitaya peel, the content of several metabolites in the peel (Fig. 5-C) increased significantly, except for (*E*)-2-hexen-1-ol. (*E*)-2-Octenal was found to be a special differentially accumulated aldehyde in this study. During pitaya development, its levels tended to decrease in both control and blue light treatment groups, but supplemental blue light significantly increased the accumulation of (*E*)-2-octenal at various stages of peel development from 25 to 35 DAA. It is reported that (*E*)-2-octenal was identified as the most efficient airborne signal in *Nicotiana benthamiana* plants induced by tobacco mosaic virus (TMV), which can prime the jasmonic acid (JA)/ET pathway and then activates immune responses, ultimately leading to enhanced TMV resistance in adjacent *N*. *benthamiana* plants (Hong *et al.* 2023). Thus, blue light treatment significantly affected the accumulation pattern of (*E*)-2-octenal, and has the potential to improve fruit resistance to biotic stress by promoting the accumulation of (*E*)-2-octenal volatiles. Furthermore, five important volatile compounds, including three acids: (9*Z*,12*Z*,15*Z*)-octadecatrienoic acid, vanillic acid, and pipecolic acid; one aldehyde: (*E*)-2-octenal, and one other compound: benzene-1,2,4-triol were enhanced after blue light treatment. With a vanilla-like smell and taste, vanillic acid has always been in high demand in the pharmaceutical, cosmetic, food, flavor, alcohol and polymer industries. It could also regulate cardiovascular diseases and may have therapeutic utility clinically (Lashgari *et al.* 2023). Pipecolic acid is a putative mediator of encephalopathy of cerebral malaria, with neuromodulation roles (Keswani *et al.* 2022). These findings suggest that blue light treatment significantly promoted the accumulation of bioactive compounds in the peel. Additionally, it was reported that (*E*)-2-hexen-1-ol was closely correlated with *Rubus coreanus* (RC) fruit ripening, with its content increasing during RC fruit ripening (Yu *et al*. 2019). Compared with the control group, (*E*)-2-hexen-1-ol decreased markedly after blue light treatment. (*E*)-2-Hexen-1-ol is an alcohol compound with a grass-like aroma, and the decrease in its content caused by blue light treatment helps to diminish grassy notes to enhance the overall sensory profile of the pitaya fruit. In addition to enhancing the accumulation of volatile compounds in the peel of pitaya fruit, blue light treatment can also increase the release of bioactive compounds to a certain extent.

Previous studies have irradiated grape leaves with blue light, and it was found that blue light improved fruit composition (Li C X *et al*. 2017). Six acids (Fig. 5-D) gradually accumulated with fruit development in the pitaya pulp: palmitoleic acid, *cis*-7-hexadecenoic acid, *n*-decanoic acid, octanoic acid, pentanoic acid, and hippuric acid. Among them, the level of hippuric acid was significantly increased by blue light treatment, and its derivatives showed good antiretroviral potential, maximum fungicidal and cytotoxic activities (Tehreem *et al.* 2019). In addition, as organic acids are used as antimicrobial agents in the food industry (Coban 2020), it could be hypothesized that blue light treatment could potentially endow pitaya fruits with better antibacterial properties, which can help reduce the probability of fruit decay during storage, and thus potentially extend the shelf life of pitaya fruits.

Compared with the control, the levels of 3-methyl-3-buten-1-ol and 2-ethyl-1-hexanol were slightly decreased by the blue light in the pulp. Related studies have shown that aldehydes have antibacterial activity and are effective agents in regulating microbial growth (Darwin and Stanley 2022). The contents of differential aldehydes (Fig. 5-D) increased significantly after blue light treatment, and the change was most obvious for benzeneacetaldehyde. Benzeneacetaldehyde, detected in the flowers of *Rhododendron* species (Qian *et al.* 2019) and in the leaves of *Cantium parviflorum* Lam. (Kala and Ammani 2017), has been reported to possess antioxidant (Tanapichatsakul *et al.* 2017) and antimicrobial (Kala and Ammani 2017) properties, and has a fruity, floral, and sweet odour. The same patterns were observed for 2-methylbutanal and 3-methylbutanal. Therefore, we hypothesize that blue light treatment can increase the biotic resistance of pitaya fruit by increasing the content of aldehyde compounds especially benzeneacetaldehyde in the pulp. Moreover, aldehydes are important aroma components of pitaya fruits (Wu *et al.* 2020a; Wu Q *et al.* 2023), so the enhancement of these compounds suggests that blue light treatment increased the representative flavor of pitaya. To a certain extent, blue light treatment enhances the accumulation of characteristic components in pitaya and helps promote the growth and development of the fruit. Overall, the blue light treatment induced a positive response and increased the accumulation of aldehydes and acids in the pulp of pitaya, which could potentially enhance the biotic resistance and flavor characteristics of the fruit.

## 5. Conclusion

In pitaya, supplemental blue light significantly increased fruit weight by promoting pulp biomass accumulation, improved fruit firmness by increasing pectin content, retarded hemicellulose degradation, and enhanced the activity of POD and SOD as well as the content of flavonoids, thereby improving the antioxidant capacity of the fruit. Specifically, blue light treatment significantly altered alanine, aspartate, and glutamate metabolism, promoted the accumulation of bioactive ingredients in the peel, and significantly altered the accumulation of volatile compounds — especially increasing organic acids, esters and terpenes in the pulp — thereby affecting fruit flavor.

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## Declaration of competing interest

The authors declare that they have no conflict of interest.

## Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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