

Effects of Monochromatic Red, Blue and Combined Red– Blue LED Light on Growth, Photosynthesis and Leaf Metabolome in Kiwifruit Seedlings

yanzong zhang

Zhengzhou Fruit Research Institute

Chenchen zhang

College of Horticulture and Plant Protection, Henan University of Science and Technology

Ming Li

Zhengzhou Fruit Research Institute

Dawei Cheng

Zhengzhou Fruit Research Institute

Xiaoxu Sun

Zhengzhou Fruit Research Institute

Hong Gu

Zhengzhou Fruit Research Institute

Lan Li

Zhengzhou Fruit Research Institute

Jinyong Chen

chen.jinyong@caas.cn

Zhengzhou Fruit Research Institute

Research Article

Keywords: LED light, Growth, Photosynthesis, Metabolism, kiwifruit

Posted Date: September 17th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10877340/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Effects of Monochromatic Red, Blue and Combined Red–Blue LED Light on Growth, Photosynthesis and Leaf Metabolome in Kiwifruit Seedlings

Yanzong Zhang^{1,3}, Chenchen Zhang^{1,4}, Ming Li^{1,2,3}, Dawei Cheng^{1,2,3}, Xiaoxu Sun^{1,2,3}, Hong Gu^{1,2,3}, Lan Li^{1,2,3*} and Jinyong Chen^{1,2,3*}

1 Zhengzhou Fruit Research Institute, Chinese Academy of Agricultural Sciences, Zhengzhou 450009, China;

zhangyanzong3137@163.com (Y. Z.); zcc922970@163.com (C. Z.); liming07@caas.cn (M. L.); chengdawei@caas.cn (D.C.); sunxiaoxu@caas.cn (X. S.); guhong@caas.cn (H. G.)

2 Zhongyuan Research Center, Chinese Academy of Agricultural Sciences, Xinxiang 453500, China

3 National Key Laboratory for Germplasm Innovation & Utilization of Horticultural Crops, Zhengzhou 450009, China;

4 College of Horticulture and Plant Protection, Henan University of Science and Technology, Luoyang 471023, China

* Correspondence: lilan01@caas.cn (L. L.); chenjinyong@caas.cn (J. C.).

Abstract

Background Light quality is a major environmental factor regulating plant growth, development, and metabolism. In protected cultivation, covering materials, seasonal variation, and geographic conditions often limit light intensity or alter its spectral composition. Light-emitting diode (LED) supplementation, particularly with red and blue light, is an effective strategy for improving photosynthetic performance and carbon metabolism. Kiwifruit seedlings were exposed to white light (W), blue light (B), red light (R), and combined red and blue light. Combined treatments used red-to-blue (R) ratios of 6:1 (R6B1), 3:1 (R3B1), and 1:1 (R1B1). Growth, photosynthetic characteristics, carbohydrate metabolism, and leaf metabolite profiles were then compared.

Results R6B1 significantly promoted plant height, leaf expansion, and biomass accumulation. R3B1 significantly enhanced the net photosynthetic rate and stomatal conductance. R3B1 also increased leaf concentrations of sucrose, glucose, fructose, and starch. It enhanced the activities of sucrose phosphate synthase (SPS), sucrose synthase in the synthetic direction (SS-II), acid invertase (AI), neutral invertase (NI), soluble starch synthase (SSS), and total amylase (AMY). These results indicate that an appropriate red-to-blue ratio promotes photosynthetic carbon assimilation and sugar accumulation by coordinating carbohydrate synthesis and degradation. Metabolomic profiling of representative W, B, R, and R3B1 treatments identified 2,741 metabolites, primarily comprising terpenoids, flavonoids, phenolic acids, and

lipids. Compared with W, B induced the largest number of differentially accumulated metabolites. These metabolites were predominantly enriched in flavonoid biosynthesis and flavone and flavonol biosynthesis. Differentially accumulated metabolites under R were mainly associated with isorhamnetin O-glycoside biosynthesis and unsaturated fatty acid biosynthesis. Those under R3B1 were primarily enriched in linoleic acid metabolism and flavonoid biosynthesis.

Conclusions Collectively, red and blue light ratios differentially regulate growth, photosynthetic carbon metabolism, and secondary metabolism in kiwifruit seedlings. These findings provide a scientific basis for optimizing supplemental-lighting strategies in protected kiwifruit cultivation.

Keywords: LED light; Growth; Photosynthesis; Metabolism; kiwifruit

1. Introduction

Light is a key environmental factor driving photosynthesis during plant growth and development, and affects plant morphogenesis, physiological processes, and developmental regulation [1]. In horticultural production systems, dense canopies, greenhouse plastic covering materials, geographic latitude, seasonal changes, and weather conditions often result in insufficient light intensity or poor light quality. Suboptimal light environments can lead to slow growth, reduced photosynthetic capacity, abnormal flower bud differentiation, and undesirable plant architecture, ultimately affecting crop yield and quality [2]. In recent years, light-emitting diode (LED) sources have been widely applied in plant factories and protected agriculture because of their low energy consumption, adjustable wavelengths, and long service life [3, 4]. Red and blue light are the two most commonly used spectral regions in supplemental lighting for plants, as they are highly absorbed by leaves and serve as the primary energy sources for photosynthesis [5, 6]. Red light can effectively promote plant growth and photosynthesis [7], and has been shown to increase the yield of tomato and parsley [8, 9], expand leaf area in lettuce [10], and significantly enhance chlorophyll content and net photosynthetic rate in grapevine [11]. In contrast, blue light contributes to the accumulation of primary and secondary metabolites in strawberry [12], improves antioxidant capacity and nutritional quality in tomato and coriander [13, 14]. In addition, the ratio of red to blue light plays an important regulatory role in plant growth. It has been reported that a red-to-blue light ratio of 8:1 significantly increases the net photosynthetic rate and maximum quantum efficiency of Photosystem II (PSII) in potato, while also suppressing excessive stem elongation [15]. In cucumber seedling production, when the proportion of red light exceeded that of blue light, seedling

height, leaf area, stem diameter, Dickson quality index (DQI), relative chlorophyll content, and net photosynthetic rate were significantly higher than those under blue-light-dominant treatments [16]. In studies on basil grown under artificial lighting, LED sources were found to be markedly superior to fluorescent lamps, especially under the R3B1 treatment, which significantly increased yield, chlorophyll content, water- and energy-use efficiency, antioxidant activity, and mineral element accumulation [17]. In melon, increasing the proportion of red light under different red/blue combinations progressively enhanced seedling height, stem diameter, leaf area, and stomatal aperture, with the R7B3 treatment producing the optimal morphological performance [18]. In blackberry tissue-cultured plantlets, LED lighting with a red-to-blue ratio of 1:2 significantly increased leaf area as well as chlorophyll and carotenoid contents [19].

Sugars are major energy sources in plants, supplying energy for growth, metabolism, and reproduction. Enzymes play indispensable roles in sugar metabolism, and the major enzymes involved include sucrose synthase (SUS), sucrose phosphate synthase (SPS), invertase (INV), UDP-glucose pyrophosphorylase (UGPase), and glycosyltransferases (GTs) [20]. Changes in light conditions can significantly affect plant sugar metabolism, thereby regulating sugar synthesis and accumulation [21]. Previous studies have shown that red light significantly increases glucose, fructose, and sucrose contents in grapes by enhancing sucrose synthase activity in the synthetic direction (SS-II) and acid invertase (AI) activity [22]. Blue light has also been reported to enhance the activities of sucrose synthase (SS) and sucrose phosphate synthase (SPS) during grape ripening [23]. Different light qualities, particularly appropriate red-to-blue light ratios, can significantly regulate plant sugar metabolism and related enzyme activities. For example, continuous irradiation under different red-to-blue light ratios increased the activities of synthetic enzymes such as sucrose synthase (SS), sucrose phosphate synthase (SPS), and ADP-glucose pyrophosphorylase (AGPase), thereby promoting sucrose and starch accumulation in lettuce. However, the activities of these synthetic enzymes decreased with increasing proportions of blue light, whereas the activities of sugar-conversion-related enzymes, such as AI, NI, and α - and β -amylases, increased [24]. In red-fleshed pitaya 'Zimilong', LED supplemental lighting at a red-to-blue ratio of 2:1 significantly increased soluble solids and sucrose contents in ripe fruits, enhanced SPS and SS activities, and inhibited AI and NI activities [25].

In recent years, with the rapid development of high-throughput analytical technologies, metabolomics has been widely applied to investigate plant responses to various environmental factors,

including light quality, temperature, drought, and nutrient availability, and to elucidate the underlying metabolic regulatory networks [26]. The light environment is one of the major factors influencing plant metabolism. Different light qualities can significantly regulate the synthesis and accumulation of various metabolites in plants. For example, red light can modulate the expression of key genes (*PAL* and *CHS*) involved in the phenylpropanoid pathway, thereby promoting the biosynthesis of anthocyanins, flavonoids, and phenolic compounds [27]. Red light can also enhance terpene biosynthesis by regulating the expression of genes involved in the MEP/MVA pathways [28]. On the other hand, blue light can induce the expression of transcription factors such as HY5 and MYB, thereby activating key genes in the phenylpropanoid pathway, including *PAL*, *CHS*, and *4CL*, and promoting the accumulation of flavonoids, anthocyanins, and phenolic compounds [29, 30]. Moreover, in many plant species, blue light has been shown to significantly increase the contents of antioxidant compounds such as phenolics and flavonoids and to enhance antioxidant capacity [31–33]. Compared with monochromatic light, combined red and blue light often exerts a more pronounced regulatory effect on secondary metabolism. For example, the R1B3 treatment promoted anthocyanin accumulation in pepper, whereas the R1.6B1 treatment significantly increased flavonoid and flavonol contents and enhanced antioxidant capacity in *Crocus sativus* [34].

Kiwifruit is a dioecious fruit crop belonging to the genus *Actinidia* in the family Actinidiaceae. Owing to its unique flavor and high nutritional value, it is highly favored by consumers and has become an important fruit in the world [35]. As a woody vine fruit crop, kiwifruit is characterized by vigorous shoot growth and a complex canopy structure, which can easily cause mutual shading between leaves and fruits, thereby reducing photosynthetic efficiency and ultimately affecting yield and fruit quality. Artificial supplemental lighting can improve the canopy light environment, compensate for insufficient natural light, promote the accumulation of photosynthetic assimilates, and thus enhance fruit quality and commercial value [36]. Although LED supplemental lighting has been extensively studied and applied in horticultural crops such as vegetables, flowers, and medicinal plants, its application in fruit trees, particularly kiwifruit, remains limited. Therefore, this study used kiwifruit seedlings to evaluate the potential of LED lighting for optimizing the light environment and promoting plant growth and development under practical production conditions.

2. Materials and Methods

2.1 Plant Materials and Treatments

The experimental materials were obtained from the kiwifruit germplasm nursery at the Zhengzhou Fruit Research Institute, Chinese Academy of Agricultural Sciences. Uniform and vigorous one-year-old potted seedlings of *Actinidia deliciosa* ‘Zhongmi No. 2’ were selected as the experimental materials. Seedlings were pruned back to retain two to three buds per plant. After bud break, only one vigorous shoot was retained per seedling. When the third fully expanded functional leaf had developed, the seedlings were transferred to an artificial climate chamber and exposed to different light treatments. LED light sources (supplied by Henan Zhishengpu Electronic Technology Co., Ltd.) were used in this experiment, including white light (400–770 nm, W), red light (660 nm, R), and blue light (450 nm, B). The photosynthetic photon flux density was set at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ according to the light compensation point and light saturation point of kiwifruit[37], with the ambient temperature maintained at 25°C . Six light-quality treatments were established, as shown in Figure 1, and the detailed treatment conditions are presented in Table 1. The treatments were applied for 4 weeks. Each treatment included 15 plants, with three biological replicates of five plants each. Hoagland nutrient solution was applied weekly to ensure proper growth. At the end of the 4-week treatment period, leaf samples were collected, immediately frozen in liquid nitrogen, and stored at -80°C .

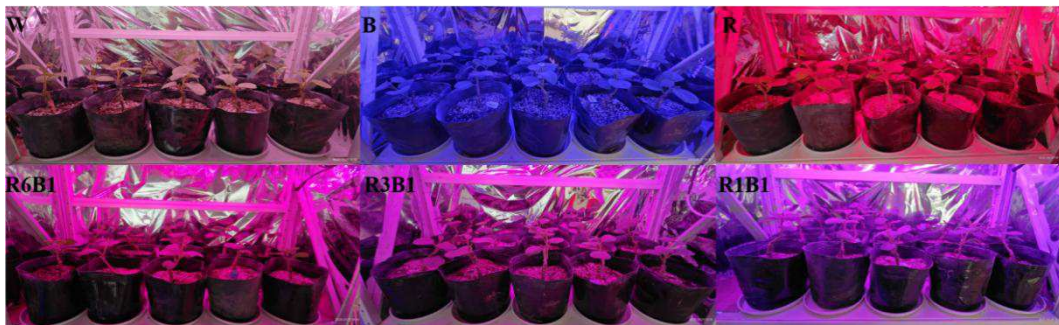


Figure 1. Experimental environment of kiwifruit seedlings under different light-quality treatments

Table 1. Supplemental lighting treatment conditions

Treatment	Photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	Photoperiod
White (W)	200	14 h (6:00–20:00)
Blue (B)	200	14 h (6:00–20:00)
Red (R)	200	14 h (6:00–20:00)
R:B=6:1 (R6B1)	200	14 h (6:00–20:00)
R:B=3:1 (R3B1)	200	14 h (6:00–20:00)

2.2 Measurement of Morphological Traits

Plant height was measured weekly using a ruler, and basal stem diameter was measured using a vernier caliper. The leaf area, leaf length, leaf width, and leaf perimeter of the uppermost fully expanded functional leaf were determined using a leaf area meter (YMJ-B, TOP Cloud-Agri, Hangzhou, China).

2.3 Biomass Determination

At the end of the supplemental lighting treatments, the fresh weight of the aboveground parts was measured using an electronic balance. The samples were then oven-dried at 105 °C for 15 min, followed by drying at 65 °C to a constant weight, and the dry weight was recorded using an electronic balance.

2.4 Determination of Photosynthetic Pigment Contents

The contents of photosynthetic pigments were determined according to the method described by Zou [38]. Fresh leaf samples (0.2 g) were placed in 15 mL centrifuge tubes and extracted with 10 mL of 95% ethanol for 48 h. The absorbance was then measured at 665, 649, and 470 nm using a microplate reader (SpectraMax i3x, Molecular Devices, San Jose, CA, USA).

2.5 Determination of Photosynthesis-Related Parameters

During the fourth week, the net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (Tr) were measured using a CIRAS-3 portable photosynthesis system (PP Systems, Boston, MA, USA). Five functional leaves at the same position were randomly selected from each treatment for measurement.

2.6 Determination of Carbon Metabolite Contents

Starch content was determined using a commercial assay kit provided by Jiangsu Aidisheng Biological Technology Co., Ltd., and sucrose content was determined using a commercial assay kit provided by Beijing Solarbio Science & Technology Co., Ltd. All measurements were performed according to the manufacturers' instructions, with three biological replicates for each treatment. Glucose and fructose contents were determined by high-performance liquid chromatography (HPLC) according to the method described in GB 5009.8—2023 National Food Safety Standard: Determination of fructose, glucose, sucrose, maltose, and lactose in foods, with appropriate optimization based on the recommended parameters. The instrumental conditions were as follows: an amino column (4.6 mm × 250 mm, 5 μm particle size, packed with aminopropyl-bonded silica) or an equivalent alternative column were used. The mobile phase consisted of acetonitrile and water (70:30, v/v), with a flow rate of 1.0 mL min⁻¹. The

column temperature was maintained at 40 °C, and the injection volume was 10 µL. An evaporative light-scattering detector (ELSD) was used, with the drift tube temperature set at 80–90 °C and the nitrogen flow rate at 2.5 L min⁻¹. Quantitative analysis was performed based on peak areas and standard curves. All measurements were conducted with three biological replicates.

2.7 Determination of Activities of Carbon Metabolism-Related Enzymes

The activities of sucrose phosphate synthase (SPS), sucrose synthase in the synthetic direction (SS-II), neutral invertase (NI), acid invertase (AI), soluble starch synthase (SSS), and total amylase (AMY) were determined using plant enzyme activity assay kits provided by Jiangsu Aidisheng Biological Technology Co., Ltd. All measurements were performed according to the manufacturer's instructions, with three biological replicates for each treatment.

2.8 Metabolome analysis

2.8.1 Dry Sample Extraction

Using vacuum freeze-drying technology, the leaf samples were placed in a lyophilizer (Scientz-100F), then ground (30 Hz, 1.5 min) to powder form by using a grinder (MM 400, Retsch). Next, weigh 30 mg of sample powder using an electronic balance (MS105DM) and add 1500 µL of -20 °C pre-cooled 70% methanolic aqueous internal standard extract (less than 30 mg added at the rate of 1500 µL extractant per 30 mg sample). Vortex once every 30 min for 30 s, for a total of 6 times. After centrifugation (rotation speed 12000 rpm, 3 min), the supernatant was aspirated, and the sample was filtered through a microporous membrane (0.22 µm pore size) and stored in the injection vial for UPLC-MS/MS analysis.

2.8.2 UPLC Conditions

The extracted samples were analyzed using an UPLC-ESI-MS/MS system (UPLC, ExionLC™ AD, <https://sciex.com.cn/>) and Tandem mass spectrometry system (<https://sciex.com.cn/>). The analytical conditions were as follows, UPLC: column, Agilent SB-C18 (1.8 µm, 2.1 mm * 100 mm); The mobile phase consisted of solvent A, pure water with 0.1% formic acid, and solvent B, acetonitrile with 0.1% formic acid. Sample measurements were performed with a gradient program that employed the starting conditions of 95% A, 5% B. Within 9 min, a linear gradient to 5% A, 95% B was programmed, and a composition of 5% A, 95% B was kept for 1 min. Subsequently, a composition of 95% A, 5.0% B was adjusted within 1.1 min and kept for 2.9 min. The flow velocity was set as 0.35 mL per minute, the column oven was set to 40 °C and the injection volume was 2 µL. The effluent was alternatively connected to an ESI-triple quadrupole-linear ion trap (QTRAP)-MS.

2.8.3 Principal Component Analysis (PCA)

PCA (principal component analysis) was performed by the statistics function `prcomp` within R (www.r-project.org). The data were processed by UV (unit variance scaling) before PCA.

2.8.4 Hierarchical Clustering Analysis (HCA) and Pearson Correlation Coefficient (PCC) Analysis

HCA and PCC analysis were performed using the `ComplexHeatmap` package in R.

2.8.5 Screening of Differential Metabolites

For comparisons between two groups, differential metabolites were screened based on the following criteria: variable importance in projection (VIP)>1 and an absolute value of $\log_2$ fold change ($|\log_2FC|$) ≥ 1.0 .

2.8.6 Kyoto Encyclopedia of Genes and Genomes (KEGG) Annotation and Enrichment Analysis

The identified metabolites were annotated using the KEGG Compound database (<http://www.kegg.jp/kegg/compound/>), and the annotated metabolites were subsequently mapped to the KEGG Pathway database (<http://www.kegg.jp/kegg/pathway.html>) for pathway analysis.

2.9 Data Processing and Statistical Analysis

Experimental data were first organized and preprocessed using Microsoft Excel. Statistical analyses were performed in the R software program. Significant differences among treatments were assessed by one-way analysis of variance (ANOVA) followed by Duncan's multiple range test at $P<0.05$. Figures were generated using Origin 2024.

3. Results

3.1 Effects of Different Light Qualities on Morphogenesis of Kiwifruit Seedlings

Plant height, stem diameter, and leaf traits, including leaf area, leaf length, leaf width, and leaf perimeter, of kiwifruit seedlings increased over time under all light-quality treatments, although differences were observed under different treatments (Figure 2). The R6B1 treatment showed the fastest increases in plant height, leaf area, leaf length, leaf width, and leaf perimeter, reaching 30.66 cm, 12,372.7 mm², 119.3 mm, 129.36 mm, and 424.15 mm, respectively, at 28 d, which were higher than those under the other treatments. In contrast, these growth parameters were lowest under the B treatment. Differences in stem diameter were relatively small, with the R and W treatments showing slightly higher values than the combined light and B treatments.

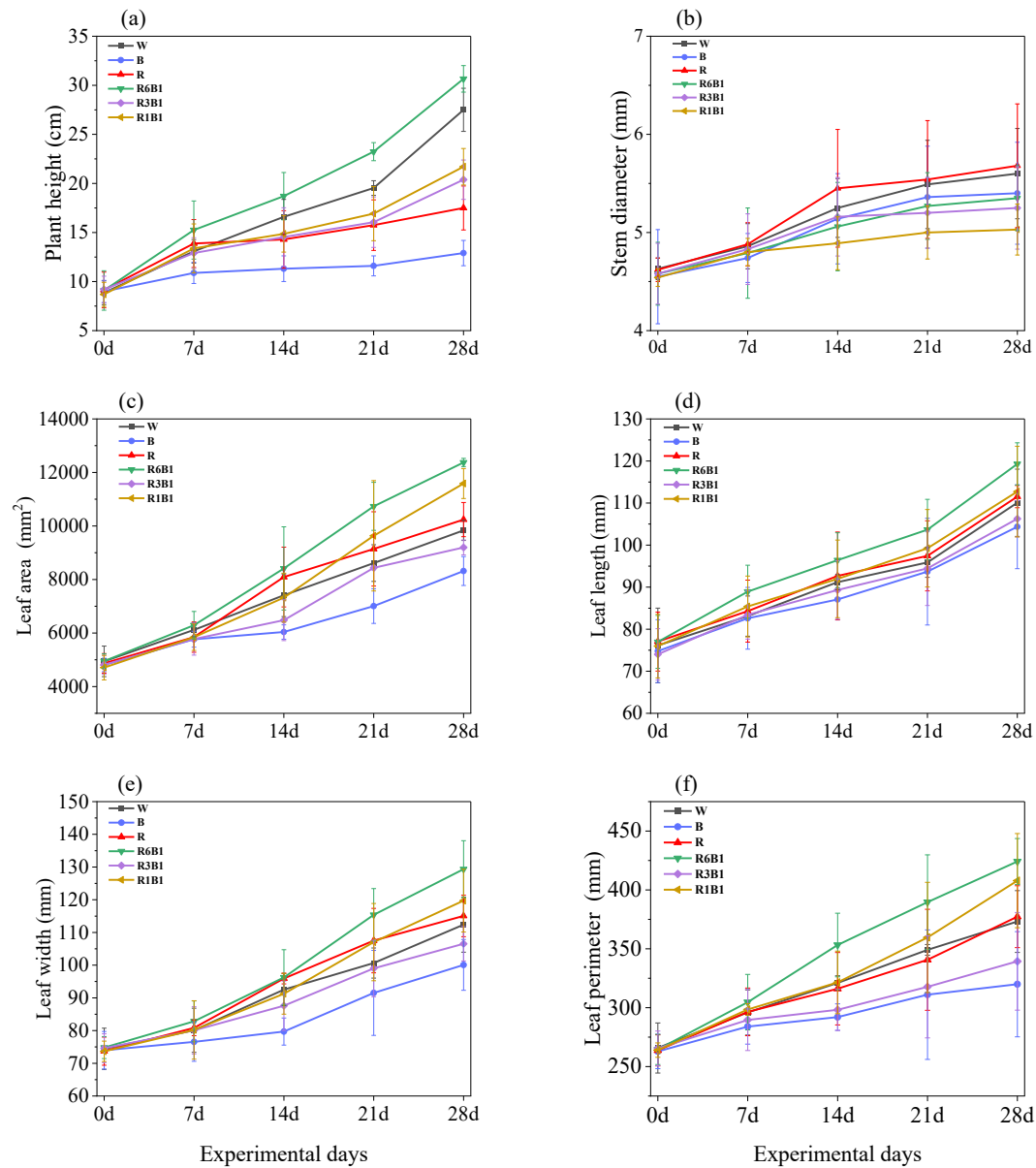


Figure 2. Effects of different light qualities on the morphogenesis of kiwifruit seedlings

Note: W (white light), B (blue light), R (red light), R6B1 (red–blue ratio 6:1), R3B1 (red–blue ratio 3:1), and R1B1 (red–blue ratio 1:1). Panels a, b, c, d, e, and f represent plant height, stem diameter, leaf area, leaf length, leaf width, and leaf perimeter, respectively.

3.2 Effects of Different Light Qualities on the Biomass of Kiwifruit Seedlings

Biomass accumulation in kiwifruit seedlings varied among different light-quality treatments (Figure 3). Among the treatments, R6B1 showed the best performance in both fresh weight and dry weight, with increases of approximately 25% and 29%, respectively, compared with W. The R1B1 treatment also showed an increase relative to W, with fresh weight increasing by approximately 11%. In contrast, the B treatment resulted in the lowest biomass accumulation, with fresh weight and dry weight decreasing by approximately 30% and 42%, compared with W. The R treatment also showed lower biomass than W,

with decreases of approximately 19% and 22% in fresh weight and dry weight.

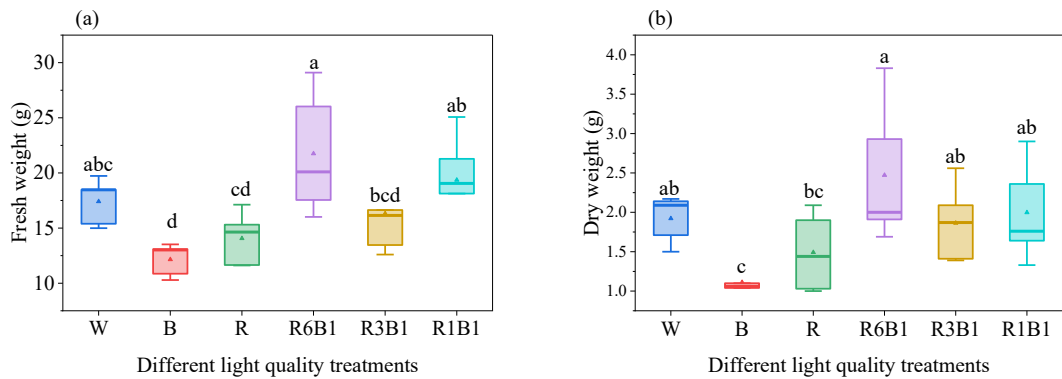


Figure 3. Effects of different light qualities on the biomass of kiwifruit seedlings

Note: W (white light), B (blue light), R (red light), R6B1 (red-blue ratio 6:1), R3B1 (red-blue ratio 3:1) and R1B1 (red-blue ratio 1:1). Duncan's multiple range test was used for significance analysis. Different letters indicate significant differences between treatments at the $P < 0.05$ level. Panels a and b represent fresh weight and dry weight, respectively.

3.3 Effects of Different Light Qualities on the Photosynthetic Pigment Contents of Kiwifruit Seedlings

Different light-quality treatments significantly affected the contents of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids in kiwifruit seedling leaves (Figure 4). The R1B1 treatment resulted in the highest photosynthetic pigment contents. Chlorophyll a, total chlorophyll, and carotenoid contents under R1B1 increased by approximately 8%, 6%, and 13% compared to W, whereas the difference in chlorophyll b content between the R1B1 and W treatments was not significant. In contrast, the B treatment showed the lowest photosynthetic pigment contents, with chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents decreasing by approximately 24%, 32%, 26%, and 13%, compared with W. Under the R treatment, chlorophyll a and total chlorophyll contents decreased by approximately 12% and 16% relative to W, whereas no significant differences in pigment contents were observed between the R6B1 and W treatments.

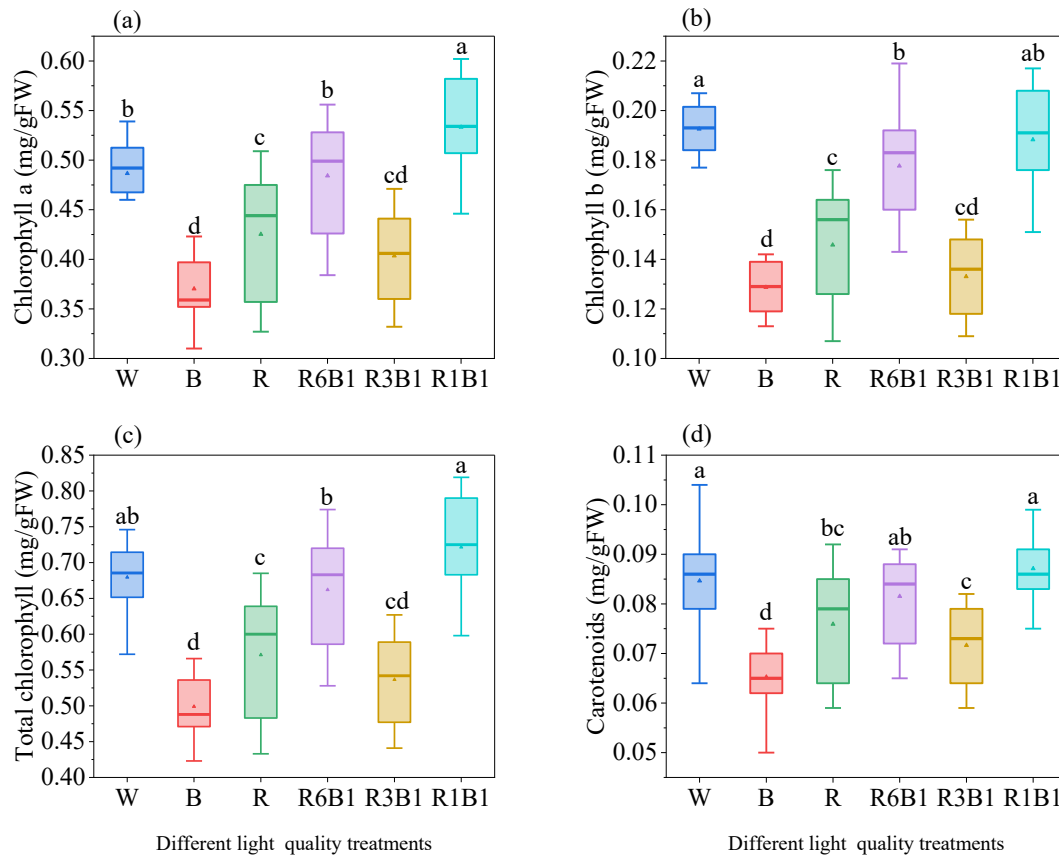


Figure 4. Effects of different light qualities on photosynthetic pigment contents in kiwifruit seedlings

Note: W (white light), B (blue light), R (red light), R6B1 (red-blue ratio 6:1), R3B1 (red-blue ratio 3:1) and R1B1 (red-blue ratio 1:1). Duncan's multiple range test was used for significance analysis. Different letters indicate significant differences between treatments at the $P < 0.05$ level. Panels a, b, c and d represent chlorophyll a, chlorophyll b, total chlorophyll and carotenoids, respectively.

3.4 Effects of Different Light Qualities on Leaf Photosynthetic Parameters in Kiwifruit Seedlings

The effects of different light qualities on the photosynthetic parameters of kiwifruit seedlings were investigated (Table 2). For the net photosynthetic rate (P_n), the R3B1 treatment was significantly higher than the other treatments, reaching $15.67 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas no significant differences were observed among the remaining treatments. The intercellular CO_2 concentration (C_i) differed significantly among treatments. Treatments with a higher proportion of blue light generally showed higher C_i values. The B and R1B1 treatments had C_i values of 336.17 and $332.83 \mu\text{mol mol}^{-1}$, respectively, both of which were significantly higher than those of the other treatments, whereas the R3B1 treatment showed the lowest C_i value ($308.17 \mu\text{mol mol}^{-1}$). For stomatal conductance (G_s), the R3B1 treatment reached $1120.83 \text{ mmol m}^{-2} \text{s}^{-1}$, which was significantly higher than that of the other treatments, whereas the B and R1B1

treatments showed the lowest values, 411.50 and 505.00 mmol m⁻² s⁻¹, respectively. The transpiration rate (Tr) showed a trend similar to that of Gs. The highest Tr was observed under the R3B1 treatment (7.80 mmol m⁻² s⁻¹), which was significantly higher than that under the other treatments, whereas the B and R1B1 treatments showed the lowest values, at 5.23 and 5.40 mmol m⁻² s⁻¹, respectively.

Table 2. Effects of different light qualities on leaf photosynthetic parameters of kiwifruit seedlings

Treatment	Pn ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Ci ($\mu\text{mol mol}^{-1}$)	Gs ($\text{mmol m}^{-2} \text{s}^{-1}$)	Tr ($\text{mmol m}^{-2} \text{s}^{-1}$)
W	13.62±1.31b	315.50±4.89b	641.83±145.41cd	6.48±0.25d
B	13.02±0.74b	336.17±7.44a	411.5±73.86e	5.23±0.28e
R	14.02±0.66b	312.67±5.92bc	911.00±173.74b	7.36±0.29b
R6B1	13.88±0.37b	315.50±6.92bc	772.67±100.86bc	6.84±0.26c
R3B1	15.67±1.28a	308.17±5.23c	1120.83±73.33a	7.80±0.29a
R1B1	13.35±0.47b	332.83±5.64a	505.00±113.62de	5.40±0.40e

Note: W (white light), B (blue light), R (red light), R6B1 (red-blue ratio 6:1), R3B1 (red-blue ratio 3:1) and R1B1 (red-blue ratio 1:1). Duncan's multiple range test was used for significance analysis. Different letters indicate significant differences between treatments at the $P < 0.05$ level. Pn, Ci, Gs and Tr represent net photosynthetic rate, intercellular CO₂ concentration, stomatal conductance and transpiration rate, respectively.

3.5 Effects of Different Light Qualities on the Accumulation of Carbon Metabolites in Kiwifruit Seedlings

Different light qualities significantly affected the accumulation of carbon metabolites in kiwifruit seedling leaves (Figure 5). Compared with the W treatment, the R3B1 treatment increased starch, fructose, glucose, and sucrose contents by 18%, 41%, 18%, and 30%, respectively, showing the most pronounced effect. The R treatment also significantly promoted carbon metabolite accumulation, with starch, fructose, glucose, and sucrose contents increasing by 10%, 25%, 14%, and 11%, respectively, compared with W. In contrast, the R6B1 treatment effect on carbon metabolite accumulation was relatively limited, with starch, fructose, glucose, and sucrose contents increasing by approximately 1%, 5%, 3%, and 3%, respectively, compared with W, and these differences did not reach significant levels. Metabolite contents under the R1B1 treatment were generally comparable to those under W, with no significant differences observed. In contrast, the B treatment reduced starch, fructose, glucose, and sucrose contents by approximately 8%, 7%, 9%, and 4%, respectively, relative to W.

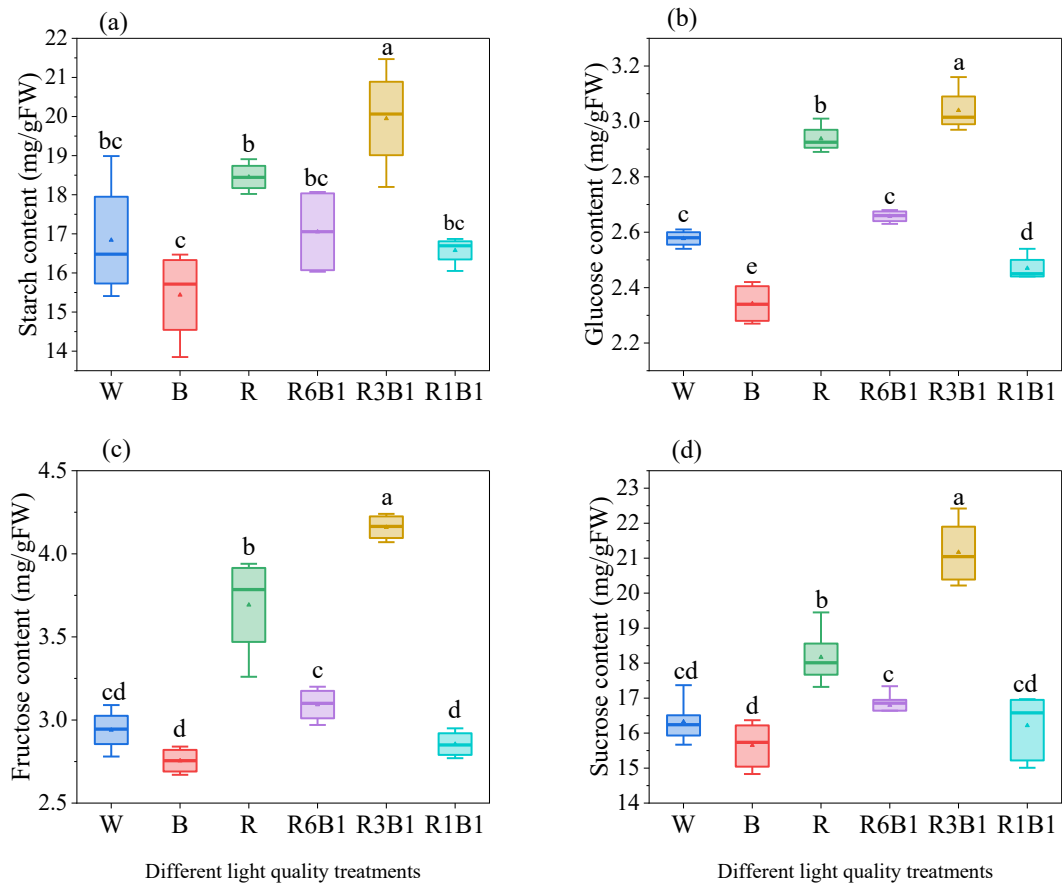


Figure 5. Effects of different light qualities on carbon metabolite accumulation in kiwifruit seedlings

Note: W (white light), B (blue light), R (red light), R6B1 (red-blue ratio 6:1), R3B1 (red-blue ratio 3:1) and R1B1 (red-blue ratio 1:1). Duncan's multiple range test was used for significance analysis. Different letters indicate significant differences between treatments at the $P < 0.05$ level. Panels a, b, c and d represent starch, glucose, fructose and sucrose, respectively.

3.6 Effects of Different Light Qualities on Carbon Metabolism-Related Enzyme Activities in Kiwifruit Seedlings

Different light-quality treatments significantly affected the activities of carbon metabolism-related enzymes in kiwifruit seedling leaves (Figure 6). Compared with the W treatment, amylase activity reached the highest level under the R3B1 treatment, increasing by approximately 11%. The activity of soluble starch synthase (SSS) was also significantly enhanced under R3B1, reaching approximately twice that of the W treatment, while sucrose phosphate synthase (SPS) activity increased significantly by about 20% compared with W. In addition, sucrose synthase activity in the synthetic direction (SS-II) was highest under the R3B1 treatment, showing an increase of approximately 25% relative to W, and acid invertase (AI) activity was also significantly elevated, increasing by about 54%. Neutral invertase (NI) activity likewise reached its peak under the R3B1 treatment, with an increase of approximately 31%

compared with W. The R treatment ranked second, with all enzyme activities being significantly higher than those under W. The R6B1 treatment also promoted the activities of some enzymes, such as SSS, NI, and AI, to a certain extent, whereas the R1B1 and B treatments generally showed lower enzyme activities, with the B treatment in particular exhibiting a clear inhibitory effect relative to W.

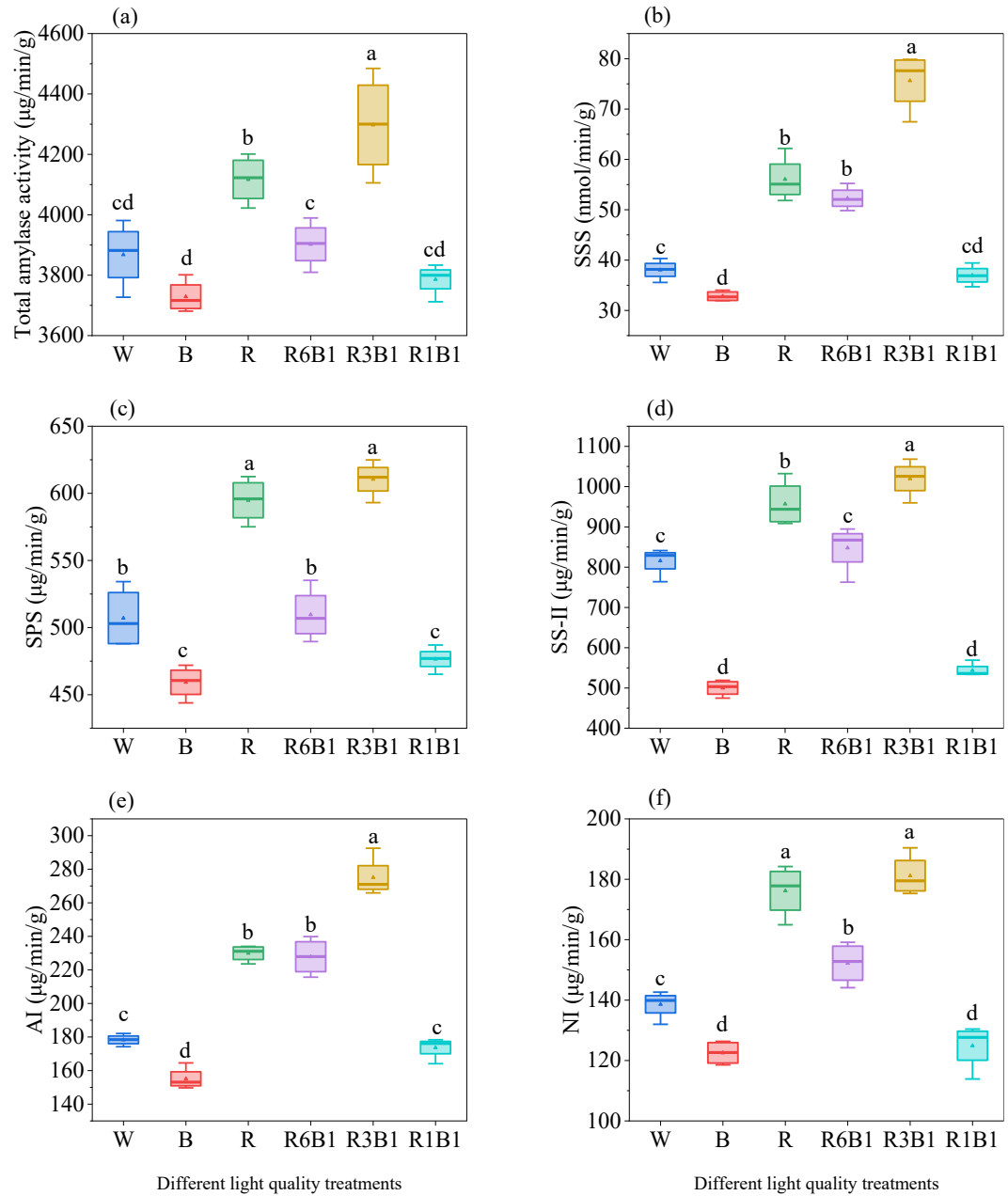


Figure 6. Effects of different light qualities on the activities of carbon metabolism-related enzymes in kiwifruit seedlings

Note: W (white light), B (blue light), R (red light), R6B1 (red-blue ratio 6:1), R3B1 (red-blue ratio 3:1) and R1B1 (red-blue ratio 1:1). Duncan's multiple range test was used for significance analysis. Different letters indicate significant differences between treatments at the $P < 0.05$ level. Panels a, b, c, d, e and f represent total amylase, soluble starch synthase (SSS), sucrose phosphate synthase (SPS), sucrose synthase activity in the synthetic direction (SS-II), acid invertase (AI) and neutral invertase (NI), respectively.

3.7 Comprehensive Analysis

Principal component analysis (PCA) was used to comprehensively evaluate morphogenesis, photosynthetic characteristics, and carbon metabolism in kiwifruit seedlings under different light-quality treatments, with principal components extracted according to the criterion of eigenvalues > 1 . The variance contribution rates of the first three principal components (PC1, PC2, and PC3) were 59.12%, 28.32%, and 7.19%, respectively, with a cumulative contribution rate of 94.63%, indicating that most of the variation among the measured traits could be explained by these three principal components (Table 3). The loadings of each trait on the three principal components are shown in Table 4. Based on the weighted scores of each principal component, a comprehensive score (Z value) was calculated and used to rank the different treatments (Table 5). The results showed that the R3B1 treatment had the highest comprehensive score ($Z = 3.43$), indicating that it performed better than the other treatments.

Table. 3 Variance explanation of principal component analysis for growth, photosynthetic and carbon metabolism indices of kiwifruit seedlings under different light quality treatments

Principal component	Eigenvalue	Variance contribution rate (%)	Cumulative variance contribution rate (%)
PC1	13.60	59.12%	59.12%
PC2	6.51	28.32%	87.43%
PC3	1.65	7.19%	94.63%

Table. 4 Principal component loading matrix of growth, photosynthetic and carbon metabolism indices of kiwifruit seedlings

Indices	PC1	PC2	PC3
Plant Height	0.021	0.888	-0.379
Stem diameter	0.079	0.248	-0.944
Leaf area	-0.132	0.908	0.024
Fresh weight	-0.062	0.943	0.024
Dry weight	0.120	0.942	-0.045
Chlorophyll a	-0.365	0.867	0.272
Chlorophyll b	-0.467	0.839	0.038
Total chlorophyll	-0.386	0.872	0.219

Carotenoids	-0.423	0.711	0.384
Pn	0.940	0.059	0.176
Ci	-0.869	-0.342	0.258
Gs	0.988	0.155	0.001
Tr	0.955	0.211	-0.173
Starch	0.967	0.106	0.222
Fructose	0.982	-0.072	0.168
Glucose	0.976	0.118	0.061
Sucrose	0.955	-0.065	0.244
Total amylase	0.991	-0.003	0.123
SSS	0.973	0.081	0.076
SPS	0.970	0.006	0.073
SS-II	0.922	0.256	-0.215
AI	0.957	0.203	0.007
NI	0.975	0.069	-0.070

Table. 5 Comprehensive scores and rankings of principal components for kiwifruit seedlings under different light quality

treatments		
Treatment	Comprehensive score	Ranking
R3B1	3.43	1
R	1.46	2
R6B1	0.77	3
W	-0.60	4
R1B1	-1.56	5
B	-3.50	6

3.8 Overall Characteristics of Metabolomic Data

Based on the results of the previous comprehensive analysis, representative treatments, including white light (W), blue light (B), red light (R), and the optimal red–blue combined light treatment (R3B1), were selected for widely targeted metabolomics analysis to elucidate the potential mechanisms by which different light qualities regulate the growth of kiwifruit seedlings at the metabolic level. To characterize

the overall variation in metabolomic profiles of kiwifruit leaves under different light-quality treatments, principal component analysis (PCA), sample correlation analysis, hierarchical clustering analysis (HCA), and metabolite classification were performed (Figure 7). The PCA results showed that PC1 and PC2 explained 28.46% and 19.78% of the total variation, respectively (Figure 7A). Samples from different treatments were clearly separated in the principal component space, whereas the three biological replicates within each treatment were tightly clustered, indicating good experimental reproducibility and a significant effect of light quality on metabolite composition in kiwifruit leaves. Sample correlation analysis showed that the correlation coefficients among biological replicates were high ($r > 0.83$), further confirming the reliability of the data (Figure 7B). Hierarchical clustering analysis of all detected metabolites revealed that samples from different light-quality treatments formed relatively independent clusters, indicating distinct patterns of metabolite accumulation among treatments (Figure 7C).

A total of 2741 metabolites were identified across all kiwifruit leaf samples. Based on their chemical structures and functional characteristics, these metabolites were classified into 13 categories (Figure 7D). Among them, terpenoids accounted for the largest proportion (21.78%), followed by flavonoids (15.58%) and other compounds (14.99%). In addition, phenolic acids (11.16%) and lipids (11.13%) also represented relatively high proportions, each exceeding 10% of the total metabolites. Alkaloids (6.35%), lignans and coumarins (5.87%), and amino acids and derivatives (4.82%) were present at moderate levels. Overall, kiwifruit leaves contained a wide diversity of metabolites, with secondary metabolites (such as terpenoids, flavonoids, and phenolic acids) accounting for a substantial proportion of the metabolomic profile.

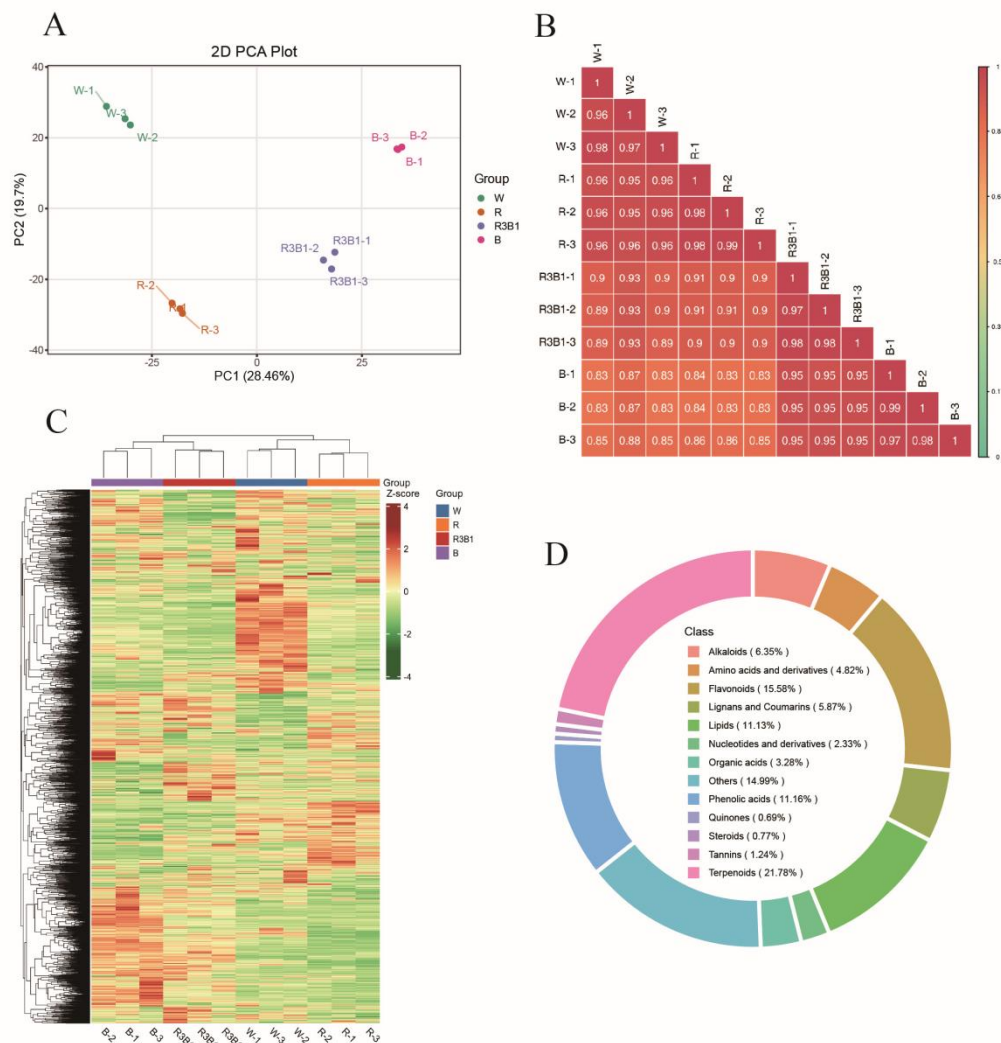


Figure 7. Overall analysis of metabolomic characteristics in kiwifruit leaves under different light-quality treatments

Note: Panels A, B, C and D represent principal component analysis (PCA), sample correlation analysis, hierarchical clustering analysis (HCA), and metabolite classification, respectively.

3.9 Screening of Differential Metabolites under Different Light-Quality Treatments

Using white light (W) as the control, pairwise comparisons were performed between the blue light (B), red light (R), and red–blue combined light (R3B1) treatments and the W treatment. Based on the screening criteria of variable importance in projection ($VIP > 1$) from orthogonal partial least squares-discriminant analysis (OPLS-DA) and fold change ($|\log_2FC| \geq 1$), differential metabolites in kiwifruit leaves under different light-quality treatments were systematically identified, and the results were visualized using a combined volcano plot (Figure 8).

In the B vs W comparison, a total of 549 differential metabolites were identified, including 308

significantly upregulated metabolites, 241 significantly downregulated metabolites, and 2181 metabolites showing no significant difference. The R vs W comparison showed the fewest differential metabolites, with a total of 356 identified, including 106 upregulated metabolites, 250 downregulated metabolites, and 2363 metabolites with no significant difference. In the R3B1 vs W comparison, 494 differential metabolites were identified, including 206 upregulated metabolites, 288 downregulated metabolites, and 2238 metabolites showing no significant difference.

To further clarify the common and specific metabolic responses of kiwifruit leaves to different light-quality treatments, a Venn diagram of differential metabolites from the three comparison groups was constructed (Figure 8D). The results showed that 107 differential metabolites were shared among the three comparisons, suggesting that these metabolites may represent core targets of light-quality-regulated metabolism in kiwifruit leaves and may participate in fundamental light-responsive metabolic pathways. Meanwhile, each comparison also contained a large number of unique differential metabolites. The B vs W comparison had the largest number of unique differential metabolites (224), followed by R3B1 vs W (161), whereas R vs W had the fewest, with only 129.

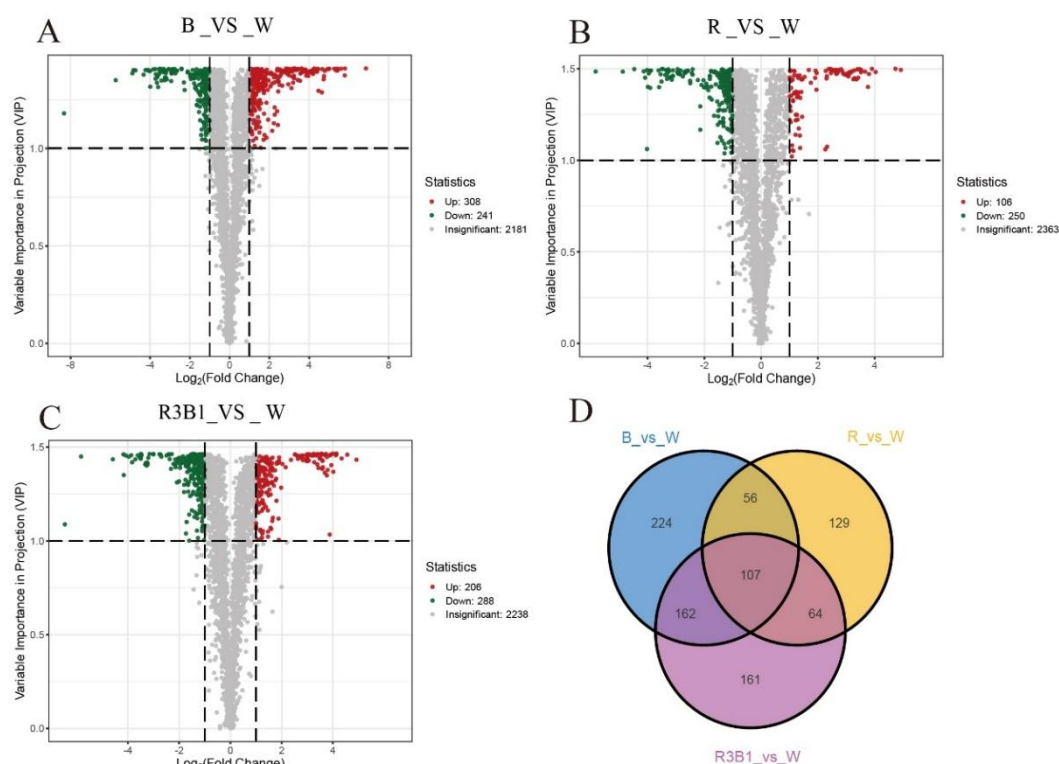


Figure 8. Volcano plot and Venn diagram of differential metabolites in kiwifruit leaves under different light-quality treatments

Panels A, B and C represent volcano plots showing the distribution of significantly upregulated and downregulated metabolites in B vs W, R vs W, and R3B1 vs W comparisons, respectively. Panel D represents the Venn diagram illustrating the common and specific differentially accumulated metabolites among the three comparisons.

3.10 KEGG Enrichment Analysis of Differential Metabolites and Changes in Flavonoid Metabolism under Different Light-Quality Treatments

To further elucidate the effects of different light qualities on metabolic pathways in kiwifruit leaves, KEGG pathway enrichment analysis was performed on the differential metabolites identified in the blue light (B), red light (R), and red–blue combined light (R3B1) treatments, using white light (W) as the control (Figure 9). In the B vs W comparison, differential metabolites were mainly enriched in flavonoid biosynthesis, flavone and flavonol biosynthesis, and isorhamnetin O-glycosides biosynthesis. In the R vs W comparison, differential metabolites were mainly enriched in isorhamnetin O-glycosides biosynthesis and biosynthesis of unsaturated fatty acids. In the R3B1 vs W comparison, differential metabolites were mainly enriched in linoleic acid metabolism and flavonoid biosynthesis.

Given that the flavonoid biosynthesis pathway was significantly enriched in multiple comparisons under different light-quality treatments, metabolites related to this pathway were further subjected to hierarchical clustering analysis (Figure 9D), which revealed clear differences in metabolite accumulation patterns among treatments. Overall, most metabolites showed relatively high abundance in the B treatment. In particular, myricetin, naringenin 7-O-beta-D-glucoside, phlorizin, dihydromyricetin, quercetin, naringenin, phloretin, and tricetin accumulated at relatively high levels under B treatment. The abundance of most metabolites was relatively low in the R treatment, with only a few metabolites, such as (+)-gallocatechin and leucocyanidin, showing relatively high levels. In the R3B1 treatment, only few metabolites, including pinocembrin, phlorizin, quercetin, and vitexin, showed relatively high abundance, whereas most of the remaining metabolites were maintained at moderate or low levels. In the W treatment, fustin exhibited relatively high abundance, whereas the other metabolites exhibited relatively small overall changes. These results indicate that flavonoid biosynthesis is an important metabolic pathway responsive to different light qualities, and that the B treatment had a more pronounced effect on the accumulation of metabolites associated with this pathway.

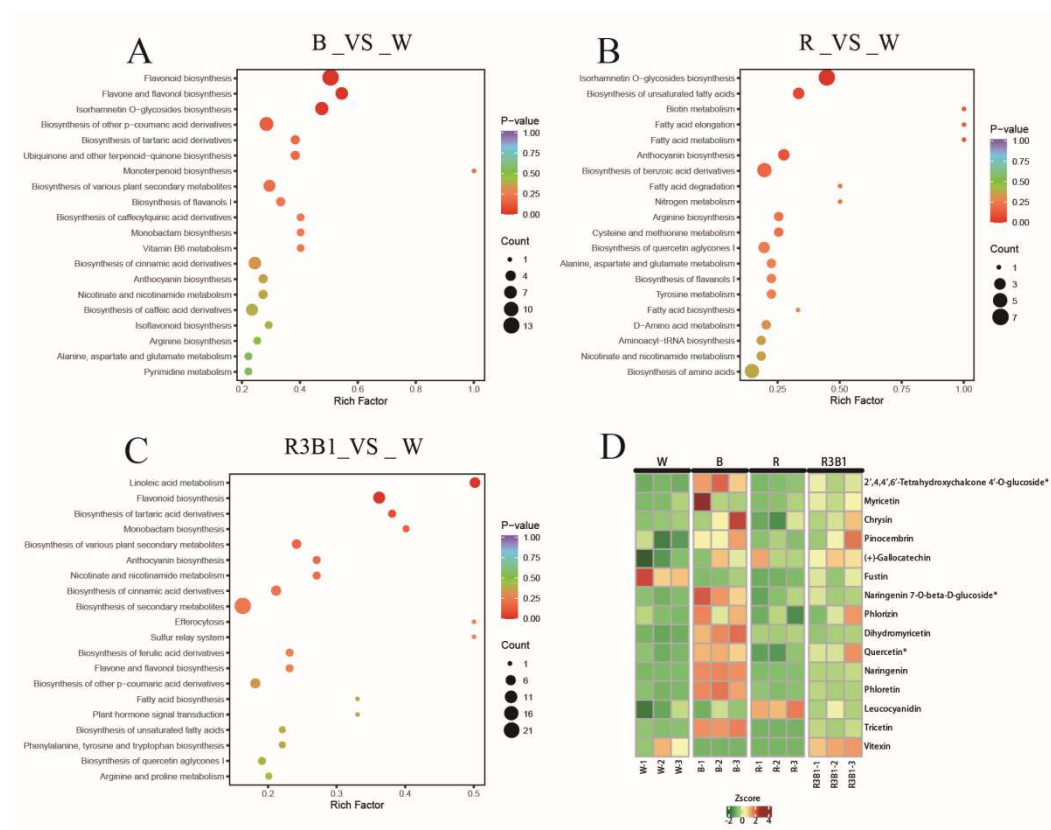


Figure 9. KEGG enrichment analysis of differential metabolites and heatmap of flavonoid biosynthesis-related metabolites under different light-quality treatments

Panels A, B and C represent KEGG pathway enrichment analyses of differentially accumulated metabolites identified in blue light versus white light (B vs W), red light versus white light (R vs W), and red–blue combined light versus white light (R3B1 vs W) comparisons, respectively. Panel D represents the heatmap visualization of flavonoid biosynthesis-related metabolites under different light-quality treatments.

4. Discussion

4.1 Combined Red and Blue Light Promotes the Growth of Kiwifruit Seedlings

Light quality plays a crucial role in regulating plant growth. Red and blue light can significantly affect plant morphology, and architecture is one of the most direct manifestations of plant adaptation to the light environment [39]. Monochromatic red and blue light have been shown to significantly affect morphogenesis in many species. Previous studies have shown that biomass accumulation in pepper was significantly reduced under red LED light [40]. In sweet pepper seedlings, the red light significantly promoted hypocotyl elongation, first internode elongation, and leaf expansion, but inhibited biomass accumulation, whereas blue light significantly suppressed plant height and internode elongation [41]. Similarly, during early photomorphogenesis in tomato, red light promoted hypocotyl elongation,

cotyledon expansion, plant height, and leaf area, whereas blue light resulted in a more compact plant architecture, reduced plant height, and lower biomass accumulation[42]. These indicate that red light generally promotes stem and leaf elongation, whereas blue light tends to inhibit elongation growth and alter plant architecture, although its effects on biomass may be species-dependent.

In the present study, plant height and biomass accumulation of kiwifruit seedlings under red and blue light were both lower than those under white light, with the lowest values observed under blue light. The growth responses of kiwifruit seedlings to monochromatic light may therefore exhibit a certain degree of species specificity, and may also be influenced by other factors such as temperature, relative humidity, irrigation, and fertilization. The stronger inhibitory effect of blue light on elongation growth and biomass accumulation in kiwifruit seedlings may be related to its role in restricting cell elongation and leaf expansion. Compared with monochromatic light, combined light is generally more favorable for seedling growth, and red–blue combined light is widely regarded as the optimal light quality for promoting plant growth [43]. In the present study, the R6B1 treatment performed best in promoting plant height, leaf area, leaf morphological traits, and biomass accumulation in kiwifruit seedlings, outperforming monochromatic red light, monochromatic blue light, and other mixed-light treatments. Although no direct reports are currently available on the growth performance of kiwifruit seedlings under this specific light ratio, previous studies have shown that a relatively high proportion of red light in red–blue combined light generally promotes the growth and development of various plants, such as cucumber [16] and apple [44]. Given the species-specific responses of plants to light quality, the present study provides new experimental evidence for light-quality regulation of growth in kiwifruit seedlings. Further studies are needed to elucidate the underlying mechanisms by which different red-to-blue light ratios regulate kiwifruit morphology.

Although stem diameter did not differ significantly among treatments, this does not necessarily indicate that light quality has no effect on stem diameter. Previous studies have shown that red light and red–blue combined light (1R1B and 3R1B) significantly increased stem diameter in tomato seedlings [45]. In the present study, there were no significant variation for stem diameter, which may be due to the relatively short duration of supplemental lighting or to the lower sensitivity of stem diameter to light quality at the seedling stage. Future studies could extend the treatment period or integrate stem diameter measurements with indicators such as lignification to further elucidate the mechanisms underlying light-quality regulation of stem growth.

4.2 Combined Red and Blue Light Promoted Photosynthesis in Kiwifruit Seedlings

Photosynthetic pigments play important roles in light absorption, energy transfer, and light energy utilization, and their contents may vary under different light-quality conditions [46]. In the present study, the R1B1 treatment promoted photosynthetic pigment biosynthesis in kiwifruit seedlings, which is consistent with the results reported by Zhang et al. [47] in tomato. This effect may be attributed to the synergistic roles of red and blue light in regulating photosynthetic pigment synthesis [48]. In contrast, chlorophyll and carotenoid contents were significantly reduced under the R treatment, and similar results have also been reported in apple and cauliflower microgreens [49, 50]. Although some studies have shown that the R3B1 and blue-light treatments are favorable for photosynthetic pigment synthesis [51–53], these two treatments showed relatively poor performance in the present study, possibly because the responses of photosynthetic pigment synthesis to light are highly species-dependent [54].

The chlorophyll content of kiwifruit leaves was highest under the R1B1 treatment, but the net photosynthetic rate was not the highest. This indicates that leaf photosynthesis is influenced by multiple factors, and that chlorophyll content alone cannot fully reflect photosynthetic capacity, highlighting the complexity of plant photosynthetic responses to light quality [47]. Photosynthetic rate is a key determinant of plant assimilatory capacity and yield. In the present study, the R3B1 treatment significantly increased the net photosynthetic rate and stomatal conductance of kiwifruit seedlings, while the transpiration rate was also relatively high, indicating that this treatment enhanced photosynthetic capacity. The enhanced photosynthetic capacity under R3B1 may be closely related to adaptive changes in leaf anatomical structure. Palisade tissue (PT) improves light penetration, whereas spongy tissue (SPT) enhances light scattering and gas exchange, together contributing to higher light-use efficiency [55]. Similarly, R3B1 combined light can increase PT and SPT length, thereby improving leaf photosynthetic structure and promoting photosynthesis [53]. In contrast, blue light significantly reduced the net photosynthetic rate of blueberry [56]. In rice, blue light significantly decreased intercellular CO₂ concentration, stomatal conductance, and transpiration rate [39]. In the present study, blue light reduced the net photosynthetic rate, stomatal conductance, and transpiration rate, while increasing intercellular CO₂ concentration. These results are partly consistent with previous findings, although some differences were also observed. These discrepancies may be associated with differences in plant species, environmental temperature, and light intensity.

4.3 Combined Red and Blue Light Promoted Carbon Metabolism in Kiwifruit

Seedling Leaves

Sucrose is the major product of photosynthesis in leaves (source tissues) and is transported to sink tissues as an important source of carbon and energy [57]. Sucrose, glucose, and fructose are indispensable substrates for plant growth, development, and various physiological processes, whereas starch is the major storage carbohydrate accumulated in chloroplasts. Thus, light quality can affect plant growth and development by regulating carbon metabolism [45]. Several studies have shown that red light can promote sucrose and starch accumulation in cotton and increase fructose and glucose contents in tomato seedlings, whereas blue light inhibits sucrose and starch synthesis in tomato and strawberry [45, 58–60]. These findings were also consistent with the present study. In addition, some studies have indicated that supplementing red light with an appropriate proportion of blue light can also promote carbohydrate accumulation [61]. In the present study, leaf sucrose, glucose, fructose, and starch contents were all higher under the R3B1 treatment than under the R6B1 and R1B1 treatments, which may be associated with the stronger photosynthetic capacity under R3B1 [45]. The R3B1 treatment increases starch, glucose, and sucrose contents in eggplant seedlings [62], as well as glucose, fructose, and sucrose contents in tomato fruits [63], which is consistent with our findings.

In plants, sucrose synthesis, accumulation, and transport depend on the coordinated actions of sucrose metabolism-related enzymes, including sucrose phosphate synthase (SPS), sucrose synthase in the synthetic direction (SS-II), acid invertase (AI), and neutral invertase (NI). Meanwhile, starch synthesis and accumulation are also regulated by enzymes such as soluble starch synthase (SSS) and total amylase, which together participate in the dynamic balance and allocation of carbohydrates. SPS is a key enzyme in sucrose biosynthesis, invertases (AI and NI) are involved in sucrose degradation, whereas sucrose synthase has a bidirectional catalytic function [64–66]. The increased activities of SPS and SS-II under the R3B1 treatment were consistent with the higher sucrose content in leaves, indicating that enhanced sucrose synthesis contributes to carbohydrate accumulation. Similar studies have shown that light conditions affect sucrose metabolism in tomato seedling leaves, and that increases in sucrose, glucose, and starch contents are mainly associated with enhanced activities of sucrose metabolism-related enzymes [45, 60]. At the same time, AI and NI activities were also elevated under the R3B1 treatment, which may facilitate the conversion of part of the sucrose into glucose and fructose, thereby maintaining sugar homeostasis and energy supply. In addition, with respect to starch metabolism, the R3B1 treatment also increased the activities of SSS and total amylase to some extent, which was

consistent with the relatively high starch content in leaves. This result is similar to findings previously reported in lettuce [24, 67]. Collectively, these results suggest that the R3B1 treatment promoted sugar accumulation and plant growth by enhancing the activities of enzymes involved in sucrose and starch metabolism.

4.4 Combined Red and Blue Light Promoted the Accumulation of Flavonoid- and Lipid Metabolism-Related Metabolites in Kiwifruit Seedling Leaves

As an important environmental regulatory factor, light quality not only affects plant morphogenesis, but also plays a key role in regulating the synthesis and accumulation of metabolites in plants. Widely targeted metabolomics enables the systematic detection of a wide range of metabolites and the identification of differential metabolites that accumulate under changing environmental conditions, thereby facilitating the elucidation of metabolic responses to external stress [68]. At present, metabolomics studies on the effects of light quality have been reported in various horticultural crops, such as grape [69], pitaya [70], strawberry [71], and tomato [72], whereas such studies in kiwifruit remain limited. Therefore, investigating metabolite variation in kiwifruit leaves under different light-quality conditions is important for understanding the mechanisms by which light regulates plant metabolism.

In the present study, widely targeted metabolomics based on UPLC-MS/MS was used to systematically analyze the metabolite composition of kiwifruit leaves under different light-quality treatments. A total of 2741 metabolites were identified, mainly comprising terpenoids, flavonoids, phenolic acids, and lipids, among which secondary metabolites accounted for a relatively large proportion. Previous studies have shown that changes in the light environment can induce the synthesis of specific secondary metabolites in plants, particularly flavonoids, phenolics, and terpenoids, which play important roles in plant adaptation to environmental changes [73].

Differential metabolite screening showed that the B treatment generated the largest number of differential metabolites, followed by R3B1, whereas the R treatment produced the fewest. According to the enrichment analysis, differential metabolites under the B treatment were mainly enriched in the flavonoid biosynthesis and flavone and flavonol biosynthesis pathways, indicating that blue light has a strong inductive effect on secondary metabolism in kiwifruit leaves, particularly on flavonoid metabolism. Similar phenomena have also been reported in other plants. For example, in rice grains, the B treatment was also associated with enhanced flavonoid accumulation, suggesting that the promotive

effect of blue light on flavonoid metabolism may be relatively widespread [30]. Combined with the phenotypic results, the marked growth inhibition observed under the B treatment suggests that monochromatic blue light may impose a certain degree of stress on normal seedling growth. The enhancement of flavonoid biosynthesis may therefore represent an adaptive response of kiwifruit seedlings to blue-light stress by promoting the accumulation of antioxidant-related secondary metabolites and thereby alleviating stress damage. In contrast, under the R treatment, differential metabolites were mainly enriched in isorhamnetin O-glycosides biosynthesis and biosynthesis of unsaturated fatty acids, whereas under the R3B1 treatment they were mainly enriched in linoleic acid metabolism and flavonoid biosynthesis. These results indicate that different light qualities exert distinct regulatory effects on metabolism in kiwifruit leaves. The R treatment appeared to preferentially affect flavonol glycosylation and lipid metabolism, whereas the R3B1 treatment simultaneously influenced both lipid- and flavonoid-related metabolic pathways, showing a more integrated regulatory pattern than monochromatic light.

5. Conclusion

This study revealed how different LED light-quality treatments regulate the growth and metabolism of kiwifruit seedlings. The R6B1 treatment significantly promoted plant morphogenesis and biomass accumulation, whereas the R3B1 treatment significantly enhanced photosynthetic capacity. At the same time, the R3B1 treatment effectively increased the contents of major soluble sugars and starch in leaves. It also significantly enhanced the activities of key carbon metabolism-related enzymes, including total amylase, sucrose phosphate synthase (SPS), sucrose synthase in the synthetic direction (SS-II), acid invertase (AI), neutral invertase (NI), and soluble starch synthase (SSS), thereby promoting carbohydrate homeostasis and energy supply in kiwifruit seedlings. Principal component analysis further indicated that the R3B1 treatment was optimal for the overall performance of kiwifruit seedlings in terms of growth, photosynthesis, and carbon metabolism. Different light qualities also exerted distinct regulatory effects on metabolite accumulation in kiwifruit seedling leaves. The B treatment tended to induce the accumulation of antioxidant-related secondary metabolites such as flavonoids, which may represent an adaptive response of seedlings to blue-light stress. The R treatment mainly affected the flavonol glycosylation branch and lipid metabolism, whereas the R3B1 treatment combined features of both, promoting the accumulation of flavonoid- and lipid metabolism-related metabolites and exhibiting a more balanced and integrated regulatory pattern. These findings provide a theoretical basis for optimizing

light-quality regulation to improve light-use efficiency and promote kiwifruit growth and development in kiwifruit production.

DECLARATIONS

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

All data generated or analysed during this study are included in this manuscript and its supplementary information files.

Competing interests

The authors declare that they have no competing interests.

Funding: This work was supported by the National Key Research and Development Program (2022YFD1600700), the Scientific and Technological Project in Henan Province (242102110221), the Special Fund for Henan Agriculture Research System (HARS-22-09-S) and the Agricultural Science and Technology Innovation Program, Chinese Academy of Agricultural Sciences (CAAS-ASTIP-2025-ZFRI-03).

Author Contributions: Conceptualization, L. L., J. C.; methodology, Y. Z., M. L., D. C., X. S. and H. G.; software, Y. Z., X. S. and H. G.; validation, C. Z. and L. L.; formal analysis, X. S. and H. G.; investigation, Y. Z.; resources, M. L., D.C., C. Z. and L. L.; data curation, Y. Z., M.L., D. C., C. Z. and L. L.; writing—original draft preparation, Y. Z.; writing—review and editing, Y. Z., J. C.; visualization, C. Z. and L. L.; supervision, L. L., J. C.; project administration, J. C.; funding acquisition, J. C.. All the authors have read and approved the final manuscript.

Acknowledgements

Not applicable.

REFERENCES

1. Demotes-Mainard S, Péron T, Corot A, Bertheloot J, Le Gourrierc J, Pelleschi-Travier S, et al. Plant responses to red and far-red lights, applications in horticulture. *Environ Exp Bot.* 2016;121:4-21.
2. Zhou H, Liu S, Yang Y, Yang A, Liu L, Yu F. Effect of light quality on the growth and

- photosynthetic characteristics of *Cinnamomum camphora* rooted cuttings. Scand J For Res. 2021;36:532-538.
3. Piovene C, Orsini F, Bosi S, Sanoubar R, Bregola V, Dinelli G, et al. Optimal red:blue ratio in led lighting for nutraceutical indoor horticulture. Sci Hortic. 2015;193:202-208.
4. D'Souza C, Yuk HG, Khoo GH, Zhou W. Application of light-emitting diodes in food production, postharvest preservation, and microbiological food safety. Compr Rev Food Sci Food Saf. 2015;14:719-740.
5. Meng C, Chory J, Fankhauser C. Light signal transduction in higher plants. Annu Rev Genet. 2004;38.
6. Liang Y, Kang C, Kaiser E, Kuang Y, Yang Q, Li T. Red/blue light ratios induce morphology and physiology alterations differently in cucumber and tomato. Sci Hortic. 2021;281:109995.
7. Al Murad M, Razi K, Jeong BR, Samy PMA, Muneer S. Light Emitting Diodes (LEDs) as Agricultural Lighting: Impact and Its Potential on Improving Physiology, Flowering, and Secondary Metabolites of Crops. Sustainability. 2021;13:1985.
8. Lu N, Maruo T, Johkan M, Hohjo M, Tsukagoshi S, Ito Y, et al. Effects of Supplemental Lighting with Light-Emitting Diodes (LEDs) on Tomato Yield and Quality of Single-Truss Tomato Plants Grown at High Planting Density. Environ Control Biol. 2012;50:63-74.
9. Carillo P, El-Nakhel C, De Micco V, Giordano M, Pannico A, De Pascale S, et al. Morpho-metric and specialized metabolites modulation of parsley microgreens through selective LED wavebands. Agronomy. 2022;12:1502.
10. Izzo GL, Mickens AM, Aronne G, et al. Spectral effects of blue and red light on growth, anatomy, and physiology of lettuce. Physiol Plant. 2021;172:2191-2202.
11. Wang S, Wang X, Shi X, Wang B, Zheng X, Wang H, et al. Red and Blue Lights Significantly Affect Photosynthetic Properties and Ultrastructure of Mesophyll Cells in Senescing Grape Leaves. Hortic Plant J. 2016;2:82-90.
12. Lauria G, Lo Piccolo E, Ceccanti C, et al. Supplemental red LED light promotes plant productivity,'photomodulates' fruit quality and increases *Botrytis cinerea* tolerance in strawberry. Postharvest Biol Technol. 2023;198.
13. He R, Wei J, Zhang J, et al. Supplemental blue light frequencies improve ripening and nutritional qualities of tomato fruits. Front Plant Sci. 2022;13.

14. Nguyen TPD, Kitayama M, Lu N, et al. Improving secondary metabolite accumulation, mineral content, and growth of coriander (*Coriandrum sativum* L.) by regulating light quality in a plant factory. *J Hortic Sci Biotechnol.* 2020;95:356-363.
15. Paradiso R, Arena C, Rouphael Y, et al. Growth, photosynthetic activity and tuber quality of two potato cultivars in controlled environment as affected by light source. *Plant Biosyst.* 2019;153:725-735.
16. Jin D, Su X, Li Y, et al. Effect of red and blue light on cucumber seedlings grown in a plant factory. *Horticulturae.* 2023;9.
17. Pennisi G, Blasioli S, Cellini A, Maia L, Crepaldi A, Braschi I, et al. Unraveling the Role of Red:Blue LED Lights on Resource Use Efficiency and Nutritional Properties of Indoor Grown Sweet Basil. *Front Plant Sci.* 2019;10.
18. Zhao S, Li X, Kang Y, Lin Y, Wu Y, Yang Z. Photomorphogenesis and Photosynthetic Trait Changes in Melon Seedlings Responding to Red and Blue Light. *Horticulturae.* 2024;10:961.
19. Dewir YH, Al-Ali AM, Rihan HZ, Alshahrani T, Alwahibi MS, Almutairi KF, et al. Effects of Artificial Light Spectra and Sucrose on the Leaf Pigments, Growth, and Rooting of Blackberry (*Rubus fruticosus*) Microshoots. *Agronomy.* 2022;13:89.
20. Zabolina OA, Zhang N, Weerts R. Polysaccharide Biosynthesis: Glycosyltransferases and Their Complexes. *Front Plant Sci.* 2021;12.
21. Wu W, Chen L, Liang R, Huang S, Li X, Huang B, et al. The role of light in regulating plant growth, development and sugar metabolism: a review. *Front Plant Sci.* 2025;15.
22. Nassarawa SS, Luo Z. Effect of Light Irradiation on Sugar, Phenolics, and GABA Metabolism on Postharvest Grape (*Vitis vinifera* L.) During Storage. *Food Bioprocess Technol.* 2022;15:2789-2802.
23. Shi X, Lin L, Huang Q, Bai X, Bai Y, Huang G, et al. Response mechanism of Shine Muscat grape winter berries quality and sugar metabolism to light quality. *J South Agric.* 2024;55:2286-2294.
24. Liu J, Liu W. Regulation of accumulation and metabolism circadian rhythms of starch and sucrose in two leaf-color lettuces by red:blue ratios of LED continuous light. *Environ Exp Bot.* 2022;196:104811.
25. Chen X, Yin Y, Zhu L, Tao N, Man K, Jia H. Effect of supplemental lighting with different light

- quality on fruit quality and related enzymes activities in pitaya. *Acta Agric Zhejiangensis*. 2019;31:1079-1085.
26. Głuchowska A, Zieniuk B, Pawełkiewicz M. Unlocking Plant Resilience: Metabolomic Insights into Abiotic Stress Tolerance in Crops. *Metabolites*. 2025;15:384.
 27. Pashkovskiy P, Vereshchagin M, Kartashov A, et al. Influence of additional white, red and Far-red light on growth, secondary metabolites and expression of hormone signaling genes in scots pine under sunlight. *Cells*. 2024;13.
 28. Mokhtari A, Ebrahimi M, Azadi P, et al. Elucidating the regulatory network of valerenic acid biosynthesis in *Valeriana officinalis* hairy roots under different light qualities: A coexpression perspective. *Ind Crops Prod*. 2025;226.
 29. Wang P, Chen S, Gu M, et al. Exploration of the effects of different blue LED light intensities on flavonoid and lipid metabolism in tea plants via transcriptomics and metabolomics. *Int J Mol Sci*. 2020;21.
 30. Zhang P, Tang Y, Zhang J, Liu J, Li L, Li H, et al. Multi-omics analysis of the accumulation mechanism of flavonoids in rice caryopsis under blue light. *Plant Cell Rep*. 2025;44.
 31. Darko E, Hamow KA, Marček T, et al. Modulated light dependence of growth, flowering, and the accumulation of secondary metabolites in chilli. *Front Plant Sci*. 2022;13.
 32. Fayeizadeh RM, Ansari AN, Mahmoodi Sourestani M, et al. Management of secondary metabolite synthesis and biomass in basil (*Ocimum basilicum L.*) microgreens using different continuous-spectrum LED lights. *Plants*. 2024;13.
 33. Lee S, Park CH, Kim JK, et al. LED lights influenced phytochemical contents and biological activities in kale (*Brassica oleracea L. var. acephala*) microgreens. *Antioxidants*. 2023;12.
 34. Trivellini A, Toscano S, Romano D, Ferrante A. The Role of Blue and Red Light in the Orchestration of Secondary Metabolites, Nutrient Transport and Plant Quality. *Plants*. 2023;12:2026.
 35. Garcia CV, Quek S-Y, Stevenson RJ, Winz RA. Kiwifruit flavour: A review. *Trends Food Sci Technol*. 2012;24:82-91.
 36. Zhang Y, Li L, Sun X, Gu H, Cheng D, Li M, et al. Research progress in effects of artificial light supplementation on the growth and development of fruit trees. *J Fruit Sci*. 2024;41:2595-2605.
 37. Dong L, Sun Y, Zhang J, Zhang C. Analysis of photosynthetic characteristics of six kiwifruit

varieties. Chin Agric Sci Bull. 2024;40:61-66.

38. Zou Q. Experimental guidance of plant physiology. Beijing: China Agriculture Press, 2003.

39. Ren M, Liu S, Tang C, Mao G, Gai P, Guo X, et al. Photomorphogenesis and Photosynthetic Traits Changes in Rice Seedlings Responding to Red and Blue Light. Int J Mol Sci. 2023;24:11333.

40. Sager JC, Brown CS, Schuerger AC. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. 1995.

41. Li Y, Xin G, Shi Q, et al. Response of photomorphogenesis and photosynthetic properties of sweet pepper seedlings exposed to mixed red and blue light. Front Plant Sci. 2023;13.

42. Izzo LG, Hay Mele B, Vitale L, Vitale E, Arena C. The role of monochromatic red and blue light in tomato early photomorphogenesis and photosynthetic traits. Environ Exp Bot. 2020;179:104195.

43. Wei Y, Wang S, Yu D. The Role of Light Quality in Regulating Early Seedling Development. Plants. 2023;12:2746.

44. Chung G-J, Lee J-H, Oh M-M. Growth and Acclimation of In Vitro-Propagated M9 Apple Rootstock Plantlets under Various Visible Light Spectrums. Agronomy. 2020;10:1017.

45. Li Y, Xin G, Wei M, et al. Carbohydrate accumulation and sucrose metabolism responses in tomato seedling leaves when subjected to different light qualities. Sci Hortic. 2017;225:490-497.

46. Gupta SD, Jatothu B. Fundamentals and applications of light-emitting diodes (LEDs) in in vitro plant growth and morphogenesis. Plant Biotechnol Rep. 2013;7:211-220.

47. Zhang X, Wang D, Dong F, Zhang Y, Liu S, Sun X. Effects of different proportions of red and blue light on growth and photosynthetic characteristics of tomato seedlings. Jiangsu Agric Sci. 2019;47:136-138.

48. Mao R, Guo S. Performance of the mixed LED light quality on the growth and energy efficiency of *Arthrospira platensis*. Appl Microbiol Biotechnol. 2018;102:5245-5254.

49. Li Z, Chen Q, Xin Y, et al. Analyses of the photosynthetic characteristics, chloroplast ultrastructure, and transcriptome of apple (*Malus domestica*) grown under red and blue lights. BMC Plant Biol. 2021;21:483.

50. Pavlović S, Girek Z, Damnjanović J, et al. The Influence of Different LED Light Treatments on

- the Growth and Salt Stress Tolerance of Cauliflower Microgreens In Vitro. *Horticulturae*. 2024;10.
51. Kurilčik A, Miklušytė-Čanova R, Dapkūnienė S, Žilinskaitė S, Kurilčik G, Tamulaitis G, et al. In vitro culture of *Chrysanthemum* plantlets using light-emitting diodes. *Open Life Sci*. 2008;3:161-167.
52. Anuchai J, Hsieh CH. Effect of change in light quality on physiological transformation of in vitro *Phalaenopsis* 'Fortune Saltzman' seedlings during the growth period. *Hortic J*. 2017;86:395-402.
53. Li Y, Liu Z, Shi Q, et al. Mixed red and blue light promotes tomato seedlings growth by influencing leaf anatomy, photosynthesis, CO₂ assimilation and endogenous hormones. *Sci Hortic*. 2021;290.
54. Cope KR, Snowden CM, Bugbee B. Photobiological Interactions of Blue Light and Photosynthetic Photon Flux: Effects of Monochromatic and Broad-Spectrum Light Sources. *Photochem Photobiol*. 2014;90:574-584.
55. Evans JR. Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia*. 1989;78:9-19.
56. An H, Zhang J, Zhang L, Li S, Zhou B, Zhang X. Effects of Nutrition and Light Quality on the Growth of Southern Highbush Blueberry (*Vaccinium corymbosum* L.) in an Advanced Plant Factory with Artificial Lighting (PFAL). *Horticulturae*. 2023;9:287.
57. Qazi HA, Paranjpe S, Bhargava S. Stem sugar accumulation in sweet sorghum – Activity and expression of sucrose metabolizing enzymes and sucrose transporters. *J Plant Physiol*. 2012;169:605-613.
58. Li H, Xu Z, Tang C. Effect of light-emitting diodes on growth and morphogenesis of upland cotton (*Gossypium hirsutum* L.) plantlets in vitro. *Plant Cell Tissue Organ Cult*. 2010;103:155-163.
59. Choi HG, Moon BY, Kang NJ. Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. *Sci Hortic*. 2015;189:22-31.
60. Zhan X, Yang Q, Wang S, Wang Y, Fan X, Bian Z. The Responses of Sucrose Metabolism and Carbon Translocation in Tomato Seedlings under Different Light Spectra. *Int J Mol Sci*. 2023;24:15054.

61. Hu J, Dai X, Song T, Yang X, Wang Q, Sun G. Effect of different proportions of red and blue light on carbon-nitrogen metabolism and endogenous hormones in mulberry seedlings. *Pratac Sci.* 2018;35:2489-2499.
62. Di Q, Li J, Du Y, et al. Combination of red and blue lights improved the growth and development of eggplant (*Solanum melongena L.*) seedlings by regulating photosynthesis. *J Plant Growth Regul.* 2021;40:1477-1492.
63. Dong F, Wang C, Sun X, Bao Z, Dong C, Sun C, et al. Sugar metabolic changes in protein expression associated with different light quality combinations in tomato fruit. *Plant Growth Regul.* 2019;88:267-282.
64. Stein O, Granot D. An overview of sucrose synthases in plants. *Front Plant Sci.* 2019;10.
65. Ruan YL. Sucrose metabolism: gateway to diverse carbon use and sugar signaling. *Annu Rev Plant Biol.* 2014;65:33-67.
66. Lombardo AV, Osorio S, Borsani J, et al. Metabolic profiling during peach fruit development and ripening reveals the metabolic networks that underpin each developmental stage. *Plant Physiol.* 2011;157:1696-1710.
67. Chen X-L, Wang L, Li Y-L, Yang Q-C, Guo W. Alternating red and blue irradiation affects carbohydrate accumulation and sucrose metabolism in butterhead lettuce. *Sci Hortic.* 2022;302:111177.
68. Deng Y, Ma Z, Li Z, Hou J. Study on growth and metabolic changes of *Lilium pumilum* DC. tissue culture seedlings under LED light quality treatment based on metabolomics. *Jiangsu Agric Sci.* 2024;52:150-159.
69. Dong T, Zhang P, Hakeem A, Liu Z, Su L, Ren Y, et al. Integrated transcriptome and metabolome analysis reveals the physiological and molecular mechanisms of grape seedlings in response to red, green, blue, and white LED light qualities. *Environ Exp Bot.* 2023;213:105441.
70. Huang W, Yang G, Liu D, Li Q, Zheng L, Ma J. Metabolomics and transcriptomics analysis of vitro growth in pitaya plantlets with different LED Light spectra treatment. *Ind Crops Prod.* 2022;186:115237.
71. Chen X, Cai W, Xia J, Yu H, Wang Q, Pang F, et al. Metabolomic and Transcriptomic Analyses Reveal that Blue Light Promotes Chlorogenic Acid Synthesis in Strawberry. *J Agric Food Chem.* 2020;68:12485-12492.

- 793 72. Xiao L, Shibuya T, Watanabe T, Kato K, Kanayama Y. Effect of Light Quality on Metabolomic,
794 Ionomic, and Transcriptomic Profiles in Tomato Fruit. *Int J Mol Sci.* 2022;23:13288.
- 795 73. Wu W, Wu H, Liang R, Huang S, Meng L, Zhang M, et al. Light regulates the synthesis and
796 accumulation of plant secondary metabolites. *Front Plant Sci.* 2025;16.