

# Positive effect of red/blue light supplementation on the photosynthetic capacity and fruit quality of 'Yanli' strawberry

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## Abstract

In order to meet people's demand for strawberry during winter and early spring, strawberry is usually cultivated in solar greenhouses with forcing cultivation in northern China. However, low light intensities and short-days are the major obstacles that restrict strawberry growth. Therefore, it is crucial to solve the problem of insufficient light in strawberry production. In this study, we established LED facilities to supplement the red/blue light (R/B = 4:1) before sunrise and after sunset in the solar greenhouse. We found that the plant height of the strawberry under supplemental R/B light was 13%–17% higher than that of the control, and the crown diameter of the plants was increased by 1.07–1.38 fold compared with the control for two consecutive years. The net photosynthetic rate of strawberry plants was 19% higher than that of the control. In addition, the strawberry primary fruits' fresh weight during the stage of full ripeness and the total fruit weight/plant was 18%–24% and 27%–33% higher than that of control for two years, respectively. Fruit soluble solid content and firmness were increased by 1.05–1.21 fold and 1.06–1.18 fold compared with those of control during the two years, respectively. Moreover, we found some differentially expressed genes between red/blue light supplementation and control by RNA-seq, including light-responsive genes (*PRR95/LHY/CDF3/CO16/bHLH63/BBX21/PAR1/SIGE*) and sucrose metabolism-related genes (*SWEET9/BAM1*). This study provided a foundation for revealing the mechanism of red/blue light supplementation on photosynthesis and fruit quality of strawberries and could help to improve the cultivation techniques for 'Yanli' strawberry.

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## INTRODUCTION

Strawberry is an important economic crop with delicious and nutritious fruit<sup>[1,2]</sup>. In north China, strawberry is usually cultivated in solar greenhouses with forcing cultivation during the winter and early spring season. Forcing cultivation has the advantages of breaking dormancy and prolonging the harvest time in strawberry. However, under this condition, low light intensities and short-days are the major obstacles that restrict strawberry growth and development. There are many reasons for this problem, including short sunshine time and frequent hazy weather in winter, covering for heat preservation, and reducing light transmittance after the surface of the shed film absorbs dust, etc. These conditions may lead to reduced photosynthesis and thus affect plant growth and development of strawberry. Therefore, it is crucial to solve the problem of insufficient light in strawberry production.

The artificial supplemental light source is an important cultivation technology for strawberry plants grown in greenhouses<sup>[3,4]</sup>. LED (Light Emitting Diode) was widely used in horticultural production in controlled environments due to the advantages of small size, relatively low heat release, great wavelength controllability, long lifetime, and low power consumption<sup>[5,6]</sup>. Different light wavelengths have different effects on strawberry plants' development and fruit quality<sup>[7,8]</sup>. To improve light-use efficiency in a greenhouse, more and more researchers pay attention to which corresponding light

wavelengths are required for different growth and development processes of plants<sup>[9]</sup>.

Red light is one of the most efficient light qualities for powering plants' photosynthesis<sup>[10,11]</sup>, but monochromatic red light may cause abnormal phenotypes because of a lower photosynthetic rate in several crop plants, such as leaf curling and leaf thickness, etc<sup>[12,13]</sup>. Adding blue light can suppress these symptoms<sup>[12–14]</sup>. Other studies showed that red and blue light mixed wavelength is beneficial to enhance strawberry production and fruit quality<sup>[15,16]</sup>. However, the effective model of R/B light supplementation in strawberry cultivar 'Yanli' is poorly understood.

Strawberry cultivar 'Yanli' was released from Shenyang Agricultural University, China. The fruit has excellent flavor and aroma and the exterior is a regular conic shape and bright red. It is grown in different provinces of China, especially cultivated by forcing cultivation in solar greenhouses in northern China<sup>[17]</sup>. Therefore, it is necessary to study its effective cultivation practices. We established LED facilities to supplement the red/blue light (R/B = 4:1) for 'Yanli' before sunrise and after sunset in the solar greenhouse. The results showed that the photosynthetic efficiency, soluble solid content and yield were increased. In addition, we initially screened the candidate genes for improving photosynthesis and fruit quality in 'Yanli' strawberry under the condition of red/blue light supplementation by RNA-seq. These results will help to perfect the cultivation techniques for strawberry cultivar 'Yanli'.

## MATERIALS AND METHODS

### Plant material and growth conditions

'Yanli' (*Fragaria × ananassa* Duch.) plants were grown in the greenhouse at Shenyang Agricultural University (Liaoning province, China). Runner plants of 'Yanli' were planted in the greenhouse in early September every year. After 30 d, 20 of them were subjected to the condition of a mixture of red (R) and blue (B) light at 06:30–08:00 AM (before sunrise) and 15:50–19:00 PM (after sunset) daily. Supplemental light treatments were provided using LED lamps (North Brilliancy Technology Co., LTD, Shenzhen, China). These LED lamps were installed at 1.5 m above the strawberry plants. The photosynthetic photon flux density (PPFD) was measured by a quantum sensor (LI-250A, LI-COR, USA), and the PPFD ratio of red ( $3.9261 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) to blue ( $0.9716 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) to supplemental light (R/B) was 4:1. Plants without any supplemental light were used as control.

### Measurements of growth and physiological traits

The height and crown diameter of strawberry plants were measured before reproductive growth. Plant height was measured from the ground to the highest blade. The crown diameter was the diameter of the leaf clusters. Primary fresh fruits were weighed. During the ripening stages of strawberry, the soluble solid content (SSC) of the strawberry juice was measured by a digital pocket refractometer ATAGO PAL- $\alpha$  (Atago Co. Ltd., Tokyo, Japan), and the firmness of fresh fruit was measured using a texture analyzer (GY-4, Handpi). Two opposite sites on the fruit shoulder were measured for each fruit, and the average firmness value of each fruit was recorded. Photosynthetic indexes, including net photosynthetic rate (Pn), stomata conductance (Gs), intercellular CO<sub>2</sub> (Ci), and transpiration rate (Tr), were measured with a portable photosynthesis system (CIRAS-2, PP Systems, Massachusetts, USA) within the hours of 8:30–11:30 AM under sunny conditions. Third fully opened and new leaves from each plant were used for the photosynthetic indexes data. Twenty plants were measured for treatment and control, and three fruits were measured per plant.

### RNA extraction and sequencing

After 50 d of irradiation, the fully opened and new leaves of treated strawberry plants and controls in three biological replicates were selected for sampling and frozen in liquid nitrogen. Total RNA was extracted by a modified CTAB method<sup>[18]</sup>. RNA concentration was measured using a NanoDrop 2000 (Thermo Fisher Scientific, Wilmington, DE, USA). cDNA library and high-throughput sequencing were conducted by Biomarker Technologies Co, LTD (Beijing, China). The Illumina HiSeq™ platform was performed. Reads from each library were *de novo* assembled separately. Gene expression levels were measured in the RNA-Seq analysis as fragments per kilobase per million mapped fragments (FPKM).

### Statistical analysis

The data for the physiological parameters were analyzed using DPS 7.05 software. Significant differences between treatment and control were evaluated with Student's *t*-test, and the significance level was set at \*  $p < 0.05$  and \*\*  $p < 0.01$ , respectively.

## RESULTS

### Effects of supplemental red/blue light on growth and photosynthetic indexes

Aiming to elucidate whether red/blue (R/B) light supplementation affects the growth and development of 'Yanli' strawberry, we compared the plants growing under R/B light supplementation and control conditions. We found that R/B light supplementation significantly increased the growth of strawberry plants in two years (Supplemental Fig. S1). During 2019–2020 and 2020–2021, the plant height of the strawberry under supplemental R/B lighting was 17% and 13% higher than that of the control, respectively (Table 1). Meanwhile, the crown diameter of the plants under light treatment was increased by 1.38-fold and 1.07-fold compared with that in the control during the two years, respectively (Table 1). To further explore the effect of supplemental R/B light on the photosynthesis of 'Yanli' strawberry, we measured the photosynthetic parameters of 'Yanli' strawberry plants during the flowering and fruit setting stage. The results showed that the Pn, Gs and Tr of strawberry plants under R/B light supplementation were 19%, 55% and 27% higher than those in the control, respectively (Fig. 1).

### Effects of supplemental R/B light on strawberry yield and fruit quality

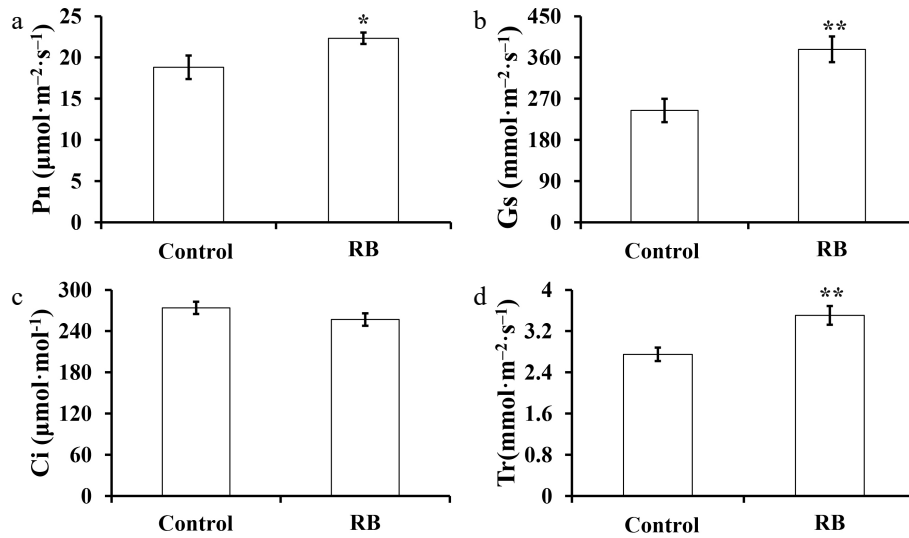
To investigate whether supplemental R/B light affected strawberry yield and fruit quality, we analyzed strawberry primary fruit fresh weight, total fruit weight/plant, SSC, and the fruit firmness under supplemental R/B light and control. As shown in Fig. 2a, the R/B light supplementation led to a remarkable improvement (18% and 24%) in the strawberry primary fruit fresh weight during the stage of full ripeness compared with that in control conditions during the years 2019–2020 and 2020–2021. And total fruit weight/plant under supplemental R/B light was 27% and 33% higher than that of the control during two consecutive years, respectively (Fig. 2b). Under R/B light supplementation, strawberry fruit SSC was increased by 1.21-fold and 1.05-fold compared with that in the control during the two years, respectively (Fig. 2c). Similarly, fruit firmness was also increased by 1.18-fold and 1.06-fold compared with that in the control for two years, respectively (Fig. 2d). These results suggested that supplemental R/B light could improve 'Yanli' strawberry yield and fruit quality.

### Transcriptome sequencing

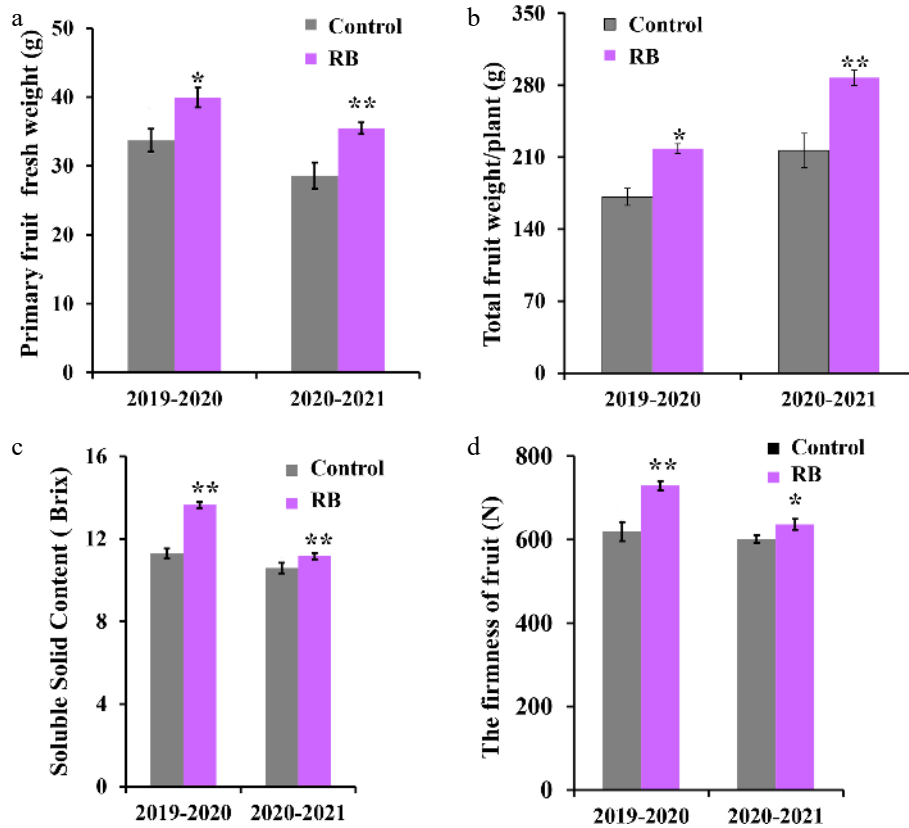
To study the effect of supplemental R/B light on 'Yanli' strawberry plants, total RNA from six samples (CK-1, CK-2, CK-3 and RB-1, RB-2, RB-3) were used for RNA-seq. The treatment and control group respectively contain three biological repeat samples. After filtering dirty tags from the raw data, a total of 38.36 Gb of clean data were obtained, with an average of 6.21 Gb of clean reads per sample. Of the clean reads, the average

**Table 1.** Comparison of strawberry plant height and crown diameter between red/blue light supplementation and control.

Year	Light treatment	Plant height (cm)	Crown diameter (cm)
2019–2020	Control	17.11	22.42
	RB	19.96**	30.86**
2020–2021	Control	17.22	24.23
	RB	19.44*	26.04**



**Fig. 1** Effect of R/B light supplementation on photosynthetic parameters of strawberry cultivar 'Yanli' cultured in solar greenhouse. (a)–(d) net photosynthetic rate (Pn), stomata conductance (Gs), intercellular CO<sub>2</sub> (Ci), and transpiration rate (Tr). Vertical bars represent the SD. Statistical significance was measured using Student's *t*-test. (*n* = 20, \* *p* < 0.05, \*\* *p* < 0.01).



**Fig. 2** Effect of R/B light supplementation on production and fruit quality of strawberry cultivar 'Yanli' cultured in solar greenhouse. (a) Primary fruit fresh weight, (b) total fruit weight/plant, (c) soluble solid content and (d) firmness of the 'Yanli' fruit under R/B light supplementation and control. Vertical bars represent SD. Statistical significance was measured using Student's *t*-test. (*n* = 20, \* *p* < 0.05, \*\* *p* < 0.01).

GC content is approximately 46.96%, and the Q30 percentage was over 93.05%. The percentage of clean reads mapped to the unigen database ranged from 79.07% to 80.42% (Table 2).

The FPKM values were used to analyze the gene expression levels in the RNA-seq analysis. R (Pearson correlation coefficient)

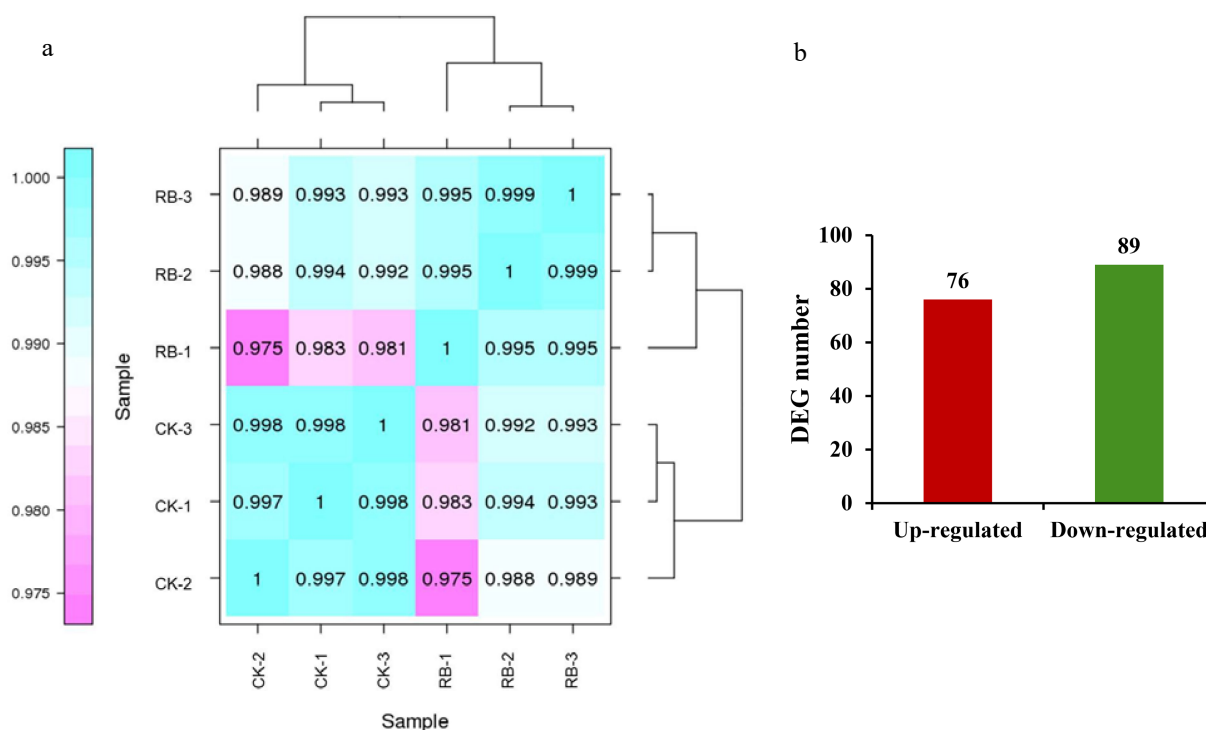
was used as the evaluation index of correlation between each sample, the results of Fig. 3a showed that there was a strong correlation between the three biological replicates from each group. 1.5 fold change and *P* value less than 0.05 were used to define differentially expressed genes (DEGs). A total of

**Table 2.** Summary of transcriptome data.

Sample	Clean read number	Clean base number	GC content <sup>a</sup>	% ≥ Q30 <sup>b</sup>	Mapped reads	Mapped ratio
CK-1	21,222,192	6,353,022,700	46.98%	93.13%	16,779,949	79.07%
CK-2	23,479,291	7,032,924,424	47.23%	93.04%	18,653,551	79.45%
CK-3	20,727,367	6,210,109,126	47.07%	93.09%	16,668,439	80.42%
RB-1	20,756,139	6,218,258,998	46.63%	93.07%	16,594,034	79.95%
RB-2	20,842,520	6,243,435,538	46.83%	92.85%	16,552,377	79.42%
RB-3	21,022,752	6,297,302,712	46.99%	93.09%	16,753,654	79.69%

<sup>a</sup> GC Content: the percentage of G and C bases in the total bases in clean reads.

<sup>b</sup> % ≥ Q30: the percentages of clean reads with Phred qualities scores over 30.



**Fig. 3** Overview of the transcriptome sequencing under supplemental R/B lighting in strawberry leaves. (a) Pearson correlation between samples analysis. (b) Number of up- and down-regulated expressed genes. CK-1, CK-2, CK-3 are controls, RB-1, RB-2, and RB-3 are the experimental groups treated with supplemental R/B lighting.

165 DEGs were identified, among which 76 were up-regulated and 89 were down-regulated by supplementing R/B light, respectively (Supplemental Table S1, Fig. 3b).

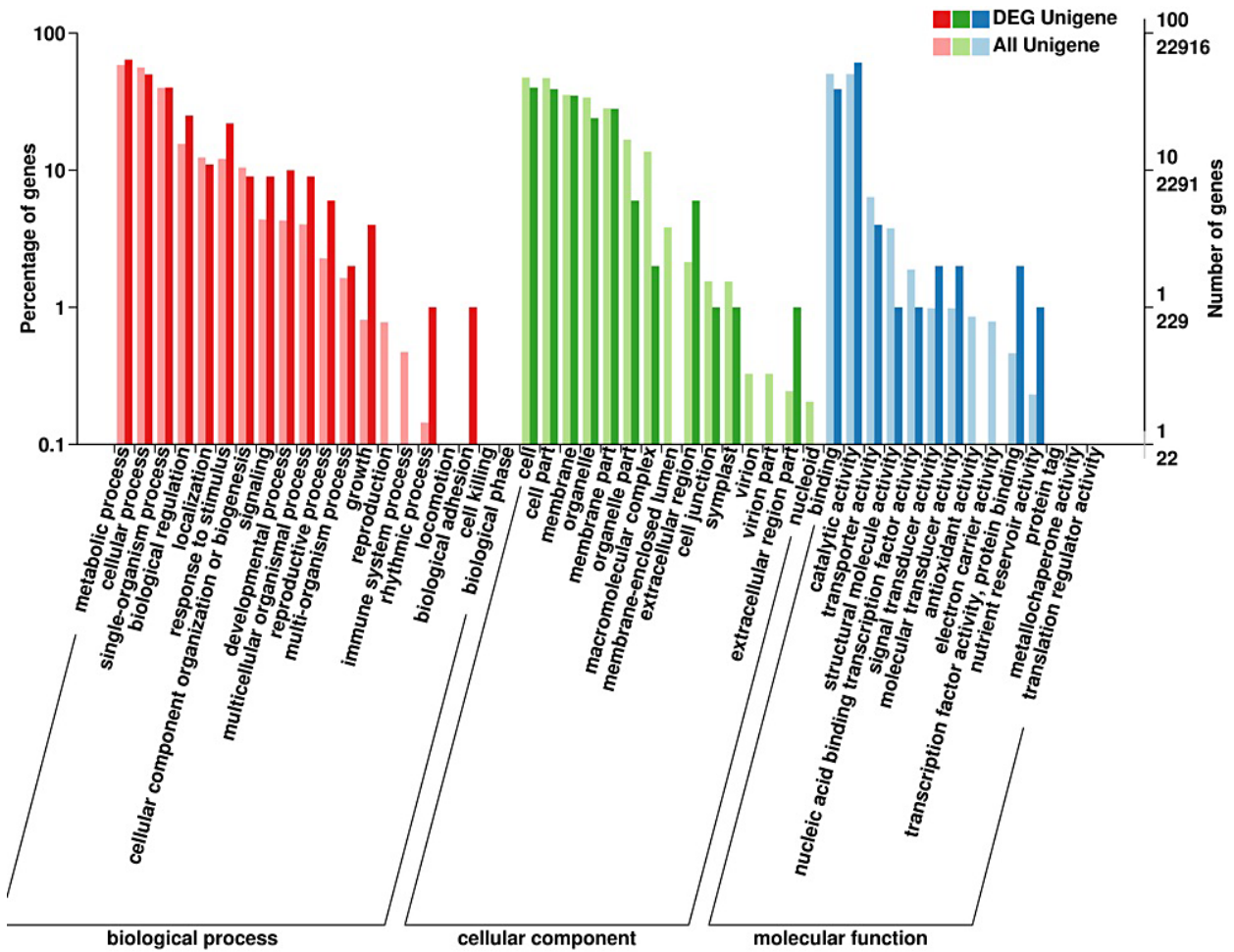
### GO and KEGG pathway enrichment

GO (Gene ontology) functional classes showed that the putative function of DEGs. The enriched genes were classified into three major categories, including Biological Processes (BP), Cellular Components (CC), and Molecular Functions (MF). Metabolic process, cellular process and single-organism process were enriched mainly in biological processes. Among CC, cell, cell part, membrane, membrane part and organelle were the main terms. Molecular functions such as binding, catalytic activity and transporter activity were mainly enriched (Fig. 4). And TopGO was used to analyze the function enrichment of DEGs, including in the oxidation-reduction process (GO:0055114,  $KS = 9.5e-10$ ), photosynthesis (GO:0015979,  $6.7e-05$ ), chloroplast thylakoid membrane (GO:0009535,  $0.00014$ ; Supplemental Table S2). The annotated unigenes were classified into 14 COG (Cluster of Orthologous Groups of proteins) categories (Fig. 5). And the largest group is 'carbohydrate transport and metabolism'.

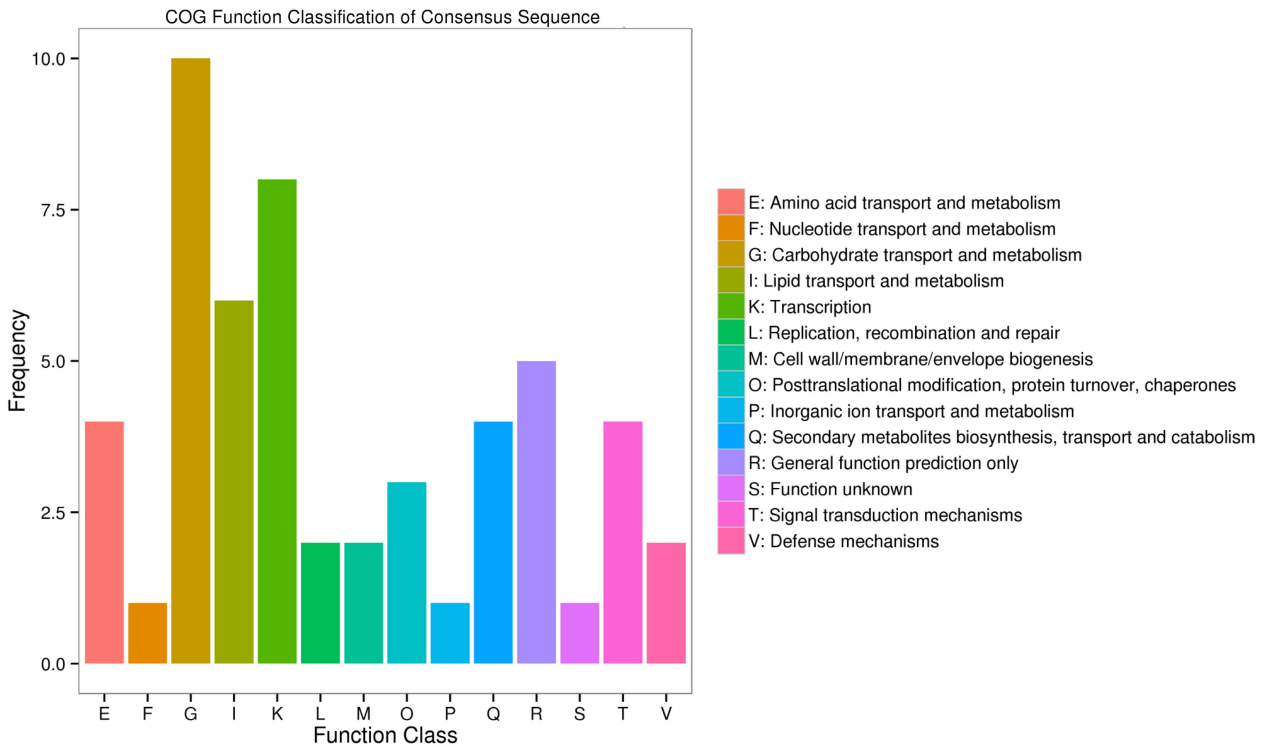
In addition, KEGG (Kyoto Encyclopedia of Genes and Genomes) annotation was used to analyze the functional enrichment of DEGs. There were 18 significantly enriched KEGG pathways (Fig. 6). In the comparison of the control and R/B light supplementation groups, the identified DEGs were mainly enriched in plant hormone signaling transduction, base excision repair, circadian rhythm-plant, and alpha-Linolenic acid metabolism.

### Transcriptomic analysis of some DEGs in response to red/blue light supplementation

Transcription factors (TFs) play an important role in plant response to changing environments<sup>[19]</sup>. In 'Yanli' leaves, the expressions of a total of 13 TF genes were significantly affected by supplementing R/B light. These TF genes belong to different families (NAC, PRR, MYB, bZIP, ZAT, CDF, CO, bHLH, BBX and PAR) (Table 3). The gene families including PRR, MYB, CDF and CO play an important role in the regulation of the circadian clock<sup>[20–23]</sup>. bHLH, BBX and PAR participate in the light signal transduction<sup>[24–26]</sup>. We found that *PRR95* (PRR family), *LHY* (MYB family) and *CDF3* (CDF family) were up-regulated, while *CO16* (CO family), *bHLH63* (*Arabidopsis thaliana* CIB1 homologous



**Fig. 4** Gene ontology (GO) enrichment analysis of differentially expressed genes in strawberry leaves by supplementing R/B light.



**Fig. 5** Histogram of COG (cluster of orthologous groups) classification.

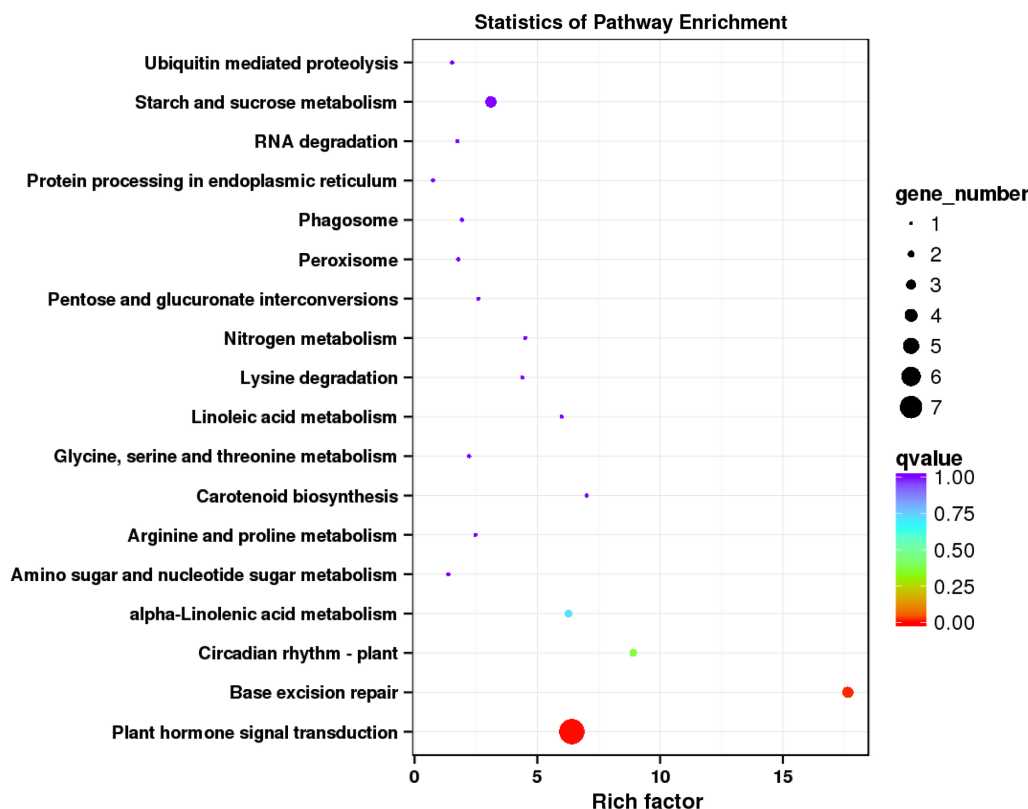


Fig. 6 KEGG enrichment analysis of DEGs regulated by supplementing R/B light in strawberry leaves.

Table 3. List of differentially expressed TF genes.

Gene family	TF name	Annotation function	logFC	Regulation
NAC	NAC72	NAC domain-containing protein 72-like	0.931857	Up
PRR	PRR95	Two-component response regulator-like PRR95	0.893515	Up
MYB	LHY	Protein LHY-like	0.657352	Up
bZIP	TRAB1	bZIP transcription factor TRAB1	0.651141	Up
ZAT	ZAT8	Zinc finger protein ZAT8-like	0.628283	Up
CDF	CDF3	Cyclic dof factor 3	0.641524	Up
CO	CO16	Zinc finger protein CONSTANS-LIKE 16	-0.66291	Down
bZIP	bZIP34	Basic leucine zipper 34	-1.07449	Down
bZIP	bZIP61	Basic leucine zipper 61-like	-0.9109	Down
bHLH	bHLH63	Transcription factor bHLH63	-0.66341	Down
BBX	BBX21	B-box zinc finger protein 21	-0.67538	Down
PAR	PAR1	Transcription factor PAR1	-0.61181	Down
MYB	RAD	Transcription factor RADIALIS-like	-0.61324	Down

gene, bHLH family), *BBX21* (BBX family) and *PAR1* (PAR family) were down-regulated in 'Yanli' leaves during supplementing R/B light. In addition, we found that the *SIGE* regulating the expression of the chloroplast genes in the light-signaling pathway was upregulated (Supplemental Table S1). The results indicated that these TFs and *SIGE* maybe participate in the photosynthesis process of 'Yanli' during R/B light supplementation.

## DISCUSSION

Light is one of the most vital environmental factors for plant growth and development. Too much or too little light can have adverse effects on some horticultural crops [27–29]. In winter, the cultivation of horticultural crops in solar greenhouses is widely used to meet people's nutritional needs, in northern China [30]. In addition to insufficient light time in northern winter, low

PPFD under greenhouse conditions is also one of the important factors restricting the yields and quality of horticultural crops [28,31]. More and more studies found that combined red and blue light supplementation have a widely positive effect on the process of growth and development, and fruit quality for horticultural plants [32–34]. There are also individual differences between different red and blue ratios, different horticultural plants and different varieties [15,32,35]. The supplementation of red/blue (4:1) light for 3 h every day improved the growth of pepper seedlings in solar greenhouse [36]. Tomatoes grown under red/blue light (ratio = 3:1) have optimum growth [37]. In order to explore suitable cultivation measures for the 'Yanli' strawberry, and LED red and blue light (ratio = 4:1) was supplemented without changing other conditions in the solar greenhouse. Combined with transcriptome analysis and phenotypic identification, we found that supplementation of

## Effective cultivation techniques on strawberry

red and blue light could improve photosynthesis, yield and soluble solid content in strawberry cultivar 'Yanli'.

For plant morphology and physiological indicators, we observed that the plant height, crown diameter and photosynthesis were significantly increased in 'Yanli' strawberry under R/B light supplementation before sunrise and after sunset every day. Previous studies have also shown that red and blue light can improve plant growth and photosynthesis. Strawberry quality and production were improved by promoting the stomatal opening and accumulation of the photosynthetic products under the condition of supplementary morning lighting with blue light<sup>[5]</sup>. In addition, we compared the transcriptomes of the leaves of 'Yanli' strawberry plants under supplementary red and blue light and control.

Many TFs regulate photosynthesis gene expression and response to changing environmental conditions<sup>[30,38]</sup>. We found several different expression TF genes in 'Yanli' leaves between supplementing R/B light and control. *PRR95*, *LHY* and *CDF3* were up-regulated, *bHLH63*, *BBX21* and *PAR1* were down-regulated. Among them, PRR and LHY are the downstream photoreceptors and the key component of the circadian clock<sup>[39]</sup>. Photosynthesis is regulated by the circadian rhythm, and it is very important that the circadian clock coordinates photosynthesis to improve the efficiency of light-energy capture and carbon fixation<sup>[20]</sup>. In *Jatropha curcas*, CDFs (cycling dof factors) responded to the photoperiod<sup>[23]</sup>. CDFs also play an important role in improving photosynthetic efficiency, coordinating carbon/nitrogen balance and promoting plant growth<sup>[40]</sup>. For *CIB1* (CRYPTOCHROME-INTERACTING BHLH 1), *FvebHLH63* homologous gene, previous studies show that *CIB1* negatively regulates the photosynthetic rate in soybean<sup>[41]</sup>. BBXs play an important role in photomorphosis. BBXs and HY5 are components that control a variety of light-regulated genes expression<sup>[42–44]</sup>. PAR regulated hypocotyl length under simulated shade in Arabidopsis<sup>[45]</sup>. The function of PAR1 in strawberry needs to be further studied. Besides, RNA polymerase sigma factor gene *SIGE* (a homolog of *SIG5* in Arabidopsis) was upregulated by supplementing R/B light. *SIG5* is mainly induced by red light and blue light to participate in photosynthesis<sup>[46,47]</sup>. *SIG5* regulates the chloroplast genes *psbD* and *psbA* (PSII core proteins) in chloroplasts at the post-transcriptional level<sup>[48,49]</sup>. In the present study, transcriptome analysis indicated *PRR95*, *LHY*, *CDF3*, *CO16*, *bHLH63*, *BBX21*, *PAR1* and *SIGE* exhibited different expressions between supplementary R/B light and control in 'Yanli'. We speculate that these eight differentially expressed genes maybe participate in the photosynthesis process of 'Yanli' during R/B light supplementation.

For fruit quality and yield, previous studies have shown that tomato fruit quality was improved by increased photosynthetic efficiency under red and blue LED (red : blue = 8:2) supplementation in the greenhouse<sup>[50]</sup>. In the condition of an artificial climate chamber, supplementing R/B light in the morning promoted the accumulation of health-promoting substances in the tomato fruits, such as vitamin C, organic acids, carotenoids, etc. While the content of sugars, flavonoids, and aromatic substances in tomato fruits were significantly increased by supplementing R/B light at night<sup>[51]</sup>. In addition, the photosynthetic activity, and fruit productivity were increased in strawberry plants under different ratios of red and blue LED light<sup>[52,53]</sup>. In this study, we found that the SSC content, primary fruit weight, and fruit weight per plant were increased by R/B

light supplementation in 'Yanli' strawberry. At the same time, transcriptome analysis found that the expression of genes related to sucrose transport (sugar transporter: *SWEET9-like*, c50514.graph\_c0) and amylolysis (beta-amylase: *BAM1*, c61305.graph\_c0) were up-regulated (Supplemental Table S1). This may be related to strawberry fruit quality. Some studies showed that there were no effects on the strawberry fruit firmness after monochromatic red or blue light treatment<sup>[54,55]</sup>. However, our studies found that the strawberry fruit firmness was increased by supplementing R/B light. This is probably a consequence of different strawberry varieties or different cultivation environments. Next, we will further explore the differentially expressed genes in 'Yanli' between R/B light supplementation and control.

For the most suitable ratio of supplementary R/B light and the photoperiod for strawberry cultivars 'Yanli', we are investigating the growth and development of 'Yanli' strawberry plants in the artificial climate culture chamber under different R/B light ratio and photoperiod, so as to be applied to 'Yanli' cultivation and production more accurately. Different red and blue ratios have different effects on different species or different traits of the same species<sup>[35,37]</sup>. In this study, we found that the growth, photosynthesis, yield and fruit quality of 'Yanli' strawberries were improved under R/B light (red : blue = 4:1) supplementary in solar greenhouses of northern China. The cost for LED lights is about \$600 per thousand square meters, and the LED lights could be used for 3–5 years. The economic benefits far outweigh the costs of LED lights. Therefore, these studies provide evidence for establishing the effective cultivation measures of 'Yanli' strawberry. The internal molecular mechanism still needs to be further studied.

## ACKNOWLEDGMENTS

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## Conflict of interest

Zhihong Zhang is the Editorial Board member of the journal *Fruit Research*. He was blinded from reviewing or making decisions on the manuscript. The article was subject to the journal's standard procedures, with peer-review handled independently of this Editorial Board member and his research group.

## Dates

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