Effect of light quality on polyphenol biosynthesis in three varieties of mung bean sprouts with different color seed coats

Yaoyao Cheng1 · Honglin Chen2 · Yihan Zhao1 · Xuzhen Cheng2 · Lixia Wang2 · Xinbo Guo1

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Abstract

We investigated the mechanism of the effect of different light qualities on the synthesis and regulation of mung bean sprouts. Light quality acts as a signal molecule, strongly enhancing polyphenol biosynthesis in sprouts.

Mung bean (Vigna radiata) sprouts are a popular sprouting vegetable all over the world and are an excellent source of polyphenols with high antioxidant activity. This study investigated the effects of light qualities on the kinetic changes and metabolic regulation mechanism of light signal-mediating polyphenols in three mung bean sprout cultivars. Experimental results showed that three light qualities significantly enhanced the contents of caffeic acid, rutin, vitexin, genistin and delphinidin 3-glucoside. Interestingly, ferulic acid and vitexin responded selectively to blue light and red light, severally. Most genes involved in polyphenol biosynthesis were activated under different light quality conditions, resulting in an overaccumulation of phenylpropanoids. Pearson correlation analysis showed that PAL, F3H, F3′H and F3′5′H expression correlated highly with rutin, whereas ANS expression paralleled anthocyanin biosynthesis. Moreover, MYB111, MYB3, MYB4, MYB1 and MYC2 were critical regulators of polyphenol biosynthesis in mung bean sprouts. These changes were likely due to the changes in the expression of the photoreceptor genes CRY-D, PHOT2, PHYE and light response genes (PIF3 and HY5). Our results provide insights into polyphenol biosynthesis in sprouts and microgreens.

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Lixia Wang
wanglixia03@caas.cn

Xinbo Guo
guoxinbo@scut.edu.cn

1 School of Food Science and Engineering, Ministry of Education Engineering Research Centre of Starch & Protein Processing, Guangdong Province Key Laboratory for Green Processing of Natural Products and Product Safety, South China University of Technology, Guangzhou 510640, China

2 Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, Beijing 100081, China
Introduction

Epidemiological studies suggest that increasing dietary intake of fruits and vegetables has emerged as an effective way to reduce the risk of chronic disease (del Río-Celestino and Font 2020). The beneficial effects are attributed at least in part to secondary metabolites, including flavonoids and phenolic acids. Polyphenol compounds are considered as effective antioxidants by scavenging reactive free radicals, chelating iron and inhibiting lipid peroxidation, thereby reducing the harmful effects of oxidative stress in humans (Deng and Lu 2017). Mung bean (Vigna radiata) sprouts are rich sources of flavonoids, phenolic acids, saponins and vitamins with health-benefiting biological activities, including antioxidant, antihypertensive, antitumor effects, etc. The main components of mung bean sprouts with antioxidant activity seemed to be polyphenols (Gan et al. 2016). Thus, mung bean sprouts are an excellent source of polyphenols with high antioxidant activity, including caffeic acid and rutin, whose regular consumption can reduce the incidence of multiple chronic diseases (Ganesan and Xu 2018). In addition, the color and genotype of mung bean seeds may affect the type, amount and activity of polyphenol compounds, which might lead to differences in polyphenol profile among mung bean cultivars after germination (Tajoddin et al. 2014), for instance, black mung beans have a higher antioxidant capacity and anthocyanin content (Yao et al. 2013).

Light is a crucial external factor that affects growth and development, photomorphogenesis and nutrient synthesis during plant germination (Palma et al. 2021). Monochromatic lights are considered as an effective technique for enhancing plant growth and metabolite accumulation (such as polyphenols) at a lower energy cost (Zhang et al. 2020a, b). The accumulation of polyphenol compounds can protect plants from oxidative stress damage caused by precise light wavelengths (Liu et al. 2018). Red and blue lights are the most studied light spectral regions in indoor agriculture for optimizing specific metabolites (Appolloni et al. 2022). In addition, recent studies have proved that...
light quality (LQ) strongly affects the accumulation of phenolic compounds and the expression of related genes in sprouts. For instance, Zhang et al. (2019a, b, 2020a, b) observed that polyphenol profiles and gene expression in soybean microgreens performed great differences under various light spectra. It has been widely studied that several transcription factors, such as bHLH and MYB families, involved in light signal transduction pathways and regulated the polyphenol biosynthesis in response to light (Naing and Kim 2018; Yu et al. 2021).

Light triggers polyphenol biosynthesis, which involves the coordinated regulation of transcription factors of multiple light signals (Rai et al. 2021). It has been well documented that plants perceive and transmit light signals through photoreceptors, and at least five types of photoreceptors have been identified in the model plant Arabidopsis thaliana, namely red/far-red light receptors (Phytochromes, PHYs), blue light receptors (Zeitlupes, ZTL; Phototropins, PHOTs; Cryptochromes, CRYs) and ultraviolet light receptors (UV resistance locus 8, UVR8) (Sheerin and Hiltbrunner 2017). Photoreceptor-mediated signaling mechanisms have been shown to involve multiple transcriptional regulators, including COP1, HY5, PIFs, SPA1, FAR1, LAF1, among others (Li et al. 2022). Photoreceptors regulate photomorphogenic development via direct physical interaction with the negative regulator COP1. The photomorphogenic positive regulator HY5, a direct target of COP1, is associated with the activation of transcription factors (TFs) and structural genes in the phenylpropanoid pathway in response to light signals (Li et al. 2022). PIFs can also interact with light-activated photoreceptors and participate in polyphenol biosynthesis by directly binding to the promoters of related genes (Sheerin and Hiltbrunner 2017). Consequently, transcriptional regulatory networks mediate light signaling transduction by coordinating the activation and inhibition of specific downstream genes and play a key role in light-regulated polyphenol biosynthesis (Rai et al. 2021). However, few studies have examined the molecular mechanism of light perception and subsequent regulation of gene expression in mung bean sprouts.

To the best of our knowledge, the systematic profiling analyses of polyphenol profiles under different light qualities in mung bean sprouts have not yet been clearly revealed. Based on previous studies, we hypothesized that light quality affected the metabolism of mung bean sprouts, which may lead to the biosynthesis of specific metabolites. The objective was to investigate the relevant molecular mechanisms in different cultivars, expecting to better understand how polyphenol biosynthesis was regulated by diverse light quality conditions. The prospective findings would provide insights into the molecular mechanisms underpinning the production of light-responsive polyphenols in mung bean sprouts, facilitating their nutritional quality.

### Materials and methods

#### Plant materials and growth conditions

The pigmented mung beans are a precious mung bean germplasm resource, including yellow, green and black mung beans, etc. The three different colored mung bean (Vigna radiata) varieties used in the experiment were provided by Institute of Crop Science, Chinese Academy of Agricultural Sciences (Beijing, China), including Su Huang No.1 (yellow seeds, SH1), Zhong Lv No.5 (green seeds, ZL5) and Zhong Lv No.13 (black seeds, ZL13). Mung bean seeds (20 g) were surface-sterilized with 70% (v/v) ethanol for 1 min and then soaked with tap water (400 mL) at room temperature for 6 h to stimulate germination. Then seeds were placed into a germinating box (15 × 20 cm) within an artificial climate chamber (RQH-01Y, Hengfeng, Hubei, China) with 90% humidity and 25°C. The frequency of irrigation was 12 h/d with tap water. The different light quality treatments were as follows: dark culture was used as the control (CK), red light (λ = 620–625 nm, 6–7 μmol·m⁻²·s⁻¹, RL), blue light (λ = 460–465 nm, 15–16 μmol·m⁻²·s⁻¹, BL) and white light (6000 K, 24–25 μmol·m⁻²·s⁻¹, WL). The photoperiod was 24 h continuous light. After 6 days of germination, the sprouts were collected excluding the seed coat and stored at -80°C until analysis. According to light-growing conditions and mung bean seed cultivars, samples were named CK-1, CK-5, CK-13, RL-1, RL-5, RL-13, BL-1, BL-5, BL-13, WL-1, WL-5 and WL-13 (Fig. 1).

#### RNA extraction, cDNA synthesis and quantitative real-time PCR analysis

Total RNA was extracted from frozen samples using an HP Plant RNA Kit (Tiangen Biotech, Beijing, China). Extracted RNA was reversed to cDNA using FastKing RT Kit with gDNase (Tiangen Biotech, Beijing, China). Real-time fluorescence quantitative PCR was determined using LightCycler® 480 Real-Time PCR System (F. Hoffmann-La Roche Ltd., Basel, Switzerland) and Talent qPCR Premix with SYBR Green (Tiangen Biotech, Beijing, China) according to the manufacturer's instructions. Each reaction system was 0.4 μM gene-specific primer and 1.0 μL cDNA template, 5 μL SuperReal PremiX Plus, the final volume was 10 μL. The qRT-PCR cycle parameters were set to 95°C for 15 min, followed by heating at 95°C for 10 s and annealing at 60°C for 30 s for a total of 40 cycles. The Actin (NCBI accession XM_014638363.2) was chosen as endogenous control, and specific primers were designed by Primer5, as listed in Supplemental Table 1. Relative
expression levels of target genes were analyzed by the $2^{-\Delta\Delta Ct}$ method according to the Ct value. The CK sprouts treated by dark, blue, red and white lights were collected on the 6th day (color figure online).

Fig. 1 Mung bean sprouts after dark, blue, red and white light treatments. CK-1, CK-5, CK-13, RL-1, RL-5, RL-13, BL-1, BL-5, BL-13, WL-1, WL-5 and WL-13 indicate that three genotypes of mung bean sprouts were used as a control group. Results were reported as mean ± SE (n = 3).
Extraction and determination of polyphenols

The extraction of polyphenols was determined according to the method described by Lu et al. (2019) with some modifications. In brief, fresh samples (2.00 g) were extracted with 80% acetone solution (90 mL, pH = 2), finally dissolved in 70% methanol solution (10 mL, pH = 2) and stored at -20 °C until further analysis. The polyphenols in sprout extracts were analyzed qualitatively and quantitatively by high-performance liquid chromatography (HPLC) system (Waters Corporation, Milford, MA, USA) as described previously and slightly modified (Lu et al. 2019). Briefly, the phytochemicals were separated at 35 °C on a Waters 2998 photodiode array detector and a C18 column (250×4.6 mm, 5 μm). The polyphenols were analyzed at 254, 320 and 520 nm using mobile phases (A: 0.1% trifluoroacetic acid in water; B: acetonitrile). The loading flow rate was 1.0 mL/min and the injection volume was 30 μL. The polyphenol component contents were identified and quantitated via the external standard method on the basis of retention time. Each polyphenol compound detected was reported as micrograms per gram in fresh weight (μg/g FW) with three replicates. The lignin contents in mung bean sprouts were measured using the AcBr method described in the reference (Gu et al. 2021) and were expressed in A260/g FW.

Statistical analysis

Differences among the mung bean sprouts were determined by IBM SPSS 25.0 (SPSS Inc., Chicago, IL, USA). The one-way ANOVA and Tukey’s multiple comparison post-tests were performed to analyze the significant differences between groups (p < 0.05). A Pearson test was performed to determine the correlation analysis of the data.

Results

Effect of light quality on polyphenol profiles in mung bean sprouts

The chromatographs of the polyphenol components discovered in mung bean sprouts at three wavelengths of 254, 320 and 520 nm are shown in Supplemental Fig. 1. Variations in the polyphenol profiles and lignin contents of mung bean sprouts under light quality treatments are shown in Fig. 2 (A–I) and Supplemental Fig. 2. Nine compounds of polyphenols, including three phenolic acids, two flavones, three isoflavones and one anthocyanin, were identified in mung bean sprouts. Light irradiation was beneficial to increase polyphenols in three cultivars. Caffeic acid, a characteristic metabolite of detected phenolic acids, occupied the maximum levels and exhibited a 38.57%–60.16% contribution to the total in all samples. In the dark control, there was no significant difference in caffeic acid content among the three sprout cultivars, whereas caffeic acid of ZL13 was more strongly induced than in other cultivars in response to light. However, caffeic acid content was significantly increased under light qualities and reached up to 99.33 ± 9.87 μg/g FW at RL-13, which was approximately 3.6 times higher than CK-13. A similar pattern was observed in three cultivars where caffeic acid content was 1.2–1.4 times higher in both WL and RL than in BL. Rutin, a characteristic metabolite of detected flavones, had a more than 2.5 times increase under three LQs compared to CK from 17.30 ± 2.01 μg/g FW (at CK-13) to 76.59 ± 3.54 μg/g FW (at WL-13). The rutin content in cultivar ZL13 was higher than the other cultivars, regardless of whether the light was present or not, and rutin content peaked under WL. Interestingly, ferulic acid was detected only in the BL and WL groups. SH1 achieved the highest content of ferulic acid (56.91 ± 11.88 μg/g FW) under BL, which was 5.0 and 16.3 folds as compared with ZL5 and ZL13, respectively. A significant increase in vitexin concentration was observed under light conditions, with the most effective enhancement under RL. Three isoflavones, daidzin, glycitin and genistin, were identified in mung bean sprouts. WL and BL could produce the same effect by stimulating the accumulation of daidzin in three cultivars, whereas daidzin content at RL-1 reached a peak and constant value of 12.24 ± 0.89 μg/g FW. However, the amounts of glycitin, genistin and p-coumaric acid were found to be relatively low. Glycitin and p-coumaric acid only appeared in CK and RL, and their contents were down-regulated by RL, whereas genistin was detected in the RL and BL groups. Delphinidin 3-glucoside, as a unique anthocyanin appeared only in ZL13 with abundant amounts under RL (6.84 ± 0.80 μg/g) and WL (5.55 ± 0.56 μg/g) followed under BL (2.36 ± 0.24 μg/g), whereas it was not detected under CK. In addition, three LQs increased obviously lignin contents in the three cultivars. Generally, these observations revealed that LQ boosted the accumulation of different polyphenols (caffeic acid, rutin, ferulic acid, vitexin, daidzin, genistin and delphinidin 3-glucoside), especially the enhancement of caffeic acid and rutin under WL. Different polyphenol compounds responded differently to the single light quality.

Effect of light quality on regulating polyphenol biosynthesis at transcription levels

To gain insight into the light regulation of the polyphenol biosynthesis in mung bean sprouts, nineteen key genes involved in the phenylpropanoid biosynthesis pathway were selected for quantitative RT-PCR analysis (Fig. 3). Most genes were up-regulated in mung bean sprouts under LQ treatments compared to CK. Among the three light conditions, WL had the
highest transcript levels of \textit{PAL}, \textit{C4H}, \textit{CHS}, \textit{F3H}, \textit{DFR} and \textit{ANR} in three cultivars (\(p < 0.05\)); meanwhile, RL and BL likewise boosted their expression except for \textit{C4H}. \textit{4CL} expression was obviously enhanced under three LQs in ZL13 and SH1 (\(p < 0.05\)), particularly showing higher values under WL and RL than under BL. Besides, the \textit{FLS}, \textit{F3′H} and \textit{UDPG} genes of three cultivars exhibited higher levels in response to both WL and BL, as compared to RL, with up to a maximum of 6.88, 6.59 and 3.80 times versus CK, severally. Notably, the \textit{F3H}, \textit{F3′H} and \textit{F3′5H} genes in ZL13 were more sensitive to LQs than the other two cultivars with at least 3.5 times higher than CK. In particular, \textit{ANS} and \textit{F3′5H} in ZL13 were strongly induced more than 15.63 and 5.72 times by three LQs, respectively. By contrast, a slight effect of LQs on their expression was found in ZL5 and SH1. Three LQs obviously stimulated \textit{IFS} expression except for ZL5, with the highest levels reaching 8.77 times (at RL-1) and 10.98 times (at BL-1) in comparison with controls. The transcription of \textit{HID} was activated by LQs in SH1 and ZL13 except for at BL-1, while remaining constant in ZL5. Notably, LQs inhibited the expression of \textit{COMT}, \textit{F6H} and \textit{IF7GT}. In general, the expression levels of most genes in the polyphenol biosynthetic pathway were induced by LQs, especially WL, and ZL13 was more sensitive in response to light.
Effect of light quality on the regulatory transcription factor involved in polyphenol accumulation

The specific mechanisms of transcription factors (TFs) involved in the light regulation of polyphenol accumulation were further analyzed as shown in Fig. 4A. BL down-regulated the expression levels of MYB4 to reach the lowest values, while RL induced MYC2 expression in three cultivars versus control. MYBL1 expression was suppressed by approximately 45% under RL and BL in three cultivars, whereas no significant changes between the WL and CK groups were
observed in sprouts. LQs promoted the up-regulation of \textit{MYB111} expression, in particular, \textit{MYB111} was increased over four times by WL and BL. In contrast, \textit{MYB3} exhibited an apparent dissimilar pattern in the three cultivars. \textit{MYB3} expression remained consistent in ZL5 and was decreased by 32% under RL and BL in SH1, whereas it increased more than 1.29 times under three LQs in ZL13.

Effect of light quality on the regulation of light signal transduction pathways

Due to the close association of light perception and signaling with polyphenol synthesis, we selected 13 genes from the regulatory network of light signaling transduction for further study (Fig. 4B, 4C). LQ obviously influenced the expression of photoreceptor genes. Among blue photoreceptors, \textit{CRY-D} and \textit{PHOT2} were induced by LQs in three cultivars and were strongly sensitive in response to WL (more than five times versus control) and BL (more than 2.6 times versus control), respectively. The identical spectral response patterns were found in both SH1 and ZL13 that \textit{PHYE} expression was stimulated by three LQs, reaching the highest values under WL (2.6 times versus control), followed by BL and RL. However, the relative expression of \textit{PHYE} in ZL5 remained little/no effect between light and dark conditions. On the other hand, RL and BL inhibited \textit{CRY1} and \textit{PHYA} genes.
Among the identified transcriptional regulators involved in photoreceptor-mediated signaling mechanisms, the expression levels of *COP1* and *SPA1* were increased by three LQs. By comparison, the response of *SPA1* to both WL and BL was more distinct. In three cultivars, BL and RL inhibited the expression of *FAR1*, *LAF1*, *FHY1* and *FHY3* with a more than 50% decrease versus dark control. The *HY5-1* and *HY5-2* of the three cultivars had a similar pattern in that LQs significantly stimulated their expression, especially BL and WL. Besides, the expression of *PIF3* was decreased by about 85% under RL and WL in three cultivars, whereas exhibited a modest change under BL. *BBX20*, *BBX21* and *BBX22* were inhibited under BL, at which they reached the lowest expression levels.

Correlations between polyphenol compounds and relative gene expression

Correlations between measured compounds and relative expression levels of key genes are shown in Fig. 5. The number of samples used for correlation analysis was 32, including 3 replicates of each genotype. Highly significant positive correlations appeared among polyphenol compositions (delphinidin 3-glucoside, rutin and caffeic acid) and these genes (*PAL*, *F3H*, *F3’5’H* and *F3’H*) (*p* < 0.01). In addition, the expression of *ANS* was positively correlated with the content of delphinidin 3-glucoside, and *F6H* expression exhibited a positive relationship with glycitin.

Correlations between structural genes and transcription factors, genes in light signaling transduction pathways are shown in Fig. 6. The number of samples used for correlation analysis was 12, including 3 replicates of each genotype. *HY5-1*, *HY5-2*, *CRY-D*, *PHOT2* and *PHYE* were positively correlated with many structural genes involved in polyphenol biosynthesis pathway, whereas *PIF3* exhibited a negative relationship with some structural genes. Moreover, *MYB111* was highly significantly and positively correlated with the *PAL*, *4CL*, *FLS*, *DFR* and *UDPG* genes. Notably, *MYB3* showed positive correlations with *F3H*, *ANR* and *ANS*.

**Discussion**

The polyphenols varied in their response capability to different light qualities

Previous studies have shown that light quality would significantly impact on the production of polyphenols under low light intensity (Craver et al. 2017; Tantharapornrerks et al. 2021). In this study, different low light intensities were used, thus specific light wavelengths play the majority effect in polyphenol accumulation. Light is an important external factor in the regulation of polyphenol biosynthesis in plants. Light stress can induce the accumulation of reactive oxygen species (ROS) in plants, resulting in photooxidative damage, and polyphenols can improve the tolerance of plants to oxidative stress (Zoratti et al. 2014). Accumulation of flavonoid compounds in *Catharanthus roseus* seedling adapted to light stress by effectively suppressing ROS levels (Yu et al. 2021). Among detected polyphenols, the concentrations of caffeic acid, rutin, ferulic acid, vitexin, daidzin, genistin and delphinidin 3-glucoside were increased by LQs (Fig. 2). Therefore, protecting sprouts from oxidative stress response might be responsible for the large accumulation of polyphenol compounds under different LQs. Caffeic acid was correlated with many structural genes involved in polyphenol biosynthesis pathway, whereas *PIF3* exhibited a negative relationship with some structural genes. Moreover, *MYB111* was highly significantly and positively correlated with the *PAL*, *4CL*, *FLS*, *DFR* and *UDPG* genes. Notably, *MYB3* showed positive correlations with *F3H*, *ANR* and *ANS*.
the predominant component of polyphenols in mung bean sprouts, similarly to the previous report (Ebert et al. 2017). The caffeic acid content was significantly higher under RL and WL than under BL, while ferulic acid appeared in BL-treated sprouts (Fig. 2A, B). Caffeic acid is the precursor for the formation of ferulic acid (Neelam et al. 2020), which explained the phenomenon together with the higher contents of caffeic acid in the WL and RL groups as well as the highest contents of ferulic acid in the BL group. Similarly, the concentration of ferulic acid was dramatically increased under BL than RL in pea sprouts (Liu et al. 2016). Moreover, caffeic acid and ferulic acid, with high antioxidant capacity and antibacterial activity, contribute to preventing diabetes and cancers as well as protecting kidney (Deng and Lu 2017; Neelam and Sharma 2020). Interestingly, caffeic acid is also a key precursor of lignin formation which is a product of the phenylpropanoid pathway (Bubna et al. 2011). As a core component of cell walls, the rapid synthesis of lignin is an important protective mechanism of plants against environmental stress (Gu et al. 2021). This was responsible for the large accumulation of lignin in mung bean sprouts under light conditions (Supplemental Fig. 2). Changes in polyphenol accumulation and components reflected the response of plants to different LQ conditions (Liu et al. 2016). The distribution pattern and trend of most polyphenol compounds regulated by different LQs in the three varieties were consistent. In this study, rutin and vitexin responded most strongly to WL and RL, severally, and daidzin responded to BL and WL to the same extent, as well as the above-mentioned components (caffeic acid, ferulic acid and lignin) also responded selectively to LQs (Fig. 2). In particular, rutin, a high antioxidant, has extensive pharmacological activities such as anticoagulant and antithrombotic (Choi et al. 2015). A study reported that RL enhanced significantly the accumulation of vitexin, isovitexin and rutin compared with BL in common buckwheat sprouts (Lee et al. 2014), while WL showed the highest concentrations of daidzin in soybean sprouts as compared to RL and BL (Zhang et al. 2019a, b). RL and BL have been extensively reported in the increase of plant secondary metabolites as their photoreceptors were involved in the accumulation of phenolic acids and flavonoids (Appolloni et al. 2022). Notably, the key to precise stimulation of polyphenol components was the manipulation of different light qualities in mung bean sprouts. There is long-standing evidence that BL is more effective for the accumulation of polyphenols than RL (Zhang et al. 2020a, 2020b).
which is discrepant with our results that individual polyphenols responded differently to BL and RL. This dissimilar finding might result from species differences. Due to this diverse response, monochromatic lights can be applied to increase the targeted polyphenol concentrations. As previously reported, caffeic acid and p-coumaric acid of Salvia miltiorrhiza seedlings were enhanced under high BL:RL ratios (7B:3R) compared with WL (Zhang et al. 2020a, b).

Notably, the combination of monochromatic light might be more beneficial to the accumulation of polyphenol metabolites; thus further endeavors should be focused on elucidating optimal BL:RL ratios to optimize the accumulation of the polyphenols in mung bean sprouts. Additionally, WL had equal or superior effects on enhancing polyphenols compared to RL and BL (Zhang et al. 2019a, b), as white light is a complex that encompasses all wavelengths of the visible spectrum. Similar results were obtained in this study, and WL appeared to be the optimal light source to produce mung bean sprouts rich in polyphenol components.

In addition, it was previously reported that polyphenol compositions among diverse mung bean sprout cultivars were similar with slight differences, but amounts were likely to vary widely (Ebert et al. 2017). In dark-treated sprouts, rutin, daidzin and glycitin were richer in ZL13 (black cultivar) than in the other two cultivars (Fig. 2). The results were expected because black mung bean seeds were ample in polyphenol compounds (Yao et al. 2013), with greater polyphenol accumulation after germination. After being exposed to light, ZL13 obtained the highest concentrations of the main components, caffeic acid and rutin, especially anthocyanins were detected only in ZL13. The accumulation of anthocyanin is directly bound up with light, resulting in protecting plants from oxidative damage by absorption of excess light (Mastropasqua et al. 2020). Light is a precondition for anthocyanin synthesis, which is consistent with our findings that the traditional cultivation of mung bean sprouts in dark did not trigger anthocyanin production. It was reported that light quality effectively accelerated anthocyanins accumulation in Chinese kale sprouts (Qian et al. 2016). Moreover, there was a discrepancy in the response of anthocyanin synthesis to different LQs (Kadomura-Ishikawa et al. 2013), coinciding with a more effective enhancement under RL and WL than BL (Fig. 2F). Besides, delphinidin 3-glucoside was only detected in light-treated sprouts of ZL13 (black cultivar) in this study, which was likely attributable to the unique sensitivity of ZL13 in response to light quality. Due to mutations in the structural genes or TFs related to anthocyanin biosynthesis, many plant cultivars also have peculiar varieties in which light fails to stimulate anthocyanin production (Zoratti et al. 2014).

Overall, the differences between polyphenols were closely related to light qualities and cultivars. White light was an effective way to enhance specific polyphenol metabolites in mung bean sprouts. Black mung bean sprouts (ZL13) were rich in polyphenol metabolites and were excellent sources of natural antioxidants for health promotion.

**Light quality regulated the expression of polyphenol-related structural genes to promote polyphenol accumulation**

Polyphenol accumulation was widely regulated at the transcriptional level, and most genes related to the phenylpropanoid pathway could be activated by light (Naing and Kim 2018). The expression levels of most detected genes were notably up-regulated by light, while COMT, F6H and IF7GT were down-regulated by LQs. These data implied that light increased polyphenol accumulation via promoting phenylpropanoid biosynthesis once the sprouts were exposed to light. Early genes of the phenylpropanoid pathway, such as PAL, C4H, 4CL, CHS and CHI, are primarily regulated by WL (Fig. 3), and the up-regulation of the first two genes resulted in higher caffeic acid and ferulic acid levels, which caused a further increase in lignin biosynthesis. Notably, the expression level of 4CL paralleled the lignin accumulation (Supplemental Fig. 2, Fig. 3). Simultaneously, the expression of 4CL and CHS could be induced by blue and red lights, which was consistent with the result of Liu et al. (2018) in Cyclocarya paliurus. CHS, a critical enzyme catalyzing the initial step in flavonoid biosynthesis, can be activated by light (Lillo et al. 2008).

The discrepancy in relative gene expression levels reflected the response of sprouts to different cultivars and light quality conditions (Fig. 3). Three LQs stimulated the transcription of F3H, F3′H, FLS, UDPG3GT, DFR, F3′5′H, ANS, ANR, HID and IFS to varying degrees (Fig. 3). Zhang et al. (2019a, b) also reported that BL, RL and WL could activate the expression of six major structural genes (CHS, CHI, F3′H, F3H, FLS and IFS) in soybean microgreens grown, especially BL. Moreover, at the transcriptional level, we discovered that ZL13 was the most sensitive to light among the three species, followed by SH1, whereas the sensitivity of ZL5 was relatively low (Fig. 3). These differences can be attributed to species diversity. In particular, both RL and BL were found to up-regulate the transcript levels of PAL and ANR only in ZL13, while F3H and ANS contained considerably high expression levels in ZL13 under three LQs (Fig. 3), which coincided with the accumulation of anthocyanin (delphinidin 3-glucoside) (Fig. 2F). F3H is located in a central position of flavonoid pathway, and ANS is a key enzyme that directs flavonoid flux into anthocyanin, both of them can be activated by light (Lillo et al. 2008). Analogously, in hypocotyls of radish sprouts continues, F3H, ANS expression as well as PAL activity were closely related to anthocyanin accumulation (Su et al. 2016). According to correlation analysis, delphinidin
3-glucoside was highly significantly and positively correlated with the gene expression of \(PAL (R^2 = 0.452, p < 0.01)\), \(F3H (R^2 = 0.774, p < 0.01)\) and \(ANS (R^2 = 0.884, p < 0.01)\) (Fig. 5). The above data indicated that \(PAL\), \(F3H\) and \(ANS\) might be the key genes involved in anthocyanin synthesis in ZL13.

Indeed, the rutin content of ZL13 was consistently higher than that of the other two cultivars under all LQs, in accordance with the expression levels of \(F3H\), \(F3'H\) and \(F3'5'H\). Besides, the expression of \(PAL\), \(C4H\), \(CHI\), \(CHS\), \(F3H\), and \(F3'5'H\) peaked unaniostously at WL-13 (Fig. 3), coinciding with the highest content of rutin under WL (Fig. 2D). Certainly, similar but weaker associations were found in both SH1 and ZL5. Pearson’s analysis of three cultivars after light treatments showed that the relative gene expression of \(PAL\), \(F3H\), \(F3'H\) and \(F3'5'H\) was highly significantly correlated with the rutin content (the correlation coefficients reaching 0.630, 0.916, 0.860 and 0.884, respectively) (Fig. 5). Therefore, these genes played important roles in flavonoid biosynthesis in mung bean sprouts. As previously reported (Zhang et al. 2019a, b), rutin accumulation was closely related to the activation of \(F3'H\) expression. They also indicated that RL and BL strongly induced \(PAL\), \(CHI\), \(F3H\), \(FLS\) and \(F3'H\), as well as flavonoid accumulation in tartary buckwheat sprouts. According to the data, the highest level of daizin in SH1 resulted from the joint action of \(IFS\) and \(HID\) (Fig. 2G, 3). In addition, \(F6H\) transcription was repressed by all LQs in three cultivars, consistent with the down-regulation of glycitin content by light. Correspondingly, \(F6H\) showed a high correlation value with glycitin as 0.676 \((p < 0.01)\) (Fig. 5). Overall, these findings revealed that different polyphenol biosynthesis-related genes were induced by different LQs, manifesting that the light-promoted synthesis of polyphenol compounds is a complicated process.

**Light quality regulated the expression of polyphenol-related TFs to regulate structural genes of polyphenol synthesis pathway**

Numerous previous studies have shown that TFs play essential roles in light-induced polyphenol metabolism, including MYB and bHLH (Naing and Kim 2018). It was known that MYBs were involved in the transcriptional regulation of polyphenol biosynthetic genes. In *Arabidopsis*, MYB11, MYB12, and MYB111 can independently activate related genes ([*CHS*, *CHI*, *F3H*, and *FLS*) which together determine the flavonol content (Mondal and Roy 2018). In accordance with *FLS*, *F3H*, *F3'H* and *UDPG*, the expression of *MYB111* was significantly induced by light in three cultivars, especially by BL and WL (Figs. 3 and 4A). Meanwhile, *MYB111* showed high correlation value with *FLS*, *DFR* and *UDPG* \((p < 0.01, \text{Fig. 6})\). Consequently, MYB111 likely acted as a polyphenol-specific activator in light-treated sprouts.

MYC2 (bHLH TF) positively regulated polyphenol biosynthesis and overexpression of *Arabidopsis MYC2* promoted biosynthesis of phenolic acid in *Salvia miltiorrhiza* hairy roots (Gallego et al. 2018; Shi et al. 2020). MYC2 might be linked to RL-induced polyphenol biosynthesis on account of the significant induction of *MYC2* under RL (Fig. 4A). MYB3 acting as an inducer was associated with the up-regulation of structural genes of anthocyanin synthesis (Naing and Kim 2018). Distinctly, LQs-activated *MYB3* expression only was found in ZL13 (Fig. 4A), which paralleled the anthocyanin accumulation (Fig. 2). Meanwhile, *MYB3* exhibited a high correlation with the *F3H* and *ANS* genes as 0.64 and 0.73, respectively \((p < 0.01, \text{Fig. 6})\). These results revealed that *MYB3* potentially controlled the expression of genes-related anthocyanin biosynthesis to promote the accumulation of delphinidin-3-O-glucoside. Additionally, the expression of many *MYBs* appeared to be light-induced in vegetable crops, similar to *MYB111*, *MYC2* and *MYB3* in mung bean sprouts we studied. Several repressors of phenylpropanoid biosynthesis were also MYB TFs, including MYB1, MYB4 and MYB6 (Liu et al. 2020). *MYB1* was down-regulated in response to RL and BL, while *MYB4* was selectively inhibited in response to BL (Fig. 4A). Their down-regulation increased polyphenol levels by strongly promoting the transcript of related genes. Collectively, these data showed that LQs in mung bean sprouts potentially influenced the expression of structural genes and TFs involved in polyphenol synthesis.

**Light signal transduction pathway**

As shown in Fig. 4B and C, sprouts utilized a series of photoreceptors to perceive and respond to light with diverse wavelengths. In blue light receptors, the expression of *CRY-D* and *PHOT2* (blue light-sensitive photoreceptor) was conformably up-regulated under WL and BL in three cultivars (Fig. 4B). Nevertheless, previous studies have shown that the transcriptional levels of photoreceptor genes might not be specific to a particular wavelength of light (Nawae et al. 2021). *PHYE* (red light-sensitive photoreceptor) had the highest levels under WL instead of RL in this study (Fig. 4B). Analogously, the expression of *PHYB* (red light-sensitive photoreceptor) under BL was higher than that under RL in *Centella asiatica* (Nawae et al. 2021). Light-induced accumulation of polyphenols required the involvement of photoreceptors. It was reported that only PHOT2 was identified as a photoreceptor that promotes anthocyanin biosynthesis in strawberry fruit (Kadomura-Ishikawa et al. 2013). Moreover, Liu et al. (2020) suggested that CRY3 could act as a critical photoreceptor in broccoli head flowers to regulate anthocyanin production. Although it was more
commonly reported that RL-regulated polyphenol accumulation depended mainly on PHYA, PHYE may also be involved in RL regulation (Liu et al. 2015). Consistent with the polyphenol accumulation pattern, relatively high levels of CRY-D, PHOT2 and PHYE expression were also observed in light-grown mung bean sprouts (Fig. 4B).

PHYs, PHOTs or CRYs could interact with COP1/SPA1 complex, which is a central repressor of photomorphogenesis, to prevent the complex from targeting activators (e.g., HY5, LAR1, LAF1 and MYBs) of the light response for degradation (Kadomura-Ishikawa et al. 2013; Sheerin and Hiltbrunner 2017). Moreover, these light-dependent TFs have also been widely reported to positively regulate the expression of key enzyme genes required to produce polyphenol components. In sprouts, COP1, SPA1 and HY5 were up-regulated by three LQs, particularly SPA1 and HY5 were induced more obviously under BL and WL in line with CRY-D, PHOT2 and PHYE (Fig. 4C). These results revealed that the COP1/SPA complex might interact with photoreceptors (CRY-D, PHOT2 and PHYE) to form a self-regulatory feedback loop by dissociation of COP1. Similar results have been found by Gallego et al. (2018). HY5 can bind to the promoters of COP1 and SPA1 and stimulate their transcription (Yadav et al. 2020), which may be a negative feedback mechanism, resulting in more excellent stabilization of HY5. In addition, the down-regulated expression of FHY1, FHY3, LAF1 and FAR1 (downstream positive regulators) of light signaling was explained by the up-regulation of COP1 and SPA1 (Fig. 4C). It was noted that COP1 may be involved in BL-induced flavonoid biosynthesis in various ways (Zheng et al. 2019). HY5, the master positive regulator of light signaling, could bind the promoters of flavonoid biosynthesis-related genes and TFs (such as CHS, CHI, F3H, F3’H, DFR, and TFs) and activate their transcription (Sheerin and Hiltbrunner 2017). The expression patterns on strong stimulation under BL and WL of FLS, F3H, F3’H, UDPG and MYB111 were convinced with that of both HY5-1 and HY5-2 (Figs. 3 and 4). Meanwhile, HY5s showed positive correlations with many structural genes (p < 0.05, Fig. 6). Consequently, the regulation of related genes was mediated by HY5s, which might stimulate polyphenol biosynthesis of mung bean sprouts in response to light signals, as has been previously found in Catharanthus roseus seedlings (Yu et al. 2021). PIFs, constitutive repressors of photomorphogenesis, can interact with photoreceptors to regulate downstream light-responsive factors (Liu et al. 2015). A previous study has shown that PIF3 was likely phosphorylated and degraded very rapidly when dark-grown seedlings were transferred to RL (Heng et al. 2019). The PIF3 expression in three cultivars was decreased under RL and WL rather than under BL (Fig. 4C), revealing that the degradation of PIF3 occurred preferentially under RL. A study on Arabidopsis seeds observed that RL up-regulated anthocyanin content and the expression levels of CHS, F3’H and DFR in pif3 mutants compared with wild-type (Liu et al. 2015). These supported that PIF3 might negatively regulate RL and WL-induced 4CL expression in mung bean sprouts.

Altogether, based on the data and results previously reported, we proposed a new working model illustrating a possible mechanism for light-regulated polyphenol biosynthesis in mung bean sprouts (Fig. 7). On the one hand, light-triggered CRY-D-, PHOT2-, PHYE-COP1-SPA1 interaction induced the transcriptional activation of HY5, which is likely to bind directly to the promoter of several vital genes and TF (such as MYB111) involved in polyphenol biosynthesis synthesis pathway and thus activates their expression, subsequently leads to massive accumulation of polyphenols. Meanwhile, the COP1/SPA1 complex suppressed the expression of its downstream light-responsive genes, including LAF1, FAR1, FHY1 and FHY3. On the other hand, red light-activated photoreceptors led to the degradation of PIF3, relieving their repression of polyphenol biosynthetic genes including 4CL. Ultimately, the accumulated polyphenols act as a protective screen for mung bean sprouts to cope with light stress, which was of practical significance for nutritional fortification of sprouts as well as light adaptation. Although the analysis of factors in response to light stimulation has been accomplished, the regulated interaction of the selected factors from specific light sensing to polyphenol biosynthesis of mung bean sprouts remains unclear and requires further exploration.

**Conclusion**

In summary, our results showed that the light conditions could improve the nutritional quality of mung bean sprouts by inducing polyphenol biosynthesis. The differences in polyphenol accumulation were closely related to light qualities and cultivars. Different light conditions significantly enhanced the accumulation of caffeic acid, rutin and delphinidin 3-glucoside (only detected in ZL13), especially white light (the highest intensity), whereas ferulic acid and vitexin responded selectively to blue and red light, respectively. Most genes in phenylpropane pathway were activated under light quality and significantly modulated polyphenol production, which was closely associated with CRY-D, PHOT2, PHYE, HY5s and PIF3 contributing to light signaling perception and transduction. Correlation analyses indicated that PAL, F3H, F3’H and F3’5’H correlated highly with rutin. Moreover, ANS expression was positively correlated with the synthesis of anthocyanins for ZL13, which paralleled the expression of MYB3. Besides, MYB111, MYB3, MYB4, MYB1 and MYC2 seemed to be transcription factors involved in polyphenol biosynthesis. This study provides insights into the transcriptional regulation of specific intermediates in the...
phenylpropanoid pathway and the molecular mechanism of light-mediated polyphenol production.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.
Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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