



Effect of Light Irradiation on Sugar, Phenolics, and GABA Metabolism on Postharvest Grape (*Vitis vinifera* L.) During Storage

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Abstract

The impact of red and blue light-emitting diodes (LEDs) irradiation on the sugar metabolism and γ -aminobutyric acid in postharvest table grapes stored at 4 °C for 21 days after harvest were explored. Grape clusters were exposed to red and blue light irradiation at the same intensity (500 lx). The findings revealed that red and blue light treatments enhanced total soluble solids (TSS) and total acidity (TA) content. Furthermore, red-light irradiation retained higher phenolic compound during storage than blue light and control. Red-light radiation sustained higher levels of phenolic biosynthesis-related enzymes, including phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), cinnamate 4-hydroxylase (C4H), and *p*-coumarate ligase (4CL), than blue light irradiation and control. The results showed that red light increased glucose, fructose, and sucrose levels, which were 32.19, 33.18, and 2.95 mg g⁻¹, compared with those in blue light and control at the end of storage and enhancing the sucrose synthase synthesis (SS-synthesis) and acid invertase (AI), while blue light enhanced sucrose synthase cleavage (SS-cleavage). In addition, red light irradiation increased glutamic acid decarboxylase (GAD) activity while red and blue light irradiation inhibited γ -aminobutyric acid transaminase (GABA-T) activity by 22.14 and 20.71 U g⁻¹ at 21 days of storage, compared to control, leading to γ -aminobutyric acid (GABA) accumulation. These findings suggest that red and blue light will help in maintaining the quality of grape during postharvest storage.

Keywords Red light irradiation · Blue light irradiation · Grape berries · Postharvest · Quality · Sugar metabolism · GABA shunt activity

Introduction

Table grape is highly perishable after harvest due to significant water losses induced by rachis, which results in browning, weight loss, and fruit softness. Also, the amount of sugar in grape berries is one of the key factors determining its quality (Balic et al., 2012). Its metabolism has a substantial influence on the quality of its produce. Sugars are produced by photosynthesis in the leaves and accumulate in the fruit via many physiological mechanisms (Falguera et al., 2013). The sweetness of grape berries is influenced by the buildup of soluble sugars throughout fruit growth. Sugar catabolism in postharvest grape berries alters the composition and amount of soluble sugars, altering fruit flavor, an essential requirement for customer acceptance (Lu et al., 2018). Global interest is rising in finding a more efficient, non-hazardous, and cost-effective alternative strategy to chemical treatments for improving and sustaining the quality of grapes during postharvest storage.

Chemical additives such as sulfur dioxide (Xue & Yi, 2017), spermine (Harindra Champa et al., 2015), nitric

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oxide (Song et al., 2022), chitosan (Lo'ay & Dawood, 2017), and salicylic acid (Nia et al., 2022) used in grapes to extend postharvest shelf life may endanger consumers health. As a newly emerging technique in postharvest fruit and vegetable storage, the application of light-emitting diodes (LEDs) has gained popularity in fruit preservation because of their cost-effectiveness, non-thermal sterilizing, ease of operation, high efficiency, and relatively cold emitting surfaces (Nassarawa et al., 2020). LEDs radiation is also a feasible postharvest treatment alternative for improving nutritional content and preventing senescence in fruit and vegetable during storage (Khan et al., 2022). LEDs light has been used as a postharvest treatment to stimulate the production of total phenolic and total flavonoid content in tomatoes (Castagna et al., 2014), grapes (Barut Gök, 2021), blueberry (Xu & Liu, 2017), okra (Wilawan et al., 2019), pear (Falguera et al., 2014), pakchoi (Xijia et al., 2022), watermelon (Pendyala et al., 2020), fresh-cut pineapple (Bhavaya et al., 2021), tomatoes (Jagadeesh et al., 2011), fresh-cut apple (Gómez et al., 2015), fresh-cut endive (Hägele et al., 2016), and strawberries (Avalos-Llano et al., 2020). Red-light irradiation increased the accumulation of soluble sugars in postharvest citrus fruit by modifying the sucrose metabolism enzyme activity (Yuan et al., 2017). Blue light at 10 °C for 8 days extended the shelf life and increase soluble sugar content in Chinese bayberry (Shi et al., 2016). During the storage of lime fruit, red light treatment increased the concentration of soluble sugars and maintained the flavor of lime (Kaewsuksaeng et al., 2011). Similarly, blueberry fruit treated with red and blue light during postharvest storage increase the soluble sugar content (Xu et al., 2016). During 35 days of storage at 13 °C, UV-C LED treatment significantly increased sugar content and increased GAD activity while inhibited GABA-T activity in tomato fruit (Yan et al., 2021). In postharvest tomatoes, blue light irradiation was more effective than red-light irradiation in promoting GABA accumulation (Dhakal & Baek, 2014a; Xu et al., 2014a).

To our best knowledge, no comprehensive study of the influence of red and blue light radiation on sugar metabolism and the aminobutyric acid shunt pathway in postharvest grape clusters has been conducted. To provide a better understanding of the impact of red and blue light irradiation on sucrose metabolism and the aminobutyric acid shunt pathway during postharvest storage of grape clusters, the current study investigates the influence of continuous LEDs light on specific wavelengths 660 nm (red) and 450 nm (blue) on sugar content and the aminobutyric acid shunt pathway in postharvest grape clusters during storage. In addition, the phenolic compounds and phenolic biosynthesis-related enzymes in grape clusters were studied.

Materials and Methods

Fruit Sample Collection and LEDs Light Treatments

Table grape clusters (cv. Kyoho) were picked from an orchard in Zhejiang Province, Hangzhou, China, and immediately transferred to an agro-product postharvest facility for pre-cooling to dissipate field heat. Thirty-six grape clusters without any defect were chosen and divided into three groups at random (12 grape clusters in each group). The lighting system panel with a length of 63 cm and a width of 52.5 cm and contained eight LEDs bar in each panel consisting of red or blue LEDs were assembled on refrigerator chambers. One refrigeration was made to contain 12 grape clusters; grape clusters were placed under continuous red light irradiation (Systion, Inc., Saitama Portugal; wavelength 660 nm; power 13 W; length 60 cm and width 3 cm) at a distance of 20 cm from the red light emission, while another 12 grape clusters were kept in the second refrigeration under continuous blue light irradiation (Systion, Inc., Saitama Portugal; wavelength 450 nm; power 6 W; length 60 cm and width 3 cm) at a distance of 20 cm from the blue light emission. During the light illumination, all the grapes clusters in both treatments were placed between the two sets of the panel to avoid the shadow distance between the bottom and upper parts of the bunches and to obtain the same illumination energy. The control group was stored in darkness without any light supply. The light intensity which was applied in both the red and blue lights was set to 500 lx and measured with a lux-meter (PM 6612L). All grape samples were stored at 4 °C throughout the whole storage period. The temperature and humidity within the incubators were 5.5 ± 1 °C and 50.5 ± 4 %, respectively. On days 0, 7, 14, and 21, three clusters of berries from each treatment were removed, mixed, and 10 berries in three replicates were randomly sampled for titratable acidity (TA) and total soluble sugars (TSS). Grapes from early harvest were used as 0 day. Subsequent the quality analyses, the remaining berries from each of the three replicates were randomly sampled, mixed, and instantly refrigerated with liquid nitrogen and kept at -80 °C for later use.

Fruit Quality Measurement

Total Soluble Solids and Total Acidity Content in Berries

The total soluble solids and total acidity in berries were determined on fresh squeezed grape juice (3 replicates from 10 berries) using a pocket refractometer meter (PAL-BXI-ACID F5; Atago, Japan), and the results were expressed as percentage.

Chemical Analyses

Determination of Bioactive Compound

The frozen grape tissue (5 g) (3 replicates from 10 berries) was homogenized in 9 mL of 95 % (v/v) methanol. After 24 h of incubation at 25 °C in the dark, the homogenate was centrifuged at $13,000\times g$ for 5 min at 4 °C. The extract was used to determine the total phenolic, total flavonoid, and total anthocyanin content using the method of Farhadi et al. (2016). UV-5800PC spectrophotometers were used to measure the absorbance of the following supernatant at 280 nm (phenolic) and 325 nm (flavonoid). Phenolic and flavonoid content was calculated using gallic acid (phenolic) and rutin (flavonoid) as a standard and results were expressed as milligrams per gram fresh weight. The anthocyanin content was determined using a pH differential method. The result was expressed as milligrams per gram cyanidin 3-glucoside fresh weight.

Determination of Phenolic Biosynthesis-Related Enzymes

The frozen grape tissue (5 g) (3 replicates from 10 berries) was extracted in 0.3 mmol L^{-1} sodium phosphate buffer (pH 8.0) containing 30 mM β -mercaptoethanol for the PAL and TAL assays. For the C4H and 4CL tests, 5 g of frozen grape tissue was extracted with 5 mL of 0.3 M Tris–HCl buffer (pH 7.0) containing 0.2 M dithiothreitol and 25 % glycerol. The reaction mixture was centrifuged for 20 min at $12,000\times g$, and the supernatant was collected for enzymatic activity determination. PAL and TAL activity was measured based on the previous method of Zeng et al. (2015). The method defined by Li et al. (2019) was used to conduct the C4H and 4-CL activities. The result was expressed as units per gram protein fresh-weight basis.

Determination of Soluble Sugars

The glucose, fructose, and sucrose contents were determined in grape samples. For extraction, 50 mL of distilled water was added to 5 g of frozen grape tissue (3 replicates from 10 berries). The mixture was extracted in a water bath for 20 min at 80 °C; after cooling at room temperature, 20 mL of 3% sulfosalicylic acid and 30 mL of distilled water were added to the mixture. The mixture was then allowed to cool for 15 min at room temperature. Ten milliliters of the reaction mixture was transferred to a 10-mL tube and allowed to settle for 15 min before filtering through a 0.45- μm filter and proceed with ion chromatography analyses. The sugars extracted were analyzed using an ion chromatography Dionex CarboPac PA10 column (4 mm \times 250 mm) to separate soluble sugars. The mobile phases were 120 mM NaOH (A) and H₂O (B) at a flow rate of 1.0 mL min^{-1} . The

injection volume was 10 μL , and the column temperature was 25 °C. Glucose, fructose, and sucrose were used to make the calibration standard curves. The result was expressed as milligrams per gram fresh-weight basis.

Determination of SS-Cleavage, SS-Synthesis, and Acid Invertase

The frozen grape samples (5 g) (3 replicates from 10 berries) were homogenized in 10 mL of 50 mmol L^{-1} sodium phosphate buffer (pH 7.8) containing 10 mM MgCl₂, 2.0 mL L^{-1} β -mercaptoethanol, 2.0 g L^{-1} PVPP, and 2.0 mL L^{-1} Triton X-100. The reaction mixture was centrifuged for 15 min at $12,000\times g$ at 4 °C. The extract was used for testing. The SS-cleavage, SS-synthesis, and acid invertase assays were performed using a detection kit in accordance with the manufacturer's instructions (Nanjing Herb Source Bio-Technology Co., Ltd., China). The result was expressed as units per gram fresh-weight basis.

Determination of GABA Content

(5 g) of frozen grape samples (3 replicates from 10 berries) was homogenized in 9 mL of PBS (pH 7.4). The reaction mixture was centrifuged for 20 min at 4 °C at $3000\times g$. The extract was used for GABA determination. The UV 5800PC spectrophotometer was used to measure absorbance at 450 nm. GABA was determined using a plant GABA ELISA assay kit (Nanjing Herb Source Bio-Technology). The GABA content was determined using a GABA standard curve and expressed in micromoles of GABA equivalent per gram of fresh weight ($\mu\text{mol g}^{-1}$).

To determine the GAD and GABA-T activities, frozen grape tissues (5 g) (3 replicates from 10 berries) were extracted in 9 mL of PBS (pH 7.4). The supernatants were used for the GAD and GABA-T tests after centrifugation at $5000\times g$ for 15 min at 4 °C. The activity of GAD and GABA-T assays was measured according to manufacturer's instructions using the plant GABA-T ELISA assay kit and the plant GAD ELISA assay kit (Nanjing Herb Source Bio-Technology). The results was expressed as units per gram fresh-weight basis.

Statistical Analyses

The results were processed using IBM SPSS (version 25). The data were analyzed using one-way analysis of variance (ANOVA), and the values were presented as the mean \pm standard deviation of three replications. The multiple comparison of the means between the treated samples and the control was determined using Duncan's multiple ranges ($P < 0.05$).

Results

Impact of Red and Blue Light Emission on TSS and TA

During the postharvest storage period, the TSS content of grape samples increased slightly from 16.30% to 16.63%, 16.93%, and 17.45% in both treatments (Fig. 1a). However, treated grape samples had slightly higher soluble solids than the control samples. The results showed that red light irradiation maintained a significant higher increase in TSS from 7 to 21 days of storage. TA content of grape samples in both treatments decreased. TA declined from 0.69% to 0.59%, 0.62%, and 0.63%. The TA content of berries treated with red light retained a slightly higher level on the 7–21 days of storage than blue light and control berries (Fig. 1b).

Impact of Red and Blue Light Radiation on Phenolic Compounds

The total phenolic content of treated and control grape samples gradually increased (Fig. 2a). The red light treatment resulted in the greatest increase in phenolic content in grape samples. On day 21, the total phenolic content of the control fruit was 3.01 mg g^{-1} , which was significantly ($P < 0.05$) lower than that of the red and blue light treatments (3.58 mg g^{-1} and 3.22 mg g^{-1}) at the end of storage. Red

light treatment exhibited higher total flavonoid content of grape samples during the whole storage (Fig. 2b). The flavonoid content of red and blue light was 1.09 mg g^{-1} and 1.03 mg g^{-1} higher than control fruit (0.97 mg g^{-1}) at the storage end. A significant ($P < 0.05$) difference in the total phenolic and total flavonoid content of grape samples between the treatments and the control was observed. Figure 2c depicts changes in total anthocyanin content in grape samples. The overall anthocyanin content of both control and treated grapes increased during storage. Grape samples exposed to red light had significantly ($P < 0.05$) higher total anthocyanin levels than blue light and control fruit from 7 to 21 days. The anthocyanin content of grape samples treated with red light was 2.58 mg g^{-1} at the end of storage, which was greater than the blue light and control.

Impact of Red and Blue Light Radiation on Phenolic Biosynthesis-Related Enzymes

The result of PAL activity is presented in Fig. 3a; the PAL activity in grape samples increased in both treatments. However, after 7 days of storage, red light radiation has retained higher PAL activity. In comparison to the control, red and blue light radiation had higher PAL activity (30.10 U g^{-1} and 29.24 U g^{-1}) at the end of storage. In this experiment, TAL activity increased within 14 days of storage in all the treatments, and then declined at the end of

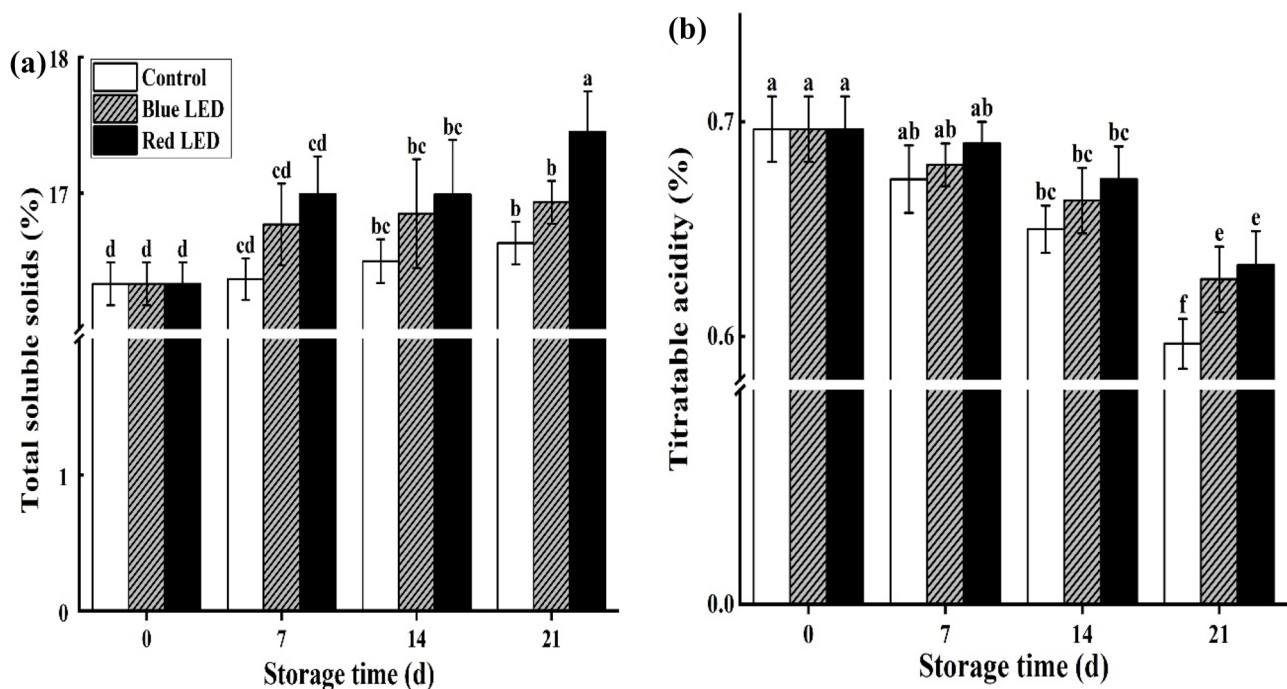


Fig. 1 Impact of red and blue light exposure on **a** TSS and **b** TA during storage at 4 °C in grape berries. The standard deviation is defined by the data shown (SD, $n=3$). Significant changes between treatments ($P < 0.05$) are represented by different letters

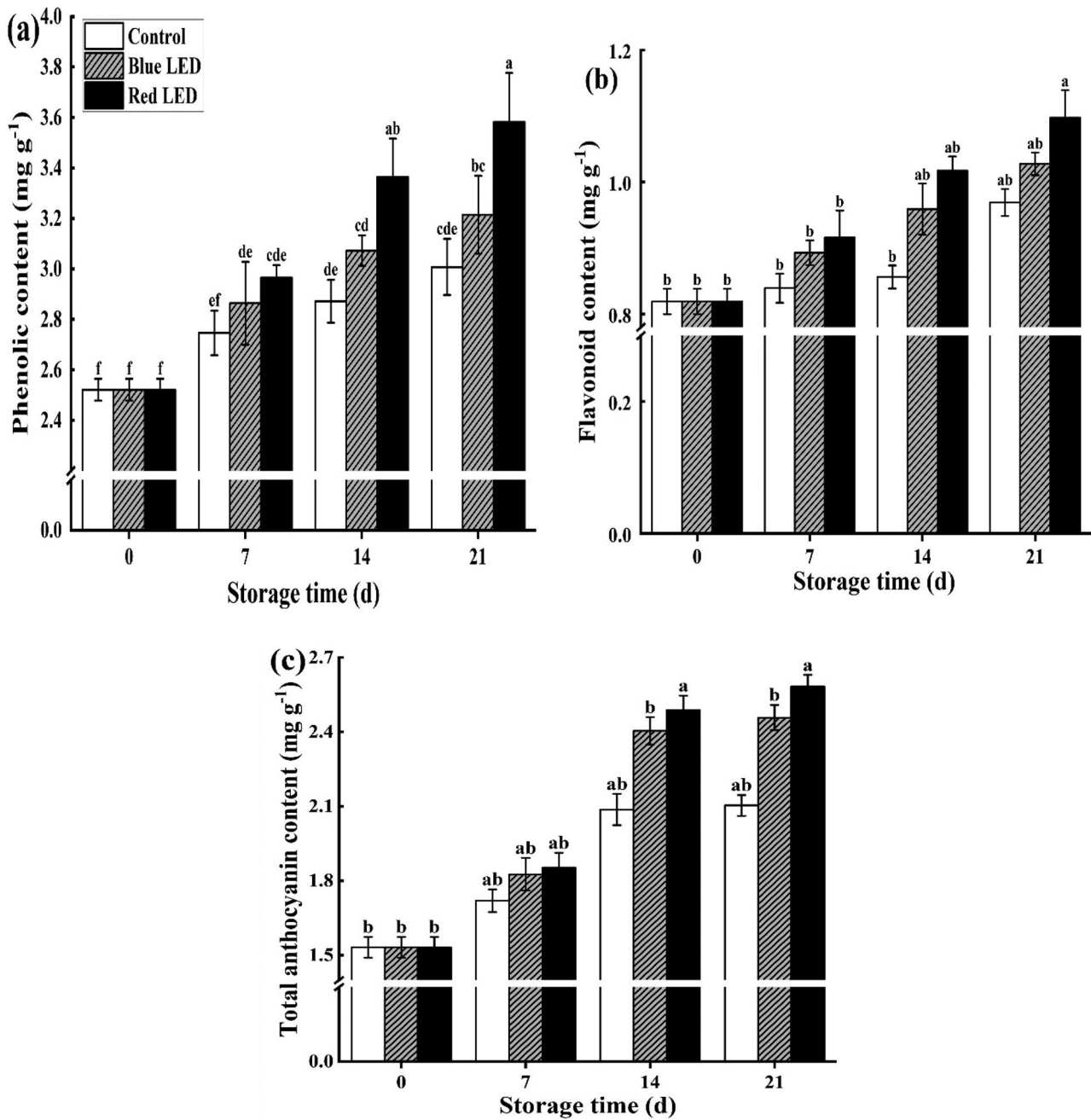


Fig. 2 Impact of red and light exposure on **a** total phenolic content, **b** total flavonoid content, and **c** total anthocyanin content of grape berries stored at 4 °C. The standard deviation is represented by the

data shown (SD, *n*=3). Different letters reflect significant differences (*P*<0.05) between the treatments

storage closest to the initial storage level of around 27.44, 29.69, and 30.51 U g⁻¹ (Fig. 3b). Red light treatment had the highest TAL activity than blue light and control during the whole storage. During storage, the C4H and 4CL activity decreased progressively as storage time prolonged (Fig. 3c, d). However, C4H activity in grape berries treated

with red light was significantly (*P*<0.05) higher than blue light and control throughout the entire storage (Fig. 3c). C4H activity in red light treatment was 38.52 U g⁻¹ higher than the control and blue light treatment at the end of storage. A similar pattern to C4H activity was observed for 4CL activity (Fig. 3d).

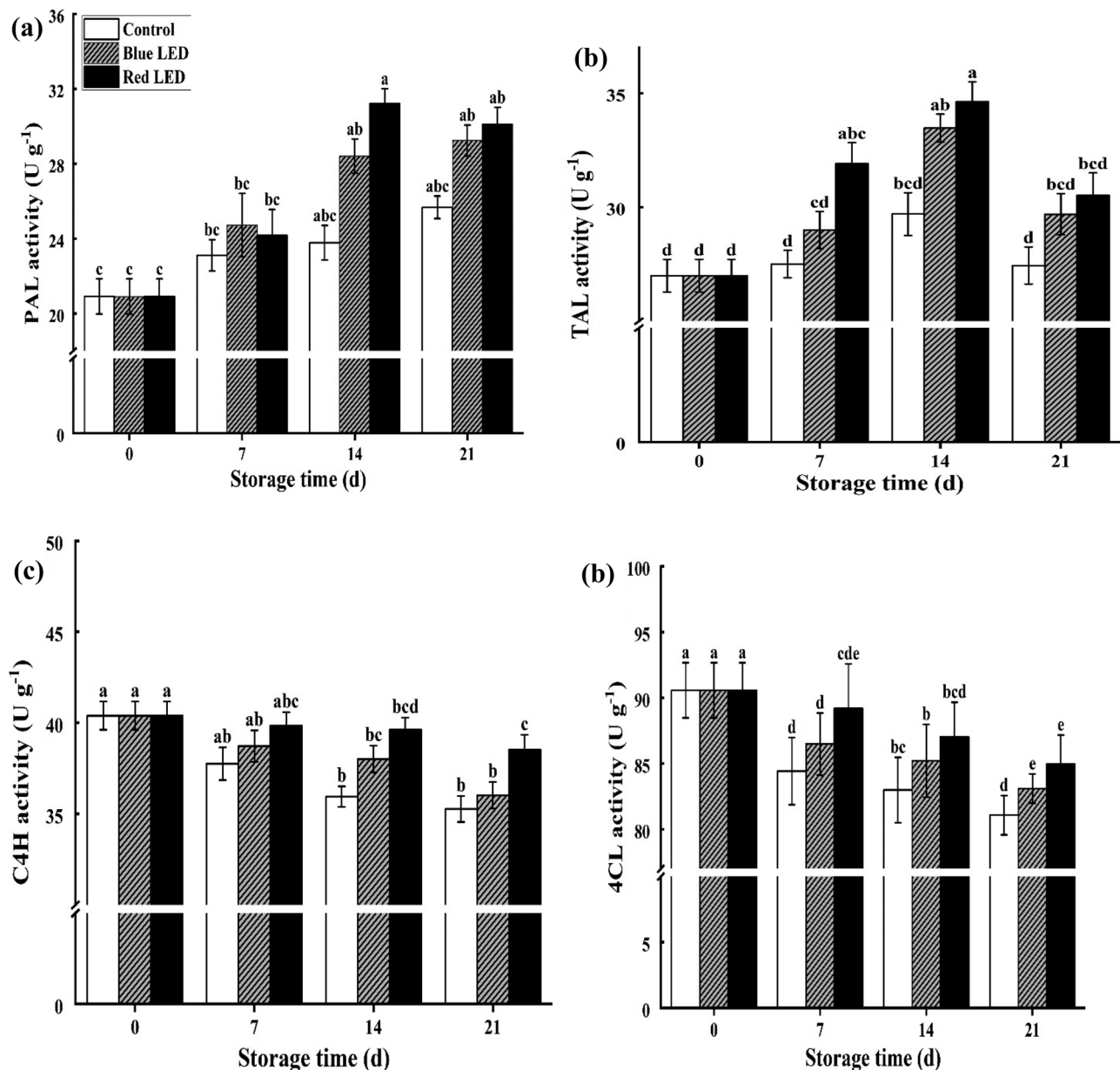


Fig. 3 Impact of red and blue light exposure on **a** PAL, **b** TAL, **c** C4H, and **d** 4-CL enzyme activities during storage at 4 °C in grape berries. Standard deviation (SD, $n=3$) is expressed by the data

shown. Significant variations ($P < 0.05$) between treatments are indicated by different letters

Impact of Red and Blue Light Radiation on Soluble Sugars

Changes in glucose, fructose, and sucrose showed a similar pattern in both treatments (Fig. 4). The content of glucose, fructose, and sucrose increased in both control and red and blue light-treated grapes (Fig. 4a–c). The content of glucose and fructose at the end of storage in the control berries was 29.31 and 30.72 mg g⁻¹, respectively, whereas the content under red and blue light was (30.64 and 32.19 mg g⁻¹) (glucose) and (32.36 and 33.18 mg g⁻¹) (fructose), respectively,

which was significantly ($P < 0.05$) higher than the control berries. There was virtually little sucrose in the grape samples (Fig. 3c). The sucrose content of grape samples stored under red light treatments were significantly ($P < 0.05$) higher than blue light and control berries.

Impact of Red and Blue Light Radiation on Sucrose Metabolism-Related Enzyme Activities

Figure 5a shows that SS-synthesis activity increased throughout the storage time in all treatments. The activities

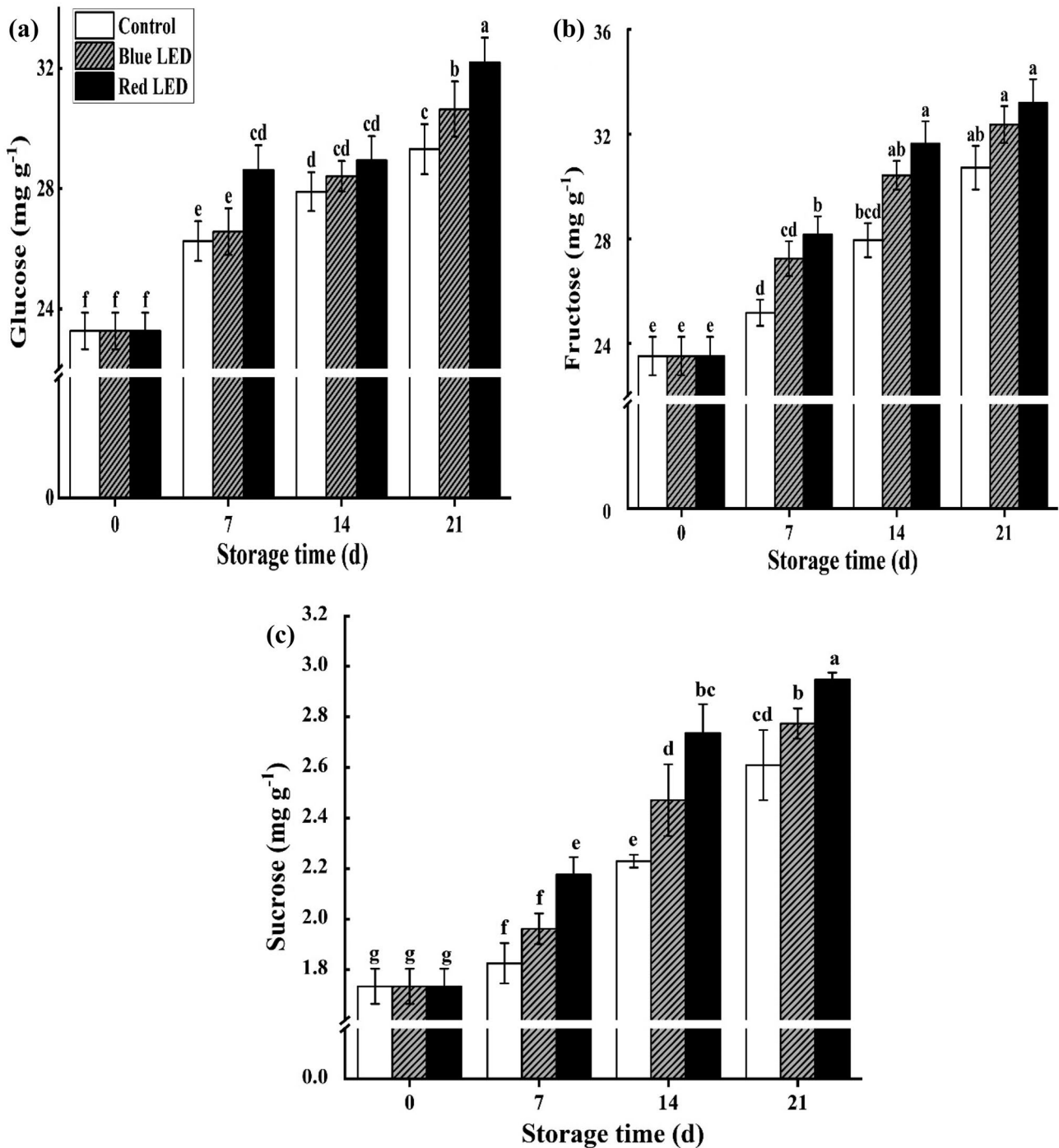


Fig. 4 Impact of red and blue light exposure on **a** glucose, **b** fructose, and **c** sucrose in grape berries during 4 °C storage. The standard deviation is represented by the data shown (SD, *n* = 3). Different letters reflect significant differences (*P* < 0.05) between the treatments

of SS-synthesis in blue light treatment was significantly (*P* < 0.05) higher than the red light treatment and control. This trend did not change throughout the storage. After 21 days of storage, blue light treatment resulted in 0.31 U g⁻¹ higher than red light and control samples. Changes

in the SS-cleavage activity during storage are shown in Fig. 5b. SS-cleavage activity decreased in both treatments. The SS-cleavage in red light treatment was maintained slightly higher than the blue light and control samples during the whole storage. Compared to blue light and control

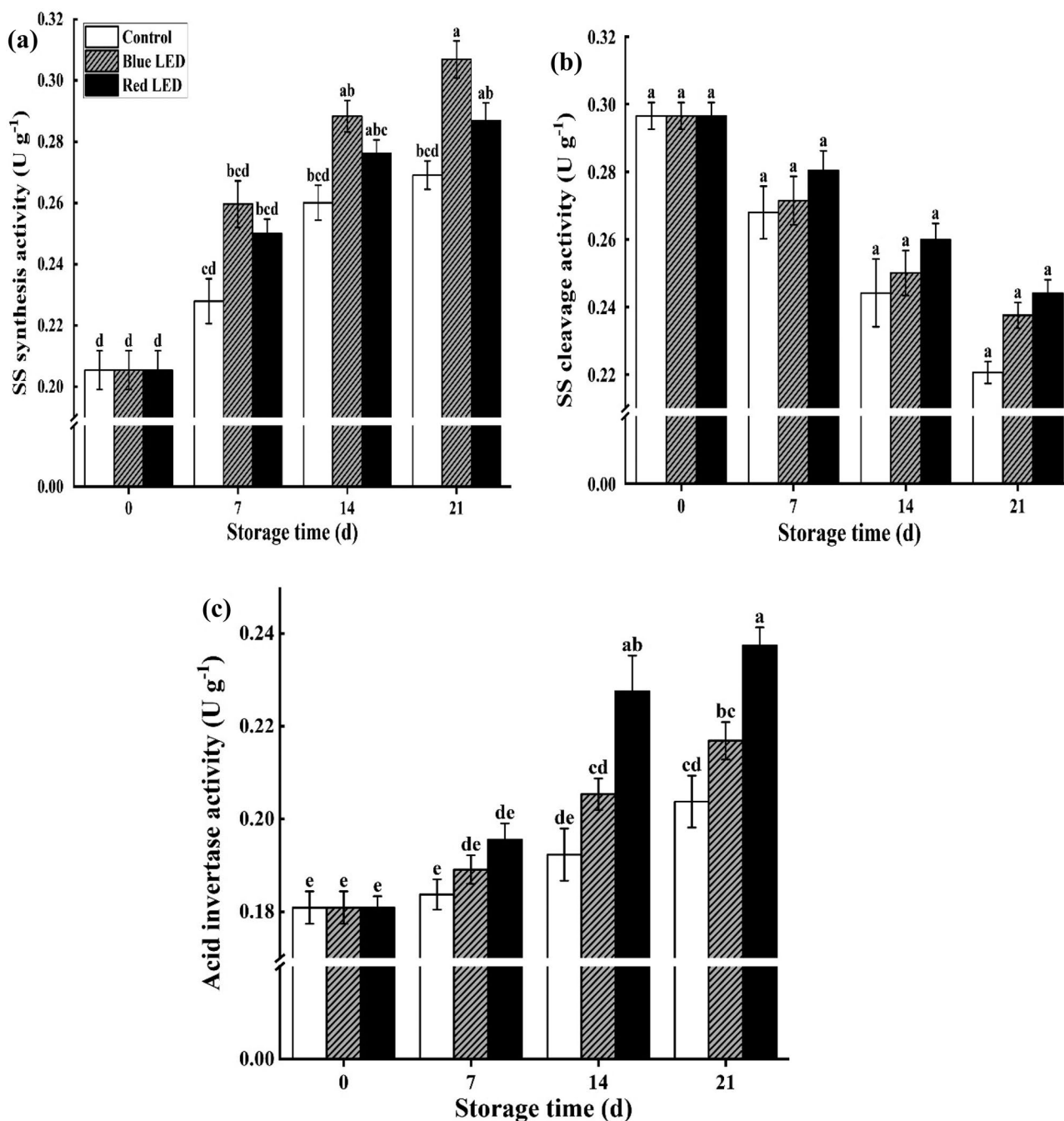


Fig. 5 Impact of red and blue light radiation on **a** SS-synthesis, **b** SS-cleavage, and **c** acid invertase activities during storage at 4 °C in grape berries. Standard deviation (SD, $n=3$) is expressed by the data

shown. Different letters represent significant differences ($P < 0.05$) between treatments

fruit, red light treatment resulted in 0.24 g U g^{-1} slightly higher in SS-cleavage activity in grape berries at the end of storage. There were no significant ($P > 0.05$) differences between the treated and control samples. The acid invertase activities continued to increase during storage (Fig. 5c).

Compared with the control and blue light treatment, acid invertase was significantly ($P < 0.05$) higher in grape berries exposed to red light. At the end of storage, acid invertase activity in red and blue light treatments was 0.24 g U g^{-1} and 0.22 g U g^{-1} higher than in control samples.

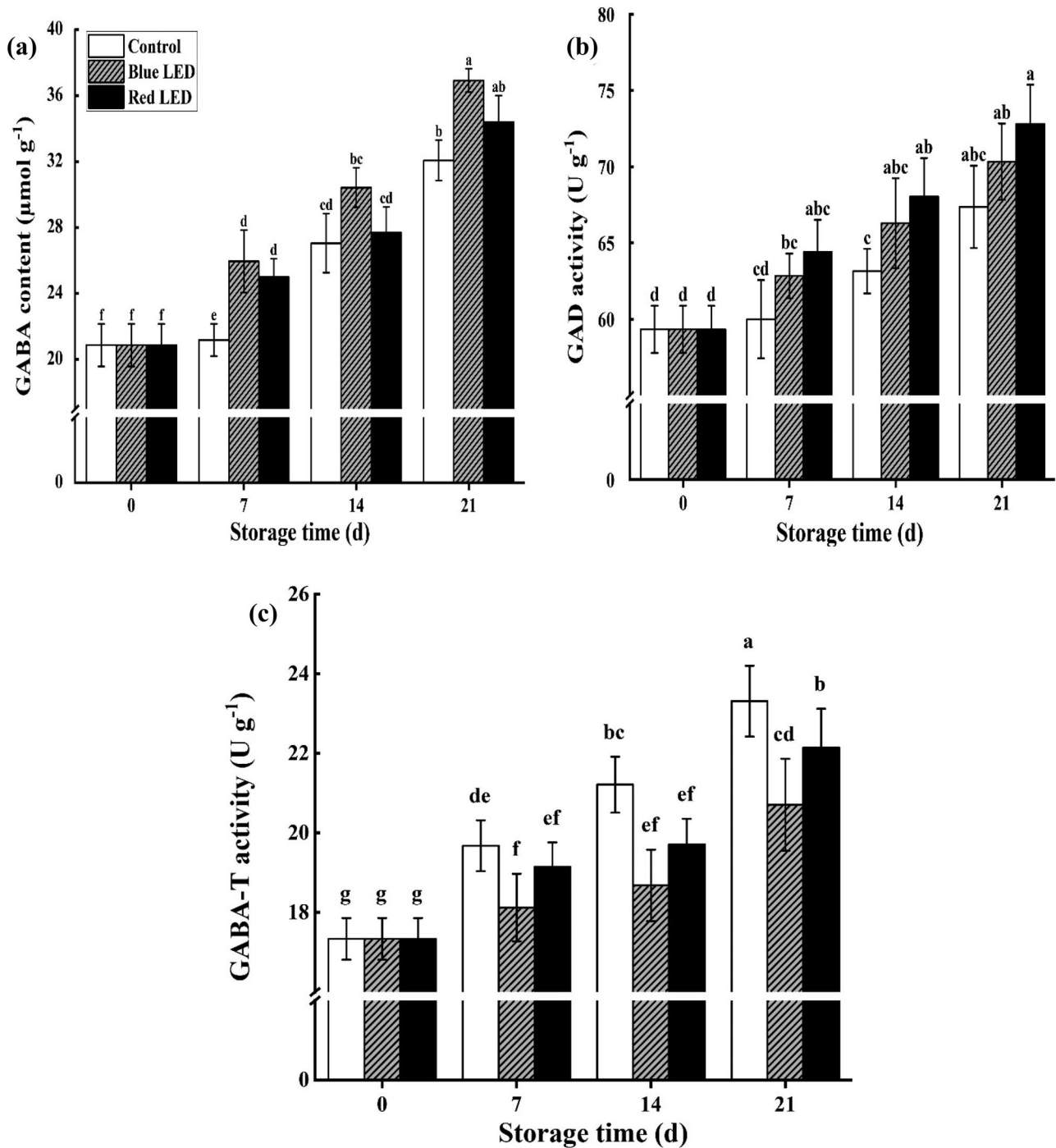


Fig. 6 Impact of red and blue light exposure on **a** GABA content, **b** GAD activity, and **c** GABA-T activity in grape berries during storage at 4 °C. The standard deviation is represented by the data shown

(SD, $n=3$). Different letters reflect significant differences ($P < 0.05$) between the treatments

Impact of Red and Blue Light Radiation on GABA Content, GAD, and GABA-T Activities

As demonstrated in Fig. 6a, the content of GABA increased in both treatments during the whole storage period as the storage time increased. Grape berries exposed to blue light

treatment exhibited higher GABA content than red light treatment and control berries. Blue light treatment had the highest GABA content ($36.94 \mu\text{mol g}^{-1}$) at the storage end, followed by red light treatment ($34.89 \mu\text{mol g}^{-1}$). As exhibited in Fig. 6b, the GAD activity showed a similar pattern with GABA content; the GAD activity presented an

increasing trend in both the treatments throughout the storage. During the whole storage period, the red light treatment significantly ($P < 0.05$) retained higher GAD activity than blue light and control, and the red light-treated sample had the most increased GAD activity (72.81 U g^{-1}) at the end of storage. As depicted in Fig. 6c, GABA-T activity increased continuously in all treatments. It was, however, lower in treated grape berries than in control berries. GABA-T activity in the control fruit was significantly ($P < 0.05$) higher (23.31 U g^{-1}) than in the treated samples at the end of the storage period.

Discussion

The amount of sugar in fruit is one of the key factors determining its quality. The changes in sugar content and composition in the fruit are also affected by respiration. Moreover, abiotic stress affects sugar metabolism in fruit as well. Here, we present a non-chemical technique for determining the influence of light quality, intensity, and storage duration on the quality of post-harvested table grapes. LED light controls the physiological metabolism in horticultural crops, which influences color and quality (Nassarawa et al., 2020, 2022a, b). LEDs light irradiation of harvested horticultural crops at the postharvest stage has become a more prevalent and efficient method of extending their shelf life and maintaining their visual quality (Nassarawa et al., 2020). TSS and TA are considered the most reliable measures of fruit flavor (Sheng et al., 2018). Increasing TSS levels in fruit suggest that the ripening process is speeding up and longer fruit shelf life, and lower TSS, on the other hand, indicates slower ripening. We found that red and blue light treatments, as shown in Fig. 1a, retained a higher TSS content than berries under control, with the slight highest recorded under red light treatment. These findings revealed that red and blue light could regulate total soluble solids and preserve grape berries' quality during the storage period. Similar outcomes were reported in tomatoes (Dhakal & Baek, 2014b), peaches (Gong et al., 2015), Chinese bayberries (Shi et al., 2016), and grape (Nassarawa et al. 2022a). During storage, TA decreased, but both treatments delayed this decline (Fig. 1b). Red and blue light treatment alleviated the decrease in TA during storage, further suggesting the role of red and blue light in delaying fruit maturation and ripening. This outcome was in line with previous research on grape berries (Azuma et al., 2019).

Phenolic compounds are health-promoting secondary metabolites found in fruit and vegetable that contribute to antioxidant activity. Light acts as stress that promotes the biosynthesis of these compounds (Nassarawa et al., 2020). The phenylpropane route produces phenolics and flavonoids, which are essential secondary metabolites in grapes.

Chalcone-flavanone isomerase (CHI), flavanone-3-hydroxylase (F3H), and chalcone synthase (CHS) catalyze the conversion of phenylalanine to phenolic content, which are then converted into flavonoids by the catalysis of PAL, TAL, 4CL, and C4H (Nassarawa et al., 2020). Previous studies have shown that red lights have been demonstrated to enhance the synthesis of phenolic compound in grapes by improving phenolic biosynthesis-related enzymes (Pinto et al., 2016). Similarly, our current study found that red light treatments retained higher total phenolic content compared with blue light and control, suggesting that red light activated the phenylpropanoid and flavonoid biosynthesis pathways (Fig. 2a). Also, it has been reported that red light radiation increased the phenolic content of some fruits and vegetables, including grape (Falguera et al., 2013), red prickly pear (Ortega-Hernández et al., 2018), and strawberries (Xu et al., 2014b). Our analysis showed that at constant intensity (500 lx), red light irradiation had the higher flavonoid content in grape berries than those in blue light and control, as shown in Fig. 2b. Our findings were similar to Shen et al. (2013) in satsuma mandarin, mushroom (Jiang et al., 2010), blueberries (Wang et al., 2009), and grape (Nassarawa et al., 2022a, b), who found that red light irradiation increased flavonoid content. Shao et al. (2020) also noted that red light treatment for 20 days ($500 \mu\text{mol m}^{-2} \text{ s}^{-1}$) at $23 \text{ }^\circ\text{C}$ had significant stimulating impacts on the increase of total flavonoid content in lettuce. We believe that flavonoid biosynthesis is a complicated process that can be inclined by various factors, including storage conditions and postharvest treatments, which may influence total flavonoid content changes during storage.

Anthocyanins are a group of flavonoids found naturally in plants liable for fruit color (Azuma et al., 2019). Environmental conditions cause the proliferation of anthocyanin by major groups of higher plants (Xu et al., 2014a). Our present study found that red light irradiation has higher anthocyanin content during storage in postharvest grape than those in blue light treatment and control (Fig. 2c). This demonstrated that red light could be a viable method for increasing anthocyanin accumulation and maintaining a postharvest grape product of high quality after harvest. Similar findings showed that red light treatment increases the anthocyanin content in red cabbage (Wu et al., 2017). Also, red light radiation enhanced the accumulation of anthocyanin in postharvested grape at 3 days (Azuma et al., 2012). Similar findings were obtained by Choi et al. (2015), who found that the irradiation of red-light in treated grape was significantly higher than those in control. To study more about the impact of red and blue light irradiation on phenolic biosynthesis-related enzymes, the enzymes involved in the phenylpropanoid pathway were also investigated. The phenylpropanoid pathway is made up of two enzymes called PAL

and TAL. PAL catalyzes L-phenylalanine to *trans*-cinnamic acid conversion. TAL works similarly to PAL as it transforms L-tyrosine to ammonia and *p*-coumaric acid (Shing et al., 2016). PAL and TAL were also exposed to be the first essential enzymes in the phenolic metabolism catalyst for converting phenylalanine to cinnamic acid. Cinnamic acid degrades into phenolic compound (Li et al., 2014). Thus, in our current study, PAL and TAL were enhanced by red and blue light during postharvest storage, with the highest recorded under red light treatment (Fig. 3a, b). The results showed that red light treatment was more efficient in enhancing the activities of PAL and TAL, which suggested that red light could potentially improve and sustain PAL and TAL activities. These findings demonstrate that an increase in phenolic compounds was associated with an increase in PAL and TAL activities. These results were positively interrelated to phenolic compound, and Pinto et al. (2016) found a similar relationship between PAL, TAL, and phenolic compound accumulation in grape berries. Similar findings have been reported by Pombo et al. (2011), who noted that red light improved the activities of PAL and TAL in treated strawberries. Similarly, table grape treated with red and blue light yielded similar results, in which red light stimulated the expression of phenolic biosynthesis-related enzymes (Crupi et al., 2013). Study shows that red light treatment enhanced the activities of PAL and TAL, demonstrating that PAL and TAL are active in response to phenolic compound treatments (Pombo et al., 2011). C4H and 4-CL are also essential regulators in the phenylpropanoid pathway, contributing to anthocyanin synthesis (Li et al., 2014). The mediating activities of anthocyanin metabolic enzymes can control anthocyanin accumulation. In our current study, C4H and 4-CL decreased during storage (Fig. 3c, d). We found that red light exposure was more effective than blue light exposure in enhancing C4H and 4-CL activities. The findings were consistent with those of the previous study that red light treatment enhanced enzyme activities in strawberry fruit (Xu et al., 2014b). We hypothesized that our findings showed that red and blue light treatment can regulate phenolic biosynthesis-related enzymes, resulting in an increase in phenolic compound in grape berries during storage.

During the postharvest storage of fruit, soluble sugars play an important role in cell signaling and resistance to external stress factors (Sun et al., 2014). Previous research has shown that glucose, fructose, and sucrose are the three main sugar components in grape fruit and sucrose stimulates the activity of certain antioxidant enzymes that eliminate reactive oxygen species (ROS) (Li et al., 2017). In our current study, red light treatment had the highest concentrations of glucose, fructose, and sucrose in grape berries compared with those in blue light (Fig. 4a–c). Our findings showed

that irradiation with red and blue light at an intensity of 500 lx efficiently regulated and promoted the conversion of sucrose to hexose in vacuoles. Li et al. (2017) reported that red light treatment enhanced the activity of sucrose metabolism-related enzyme activities, leading to a higher level of soluble sugar in tomato fruit. Similar findings were also reported in Chinese bayberry fruit (Shi et al., 2016) and lime (Kaewsuksaeng et al., 2011). The reversible conversion of sucrose to fructose, glucose, and uridine diphosphate glucose (UDPG) can be catalyzed by SS-synthesis and SS-cleavage. The primary purpose of sucrose synthesis is to produce sucrose. Sucrose phosphate synthase (SPS) is an enzyme involved in the irreversible conversion of UDPG and 6-phosphate-fructose to sucrose. Our recent study showed that SS-synthesis was higher under the blue light, while SS-cleavage and acid invertase activities were higher under red light treatments than those in control (Fig. 5a–c); this was concurrent with high soluble sugar levels in treated berries. Similar results were also observed in Chinese bayberry fruit (Shi et al., 2016) and grape (Rodyoung et al., 2016). We hypothesized that higher enzyme activity in sucrose synthesis contributed to maintaining the quality of grape berries during postharvest storage.

In higher plants, GABA is mostly metabolized through a short mechanism called GABA shunt. GAD and GABA-T are two important enzymes in the GABA shunt. The GABA-T pathway converts glutamate to succinic semialdehyde after being catalyzed by GAD (Khan et al., 2021). Our findings revealed that blue-light treatment increased GABA content than red-light and control fruit during storage at 4 °C (Fig. 6a). However, the higher GAD activity was observed in red light compared to blue-light and control fruit (Fig. 6b). Nevertheless, control sample had the highest GABA-T activity than treated samples (Fig. 6c). Compared with control fruit, treated samples inhibited the GABA-T activity. Based on these findings, we hypothesize that red and blue light treatment at 4 °C can impact the GABA shunt pathway by promoting GAD activity and inhibiting GABA-T activity, resulting in GABA accumulation, which could be an adaptive mechanism for protecting against senescence from grape berries. Also, higher GABA content and GAD activity in grape berries during 4 °C storage, which leads to phenolic compound accumulation, could be due to inhibition of GABA-T, which is responsible for supplying skeleton carbon in prolyl endopeptidase (PEP) form and is linked to Er4P, which may act as a starter of the phenylpropanoid pathway. Yan et al. (2021) reported that UV-C LED exposure increased GABA content and GAD activity while inhibiting GABA-T activity in tomato fruit. The increase in the GABA content in tomato fruit stored under blue-light treatment was reported by Dhakal and Baek (2014b).

Conclusion

The current study investigates the positive influences of red and blue light radiation on postharvest grape berries quality during storage. The quality characteristic was maintained by red or blue light treatment during storage. Blue light treatment had less influence on phenolic compound during storage than red light treatment. Red light treatment at 500 lx was more efficient in enhancing phenolic biosynthesis-related enzymes than blue light treatment. The red light treatment was also efficient in stimulating soluble sugars and maintaining higher SS-cleavage and acid invertase in grape berries, while blue light treatment increased SS-synthesis during storage. Our results also showed that treated samples increased GAD activity by inhibiting GABA-T activity, which led to GABA accumulation. In summary, our findings suggest that irradiation with red or blue light treatment is likely a useful technique for maintaining sugar metabolism and the γ -aminobutyric acid shunt pathway, improving grape berries' quality and extended postharvest storage life.

Author Contribution SSN: writing—first draft, revision and editing, conceptualization, data curation, formal analysis. ZL: conceptualization, funding, resources, review, and editing.

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Data Availability Statement On reasonable request, the datasets generated and/or analyzed during the current study are available from the corresponding author.

Declarations

Conflict of Interest The authors declare no competing interests.

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