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# Preharvest UV-B Treatment Improves Strawberry Quality and Extends Shelf Life

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**Abstract:** Postharvest ultraviolet B (UV-B) radiation has been used to control pathogen incidence on fresh produce, but little attention has been paid to preharvest UV-B effect on strawberry fruit quality and storage. In this study, strawberry (*Fragaria × ananassa* Duch. cv Albion) plants grown in greenhouse were irradiated with UV-B lamps with an intensity of 0.7362 J/s m$^2$ for 1 and 2 h every day from 5–7 pm after flowering. Fruits were harvested at red stage for quality evaluation. The results indicated that the preharvest UV-B-treated fruits had lighter color (increased L*) than the control. Total soluble solids (TSS), total phenolics content (TPS) and total anthocyanin content (TAC) of UV-B-treated fruits were higher than for the control fruits. There were no significant differences in any of the quality traits between UV-B one-hour and two-hour treatments. We further evaluated the fruit quality when stored at 5 °C on day 7 and day 14. Compared to untreated control, UV-B-treated fruits retarded decrease in L*, TSS, TPS, TAC and firmness, and reduced fruit decay. Examination of expression of genes related to UV-B signaling indicated that *HY5* was the major component of UV-B signaling during the green and white stages. However, anthocyanin genes were highly responsive to UV-B treatment during the red stage. Our results suggest that utilization of a low dose of UV-B radiation during the growth stage can improve strawberry fruit quality, and extend shelf life. This research facilitates the utilization of preharvest UV-B treatment for improving fruit quality in controlled environment agriculture.

**Keywords:** *Fragaria × ananassa*; ultraviolet radiation; fruit quality; shelf life; postharvest

## 1. Introduction

Ultraviolet radiation (UV) is a form of electromagnetic radiation with a light spectrum from 200 to 400 nm. It usually includes three classes, UV-A, UV-B and UV-C, based on the wavelength. UV-C is short-wave UV, below 280 nm, that can kill pathogens and trigger the biosynthesis of secondary metabolites in plants [1,2]. However, UV-C often causes damage to plants, too [3]. On the other hand, UV-B (280–315 nm) radiation affects many aspects of plant growth and development, such as control of plant height and yield, and acts at the molecular level on signal transduction and gene expression [1,4]. The mechanism of UV-B perception and signal transduction involves UV Resistance locus 8 (UVR8) and the bZIP transcription factor *Elongated Hypocotyl 5* (*HY5*) [5]. UVR8 itself is a constitutively expressed protein that functions as a UV-B photoreceptor regulating *HY5* expression [5].

Postharvest UV-B treatments have been used to control postharvest diseases, extend shelf life, and improve nutritional benefits of many vegetables and fruits [6,7]. Exposure to low-dose UV-B radiation has been shown to reduce broccoli weight loss, delay yellowing, and improve chlorophyll retention [8]. In grapes, a higher level of resveratrol was identified in the skins of UV-B-treated grapes stored for 7 d under cold conditions [9]. UV-B radiation can stimulate the expression of genes involved in anthocyanin biosynthesis in blueberry fruit [10]. In tomato, postharvest UV-B irradiation maintained fruit sensory qualities and enhanced antioxidant capacity during storage [11]. The content of cyanidin 3-glucoside, quercetin 3-glucuronide and kaempferol 3-glucoside in strawberry increased with solar

UV-B treatment [12]. The beneficial effect of UV-B on anthocyanin accumulation also has been demonstrated in various fruits, including apples [13], grapes [9], pears [14], and blueberries [15]. Expression of several anthocyanin biosynthetic genes, such as flavonol synthase (*FLS*) and hydroxycinnamoyl CoA: shikimate hydroxycinnamoyl transferase (*HCT*), was upregulated by UV-B [16–19]. However, limited research has been performed on the effects of preharvest UV-B application.

Strawberry is one of the most popular horticultural crops due to its characteristic flavor and nutraceutical value. Strawberry fruits are rich in natural antioxidants, such as anthocyanins [20], which are beneficial for human health [21]. Most strawberries grow in open fields. However, as the cost of growing fruit in open fields increases due to water shortages and challenges with pests, as well as increasing consumer demand regarding fruit quality, the strawberry production in controlled environment is increasing, especially in urban areas [22]. The controlled environment agriculture provides opportunities to optimize the fruit development including light control to obtain the desired produce. In this study, we utilized UV-B irradiation to treat strawberry fruits during the growth stage in a greenhouse and investigated its impact on fruit quality and shelf life.

## 2. Materials and Methods

### 2.1. Plant and Fruit Materials

Strawberry plants (*Fragaria* × *ananassa* Duch. L. cv. Albion) were grown in a greenhouse at 26 °C with 14 h light (from 6 am to 8 pm) every day. The average light intensity over the plant growth period was about 140 µmol/s m$^2$, and no UV-B irradiation was detected inside the greenhouse. Fruits were harvested at three developmental stages based on size and color of receptacles and achenes: green stage, young fruit with green achenes and receptacle; white stage, white receptacles and tanning achenes; red stage, full size fruit with fully red receptacles.

### 2.2. UV-B Treatments

Strawberry plants were irradiated with UV-B lamps (280–320 nm, Q-Panel 313, Cleveland, OH, USA). The lamps were ~30 cm above the plants with an intensity of 0.7362 J/s m$^2$ for 1 and 2 h every day from 5–6 or 5–7 pm after flowering. The experiment was completely randomized with 3 treatments: (1) no UV-B radiation (control); (2) UV-B for 1 h; and (3) UV-B for 2 h. Fruits at the red stage were harvested and used for postharvest quality trait analyses.

### 2.3. Analysis of Color, Texture, Water Loss and Decacy Incidence

Fruit surface color was determined with a Chroma meter CR-400 (Konica Minolta Sensing, Inc., Tokyo, Japan) as described [23]. The chromaticity coordinates are: L* for lightness (black = 0, white = 100), a* for red/green color (redness > 0, greenness < 0) and b* for yellow/blue color (yellowness > 0, blueness < 0). Chroma (C) was calculated using the equation $C = \sqrt{(a^*)^2 + (b^*)^2}$. A total of 24 fruits from each treatment were measured.

Firmness was assessed as the maximum penetration force (N) reached during tissue breakage using a TA-XTplus Texture Analyzer (Texture Technologies Corp, New York City, NY, USA) with a 10-mm-diameter cylinder probe [23]. The penetration depth and the cross-head speed were 3 mm and 1 mm s$^{-1}$, respectively. Fruits were sliced into halves, and each half was measured in the central zone. Eighteen fruits of each treatment were used for fruit firmness evaluation.

Water loss and decay incidence were calculated on the fruit weight changes and fruit decay ratios during storage. Twelve fruits were put in a clear plastic egg carton. A total of 120 fruits (10 cartons) were used for each treatment. The fruits were kept at a temperature of 5 °C and 75% relative humidity.

### 2.4. Determination of Quality Attributes

Total phenolic content (TPC) was evaluated following a method described previously [24], with modifications. Briefly, 100 mg of lyophilized fruit powder was added into 5 mL of 80% methanol, and centrifuged at $6650\times g$ for 10 min. Then, 250 µL aliquots of the supernatants were mixed with 25 µL of 0.1% Fast Blue BB solution and 25 µL of 5% NaOH. The absorbance of samples was measured at 420 nm using a high-performance microplate spectrophotometer (Agilent, Santa Clara, CA, USA). Results are expressed as milligrams of gallic acid equivalent (mg GAE) per gram of dry weight. The measurements were performed in triplicate.

Total anthocyanin contents (TAC) were assessed using a pH differential method [25]. Absorbance at 510 nm and at 700 nm in buffer at pH 1.0 and pH 4.5 was calculated using $A = (A510 - A700)\,pH1.0 - (A510 - A700)\,pH4.5$ with a molar extinction coefficient for pelargonidin-3-glucoside of 15,600. Results are expressed as milligrams of pelargonidin-3 glucoside equivalent (mg PGE) per gram of dry weight. The measurements were performed in triplicate.

Total soluble solids (TSS) were estimated as described [23] with an Atago PR-101 digital refractometer (Atago Co., Ltd., Tokyo, Japan) at 20 °C. The measurements were performed in triplicate.

### 2.5. RNA Extraction and RT-qPCR

Total RNA was extracted from frozen tissue using the RNeasy Plant Mini Kit (Qiagen, Germantown, MD, USA). Reverse transcription reaction and quantitative real-time PCR (RT-qPCR) was essentially performed as described [26]. One µg of total RNA was used to synthesize cDNA with iScript kit (Bio-RAD, Hercules, CA, USA), and PCR analysis of cDNA was conducted on a CFX96 Real-Time System (Bio-RAD, Hercules, CA, USA). The gene-specific primers were designed with Primer3 software (http://bioinfo.ut.ee/primer3-0.4.0/primer3/ (accessed on 1 January 2023) from their coding regions, where they share low homology between the gene paralogues. The primer pairs used in this study are listed in Table 1. All the reactions were run in triplicate from three independent experiments. Relative quantification of specific genes was determined using the cycle threshold $2^{\Delta\Delta Ct}$ method. Relative expression levels were normalized based on the housekeeping gene *FaACTIN* (JN616288).

**Table 1.** List of primers used for gene expression analysis.

| Gene Name | Gene ID | Forward Sequence (5′-3′) | Reverse Sequence (3′-5′) |
|---|---|---|---|
| *FaACTIN* | JN616288 | TCACCACCACTGCTGAACGGGA | TGCAAGCTTCTCCTTCATGTCACGG |
| *FaHY5* | KP984791 | TGTTGCAAGACCAAGCCACGAGC | AGACCTCTCACTGCTGGAAGGCA |
| *FaUVR8* | KU647690 | AGGGAAGATTTGGGTGTCACCGTCA | GCCGTATGCGTTTCCCGTCGGTTT |
| *FaMYB10* | EU155162.1 | GACGGCTTCATACGCAAAGA | TCTGTGGTGGTTCTGTTGGT |
| *FaPAL1* | KX450226 | GCCAAGGAGGAGGACTACTACATGACC | TCCGCCGCCAAGTTCCAGTTCA |
| *FaCHS1* | AY997297 | ACGGCCCAAACTATCCTTCCCGA | GCCCAACTTCACGAAGATGCCCGT |
| *FaF3H1* | AY691919 | CGGTGCAGGATTGGCGCGAGA | CTGCTGTGGTTTGAGTTCACCAC |
| *FaDFR1* | KC894047 | GCCGGAAAGTAAAGATGACTGG | GCTTCATTTCCAGTGAGTGGTG |
| *FaANS* | AY695817 | TCGAGAGTTTGGCCAGCAGCGGGAT | TGAGGCCCTTCGGTGCTCTTCTCGT |
| *FaUGT1* | LC312710 | GGAATCATCTTCGGAAACTTGG | TGCACTTGCTGGTGGTTCTAGT |
| *FaFLS* | DQ087252 | CCCGGCGGAGTACATTAGGTCGGA | ACGGTGGTGATTCCCGGCTGCT |
| *FaLAR* | DQ087253.1 | GCAATATCACGGCTACTTGTGC | GAAAATGCAGCTTCCTTGCTTT |
| *FaANR* | DQ664192.1 | CCGATGAAAATGATTGGTCTGA | GTCTGGAGTGAGAGAAGCACCA |

HY5: ELONGATED HYPOCOTYL 5; UVR8: ultraviolet-B receptor 8; PAL1: Phenylalanine ammonia lyase 1; CHS1: Chalcone synthase 1; F3H1: flavanone 3-hydroxylase 1; DFR1: Dihydroflavonol 4-reductase 1; ANS: Anthocyanidin synthase; UGT1: UDP-glucose glucosyltransferase 1; FLS: Flavonol synthase; LAR: leucoanthocyanidin reductase; ANR1: Anthocyanidin reductase.

### 2.6. Statistical Analysis

SPSS (SPSS for Windows, SPSS Inc., Chicago, IL, USA) was used for statistical analysis. Two-way ANOVA was performed, and Tukey–Kramer post hoc test at a 95% confidence

level was used to evaluate the effect of postharvest storage and the UV-B irradiation at a significance level of 0.05 ($p < 0.05$).

## 3. Results

### 3.1. Effect on Fruit Appearance

Both UV-B 1 h and UV-B 2 h treated plants exhibited similar growth to control (no treatment). Ripe fruits (red stage) were collected and used for all analyses. The individual fruit weight ranged from 12 to 14 g, and the average single fruit weight for UV-B 1 h, UV-B 2 h and control were 12.9, 13.0 and 12.9 g, respectively. As shown in Figure 1, there were no clear differences in fruit size between UV-B treatments and control, either. As for fruit appearance, at day 0 (harvest day), there were no significant differences in fruit redness (a*), blueness (b*) and chroma (C) (Figures 1 and 2). However, the lightness (L*) value of UV-B-treated fruits was significantly higher than the no treatment control, suggesting that the UV-B-treated fruits maintained a fresher appearance, as darkening/dulling is an indication of senescence in strawberry fruits.
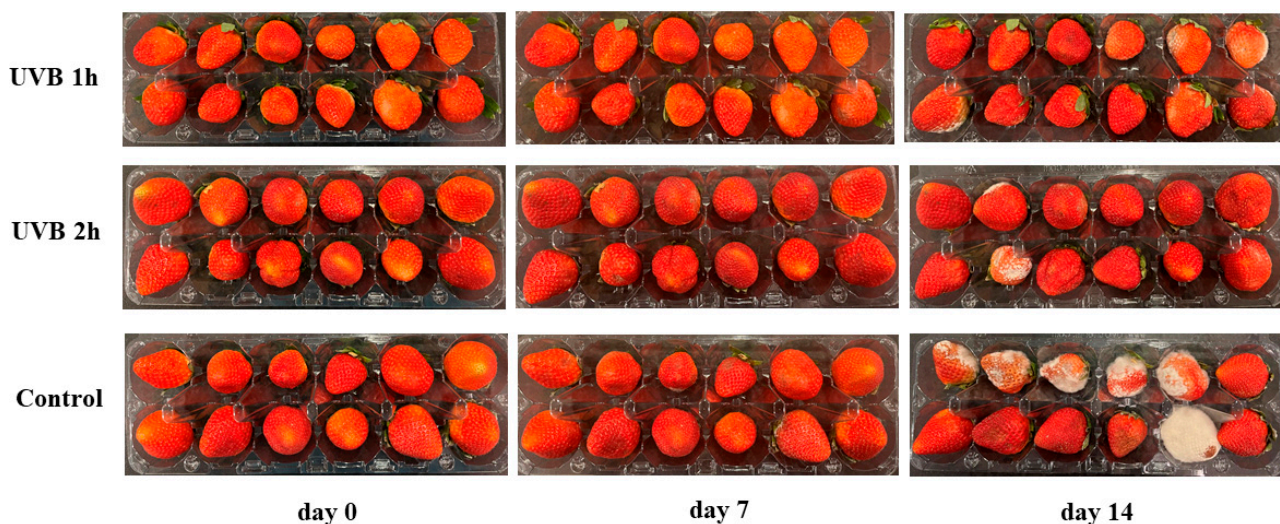


**Figure 1.** Effect of preharvest UV-B treatment on fruit appearance and shelf life. Red fruits were harvested from plants treated with different durations of UV-B (0.7362 J/s m$^2$) treatment and control (no treatment). Fruits were stored at 5 °C and 75% relative humidity. Photos were taken on day 0 (harvest day) and days 7 and 14 after harvest.

During the storage period, L*, a*, b* and C of strawberry fruit gradually decreased (Figure 2). However, fruits receiving UV-B treatment for one or two hours had higher L* and a* than the control. There was no significant difference between one- and two-hour UV-B treatments. Blueness (b*) and chroma (C) also gradually decreased during storage. However, UV-B treatments did not show a significant influence on them. Therefore, UV-B-treated fruits had greater lightness and a redder surface color than the no-treatment control.

### 3.2. Effect on Fruit Quality Traits

The total soluble solids (TSS), total phenolic content (TPC) and total anthocyanin content (TAC) in UV-B-treated fruits were significantly higher than in untreated fruits on harvest day (day 0) (Figure 3). However, there were no significant differences in fruit firmness between UV-B-treated and untreated fruits on harvest day (day 0).
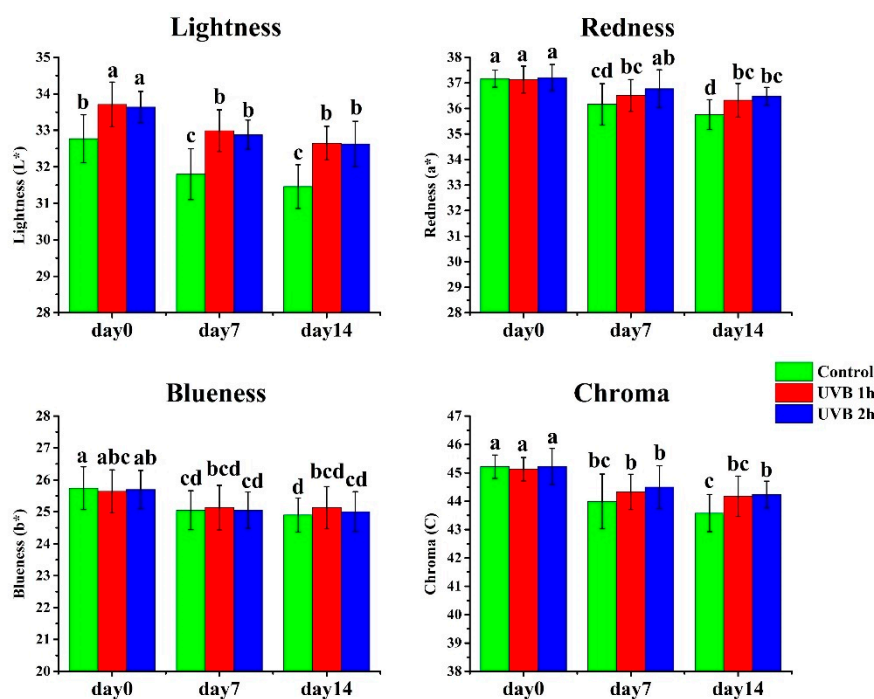
**Figure 2.** Effects of UV-B treatment on surface color of strawberry fruits. The data are based on ten biological replicates. * $p < 0.05$.
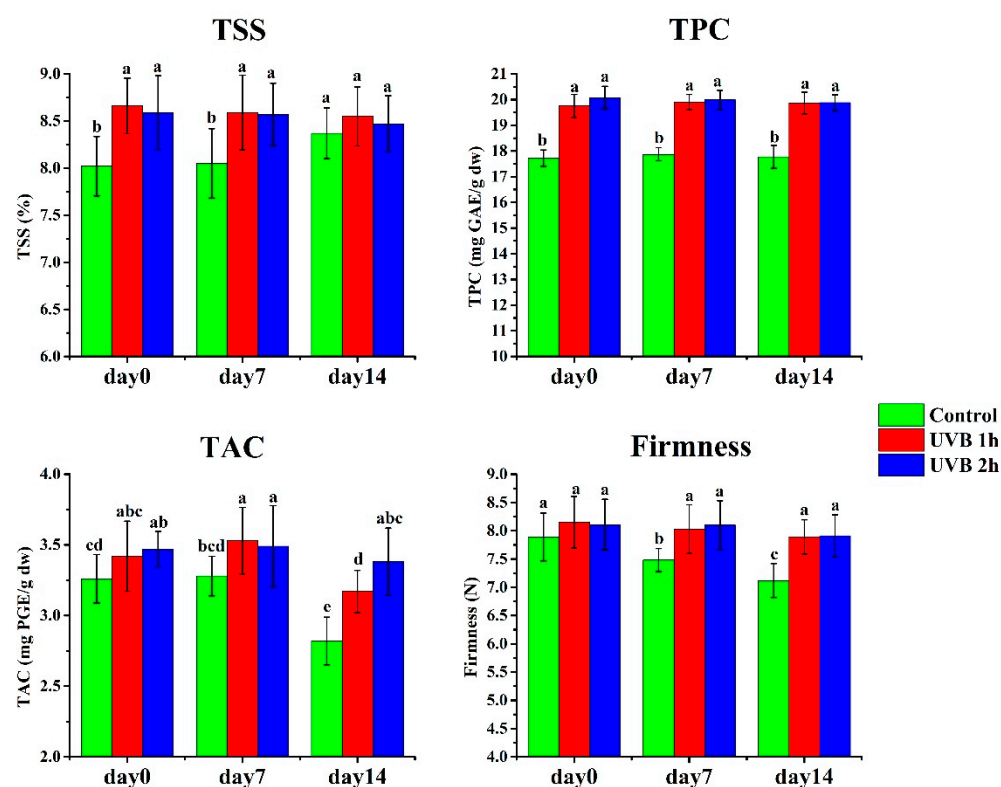


**Figure 3.** Effects of UV-B treatment on strawberry fruit quality. TSS, total soluble solids (Brix%); TPC, total phenolic content (mg GAE/g dry weight)), and TAC, total anthocyanin content (mg PGE/g dry weight). The data are based on ten biological replicates.

During the 14-day storage period, TSS of fruits receiving 1 h and 2 h UV-B treatments was significantly higher than the control fruits on day 7, while no significant differences in

TSS were observed on day 14. In comparison, TPC and TAC in 1 h and 2 h UV-B-treated fruits were significantly higher than the control fruits on both days 7 and 14. As for fruit firmness, there were no significant differences on day 0, but it steadily declined during storage. However, UV-B-treated fruits were firmer than the untreated fruits all the time. UV-B-treated fruits had higher TSS, TPC and TAC, and maintained greater firmness than control fruits during storage.

In addition, we observed the occurrence of fruit decay (mainly *Botrytis*) in control fruit on day 5, with a decay ratio of 10% on day 7, reaching 43.3% on day 14 (Figures 1 and 4). In contrast, the UV-B-treated fruits, especially those treated with 2 h UV-B daily, exhibited a lower decay ratio than the controls. On day 7, one- and two-hour UV-B-treated fruits had decay ratios of 7% and 3%, respectively. On day 14, the decay ratio for one- and two-hour UV-B-treated fruits were 33% and 25%. These results indicate that preharvest UV-B treatments can dramatically reduce fruit decay incidence during storage and extend shelf life.
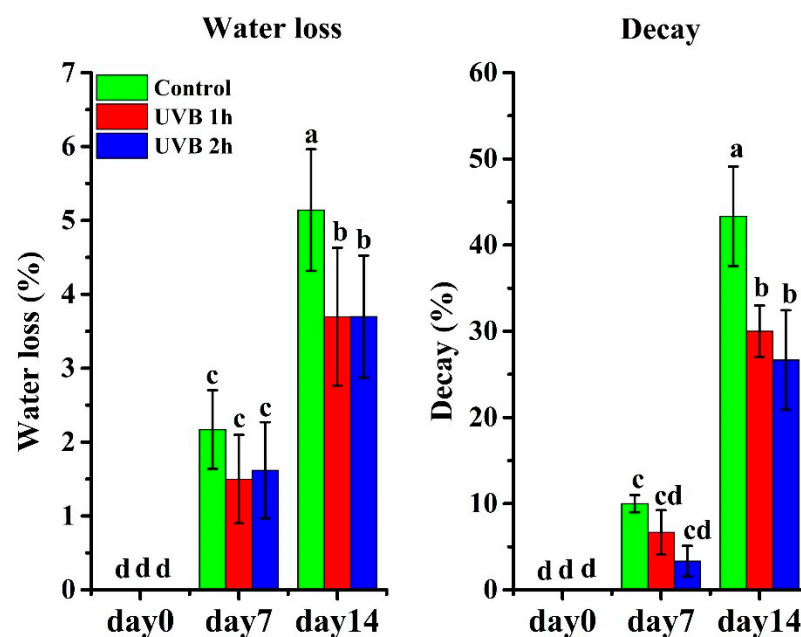


**Figure 4.** Effects of UV-B treatment on water loss and decay incidence of strawberry fruits. The data are based on ten biological replicates.

### 3.3. Expression of UV-B Responsive Genes in Fruits during Growth Stage in Response to UV-B Treatment

To investigate how fruits respond to UV-B treatments during fruit development, we treated fruits at green, white and red stages with UV-B and examined the expression changes in the genes involved in the UV-B pathway. As shown in Figure 5, the expression of the *FaHY5* gene was significantly induced by the UV-B treatment in green- and white-stage berries, while the expression level in red berries was the lowest, and had no obvious response to UV-B treatment. We also examined the expression pattern of *FaUVR8*. In all berry stages, *FaUVR8* was constitutively expressed and showed no response to UV-B treatment. The results were consistent with previous findings in grape, tomato and *Arabidopsis* showing that *UVR8* does not respond to UV-B and *FaHY5* shows a significant UV-B regulation [5,19,27].
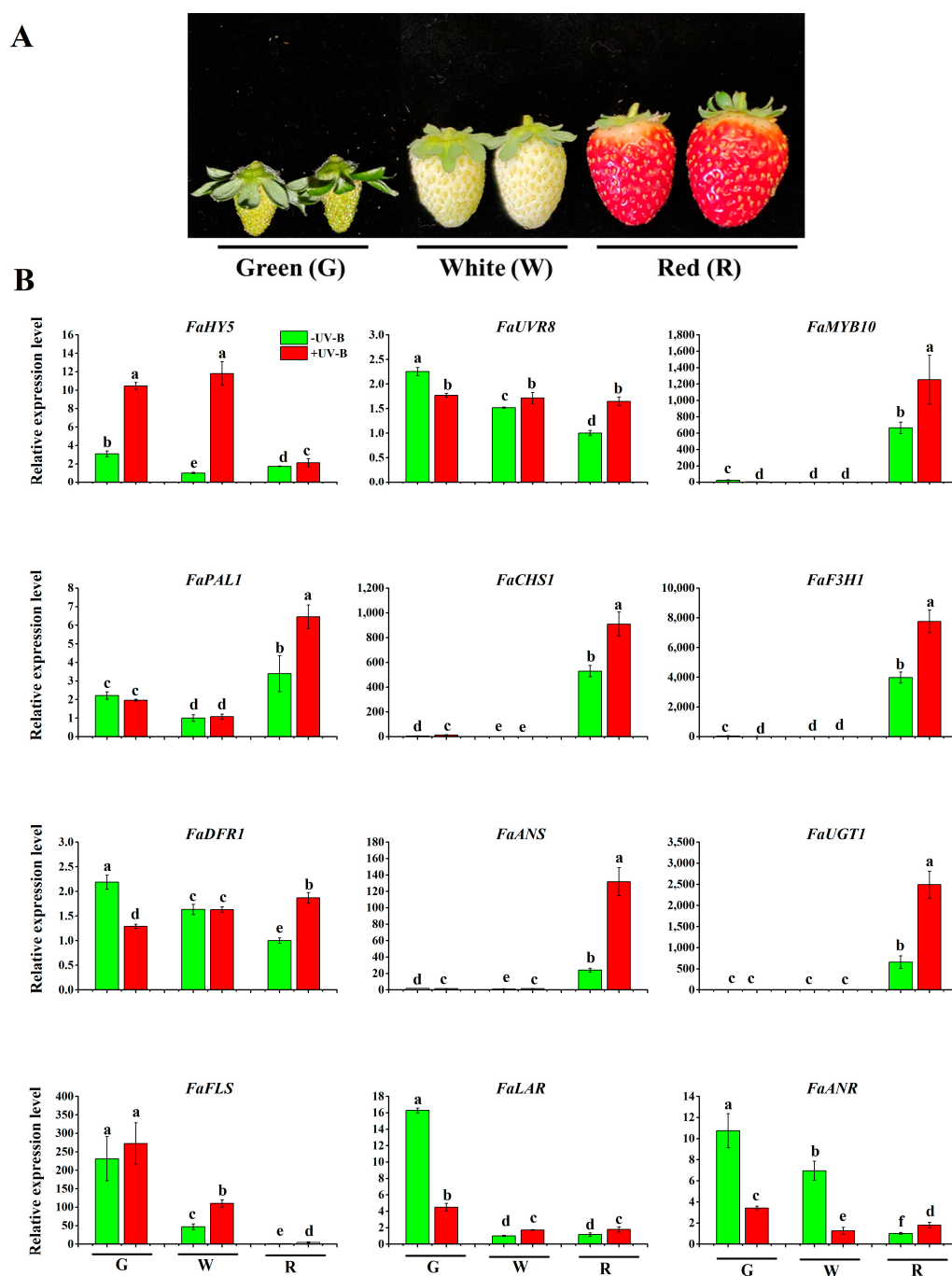
**Figure 5.** Expression patterns of UV-B signaling pathway and anthocyanin biosynthetic genes in strawberry fruits after UV-B 1 h treatment. (**A**) Fruit images at different stages. (**B**) Comparison of gene expression levels. G: fruit at the green stage; W: fruit at the white stage; R: fruit at the ripe stage; RNA levels were quantified and normalized to the level of *FaACTIN*. Values are means ± SD of three replicates. The data are based on three biological replicates.

We further analyzed the expression changes in genes involved in the phenylpropanoid pathway, as well as flavonoids, anthocyanins and proanthocyanidins biosynthesis, because these genes determine fruit color and phenolic content (Figure 5). *MYB10* is a key transcription factor in regulating flavonoid and anthocyanin biosynthesis. It is highly expressed in the red stage, and showed a positive response to UV-B treatment. In the general phenylpropanoid pathway, expression of *PAL1* was detected in all stages. However, it had the highest expression in the red stage, and UV-B further boosted its expression.

As for *CHS1 and F3H1*, they were dominantly expressed in the red stage. UV-B treatment further stimulated its expression level. In the flavonoid pathway, there are three expression patterns. First, *FaLAR* and *FaANR*, which were involved in proanthocyanidin biosynthesis, were highly expressed in the green stage, and hardly detected in the red stage. UV-B treatment reduced their expression. Second, *FLS* for flavonoid biosynthesis followed a similar expression pattern to that of *LAR* and *ANR*. However, UV-B stimulated its expression. Last, *ANS* and *UGT1* for anthocyanin biosynthesis exhibited the highest expression in the red stage, while almost no expression occurred during the green and white stages. UV-B treatment boosted their expression levels by 2–4 folds. These results demonstrate that UV-B can increase anthocyanin biosynthesis in the red stage and flavonoid biosynthesis in the green and white stages.

## 4. Discussion

Flesh fruits, such as strawberry, are perishable, and their postharvest quality and shelf life are greatly affected by preharvest practice. In this study, we found that the long-term preharvest application of low doses of UV-B improved the fruit quality and shelf life of strawberry fruits.

Plants can perceive UV-B using the UV-B photoreceptor *UVR8*, which is linked to a specific molecular signaling pathway and leads to UV-B acclimation [5]. In general, the basic leucine zipper (bZIP) transcription factor *HY5* plays a significant role in relaying UV-B signaling [28]. The interaction between UVR8 and HY5 is confirmed to play a well-characterized and central role in the UV-B signaling pathway according to *Arabidopsis* studies [5]. In this study, we observed that *FaHY5* was induced significantly in green and white stages. However, the expression of *FaHY5* was relatively low in the red stage. This phenomenon has been reported in other crops [29–31]. For example, Loyola et al. (2016) reported that *VvHY5* was induced in response to low and high UV-B irradiance in green-stage berry skins [30]. *VvHYH* (*HY5 homologue*) expression increased in response to UV-B at ripening, and more strikingly by the low radiant exposure treatment before ripening. Li et al. (2021) [31] reported that preharvest long-term UV-B radiation can increase *HY5* in the green stage, but not in the mature stage, in blueberry fruit. *HY5* may play a key role in responding to UV-B in promoting strawberry fruit development before the red stage.

In the red stage, strawberry fruits undergo color change and the accumulation of anthocyanins, with anthocyanin biosynthesis genes being highly expressed. Those anthocyanin genes are all upregulated by UV-B treatment, while most of them have low expression in the green and white stages. Therefore, *HY5* may not be the major component for high anthocyanin accumulation induced by UV-B in strawberry fruits. Li et al. (2021) [31] suggested that the abscisic acid (ABA) pathway could be involved in UV-B perception and anthocyanin accumulation in blueberry fruit, since UV-B irradiation boosted ABA biosynthesis [31,32]. In strawberry, exogenous ABA application can promote *MYB* expression, accelerate fruit ripening, and increase anthocyanin content [33,34]. Kadomura-Ishikawa et al. (2015) suggested that light and ABA independently regulated *FaMYB10*. In this study, *FaMYB10* and anthocyanin structural genes were upregulated by UV-B treatments. It is still unclear whether UV-B irradiation can increase ABA biosynthesis in strawberry [33].

The abundant phenolic and anthocyanin compounds are regarded as important beneficial antioxidants in strawberries [20]. Postharvest UV-B displayed positive effect on total phenolic and anthocyanin in grapes [9], apples [13] and pears [14]. In this study, the UV-B-irradiated strawberry fruits were found to be redder during the growth stage than control, and UV-B treatment was correlated with high anthocyanin content, too. In addition, preharvest UV-B treatment also enhanced the TCC or sugar content of strawberry fruit, possibly by increasing the sugar transport to fruits. Li et al. (2021) reported that preharvest long-term exposure to UV-B radiation of blueberry plants promoted fruit growth, sugar and anthocyanin contents [31]. In peach, UV-B irradiation enhanced anthocyanin content and sugar accumulation in fruit by increased sorbitol transport to fruit from leaves [35]. UV-B also increased the flavonoid pathway genes and flavonol content of grape berries in

a controlled environment [36]. Thus, it could be a general phenomenon that preharvest UV-B promotes the accumulation of sugar and phenolics in fruit. Furthermore, we also observed that preharvest UV-B irradiation has a significant maintenance effect on TAC, TPC and firmness of fruits during storage, as compared to untreated fruits. These events combined, especially high antioxidants, likely contributed to the lower occurrence of fruit decay in strawberry for UV-B-treated fruits. Our study is the first to examine changes in postharvest quality and shelf life in strawberry fruits in response to UV-B treatment during the growth stage.

It should be noted that UV-C (200–280 nm) is often used for preharvest and postharvest treatment of fruits and vegetables, too [1,2,6]. However, UV-C has some extremely inhibitory and damaging effects on plant cells, although it is more effective for postharvest treatment to reduce fungal infections compared to UV-B treatment [3,6]. For example, UV-C inhibited quality formation in strawberry fruit at large green stage during plant growth [34]. Instead, UV-B causes much less damage to plants. We did not observe any inhibitory effect of UV-B treatment on strawberry plant growth and fruit development.

In summary, long-term preharvest irradiation with UV-B ($0.7362$ J/s m$^2$) had a pronounced effect on improving strawberry fruit color, phenolic and anthocyanin content, and maintaining fruit firmness during postharvest storage, thus extending shelf life. No significant differences were observed between 1 h and 2 h UV-B treatment. Our investigation revealed that that UV-B signal was mainly modulated through the upregulation of *HY5* associated with UV-B signal transduction pathway on the early stage of strawberry fruit development. On the red stage, UV-B radiation significantly stimulated the anthocyanin genes independent of *HY5*. Although most strawberries grow in open fields, and it is costly to add UV-B treatment in fields, the production of strawberries in controlled environments grows rapidly, particularly in urban areas [22]. This makes it feasible to manipulate plant growth conditions, such as through UV light management. Thus, this study provides an effective approach for utilizing preharvest UV-B radiation to improve strawberry fruit appearance and nutritional quality and extend shelf life in controlled-environment agriculture.

**Author Contributions:** Conceptualization, T.Y.; methodology, X.Z. and F.T.; writing—original draft preparation, X.Z.; writing—review and editing, T.Y. and F.T.; visualization, X.Z., F.T. and T.Y.; supervision, T.Y.; project administration, T.Y. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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