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Early postharvest application of LED lighting enhances strawberry quality during storage

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ABSTRACT

Strawberry (*Fragaria* × *ananassa* Duch.) perishability challenges postharvest quality retention. Traditional postharvest methods have limitations, and early harvesting to extend shelf-life often compromises sensory attributes. This study investigated whether 24 h or 48 h treatments performed at the beginning of postharvest with Red, Blue, Far-Red, or UV-A light-emitting diode (LED) light could improve 'Elsanta' strawberry quality during subsequent 7-day storage at suboptimal temperature (5 °C). Fruit quality attributes, including firmness, weight loss, soluble solids content (SSC), titratable acidity (TA), anthocyanins, and volatile organic compounds (VOCs), were assessed. While LED treatments did not significantly affect firmness, they generally increased weight loss compared to dark controls (particularly after 48 h Blue/Red/Far-Red exposures). Light effects on SSC were complex and duration-dependent. Notably, all LED treatments significantly enhanced total anthocyanin content (especially after 48 h exposure), although instrumental color measurements remained unchanged. Compared to dark controls Blue and Red light (especially after 48 h) significantly increased the concentration of key aroma-related VOCs, for the most esters. In conclusion a brief, early postharvest LED exposure, particularly using Blue and Red light, can trigger lasting beneficial effects, enhancing nutritionally relevant anthocyanins and aroma-defining VOCs during storage at 5 °C. This suggests an 'early signal' mechanism and offers a potentially practical strategy to improve strawberry quality, mitigating negative impacts of commercial early harvesting practices and potentially benefiting other non-climacteric fruits.

1. Introduction

Strawberries (*Fragaria* × *ananassa* Duch.) are globally popular and economically important berry fruits, valued for their unique flavor, aroma, and nutritional profile. However, strawberries are highly perishable, presenting significant challenges for postharvest management and quality retention throughout the supply chain (Giampieri et al., 2012; Priyadarshi et al., 2024).

A key challenge is balancing fruit quality with shelf life. Harvesting immature fruit extends shelf life, but compromises flavor and nutritional value, as fruits may fail to develop optimal aroma, sweetness, or nutrient content (Van de Poel et al., 2014). Conversely, harvesting fully ripe strawberries maximizes quality but drastically reduces postharvest longevity and increases susceptibility to decay and damage (Nunes et al., 2006).

Traditional postharvest methods have limited efficacy. Low-temperature storage (optimally 0–1 °C) slows metabolism but is difficult to maintain consistently, and temperatures below 0 °C can induce chilling injury (Lu et al., 2025). Modified atmosphere packaging (MAP) and controlled atmosphere (CA) storage can delay senescence but may cause off-flavors or uneven ripening in strawberries (Perez et al., 2001; Pelayo et al., 2003; Zhang et al., 2007). Unlike climacteric fruits, strawberries show minimal response to ethylene inhibitors (Jiang et al., 2001), further limiting management options.

Given these limitations, novel postharvest approaches are needed. In this context, priming of defence mechanisms emerges as a promising strategy to enhance the resilience of fruits, and consequently their storability. Priming involves a brief pre-treatment or pre-conditioning

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that activates various physiological mechanisms, preparing the fruit to better cope with subsequent stresses. Examples of priming include treatments with chemical compounds, nutritional substances, or controlled environmental stresses. In the postharvest field, exposure to specific light spectra is gaining attention as an innovative form of priming (Bárcena, Martínez, Costa, 2025). Applying light-emitting diode (LED) technology to enhance fruit postharvest performances is an innovative method gaining attention (Xu et al., 2014a; Nassarawa et al., 2021; Lu et al., 2025). This technology has shown promise across a range of commodities, from delaying senescence in leafy greens and broccoli (*Brassica oleracea*) sprouts (Castillejo et al., 2021) to enhancing phytochemicals in various fruits and vegetables during storage (Mditshwa et al., 2024; Wang et al., 2025). Beyond their energy efficiency and spectral precision, LEDs enable the postharvest modulation of key physiological and metabolic processes, opening new avenues for quality enhancement strategies (Bantis et al., 2018; Castillejo et al. 2021; Perera et al., 2022).

LED lighting can positively influence postharvest fruit quality by enhancing sugar accumulation (e.g., in strawberries under blue light (Xu et al., 2014a; Lu et al., 2025)), and the biosynthesis of phenolic compounds, including anthocyanins (e.g., in strawberries under blue light (Xu et al., 2014b; Zhang et al., 2018)), potentially improving taste color and antioxidant capacity. Aroma modulation through postharvest LED application represents a nascent but promising frontier, with preliminary studies revealing significant changes in volatile emission in different fruit (Gong et al., 2015; Kim et al., 2023; Li et al., 2023), although strawberry-specific data are limited (Campbell et al. 2020).

While most studies investigate the effects of continuous light exposure during the entire storage period, the potential of applying a short, intense light treatment only during the initial postharvest phase remains largely unexplored. This 'early signal' approach presents a significant practical advantage, as it could trigger lasting beneficial metabolic changes without the high energy cost and logistical complexity of illuminating produce throughout the cold chain. The research gap, therefore, lies in understanding whether such a brief photostimulation can induce persistent improvements in quality attributes, particularly under commercially relevant suboptimal storage temperatures. Since the cooling process (i.e., initial refrigeration and maintaining the cool temperature) may account up 19.7 % and 15.7 % of the cumulative energy demand (Boschiero et al., 2019), even the increase of 1° or 2° C of the postharvest temperature may result in a significant reduction of the cost and environmental impacts of cold storage. This approach could offer a novel, energy-efficient strategy to enhance the sensory and nutritional value of fruits like strawberries, mitigating the quality loss often associated with harvesting at commercial maturity to extend shelf-life

Therefore, this study aimed to demonstrate that an early, short light treatment can trigger lasting physiological responses that positively influence fruit quality during subsequent dark storage To this end, we investigated the effects of different LED light spectra (Red, Blue, Far-Red, UV-A) applied for either 24 or 48 h at the beginning of postharvest on key quality parameters (color, firmness, SSC, TA, anthocyanins, and VOC profile) of 'Elsanta' strawberries stored at a suboptimal temperature (5 °C)

2. Materials and methods

2.1. Plant material

Strawberry *(Fragaria* x *ananassa* cv 'Elsanta') fruits were harvested at commercial maturity (> 80 % red surface) and immediately transferred to an experimental climate chamber at the University of Bologna, Italy. Fruits were sorted for uniform size and maturity using a DA Meter (T.R. Turoni®, Italy), a non-destructive device measuring chlorophyll degradation as an indicator of ripeness, selecting those with an index of the absorption (I_{AD}) between 1.75 and 2.05 (Costa et al., 2016). Each fruit was marked with a numbered tag on the stem for tracking during non-destructive measurements.

2.2. Storage conditions, lighting treatments and sampling

A randomized block design (3 blocks) was used. Strawberries (30 fruit per tray) were placed calyx-down in white plastic trays within separate light-proof compartments (0.24 m^2, 0.15 m^3). The climate chamber was maintained at 5 ± 1 °C and 80–85 % relative humidity (RH), simulating suboptimal commercial storage conditions.

Eight LED lighting treatments were applied only during the initial storage period: Red (peak 660 nm), Blue (peak 465 nm), Far-Red (peak 730 nm), and UV-A (peak 350 nm). Each spectrum was applied at two durations: 24 h total (12 h day 1 + 12 h day 2) or 48 h continuous, followed by darkness for the remainder of the 7-day experiment. A dark-stored group served as control. Dimmable LED lamps (Flytech LED Technology®, Italy) were used, and spectral distribution was measured with a CL-500A spectrophotometer (Konica Minolta®, Japan). Photosynthetic Photon Flux Density (PPFD) was set at 80 μmol m^{-2} s^{-1} for Red, Blue, Far-Red, and 30 μmol m^{-2} s^{-1} for UV-A, measured at the fruit surface using a QSO sensor (Apogee Instruments®, USA) connected to a ProCheck reader (Decagon Devices Inc.®, USA).

Non-destructive and destructive measurements (described in 2.3–2.9) were taken at 0, 4, and 7 days. Seven strawberries per block per lighting treatment were used for non-destructive measurementswith the same fruits were measured at each time point (0, 4 and 7 days). For destructive analyses (dry weight, firmness, soluble solids content and titratable acidity), 20 strawberries per lighting treatment per time point were used. Regarding biochemical analysis (anthocyanin and VOC), 20 strawberries per lighting treatment per time point were frozen with liquid nitrogen and stored at −80 °C until the analysis.

2.3. Fruit weight loss

Fruit weight loss was calculated using the following equation:

$$\frac{(m_i - m_f)}{m_i} \quad x \quad 100,$$

where m_i corresponds to the initial mass (0 d) and m_f is the sample mass, evaluated at each time point.

2.4. Color determinations

Surface color was determined with a colorimeter (Chroma Meter CR-400, Konica Minolta®, Tokyo, Japan) through the CIE Lab color space analysis, where the L* component represents the lightness from black (0) to white (100), a* component ranges from green (-) to red (+), and b* component from blue (-) to yellow (+). Four measurements per fruit at the equatorial level were averaged.

2.5. Fruit flesh firmness analysis

Firmness was assessed using a texture analyzer (FTA GÜSS®, Strand, South Africa) with a 3 mm cylindrical probe. Four measurements on opposite sides of the equatorial diameter per fruit were averaged.

2.6. Soluble solids content and titratable acidity

Individual strawberries were juiced using a centrifugal extractor. Juice was filtered. Soluble solids content (SSC, °Brix) was measured using a PAL-1 digital refractometer (Atago Co. Ltd.®, Japan). Titratable acidity (TA, g L^{-1} citric acid equivalent) was determined by automatic titration (Compact-S, Crison®, Italy) of 2 mL juice diluted with 20 mL deionized water to a pH 8.1 endpoint using 0.1 N NaOH. The SSC/TA ratio, an indicator of perceived sweetness balance, was calculated.

2.7. Dry weight

Strawberry were dried at 65°C for 72 h. Dry weight (%) analysis was determined by the following equation:

$$\frac{m_d}{m_f} \quad x \quad 100,$$

where m_d corresponds to the dry mass and m_f is the fresh sample mass, evaluated at each time point.

2.8. Anthocyanins analysis by HPLC-DAD

Fruit extracts were filtered (mesh size 0.45 μm) and analyzed following the method described in Mattivi et al. (2006) using a High Performance Liquid Chromatography (HPLC) Waters 1525 (Waters, Milford, MA) equipped with a diode array detector (DAD) and a Phenomenex (Castel Maggiore, BO, Italy) reversed-phase column (RP18, 250 mm × 4 mm, 5 μm). Anthocyanins were quantified at 520 nm using an external calibration curve with malvidin-3-glucoside chloride as the standard (Sigma-Aldrich). Results were expressed as mg g^{-1} Fresh Weight (FW).

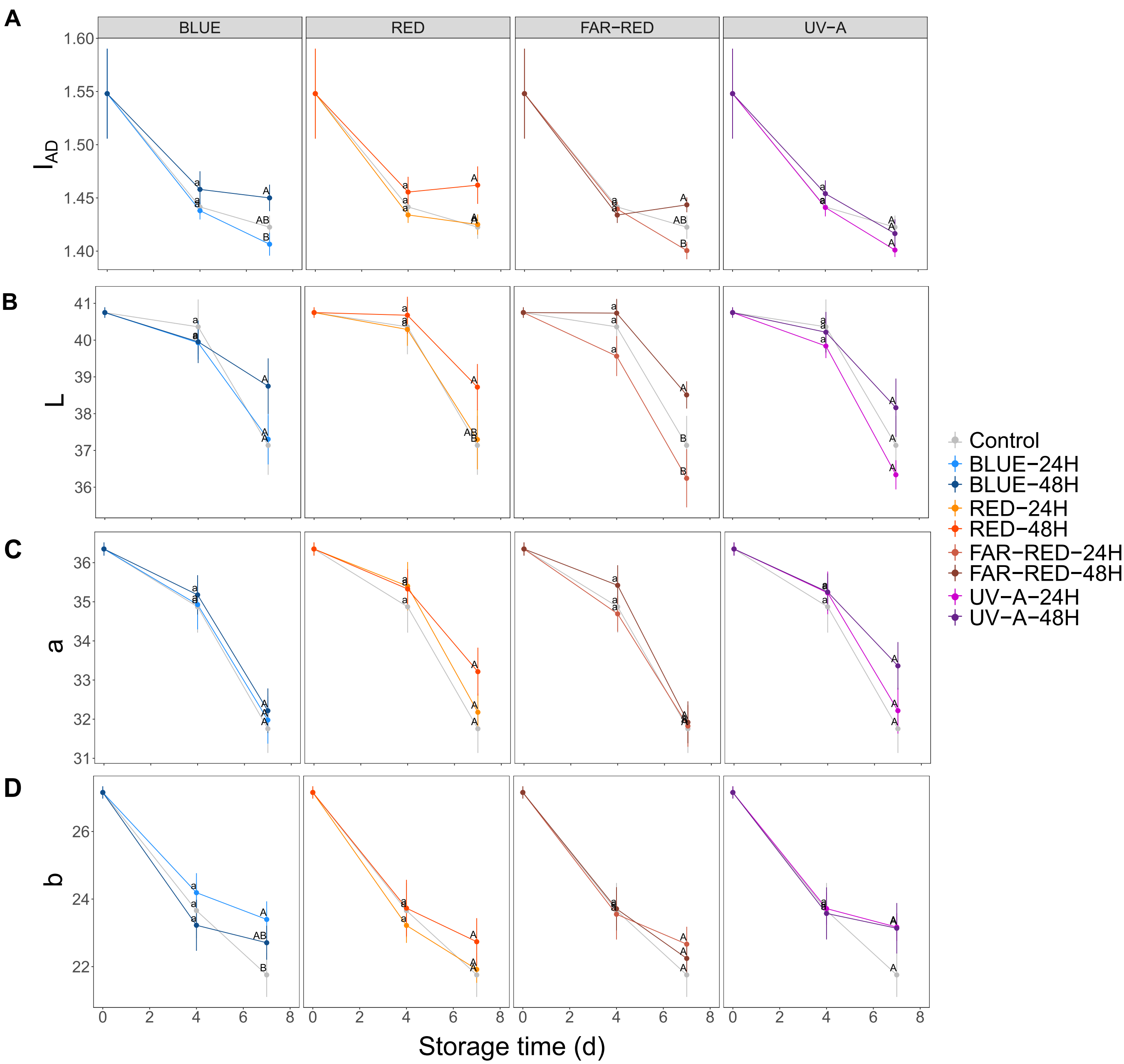

Fig. 1. Non-destructive colorimetric analysis of strawberries during storage at 5 °C. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Each panel displays the results for a specific colorimetric parameter over the storage period: (A) I_{AD} index (Absorbance difference, A670 - A720), (B) L*, (C) a*, and (D) b* value. Within each panel, data for each LED treatment (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 20 replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7.

2.9. VOC analysis by PTR-ToF–MS

Frozen powdered strawberry samples (0.5 g, stored at −80 °C) were weighed into 20 mL glass vials with 0.5 mL deionized water, 200 mg NaCl, 2.5 mg ascorbic acid, and 2.5 mg citric acid (Farneti et al., 2020). Analysis used a Proton Transfer Reaction Time-of-Flight Mass Spectrometry (PTR-ToF-MS) 8000 (Ionicon Analytik GmbH, Austria) with parameters described in Farneti et al. (2020). Automated sampling used a GERSTEL MPS autosampler. After 20 min of incubation at 40°C 2.5 mL of static headspace were injected into SHS module (Ionicon Analytik GmbH, Austria) which had following settings: temperature of the module 110°C, flow inside the module 90 sccm, flow inlet 40 sccm Samples were analyzed in triplicate. Spectral analysis followed Farneti et al. (2017).

PTR-ToF-MS data pre-processing was following: removal of peaks not significantly different from blank and peaks with > 99 % correlation (isotopes) (Farneti et al., 2017).

2.10. Statistical analysis

Statistical analyses were performed to test the effects of the different lighting conditions on strawberry fruit quality parameters. A non-parametric ANOVA (Kruskal–Wallis test) was used to compare light-treated samples against the dark-stored control at each time point, with differences considered significant at $p \leq 0.05$. These univariate analyses were conducted using SPSS (v. 28, IBM®, Armonk, NY, USA). For multivariate analysis (Principal Component Analysis, PCA) and data visualization, the R software (v.3.4.1, R Foundation for Statistical Computing, Vienna, Austria) was utilized, employing the 'mixOmics' and 'ggplot2' packages.

3. Results

3.1. Effect of lighting treatments on fruit ripening and color development

Strawberries continued ripening during storage, indicated by a decline in the chlorophyll-related I_{AD} index, which primarily occurred within the first four days and then stabilized (Fig. 1A). LED treatments did not cause statistically significant differences in I_{AD} compared to the dark control after 4 days of storage. However, a non-significant trend suggested slightly higher I_{AD} values after 7 days in fruits exposed to 48 h LED treatments compared to 24 h treatments, indicating a modest delay in the loss of chlorophyll-related pigments, with statistically significant differences observed for Blue and Far-Red treatments at 48 h exposure when compared to the dark control.

Colorimetric analysis (Lab*) revealed subtle, continuous changes (Figs. 1B, 1C; 1D). Lightness (L* values), redness (a* values) and yellowness (b* values) gradually decreased over 7 days, though differences were not always statistically significant between LED treatments. Mirroring the I_{AD} values, light treatments did not induce significant differences after 4 days of storage, whereas some significant differences emerged after 7 days, particularly for L* values in the 48-hour Blue, Red and Far-Red LED treatments relative to the dark control. After 7 days, fruits under 48 h LED exposure tended to maintain higher L* values than control and 24 h treatments (Fig. 1B). This trend was notable for Red and UV-A treatments, which also indicated a tendency towards higher a* values after 48 h exposure (Fig. 1C). Yellowness (b*) decreased during the first four days and then stabilized, with statistically significant differences from the control observed only for the Blue LED treatment (Fig. 1D).

3.2. Effect of lighting treatments on fruit weight loss and firmness

Postharvest LED treatments with Blue, Red and Far-Red significantly increase fruit weight loss compared to the dark control (Fig. 2). UV-A exposure caused weight loss comparable to the control independently from the duration of the exposure and for storage time. Weight loss depended on the duration of the exposure. For Blue and Red treatments, 48 h exposure resulted in significantly greater weight losses than 24 h exposure after 4 and 7 days. The Far-Red treatment for 48 h resulted in a higher weight loss at 4 days of storage, while at 7 days, no difference was observed between the 24 and 48 h exposure.

Despite significant differences in weight loss, fruit firmness did not differ statistically between LED treatments and the dark control, independently from the durations of the exposure (24 or 48 h) and the time of storage (4 or 7 days). (Fig. 3).

3.3. Effect of lighting treatments on dry matter, soluble solid content and titratable acidity

Control fruits showed a decline in dry matter (DM), from ~10 % initially to ~9 % after 4 days (Supplementary Fig. S1). Fruits treated with Blue and Red LEDs for 48 h maintained significantly higher DM percentages, close to harvest levels. This higher DM correlated positively with higher fresh weight loss observed under these treatments.

Soluble solid content (SSC) increased throughout storage in all treatments (Fig. 4A). Control fruit SSC increased from ~9 °Brix to ~11 °Brix over 7 days. UV-A and Red light treatments resulted in SSC levels comparable to the control. However, 24 h Far-Red light exposure led to significantly higher SSC (~13 °Brix) after 7 days. Blue light treatments yielded distinct, duration-dependent results: 48 h exposure resulted in lower SSC than controls at 4 and 7 days, whereas 24 h exposure

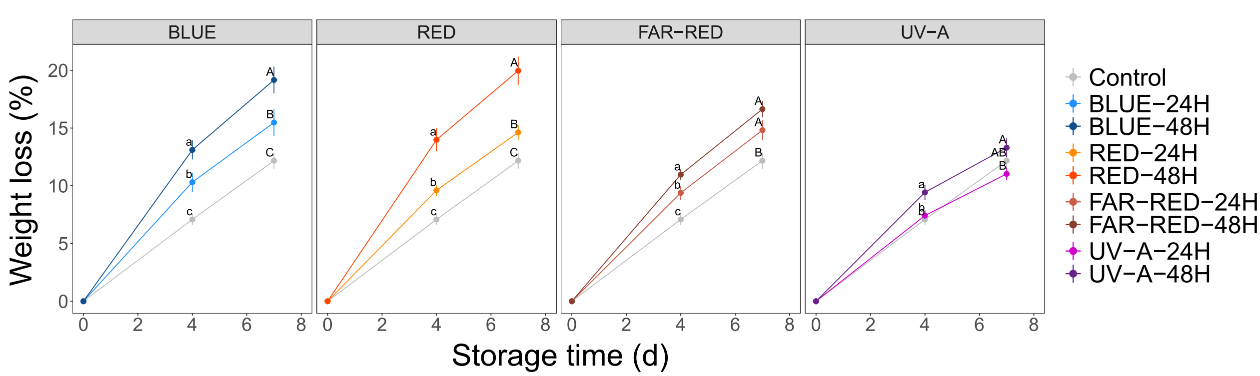

Fig. 2. Weight loss (%) of strawberries during storage at 5 °C. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Data for each LED treatment type (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 20 replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7.

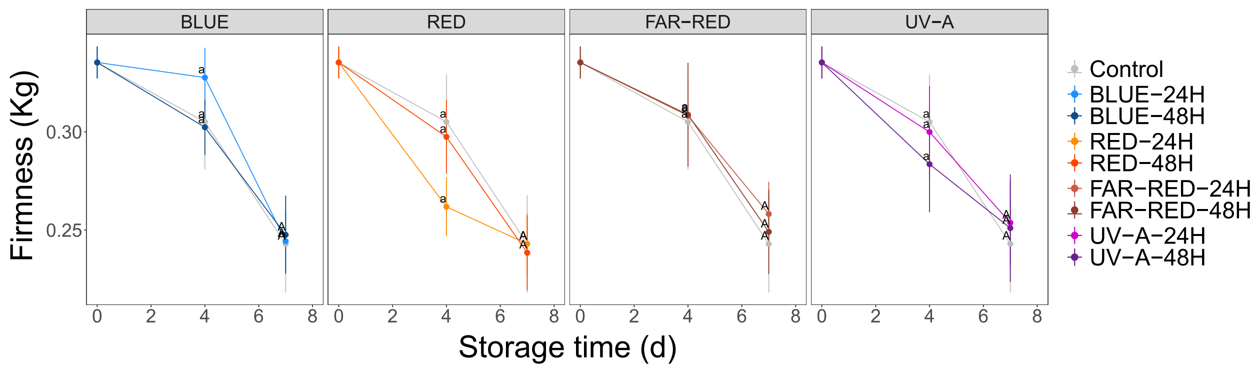

Fig. 3. Firmness (Kg) of strawberries during storage at 5 °C. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Data for each LED treatment type (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 20 replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7.

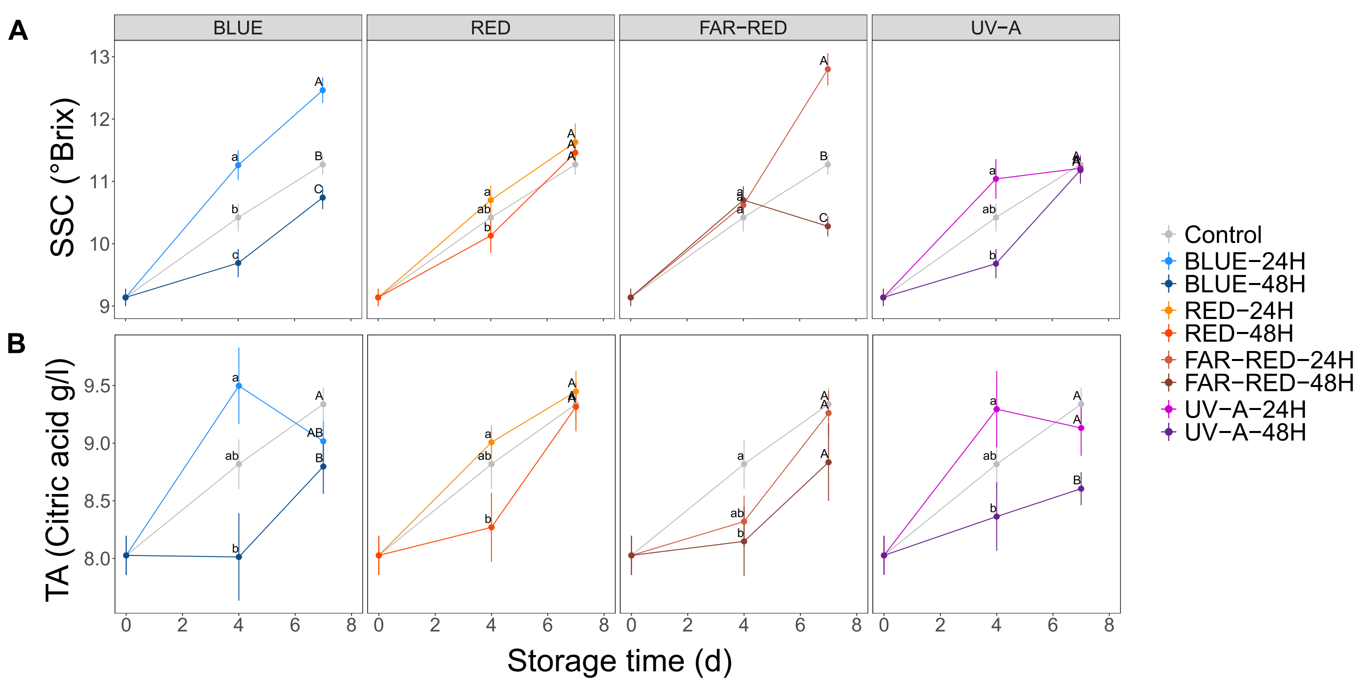

Fig. 4. Soluble solids content and titratable acidity of strawberries during storage at 5 °C. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Each panel displays the results for a specific quality trait over the storage period: (A) Soluble solids content (SSC, °Brix) and (B) titratable acidity (TA, g L^{-1} of citric acid equivalent). Data for each LED treatment (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 10 replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7.

significantly enhanced SSC accumulation at both time points. These SSC variations did not correlate with fresh weight loss patterns. This suggests that SSC dynamics reflect active metabolic adjustments rather than a mere concentration effect due to dehydration.

Titratable acidity (TA) showed a modest increasing trend during storage, with controls rising from ~7.5 to ~9 g/L (Fig. 4B). LED treatments did not induce major significant changes with 24 h exposure, despite slight elevations in TA were noted after 4 days under 24 h expositions to Blue, Red, and UV light compared to the control. On the other hand, 48 h exposition with all LED treatments tended to reduce TA in comparison with control fruit. These TA fluctuations were not correlated with fresh weight loss.

3.4. Effect of lighting treatments on total anthocyanin content

HPLC analysis confirmed pelargonidin-3-O-glucoside as the predominant anthocyanin (~95 % of total) (Data not shown). Control fruits showed a slight, non-significant increase in total anthocyanin content during storage (0.25–0.28 mg g^{-1} FW). All four LED wavelength treatments resulted in a significant rise of total anthocyanin content compared to the control at both 4 and 7 days (Fig. 5). The effect was most pronounced under 48 h exposure, resulting in ~20 % higher anthocyanin levels than controls after 7 days (mean ~0.34 mg g^{-1} FW vs. 0.28 mg g^{-1} FW). Notably, these significant increases in anthocyanin content did not correlate with the measured colorimetric parameters (L*, a* and b* values).

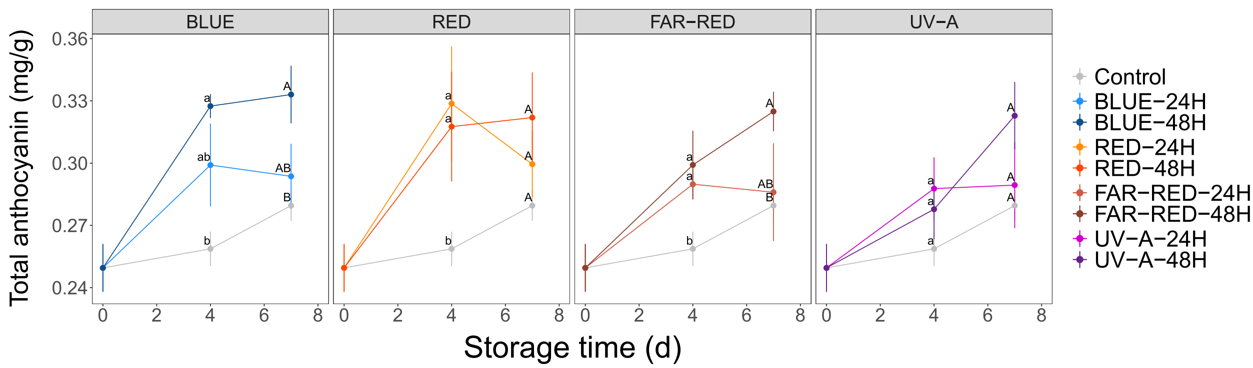

Fig. 5. Total anthocyanin content (mg g^{-1} FW) of strawberries during storage at 5 °C. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Data for each LED treatment type (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 10 replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7.

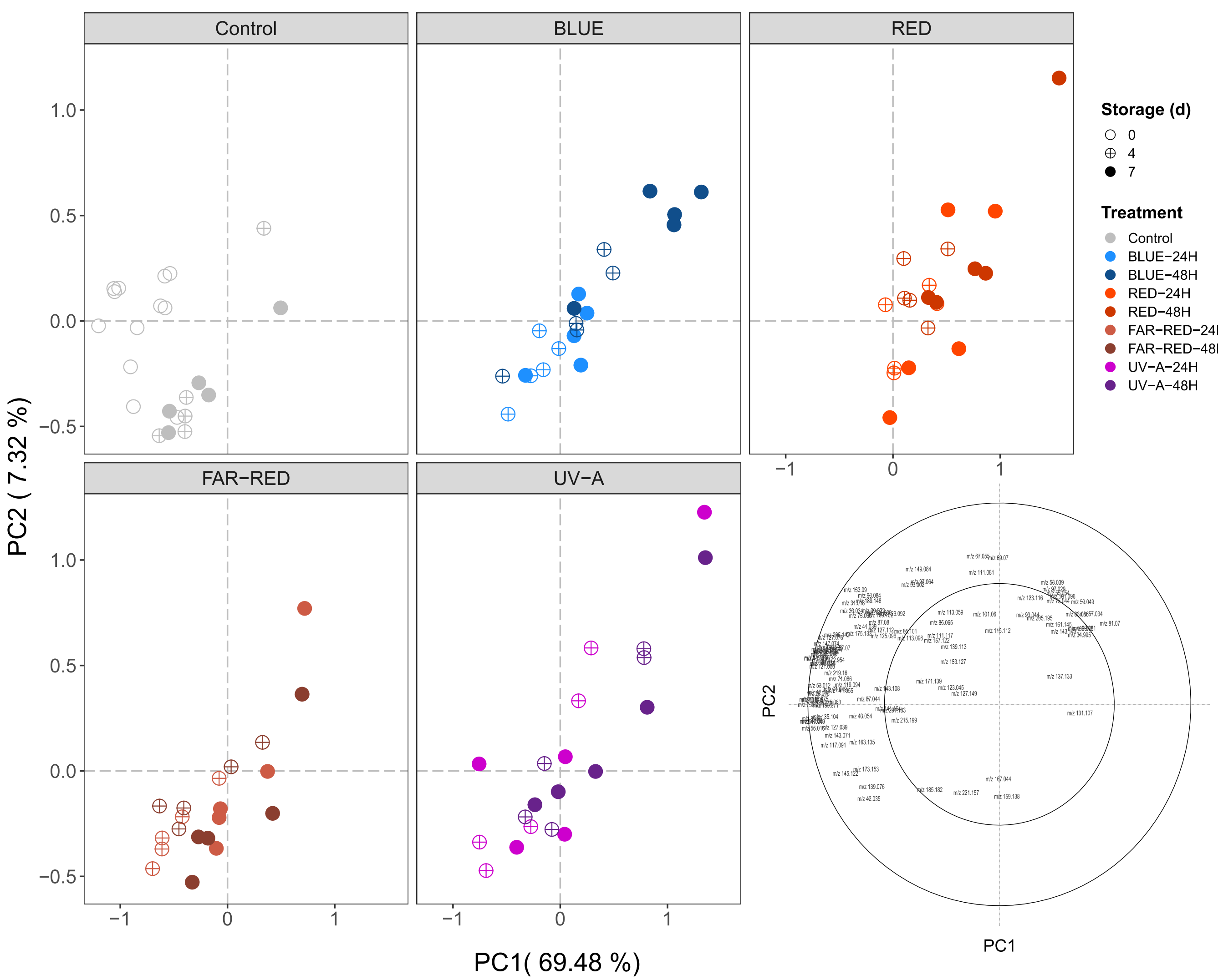

Fig. 6. Principal Component Analysis (PCA) of the volatile compound profile of strawberries during storage at 5 °C, measured by PTR-ToF-MS. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h, or kept in darkness (Control). The PCA was performed on the log-transformed concentration data of all detected mass features (*m/z*) across the entire dataset. To improve clarity, the PCA score plots are presented separately for each LED treatment type. Each individual plot visualizes the separation between the control samples and those treated for 24 h or 48 h with that specific LED light, considering changes over the storage period. Each data point represents the mean value derived from 3 technical replicates.

3.5. Effect of lighting treatments on Volatile Organic Compound (VOC) profile analysis

PTR-ToF-MS analysis detected 109 mass peaks that were significantly different from blank controls after filtering. Tentative identification (t.i.) based on comparison with internal spectral libraries, GC-MS data, and literature (Ulrich et al., 2018; Farneti et al., 2017; Farneti et al., 2021.) allowed assigning putative chemical formulas to 94 detected mass peaks and identities to 71 ones (summarized in Supplementary Table S1). Key compound classes characteristic of strawberry aroma were identified, including esters, aldehydes, alcohols, and furanones.

3.5.1. Overall evolution of VOC profiles during storage

Principal Component Analysis (PCA) of the complete VOC dataset revealed distinct patterns of evolution during storage influenced by the light treatments (Fig. 6). The first principal component (PC1) explained 69.48 % of the total variance, while the second principal component (PC2) explained 7.32 %. In contrast to LED-treated fruits, control fruits showed limited change along PC1. Their progression was primarily along PC2 between day 0 and day 4, with relatively little change thereafter until day 7. This suggests VOC profile stabilization under dark storage at 5°C. Conversely, Blue and Red LED treatments, induced more pronounced shifts along PC1, especially between day 0 and day 4 (or day 7). The loadings plot associated with the PCA (Fig. 6, bottom right panel) indicated that PC1 was positively correlated with increased concentrations of several VOCs, including many esters like *m/z* 117.090 (t.i. C6 esters like methyl isovalerate, ethyl butyrate or butyl acetate), *m/z* 145.122 (t.i. C8 esters like isobutyl butyrate, butanoic acid butyl ester or ethyl hexanoate), *m/z* 131.106 (t.i. C7 esters like isopropyl butanoate, ethyl isovalerate or isoamyl acetate), and furanones like *m/z* 143.070 (t.i. 2,5-dimethyl-4-methoxy-3(2 H)-furanone). Far-Red treatment seemed to have a comparable influence of VOCS emission to control fruit, with minor differences along PC1. Finally, UV-A exposure appeared to result in greater variability among replicate samples at day 7 compared to other light treatments or the control.

Analysis of individual mass peak trends revealed the dynamic nature of the aroma profile during storage (Fig. 7, Supplementary Fig. S2). The aroma profile of control fruits evolved over the 7 days: some compounds generally increased (e.g., *m/z* 117.091 (t.i. C6 esters), *m/z* 145.122 (t.i. C8 esters), *m/z* 173.153 (t.i. C10 esters)), some remained relatively stable (e.g., *m/z* 47.049 (t.i. ethanol), *m/z* 143.070 (t.i. 2,5-dimethyl-4-methoxy-3(2 H)-furanone)), and others showed a tendency to decrease compared to initial levels like *m/z* 75.044 (t.i. methyl acetate), *m/z* 83.085 (t.i. cis-3-hexen-1-ol), *m/z* 99.080 (t.i. E-2-hexenal), *m/z* 101.096 (t.i. hexanal), *m/z* 103.075 (t.i. C5 esters methyl butyrate), *m/z* 137.132 (monoterpenes), *m/z* 143.143 (t.i. nonanal). Significantly, all LED treatments consistently resulted in concentrations statistically higher than the control at day 4 or day 7.

3.5.2. Specific preservation of aroma compounds by LED treatments

Several compounds that tended to decrease during storage in control fruits, such as t.i. methyl acetate (*m/z* 75.044), cis-3-hexen-1-ol (*m/z* 83.085), E-2-hexenal (*m/z* 99.080), hexanal (*m/z* 101.096), dihydro-2-methyl-3(2 H)-furanone (*m/z* 101.059, also t.i as 2,3-pentanedione), methyl butyrate (*m/z* 103.075), monoterpenes (*m/z* 137.132), and nonanal (*m/z* 143.143), were often maintained at levels closer to those at harvest (day 0) under specific LED treatments, particularly Blue and Red light (Fig. 7, Fig. 8A, Supplementary Fig. S2)

Furthermore, LED treatments significantly increased the concentration of many strawberry key VOCs relative to the control by day 4 and/or day 7. Enhanced levels were observed across several chemical classes. This included some alcohols (e.g. ethanol (*m/z* 47.049), butanol (*m/z* 57.07), 3-methyl-3-buten-2-ol (*m/z* 71.086) and the important strawberry furanones 2,5-dimethyl-4-methoxy-3(2 H)-furanone (*m/z* 143.070) or 2(3 H)-furanone, 5-ethenyldihydro-5-methyl- (*m/z* 127.076). Increases were also detected for some aldehydes (e.g., *m/z* 45.033 (t.i acetaldehyde), *m/z* 71.049 (t.i. butenal), *m/z* 73.065 (t.i. butanal), *m/z* 87.08 (t.i. pentanal)) and other compounds potentially representing fragments or less certain identifications.

3.5.3. Enhancement of ester compounds by Blue and Red LEDs

The most notable impact of Blue and Red treatments was the significant enhancement of numerous esters, which are crucial for strawberry flavour. Examples of t.i. esters with increased concentrations include: methyl acetate (*m/z* 75.044), ethyl acetate (*m/z* 89.059), methyl propanoate (*m/z* 87.043), ethyl propanoate (*m/z* 87.080), methyl butanoate (*m/z* 103.075), C6 esters like ethyl butanoate/isomers (*m/z* 117.091), C7 esters like methyl hexanoate/isomers (*m/z* 131.107), C8 esters like ethyl hexanoate/isomers (*m/z* 145.122), and potentially ethyl octanoate (*m/z* 173.153), among others detailed in Supplementary Table S1 and Supplementary Figure S2.

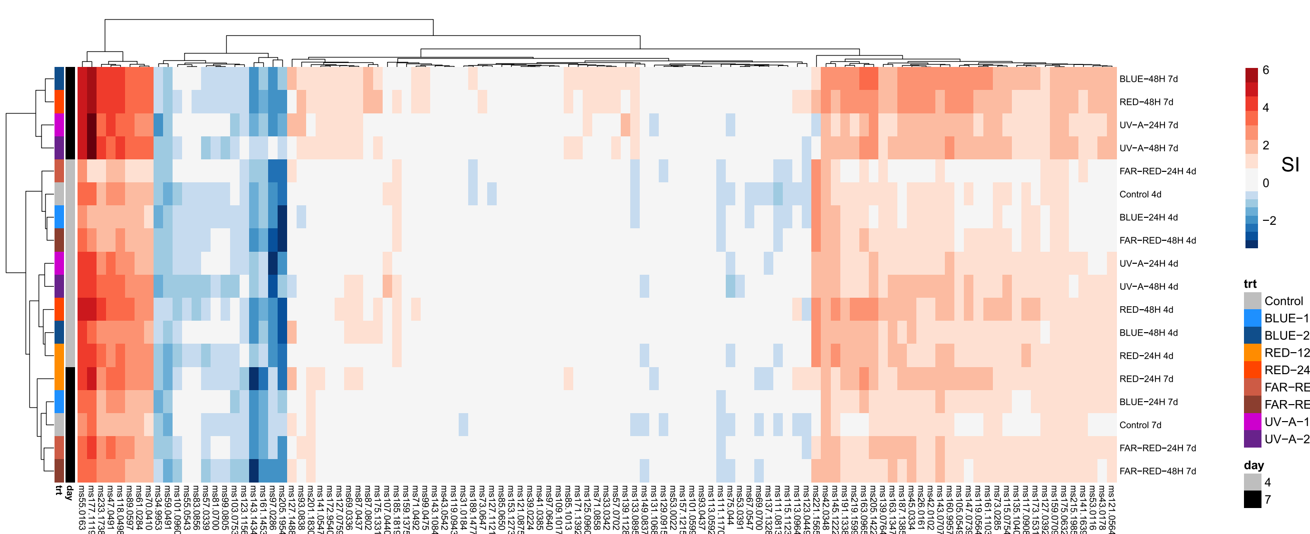

Fig. 7. Heatmap illustrating relative changes in strawberry VOC profiles (PTR-ToF-MS) at day 4 and day 7 of storage at 5 °C. Fruits were treated with different LED treatmens (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h, or kept in darkness (Control). Cell color intensity represents the Log2-transformed fold change for each VOC (column) under each treatment condition (row) at the specified storage day (4 or 7), relative to the mean concentration at day 0. Hierarchical clustering dendrograms show similarities between treatment responses (rows) and VOC patterns (columns).

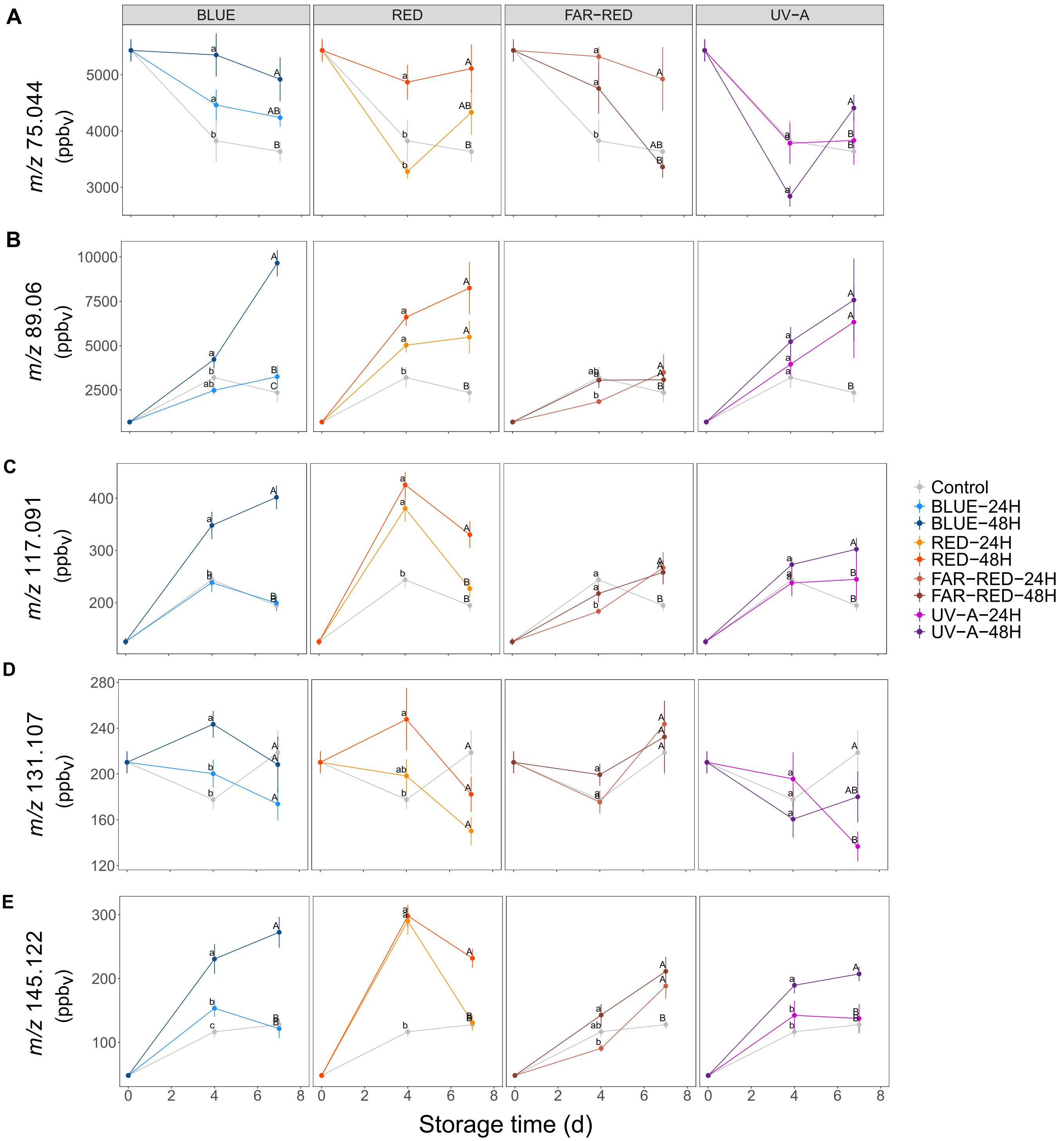

Fig. 8. Time-course of key ester concentrations (ppbv) in strawberries during storage at 5 °C, measured by PTR-ToF-MS. Fruits were treated with different LED treatments (Blue, Red, Far-Red, or UV-A) for 24 h or 48 h prior to storage, or kept in darkness (Control). Each panel displays the results for a specific VOC over the storage period: (A) *m/z* 75.044 (C3 ester: t.i. methyl acetate), (B) *m/z* 89.06 (C4 ester: t.i. Ethyl Acetate) (C) *m/z* 117.091 (C6 ester: t.i. methyl isovalerate, ethyl butyrate, Butyl acetate), (D) *m/z* 131.107 (C7 ester t.i. Isopropyl Butanoate, Ethyl Isovalerate, Isoamyl Acetate), (E) *m/z* 145.122 (C8 ester t.i. Isobutyl butyrate, Butanoic Acid Butyl Ester, Ethyl Hexanoate). Within each panel, data for each LED treatment type (compared to the dark control) are presented in separate plots. Data points represent the mean ± standard deviation of 5 biological replicates. Statistical analysis was performed independently for day 4 and day 7 to compare the control against the 24 h and 48 h durations for each specific LED treatment. Different letters indicate significant differences ($p < 0.05$) at a given time point: lowercase letters for day 4 and uppercase letters for day 7. Plots of all mass peaks are reported in the Supplementary Fig. S2.

The 48 h exposure often yielded the highest concentrations at both 4 and 7 days compared to the 24 h exposure and the dark control. The time-course evolution for five specific esters which significantly contribute to strawberry aroma is shown in Fig. 8. The LED treatments increased their concentration, compared to the dark control, during storage at 5°C: methyl acetate (*m/z* 75.044), ethyl acetate (*m/z* 89.06), a C6 ester like ethyl butanoate (*m/z* 117.091), a C7 ester like methyl hexanoate (*m/z* 131.107), and a C8 ester like ethyl hexanoate (*m/z*

145.122). Collectively, these examples demonstrate that early postharvest exposure to Blue and Red light, especially for 48 h, substantially modulates the ester profile during subsequent 5 °C storage, either mitigating the decreases observed in controls or, more frequently, stimulating the accumulation of these VOCs. The complete dataset for all monitored *m/z* features is provided in Supplementary Figure S2.

4. Discussion

4.1. LED treatments affect fruit weight loss without altering firmness: an interplay of metabolism and water dynamics

Fruit texture is a pivotal quality attribute influencing marketability and consumer acceptance. On the other hand, maintaining fresh weight is crucial for fruit sellers. Texture is primarily determined by cell wall and middle lamella integrity, involving components like pectin, hemicellulose, and cellulose, and the activity of modifying enzymes (Vicente et al., 2002; An et al. 2023). Softening during storage typically results from cell wall degradation catalyzed by enzymes such as polygalacturonase (PG) and pectin methylesterase (PME) (Jiménez-Bermudez et al., 2002; Salentijn et al., 2003, Figueroa et al., 2010).

Our results indicated that while early LED exposure significantly influenced fruit weight loss (Fig. 2), it did not statistically alter fruit firmness compared to dark-stored controls under our experimental conditions (5 °C storage) (Fig. 3). This finding contrasts with several studies demonstrating that specific light treatments can delay softening in various fruits. For example, LED light inhibited cellulase activity in apricots (*Prunus armeniaca)*, preserving firmness (Bai et al., 2025), and downregulated genes encoding cell wall-loosening endoglucanases in peaches (*Prunus persica)* (Gong et al., 2015). Specific to strawberries, Blue and Red light exposure has been linked to reduced PG activity and maintained firmness (Xu et al., 2014; Lu et al. 2025). Furthermore, pulsed light application was reported to maintain hardness in fresh-cut strawberries, possibly *via* stress-induced cell wall strengthening (Avalos-Llano et al., 2018).

However, our findings align with those of Chong et al. (2022), who also observed no significant LED effect on strawberry firmness. The lack of textural modification in our study likely stems from a combination of factors. Methodological variations, including specific LED wavelengths, intensities, the chosen cultivar ('Elsanta'), the ripening stage of fruit at the time of treatment and the relatively short treatment duration (24–48 h), could play a role. Critically, the suboptimal storage temperature (5 °C) employed deliberately in our design likely slowed the natural enzymatic softening processes significantly, potentially masking more subtle effects of the light treatment on cell wall metabolism that might be apparent at higher storage temperatures.

Conversely, fresh weight loss, primarily due to transpiration and respiration, was significantly affected by the LED treatments. We observed that Blue, Red, and Far-Red light, especially at 48 h duration, induced greater weight loss than the dark control and UV-A treatment. This finding is contrary to several reports where light treatments reduced weight loss. For instance, white LED light decreased weight loss in 'Zaosu' pears (*Pyrus communis*), potentially by inhibiting respiration and ethylene production (Mi et al., 2023), Red light reduced weight loss in grapes (Nassarawa et al., 2022), and UV-B/UV-C combination reduced it in peaches (Abdipour et al., 2019). The proposed mechanism for reduced weight loss often involves decreased respiration or transpiration, linked to photoreceptor-mediated regulation, such as a known role of blue light in stomatal closure (Gong et al., 2015; Yang et al., 2020). However, strawberry fruit is characterized by a stomatal density lower than 1 per mm^2 (Blanke, 2002). Furthermore, strawberry cuticles are very thin since the amount of cutin and wax decrease at the late stage of fruit development (Straube et al., 2024). A recent study identified the abscission zone, the junction between calyx and receptacle, and the seedless zone as the most important pathways for water loss (Hurtado et al., 2023). Thus, transpiration through fruit stomata is negligible and any mechanisms affecting stomata opening, such as Blue light, is likely ineffective in reducing water losses.

We propose that under our conditions (early treatment pulse at 5 °C), the increased weight loss associated with Blue, Red, and Far-Red light reflects a heightened metabolic activity stimulated by the light signal via photoreceptors (cryptochromes, phytochromes). This stimulation is evidenced by the enhanced synthesis of anthocyanins and VOCs observed in these treatments (see Sections 4.3, 4.4). This increased metabolic activity, even at 5 °C, likely elevated respiration rates, a primary driver of water loss alongside transpiration. This represents a physiological trade-off for the biosynthesis of quality-related compounds, where the energy and carbon expenditure on secondary metabolism contributes to greater overall weight loss. Finally, it is possible that any potential light-induced stomatal closure effect (Yang et al., 2020) was overridden by the overall metabolic stimulation under these specific suboptimal temperature conditions. The moderate weight loss under UV-A, similar to the control, was likely influenced by its limited applied intensity (30 μmol $m^{-2}s^{-1}$), the maximum achievable with our experimental setup. This observation might also reflect a distinct stress response or a lesser impact on general metabolism compared to Blue/Red/Far-Red light.

While firmness itself was not significantly altered, light signals are known to influence genes encoding cell wall enzymes like PME inhibitors (PMEI) and cellulase (Bai et al., 2025). The lack of correlation between weight loss and firmness changes in our study further suggests that water dynamics and cell wall structural modifications were independently regulated under these postharvest light treatment conditions. These results highlight the complex interplay between light signaling, metabolic activity, water retention, and cell wall processes, emphasizing how the net effect on quality attributes depends strongly on the specific light parameters and the environmental context (e.g., suboptimal temperature).

4.2. LED lighting alters sugar-acid balance through complex modulation of carbohydrate metabolism

The balance between sugars (primarily sucrose, glucose, fructose) and organic acids (mainly citric and malic acid) is a critical determinant of strawberry sensory quality, influencing perceived sweetness, acidity, and overall flavor acceptability (Keutgen and Pawelzik, 2007). While sugars are largely accumulated during fruit development, their levels, along with acidity, undergo significant postharvest modulation driven by enzymatic activity and metabolic regulation (Pott et al. 2020).

Emerging evidence demonstrates that light, particularly specific LED wavelengths, acts as an active metabolic signal capable of influencing postharvest carbohydrate metabolism, rather than merely being a passive environmental factor. Studies across various fruit species, including tomatoes (*Solanum lycopersicum*), cherries (*Prunus avium*), sweet oranges (*Citrus x sinensis*), and apricots, have shown that LED treatments can modulate sugar and acid content (Zhang et al., 2017; Hu et al., 2019; Nassarawa et al., 2021; Bai et al., 2025). Blue (~ 470 nm) and Red (~ 660 nm) light appear particularly effective, often stimulating carbohydrate metabolism by influencing key enzymes involved in sugar biosynthesis, interconversion, and transport, such as sucrose phosphate synthase (SPS), sucrose synthase (SS), and invertases (Xu et al., 2014; Bai et al., 2025). For instance, Hu et al. (2019) found that both LED and UV irradiation significantly increased soluble sugar and organic acid content in postharvest sweet oranges.

In our study, soluble solid content (SSC) generally increased during the 7-day storage at 5 °C, consistent with ongoing ripening processes (Fig. 4**A**). However, the early LED treatments induced distinct wavelength- and duration-specific responses superimposed on this trend. UV-A and Red light exposures resulted in SSC levels comparable to the dark control, suggesting minimal interference with the intrinsic ripening trajectory under these conditions. In contrast, a significant enhancement of SSC was observed under 24 h Far-Red light exposure. Most notably, Blue light treatments produced divergent results based on duration: the 24 h treatment significantly increased SSC compared to controls at both 4 and 7 days, whereas the continuous 48 h treatment led to significantly lower SSC levels.

This complex Blue light response contrasts with previous reports on strawberries where Blue light consistently enhanced sugar accumulation. Xu et al. (2014) found Blue light enhanced SSC activity, promoting sugar accumulation, while Kim et al. (2011) reported Blue light stimulated glucose sensor pathways and carbohydrate metabolism, increasing SSC. The divergent effect observed in our study (enhancement at 24 h vs. suppression at 48 h) suggests a potentially complex interplay between signaling duration, intensity, and the fruit's physiological state under the suboptimal 5°C condition. It is plausible that the shorter 24 h pulse effectively stimulated sugar metabolism pathways, while the prolonged 48 h exposure might have triggered a different metabolic or stress response, possibly altering carbon partitioning or inhibiting key enzymes over time. The significant SSC increase under 24 h Far-Red light also highlights the specific role of phytochrome signaling in potentially modulating carbohydrate pools differently from cryptochrome (Blue light) mediated responses, warranting further investigation. Importantly, these diverse SSC changes did not correlate with fresh weight loss patterns, confirming they represent specific metabolic adjustments rather than mere concentration effects due to dehydration.

The impact of the early LED treatments on titratable acidity (TA) was less pronounced and consistent than on SSC (Fig. 4B), further confirming that the increase in SSC and TA is not merely a concentration effect related to water loss. While some studies report that Blue/Red light combinations can slightly reduce citric and malic acid levels in strawberries, potentially improving the sugar-to-acid ratio (Kim et al., 2011; Xu et al., 2014), and LED treatments decreased levels of other acids like succinic acid in apricots (Bai et al., 2025), we observed only minor, transient increases in TA, primarily after 4 days under 24 h Blue, Red, and UV treatments. These subtle changes uncorrelated with weight loss, suggesting that under the conditions of an early light pulse at 5 °C, the primary effect was on sugar metabolism, with less impact on the regulation of the main organic acid pools contributing to TA.

From a mechanistic standpoint, these metabolic shifts are likely initiated by photoreceptors (cryptochromes, phytochromes) activating signaling cascades that modulate the expression and activity of key metabolic enzymes. Light-responsive genes involved in carbohydrate metabolism include those encoding hexokinase (HK), SS, SPS, and invertase (Xu et al., 2014; Zhang et al., 2017; Bai et al., 2025). Similarly, light can influence genes encoding enzymes central to organic acid metabolism, such as malate dehydrogenase (MDH) and TCA cycle enzymes like malate synthase and citrate synthase (Bai et al., 2025). Our results, particularly the divergent Blue light effect and the specific Far-Red response, underscore the complexity of these regulatory networks and how the net outcome on sugar-acid balance critically depends on the specific light parameters (wavelength, duration, intensity) interacting with the fruit's physiological state and storage environment.

While tailored LED treatments hold promise for optimizing fruit quality by modulating sugar-acid balance, as suggested for other berries (Nassarawa et al., 2021), our findings highlight that predicting and achieving specific outcomes requires a precise understanding of these complex light-physiology interactions, especially under non-ideal conditions.

4.3. *Early LED lighting enhances strawberry anthocyanin biosynthesis without altering perceived color*

Fruit color is a paramount quality attribute, strongly influencing consumer perception of freshness and ripeness, and thus purchasing decisions (Sparacino et al., 2024). In strawberries, the characteristic red hue is primarily imparted by anthocyanins, with pelargonidin-3-O-glucoside being the most abundant form, crucial for both visual appeal and nutritional value due to its antioxidant properties (Aaby et al., 2012; Giampieri et al., 2012; Afrin et al. 2016). While redness is often associated with ripeness and flavor, this link is not always direct.

Our analysis confirmed pelargonidin-3-O-glucoside constituted ~95 % of total anthocyanins in 'Elsanta' strawberries, consistent with typical profiles (Aaby et al., 2012). While control fruits showed only a marginal increase during storage at 5 °C, a key finding of our study was the significant enhancement of total anthocyanin content by all four tested LED wavelength treatments (Red, Blue, Far-Red, UV-A) applied during the initial 24–48 h postharvest period (Fig. 5). This effect was particularly pronounced with the 48 h exposure, leading to ~20 % higher anthocyanin levels compared to controls after 7 days.

This result strongly supports the role of light as a potent elicitor of secondary metabolism postharvest. Anthocyanins are synthesized via the complex interplay of the pentose phosphate pathway (PPP), shikimate pathway, and the downstream general phenylpropanoid and flavonoid pathways. Light quality and quantity are well-known regulators of these pathways (Xu et al., 2014a, Xu et al., 2014b; Xu et al., 2018). Specific LED wavelengths have shown significant potential to modulate anthocyanin biosynthesis. Blue light (~470 nm), acting primarily through cryptochrome photoreceptors, is known to enhance the expression of key structural genes like phenylalanine ammonia-lyase (PAL), chalcone synthase (CHS), and dihydroflavonol 4-reductase (DFR) in various species, including strawberries (Xu et al., 2014a; Xu et al., 2014b; Xu et al., 2018). Blue light may also induce enzymes in precursor pathways like glucose-6-phosphate dehydrogenase (G6PDH) and shikimate dehydrogenase (SKDH) (Xu et al., 2014b). Similarly, Red light (~660 nm), perceived by phytochromes, can also promote anthocyanin accumulation, often synergistically with Blue light (Kim et al., 2011; Zhang et al., 2017; Zhang et al., 2018). Studies using white LED light have also demonstrated increased expression of PAL and other flavonoid biosynthetic genes, leading to higher anthocyanin content in fruits like apricots (Bai et al., 2025). Furthermore, light might also contribute to anthocyanin stability by inhibiting degradation enzymes (Vergara-Domínguez et al., 2016).

Interestingly, in our study, the significant increase in anthocyanins was observed across all tested wavelengths, with the duration of exposure (48 h > 24 h) appearing more critical than the specific spectrum. This contrasts with studies often highlighting the particular effectiveness of Blue or Red light. Several factors might explain this: i) potential saturation of photoreceptor signaling pathways at the applied intensity (80 μmol m^{-2} s^{-1}), making duration the prime factor; ii) functional redundancy or crosstalk between different photoreceptor pathways (phytochromes, cryptochromes, potentially UVR8 for UV-A) under these specific conditions; iii) interaction with the suboptimal temperature (5 °C), which might alter the sensitivity or downstream output of specific light signaling pathways.

Despite the marked (~20 %) biochemical increase in anthocyanin concentration, we did not observe a corresponding statistically significant change in the objective colorimetric parameters L* (lightness) or a* (redness) (Fig. 1). This apparent disconnection between pigment content and perceived color is not entirely unexpected. Visual color results from complex interactions within the fruit tissue. Factors beyond total pigment concentration, such as the specific chemical structure of anthocyanins, their localization and concentration within the vacuole, the vacuolar pH (which affects anthocyanin hue), and co-pigmentation effects (interaction with other phenolics like flavonols or flavan-3-ols) significantly influence the final color shade and intensity (Kalt et al., 1993; Giampieri et al., 2012; Xu et al., 2014b). It is possible that the early light treatments primarily boosted the quantity of anthocyanins without significantly altering these other cellular factors that modulate color expression under these storage conditions, or that the changes were below the detection threshold of the colorimeter.

Furthermore, the spatial distribution of the newly synthesized anthocyanins within the fruit tissue could be a critical factor. If the light-induced accumulation occurs primarily in sub-epidermal cell layers rather than in the epidermis itself, it would increase the total measurable pigment content without significantly altering the surface coloration perceived by a colorimeter. This highlights a potential disconnect between bulk biochemical analysis and surface-level optical properties.

Nonetheless, the significant increase in anthocyanin content driven by the early LED treatment is relevant from a nutritional perspective, enhancing the potential health benefits associated with strawberry consumption. This highlights that light treatments can effectively boost the accumulation of valuable phytochemicals during postharvest, even if the effect is not immediately obvious through simple colorimetric assessment.

4.4. Early LED lighting treatments positively remodel the strawberry aroma profile, notably enhancing ester biosynthesis

The characteristic aroma of strawberry is a complex blend resulting from over 360 VOCs, with esters, furanones (like mesifurane and furaneol), and certain terpenes being primary contributors to the perceived sensory quality (Ulrich et al., 2018; Schwieterman et al., 2014). VOC biosynthesis is tightly regulated, involving precursors derived from fatty acid, amino acid, and carbohydrate metabolism, and is significantly influenced by pre- and postharvest environmental factors, including light quality and quantity (Forney et al., 2000; Campbell et al., 2020). Given this, LED technology presents an innovative tool for potentially modulating fruit aroma profiles postharvest.

The untargeted VOC analysis performed using PTR-ToF-MS revealed that a post-harvest application of LED light (particularly Blue and Red) for just 24 – 48 h significantly impacted the VOC profile of strawberries during subsequent storage at 5°C, compared to dark control (Figs. 6–8). A crucial observation from the heatmap analysis (Fig. 7) and individual mass peak plots (Fig. 8, Supplementary Fig. S2) was that the effects were overwhelmingly positive in terms of concentration: when significant differences occurred, LED-treated fruit always showed higher concentrations of aroma-relevant compounds, never lower. Furthermore, LEDs helped maintain higher levels of certain VOCs, such as cis-3-Hexen-1-ol (*m/z* 83.085, associated with green/grassy notes) and methyl acetate (*m/z* 75.044), which tended to decrease in control fruit during storage. This suggests that the early light treatment may help preserve specific biosynthetic pathways or maintain precursor pools that are otherwise depleted during storage at 5 °C

While research specifically investigating postharvest LED effects on strawberry VOCs is limited (Campbell et al., 2020), studies in other systems demonstrate light's regulatory role. For instance, dark treatment reduces floral benzenoid/phenylpropanoid volatiles in petunia (*Petunia* × *hybrida*), while Red and Far-Red light can increase specific emissions, indicating light-dependency (Colquhoun et al., 2013). In tomato, Red and Blue light increased concentrations of volatiles associated with flavor perception (Wang et al., 2022). Light spectra can influence volatiles derived from various precursor pathways, including carotenoids (e.g., β-ionone), lipids (e.g., hexanal and hexenal), and amino acids (Wang et al. 2022; Lauria et al. 2023).

The most striking finding in our study was the significant enhancement of numerous esters under Blue and Red light, particularly with 48 h exposure (Fig. 8, Supplementary Table S1). Key esters showing increased concentrations included methyl acetate (*m/z* 75.044), ethyl acetate (*m/z* 89.059), methyl butanoate (*m/z* 103.075), ethyl butanoate (and/or isomers, *m/z* 117.091), methyl hexanoate (and/or isomers, *m/z* 131.107), and ethyl hexanoate (and/or isomers, *m/z* 145.122), among many others (Supplementary Table S1, Supplementary Fig. S2). Esters are paramount for the desirable fruity, sweet, and floral notes characteristic of ripe strawberries (Ulrich et al., 2018; Schwieterman et al., 2014). Their biosynthesis primarily involves the enzymatic esterification of alcohols with acyl-CoA thioesters, catalyzed by alcohol acyltransferases (AATs). Alcohols can be derived from pathways like glycolysis/fermentation (e.g., ethanol) or fatty acid/amino acid catabolism (e.g., hexanol), while acyl-CoAs are typically generated via fatty acid β-oxidation or branched-chain amino acid catabolism.

Our results strongly suggest that the early Blue and Red light signals, likely perceived by cryptochromes and phytochromes respectively, trigger downstream events that boost ester production during subsequent storage. This enhancement likely occurs via several non-mutually exclusive mechanisms operating concurrently or synergistically. One primary possibility involves the direct upregulation of genes encoding key alcohol acyltransferases (AATs); light signaling pathways might increase the transcription or translation of specific AAT genes responsible for synthesizing the observed esters. In addition, the increased ester formation could stem from enhanced availability of necessary precursors. For instance, light may stimulate metabolic pathways providing specific alcohols, potentially through altered glycolysis or fermentation (consistent with the trend of increased ethanol, *m/z* 47.049, observed particularly under Blue light – Supplementary Fig. S2), or by influencing lipid or amino acid catabolism to increase the supply of specific acyl-CoA thioesters required for esterification. Furthermore, maintaining a favorable cellular energy and redox state could be another contributing factor. The early light exposure might help sustain adequate ATP levels or an appropriate redox balance (e.g., NADPH/NADP+ ratio) during the 5 °C storage, thereby supporting the energy-intensive processes of both precursor synthesis and the enzymatic activity of AATs. Beyond direct transcriptional control, a higher level of regulation may be at play. Light signals are known to interact with plant hormone signaling pathways. It is plausible that the initial light exposure modulates the balance of key hormones (e.g., auxins, jasmonates), or mRNA methylation, which then act as secondary regulators to orchestrate the coordinated upregulation of the entire ester biosynthesis network, from precursor supply to final enzymatic esterification (Zhou et al. 2021).

While direct evidence for light regulation of AATs postharvest in strawberries is scarce, our findings align conceptually with reports where Blue light increased emission concentrations of esters like octyl butyrate, hexyl butyrate, ethyl caproate, and methyl acetate in strawberries (Campbell et al., 2020). Our study significantly expands on this, showing a broad enhancement across numerous esters induced by both Blue and Red light applied early postharvest and effective during storage at a suboptimal temperature. The stronger effect observed with 48 h exposure suggests a dose-response relationship for activating these biosynthetic pathways.

The less pronounced effects of Far-Red light and the higher variability under UV-A (Fig. 6) suggest that different wavelengths engage these pathways with varying efficiency or trigger additional, possibly competing, responses. UV-A, known to induce stress responses, might lead to more heterogeneous metabolic adjustments related to aroma compound biosynthesis across individual fruits.

Overall, the substantial positive impact of early Blue and Red light exposure on the ester profile represents a significant finding. It suggests a novel strategy to not only maintain but potentially enhance the desirable aroma characteristics of strawberries during postharvest, particularly under commercially relevant suboptimal temperature storage, by specifically stimulating the pathways responsible for their key volatile constituents. This highlights the potential of using targeted light treatments as a non-chemical tool to improve fruit sensory quality.

5. Conclusion

This study demonstrates that applying LED light (particularly Blue and Red spectra) for just 24–48 h immediately after harvest can significantly enhance important quality attributes of 'Elsanta' strawberries during subsequent storage at a suboptimal temperature (5 °C). While firmness was unaffected, the early light treatment significantly boosted total anthocyanin content and, crucially, increased the concentration of key aroma-active VOCs, especially esters, compared to dark-stored controls. These benefits occurred despite an increase in fresh weight loss, suggesting a metabolic trade-off. The effects were dependent on light wavelength and duration, highlighting the potential for targeted manipulation.

We propose these lasting effects stem from an 'early signal' mechanism: the initial 24 −48 h light exposure acts as a powerful photomorphogenic trigger, likely mediated by phytochrome and cryptochrome photoreceptors. This initial signal appears to activate downstream pathways regulating secondary metabolism (anthocyanins, VOCs/esters) and influence primary metabolism (sugars), enhancing the fruit's metabolic competence during subsequent dark storage, even under the mild chilling stress of 5 °C.

Crucially, this ability to stimulate key quality pathways during postharvest suggests a potential strategy to reconcile shelf-life extension with quality development. It might allow harvesting strawberries at a slightly earlier maturity stage – a common practice to improve handling and storage longevity – while utilizing the early light treatment to promote the synthesis of desirable aroma compounds (esters) and health-promoting anthocyanins during storage. This could mitigate the quality trade-offs often associated with early harvesting, leading to fruit that is both durable and possesses enhanced organoleptic and nutritional value upon reaching the consumer. Such an approach holds promise beyond strawberries, potentially offering similar benefits for other non-climacteric fruits, particularly berries, which face analogous challenges in balancing postharvest life with the full development of sensory and phytochemical quality attributes.

This concept of using a short, initial light treatment to pre-condition fruit offers an innovative approach for postharvest management. It presents a potentially more practical and energy-efficient strategy than continuous lighting to trigger lasting physiological benefits, thereby improving strawberry quality retention and consumer appeal, especially within less-than-ideal cold chains. Future research should focus on optimizing cultivar-specific protocols (spectrum, intensity, duration), further elucidating the underlying molecular mechanisms (gene expression, enzyme activity) responsible for these persistent effects, and exploring potential synergistic effects with other postharvest treatments. This work pave the way for developing light-based technologies to enhance fruit quality and reduce losses in the supply chain for strawberries and potentially other perishable fruits. Nevertheless, further investigations are required to elucidate the molecular mechanisms underlying the observed effects and to explore the signaling pathways modulated by light perception. These studies should include gene expression analyses related to the biosynthesis of anthocyanins and other color-modifying compounds (e.g., flavonols), as well as genes involved in metabolic processes associated with fruit softening.

CRediT authorship contribution statement

Pastore Chiara: Investigation. **Pistillo Alessandro:** Resources, Methodology. **Prosdocimi Giorgio Gianquinto:** Supervision. **Crepaldi Andrea:** Resources. **Pennisi Giuseppina:** Resources, Methodology. **Khomenko Iuliia:** Investigation, Formal analysis. **Paucek Ivan:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Orsini Francesco:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Biasioli Franco:** Supervision. **Farneti Brian:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Spinelli Francesco:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.postharvbio.2025.114018.

Data availability

Data will be made available on request.

References

Aaby, K., Mazur, S., Nes, A., Skrede, G., 2012. Phenolic compounds in strawberry (Fragaria x ananassa Duch.) fruits: composition in 27 cultivars and changes during ripening. Food Chem. 132 (1), 86–97. https://doi.org/10.1016/j.foodchem.2011.10.037.

Abdipour, M., Hosseinifarahi, M., Naseri, N., 2019. Combination method of UV-B and UV-C prevents post-harvest decay and improves organoleptic quality of peach fruit. Sci. Hortic. 256, 108564. https://doi.org/10.1016/j.scienta.2019.108564.

Afrin, S., Gasparrini, M., Forbes-Hernandez, T.Y., Reboredo-Rodriguez, P., Mezzetti, B., Varela-López, A., Battino, M., 2016. Promising health benefits of the strawberry: a focus on clinical studies. J. Agric. Food Chem. 64 (22), 4435–4449. https://doi.org/10.1021/acs.jafc.6b00857.

An, X., Li, Z., Wegner, G., Zude-Sasse, M., 2023. Effect of cell size distribution on mechanical properties of strawberry fruit tissue. Food Res. Int. 169, 112787. https://doi.org/10.1016/j.foodres.2023.112787.

Avalos-Llano, K.R., Martín-Belloso, O., Soliva-Fortuny, R., 2018. Effect of pulsed light treatments on quality and antioxidant properties of fresh-cut strawberries. Food Chem. 264, 393–400. https://doi.org/10.1016/j.foodchem.2018.05.028.

Bai, C., Zheng, Y., Watkins, C.B., Ma, L., Jiang, Y., Chen, S., Zuo, J., 2025. Multiomics analyses of the effects of LED White light on the ripening of apricot fruits. J. Adv. Res. 67, 1–13. https://doi.org/10.1016/j.jare.2024.01.008.

Bantis, F., Smirnakou, S., Ouzounis, T., Koukounaras, A., Ntagkas, N., Radoglou, K., 2018. Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). Sci. Hortic. 235, 437–451. https://doi.org/10.1016/j.scienta.2018.02.058.

Bárcena, A., Martínez, G., Costa, L., 2025. The use of visible LEDs as technology to delay postharvest senescence of vegetables: a review. Plant Mol. Biol. Rep. 43, 11–22. https://doi.org/10.1007/s11105-024-01480-3.

Blanke, M., 2002. Photosynthesis of strawberry fruit. Acta Hortic. (567), 373–376. https://doi.org/10.17660/ActaHortic.2002.567.81. 〈https://doi.org/10.17660/ActaHortic.2002.567.81〉.

Boschiero, M., Zanotelli, D., Ciarapica, F.E., Fadanelli, L., Massimo Tagliavini, M, 2019. Greenhouse gas emissions and energy consumption during the post-harvest life of apples as affected by storage type, packaging and transport. J. Clean. Prod. 220, 45–56. https://doi.org/10.1016/j.jclepro.2019.01.30.

Campbell, S.M., Sims, C.A., Bartoshuk, L.M., Colquhoun, T.A., Schwieterman, M.L., Folta, K.M., 2020. Manipulation of sensory characteristics and volatile compounds in strawberry fruit through the use of isolated wavelengths of light. J. Food Sci. 85 (3), 771–780. https://doi.org/10.1111/1750-3841.15044.

Castillejo, N., Martínez-Zamora, L., Gómez, P.A., Pennisi, G., Crepaldi, A., Fernández, J. A., Orsini, F., Artés-Hernández, F., 2021 Jan 15. Postharvest LED lighting: effect of red, blue and far red on quality of minimally processed broccoli sprouts. J. Sci. Food Agric. 101 (1), 44–53. https://doi.org/10.1002/jsfa.10820.

Chong, L., Ghate, V., Zhou, W., Yuk, H.G., 2022. Developing an LED preservation technology to minimize strawberry quality deterioration during distribution. Food Chem. 366, 130566. https://doi.org/10.1016/j.foodchem.2021.130566.

Colquhoun, T.A., Schwieterman, M.L., Gilbert, J.L., Jaworski, E.A., Langer, K.M., Jones, C.R., Folta, K.M., 2013. Light modulation of volatile organic compounds from petunia flowers and select fruits. Postharvest Biol. Technol. 86, 37–44. https://doi.org/10.1016/j.postharvbio.2013.06.013.

Costa, G., Rocchi, L., Farneti, B., Busatto, N., Spinelli, F., Vidoni, S., 2016. Use of nondestructive devices to support pre-and postharvest fruit management. Horticulturae 3 (1), 12. https://doi.org/10.3390/horticulturae3010012.

Farneti, B., Emanuelli, F., Khomenko, I., Ajelli, M., Biasioli, F., Giongo, L., 2020. Development of a novel phenotypic roadmap to improve blueberry quality and storability. Front. Plant Sci. 11, 1140. https://doi.org/10.3389/fpls.2020.01140.

Farneti, B., Khomenko, I., Grisenti, M., Ajelli, M., Betta, E., Algarra, A.A., Giongo, L., 2017. Exploring blueberry aroma complexity by chromatographic and direct-injection spectrometric techniques. Front. Plant Sci. 8, 617. https://doi.org/10.3389/fpls.2017.00617.

Farneti, B., Khomenko, I., Pietrella, M., Martinatti, P., Emanuelli, F., Aprea, E., Maltoni, M.L., Baruzzi, G., Biasioli, F., Giongo, L., 2021. Development of a new phenotypic roadmap to improve strawberry aroma based on direct injection mass spectrometry. ISHS 2021. Proc. IX International Strawberry Symposium Acta Hortic. (1309). https://doi.org/10.17660/ActaHortic.2021.1309.138.

Figueroa, C.R., Rosli, H.G., Civello, P.M., Martínez, G.A., Herrera, R., Moya-León, M.A., 2010. Changes in cell wall polysaccharides and cell wall degrading enzymes during ripening of fragaria chiloensis and fragaria × ananassa fruits. Sci. Hortic. 124 (4), 454–462. https://doi.org/10.1016/j.scienta.2010.02.003.

Forney, C.F., Kalt, W., Jordan, M.A., 2000. The composition of strawberry aroma is influenced by cultivar, maturity, and storage. HortScience 35 (6), 1022–1026. https://doi.org/10.21273/HORTSCI.35.6.1022.

Giampieri, F., Tulipani, S., Alvarez-Suarez, J.M., Quiles, J.L., Mezzetti, B., Battino, M., 2012. The strawberry: composition, nutritional quality, and impact on human health. Nutrition 28 (1), 9–19. https://doi.org/10.1016/j.nut.2011.08.009.

Gong, D., Cao, S., Sheng, T., Shao, J., Song, C., Wo, F., Yang, Z., 2015. Effect of blue light on ethylene biosynthesis, signalling and fruit ripening in postharvest peaches. Sci. Hortic. 197, 657–664. https://doi.org/10.1016/j.scienta.2015.10.034.

Hu, L., Yang, C., Zhang, L., Feng, J., Xi, W., 2019. Effect of light-emitting diodes and ultraviolet irradiation on the soluble sugar, organic acid, and carotenoid content of postharvest sweet oranges (Citrus sinensis (L.) Osbeck). Molecules 24 (19), 3440. https://doi.org/10.3390/molecules24193440.

Jiang, Y., Joyce, D.C., Terry, L.A., 2001. 1-methylcyclcopropene treatment affects strawberry fruit decay. Postharvest Biol. Technol. 23, 227–232. DOI::10.1016/s0925-5214(01)00123-5.

Jiménez-Bermudez, S., Redondo-Nevado, J., Munoz-Blanco, J., Caballero, J.L., López-Aranda, J.M., Valpuesta, V., Mercado, J.A., 2002. Manipulation of strawberry fruit softening by antisense expression of a pectate lyase gene. Plant Physiol. 128 (2), 751–759. https://doi.org/10.1104/pp.010671.

Kalt, W., Prange, R.K., Lidster, P.D., 1993. Postharvest color development of strawberries: influence of maturity, temperature, and light. Can. J. Plant Sci. 73 (2), 541–548. https://doi.org/10.4141/cjps93-074.

Keutgen, A., Pawelzik, E., 2007. Modifications of taste-relevant compounds in strawberry fruit under NaCl salinity. Food Chem. 105 (4), 1487–1494. https://doi.org/10.1016/j.foodchem.2007.05.033.

Kim, B.S., Lee, H.O., Kim, J.Y., Kwon, K.H., Cha, H.S., Kim, J.H., 2011. An effect of light emitting diode (LED) irradiation treatment on the amplification of functional components of immature strawberry. Hortic. Environ. Biotechnol. 52, 35–39. https://doi.org/10.1007/s13580-011-0189-2.

Kim, D., Ra, I., Son, J.E., 2023. Fruit quality and volatile compounds of greenhouse sweet peppers as affected by the LED spectrum of supplementary interlighting. J. Sci. Food Agric. 103 (5), 2593–2601. https://doi.org/10.1002/jsfa.12439.

Lauria, G., Piccolo, E.L., Davini, A., Castiglione, M.R., Pieracci, Y., Flamini, G., Landi, M., 2023. Modulation of VOC fingerprint and alteration of physiological responses after supplemental LED light in Green-and red-leafed sweet basil (Ocimum basilicum L.). Sci. Hortic. 315, 111970. https://doi.org/10.1016/j.scienta.2023.111970.

Li, W., Zhang, J., Sun, J., Chen, K., Guan, X., Zhang, K., Fang, Y., 2023. Light irradiation with different wavelmengths modifies the quality traits and monoterpenes biosynthesis of postharvest grape berries during the shelf life. LWT 185, 115164. https://doi.org/10.1016/j.lwt.2023.115164.

Lu, W., Li, W., Zhao, K., Bai, X., Zhang, Y., Li, Q., Wang, X.X., 2025. Blue light irradiation combined with low-temperature storage further enhances postharvest quality of strawberries through improving antioxidant defense and cell wall metabolic activities. Food Chem. X 25, 102115. https://doi.org/10.1016/j.fochx.2024.102115.

Mattivi, F., Guzzon, R., Vrhovsek, U., Stefanini, M., Velasco, R., 2006. Metabolite profiling of grape: flavonols and anthocyanins. J. Agric. Food Chem. 54 (20), 7692–7702. https://doi.org/10.1021/jf061538c.

Mi, H., Zhou, X., Yang, J., Chen, J., Liu, B., 2023. LED White light treatment delays postharvest senescence of 'Zaosu'pear fruit with inhibited chlorophyll degradation. Horticulturae 10 (1), 32. https://doi.org/10.3390/horticulturae10010032.

Mditshwa, A., Magwaza, L.S., Tesfay, S.Z., Opara, U.L., 2024. Shining a light on postharvest decay: how Light-Emitting diodes modulate fungal Pathogen–Fruit interactions and activate plant defenses. Foods 13 (2), 294.

Nassarawa, S.S., Abdelshafy, A.M., Xu, Y., Li, L., Luo, Z., 2021. Effect of light-emitting diodes (LEDs) on the quality of fruits and vegetables during postharvest period: a review. Food Bioprocess Technol. 14, 388–414. https://doi.org/10.1007/s11947-020-02534-6.

Nunes, M.C.N., Brecht, J.K., Morais, A.M.M.B., Sargent, S.A., 2006. Physicochemical changes during strawberry development in the field compared with those that occur in harvested fruit during storage. J. Sci. Food Agric. 86 (2), 180–190. https://doi.org/10.1002/jsfa.2314.

Pelayo, C., Ebeler, S.E., Kader, A.A., 2003. Postharvest life and flavor quality of three strawberry cultivars kept at 5°C in air or air+20 kpa CO2. Postharvest Biol. Technol. 27 (2), 171–183. https://doi.org/10.1016/S0925-5214(02)00059-5.

Perera, W.P.T.D., Navaratne, S., Wickramasinghe, I., 2022. Impact of spectral composition of light from light-emitting diodes (LEDs) on postharvest quality of vegetables: a review. Postharvest Biol. Technol. 191, 111955. https://doi.org/10.1016/j.postharvbio.2022.111955.

Pott, D.M., e Lima, F.D.A., Soria, C., Willmitzer, L., Fernie, A.R., Nikoloski, Z., Vallarino, J.G., 2020. Metabolic reconfiguration of strawberry physiology in response to postharvest practices. Food Chem. 321, 126747. https://doi.org/10.1016/j.foodchem.2020.126747.

Priyadarshi, R., Jayakumar, A., de Souza, C.K., Rhim, J.W., Kim, J.T., 2024. Advances in strawberry postharvest preservation and packaging: a comprehensive review. Compr. Rev. Food Sci. Food Saf. 23, e13417. https://doi.org/10.1111/1541-4337.13417.

Salentijn, E.M., Aharoni, A., Schaart, J.G., Boone, M.J., Krens, F.A., 2003. Differential gene expression analysis of strawberry cultivars that differ in fruit-firmness. Physiol. Plant. 118 (4), 571–578. https://doi.org/10.1034/j.1399-3054.2003.00138.x.

Schwieterman, M.L., Colquhoun, T.A., Jaworski, E.A., Bartoshuk, L.M., Gilbert, J.L., Tieman, D.M., Folta, K.M., 2014. Strawberry flavor: diverse chemical compositions, a seasonal influence, and effects on sensory perception. PLoS One 9 (2), e88446. https://doi.org/10.1371/journal.pone.0088446.

Sparacino, A., Ollani, S., Baima, L., Oliviero, M., Borra, D., Rui, M., Mastromonaco, G., 2024. Analyzing strawberry preferences: Best–worst scaling methodology and purchase styles. Foods 13 (10), 1474. https://doi.org/10.3390/foods13101474.

Straube, J., Hurtado, G., Zeisler-Diehl, V., et al., 2024. Cuticle deposition ceases during strawberry fruit development. BMC Plant Biol. 24, 623. https://doi.org/10.1186/s12870-024-05327-7.

Ulrich, D., Kecke, S., Olbricht, K., 2018. What do we know about the chemistry of strawberry aroma? J. Agric. Food Chem. 66 (13), 3291–3301. https://doi.org/10.1021/acs.jafc.8b01115.

Van de Poel, B., Vandendriessche, T., Hertog, M.L.A.T.M., Nicolai, B.M., Geeraerd, A., 2014. Detached ripening of non-climacteric strawberry impairs aroma profile and fruit quality. Postharvest Biol. Technol. 95, 70–80. https://doi.org/10.1016/j.postharvbio.2014.04.012.

Vergara-Domínguez, H., Ríos, J.J., Gandul-Rojas, B., Roca, M., 2016. Chlorophyll catabolism in olive fruits (var. Arbequina and Hojiblanca) during maturation. Food Chem. 212, 604–611. https://doi.org/10.1016/j.foodchem.2016.06.020.

Vicente, A.R., Costa, M.L., Martínez, G.A., Chaves, A.R., Civello, P.M., 2002. Effect of heat treatments on cell wall degradation and softening in strawberry fruit. Postharvest Biol. Technol. 25 (2), 147–160. https://doi.org/10.1016/S0925-5214(01)00162-9.

Wang, Y., Li, Y., Feng, Y., Hou, Z., Xia, R., Wang, Z., Xin, G., 2025. Light-based improvement technology for postharvest fruits and vegetables flavor and regulation mechanism: a review. Crit. Rev. Food Sci. Nutr. 1–23. https://doi.org/10.1080/10408398.2025.2458165.

Wang, S., Jin, N., Jin, L., Xiao, X., Hu, L., Liu, Z., Yu, J., 2022. Response of tomato fruit quality depends on period of LED supplementary light. Front. Nutr. 9, 833723. https://doi.org/10.3389/fnut.2022.833723.

Xu, F., Cao, S., Shi, L., Chen, W., Su, X., Yang, Z., 2014b. Blue light irradiation affects anthocyanin content and enzyme activities involved in postharvest strawberry fruit. J. Agric. Food Chem. 62 (20), 4778–4783. https://doi.org/10.1021/jf501120u.

Xu, F., Shi, L., Chen, W., Cao, S., Su, X., Yang, Z., 2014a. Effect of blue light treatment on fruit quality, antioxidant enzymes and radical-scavenging activity in strawberry fruit. Sci. Hortic. 175, 181–186. https://doi.org/10.1016/j.scienta.2014.06.012.

Xu, P., Zawora, C., Li, Y., Wu, J., Liu, L., Liu, Z., Lian, H., 2018. Transcriptome sequencing reveals role of light in promoting anthocyanin accumulation of strawberry fruit. Plant Growth Regul. 86, 121–132. https://doi.org/10.1007/s10725-018-0415-3.

Yang, J., Li, C., Kong, D., Guo, F., Wei, H., 2020. Light-mediated signaling and metabolic changes coordinate stomatal opening and closure. Front. Plant Sci. 11, 601478. https://doi.org/10.3389/fpls.2020.601478.

Zhang, M., Meng, X., Bhandari, B., Fang, Z., 2007. Recent application of modified atmosphere packaging (MAP) in fresh and fresh-cut foods. Food Rev. Int. 23 (2), 103–127. https://doi.org/10.1080/87559120701224830.

Zhang, Y., Hu, W., Peng, X., Sun, B., Wang, X., Tang, H., 2018. Characterization of anthocyanin and proanthocyanidin biosynthesis in two strawberry genotypes during fruit development in response to different light qualities. J. Photochem. Photobiol. B 186, 225–231. https://doi.org/10.1016/j.jphotobiol.2018.07.024.

Zhou, L., Tang, R., Li, X., Tian, S., Li, B., Qin, G., 2021. N6-methyladenosine RNA modification regulates strawberry fruit ripening in an ABA-dependent manner. Genome Biol. 22, 168. https://doi.org/10.1186/s13059-021-02385-0.