

Research Paper

High daily light integral at end of production improves lettuce nutritional quality

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ABSTRACT

End-of-Production (EoP) lighting, which involves adjusting light intensity or spectrum a few days before harvest, is particularly effective in vertical farms and greenhouses using artificial lighting. Increased EoP light intensity has been found to improve lettuce nutritional quality and to extend the shelf life, but the simultaneous changes in daily light integral (DLI) and cumulative light sum (CLS, cumulative light sum received during the EoP phase) complicate the understanding of these effects. This study aims to investigate the effects of different EoP light factors, including light intensity, photoperiod, DLI and CLS on the nutritional quality of lettuce (*Lactuca sativa* L.), focusing on carbohydrates and total ascorbic acid (Vitamin C, TAsA) levels. We applied six EoP light treatments with varying light intensities (200, 240, 300, 360 and 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and photoperiods (16, 20 and 24 h d^{-1}) over six days. DLI was either 17 or 26 $\text{mol m}^{-2} \text{d}^{-1}$. High DLI in EoP lighting increased carbohydrates and TAsA levels in lettuce, regardless of whether the high DLI was achieved through longer photoperiod or higher light intensity. At a given DLI, longer photoperiod with lower light intensity resulted in higher carbohydrates and TAsA levels compared to shorter photoperiod with higher light intensity. Prolonging EoP lighting period (e.g. from 2 to 6 days) with low DLI did not affect nutritional quality despite higher CLS. Our findings show that the most effective way to enhance lettuce nutritional quality is through EoP lighting with higher DLI created by a longer photoperiod.

1. Introduction

Fresh lettuce (*Lactuca sativa* L.), a major leafy vegetable cultivated in vertical farms, is an important choice in health-conscious diets worldwide (Joint WHO/FAO Expert Consultation, 2003; Righini et al., 2023; Serafini et al., 2002). Lettuce nutritional value is often highlighted by high concentrations of carbohydrates and vitamin C (total ascorbic acid, TAsA, the sum of ascorbic acid and dehydroascorbic acid), which not only influence its flavor but also provide various health advantages (Chadwick et al., 2016; Medina-Lozano et al., 2021; Shi et al., 2022). Carbohydrates serve as the primary precursors and energy sources for the biosynthesis of various secondary metabolites, including ascorbic acid (AsA) which is an important antioxidant in lettuce (Medina-Lozano

et al., 2021). An improved content of both carbohydrates and AsA is positively correlated with the delayed deterioration of postharvest visual quality and longer shelf life of lettuce (Kandel et al., 2024; Min et al., 2021; Woltering and Seifu, 2015). Both the improved health-related benefits and longer shelf life may further contribute to a higher market value.

The concentration of carbohydrates and AsA in leafy products varies with cultivar, growing conditions, the practices of harvest and storage (Thapa et al., 2022; Zhan et al., 2013; Zhao et al., 2024). Light conditions are a crucial factor influencing the levels of these nutritional compounds and their metabolism, including light factors like intensity (photosynthetic photon flux density, PPF), photoperiod, spectrum, as well as the direction and duration of light exposure (Bian et al., 2015;

Abbreviations: AsA, total ascorbic acid; CLS, cumulative light sum; DLI, daily light integral; DMC, Dry matter content; DW, Dry weight; EoP, End of Production; FW, Fresh weight; GR, Glutathione reductase; GSH, Glutathione; LED, light-emitting diode; L-GalLDH, L-galactone-1,4-lactone; PPF, photosynthetic photon flux density; TAsA, total ascorbic acid (sum of ascorbic acid and dehydroascorbic acid).

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Min et al., 2023; Paradiso and Proietti, 2022; Wang et al., 2021; Yan et al., 2019a). Light intensity is one of the most studied light factors. Increased light intensity during growth generally elevates sugar content by enhancing photosynthesis and likely increase ASA through activation of biosynthesis-related genes and enzymes, improved respiratory electron transport, redox homeostasis disruption and sufficient precursors (Bartoli et al., 2000; Min et al., 2023; Ntagkas et al., 2018).

Vertical farming and greenhouse cultivation with artificial lighting (Light Emitting Diodes, LEDs) offers great potential for fine-tuning lighting conditions and optimizing the nutritional quality before harvest (van Delden et al., 2021). End-of-Production (EoP) lighting refers to changing the light factors shortly before harvest. EoP lighting provides the advantage in enhancing crop quality without interference with the regular growth cycle: it is ideally suited for vertical farms scenarios where artificial light is used as the only light source (Kaiser et al., 2024). Higher light intensity in EoP lighting generally improves crop quality in terms of nutrition, pigmentation and shelf life (Larsen et al., 2022; Shao et al., 2020; Zhou et al., 2021). An increased light intensity of 475 $\mu\text{mol m}^{-2} \text{s}^{-1}$ significantly increased the levels of carbohydrates and TAsA within only 6 days, and such nutritional enhancement positively correlated with a prolonged shelf life (Min et al., 2021). However, many studies on varying light intensities face the challenge in understanding the effect of different light factors due to the simultaneous changes in daily light integrals (DLI, a function of light intensity and photoperiod)

and cumulative light sum (CLS).

Our study aims to investigate which light factor—light intensity, photoperiod, DLI, or CLS—is more important in influencing the growth and nutritional quality of lettuce during EoP lighting. We established six EoP lighting treatments by different combinations of light intensities and photoperiods, which were grouped in two DLI levels and lasted for 6 days. By analyzing the changes in carbohydrate concentrations (sucrose, glucose, fructose, and starch), ascorbic acid levels, fresh weight, and dry weight during EoP light exposure, we investigated the effects of different light factors on lettuce nutritional quality.

2. Materials and methods

2.1. Plant growth and EOP light treatments

Lettuce (*Lactuca sativa* L. cv. Expertise RZ) was germinated and cultivated in a climate chamber (Philips GrowWise Research center, Eindhoven, the Netherlands). The complete experimental process including the germination phase, cultivation phase and EoP lighting phase is illustrated in Fig. 1.

Seeds were sown in plug trays (Quick Plug, Monster, the Netherlands) with one seed per plug at a plant density of 59 plants m^{-2} . The seeds were kept in a darkness for 2 days, followed by 8 days exposure to red-blue LED lighting with a PPFD of 140 $\text{m}^2 \text{s}^{-1}$ (Red: Blue =

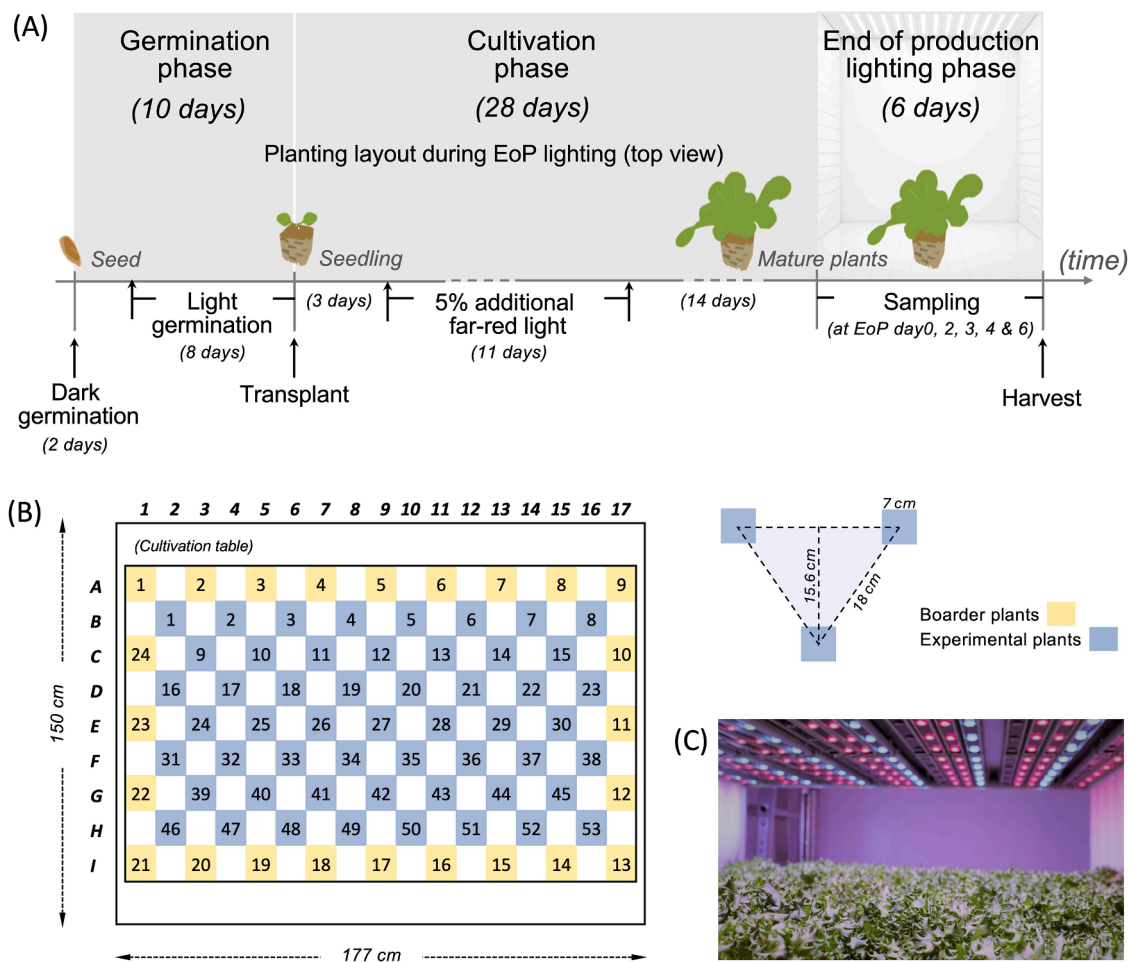


Fig. 1. Overview of the experimental setup and timeline. A) Timeline of the experiment illustrating the major phases in the experiment: germination, cultivation and the End-of-Production (EoP) lighting. The germination phase began with two days of darkness, followed by eight days under light. An additional 5 % of far-red light to the total PPFD was applied midway through the cultivation phase and stopped two weeks before the EoP lighting began. Five sampling timepoints were conducted during the EoP lighting phase to measure the change of nutritional qualities of the lettuce. (B) Schematic representation of the planting frame and plant layout during the EoP lighting phase on the cultivation table. The diagram includes detailed table dimensions, plant-to-plant spacing, and the positions and numbers of border and experimental plants. (C) Photograph taken on the first day of one EoP lighting treatment, showing the lighting position relative to the plant canopy.

88: 12, Philips Green Power LED research modules) and 16-hour photoperiod (dark period from 16:00 to 24:00).

For the cultivation phase, seedlings with two true leaves and uniform morphology were selected and transplanted into stone wool blocks (size $7 \times 7 \times 7$ cm, Grodan Rockwool, The Netherlands) at day 9 after sowing. These seedlings were then grown under a $240 \pm 2.52 \mu\text{mol m}^{-2} \text{s}^{-1}$ light with red+white LEDs (red and white Philips Green Power LED research modules, Fig. 2A) with a 20-hour photoperiod (dark period 20:00 to 0:00) (Table 1). An additional 5 % of far-red (FR) light ($12 \mu\text{mol m}^{-2} \text{s}^{-1}$, far-red Philips Green Power LED research module) was applied midway during the cultivation phase, starting 3 days after transplanting and ending two weeks before the EoP light treatments. Far-red was applied to mimic the commercial growing recipe (provided by Philips GrowWise Research center, Eindhoven, the Netherlands). Plants were positioned using a chessboard design and respaced twice to avoid shading by neighboring plants until reaching a density of $35.6 \text{ plants m}^{-2}$. Before the EoP lighting started, plants were distributed onto independent cultivation tables where individualized EoP light treatments were applied. Each table hosted 77 plants including 24 border plants. All experimental plants were rotated one or two times a week in both row and column directions to ensure uniform illumination over the plants over time. The cultivation tables were separated by white reflective plastic film, allowing enough distance between the film edge and table surface to ensure proper airflow. The airflow with a speed of $0.3 \pm 0.1 \text{ m s}^{-1}$ was provided from one end of the cultivation table via a plenum wall into the layer of a vertical farm chamber made of 4 growth layers.

After 38 days from sowing, the 6-days EoP light treatment started. The six EoP lighting treatments comprised of two DLI groups (26 and 17

$\text{mol m}^{-2} \text{d}^{-1}$). Within each DLI group, three combinations of photoperiod and light intensity (PPFD) were applied (Table 1). Each group was designed to reach the same cumulative light sum (CLS) over different treatment durations (Fig. 2B and Table 2). To minimize light interference between treatments, the light periods for all EoP light treatments started simultaneously (Table 1). The light spectrum for all EoP light treatments was similar as applied during the cultivation phase with no added far-red (Fig. 2A). The treatment of $240 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a 20-hour photoperiod was considered as the control group, which maintained similar light conditions throughout the cultivation and EoP lighting phases (Table 1). Light intensity (PPFD) was adjusted through the dimmable control of LED lamps, while the final average PPFD, PPFD distribution, and spectrum was verified using spectrometer (Jeti, Technische Instrumente GmbH, Germany) with 12 evenly distributed measurements at the height of crop canopy (~ 15 cm from the table) from each treatment (Table 1).

For seed germination phase, the average relative humidity was set at 80 %, while for cultivation and EoP lighting phases, the relative air humidity was kept at 70 % during the light period and 80 % during the dark period. CO_2 concentration was maintained at 800 ppm. The air temperature during the growth phase was set to 20°C and 18°C for the light and dark periods, respectively. During the EoP phase, the temperature was maintained at 20°C . Within each EoP light treatment, canopy-level temperature was measured using calibrated K-type thermocouples (shielded with aluminum foil to avoid direct radiation from the LED lamps) connected to TC-80 data loggers (Picotechnology Ltd., Cambridge, United Kingdom), placed at both the center and corner of each cultivation table. Temperature differences among treatments did not exceed 0.5°C . Temperature differences among treatments did not exceed 0.5°C . The irrigation solution was supplied through ebb and flood system and had the following composition: N-NO_3 , 12.9; N-NH_4 , 1.5; P-PO_4 , 1.2; K , 8.8; Ca , 4.2; Mg , 0.4; Cl , 1.5; S-SO_4 , 1.5 mmol L^{-1} ; Fe , 30.7; B , 38.3; Cu , 0.8; Zn , 3.8; Mn , 3.8; and Mo , $0.4 \mu\text{mol L}^{-1}$ ($\text{pH} = 6$ and $\text{EC} = 2.3 \text{ mS cm}^{-1}$).

2.2. Sampling and determination of fresh and dry weight

Fully expanded mature leaves with uniform size were harvested from the middle whorls of the lettuce head (Supplementary Figure 1) at 6-hours after light period started as sample materials for quality measurements. During the entire experiment, each of the 76 experimental plants in each EoP light treatment contributed at most one leaf, with four randomly selected leaves pooled to form one biological sample. This approach minimized the impact of leaf collection on plant growth and ensured uniformity with limited number of suitable leaves available from the middle whorls. Sampling during the EoP lighting phase was conducted on days 2, 3, 4, and 6, with four biological samples collected at each time point. Each biological sample is a pooled sample that consisted of four leaves, each leaf randomly selected from a different plant among the 76 experimental plants, resulting in a total of 16 leaves per sampling. On day 0 (before start of EoP lighting), leaf samples were collected from surplus plants excluded from the EoP treatments, ensuring enough plants remained for subsequent sampling.

For quality measurements, including carbohydrate concentrations (sucrose, glucose, fructose, and starch) and TASA, were performed using four biological samples. Each biological sample was immediately frozen in liquid nitrogen and stored at -80°C . The leaf dry matter content (DMC_{leaf} , defined as the ratio of dry weight to fresh weight) of each biological sample was determined along with the preparation of freeze-dried materials for carbohydrate analysis.

Addition to the DMC_{leaf} measured during EoP phase, the fresh weight of the entire lettuce heads (FW_{head} , all above-ground parts without roots) was measured. Thereafter the samples were oven-dried at 70°C for 3 days to determine lettuce head dry weight (DW_{head}) and DMC_{head} during the both the cultivation phase (on day 12, 22, 29, and 36 after sowing) and the EoP lighting phase (on day 4 and 6). These

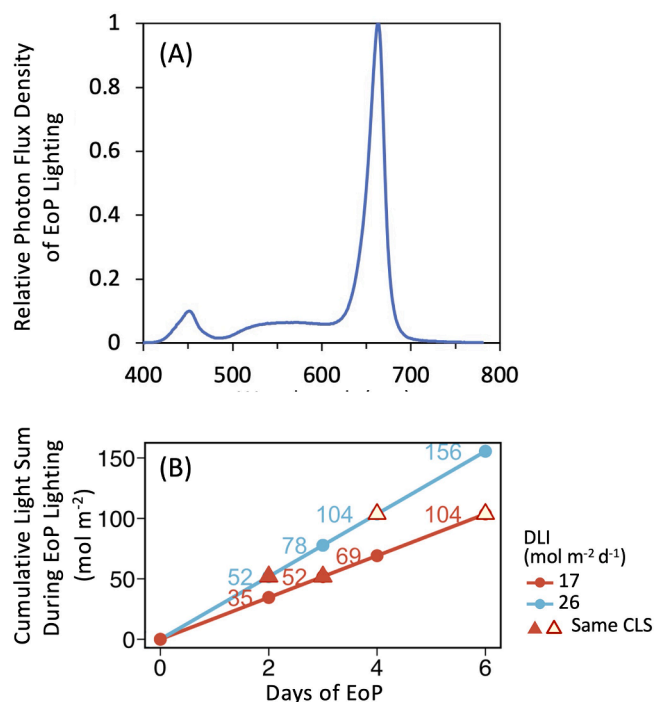


Fig. 2. The spectra and cumulative light sums of End-of-Production (EoP) lighting. (A) The relative photon distribution of red+white LEDs used during both the cultivation and the EoP lighting phase. (B) The cumulative light sum (CLS) of EoP lighting is plotted across the 6-day EoP phase for two daily light integral (DLI) levels. Different DLI groups achieved the same CLS at different time points (Triangles with yellow fill and red borders). For example, the treatment 450 – 16 h in the high DLI group reached a CLS of 104 mol m^{-2} on day 4, and the treatment 300 – 16 h in the low DLI group achieved the same CLS level on day 6. Highlighted points (yellow-filled triangles with red borders) indicate these specific conditions, with numerical values above each point representing their respective CLS values.

Table 1

Light intensity (PPFD), photoperiod and Daily light integral for the light conditions in cultivation phase and End-of-Production (EoP) lighting phase.

Treatments PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) - Photoperiod (h)	Cultivation phase		EoP lighting phase			
	Measured PPFD \pm se ^b ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Photoperiod (h)	Measured PPFD \pm se ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Photoperiod (h)	Dark period time	Daily light integral ($\text{mol m}^{-2} \text{d}^{-1}$)
450 - 16h	237 \pm 2.5	20	441 \pm 4.4	16	20:00–4:00	26 ^c
360 - 20h	237 \pm 2.5	20	352 \pm 6.5	20	00:00–4:00	26
300 - 24h	237 \pm 2.5	20	305 \pm 4.9	24	-	26
300 - 16h	237 \pm 2.5	20	294 \pm 6.4	16	20:00–4:00	17 ^c
240 - 20h (control) ^a	237 \pm 2.5	20	237 \pm 2.5	20	00:00–4:00	17
200 - 24h	237 \pm 2.5	20	200 \pm 3.1	24	-	17

^a The green shading in the background indicates the treatment with $\sim 240 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 20-hours photoperiod that is considered as the control treatment; here plants received the same PPFD and photoperiod during both cultivation and EoP phase.

^b For all treatments, lettuce received 5 % far-red light in addition to total PPFD, midway through the cultivation phase for 11 days which stopped two weeks before the EoP lighting began. The dark period starts from 20:00 and ends in 00:00 in cultivation phase.

^c The blue and red shading in the background represents two treatment groups with different daily light integral (DLI) levels: 26 and 17 $\text{mol m}^{-2} \text{d}^{-1}$, respectively.

Table 2

The Cumulative Light Sum (CLS) after 2, 3, 4 and 6 days of End-of-Production (EoP) for treatments with different Daily Light Integral (DLI).

Daily light integral ($\text{mol m}^{-2} \text{d}^{-1}$)	Cumulative light sums (CLS) during EoP lighting (mol m^{-2})			
	Day 2	Day 3	Day 4	Day 6
26	51.8^a	77.8	103.7^a	155.5
17	34.6	51.8^a	69.1	103.7^a

^a The EoP light treatments belonging to two DLI groups reached identical CLS by applying different lighting durations, as indicated in bold italics in the table.

measurements were conducted using four intact plants (without leaves harvested), each representing one biological sample.

2.3. Determination of carbohydrates

The concentration of carbohydrates was measured according to Min et al. (2021) with modifications. Carbohydrates were extracted from 15 mg freeze-dried powdered samples by mixing them with 5 mL 80 % ethanol and shaken in a water bath at 80 °C for 20 min. After centrifugation at 8500 \times g (Universal 320R, Hettich, Germany) and 4 °C for 5 min, 1 mL of the supernatant was collected and dried in a vacuum centrifuge (Savant SpeedVac SPD2010, Thermo Fisher Scientific, United states) for 1.75 h at 55 °C and 5.1 mBar for analysis of sucrose, glucose, and fructose. The remaining supernatant and precipitate were stored at -20 °C for starch analysis. The dried supernatant was mixed with 1 mL of 0.01 M HCl and placed in ultrasonic bath (Branson Ultrasonic Cleaning Bath 2800, Branson Branson, United states) at room temperature for 5 min. To elute soluble sugars, the samples were passed through the SPE column (Extract Clean SCX 100 mg per 1.5 mL, Grace, United states), which had been rinsed 3 mL of H₂O, 5 mL of 0.01 M HCl, and 0.5 mL samples before use. The eluted sample was then diluted 10 times for HPLC analysis of soluble sugars.

For starch analysis, the supernatant was carefully removed from the stored samples. The precipitate was then washed with 3 mL of ethanol, vortexed, and centrifuged at 8800 \times g for 5 min; this rinsing step was repeated three times. After rinsing, the pellet was dried in a vacuum centrifuge (Savant SpeedVac SPD2010, Thermo Fisher Scientific, United states) at 55 °C and 5.1 mbar for 20 min. 2 mL of alpha-amylase solution (1 g L⁻¹, SERVA Electrophoresis GmbH, Germany) was then added to the dried sample, and then incubated for 30 min in a water bath at 90 °C. After adding 1 mL amyloglucosidase (0.5 mg mL⁻¹ in 50 mM citrate buffer, pH=4.6), the samples were incubated in the shaking water bath for 10 min at 60 °C. Finally, the samples were centrifuged at 21,100 \times g for 5 min and diluted 20 times with Milli-Q water for the HPLC analysis of glucose.

Soluble sugars were quantified using High Performance Anion Exchange Chromatography with Pulsed Amperometric Detection (HPAEC-

PAD; Dionex ICS5000 using 250 \times 2 mm CarboPac1 column, Thermo Fisher Scientific, United states). Analysis was conducted with 100 mM NaOH at a flow rate of 0.25 mL min⁻¹. Carbohydrate concentrations were calculated based on fresh weight and expressed in mg g_{FW}⁻¹.

2.4. Determination of total ascorbic acid

The total ascorbic acid (TAsA) was measured according to Min et al. (2021) with modifications. Frozen leaf samples were ground into fine powder with liquid nitrogen and in a shaded environment. 300 mg of the ground samples were melted on ice in the dark and extracted with 1.5 mL of ice-cold 3.3 % meta-phosphoric acid (MPA). The mixed solution was then vortexed for 20 s and placed in an ultrasonic bath for 10 min at 0 °C in darkness. After 10 min centrifugation at 25,000 \times g, 100 μ L extract was filtered by 0.45 μ m cellulose filter and added with 50 μ L of 5 mM dithiothreitol (DTT) in 400 mM Tris base to convert dehydroascorbic acid (DHA) to ascorbic acid (AsA). After 15 min incubation at room temperature in darkness, 50 μ L of 8.5 % o-phosphoric acid was added to stop the reaction.

Ascorbic acid was quantified using a High-Performance Liquid Chromatography system (HPLC; P580 pump with 340S UV-VIS detector, Dionex, United states) equipped with a ProntoSIL 120-3 C18 AQ column (250 \times 3 mm, Knauer, Germany). The column was eluted with a solution containing 400 μ L L⁻¹ H₃PO₄, 2.5 mL L⁻¹ MeOH, and 0.1 mM EDTA, at a flow rate of 0.35 mL min⁻¹, followed by a wash with 30 % acetonitrile. The system was calibrated using 1 mM AsA standard prepared in 3.3 % MPA and stabilized with 2.5 mM DTT. TAsA was calculated as the sum of the directly measured AsA and the AsA converted from DHA and expressed on the basis on fresh weight in mg 100g_{FW}⁻¹.

2.5. Statistical analysis

Four biological samples ($n = 4$) were prepared for each treatment at each sampling time to determine the average values of quality traits. Polynomial regression was employed to examine changes in lettuce quality traits over time within each DLI group during the EoP lighting phase (108 total biological samples, across 2 DLI groups and 5 time points). The detailed statistical results of second-order polynomial regression, including parameter estimates (intercept, linear and quadratic coefficients for both DLI groups), standard errors, t-values, P-values, 95 % CI and model performance (R² and residual standard error), are provided in Supplementary Table 2. A two-way ANOVA analysis was conducted to assess the effects of duration (days) of EOP and DLI levels on lettuce quality and growth parameters; the significance (P-value) of main effects and interaction terms was indicated in the corresponding graphs. Normality was tested using the Shapiro-Wilk test, and homogeneity of variances was assessed with Levene's or Bartlett's test in advance. Carbohydrates and ascorbic acid data satisfied the normality

and homogeneity tests, whereas variance homogeneity for individual soluble sugars and dry matter content was assumed as these tests were not feasible.

For lettuce quality traits in response to increasing light intensity, data collected from days 2, 3, 4, and 6 were combined within each EoP light treatment. Within each DLI group, linear regression was performed to evaluate the relationship between quality traits and light intensity; the significance of regression slopes (P_{DLI17} and P_{DLI26}) of each DLI group were indicated in the corresponding graphs. Subsequently, a linear regression model with interaction terms was then applied to test whether the slopes differed significantly between the DLI groups. Next, a common-slope linear regression model was applied to test for differences in intercepts among the DLI groups (96 total observations, across 6 EoP light treatments). The common slope (ComSlope, represents the shared slope across the two DLI groups), intercept difference (IntDiff, reflects the difference in intercepts between their respective regression lines) and their corresponding significance (P -value) were indicated in the graphs. These values are only shown in the relevant figures when statistically significant. Outputs from linear regression analyses are provided in Supplementary Table 3, including parameter estimates (intercepts for both DLI and the common slope), standard errors, t -values, P -values, 95 % CI and model performance (R^2 and residual standard error). All statistical analyses were conducted in R (version 4.4.1, <http://www.R-project.org>).

3. Results

3.1. High DLI during EoP enhanced lettuce ascorbic acid level

Under the high DLI treatment ($26 \text{ mol m}^{-2} \text{ d}^{-1}$), lettuce TAsA concentration increased from 18.9 to 21.4 $\text{mg } 100\text{g}_{\text{FW}}^{-1}$ (by $\sim 13\%$) during six days of EoP lighting, whereas under the low DLI treatment ($17 \text{ mol m}^{-2} \text{ d}^{-1}$), it decreased to 16.8 $\text{mg } 100\text{g}_{\text{FW}}^{-1}$ (by $\sim 11\%$) compared with the initial level at day 0 (Fig. 3A). The interaction between DLI and EoP days was significant ($F = 6.57$, $df = 4$). At the same light intensity ($300 \mu\text{mol m}^{-2} \text{ s}^{-1}$), lettuce under continuous lighting (24 h light period, where DLI is high), showed a higher TAsA concentration compared to those under 16 h light period (Fig. 3B). In both DLI groups, the longer photoperiod with lower light intensity resulted in a higher TAsA concentration compared to a shorter photoperiod with higher light intensity (Fig. 3B).

The positive effect of high DLI on TAsA concentration was not significantly affected by the CLS. When low and high DLI groups reached the identical CLS of 52 mol m^{-2} at day 3 and day 2, and 104 mol m^{-2} at day 6 and day 4, respectively (Fig. 3B), lettuce in high DLI group exhibited 23 % higher AsA concentration compared those in low DLI group (20.7 vs $16.8 \text{ mg } 100\text{g}_{\text{FW}}^{-1}$), even though they were shorter exposed to EoP lighting.

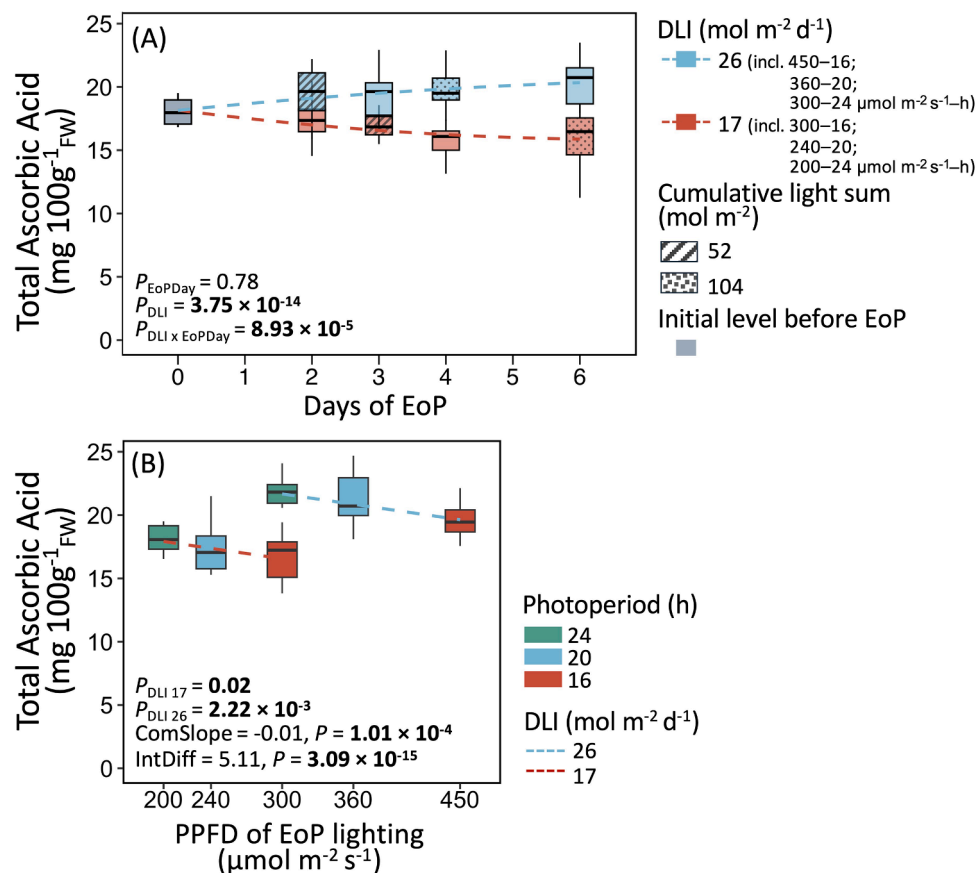


Fig. 3. The total ascorbic acid (TASA, $\text{mg } 100\text{g}_{\text{FW}}^{-1}$) levels in lettuce in response to End-of-Production (EoP) light treatments. (A) The time course of TASA concentration for each DLI group during the 6 days (5 time points) EoP lighting phase; (B) TAsA concentration of each DLI group in response to PPFD. In panel (A), each box plot from day 2 onwards is based on combination of three EoP light treatments with same DLI levels ($n = 12$). At day 0, both DLI groups share the same data collected before the start of EoP lighting ($n = 4$). Dashed lines represent the polynomial trend lines for two DLI groups each. The P -value for the main effects of DLI (P_{DLI}) and Days of EoP (P_{EoPDay}), and their interaction ($P_{\text{DLI} \times \text{EoPDay}}$) are indicated. In panel (B), each box represents the data from four sampling times (days 2, 3, 4 and 6) under the same EoP light treatment. Two linear trend lines are fitted with a common slope (ComSlope) but different intercepts (IntDiff); both values and their corresponding P -values are shown on the plot. Significant values ($P < 0.05$) in both panels are shown in bold. Center line of box plot represents median; box represent 2nd and 3rd quartiles; whiskers represent min and max value.

3.2. High DLI during EoP quickly boosted carbohydrates levels

The response of carbohydrates concentration to different light factors was similar to that observed for TAsA. Sucrose, glucose, fructose and starch, were elevated under higher DLI conditions (Fig. 4 and Supplementary Figure 2). Extended photoperiod from 16 h to 24 h at the same light intensity ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$) increased carbohydrate levels, while within each photoperiod tested (16-, 20- or 24-hours), higher light intensity (associated with higher DLI) always increased carbohydrates levels (Fig. 4B). The enhancement of carbohydrates (sucrose, glucose and starch) was quickly established after the application of high DLI and was sustained throughout the six-day EoP lighting period (Fig. 4A). Conversely, the content of carbohydrates remained low and close to the initial level over time under low DLI conditions (Fig. 4A). The interaction between DLI and EoP days was significant ($F = 12.63$, $df = 4$).

The increase of CLS over time did not significantly affect carbohydrates concentration in either high or low DLI groups (Fig. 4A). By day 6, carbohydrates level in the low DLI group ($262.5 \text{ mg g}_{\text{FW}}^{-1}$) was 8.6 % lower than that in the high DLI group on day 4 ($285.1 \text{ mg g}_{\text{FW}}^{-1}$), despite both DLI groups having the same CLS (Fig. 4A). Similarly, increasing CLS did not affect the high DLI effect on individual soluble sugars and starch (Supplementary Figure 2 A, C and D).

At both DLI levels, increased light intensity combined with shortened photoperiod led to a reduction in carbohydrates concentration compared to a lower light intensity with longer photoperiod (Fig. 4B).

Similar effects were found for fructose and starch concentration (Supplementary Figure 2 G and H), however, sucrose increased with higher light intensity and shorter photoperiod (Supplementary Figure 2 E). Glucose only decreased with higher light intensity in the low DLI group (Supplementary Figure 2 F).

3.3. High DLI during EoP enhanced lettuce yield and longer photoperiods improved dry matter content

High DLI increased the dry matter content of lettuce leaves (DMC_{leaf}) by 33 % (from 6.3 % to 8.4 %) after six-days EoP lighting (Fig. 5). Similar to carbohydrates, DMC_{leaf} increased rapidly after the start of EoP lighting with high DLI and was maintained at high level thereafter. In the low DLI group, the DMC_{leaf} of lettuce leaves remained steady over the six days EoP. The interaction between DLI and EoP days was significant ($F = 7.618$, $df = 4$). After CLS in the low DLI group increased to match the levels of the high DLI group with prolonged exposure duration, DMC_{leaf} in the low DLI group (6.8 % on day 6) was still 23 % lower than that in the high-DLI group (8.4 % on day 4) (Fig. 5A). Within each DLI group, the combination of longer photoperiod with lower light intensity resulted in higher DMC_{leaf} compared to the combination of a shorter photoperiod with higher light intensity (Fig. 5B).

Both fresh weight and dry weight of the whole lettuce head (all above-ground parts, FW_{Head} and DW_{Head} respectively) increased and the dry matter content (DW_{Head}) gradually decreased during cultivation

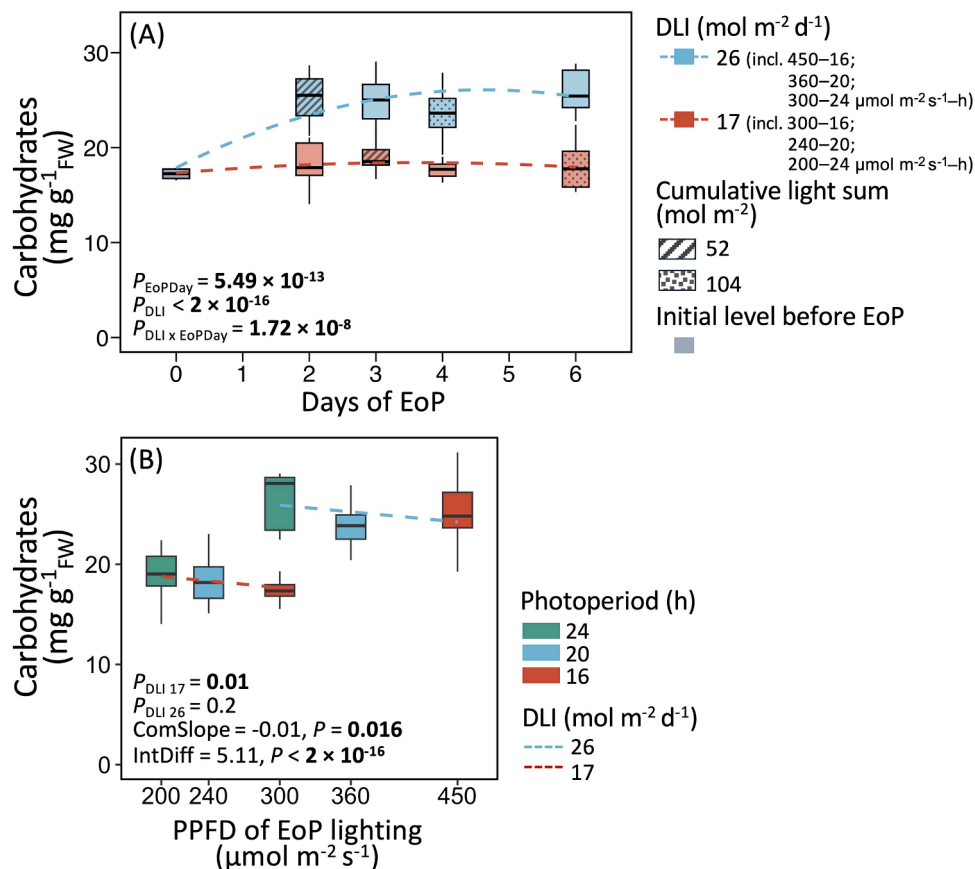


Fig. 4. Carbohydrate levels ($\text{mg g}_{\text{FW}}^{-1}$) in lettuce in response to End-of-Production (EoP) light treatments. (A) The time course of carbohydrates concentration (the sum of sucrose, glucose, fructose and starch) for each DLI group during 6 days (5 time points) EoP lighting phase; (B) The total carbohydrates concentration of each DLI group in response to PPFD. In panel (A), each box plot from day 2 onwards is based on combination of three EoP light treatments with same DLI levels ($n = 12$). At day 0, both DLI groups share the same data collected before the start of EoP lighting ($n = 4$). Dashed lines represent the polynomial trend lines for two DLI groups each. The P -value for the main effects DLI (P_{DLI}) and Days of EoP (P_{EoPDay}), and their interaction ($P_{\text{DLI} \times \text{EoPDay}}$) are indicated. In panel (B), each box represents the data from four sampling times (days 2, 3, 4 and 6) under the same EoP light treatment. Two linear trend lines are fitted with a common slope (ComSlope) but different intercepts (IntDiff); both values and their corresponding P -values are shown on the plot. Significant values ($P < 0.05$) in both panels are shown in bold. Center line of box plot represents median; box represent 2nd and 3rd quartiles; whiskers represent min and max value.

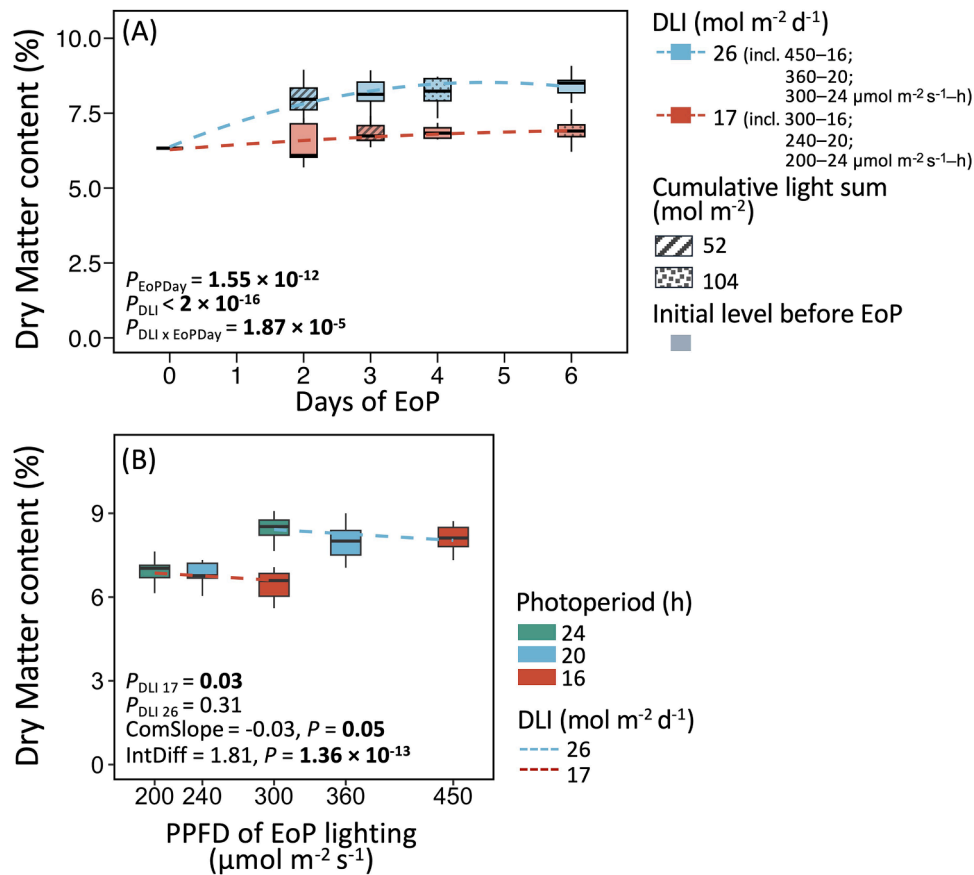


Fig. 5. Dry matter content of lettuce leaves (DMC_{leaf} , %) in response to End-of-Production (EoP) light treatments. (A) The time course of DMC_{leaf} for each DLI group during the 6 days (5 time points) EoP lighting phase; (B) DMC_{leaf} of each DLI group in response to PPFD. In panel (A), each box plot from day 2 onwards is based on combination of three EoP light treatments with same DLI levels ($n = 12$). At day 0, both DLI groups share the same data collected before the start of EoP lighting ($n = 4$). Dashed lines represent the polynomial trend lines for two each DLI groups each. The P -value for the main effects of DLI (P_{DLI}) and Days of EoP (P_{EoPDay}), and their interaction ($P_{\text{DLI} \times \text{EoPDay}}$) are indicated. In panel (B), each box represents the data from four sampling times (days 2, 3, 4 and 6) under the same EoP light treatment. Two linear trend lines are fitted with a common slope (ComSlope) but different in intercepts (IntDiff); both values and their corresponding P -values are shown on the plot. Significant values ($P < 0.05$) in both panels are shown in bold. Center line of box plot represents median; box represent 2nd and 3rd quartiles; whiskers represent min and max value.

from day 12 to day 26 (Fig. 6D, E and F; Supplementary Methods 2). During the final two days of EoP (EoP day-4 to day-6), FW_{Head} and DW_{Head} continued to increase, while DMC_{Head} decreased slightly (Fig. 6). High DLI significantly enhanced DW_{Head} , and DMC_{Head} compared to low DLI (Fig. 6B and C). No significant interaction effects were found among EoP days, DLI levels, and photoperiod on these traits (Fig. 6A, B and C), while increasing photoperiods increased DMC_{Head} (Fig. 5C).

4. Discussion

4.1. High DLI is the key factor to improve lettuce nutritional quality

Exposure to high light intensity generally increases the levels of carbohydrates and antioxidants in plants. In lettuce, these compounds are important quality attributes that potentially enhance flavor, provide health benefits, and extend the shelf life; features that may contribute to higher market value (Kim et al., 2016; Nicolle et al., 2004).

Previous studies have shown that increasing light intensity during both the cultivation and EoP phases leads to higher concentration of soluble sugars, ascorbic acid, anthocyanin, and other antioxidants in crops such as *Arabidopsis*, tomato, sweet pepper, basil, and lettuce (Cammarisano et al., 2020; Larsen et al., 2020; Liu et al., 2018; Shao et al., 2020; Yan et al., 2019b; Zhou et al., 2012). In most of these experiments different light intensities were applied while keeping the

photoperiod constant, leading to concurrent changes in DLI. DLI is defined as the total amount of photosynthetic active radiation (PAR, 400–700 nm) received per square meter over 24 h. DLI is a function of light intensity (PPFD, $\mu\text{mol m}^{-2}\text{s}^{-1}$) and photoperiod (h, hours of light period per 24-hour), it influences plant photosynthesis, biomass, morphology, and pigmentation (Blanchard et al., 2011; Gavhane et al., 2023; Zauli et al., 2024; Zhu et al., 2024). However, it remains unclear whether the enhancements in lettuce nutritional quality under EoP lighting are driven by higher light intensity, increased DLI, or both, and what the contribution of photoperiod and CLS would be.

4.1.1. Nutritional enhancement under high DLI may reflect photosynthetic performance

Our results suggest that higher DLI, either achieved by higher light intensity or longer photoperiod, is a key factor in improving lettuce nutritional quality. While we confirmed the previously reported positive effect of high DLI achieved by increased light intensity with a fixed photoperiod on lettuce carbohydrate and TAsA levels (Min et al., 2021). More importantly, we found that extending the photoperiod while maintaining the same light intensity, the elevated DLI also significantly increases both TAsA and carbohydrates concentration during EoP phase (Fig. 3B and 4B). For example, the TAsA increased with 29 % by extending the photoperiod from 16 to 24 h at 300 $\mu\text{mol m}^{-2}\text{s}^{-1}$ light intensity.

At a given DLI level during EoP, the carbohydrates and TAsA levels

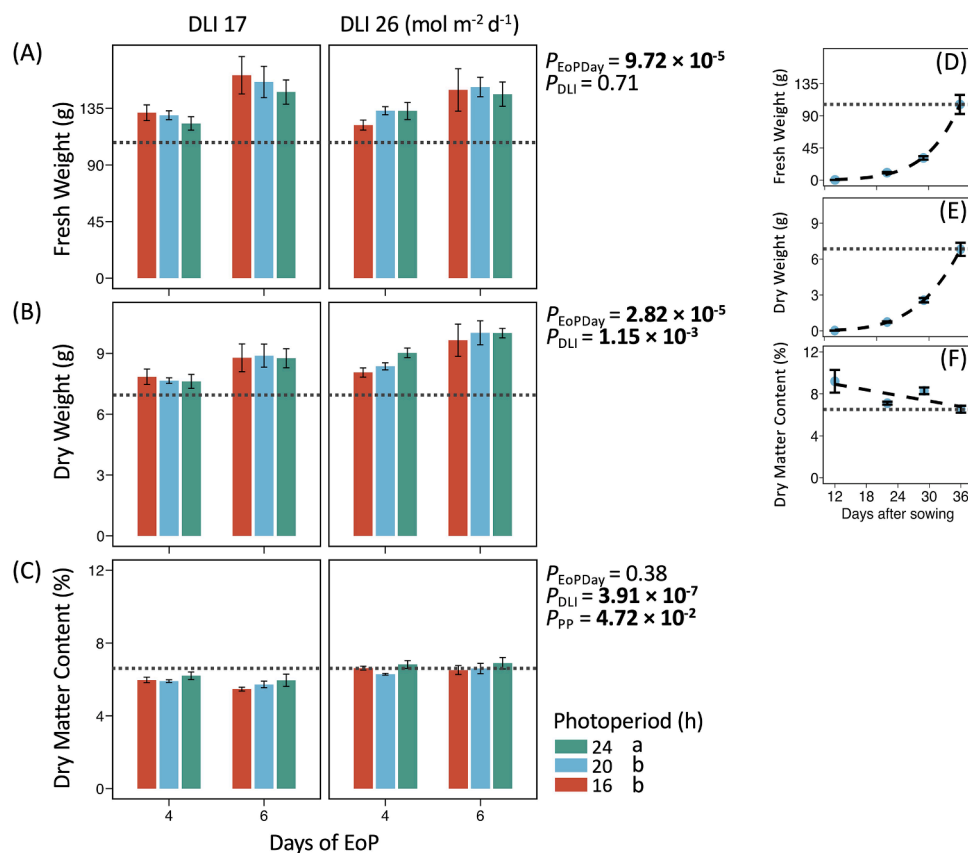


Fig. 6. The response of fresh weight (all above-ground parts; FW_{Head}, g), dry weight (DW_{Head}, g), and dry matter content (DMC_{Head}, %) of lettuce head to different photoperiods under two DLI levels. Panels (A–C) represent the FW_{Head}, DW_{Head} and DMC_{Head} during the EoP lighting phase, while panels (D–F) represent the FW_{Head}, DW_{Head} and DMC_{Head} during the cultivation phase. The black dotted line in all panels indicates the initial levels of FW_{Head}, DW_{Head} and DMC_{Head} before the EoP lighting started (EoP lighting started at 38 days after sowing). Each bar represents the average of four biological samples (n = 4). The P-value for the main effects Days of EoP (P_{EoPDay}), DLI (P_{DLI}), Photoperiod (P_{PP}) are indicated, with significant values (P < 0.05) shown in bold. Different letters in the legend of panel (C) indicate significant differences between photoperiods (P < 0.05) based on Fisher's Protected LSD. In panel D–F, dashed line indicated the growth curves for FW_{Head} and DW_{Head} (double exponential Gompertz function), and the linear regression for DMC_{Head} from 12 to 36 days after sowing, data points represent the mean value of four biological samples (n = 4). Error bars indicate the standard errors, which may be hidden by the data points when they are small.

were higher under longer photoperiods with lower light intensity compared to shorter photoperiods with higher light intensity. This suggests that lettuce exposed to lower light intensities over longer duration within a 24-hour diurnal cycle performed better in terms of nutritional quality. Similar positive effects of longer photoperiod were found previously on plant photosynthesis, fresh and dry weight during cultivation (Boucher et al., 2023; Elkins and van Iersel, 2020; Kelly et al., 2020) but their influence on nutritional quality has been less studied. This result may be explained by the reduced photosynthetic efficiency at higher light intensities. Photosynthetic light response curves measured for control plants on day 25 after sowing (cultivation phase, Supplementary Methods 1) showed that net leaf photosynthesis (A_n) increased linearly until light intensity up to about 200 μmol m⁻² s⁻¹, after which photosynthetic efficiency decreased and became non-linear (Supplementary Figure 4 and Table 1). In our EoP light treatments, light intensities in the high DLI group ranged from 300 to 450 μmol m⁻² s⁻¹ where the efficiency of leaf photosynthesis started to decline. Similar results were found in Elkins and van Iersel's (2020) research, where increasing PPFD from 189 to 794 μmol m⁻² s⁻¹ reduced ΦPSII from 0.67 to 0.28, indicating a decrease in light use efficiency under higher light intensities.

4.1.2. Relationship with photosynthetic efficiency and AsA biosynthesis

The direct link between photosynthesis and AsA biosynthesis is well studied (Ntagkas et al., 2018), with evidence showing that AsA biosynthesis is active under light with active photosynthesis but drops

sharply in darkness or with inhibited photosynthesis (Yabuta et al., 2007). This suggests that reduced photosynthetic efficiency under higher light intensity may also limit AsA biosynthesis (Müller-Moulé et al., 2004). Light as an independent regulator of the AsA biosynthesis was also confirmed by experiments showing that photosynthetic inhibitors blocked AsA accumulation even under light conditions. In addition, supplementing exogenous sucrose in darkness did not restore AsA levels to those observed in light in *Arabidopsis* leaves (Yabuta et al., 2007), and similarly, sucrose feeding failed to increase AsA levels under both light and dark conditions in off-vine tomato fruits (Ntagkas et al., 2019). This light-driven process suggests that prolonged darkness in a 24-hour cycle (short photoperiod) may disrupt these processes, resulting in decreased AsA levels. In our previous study, both carbohydrate and TAsA levels declined sharply when transfer lettuce into darkness (Min et al., 2021), a trend consistent with findings in *Arabidopsis* (Bartoli, 2006).

The increased photosynthetic efficiency at lower light intensities may also explain why longer photoperiods with lower light intensities resulted in higher carbohydrate levels at the same DLI. Carbohydrates, as key precursors for AsA biosynthesis (Wheeler et al., 1998), show positive correlations with AsA concentrations (Larsen et al., 2022; Min et al., 2021), this trend was also observed in the current experiment where higher carbohydrates level under both DLI conditions were associated with increased AsA during EoP (Supplementary Figure 3). Although the role of light in AsA accumulation is independent of sugar availability, sugars still contribute to AsA accumulation as precursors in

the biosynthetic pathway. Sugar feeding experiments have shown that exogenous precursors, such as sucrose, glucose, or *L*-galactone-1, 4-lactone (*L*-Gall) positively correlated with increased AsA under light conditions. This effect is achieved through increased precursor availability, the upregulation of key genes, and regulatory role of the photosynthetic electron transport chain in driving AsA biosynthesis (Cao et al., 2015; Xu et al., 2016; Yabuta et al., 2008).

4.1.3. Role of antioxidants and redox regulation under high DLI

AsA is a crucial antioxidant that maintains redox homeostasis and protects plants from oxidative stress. High light condition could induce ROS (reactive oxygen species) production, which stimulates AsA biosynthesis and regeneration through enhanced enzyme activity (e.g., ascorbate peroxidase, APX) to scavenge ROS and protect Photosystem I (PSI) from oxidative damage (Foyer, 2018). AsA regeneration is important for continuous ROS detoxification and is influenced by light conditions through glutathione (GSH) activity in the AsA-GSH cycle. Under high DLI, GSH, via glutathione reductase (GR), reduces DHA to AsA, sustaining antioxidant defense in plants (Zha et al., 2019). High light intensity enhances the activity of the electron transport chain in both respiration and photosynthesis, stimulating alternative oxidase (AOX) and maintaining cytochrome *c* and the plastoquinone pool in their oxidized states, which together promote AsA biosynthesis (Bartoli, 2006; Yabuta et al., 2007).

4.2. High DLI EoP lighting rapidly enhances lettuce nutritional quality, while increased cumulative light sum shows no additional benefit

Under high DLI, both carbohydrates and TAsA levels increased rapidly during the first day of EoP lighting; carbohydrates then stabilized, whereas TAsA continued to rise and peaked on EoP day 6. This rapid response aligns with previous findings in lettuce and *Arabidopsis* exposed to high light (Bartoli, 2006; Shao et al., 2020; Zhou et al., 2021). In our experiment, extending the growing period by six days under low DLI increased CLS but did not further increase carbohydrates and TAsA. Even when the low DLI treatments reached the same CLS as the high DLI group (e.g., 103.68 mol m⁻² on day 6 vs. day 4 for high DLI), both traits remained lower under low DLI, indicating that cumulative light alone cannot compensate for 'insufficient' daily light boost.

The limited benefit of higher CLS reflects the physiological dynamics of carbohydrates and TAsA. Carbohydrates and leaf dry weight respond directly to increased photosynthesis and typically reach a new steady state within 1–2 days after a change in DLI (Shen et al., 2024). In the same study, root dry weight increased only after 48 h, indicating that the early rise in assimilates largely retained within the shoot before being redistributed. After this initial adjustment, additional assimilates are preferentially directed to younger expanding leaves, the main sinks before bolting, rather than further increasing soluble sugar levels in mature leaves. TAsA accumulates more slowly and is influenced by cellular redox homeostasis; elevated DLI increases ROS and activates AsA biosynthesis and regeneration pathways (Zha et al., 2019; Shen et al., 2024). Once a new redox homeostasis is established under a given DLI, extending EoP duration increases CLS but may not provide additional oxidative stimulus to further enhance TAsA.

Developmental progression further limits the effect of prolonged EoP lighting. At day 35 after sowing, lettuce had reached commercial maturity, a stage at which sugars and antioxidants generally begin to decline (Supplementary Figure 1) (Boros et al., 2023; Min et al., 2021). The six-day EoP period represents almost one-fifth of the growth cycle, and the intermediate-whorl leaves sampled on day 6 may already be physiologically older, with reduced sink competitiveness and limited capacity to accumulate additional carbohydrates or antioxidants. Thus, prolonging EoP duration mainly advances leaf ageing rather than improving nutritional quality.

4.3. High DLI and longer photoperiods in EoP enhance lettuce growth and the accumulation of glucose, fructose, and starch

Six days of EoP lighting with high DLI effectively enhanced lettuce yield (FW_{Head} and DW_{Head}), and dry matter content (DMC_{leaf} and DMC_{Head}) at the final cultivation stage (Fig. 5 and 6). This aligns with previous research showing significantly increases in lettuce fresh weight when DLI rose from 4 to 18 mol m⁻² d⁻¹ (Kohler and Runkle, 2024; Solis-Toapanta and Géomez, 2019). Leaf DMC was increased with longer photoperiods at a constant DLI, consistent with the response of DMC_{Head} and carbohydrates concentration. However, the photoperiod effect on the whole head may be diluted by the inclusion of leaves from all maturities, and no significant effect of photoperiod was found on FW_{Head} or DW_{Head}. This is in contrast of findings of Kelly et al. (2020), who reported increases in lettuce DW and FW under longer photoperiods and lower light intensities at a constant DLI of 15.6 mol m⁻² d⁻¹, which is lower than our low DLI treatment (17 mol m⁻² d⁻¹).

In our study, sucrose, glucose, fructose, and starch exhibited similar responses to high DLI during EoP as total carbohydrate (Supplementary Figure 2, Supplementary Table 2 and 3). The short-term exposure to continuous light allows photosynthetic leaves to continuously produce and retain sugars. For lettuce at the final cultivation stage (Supplementary Figure 1), these fully expanded leaves are also the harvested products, making this sugar retention particularly beneficial. Notably, at the same DLI, sucrose decreased with longer photoperiods, while starch, glucose and fructose increased (Supplementary Figure 2. E, F, G, and H). This aligns with the findings of Mengin et al. (2017), who reported that longer photoperiods (12 h) promote *Arabidopsis* growth compared to shorter photoperiods (6 h) at a fixed DLI (4 or 8 mol m⁻² d⁻¹). Under longer photoperiods, net carbon gain during the light period was greater, and net carbon loss during the dark period was smaller. Shorter photoperiods with higher light intensity increased the accumulation rates of sugars and starch, but the limited photosynthesis duration resulted in lower total net carbon gain over a day. In contrast, longer photoperiods supported immediate use of photosynthates for growth, reducing dependence on reserves during the dark period. In our study, the shortest photoperiod (16 h) and lower DLI (17 mol m⁻² d⁻¹) both far exceeded those in Mengin et al.'s (2017) work. The greater sugar accumulation observed under longer photoperiods in our results is likely linked to the extended duration of photosynthesis.

Exposure to high light conditions with poor air circulation may increase the risk of tip burn (Yu et al., 2024), applying high DLI only during the final days before harvest may help to reduce this risk, as no tip burn was observed in this study. Increasing DLI, whether through higher light intensity, longer photoperiods, or both, results in greater energy use. Although higher quality with high yield often brings higher profit, the energy cost remains a key consideration for practical applications of light treatments. Compared with maintaining high light throughout the entire cultivation period, applying high DLI only during the final 2–6 days (approximately 6–20 % of the lettuce cultivation cycle) can deliver effective quality improvements with relatively low cumulative energy input. For vertical farms, an EoP light treatment maintaining the same light intensity as the cultivation phase (240 μmol m⁻² s⁻¹) while extending the photoperiod to 24 h for two days is recommended. This approach increases DLI and improves lettuce quality without requiring additional lighting fixtures, reducing the technical barriers for implementation. It is also important to note that prolonged continuous lighting in EoP might lead to photoinhibition (Zha et al., 2019). In greenhouse production, growers can flexibly achieve a high-DLI EoP treatment by using artificial lighting either through photoperiod extension or by supplemental lighting, depending on season and geographical location. Greenhouse-based validation will be necessary to confirm its applicability under fluctuating environmental conditions. In addition, growers may further optimize energy use and cost by scheduling lighting in accordance with daily electricity price fluctuations (Kaiser et al., 2024). Exploring light spectra during the EoP

phase presents another promising avenue for improving crop quality. Long wavelengths (red and far-red) may enhance growth, while short wavelengths (blue and UV) may stimulate secondary metabolite production (Liu et al., 2018; Thoma et al., 2020; Van Brenk et al., 2024). Since shorter wavelengths require more energy than longer ones, optimizing spectral composition may maximize nutritional benefits while minimizing energy costs (Van Brenk et al., 2024).

5. Conclusion

Higher daily light integral (DLI) applied shortly before harvest (End of Production), achieved through longer photoperiods or increased light intensity, substantially enhanced carbohydrates (+14 %), total ascorbic acid levels (+13 %), and dry matter content (+33 %) of lettuce. DLI, rather than cumulative light sum, was the critical determinant of lettuce nutritional quality. At the same DLI, longer photoperiods with lower light intensity resulted in greater nutritional improvements than shorter photoperiods with higher intensity. Based on our results, extending the photoperiod to 24 h for two days before harvest at $240 \mu\text{mol m}^{-2} \text{s}^{-1}$, could improve lettuce quality without interfering the regular growth cycle. While this study demonstrates the potential of short-term high DLI to enhance lettuce nutritional quality, further validation across different cultivars and under diverse cultivation environments will be necessary to assess the general applicability.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to correct English grammar. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRedit authorship contribution statement

Qianxixi, Min: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Leo F.M. Marcellis:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Céline C.S. Nicole:** Writing – review & editing, Funding acquisition, Conceptualization. **Ernst J. Woltering:** Writing – review & editing, Validation, Supervision, Resources, Project administration, 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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2025.114566.

Data availability

Data will be made available on request.

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