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Increasing the Red Fraction in Light-emitting Diode Supplemental Light Enhances Yield Without Affecting the Quality of Greenhouse-grown Lettuce (*Lactuca sativa* L.)

Annalisa Somma
Department of Soil, Plant and Food Sciences, University of Bari Aldo Moro, Via Amendola 165/a, 70126 Bari, Italy; and Horticulture and Product Physiology, Department of Plant Sciences, Wageningen University and Research, Wageningen, The Netherlands

Ying Liu and Lorenzo B.A. Nielen
Horticulture and Product Physiology, Department of Plant Sciences, Wageningen University and Research, Wageningen, The Netherlands

Sebastian Olschowski
Fluence, 4129 Commercial Center Drive, Austin, TX 78744, USA

Ep Heuvelink and Leo F.M. Marcelis
Horticulture and Product Physiology, Department of Plant Sciences, Wageningen University and Research, Wageningen, The Netherlands

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Abstract. **Supplemental lighting by light-emitting diodes (LEDs) in a greenhouse allows for spectral flexibility, which may enhance plant growth and morphology, yield, quality, light use efficiency, and electric energy efficiency (yield/kWh). A greenhouse experiment of two lettuce (*Lactuca sativa* L.) cultivars (green-leaved and reddish-leaved) grown under four supplemental LED light spectra at a photosynthetic photon flux density of 200 µmol·m^{-2}·s^{-1} and containing 38%, 63%, 81%, or 95% red photons (red fraction) in combination with blue, green, and far-red wavebands was conducted. Yield and growth parameters, like the total plant biomass, increased linearly with an increasing red fraction for both cultivars. In general, spectral effects were stronger in the reddish-leaved cultivar, in which leaf fresh weight increased by 35% compared with only 10% in the green-leaved cultivar. The red fraction barely affected lettuce quality (pigment, total phenolic compounds, vitamin C, total soluble sugar, starch, and mineral composition). The results indicated that a high red fraction in supplemental LED light enhances lettuce yield, light use and energy efficiency, and yield per kWh while preserving quality.**

Supplemental lighting is an important factor for greenhouse crop production in winter at high latitudes because natural light levels are low (Kusuma et al. 2022). Currently, LEDs are favored over other lamp technologies (e.g., high-pressure sodium and fluorescent lamps) because of their much higher light energy conversion efficiency (Katzin et al. 2021; Kusuma et al. 2020; Rea et al. 2023), and light-emitting diode (LED) modules have a versatile shape and compact dimension, produce less radiative heat, have a longer lifetime, can be spectral-customized, and can be dimmed (Paradiso and Proietti 2022). The possibility of fine-tuning the spectral composition allows supplemental lights to be optimized for specific purposes and genotypes (species or cultivar) because it affects physiological and metabolic processes that can lead to increased yield or improved product quality (Landi et al. 2020). The influence of the light spectrum on plant development and growth is complex and involves many processes that depend on other environmental conditions and the interactions among all the system components (Palmitessa et al. 2021; Sena et al. 2024).

Red photons represent the most effective waveband driving photosynthesis (McCree 1971). In addition, they have a lower energy content and, hence, more photons per unit of energy compared with lower wavebands, for example, blue. However, plants grown under monochromatic red light do not necessarily have optimal photosynthetic performance because red light can cause red light syndrome in plants, which is characterized by lower photosynthesis, altered morphology, and an altered metabolite profile (Hogewoning et al. 2012; Larsen et al. 2020). Therefore, supplemental LED spectra usually contain mostly red light and a small fraction of blue light or white light. Blue light is absorbed by plant chlorophylls, thus contributing to photosynthesis. Furthermore, blue light plays a role in the regulation of the stomatal opening, the reduction of stem elongation, and leaf expansion, and it can affect secondary metabolites in the plant (Hogewoning et al. 2010; Kaiser et al. 2019; Kong and Zheng 2024). Green light is known to penetrate deeper into the plant canopy compared with red light and blue light, and it can contribute to photosynthesis; therefore, the addition of green light to the artificial light spectrum can, in some cases, be beneficial for plant growth (Claypool and Heinrich Lieth 2021; Thoma et al. 2020). Further wavebands are often less regarded or applied to a smaller extent. Particular attention is given to far-red light (700–750 nm), which is abundant in sunlight. The far-red light and the red light:far-red light ratio influence metabolism, photosynthesis, and morphology as a function of the genotype and the phenological stage (Demotes-Mainard et al. 2016; Ji et al. 2021).

Lettuce (*Lactuca sativa* L.) is a worldwide-consumed leafy vegetable with interesting nutritional properties (Kim et al. 2016), and it is a well-suited crop for greenhouse cultivation (Li et al. 2021a; Wang et al. 2016). Lettuce is also the most investigated crop because of its light effects in indoor cropping systems (Nájera et al. 2023). Cultivar-specific responses to light spectra have been shown in lettuce (Frąszczak and Kula-Maximenko 2021; Gómez and Jiménez 2020; Ouzounis et al. 2016; Son and Oh 2015). A large number of lettuce cultivars are available, and these cultivars vary in their metabolic and physiological responses to light spectra (Frąszczak and Kula-Maximenko 2021). Lettuce cultivars may differ in leaf color; in green leaves, the prevalent pigments are chlorophyll a and chlorophyll b, whereas purple or reddish leaves are characterized by a high content of anthocyanins (Frąszczak and Kula-Maximenko 2021). The light spectrum is one of the most influential factors involved in the anthocyanin biosynthetic pathway (Ma et al. 2021); a high blue light fraction was found to be effective for the cryptochrome-driven production of anthocyanin (Mickens et al. 2018), whereas green light antagonizes the blue-induced response to cryptochrome, which results in the reduced accumulation of anthocyanins (Bouly et al. 2007;

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E.H. is the corresponding author. E-mail: ep.heuvelink@wur.nl.

Zhang and Folta 2012). Anthocyanins are known to absorb blue-green light, which is not used for photosynthesis (Albert et al. 2009). This difference in anthocyanin causes red leaves to have lower photosynthesis compared with green leaves of the same species when measured under the same conditions (Gould et al. 2002).

An increased fraction of red light (hereafter referred to as the "red fraction") is expected to be beneficial for crop photosynthesis and yield and to reduce the energy input needed for supplemental lights. This study aimed to determine the effects of the red fraction (replacing green and blue) in supplemental light with a fixed light intensity and photoperiod on lettuce by performing a comprehensive investigation of growth, yield, product quality, and the efficiency of supplemental lighting.

Materials and Methods

The study was performed in a closed greenhouse compartment (8 × 8 × 4 m) at Wageningen University (Wageningen, The Netherlands; 52°N, 5°E) from Nov 2021 to Mar 2022.

Plant material

Seeds of two loose-leaf lettuce (*Lactuca sativa* L.) cultivars (Lollo Rosso type, 'Satine', with reddish leaves, and Lollo Bionda type, 'Lugano', with green leaves; Rijk Zwaan, De Lier, The Netherlands) were sown in trays with 240 watered stone wool plugs (Grodan, Roermond, The Netherlands) topped with vermiculite. These trays were stored for 48 h at 4 °C in darkness to improve germination uniformity. After that, the trays were placed in a greenhouse nursery at an average 24-h temperature of 22.6 °C ± 0.5 °C (temporal variation) and relative humidity of 66.9% ± 8.4% (temporal variation). The seedlings were exposed to solar light and white supplemental LED light (Physiospec Greenhouse VYPR 2 × spectrum; Fluence Bioengineering, Austin, TX, USA). The supplemental light provided an average photoperiod of 15 h with a photosynthetic photon flux density (PPFD) of approximately 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At 10 d after sowing, seedlings at the stage of two visible true leaves were transplanted into another greenhouse compartment, where the light treatments were applied.

Growing conditions

Seedlings were transplanted and grown in a deep-water culture system in a greenhouse compartment. Each deep-water container (length, 60 cm; width, 40 cm; height, 63 cm) hosted eight plants and was equipped with a pipe for refreshing nutrient solution and an oxygenation pipe. The containers of each plot were contiguous. Each container was filled to the top with a nutrient solution and covered with a foam board. The boards were dressed in white plastic to reflect light and were pierced with eight holes for eight seedlings in stone wool plugs (Grodan, Roermond, The Netherlands) at 20 cm from each other, resulting in a planting density of 25 plants/m^2.

The average temperature during the day (when supplemental lights were on) was 22.6 °C, and the average temperature during the night (when supplemental lights were off) was 18.7 °C (Supplemental Table 1). The average relative humidity levels were 71% during the day and 83% during the night. Furthermore, the 24-h average CO_2 concentration was 655 ppm (range, approximately 580–730 ppm). The heating/cooling was provided by a ventilation air conditioning system on the sides of each greenhouse. Furthermore, a vertically oriented fan was placed above the screens in the middle of the compartment to create a uniform climate in the greenhouse. Greenhouse windows were closed during the entire experiment. Starting from transplanting, the photoperiod was 16 h. Lamps were switched off 30 min before sunset. The composition of the nutrient solution followed that reported by Min et al. (2021): NO_3^-, 12.91; NH_4^+, 0.38; $H_2PO_4^-$, 1.53; K^+, 8.82; Ca^{2+}, 4.22; Mg^{2+}, 1.15; SO_4^{2-}, 1.53; Cl^-,1.53 $mmol \cdot L^{-1}$; Fe^{3+}, 30.67; B^{3+}, 38.33; Cu^{2+}, 0.77; Zn^{2+}, 3.83; Mn^{2+}, 3.83; and Mo^+, 0.38 $\mu mol \cdot L^{-1}$ (pH = 6; electrical conductively = 2.3 $dS \cdot m^{-1}$). It was refreshed weekly with a new nutrient solution. The electrical conductivity and pH were measured weekly just before the nutrient solution was refreshed, and further checks were performed after refreshing. The nutrient solution was continuously oxygenated with an aeration pump (AirTec 4000; Vivaria, Leeuwarden, The Netherlands) that provided an average oxygen saturation of 93%, which was monitored weekly (Orion RDO oxygen probe; Thermo Fisher Scientific, Waltham, MA, USA). In addition to the supplemental light, plants received solar light (Supplemental Table 1). The greenhouse was equipped with a top screen (dek XLS Obscure Revolux A/B+B/W; Ludvig Svensson, Kinna, Sweden), thus reducing the incoming light by 75%. It was automatically closed when the outside solar radiation exceeded the threshold of 350 $W \cdot m^{-2}$ for 10 consecutive min. The solar radiation ($W \cdot m^{-2}$) outside of the greenhouse was measured every 5 min using a pyranometer sensor (Kipp en Zonen, Delft, The Netherlands). The solar PPFD inside the greenhouse was derived from the outside solar radiation data by applying a conversion factor, which varied according to the opening and closing of the top screen. To calculate the solar PPFD at the plant level, it was assumed that 1 W of solar radiation was equal to 2.1 μmol photosynthetically active radiation (McCree 1972; Thimijan and Heins 1983), and the greenhouse transmissivity was 0.57.

The health state of the plants was checked daily by visual assessments. Very limited tip burn symptoms were identified during all the growing cycles; however, they were constantly monitored and never compromised the morphology and dimension of the leaves, meaning that the growth and esthetic quality of the plants were unaffected.

Experimental design

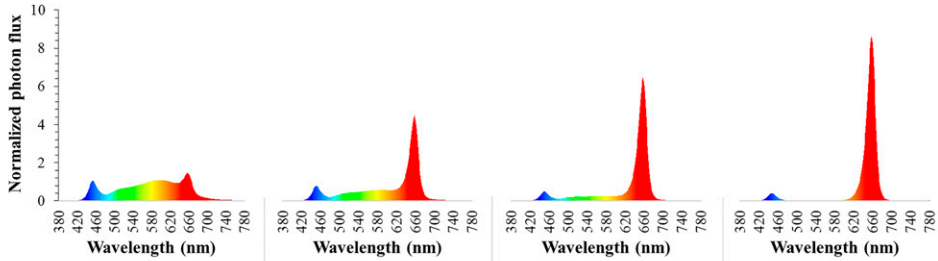
The greenhouse compartment was divided into four plots separated by light-reflecting screens (2.30 m height from ground level and approximately 25 cm above the lamp level); all four plots were also surrounded by light-reflecting screens to reduce exterior lighting effects. Each plot was exposed to a different light treatment and contained a total of 16 containers (eight for each cultivar). In each plot, for both cultivars, the external row consisted of border plants that surrounded the experimental plants. Three consecutive growing cycles were performed (approximately 6 weeks per cycle): cycle 1, November to December; cycle 2, December to January; and cycle 3, February to March. The growing cycles represented three blocks (replicates) of the experiment. The same experimental setup and conditions were applied to the three blocks. For each block, the light treatments were moved to the adjacent plot to minimize the entangling of light treatment with location in the greenhouse.

For every replicate, two harvests were performed: an intermediate harvest 36 d after sowing and a final harvest 43 d after sowing. The target weight of approximately 210 g per lettuce head was obtained at the final harvest. However, this type of lettuce could be also marketed at a smaller size with a target weight of approximately 160 g per lettuce head. Therefore, the results of growth, yield, and energy efficiency for the intermediate harvest with that target weight were additionally analyzed.

During the intermediate harvest, after the plants were collected, the position of the border plants was changed by adjusting the panels to guarantee that the remaining experimental plants were continuously surrounded by border plants and the planting density remained constant (Supplemental Fig. 1). This strategy was applied to all the plots.

Light treatments

The same four light spectra were compared (as in Kusuma et al. 2022) for greenhouse-grown tomatoes. Each plot contained six LED fixtures (VYPR 3p; Fluence Bioengineering, Austin, TX, USA). They consisted of blue plus red (R9B) or white plus red (R4, R6, R8), and they differed in the red fraction as a proportion of the PPFD (Fig. 1). By increasing the red fraction (600–699 nm) from 38% to 95%, the blue (400–499 nm), green (500–599 nm), and far-red (700–799 nm) percentages (as a proportion of PPFD) all decreased. The spectra were measured with a spectrometer (LI-180; LI-COR Inc., Lincoln, NE, USA), and the following blue light:green light:red light:far-red light ratios were observed: 19:43:38:1.2 for R4; 13:24:63:1.0 for R6; 8:11:81:0.6 for R8; and 5:0:95:0.3 for R9B (Fig. 1). The PPFD at the top of the plant canopy was 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This intensity was obtained by adjusting the lamp height (approximately 1.2 ± 0.1 m above the plants) and dimming using a control system (HCS-1 Hydro-X; TrolMaster, Xiamen, China).



	R4	R6	R8	R9B
Red	38	63	81	95
Blue	19	13	8	5
Green	43	24	11	0
Far-red	2.1	1.0	0.6	0.3
PSS	0.86	0.88	0.89	0.89
G:B	2.3	1.8	1.4	0.0
R:FR	18	60	132	295
Photon efficacy (µmol per J)	2.60	2.87	3.11	3.60

Fig. 1. Spectral photon distribution of the four treatments, R4, R6, R8, and R9B, normalized to a photosynthetic photon flux density (PPFD) of 200 µmol·m^{-2}·s^{-1}. Blue 400 to 499 nm (B), green 500 to 599 nm (G), and red 600 to 699 nm (R) as fractions of PPFD (400 to 700 nm), far-red 700 to 799 nm (FR) as a fraction of the PPFD in the range 400 to 800 nm are shown in the table. The photostationary state of phytochrome (PSS) values were calculated according to Sager et al. (1988). Photosynthetic photon efficacy was obtained from Kusuma et al. (2022).

Light treatments were applied from the day of transplanting (10 d after sowing). Before a new growing cycle, light intensity was measured using the spectrometer (LI-250A; LI-COR Inc., Lincoln, NE, USA) equipped with a Quantum Sensor (LI-190R; LI-COR Inc., Lincoln, NE, USA).

Plant measurements

All the growth, morphological, and yield measurements were performed on the harvest day. In addition, samples were collected for further analyses. A graphical summary of the experiment and the full measurements and analyses are provided in Fig. 2.

Yield, growth, and morphological measurements. Before harvest, plant height was measured as length from the foam board to the top of the center of the lettuce plant, and plant diameter was determined as the maximum diameter looking from above the plant. Yield was measured as the total fresh weight (FW) of leaves longer than 2 cm per plant. The same leaves were counted to obtain the leaf number per plant and measured using a LI-COR leaf area meter (LI-3100; LI-COR Inc., Lincoln, NE, USA) to determine the plant leaf area. Root and leaf dry weights (DWs) were determined after drying in a ventilated oven at 70 °C for 5 d. The incident light use efficiency (LUE) was calculated for the fresh and dry biomass of each treatment by dividing the leaf FW per m^2 (leaf FW × crop density) and the leaf DW per m^2 (leaf DW × crop density) by the cumulative incident light (sum of photosynthetically active radiation of LED lamps and solar light measured inside the compartment). Electric energy use efficiency was calculated by referring to the lettuce yield (leaves FW/m^2) produced per kWh of supplemental lighting. In detail, the yield was divided by the photons applied in every block for each lamp treatment and multiplied by the photosynthetic photon efficacy (Fig. 1); then, joules were converted to kilowatt-hours by multiplying by the constant 3.6×10^6 J·kWh^{-1}. Photosynthetic photon efficacy was obtained from the work of Kusuma et al. (2022), who tested the same lamps.

Lettuce quality and nutritional profile

The samples for quality analyses were obtained as pooled sample leaves from eight plants harvested 43 d after sowing for each treatment, for each block. Specifically, the selected sample leaf from each plant consisted of one fully expanded adult leaf that was also the most exposed to light among the adult leaves. The pooled leaves were quickly frozen in liquid nitrogen, ground with a frozen analytical mill (A11 basic; IKA, Staufen, Germany), and stored at –80 °C.

Phytochemical compounds. Chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, total phenolic compounds, and total flavonoids contents were measured according to the sequential colorimetric method described by López-Hidalgo et al. (2021), which was named the "rainbow protocol." A sample of 50 to 70 mg of ground fresh-frozen tissue was incubated in an iced ultrasonic bath for 10 min and subsequently centrifuged for 10 min at 8500 g_n. Only the supernatant was considered as described in the protocol.

Soluble sugars and starch analysis. The carbohydrates myo-inositol, glucose, fructose, and sucrose were measured as described by Plantenga et al. (2019) with adaptations. In brief, 15 mg of ground frozen dried material was weighed and mixed with 5 mL of 85% ethanol. The sample underwent a 10-min ultrasonic bath, a shaking water bath for 20 min at 80 °C, and centrifugation at 8500 g_n for 5 min. Then, 1 mL of supernatant (containing soluble sugars) was vacuum-dried using a vacuum concentrator (Savant SpeedVac SPD2010; Thermo Fisher Scientific) at 50 °C; the pellet was later used for starch determination. Then, 1 mL of Milli-Q water was added to the supernatant, and the sample was placed in the ultrasonic bath for 10 min and vortexed. After 10× dilution with Milli-Q water, 1 mL of this diluted sample was analyzed using high-performance anion exchange chromatography (model ICS-5000; Thermo Fisher, San Jose, CA, USA) with 100 mM NaOH, a Dionex^{TM} CarboPac^{TM} PA1 column (2 × 250 mm) plus a guard column (Thermo Fisher Scientific), flow of 0.25 mL·min^{-1}, and a pulsed amperometric detector.

The pellet meant for starch determination was washed three times with 3 mL 80% ethanol; each wash was followed by 5 min of centrifugation at 8500 g_n and discarding of the supernatant. The washed pellet was vacuum-dried (SpeedVac rotary evaporator SPD2010; Thermo Fisher Scientific) for 20 min at 50 °C. Then, 2 mL of a thermostable alpha-amylase solution (1 mg·mL^{-1} in H_2O; Rohalase) was added to the dry pellet and the suspension was incubated in a shaking water bath for 30 min at 90 °C. Thereafter, 1 mL of amyloglucosidase (0.5 mg·mL^{-1} in 50 mM citrate buffer; pH = 4.6) was added and water-bathed for 10 min at 60 °C to convert starch into glucose. After 5 min of centrifugation at 8500 g_n at room temperature, 1 mL of supernatant was further centrifuged in the same conditions. Then, 1 mL of supernatant was 10× diluted with Milli-Q water and analysed to determine the starch content, which was measured according to glucose as a breakdown product of starch by high-performance anion exchange chromatography (ICS-5000; Thermo Fisher) using 100 mM NaOH plus 25 mM sodium acetate as eluent.

Vitamin C content. Vitamin C was determined using the ascorbic acid assay (AsA) kit (MAK074; Sigma-Aldrich, St. Louis, MO, USA) according to the procedure described in the kit's technical bulletin, with minor adaptations. Namely, 20 mg of the frozen fresh sample was mixed with four volumes of cold AsA

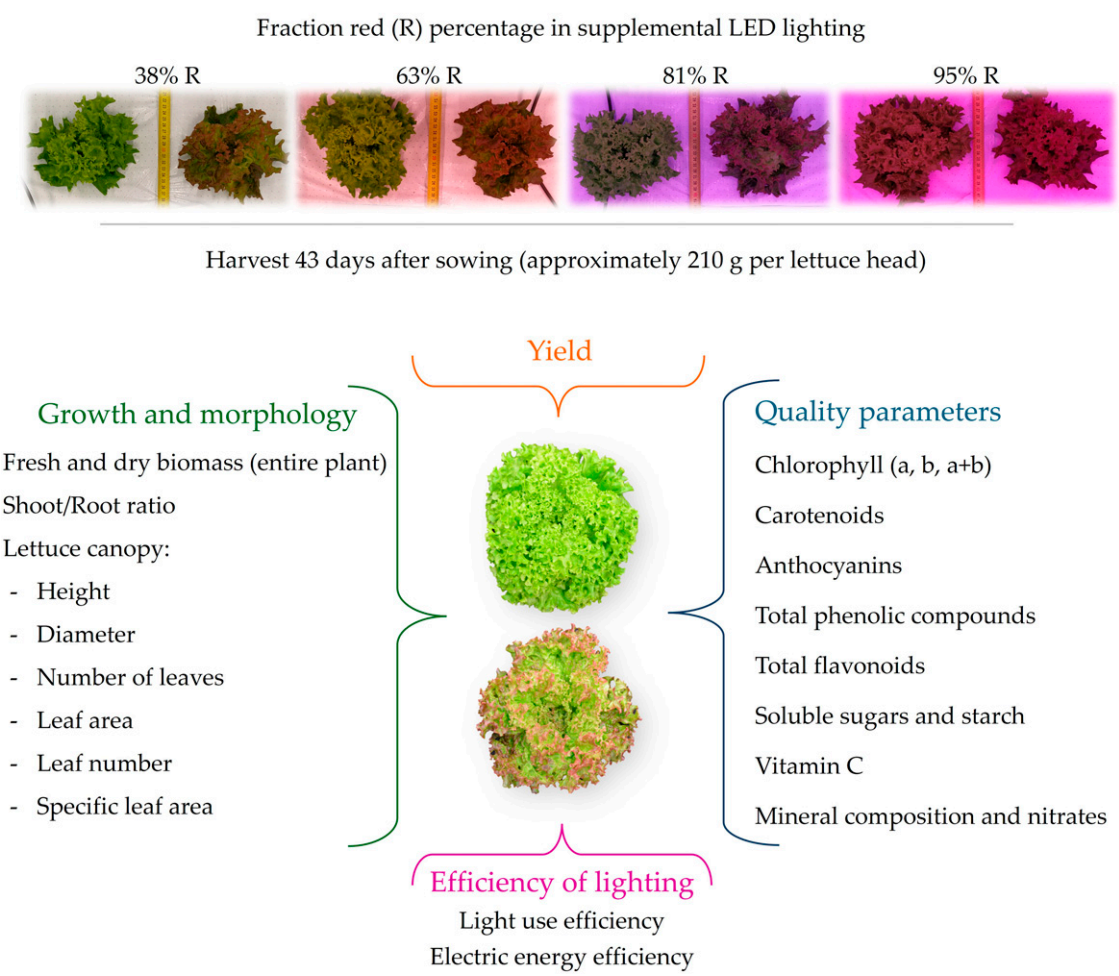


Fig. 2. Graphical summary of the experiment. From top to bottom: the four light treatments consisted of increasing the percentage of red (replacing green and blue) in the supplemental light-emitting diode (LED) light for two lettuce (*Lactuca sativa* L.) cultivars, one with reddish leaves ('Satine') and one with green leaves ('Lugano'), harvests and sample preparation for both cultivars, and measurements and analyses of lettuce samples of both cultivars.

buffer and then centrifuged at 20,800 g_n for 10 min at 4 °C. The liquid fraction was mixed with AsA buffer to a final volume of 120 µL. The assay reaction was performed by adding kit reagents to the samples. Using this assay, the AsA concentration was determined by a coupled enzyme reaction, which developed a colorimetric (570 nm) product proportional to the amount of ascorbic acid contained in the sample. The concentration of ascorbic acid in the samples was referred to as a standard curve and expressed as ng·µL^{-1}.

Anthocyanins content. Anthocyanins were determined according to Liu et al. (2022), with minor adjustments. Namely, 0.3 g of the frozen fresh leaf material was mixed with 700 µL of 70% methanol containing 1% formic acid by vortexing. After a 10-min ultrasonic bath, the samples were centrifuged for 10 min at room temperature with a relative centrifugal force of 20,800 g_n. The supernatant was directly used to determine colorimetry with a spectrophotometer (Genesys 150; Thermo Fisher Scientific) at 520 nm. The anthocyanin content was expressed as absorbance units (Au) per gram of FW.

Mineral composition. The mineral composition of oven-dried lettuce leaves from the final harvest was determined. The analyses were performed by an external laboratory (Eurofins Agro NL, Wageningen, The Netherlands; www.eurofins-agro.com). The accredited laboratory provided the boron, calcium, chloride, copper, iron, magnesium, manganese, molybdenum, nitrate, total nitrogen, phosphorus, potassium, sodium, sulfur, and zinc contents.

Statistical setup and analysis

The three independent replicates (growing cycles) of the experiment were considered as blocks in the analysis. The nitrate content and root DW, shoot/root ratio, and total plant DW were determined only during the final harvest of the second and third replicates, resulting in two blocks for these variables. A split-plot analysis of variance was conducted using the fraction of R as the main factor (with linear and quadratic components; polynomial contrasts) and the cultivar as the split factor. The effect of the replicate (block) was significant for most variables except for biomass partitioning, total flavonoids, sucrose, nitrates and sodium in 'Satine', biomass partitioning, anthocyanin, myo-inositol, sucrose, starch, potassium, and sodium in 'Lugano'. The statistical analysis was performed using Genstat (21st edition, VSN International, Hemel Hempstead, UK).

Results

Over the course of the experiment, supplemental lighting provided 74% of the total photons, whereas solar light provided the remaining 26% (Supplemental Table 1). Observations of representative plants at the time of the final harvest (43 d after sowing) are displayed in Supplemental Fig. 13 of Supplemental Material. Observations at the time of the intermediate harvest (36 d after sowing) were similar (Supplemental Material, Supplemental Table 7, Supplemental Figs. 2–10 and 12).

Yield, growth, and morphological response to increasing red fraction. The highest leaf FW (edible part of the lettuce) was produced by the highest red fraction in the supplemental lighting. Increasing the red light fraction from 38% to 95% resulted in a linear increase in the FWs and DWs of lettuce leaves

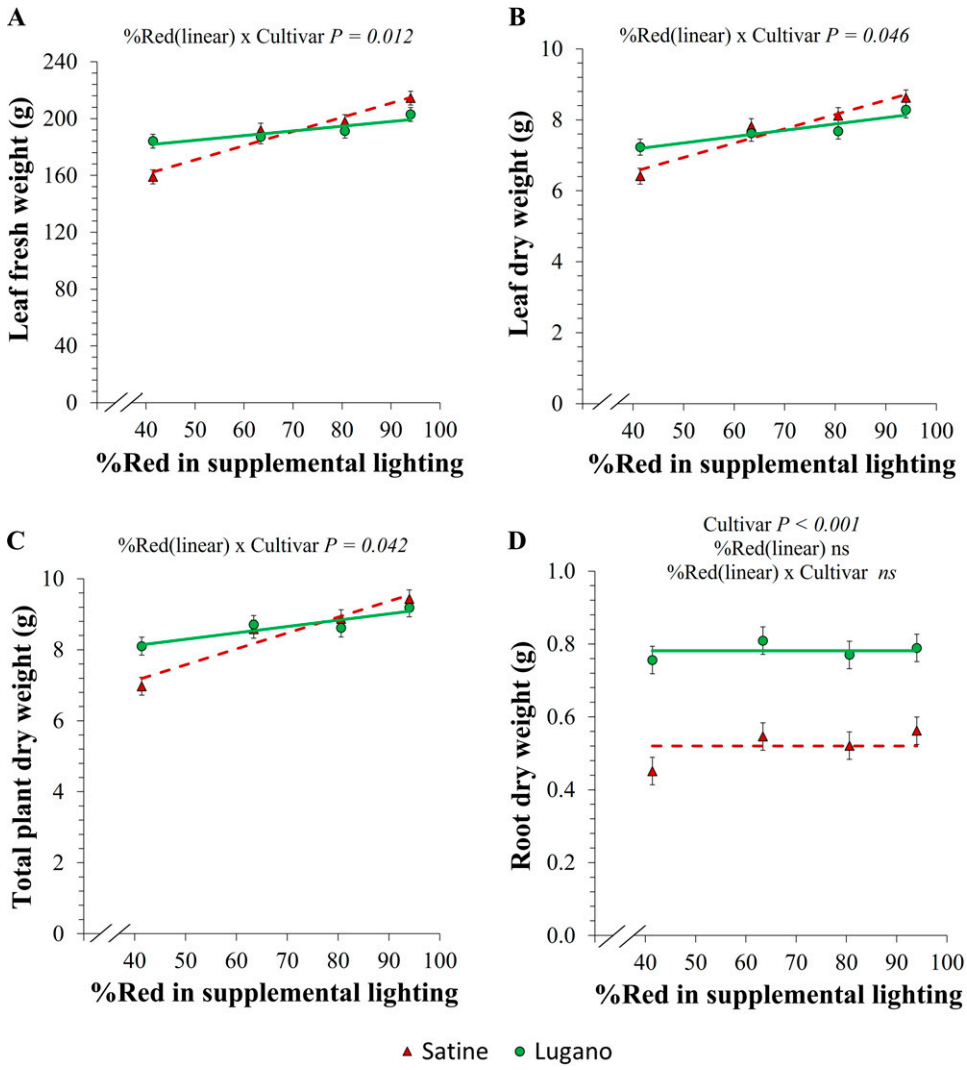


Fig. 3. (**A**) Leaf fresh weight, (**B**) leaf dry weight, (**C**) total plant dry weight, and (**D**) root dry weight as a function of the percentage (replacing green and blue) in the supplemental light for a lettuce cultivar with reddish leaves ('Satine'; red triangle) and one with green leaves ('Lugano'; green circle). Symbols are the means of three replicates of the experiment (n = 3) for panels **A** and **B** and of two replicates of the experiment (n = 2) for panels **C** and **D**. Each replicate provided an average of eight plants harvested 43 d after sowing. Vertical bars represent the standard error of the mean based on the common variance. For the interaction between the linear component of the red fraction and cultivar, the *P* values and trendlines are shown. When this interaction was not significant, *P* values for the main factors are shown (ns = not significant; hence, $P > 0.05$).

(Fig. 3) for both cultivars. For the green-leaved 'Lugano', the increment in FW was 10% weight and that in DW was 15%; the reddish-leaved 'Satine' grew by 35% (FW) and 34% (DW). The root DW (Fig. 3D) was 50% higher for 'Lugano' compared with that of 'Satine'. The DW of the entire plant linearly increased by 35% in 'Satine' and by 13% in 'Lugano' when the red fraction increased from 38% to 95% (Fig. 3C).

The incident LUE calculated for both fresh and dry leaf biomass linearly increased with the red fraction. That increase was stronger in 'Satine' (37% and 36% for fresh and dry leaf biomass, respectively) than it was in 'Lugano' (11% and 17% for fresh and dry leaf biomass, respectively), whereas the yield per kWh doubled in 'Satine' and linearly grew by 50% in 'Lugano' (Fig. 4).

The leaf area increased linearly by 487 cm^2/plant for 'Satine' and 415 cm^2/plant for 'Lugano' when the supplemental red fraction increased from 38% to 95% (Fig. 5A). The specific leaf area (SLA) was unaffected by light treatment, and it did not differ between cultivars (Supplemental Table 2). The increment in the red fraction from 38% to 95% resulted in an increase in the number of leaves in 'Satine' by 19%, whereas the number of leaves of 'Lugano' was unaffected (Fig. 5B). The leaves' dry matter content, shoot/root ratio, fraction of biomass partitioned to leaves, plant height, and plant diameter of both cultivars were not influenced by the lighting treatments in both cultivars; except for the dry matter content and SLA, the parameters differed by cultivars (Supplemental Table 2).

Effect of the red fraction on product quality. For both cultivars, chlorophyll a, chlorophyll b, the total amount of chlorophyll, carotenoids, anthocyanin, total phenolic compounds, total flavonoids, vitamin C, sugars, and starch contents were not influenced by the red light fraction (Supplemental Tables 3 and 4).

The leaves' copper, iron, magnesium, manganese, molybdenum, phosphorus, potassium, sodium, and sulfur contents were unaffected by the red fraction in supplemental light in both cultivars (Supplemental Table 5). Nitrate, boron, calcium, and zinc contents were higher in 'Lugano' compared with those in 'Satine' by 41%, 22%, 43%, and 32%, respectively (Fig. 6). The boron content showed a small decrease of 8% only in 'Lugano' (Fig. 6D). The calcium content showed a small decrease of 3% only in 'Lugano'. The total nitrogen (Fig. 6B) and chloride (Fig. 6C) contents did not differ between cultivars and showed a linear decrease with an increasing red light fraction by 3.9% and 3.8%, respectively.

Discussion

A higher red fraction in the supplemental light spectrum might be beneficial for crop growth while reducing the energy input needed for supplemental lights. This study aimed to determine the effect of the red fraction (replacing green and blue) in supplemental light on lettuce

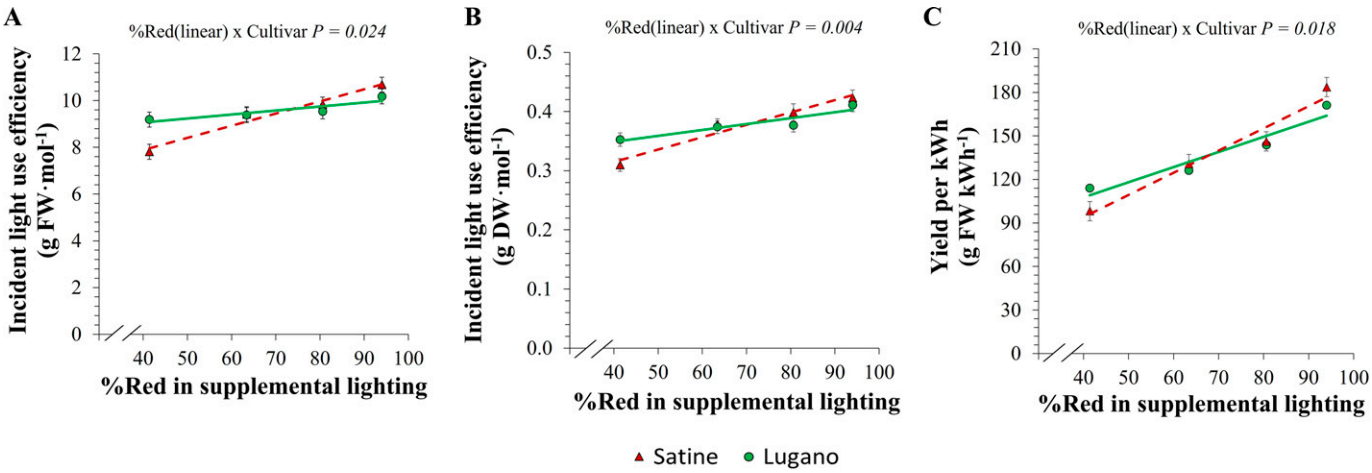


Fig. 4. Incident light use efficiency. (**A**) Ratio of leaf fresh weight (FW) divided by the cumulative incident light sum from the transplanting day, (**B**) ratio of the leaf dry weight (DW) divided by the cumulative incident light sum from transplanting day, (**C**) lettuce yield (leaf fresh weight per plant) produced per kWh of energy consumed as a function of the red percentage (replacing green and blue) in the supplemental light for a lettuce cultivar with reddish leaves ('Satine'; red triangle) and one with green leaves ('Lugano'; green circle). Symbols are the means of three replicates of the experiment (n = 3), where each replicate provided an average of eight plants harvested 43 d after sowing. Vertical bars represent the standard error of the mean based on the common variance. For the interaction between the linear component of the red fraction and cultivar, *P* values and trendlines are shown.

growth, yield, and product quality for a green-leaved and a reddish-leaved cultivar.

Lettuce yield and lighting efficiency increased with the increased red light fraction. Increasing the red fraction in an red light:blue light:green light:far-red light supplemental LED spectrum by partially replacing blue and green had a positive effect on lettuce growth and yield (Fig. 1). This is in agreement with the results of Wang et al. (2016), who reported that a higher red light/blue light ratio (particularly a red light/blue light ratio of 8 or 12) increased the shoot DW and leaf area in lettuce. Azad et al. (2020) reported a higher lettuce yield and leaf area at a higher red fraction. Pennisi et al. (2019) reported that lettuce yield, plant FW and DW, and leaf area increased with a red light/blue light ratio of up to 3 and did not increase further at a higher red light/blue light ratio. Conversely, Snowden et al. (2016) observed the highest dry yield in lettuce grown under red light/blue light ratios between 4 and 7 compared to that of lettuce grown with higher and lower ratios. These conflicting observations of the response to the red light/blue light ratio of lettuce may be the consequence of the use of different cultivars, monochromatic or broadband lights, and diverse climatic conditions. In the study by Kusuma et al. (2022) of greenhouse-grown tomatoes, using the same LED spectra as that in the current study, spectral effects appeared to be cultivar-dependent.

For both cultivars, the increase in leaf FW resulted from a linear increase in leaf DW (Fig. 3B), whereas the leaf dry matter content was unaffected by the red fraction. The increase in the leaf DW resulted from a similar increase in the total plant DW, whereas dry matter partitioning to the leaves was not significantly affected (Supplemental Table 2). Hence, the yield increase at higher red light fractions was caused by an overall increase in plant dry matter production.

The increase in the total plant DW with an increase in the red fraction may have been caused by either an increase in the leaf photosynthesis rate or an increase in intercepted light. Although no photosynthesis measurements were performed, it is known that red photons efficiently drive photosynthesis (McCree 1971). Kang et al. (2016) reported a reduced photosynthesis rate in lettuce leaves when changing the light spectrum from 80% red light and 20% blue light to 70% red light, 20% blue light, and 10% green light. An increase in intercepted light could also explain the increase in the total plant DW (Fig. 3C) because the leaf area increased with red fraction (Fig. 5) for both cultivars.

In our research, increasing the red fraction in a combined LED spectrum resulted in not only an increase in yield but also an improvement of the electric energy use efficiency of supplemental lighting (yield per kWh consumed) and, thus, LUE (Fig. 4) (Chen et al. 2021). The LUE values are in line with those reported by previous studies of greenhouse conditions with low plant density (Jin et al. 2021) as a consequence of the low coverage of the ground during the first period after transplanting (Supplemental Fig. 11). These aspects could explain the lower LUE compared with that reported by other literature that considered higher plant density and shorter growing cycles (Chen et al. 2021; Jin et al. 2023).

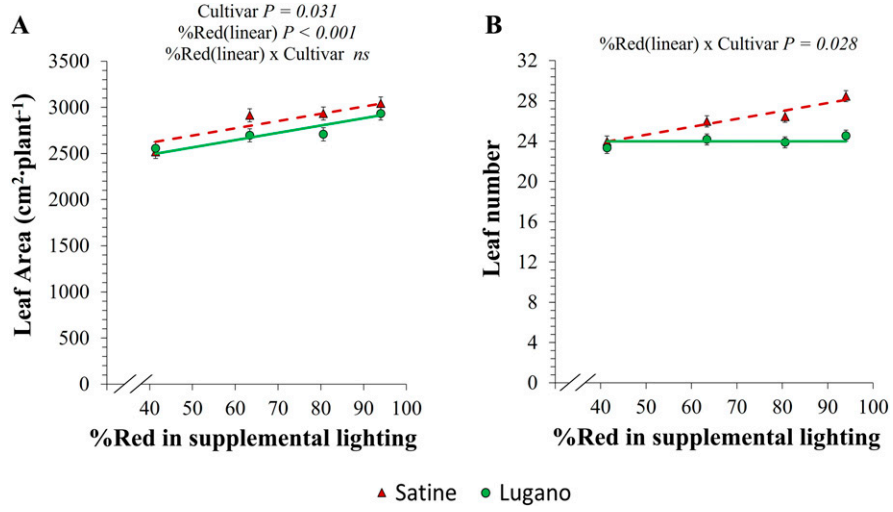


Fig. 5. (**A**) Leaf area and (**B**) number of leaves per plant as a function of the red percentage (replacing green and blue) in the supplemental light for a lettuce cultivar with reddish leaves ('Satine'; red triangle) and one with green leaves ('Lugano'; green circle). Symbols are means of three replicates of the experiment (n = 3). Each replicate provided an average of eight plants harvested 43 d after sowing. Vertical bars represent the standard error of the mean based on the common variance. For the interaction between the linear component of the red fraction and cultivar, *P* values and trendlines are shown. When this interaction was not significant, *P* values for the main factors are shown (ns = not significant; hence, $P > 0.05$).

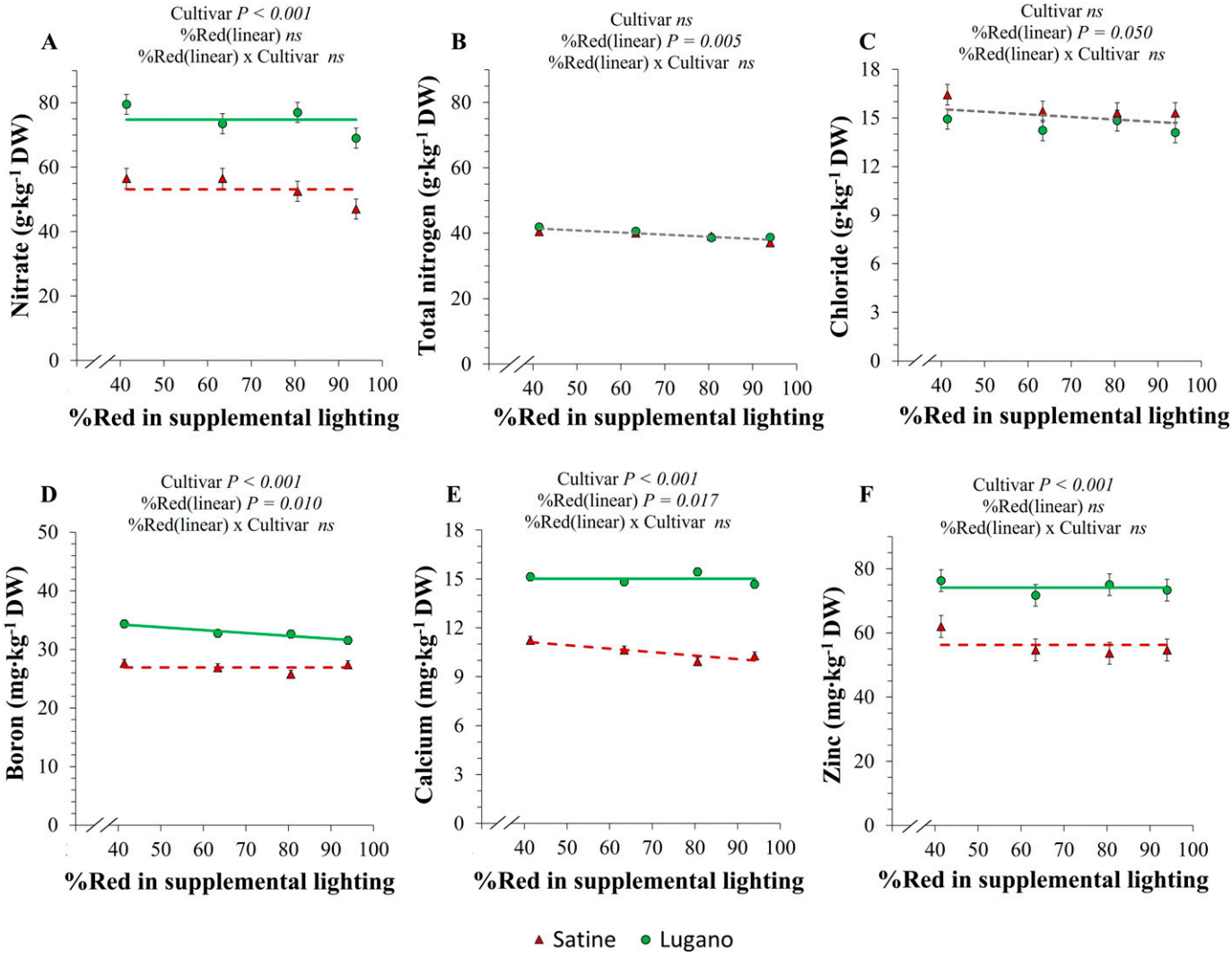


Fig. 6. Contents of (**A**) nitrate, (**B**) total nitrogen, (**C**) chloride, (**D**) boron, (**E**) calcium, and (**F**) zinc as a function of the red percentage (replacing green and blue) in the supplemental light for a lettuce cultivar with reddish leaves ('Satine'; red triangle) and one with green leaves ('Lugano'; green circle). Symbols are the means of three replicates of the experiment (n = 3) for panels **B**–**F** and the means of two replicates of the experiment (n = 2) for panel **A**. Each replicate provided an average of eight plants harvested 43 d after sowing. Vertical bars represent the standard error of the mean based on the common variance. For the interaction between the linear component of fraction red and cultivar, *P* values and trendlines are shown. When this interaction was not significant, *P* values for the main factors are shown (ns = not significant; hence, $P > 0.05$).

Red light fraction barely affected the quality of lettuce. Most of the analyzed compounds linked to lettuce quality were unaffected by the red fraction (Supplemental Tables 3 – 6). In general, although red light improves photosynthesis and carbohydrate accumulation (McCree 1971), blue light positively influences the pigments, phenolic compounds, and chlorophylls via the photoreceptors cryptochrome and phototropin (Azad et al. 2020; Fan et al. 2013; Li et al. 2021b; Paradiso and Proietti 2022). Lettuce is sensitive to red light/blue light ratios, and the contrasting results between studies of light spectra effects are imputable to experimental limitations and different environmental conditions (Chen et al. 2021; Shafiq et al. 2021; Son et al. 2017; Thoma et al. 2020), particularly in a greenhouse system (Berkovich et al. 2017).

The mineral composition of vegetables can be influenced by supplemental LED lighting, with differences between species and cultivars (Lee et al. 2022; Vaštakaitė-Kairienė et al. 2022). The understanding of the possible effects of light on plant species' mineral compositions is still poor, although the effects can involve the uptake and accumulation in the plant tissues (Pinho et al. 2017). A few variable and contrasting results have been reported in the literature regarding crops such as lettuce. During our experiment, increasing the red fraction of the spectrum significantly decreased the boron concentration in leaves of the green cultivar Lugano, decreased calcium, chlorine, zinc, and nitrate in the red cultivar Satine, and decreased the total nitrogen and chloride in both cultivars; other macro-elements and micro-elements were unaffected by the light treatments. An example of the role of light quality on the uptake of some mineral elements, such as calcium, is the triggering effect of blue light on the opening of some ion channels through the action on cryptochrome and the consequent signaling process (Lin 2002). Pennisi et al. (2019) speculated that plant growth, rather than a physiological impact of the LED light spectrum, resulted in the effect on the uptake of macro-elements.

An important aspect of lettuce quality is the nitrate concentration because nitrate metabolites can be harmful to human health; therefore, reducing the nitrate accumulation in vegetables is a considerable goal of agricultural techniques (Santamaria 2006). The nitrate concentration of the tested lettuces (Supplemental Table 6) was well below the current European maximum reference level, which is 5000 mg NO_3/kg FW for lettuce grown under cover and harvested between 1 Oct and 31 Mar (European Commission Regulation No. 915/2023), as in the present experiment.

The response to the red fraction was strongest in the reddish-leaved cultivar. An increase in the red light fraction increased leaf FW, leaf DW, incident LUE, and total plant DW more in reddish-leaved 'Satine' than it did in green-leaved 'Lugano' (Figs. 3 and 4). Only

leaf area and the total nitrogen content did not show a cultivar-specific response. Leaf DW responded differently to the red light fraction in both cultivars.

Our findings are in line with previous findings of studies that mentioned a cultivar-specific response to light spectra for lettuce (Gómez and Jiménez 2020) and tomatoes (Kusuma et al. 2022). During our research, the difference in the response between the cultivars can most likely be explained by the difference in the anthocyanin content. This class of compounds is known to absorb blue-green light, which cannot be used for photosynthesis (Albert et al. 2009). The anthocyanin content in reddish-leaved 'Satine' is higher than that in green-leaved 'Lugano' (Supplemental Table 4). Therefore, light spectra with a lower fraction of blue-green light, as is the case in light spectra with a higher fraction of red light, are expected to be more effective for the growth of 'Satine' than for the growth of 'Lugano', which could explain the stronger response of 'Satine'.

Conclusion

Lettuce production was improved by increasing the red light fraction in the white spectrum applied as a supplemental light source in a greenhouse growing system. The increment in yield was stronger in the reddish-leaved cultivar Satine than that in the green-leaved cultivar Lugano. Higher fractions of red light are also favorable for energy efficiency because less energy is needed for the same number of photons. The red fraction barely affected lettuce quality (pigment, total phenolic compounds, vitamin C, total soluble sugar, starch, and mineral composition). Further research is with particular attention on the effects of other light qualities is needed to optimize the supplemental spectrum composition for lettuce.

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