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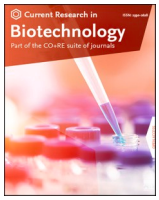

Dark interruption with red or blue LEDs mitigates powdery mildew and enhances bioactive compound accumulation in organically grown strawberries

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ABSTRACT

Disease attack of powdery mildew (Podosphaera aphanis) is a major concern in organic strawberry production in tunnels or greenhouses production. We examined the impact of dark period interruption with light from blue and red LEDs on the occurrence of powdery mildew in organically grown strawberries, plant performance and on berry quality. Strawberry cultivars (Fragaria × ananassa cvs. Honeye and Faith) were grown in a climate chamber for two months in pots filled with peat based growing media certified for organic production. The plants were drip irrigated and fertilized with liquid organic fertilizers. They were exposed to a control treatment with 18 h light using white (polychromatic) LEDs and 6 h darkness or with treatments involving white LED treatment for 14 h, followed by darkness, interrupted after 2 h by 4 h of monochromatic blue or red LED exposure and additional 4 h of darkness. A three-factorial experiment including strawberry cultivars, light regimes and pathogen inoculation was performed using six replicates (pots) per cultivar and treatment. Light regime influenced the biomass of strawberry plants irrespective of cultivar, and dark period interruption with using red or blue LEDs promoted fresh biomass of the canopy and roots as compared to the control regime. Dark interruption using blue LEDs enhanced the accumulated berry yield, increased the antioxidant activities and reduced the disease incidence as compared to the control regime and the dark period interruption using red LEDs. Blue LED treatment favored the performance of the strawberry cultivars. The obtained results are of interest for organic strawberry production to be implemented in integrated control strategies for powdery mildew with potential to replace the use of pesticides and enhance product quality.

1. Introduction

Production of strawberries in a controlled environment, e.g., high tunnel, greenhouse or indoor farming, is a strategy to extend the growing season, especially under Northern conditions, to provide stable growing conditions and to prevent crop damage from extreme weather events. In addition, by regulating environmental factors during flowering (e.g., relative humidity, duration of leaf wetness (Wilcox and Steem, 1994), the incidence of grey mold (*Botrytis cinerea*) can be significantly reduced (Xiao et al., 2001). However, powdery mildew still challenges organic strawberry production, due to the legislation and limitations on the use of disease control strategies.

Powdery mildew (*Podosphaera aphanis*) is an obligate biotrophic fungus, destructive to leaves and fruit with an impact in reducing host plant vigor, productivity and quality (Green et al., 2014; Green et al., 2002). Disease susceptibility is cultivar-dependent (Menzel, 2022; Kennedy et al., 2013) and the fungus spreads by aerial infection. Under conventional strawberry production, the control of powdery mildew relies on intensive use of fungicides (Onofre et al., 2022), a control strategy not compatible with organic farming. The development of new strategies, complying with the directives for organic farming, is thus crucial. Attack by powdery mildew is correlated to different cultivation factors, e.g., relative humidity, temperature, leaf wetness, light quality, level of carbon dioxide (Mieslerova et al., 2022; Mieslerova et al., 2013) as well as the type of plastic cover used in tunnels or greenhouses and its potential to transmit UV-light. In fact, higher infection rates (90 %)

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occur when polyethylene material that blocks UV-light is used (Onofre et al., 2022).

In Northern Europe, supplementary light is needed in controlled environment agriculture. Light-emitting diodes (LEDs) have been used in recent years to decrease light-related energy consumption in indoor and greenhouse production (Paradiso and Proietti, 2022; Nestby and Trandem (2013)), which contributes to lower greenhouse gas emission and impacts of climate changes. Irradiation with LEDs affects the microclimate (light, temperature and humidity) around plant leaves (Nestby and Trandem (2013)) and has positive effects on plant productivity and fruit quality (Appolloni, et al., 2021; Lee et al., 2020; Nestby and Trandem (2013)). Moreover, the use of LEDs has also been investigated in relation to plant disease control, such as grey mold (*Botrytis cinerea*) (Lauria, et al., 2023; Meng et al., 2023) and powdery mildew (Suthaparan et al., 2017) on strawberries.

For *Botrytis cinerea*, replacement of polychromatic white LED by red LEDfor a 16 h photoperiod has found to have a positive impact on the tolerance of strawberry plants to attack by *Botrytis cinerea* with increased the red wavelength (Meng et al., 2023). The same study has also found that exposing strawberry plants to red LED (100 μmol m^{-2} s^{-1}) for 6 h followed by 10 h white LED light (100 μmol m^{-2} s^{-1}) for 15 days enhanced the strawberry plants' tolerance to *Bortytis* species (Meng et al., 2023). Furthermore, the impact of LED light affected the phenotypic diversity of *Botrytis* species (Meng et al., 2020). The sporulation of the pathogen was enhanced under the natural daylight treatment but decreased under the red LED treatment (Meng et al., 2020). The same study pointed out the potential of red LED light to inhibit the formation of sclerotia and enhance plant resistance to all the *Botrytis* isolates used in the investigations, while blue LED light inhibited the formation of sclerotia by some of the pathogen isolates.

In relation to powdery mildew, investigations with LED light have been performed on different crops such as strawberry, cucumber and roses, but mostly in combination with ultraviolet (UV) light (275 nm to 400 nm) using doses of 1.6 or 0.8 W m^{-2} (Suthaparan et al., 2017). Limited knowledge is thus available about the control of powdery mildew under a monochromatic LED treatment. Cultivar choice occurs to be of importance when examining the application of LED light on strawberries to reduce attack by powdery mildew. The LED treatment has been shown to affect the growth and yield of both June- and everbearing cultivars (Stuemky and Uchanski, 2020).

Further, sustainable cultivation practices with the potential to reduce the use of pesticides and to meet sustainability goals are crucial. LED lights have been highlighted as a promising strategy targeting sustainable demands with respect to energy efficiency (Palacios-Intriago et al., 2024) and reduction in greenhouse gas emission. They target also food security by enabling year-round production of nutritional rich products in greenhouses as well as in urban areas, bringing production closer to the consumer and thereby reducing environmental impacts related to food transport (Gómez and Izzo, 2018). Connecting LED lights application to the control pf plant pathogens targets also the alternative disease control strategies and reducing the environmental and health impacts due to pesticides use (Gómez and Izzo, 2018).

To develop management-based control strategies, the combined impact of LED treatments and strawberry cultivar with respect to powdery mildew attack in organic indoor production remains to be examined. We hypothesized (i) that dark period interruption by blue LED affects powdery mildew occurrence, plant biomass, and berry bioactive compound content in strawberries, and (ii) that the influence is cultivar dependent. The overall aim of the study was to develop a strategy that can easily be translated to an applied context and growers' realities.

2. Materials and methods

2.1. Plant material and cultivation conditions

Frigo plants from two June-bearing strawberry cultivars (*Fragaria* × *ananassa* cvs. 'Honeoye' and 'Faith') obtained from a commercial nursery (Flevoplant B.V. Enserweg, 98307, PJ Ens, Holland) and commonly used in organic cultivation were selected for the study. The plants of each were cultivated in 1.5-L pots containing a peat-based growing medium certified for organic production and drip-irrigated on a daily basis at a rate of 150 mL $plant^{-1}$ day^{-1}. Supplementary liquid fertilization using a certified organic fertilizer (Biobact; Nilsson Garden https://www.nelsongarden.se, Sweden; NPK 7–1.3–5; pH 5.6; electrical conductivity 2.2 mS cm^{-2}) approved for use in Swedish organic farming was supplied manually once a week, at a rate of 20 mL per pot according to the manufacturer's recommendations.

The plants with respect to the treatments were placed in different climate chambers equipped with LEDs, allowing adjustment to different wavelengths according to the individual treatments and to keep the control plant mildew- free throughout the experiment. Environmental conditions in the chambers were: Day/ night temperature 20 °C respective 18 °C, photoperiod 18 h, and 75–80 % relative humidity.

2.2. Experimental set-up and treatments

This three-factorial experiment included strawberry cultivars, light regimes and presence of the pathogen as factors. Strawberry cultivars were treated with three light regimes, with and without the present pathogen. A modified version of the lighting procedure described by Suthaparan et al. (2010a) was applied, using lamps (RX30, Heliospectra-Sweden) with eight monochromatic LEDs including blue, red, and green etc., but also a white LED (polychromatic). In the current experiment the white light was integrated with either blue or red LEDs and darkness (Fig. 1). The modifications related to length of exposure to light from blue or red LEDs (Fig. 1B). Plants of each cultivar were subjected to the following treatments: (1) 18 h white LED plus 6 h darkness as a control treatment; (2) 14 h white LED plus 6 h darkness interrupted after 2 h by 4 h with blue LEDs (447,8 nm); or (3) 14 h white LED plus 6 h darkness interrupted after 2 h by 4 h with red LEDs (635 nm). Light intensity was adjusted to 100 μmol m^{-2} s^{-1} and the daily light integrals was calculated to 1,44 mol m^{-2} d^{-1} for both red and blue LED and 5,04 mol m^{-2} d^{-1} for the white light in the integrated with LED treatments. The daily light integrals for the white light in the control treatment was 6,48 mol m^{-2} d^{-1}. The experimental set-up for each treatment (light regime) and cultivar was conducted using six biological and independent replicates (pots) with one plant per pot. The experiment lasted for eight weeks.

2.3. Pathogen inoculation

Infection with powdery mildew was initiated according to the procedure described by Suthaparan et al. (2014), using *Podosphaera aphanis* inoculum isolated from diseased strawberry leaves. Healthy plants were inoculated in two ways (i) using conidial suspension and (ii) through plant-to-plant infection. For plant-to-plant infection, the pathogen was transferred to healthy plants by brushing the mycelium from diseased to healthy plants for 10 min once each day using a paint brush. The conidial suspension was produced as described by Suthaparan et al. (2014), using leaf discs from the diseased plants. These discs were incubated for seven days on plates with water agar at 20 °C and under daily illumination for 14 h using 100 μmol m^{-2} s^{-1} white light. They were then placed in distilled water containing Tween 20 (Sigma-Aldrich Chemie GmbH; 20 μl L^{-1}) and gently shaken to remove the conidia. The suspension was adjusted to a concentration of 5×10^4 conidia mL^{-1} and sprayed weekly on healthy plants at a rate of 10 mL $plant^{-1}$. Infector plants used for plant-to-plant inoculation were kept in separate greenhouse chambers.

Leaves of strawberry plants in each light treatment were either inoculated with conidia suspension and mycelium of the powdery mildew or left uninoculated. Leaf inoculation commenced two weeks after the start of the experiment. The developed leaves and runners were included in the inoculation process.

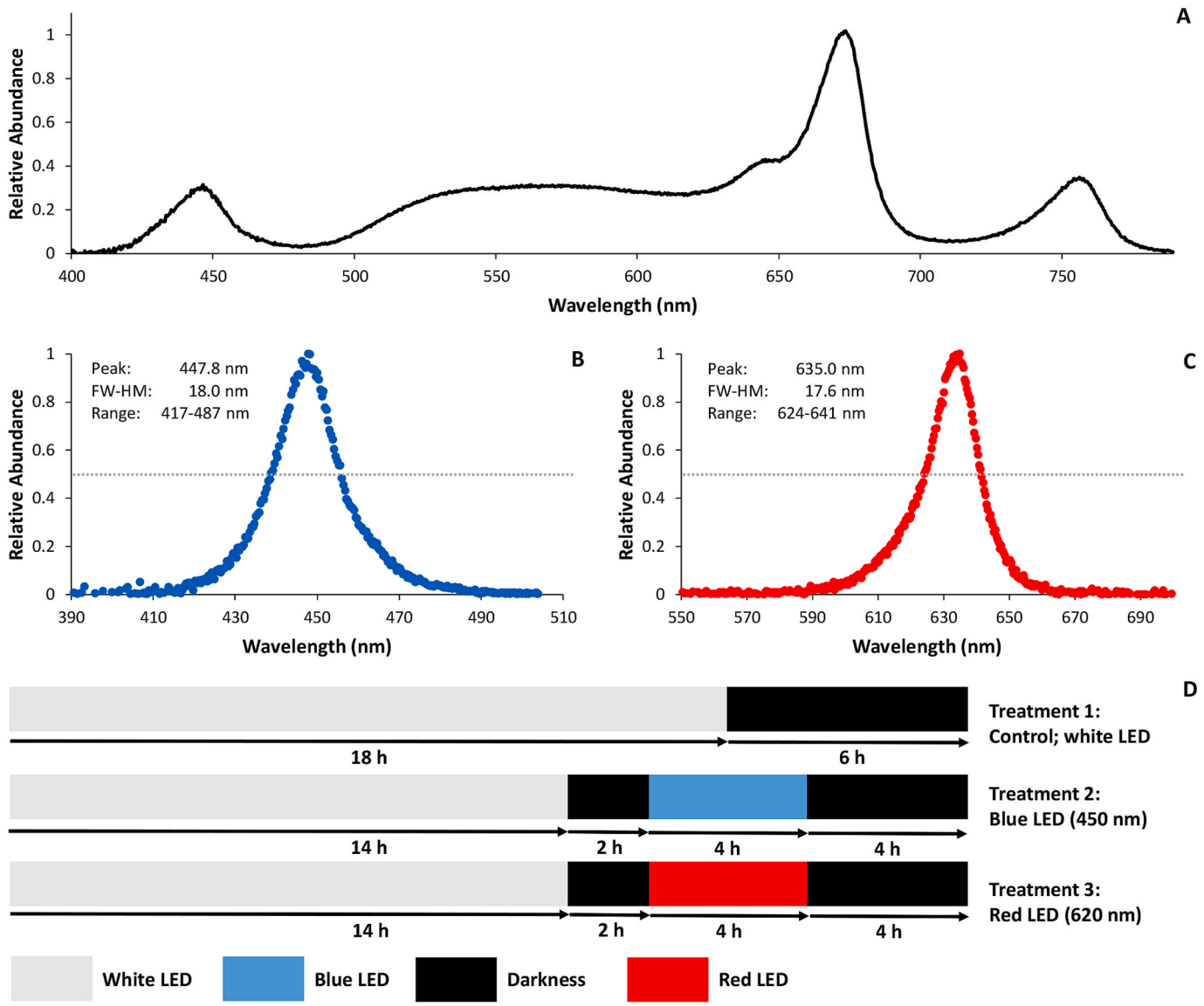

Fig. 1. Experimental design. (A) Spectral distribution (relative abundance) of light regime (white LED). Relative abundance of blue (B) and red (C) LED treatment during dark period interruption including description of light environment properties (peak, range and band width at full-width half-maximum, FW-HM). (D) Daily light regime in hours (h) for the three treatments involving dark period interruption with red and blue LED.

2.4. Plant biomass and yield

At the end of the experiment, the fresh weights of the canopy and roots were recorded separately for each plant. Flowering started two weeks after planting and berry development after four weeks of cultivation. Fruit yield was registered once a week during the last four weeks of the experimental period including the mass of ripe berries harvested during the experiment. The waste berries were discarded and were not included in the accumulated yield or number of fruits. No classifications of the berries were performed.

2.5. Bioactive compound content of strawberry fruits

Strawberry fruits were stored at –20° C prior to the quality analyses. Bioactive compound composition of strawberry fruits was evaluated with respect to total phenols (TP), anthocyanin content (AC), ascorbic acid (AA) and antioxidant capacity. One gram of freeze-dried strawberry fruit was used in the analysis. Total phenol content was determined according to the method developed by Singleton and Rossi (1965). In brief, the reaction mixture was prepared by combining 50 μL MΩ water, 12 μL extract, 12 μL Folin-Ciocalteau reagent, and 125 μL 7 % (w/v) Na_2CO_3. The mixture was allowed to stand for 75 min and absorbance was measured at 765 nm. The phenol content was determined from the calibration curve of a garlic acid standard.

The content of anthocyanin was determined according to Giusti and Rodriguez-Saona (1999). In brief, freeze dried strawberry powder was mixed with 60 % methanol and subjected to ultrasonic sonication for 60 min at 30 °C. Aliquots of 100 μL of the centrifuged supernatant (plant extract) were added to two test tubes, one of which received 900 μL pH 1.0 buffer and the other received 900 μL of pH 4.5 buffer. Absorbance was measured spectrophotometrically at 510 nm and 700 nm. The amount of anthocyanin was determined as:

$$Totalanthocyanincontent = \left(\frac{A}{\mu}\right) \times L \times M_w \times \left(\frac{W}{W_t}\right) \times 100\% \quad (1)$$

where A = absorbance (A 510 nm pH 1.0 – A 700 nm pH 1.0) − (A 510 nm pH 4.5 – A 700 nm pH 4.5) (molar absorptivity of cyanidin-3-glucoside); L = cuvette light loop in cm; M_w = molecular weight of cyanidin-3-glucoside; W = final volume (L), and W_t = weight of sample

tested (g).

For determination of ascorbic acid content, 1 mL of frozen fresh sample was mixed with 1.5 % *meta*-phosphoric acid and centrifuged for 7 min (4200 rpm). A 600 µL subsample was transferred to a vial and analyzed with HPLC (Agilent 1260 HPLC system; column: Phenomenex Kinetex C8 150 x 2.6 µm (100 A); buffer: 20 mM KH_2PO_4, pH 2.3 and 4 % methanol; flow rate: 0.65 mL min^{-1} isocratic; injection volume: 0.5 µL; and diode array detector set to $\lambda = 248$ nm (spectra collected 230–350 nm)).

Antioxidant activity was determined as scavenging activity of stable 2,2-diphenyl-1 picryl hydrazyl (DPPH) free radical assays, as described by Tahera et al., (2010) and Sharma and Bhat (2009). The diluted sample (25 µL) was mixed with 200 µL DPPH in wells of a 96-well plate and incubated for 4 h, and absorbance was measured at 517 nm against a methanol blank. Radical scavenging activity (as a percentage) was determined.

2.6. Quantification of *Podosphaera aphanis*

To estimate the amount of the pathogen on the leaves, samples were collected and subjected to culture independent analyses using qPCR. A 10 g sample of leaves from each replicate (plant) was transferred to a sterile filter bag (Separator 400, 180 mm x 300 mm x 70 µm; Grade Products Ltd., Coalville, UK) as described by Darlison et al. (2019). Phosphate-buffered saline solution was added (PBS, 50 mL, 0.01 M, pH 7.0 to each bag) and the samples were crushed and centrifuged. The pellets obtained were used for DNA extraction and for qPCR analyses of fungal amount using the ITS1 and ITS4 primer, as described by (Kasiamdari et al., 2021).

2.7. Statistical analysis

Statistical analyses were performed using Minitab statistical software for Windows (Release 18; Minitab Inc., State College, PA, USA). The data were analyzed using analysis of variance (ANOVA). Means were separated by a least significant difference (LSD) test, with $P < 0.05$ considered significant. Correlation between the investigated parameters was investigated using the General Linear Model (GLM) and Principal Component Analyses (PCA).

3. Results

Regardless of the cultivars, the light regime affected plant growth as expressed by canopy and root biomass, while significant interactions "light regime x cultivar" were observed for berry yields and number of berries (Table 1; Supplementary Table S1), as well as for antioxidant activity (%), ascorbic acid content (mg (100 g fresh weight)$^{-1}$), total phenol content and anthocyanin content (mg (kg fresh weight)$^{-1}$) (Supplementary Table S2).

The light regime related differences were further revealed through principal component analysis, including the accumulated berry weight and bioactive compound contents, where PC1 (63 %) differentiated between strawberry plants exposed to dark period interruption with either red or blue LED, and PC2 (24.1 %), which differentiated between strawberries subjected to continuous white and dark interruption with blue LED (Fig. 2). The PC2 also discriminated between plants exposed to red LED interruption and blue LED interruption in the strawberry cv. Faith irrespective of inoculation by *Podosphaera aphanis*, as well as uninoculated cv. Honeoye (Fig. 2). Antioxidant activity and ascorbic acid content had the strongest impact on PC1, whereas the accumulated berry yield and anthocyanin content were most influential for PC2.

As expected, canopy and root biomass were positively correlated and were the main modifiers for generative performance and bioactive compound contents, particularly through the root: canopy biomass (R/C) ratio, in non-inoculated strawberry plants (Table 1). Our correlation analysis showed that shoot biomass explained 66 % of the variation in

Table 1
Plant performance (canopy biomass plant^{-1}, fw, g; root biomass plant^{-1}, fw, g) and accumulated berry yield (g plant^{-1}) as well as berry number per plant of strawberries (Fragaria x ananassa; cultivar 1: 'Faith'; cultivar 2: 'Honeye') exposed to different light regimes with or without inoculation with Podosphaera aphanis. All plants were illuminated for 18 h. Control plants were exposed to continuous polychromatic white LEDs for 18 h whereas the dark period in the other two treatments was interrupted with either 2 h of illumination with monochromatic blue or red LEDs after 16 h of irradiation with white LEDs. Mean values of six independent replicates and standard deviations are presented.

	Cultivar 1 (Faith)										Cultivar 2 (Honeye)									
	Control			Blue			Red				Control			Blue			Red			
w/o inoculation with *Podosphaera aphanis*																				
Canopy fresh weight (C)	71.83	±	3.97	(ef)[a]	95.00	±	6.42	*(abc)	100.17	±	4.17	*(ab)	65.17	±	5.67	(f)	87.33	±	5.57	*(cd)	98.17	±	3.54	*(ab)
Root fresh weight (R)	53.50	±	6.47	(g)	68.17	±	7.88	*(def)	87.50	±	2.74	*(ab)	69.67	±	4.08	(cdef)	70.83	±	2.04	(cdef)	91.33	±	3.14	*(a)
Ratio C/R (%)	74.84	±	11.54	(def)	71.67	±	5.97	(ef)	87.41	±	2.34	*(bcd)	107.69	±	5.38	(a)	81.41	±	3.43	* (cde)	93.10	±	4.91	* (abc)
Accumulated berry yield	250.00	±	2.28	(b)	300.00	±	2.97	*(a)	110.00	±	2.28	*(h)	150.00	±	2.00	(f)	250.00	±	1.41	*(b)	80.00	±	2.28	*(j)
Berry number	50,3	±	1,6	* (b)	60	±	2,2	* (a)	27	±	2,1	* (e)	50,2	±	1,5	* (b)	50	±	1,4	* (b)	20,2	±	1,6	* (fg)
w inoculation with *Podosphaera aphanis*																				
Canopy fresh weight (C)	81.00	±	5.25	(de)	99.00	±	3.41	*(ab)	102.00	±	4.52	*(ab)	79.50	±	2.43	(de)	94.50	±	7.18	*(bc)	104.33	±	3.93	*(a)
Root fresh weight (R)	79.00	±	3.58	(bcd)	77.83	±	3.31	(bcde)	79.50	±	4.37	(bc)	63.33	±	5.35	(fg)	74.17	±	11.37	(cdef)	67.17	±	5.78	(ef)
Ratio C/R (%)	97.74	±	12.23	(ab)	78.66	±	6.11	* (cdef)	78.03	±	3.57	* (cdef)	79.62	±	5.61	(cdef)	79.23	±	16.21	(cdef)	64.31	±	3.77	*(f)
Accumulated berry yield	200.00	±	2.53	(e)	240.00	±	2.61	*(c)	90.00	±	3.35	*(i)	130.00	±	1.41	(g)	230.00	±	1.67	*(d)	75.00	±	1.67	*(k)
Berry number	40,3	±	2,4	* (d)	48,3	±	1,6	* (b)	22,2	±	1,5	* (f)	25,1	±	1,2	* (e)	46,2	±	2,8	* (c)	18,3	±	1,2	(g)

[a] Values within the same row and cultivar marked with and asterix are significantly different from the control as assessed by One-way ANOVA followed by Duncan's test ($\alpha = 0.05$). Different letters given in brackets indicate significant differences based on interactions between cultivar*light*inoculation with P. aphanis as assessed by the Tukey-test ($p < 0.05$).

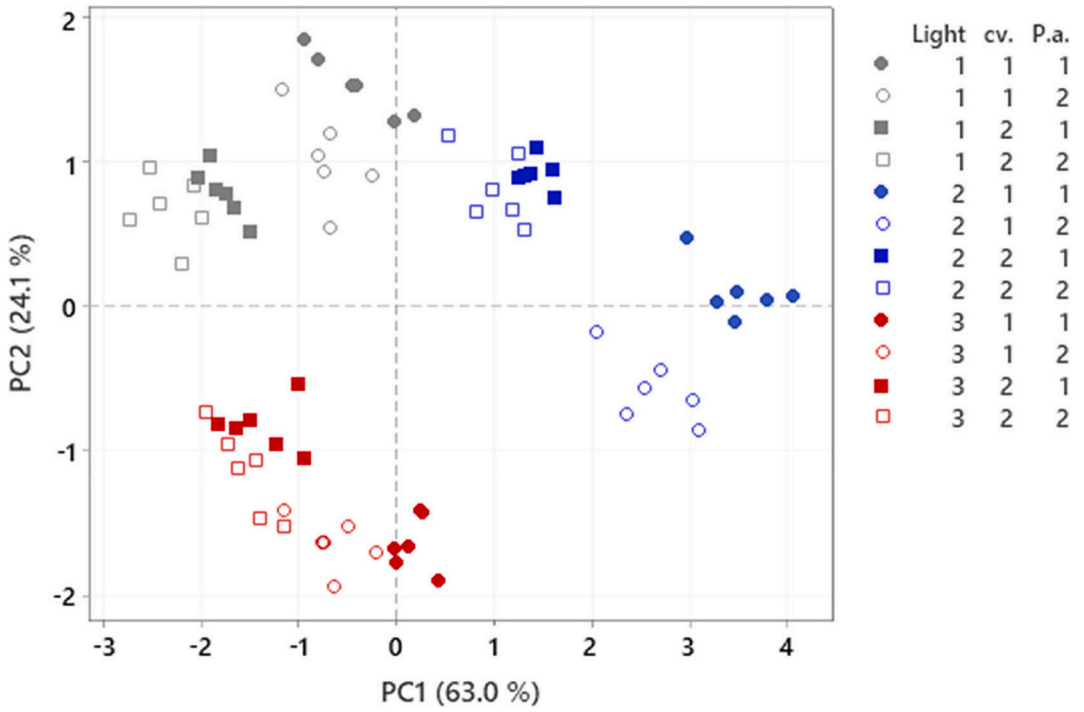

Fig. 2. Principal component analysis including accumulated berry weight and bioactive compound content (antioxidant activity, ascorbic acid content, total phenol content, anthocyanin content) of two strawberry cultivars (cv 1: Faith (circle), cv 2: Honeye (square)) exposed to either 18 h of polychromatic white LED light (control, C, grey symbols) or 6 h of white LED followed by 2 h of dark interruption with monochromatic blue (B) and red (R) LED light. The analysis displays plants with (open symbols) and without (filled symbols) artificial inoculation of *Podosphaera aphanis* (P.a.). N = 6.

root biomass ($p < 0.001$). Except in relation to root biomass, there were negative correlations between R/C ratio and the measured parameters. The canopy biomass explained between 48.4 % and 73.4 % of the variation in antioxidant activity, total phenol and anthocyanin content, but not ascorbic acid content. Positive correlations were obtained between the accumulated berry yield and antioxidant activity ($R^2 = 48.8$ %, $p = 0.003$) and ascorbic acid ($R^2 = 92.6$ %, $p < 0.001$), but not with respect to the total phenol and anthocyanin content. As expected, bioactive compounds were positively correlated (Table 1).

The key role of the R/C ratio was disrupted when the strawberry plants were inoculated with powdery mildew (Table 1). Interestingly, no significant correlation was found between the Log copy abundance of powdery mildew and canopy biomass, R/C ratio or anthocyanin content based on the mean comparison tests. For all other parameters, negative relationships were found to Log copy abundance of powdery mildew on strawberry leaves. As expected, the Log copy abundance of powdery mildew on strawberry leaves had a very strong negative impact on the accumulated berry yield ($R^2 = 91.7$ %, $p < 0.001$) (Table 1), but also on ascorbic acid content ($R^2 = 92.8$ %, $p < 0.001$) in berries (Table 2). In contrast, the ratio between root and canopy biomass only explained 42.8 % of the variations in accumulated berry yield ($p = 0.009$). As for the uninoculated plants, no correlations were observed between the accumulated berry yield and the anthocyanin content in strawberries. However, positive correlations were also obtained between the accumulated berry yield and antioxidant activity ($R^2 = 49.6$ %, $p = 0.002$) and ascorbic acid ($R^2 = 95.6$ %, $p < 0.001$), but also for the total phenol content ($R^2 = 47.6$ %, $p = 0.003$). The relationship between bioactive compounds was weaker when strawberry plants were inoculated with powdery mildew and no correlation was observed between ascorbic acid and anthocyanin content (Supplementary Tables S3 and S4).

3.1. Light regime

The results presented in Supplementary Tables S1 and S2 indicate the impact of light on growth parameters with respect to accumulated berry yield, canopy and root biomass as well as on all investigated quality parameters ($p < 0.001$). Light regime significantly affected the root and shoot plant biomass of both cultivars ($p < 0.001$), while their impact on the other parameters varied according to cultivar. Dark period interruption with red and blue LED promoted canopy and root fresh biomass compared to the control regime ($R > B$; $p > 0.001$). Significant differences ($p < 0.001$) were also found with respect to the accumulated berry yield ($p < 0.001$), but the choice of wavelength for dark period interruption was decisive for yield. While dark interruption with blue LED enhanced the accumulated berry yield compared to the control regime, the opposite was the case for dark period interruption with red LED (Table 1). Treatment with red light indicated reduction in both berry yield and number. Similar trends were found for both cultivars with respect to light regime and inoculation with powdery mildew, although the responses of the cultivars did not always result in significant differences (Tables 1 and 2, Supplementary Tables S1 and S2.

Dark period interruption positively affected the total phenol and anthocyanin content ($B > R$, $p < 0.001$). For ascorbic acid content, dark incubation with blue and red light led to opposite responses compared to the control ($p < 0.001$). Blue LED dark period interruption increased the ascorbic acid content, whereas red LED decreased the ascorbic acid content. This was observed for plants with and without artificial inoculation with powdery mildew (Tables 1 and 2).

3.2. Cultivar

In contrast to the accumulated berry yield and quality parameters ($p < 0.001$), no significant differences were recorded for the interactions between light regime and cultivars with respect to either canopy or root biomass (Supplementary Tables S1 and S2). Dark interruption with red LED further reduced the accumulated berry yield reduction in 'Honeoye' and led to significantly lower yield in 'Honeoye' compared to 'Faith'. Although blue LED dark interruption increased the accumulated berry yield in 'Honeoye' by 60 % compared to the control regime, a lower yield was obtained for Honeoye than 'Faith' under the same regime

Table 2
Bioactive compound contents in strawberries (cultivar 1: 'Faith'; cultivar 2: 'Honeye') exposed to different light regimes with or without inoculation with Podosphaera aphanis. All plants were illuminated for 18 h. Control plants were exposed to continuous polychromatic white LEDs for 18 h whereas the dark period in the other two treatments was interrupted with either 2 h of illumination with monochromatic blue or red LEDs after 16 h of irradiation with white LEDs. Mean values of six independent replicates and standard deviations are presented.

	Cultivar 1 ('Faith')									Cultivar 2 ('Honeye')								
	Control			Blue			Red			Control			Blue			Red		
w/o inoculation with *Podosphaera aphanis*																		
Antioxidant activity	64.17	±	2.64	(f)[a]	78.17	±	4.02	*(a)	71.00	±	2.19	*(bcd)	64.50	±	2.88	(ef)	76.50	±	1.87	*(a)	66.67	±	2.80	(def)
Ascorbic acid content	75.83	±	2.34	(c)	92.17	±	2.14	(a)	63.83	±	3.31	*(d)	64.17	±	2.64	(e)	83.33	±	2.88	(b)	59.83	±	5.42	*(de)
Total phenol content	21.50	±	3.56	(d)	35.00	±	3.16	*(ab)	29.17	±	3.43	*(bc)	19.33	±	2.16	(d)	26.00	±	2.61	*(cd)	25.83	±	4.02	(cd)
Anthocyanin content	229.83	±	6.65	(b)	366.67	±	3.78	*(a)	346.00	±	4.69	*(c)	197.17	±	2.79	(j)	266.17	±	4.36	*(f)	250.67	±	3.08	*(g)
w inoculation with *Podosphaera aphanis*																								
Antioxidant activity	62.67	±	2.34	(f)	75.67	±	2.16	*(ab)	69.67	±	1.63	*(cde)	62.50	±	3.45	(f)	73.17	±	3.31	*(abc)	64.50	±	1.87	(ef)
Ascorbic acid content	74.17	±	2.48	(c)	83.50	±	2.88	*(b)	57.50	±	2.59	*(e)	59.17	±	2.32	(de)	82.50	±	3.39	*(b)	57.17	±	2.32	(e)
Total phenol content	24.17	±	4.02	(cd)	36.17	±	5.19	*(a)	25.00	±	3.41	(cd)	20.67	±	3.20	(d)	26.00	±	3.90	*(cd)	24.33	±	2.88	(cd)
Anthocyanin content	223.83	±	4.62	(i)	355.50	±	2.74	*(b)	335.83	±	3.06	*(d)	170.33	±	2.73	(k)	264.67	±	3.93	*(f)	285.33	±	4.50	*(e)

[a] Values within the same row and cultivar marked with and asterix are significantly different from the control as assessed by One-way ANOVA followed by the Dunnett test ($\alpha = 0.05$). Different letters given in brackets indicate significant differences based on interactions between cultivar*light*inoculation with P. aphanis as assessed by the Tukey-test ($p < 0.05$).

(Table 1).

Comparison of bioactive compounds in the two cultivars as affected by the light regime gave an inconsistent picture. Antioxidant activity and total phenol content were comparable in the two cultivars subjected to the control regime, whereas ascorbic acid and anthocyanin contents were significantly lower in 'Honeoye' than 'Faith' (Table 1 and 2). In 'Honeoye' exposed to dark period interruption with blue LED only antioxidant activity was higher than in 'Faith'; all other bioactive compounds were recorded at a lower level in 'Honeoye' than in 'Faith'.

Bioactive compound content of inoculated plants basically displayed the same pattern in relation to the light treatments as in uninoculated plants. In general, bioactive compound formation was enhanced as compared to the control regime (B > R), when exposed to dark period interruption. Differences in bioactive compound content between the control regime and red LED dark period interruption were not always significant ('Faith' and 'Honeoye': total phenol content; 'Honeoye': antioxidant activity, ascorbic acid content). Surprisingly, in 'Honeoye', but not in 'Faith', the anthocyanin content in berries from inoculated plants subjected to red light dark period interruption significantly increased as compared to blue LED interruption ($p < 0.001$).

3.3. Powdery mildew inoculation

Log copy abundance of powdery mildew on strawberry leaves was affected by the interaction 'Light regime x cultivar' ($p < 0{,}001$) (Fig. 3). Significant differences (Tables 1 and 2, Supplementary Tables S1 and S2) were observed for light regime and cultivar ($p < 0.001$), root biomass ($p < 0.001$), accumulated berry yield ($p < 0.001$) and anthocyanin content ($p < 0.001$). Dark period interruption with blue LED significantly ($p < 0.001$) reduced the abundance of powdery mildew, while dark period interruption with red LED significantly ($p < 0.001$) promoted the Log copy abundance of powdery mildew compared to the control treatment in both strawberry cultivars. No differences were

Fig. 3. Abundance of powdery mildew (*Podosphaera aphanis*, Log number of DNA copies g^{-1} leaf fresh weight) on strawberry leaves (cultivar 1: 'Faith', filled bars; cultivar 2: 'Honeye', open bars) as affected by light regime. Control plants (grey) were subjected to continuous white LED irradiation during 18 h, whereas plants in the two other regimes were irradiated by white LED for 6 h followed by a dark period interrupted with two h of either blue (blue) or red (red) LED irradiation. Mean values and standard deviation of six replicate plants are displayed. Bars within the same cultivar, marked with different capital letters inside the bars, are significantly different according to One-way Anova followed by Dunnett test ($\alpha = 0.05$). Bars within the same treatment marked with different small letters above the bars are significantly different according to One-way Anova followed by Tukey test ($p < 0.05$).

observed between the cultivars under blue light dark period interruption, while for the two other regimes; the abundances were significantly higher in 'Honeoye' than 'Faith'.

When inoculated with powdery mildew, the two strawberry cultivars showed a similar response to the three light regimes as in non-inoculated plants. There was a trend towards higher canopy and root biomass in the presence of powdery mildew as compared to uninoculated plants. However, no differences occurred in canopy and root biomass in inoculated plants when comparing the three light regimes. On the other hand, accumulation of berries was significantly different ($p < 0.001$) with and without inoculation of powdery mildew (Tables 1, Supplementary Tables S1). With respect to the bioactive compound content, inoculation with powdery affected anthocyanin content compared to uninoculated plants ($p < 0,001$) (Tables 1, Supplementary Tables S1).

4. Discussion

The results obtained in the current study advocate strength the potential of LED light as sustainable strategy to reduce the use of pesticides towards powdery mildew and targets the sustainability goals and health aspects in food production (Gómez and Izzo, 2018). LED treatment has been widely investigated in relation to strawberry plants as a parameter to enhance plant growth and quality (Yoshida et al., 2016; Nadalini et al., 2017; Stuemky and Uchanski, 2019; Lee et al., 2020; Paradiso and Proietti, 2022; Ries and Park, 2024). In contrast to most studies, which have explored the impact of different combinations of blue, red and far-red light, the present investigation focused on dark period interruption with a monochromatic light source.

The idea of modifying the light regime is new to organically grown strawberries and with respect to powdery mildew, but not new in general. Studies by Suthaparan et al., (2010a) and Suthaparan et al., (2014) have previously applied such treatments to rose and cucumber plants, respectively, and found a tendency for a reduction in powdery mildew symptoms. In addition, most of the studies conducted thus far targeting the control of powdery mildew in strawberry have been focused on the use of UV irradiation (Onofre et al., 2022; Takeda et al., 2019; Takeda et al., 2021) using short- or neutral-day cultivars. Few studies have considered the impact of light from LEDs within the visible light spectrum. Our study, discriminating between light regime, cultivar and powdery mildew occurrence, helps to fill this gap.

The findings in the current study reveal the potential to apply dark interruption with blue or red LED to reduce the occurrence of powdery mildew (Fig. 3). The impact of darkness on the growth and development of pathogens associated with powdery mildew attack has been highlighted in other studies. Continuous exposure to darkness has been shown to suppress haustoria formation in a leaf disc assay with three powdery mildew genera (*Blumeria graminis* f.sp. *graminis*, *Erysiphe pisi*, *Sphaerotheca curcubitae*), the size of primary haustoria in *B. graminis* and the total hyphal length of *E. pisi* and *S. curcubitae* (Rie et al., 2007). However, a gradual recovery was noted when dark treated powdery mildew was re-exposed to white (polychromatic) light, a process that could be slowed down by exposure to monochromatic light in the red, white and blue spectra. Studies by Suthaparan et al., (2010b) indicated that continuous lighting using high-pressure sodium lamps had a significant impact on the reduction of powdery mildew on roses after 24 h compared to 18 h, which was associated with the highest conidia production. In contrast, our results showed the possibility of achieving a reduction in the occurrence of powdery mildew using a combination of 16 h while light and 2 h red or blue LED for the dark interruption treatments. This finding is of interest and highlights the potential of using such dark interruption as a powdery mildew reducing strategy under white LED.

Our results also revealed that the choice of light regime and of wavelength during dark period interruption significantly affected the log abundance of DNA copies of *P. aphanis* (Fig. 3). This encouraging result needs to be treated carefully; despite the strong technical significance, the biological relevance needs to be further assessed. This is of particular interest, as the reduction in accumulated berry yield could not be compensated for by light regime (Table 1).

Furthermore, our findings confirm the potential of the use of blue LED to reduce the occurrence of powdery mildew in strawberry cultivation. Applying blue LED has been shown, in previous studies, to be an effective strategy for inhibiting the viability of pathogens related to plant diseases (Meng et al., 2020) and food safety (Lawrence et al., 2022) and under medical conditions to inhibit microbial growth (Trzaska et al., 2016). The existing limited knowledge about the impact of monochromatic light sources on powdery mildew in strawberry cultivation makes the application of blue light an interesting disease control tool. However, the impact of blue light on powdery mildew has been reported for melon (Suzuki et al. 2018; Jing et al., 2018) and roses (Suthaparan et al., 2010a). The mechanisms behind the impact of the blue LEDs in the current study were not investigated, but the increase in total phenols and antioxidant activities could be one of the reasons behind the antifungal response, as highlighted by Jing et al. (2018). It could also be correlated to the development of conidia related to pathogen growth. The study performed by Suzuki et al. (2018) indicated incomplete conidia development under blue compared to red LED light. These aspects need to be examined in future studies to strength understanding of the potential of blue light in the control of powdery mildew in strawberry cultivation. The success of using blue LEDs in disease control could lead to environmental benefits, replacing the current use of fungicides and of energy-demanding UV-light to control powdery mildew. This is an area of interest for future applied research on the use of blue LEDs for disease control in horticultural production systems.

Moreover, strawberry plants' susceptibility to powdery mildew is cultivar-dependent (Menzel, 2022). In the present study, the cultivars were chosen because of their use in commercial strawberry cultivation under Swedish conditions, and not their susceptibility. However, we chose short-day cultivars and expect a similar response by other short-day cultivars (Nadalini et al., 2017). To assess the relevance of dark period interruption for powdery mildew control in commercial production, the study needs to be repeated with cultivars displaying a broad susceptibility spectrum to *P. aphanis*.

With respect to biomass, an increase in relation to red or blue LED treatment seems to be indicated compared to the control (Table 1), which suggests that the significant difference in the biomass is due to dark interruption and pathogen treatment rather than LED treatment. Both blue and red LED contributed to the biomass increase. The impact of these treatments is in line with previous investigations describing the interaction between LED treatment and plant performance (Appolloni, et al., 2021; Lee et al., 2020). Blue LED light is expected to enhance plant growth and biomass due to its impact on photosynthesis and stomatal performance (Choi et al. 2015; Suzuki et al. 2022). The impact of red LED light on biomass might be related to its impact on canopy growth and branching (Alsanius et al., 2024; Paradiso and Proietti, 2022) and shoot elongation (Samuolienė et al., 2011). However, our treatment with red LEDs produced the lowest impact on the investigated parameters. This result differs from previous studies, which have found a positive impact of red LEDs in reducing powdery mildew attack in cucumber and on growth parameters related to branching (Suthaparan et al., 2010b) as well as on the sporulation of the pathogen mycelium in the case of *Botrytis* species (Meng et al., 2020). The possibility of using red LEDs for reducing powdery mildew in strawberry cultivation cannot be ruled out based on our findings but needs to be confirmed in further analysis. The impact of dark interruption with red light on the accumulated yield in relation to lower fresh weight and number of berries (Table 1) needs also further investigation. This impact could be related to different factors including light intensity, temperature, and raises questions about the efficiency of using red light alone in strawberry cultivation. In cooperating red light with blue and even far-red LED to achieve a good yield has indicated in other studies (Samuolienė et al., 2010; Ries and Park, 2024).

Moreover, this study revealed plant health aspects of LED treatment in the control of powdery mildew, with higher antioxidant activity (Table 2). We conclude that blue LED treatment has a positive impact on quality parameters through enhancing antioxidant activity and the content of ascorbic acid, total phenols, and anthocyanin in strawberry fruits, which is in line with previous reports of e.g., enhanced content of antioxidants in strawberry fruits due to blue LED treatment (Xua et al., 2014). Other recent studies have observed the impact of red LED light on plant defense mechanisms related to pathogen attack and production of anthocyanin (Lauria et al., 2023; Xu et al., 2018). The present study also revealed enhanced content of anthocyanin in fruit of both cultivars after treatment with either blue or red LED light. This may also suggest an impact on the defense mechanism in the plants and thereby on the antifungal activities (Suzuki et al., 2018). However, the results obtained from the current study were based on the correlations between the investigated parameters with respect to impact of the treatments on quality parameters. No investigations into biological activities in the plants were carried out. This needs to be strengthened to support the use of light and dark interruption integration as a strategy to reduce the attack of powdery mildew and enhance the quality parameters.

The results obtained in this study are of interest for organic strawberry production and may lead to improved integrated control strategies for powdery mildew. The enhanced content of bioactive compounds in strawberries exposed to dark period interruption with blue LED provides added value to such a strategy. Before recommending this strategy, however, the effect needs to be verified with a broader range of strawberry cultivars and powdery mildew isolates, also considering the impact on various quality classes.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crbiot.2025.100313.

Data availability

Data will be made available on request.

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