Supplemental Far-red Light Prevents Semidormancy and Enhances Yield and Fruit Quality of Short-day Strawberry in Indoor Production

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KEYWORDS. controlled-environment agriculture, *Fragaria* ×*ananassa*, indoor farming, June-bearing strawberry, photoperiod

ABSTRACT. Optimizing the light environment for indoor strawberry production is critical for ensuring high productivity and fruit quality. Short-day (SD) strawberries require SD conditions for flower induction. However, short days can also cause semidormancy symptoms that inhibit strawberry plant growth and production. One strategy to address this challenge in SD strawberry production is extending to a long-day (LD) photoperiod to prevent semidormancy. This preliminary study investigated the effect of photoperiod adjustment and light quality modification by analyzing two SD strawberry cultivars, Earliglow and Nyohou, under three photoperiod treatments (SD, LD, or alternating SD/LD) with or without supplemental far-red (FR) treatments (44% FR, 700–800 nm over a total photon flux density of 400–800 nm). Plants under continuous SD conditions exhibited a typical semidormancy-like morphology, with shorter petioles and peduncles. The supplemental FR treatment extended petiole and peduncle length significantly, regardless of daylength. Strawberry total yield, total number of fruit, and percentage of marketable fruit were greater in plants with supplemental FR treatment regardless of cultivar. Supplemental FR light treatment also increased the total soluble solid concentration (TSS, Brix) and the Brix-to-titratable acidity ratio. The increase in productivity and fruit TSS was attributed in part to a high total photon flux density as well as improved plant morphology under supplemental FR light, which enhanced photoassimilate allocation to fruit. The addition of FR light appears to be beneficial in indoor production of SD strawberry cultivars for preventing semidormancy and enhancing yield and fruit quality.

Cultivated short-day (SD) strawberries (*Fragaria* ×*ananassa*), also known as June-bearing strawberries, are grown extensively in Europe, Asia, and the Americas in controlled environments for the production of high-quality fruit (Neri et al. 2012; Nishizawa 2021; Samtani et al. 2019). Long-day (LD), or ever-bearing, strawberry cultivars were developed more recently (Mezzetti et al. 2018), and growers select cultivars based on expected outcomes suitable for their growing environments and systems. As the productivity and fruit quality of SD strawberries in greenhouse or field production are suppressed in summer and fall because of the high temperatures associated with long days, the interest in year-round SD strawberry production using fully controlled indoor farms (i.e., vertical farms) is on the rise (Carpineti et al. 2024; Kouloumprouka Zacharaki et al. 2024; Yamasaki 2013), leading to the development of several commercial indoor farms specialized in SD strawberry production. In indoor vertical farms, flowering is induced in SD strawberries by cultivating the plants under SD conditions (Garcia and Kubota 2017a). However, it can be challenging to grow strawberry plants continuously under SD conditions because of the development of semidormancy symptoms, leading to growth reduction in plants (Sønsteby and Heide 2006). Typical semidormancy symptoms include reduced growth rate and the emergence of smaller, thicker, and more brittle leaves with shorter petioles and shorter peduncles, resulting in a stunted and compacted shoot canopy (Sønsteby and Heide 2006). In addition, flower development and fruit productivity are also reduced in semidormant plants (Bodson and Verhoeven 2005).

Previous studies showed that strawberry semidormancy symptoms could be mitigated by extending daylength, lowering temperatures, or applying exogenous gibberellic acids (GAs). After flower induction under SD conditions, strawberry plants can recover gradually from semidormancy when moved into LD environments (Sønsteby and Heide 2006, 2021). We observed extension lighting or night-interruption lighting as common practices to mitigate semidormancy in Japan, where SD cultivars are grown intensively for production in winter through spring months in greenhouse-controlled environments. However, prolonged exposure of SD plants to LD conditions must be done carefully because, in some cases, SD plants may stop perpetual flowering. Growing plants in a photoperiod just below the critical photoperiod has also reportedly helped mitigate semidormancy symptoms. For example, SD strawberry 'Korona' produced a similar number of flowers and yield under 12- and 13.5-h photoperiods, and they showed improved leaf petiole length in the 13.5-h photoperiod (Konsin et al. 2001).

Semidormancy symptoms under continuous SD conditions can be also avoided through chilling at a low temperature of 6 °C (Sønsteby and Heide 2006, 2021). This is supported by the evidence that accumulation of chilling (temperatures between –2 and 7 °C) is commonly used to break dormancy in SD strawberries (Guttridge 1958; Kronenberg et al. 1976; Tehranifar et al. 1998). However, low temperatures generally slow overall plant growth and development rate, and therefore can cause a decrease in yield (Li et al. 2021).

Treating strawberry plants with GAs was also shown to mitigate

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semidormancy symptoms (Paroussi et al. 2002). Although these chemical treatments promote vegetative growth, special attention is needed when determining the application concentration, because applying GAs at high concentrations can also inhibit flower production (Guttridge and Thompson 1964; Paroussi et al. 2002; Tafazoli and Vince-Prue 1978). Another issue is that, as far as we know, commercial use of GA applications in strawberries is currently limited to propagation, not fruit production in North America. However, the reported efficacy of exogenous GA in mitigating semidormancy may suggest an alternative nonchemical approach that can induce extension growth, such as supplemental far-red (FR) lighting.

FR light (700–800 nm) has been studied intensively recently, along with the rapid development of lighting technologies for indoor farming. When applied together with photosynthetically active radiation (PAR; 400–700 nm), FR light can enhance photosynthesis (Zhen and Bugbee 2020) and extend plant growth (Vince-Prue et al. 1976). In some species, it is also known to affect flowering induction, as summarized by Demotes-Mainard et al. (2016). The effects of FR light on extended growth and flowering induction are both mediated by phytochromes, photoreceptors that regulate plant photomorphogenesis through light signaling (Collins 1966), and the photon flux ratio between red (R) light and FR light can affect the state and amount of phytochromes (Zahedi and Sarikhani 2016). In SD strawberries grown under LD conditions, the addition of FR light promoted flowering and petiole length, which was observed with both continuous (Collins 1966) and end-of-day (EOD) FR application (Zahedi and Sarikhani 2016, 2017), contributing to both flower induction and the mitigation of semidormancy symptoms. SD strawberry plant yields were less when FR light was filtered by greenhouse film to an R-to-FR ratio of 1.57 compared with when R light was filtered to an R-to-FR ratio of 0.78 (Black et al. 2005).

The objective of our study was to determine the effects of different photoperiods with or without supplemental FR light on the production of SD strawberries for indoor farming. We hypothesized that SD strawberry plants would not exhibit semidormancy symptoms when they are grown under prolonged SD conditions with a low R-to-FR photon flux ratio. We also expected that improved plant morphology with supplemental FR lighting would benefit plant productivity in both SD and LD conditions.

Materials and methods

Plant materials. SD strawberry cultivars Earliglow and Nyohou were selected for their high sensitivity to the dormancy-inducing, prolonged SD conditions observed in our previous experiments (Lin et al. 2025). Daughter plants with visible root initials were collected from mother plants grown inside a walk-in growth chamber (GH300; Conviron, Winnipeg, MB, Canada) at The Ohio State University (Columbus, OH, USA). The daughter plants were rooted in rockwool plugs (Grodan Inc., Roermond, the Netherlands) and subirrigated with water under clear-plastic humidity domes in a reach-in growth chamber (PGC-Flex; Conviron) for 15 d. Air temperature and photosynthetic photon flux density (PPFD) inside the dome was at 24 ± 1 °C and 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with a 10 $h \cdot d^{-1}$ photoperiod. The rooted plants were transplanted into 396-mL black, square tree band containers with a coco-based substrate (Finesse; Jiffy Group, Zuid-Holland, the Netherlands) and grown for 2 months in the walk-in chamber. Air temperature, relative humidity, PPFD, and daytime CO_2 concentrations inside the growth chamber were 28 ± 1 °C, 72% ± 2%, 332 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [provided at plant canopy level with light-emitting diode (LED) lights (Gavita CT1930e; Hawthorne, Port Washington, NY, USA)] for a 16 $h \cdot d^{-1}$ photoperiod), and 1000 ± 14 $\mu mol \cdot mol^{-1}$ CO_2. Plants were fertigated by hand three times a week using a nutrient solution created by mixing a premixed commercial fertilizer (Jack's Strawberry Part A; JR Peters Inc., Allentown, PA, USA) and $Ca(NO_3)_2$ (Calcinit; Yara, Oslo, Norway), containing 80 $mg \cdot L^{-1}$ total N (72 $mg \cdot L^{-1}$ NO_3-N and 8 $mg \cdot L^{-1}$ NH_4-N), 24 $mg \cdot L^{-1}$ P, 121 $mg \cdot L^{-1}$ K, 44 Ca $mg \cdot L^{-1}$, 13 $mg \cdot L^{-1}$ Mg, 50 $mg \cdot L^{-1}$ S, 10 $mg \cdot L^{-1}$ Cl, and micronutrients. Two-month-old strawberry plants with at least five true leaves and a minimum 1-cm crown diameter were transplanted into 2.4-L black, round plastic containers with the same coconut-coir substrate.

Growing conditions and treatments. Strawberry plants were grown inside two identical reach-in growth chambers (PGC-Flex; Conviron). For the first 7 weeks, all plants were grown under a 12 $h \cdot d^{-1}$ SD photoperiod, with a 240 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD provided with LED lights (Ray44 Broad White; Fluence, Austin, TX, USA) to ensure initial flower induction. After that, plants were divided into six treatment combinations (three plants per cultivar per treatment combination, 36 plants in total) consisting of three photoperiod treatments (continuous SD, continuous LD, or alternating SD/LD every 5 weeks) and two FR treatments (with or without FR). Supplemental FR light was provided using LED lights (Ray44 Far Red; Fluence). Light spectra were measured using a spectroradiometer (PS-200; Apogee, Logan, UT, USA) for each treatment combination (Fig. 1). The photoperiod, PPFD (400–700 nm), daily light integral (DLI; 400–700 nm), supplemental FR photon flux density (PFD; 700–800 nm), R-to-FR ratio, phytochrome photostationary state, extended PPFD (400–750 nm), and extended DLI (eDLI; 400–750 nm) for the six treatment combinations are listed in Table 1. We applied relatively high FR PFDs to achieve a low R-to-FR ratio of 0.53 to 0.56, which is far below what we typically observe in incident sunlight (1.0–1.2), to observe strawberry plant responses under a significantly enhanced FR light environment. In the LD and SD growth chambers, air temperature, relative humidity, and CO_2 concentration were 18.5 ± 0.2 °C and 18.3 ± 0.3 °C, 65% ± 9% and 68% ± 9%, and 407 ± 27 and 407 ± 30 $\mu mol \cdot mol^{-1}$, respectively. Plants were fertigated twice a week with drip irrigation using a premixed commercial fertilizer (Jack's Strawberry Part A; JR Peters Inc.) and $Ca(NO_3)_2$ (Calcinit; Yara), containing 80 $mg \cdot L^{-1}$ total N (72 $mg \cdot L^{-1}$ NO_3-N and 8 $mg \cdot L^{-1}$ NH_4-N), 24 $mg \cdot L^{-1}$ P, 121 $mg \cdot L^{-1}$ K, 44 $mg \cdot L^{-1}$ Ca, 13 $mg \cdot L^{-1}$ Mg, 50 $mg \cdot L^{-1}$ S, 10 $mg \cdot L^{-1}$ Cl, and micronutrients. The fertigation volume was adjusted to maintain a 0.3 ± 0.07 daily drain-to-drip solution volume ratio. The pH and electrical conductivity of the drain solution were 6.5 ± 0.03 and 1.3 ± 0.07 $dS \cdot m^{-1}$. The experiment was conducted for 27 weeks, during which runners and old leaves were

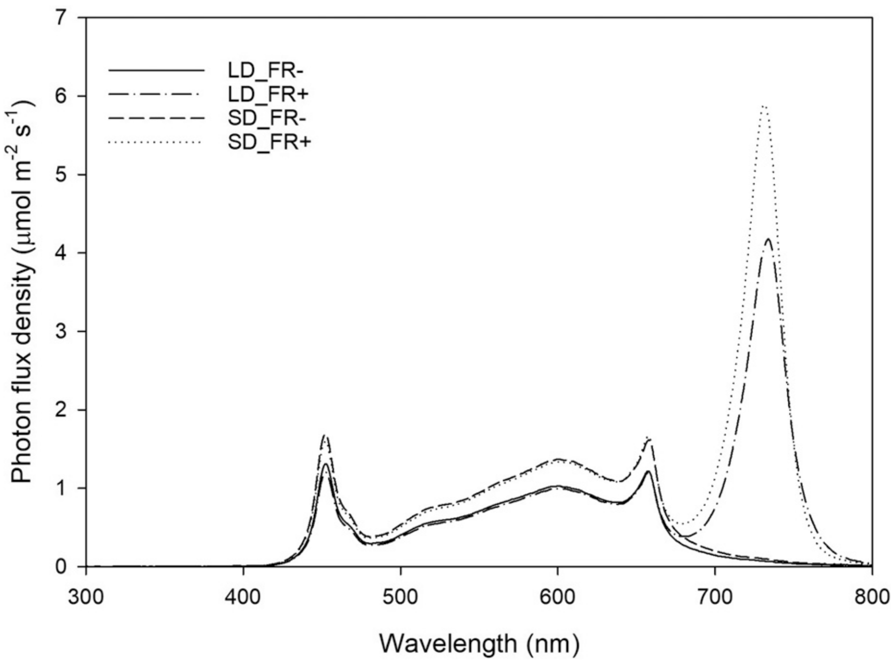

Fig. 1. Light spectra of short-day (SD) and long-day (LD) photoperiods in combination with far-red (FR) treatments: LD_FR–, LD_FR+, SDFS–, and SD_FR+. Plants receiving the SD/LD_FR– treatment combination were moved between LD_FR– and SD_FR– every 5 weeks. Plants receiving the SD/LD_FR+ treatment combination were moved between LD_FR+ and SD_FR+ every 5 weeks. Specific information about photoperiod, photosynthetic photon flux density (PPFD; 400–700 nm), daily light integral (DLI; 400–700 nm), supplemental FR photon flux density (700–800 nm), red-to-FR ratio, phytochrome photostationary state, extended PPFD (400–750 nm), and extended DLI (400–750 nm) for each treatment combination can be found in Table 1.

removed weekly, and the flowers were pollinated daily by shaking plant canopies and flicking individual flowers by hand.

Data collection. Mature strawberry fruit were harvested three times a week. Total yield per plant and the number of fruit were recorded. Strawberry fruit were deemed marketable when the fruit weighed more than 5 g, based on the current industry standard (Mucci Farms, personal communication). Harvesting was conducted from 16 to 26 weeks after transplanting. Between 16 and 21 weeks after transplant, the calyx and the top white part of the harvested fruit were removed before weighing. Pictures of representative plants were taken 22 weeks after transplanting. After 25 weeks, total soluble solid concentration (in degrees Brix) and titratable acidity (TA) were measured using 25 g of fruit sample per plant using a Pocket Brix-Acidity Meter for strawberry (PAL-BX|ACID F5; ATAGO, Bellevue, WA, USA). After 26 weeks, final plant morphological measurements were performed. Leaf petiole length was measured from two fully expanded leaves per plant using a ruler. Peduncle length was measured using two mature peduncles per plant. Leaf net photosynthetic rate was measured with a portable photosynthesis system (CIRAS-3; PPSystems, Amesbury, MA, USA) using the newest fully expanded leaf of each plant. The measurements were taken with a PLC3 Universal Leaf Cuvette (PPSystems) in the growth chambers. The cuvette temperature, vapor pressure deficit, and reference CO_2 were set at 18 °C, 1 kPa, and 400 µmol·mol^{-1}. A PPFD of 180 or 240 µmol·m^{-2}·s^{-1}, with and without supplemental FR light inside the cuvette, provided by growth chamber lights were applied for the measurement. After 27 weeks, leaf total chlorophyll concentration was measured for sample leaf disks (diameter, 28 mm) following the protocol reported by Moran (1982)

Table 1. Photoperiod, photosynthetic photon flux density (PPFD; 400–700 nm), daily light integral (DLI; 400-700 nm), supplemental far-red photon flux density (FR PFD, 700–800 nm), R-to-FR ratio, phytochrome photostationary state (PSS), extended PPFD (ePPFD, 400–750 nm), and extended DLI (eDLI, 400–750 nm) for each treatment combination.

Treatment combination	LD_FR–	LD_FR+	SD_FR–	SD_FR+	SD/LD_FR–[i]	SD/LD_FR+[i]
Photoperiod (h·d^{-1})	16	16	12	12	12/16	12/16
PPFD (µmol·m^{-2}·s^{-1})	180	180	240	240	240/180	240/180
DLI (µmol·m^{-2}·d^{-1})	10.4	10.4	10.4	10.4	10.4	10.4
FR PFD (µmol·m^{-2}·s^{-1})	5	146	7	189	3/3	78/81
R-to-FR ratio	13.6	0.53	13.3	0.56	13.3/13.6	0.56/0.53
PSS[ii]	0.860	0.560	0.859	0.566	0.859/0.860	0.566/0.560
ePPFD (µmol·m^{-2}·s^{-1})	184	307	245	418	184/245	307/418
eDLI (µmol·m^{-2}·d^{-1})	10.6	17.7	10.6	18.1	10.6	17.7/18.1

[i] Alterations between corresponding SD and LD conditions with or without FR supplementation every 5 weeks.
[ii] Phytochrome photostationary state estimated based on spectral data according to Sager et al. (1988).
LD = long day; SD = short day.

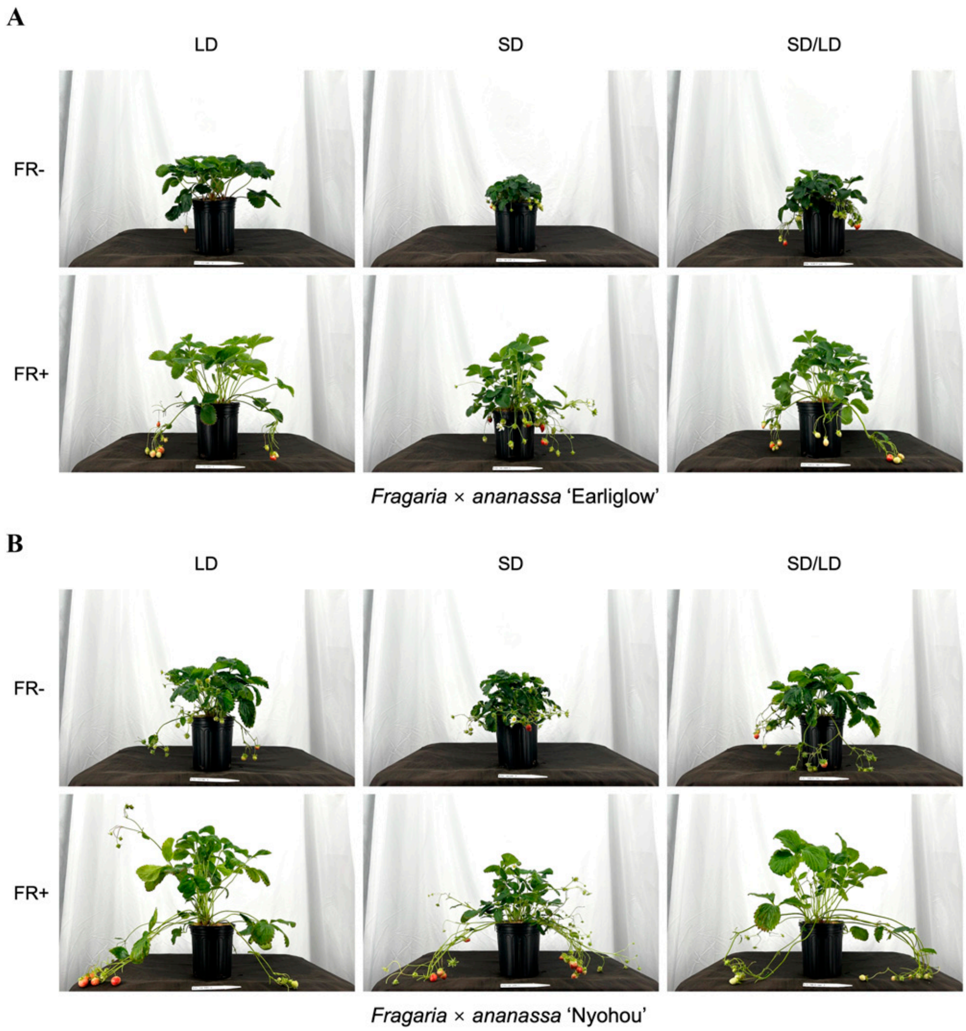

Fig. 2. Pictures of representative strawberry (*Fragaria × ananassa*) plants 22 weeks after transplant, including short-day (SD) strawberry cultivars Earliglow (A) and Nyohou (B). Photoperiod treatments include continuous long-day (LD), continuous SD, and alternating SD/LD every 5 weeks. Far-red (FR) treatments include no additional FR light [FR–; red (R)-to-FR ratio, 13.3–13.6] and the addition of supplemental FR light (FR+; R-to-FR ratio, 0.53–0.56) to a white light-emitting diode background.

using a spectrophotometer (ultraviolet-3100PC; VWR, Radnor, PA, USA).

Experimental design and statistical analysis. This study used a nested design, with growth chambers being the main plots, and cultivars and their replicates being the nested effects. All statistical analyses were conducted in R v. 4.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Because of the lack of growth chamber replication, the main-plot effect was tested using the photoperiod × FR effect as the error term, and the cultivar and interaction effects were tested using the residual error. The interaction effects, including cultivar × photoperiod, cultivar × FR, and cultivar × photoperiod × FR, were determined using analysis of variance (ANOVA) with model: $y = \mu + \text{photoperiod} + \text{FR} + \epsilon(\text{photoperiod} \times \text{FR}) + \text{cultivar} + (\text{cultivar} \times \text{photoperiod}) + (\text{cultivar} \times \text{FR}) + (\text{cultivar} \times \text{photoperiod} \times \text{FR}) + \epsilon$. Photoperiod and FR effects were determined for each cultivar using ANOVA protected mean separation via Tukey's honestly significant difference test using the R package agricolae (R Foundation for Statistical Computing).

Results and discussion

Supplemental FR light prevented semidormancy in indoor SD strawberry production. Plant morphological structure was improved with the LD photoperiod or FR supplementation (Fig. 2) 22 weeks after transplanting. Mature leaf petiole length is commonly used to evaluate plant morphological response to dormancy-inducing environments (Robert et al. 1999). In plants grown under SD conditions without supplemental FR light (SD_FR–), we observed semidormancy symptoms, including compact plant size (Fig. 2) and reduced petiole length (Table 2). Compared with the SD treatment, the leaf petioles of LD-treated plants were 34% and 54% longer, and SD/LD-treated plants had 10% and 25% longer leaf petioles, respectively, in 'Earliglow' and 'Nyohou' (Table 2). FR light supplementation also contributed to the increase of petiole length with a greater extent, causing 90% and 64% longer petioles in 'Earliglow' and 'Nyohou' than the treatment without FR supplementation (Table 2). Similar responses

Table 2. The effects of photoperiod (P), far-red (FR), and cultivar (C) on strawberry plant morphology, productivity, leaf chlorophyll content, and fruit quality.

Treatment	Petiole length (cm)	Peduncle length (cm)	No. of fruit	Marketable fruit (%)	Total chlorophyll content ($mg \cdot g^{-1}$)	Brix (%)	Brix-to-TA ratio
Earliglow							
P[i]							
LD	20.7 a	18.6 a	47 a	27 a	2.9 a	11.3 a	1.2 a
SD	15.4 c	9.9 a	50 a	22 a	2.5 a	8.6 a	1.0 a
SD/LD	17.0 b	13.2 a	51 a	19 a	2.3 a	10.5 a	1.3 a
FR[i]							
FR–	12.2 b	6.6 b	31 b	17 b	3.1 a	8.4 b	0.9 a
FR+	23.2 a	21.2 a	67 a	29 a	2.0 b	11.9 a	1.4 a
Nyohou							
P							
LD	25.2 a	26.1 a	43 a	19 a	2.4 a	9.9 a	1.1 a
SD	16.4 c	16.8 a	37 a	17 a	2.9 a	9.0 a	0.9 a
SD/LD	20.5 b	18.4 a	45 a	6 a	2.2 a	9.6 a	1.0 a
FR							
FR–	15.7 b	15.8 a	29 b	4 b	3.2 a	8.6 a	0.8 b
FR+	25.7 a	25.0 a	54 a	24 a	1.8 b	10.4 a	1.2 a
Interaction effects (ANOVA)[ii]							
P × C	***	NS	NS	*	NS	*	NS
FR × C	NS	***	NS	*	NS	***	*
P × FR × C	***	**	NS	***	NS	NS	NS

[i] The effects of photoperiod and FR treatments were determined using analysis of variance protected mean separation via Tukey's honestly significant difference test using the photoperiod × FR effect as the error term. Treatments with the same letter were not statistically different.

[ii] NS, *, **, and *** Nonsignificant or significant at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

LD = long day; SD = short day; TA = titratable acidity.

in petioles were also reported when strawberries are moved from SD to LD conditions (Sønsteby and Heide 2006, 2017) or treated with EOD FR lighting for 4 to 6 h (Zahedi and Sarikhani 2016). Similar to petioles, the peduncle length of plants with FR supplementation was 2.2 times longer than that of plants without FR supplementation in 'Earliglow' (Table 2). FR supplementation did not affect 'Nyohou' peduncle length significantly.

Supplemental FR light promoted strawberry productivity. In both 'Earliglow' and 'Nyohou', photoperiod treatments (SD, LD, and SD/LD) did not affect fruit yield significantly after 11 weeks of harvest in this study, although prolonged exposure to SD without FR supplementation may limit productivity, as we typically observe in indoor growing conditions using these SD cultivars. In contrast, supplemental FR light treatment increased fresh fruit yield per plant 2.6 times compared with the corresponding treatment without FR supplementation (Fig. 3). The total number of fruit was also increased as a result of the FR+ treatment, resulting in 116% and 86% more fruits harvested in 'Earliglow' and 'Nyohou', respectively (Table 2). FR supplementation also increased the percentage of marketable fruit by 1.7 and 6.0 times in 'Earliglow' and 'Nyohou', respectively (Table 2). Our finding is similar to a growth chamber study reported by Yamanaka et al. (2024), in which the total and average marketable fruit weights were improved in SD strawberry 'Beni hoppe' when grown with magenta LED spectra containing FR (R-to-FR ratio, 2.98) compared with white LED spectra (R-to-FR ratio, 9.19) at the same DLI. Everbearing strawberry 'Albion' treated with additional FR light in a sole-source R and blue (B) LED lighting environment with the same DLI at a high R-to-FR ratio of 5 also resulted in improved total yield and fruit number (Ries and Park 2024).

The effect of FR light on fruit production has also been studied in tomatoes (*Solanum lycopersicum*) and peppers (*Capsicum annuum*). In greenhouse-grown tomatoes, fruit production, including fresh weight and dry weight, was enhanced significantly by adding continuous supplemental FR lighting while maintaining the same DLI (Ji et al. 2019; Kalaitzoglou et al. 2019; Vincenzi et al. 2024). Greenhouse pepper plants grown with additional supplemental FR light at the same DLI displayed a yield increase and a fruit cracking reduction (Chen et al. 2024). When FR light was mixed with R and B LEDs as interlighting in greenhouse environments, total yield and individual fruit weight of sweet peppers increased during the winter (Kim et al. 2023).

In our study, although all strawberry plants were grown under the same DLI, the addition of FR light increased eDLI by 67% to 71%. The efficiency of supplemental FR photons (700–750 nm) was shown to be comparable to traditional photosynthetic photons (400–700 nm) in leaf net photosynthetic rate in 14 crop species (Zhen and Bugbee 2020). However, a greater magnitude of yield increase (160% more total yield) than the increase in eDLI (67%–71%) by supplemental FR light in our study suggests that FR light provided both physiological and morphological effects that led to greater plant productivity. In fact, the contribution of FR photons in the leaf net photosynthetic rate was not confirmed in our experiment, likely because of the long-term effect of FR light. When measured at the end of the experiment (26 weeks after the start of the FR treatment), the leaf net photosynthetic rate did not show a significant

Yield per plant			
Interaction		**P value**	
Cultivar x Photoperiod		0.10 ns	
Cultivar x Far red		0.06 ns	
Cultivar x Photoperiod x Far red		0.09 ns	
Earliglow		**Nyohou**	
Photoperiod	**Mean (g)**	**Photoperiod**	**Mean (g)**
LD	186.3 a	LD	164.3 a
SD	208.3 a	SD	120.1 a
SD/LD	211.3 a	SD/LD	164.5 a
Far red	**Mean (g)**	**Far red**	**Mean (g)**
FR-	112.4 b	FR-	83.8 b
FR+	291.5 a	FR+	215.5 a

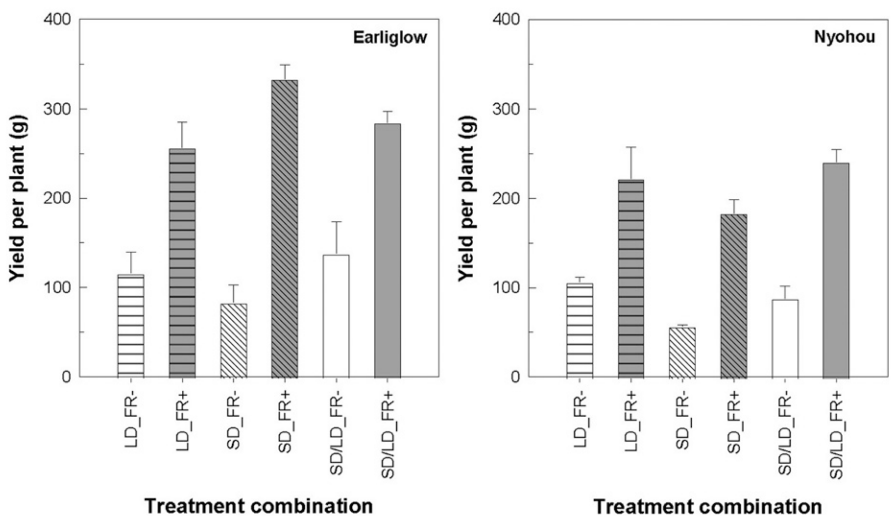

Fig. 3. The effects of long-day (LD), short-day (SD), and alternating SD/LD photoperiods with and without far-red (FR) treatments on yield per plant from 16th to 26th week after transplanting. Interaction effects among cultivar, photoperiod, and FR light are shown in the table, with ns representing no significant effect. The means of photoperiod and FR treatments for each cultivar are presented in the table under cv. Earliglow and cv. Nyohou. The effects of photoperiod and FR treatments on yield per plant were determined using analysis of variance protected mean separation via Tukey's honestly significant difference test using the photoperiod × FR effect as the error term. Treatments with the same letter in the table were not significantly different at $P \leq 0.05$. Six treatment combinations were generated, with three photoperiod treatments and two FR treatments, and the average yield of the plants in these six treatment combinations are shown in the graphs for each cultivar. The error bars represent the standard errors among the three plants in each treatment combination and were not used to determine statistical difference.

difference among treatments with and without supplemental FR light (data not shown). This may be attributed to a low chlorophyll concentration in leaves, as seen in other crop species as a long-term effect of FR light (Li and Kubota 2009). In our study, the leaves of strawberries grown with FR supplementation were a lighter green (Fig. 2) and the leaf total chlorophyll concentration was 35% and 44% less than those without FR in 'Earliglow' and 'Nyohou', respectively (Table 2). However, an improved plant architecture with a longer petiole can increase canopy light interception and thereby increase the whole-plant photosynthetic rate under supplemental FR light. Although more research is needed to understand more fully the effect of an eDLI in strawberry canopy photosynthesis, it seems that the yield improvement observed in our experiment could not be explained simply as a result of an increase in extended PAR (400–750 nm).

FR light may also affect fruit productivity as a potential regulator of sugar translocation (Ji et al. 2019, 2020). The regulatory mechanism of FR in sugar translocation to fruit was revealed by carbohydrate and gene expression analyses using tomato flowers and fruit, indicating that FR light increases the fruit sink strength through fruit sugar transportation and metabolism (Ji et al. 2020). The sink–source balance in strawberries is also known to affect leaf photosynthesis and productivity. When fruit load was less relative to source strength, 'Albion' and 'Nyohou' strawberry plants showed a diurnal decline of photosynthesis, which was associated with an unbalanced sink–source strength (Garcia and Kubota 2017b).

The effect of photoperiod on morphological improvement was less than that of FR supplementation, and productivity was unaffected by photoperiod (Table 2 and Fig. 3). When LD lighting is applied to SD plants, it is often recommended that plant responses be monitored carefully because prolonged LD might influence the SD flowering response negatively (Kubota 2023). Although we did not observe a difference in yield as a result of the photoperiod treatments within 26 weeks after transplanting, the morphological changes resulting from the photoperiod treatments may still influence fruit productivity at a later production stage. Further evaluations are necessary to determine the efficacy of LD lighting on SD strawberry cultivars in indoor vertical farms.

Supplemental FR light increased fruit Brix or Brix-to-TA ratio. In 'Earliglow', FR supplementation increased fruit Brix by 1.4 times, but did not affect the Brix-to-TA ratio significantly (Table 2). In 'Nyohou', FR supplementation did not affect Brix significantly, but it increased the Brix-to-TA ratio by 1.5 times (Table 2). The Brix-to-TA ratio correlates positively with consumer acceptability (Jayasena and Cameron 2008). No photoperiod effect was found in the Brix or Brix-to-TA ratio (Table 2). No significant difference in TA was observed in our study (data not shown).

Increasing fruit Brix by adding FR light was also reported by Ries and Park (2024) in ever-bearing strawberry 'Monterey', but not in 'Albion' grown under the same DLI, suggesting that the FR effect on fruit Brix is cultivar specific, and the effect of FR on fruit Brix may not be through a direct effect on the canopy photosynthetic rate.

Increasing the DLI can also enhance fruit Brix and the Brix-to-TA ratio in strawberries in indoor vertical farm environments (Maeda and Ito 2020) and greenhouses (Hanenberg et al. 2016). The fruit Brix of tomatoes can also be improved by intracanopy FR light under greenhouse conditions (Kim et al. 2020). As discussed in the previous section, FR light plays a role in regulating sugar allocation to fruit by potentially increasing the fruit sink strength, and therefore may have contributed to enhanced fruit quality (Brix or Brix-to-TA ratio) in addition to an improvement in productivity in our study. Further research is needed to understand more fully sugar translocation and metabolism in strawberry plants under different FR light environments.

Conclusion

By investigating the effects of two FR and three photoperiod treatments on two SD strawberry cultivars under indoor conditions with sole-source lighting, we found that strawberry productivity and fruit sugar content were increased as a result of plant morphological and physiological responses to supplemental FR light, whereas LD and SD/LD photoperiods improved plant morphological structure without affecting early fruit production or quality. The information provided in this study can contribute to our current understanding of light requirements in indoor strawberry production. Future studies may need to focus on optimizing FR lighting (e.g., PFD and timing) for indoor strawberry production to promote fruit productivity and quality while minimizing capital and operational expenses in FR lighting.

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