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Effect of Day Length on Growth, Flowering, and Yield of Three Strawberry Varieties in a Tropical Climate

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ABSTRACT

Light plays a vital role in plant growth and development, significantly affecting both the quality and quantity of strawberry fruit production. This study investigated the effects of day length on growth, flowering traits, and yield of selected strawberry cultivars by applying an environmental engineering approach. Conducted in a tropical greenhouse, the experiment involved supplemental LED lighting for three Japanese cultivars ('Haruhi', 'KS75', and 'Sakura'). The findings revealed significant interactions between LED lighting and cultivar type in terms of growth parameters before and after fruiting. Specifically, crown height and crown diameter increased by 0.21 cm and 0.30 cm, respectively, under LED lighting. Compared to conventional (non-LED) lighting, LED exposure also resulted in reduced leaf temperature and plant height, by 1.37 °C and 2.58 cm, respectively. Flowering characteristics showed notable cultivar-specific responses to LED lighting. In 'Sakura', the number of flowers per plant and per bunch increased by 11.75 and 5.87, respectively. Furthermore, the cultivar 'KS75' exhibited significantly earlier flowering, by approximately 27 d, under LED treatment compared to non-LED conditions. While fruit yield characteristics did not show significant interactions between cultivars and lighting, independent statistical analysis indicated that 'KS75' produced the highest total yield (256.54 g), average fruit weight (9.88 g), fruit diameter (26 mm), and fruit dry weight (14.50 g). On the other hand, 'Sakura' had the highest number of fruits per plant, averaging 11.52 g per plant per month. These variations are attributed to the inherent genetic differences among cultivars. In conclusion, the application of LED lighting under a 12 h d length in tropical conditions significantly influenced specific growth and flowering traits in strawberry plants. 'Sakura' responded most favorably in terms of floral characteristics, whereas 'KS75' demonstrated superior performance in generative yield traits.

Introduction

The global demand for strawberries continues to rise; however, this demand is not being met due to limitations in cultivation area. Strawberry plants thrive only under specific environmental conditions,

often restricting their cultivation to highland regions to ensure optimal fruit production. Additionally, strawberries are highly sensitive to climatic fluctuations, which can significantly affect yield and disrupt supply chains at both regional and international levels (Mitchell, 2022).

In Indonesia, strawberry cultivation faces several challenges, including the high susceptibility of existing cultivars to various diseases such as *Phomopsis*, *Pestalotia* sp., *Curvularia* sp., *Diplocarpon* sp., *Phoma* sp., *Gnomonia* sp., *Verticillium* sp., *Cercospora* sp., *Rhizoctonia* sp., and *Fusarium* sp. (Ayoubi and Soleimani, 2016; Carisse et al., 2000; Ellis, 2016; Gargita et al., 2020; Setiyawan et al., 2020; Zydlik and Zydlik, 2016). Consequently, there remains a need for the development and availability of superior cultivars that meet both quality and yield standards.

To address these challenges and achieve consistently high yields, the adoption of greenhouse cultivation systems with environmental control is essential. The regulation of environmental factors, such as light intensity, air temperature, CO_2 concentration, humidity, and wind speed, is crucial for maximizing the photosynthetic capacity of plants and enhancing fruit production (Hidaka et al., 2015). Both external (environmental) and internal (genetic) factors significantly influence plant growth and fruit yield (Díaz-Galián et al., 2020).

Among environmental factors, light and temperature play crucial roles in photosynthesis and fruit development (Miyoshi et al., 2017; Zarei et al., 2017). Since light conditions can vary based on the planting season and location (Hidaka et al., 2012), the integration of light management strategies is particularly important. Light serves as a key signal in plant growth and development through its regulation via the circadian clock system (Egea-Cortines et al., 2013). Optimizing light intensity has been shown to improve both yield and fruit quality in strawberries (Torres-Quezada et al., 2015).

The use of supplemental lighting in greenhouse systems, especially in tropical regions, can help standardize growing conditions and support year-round production. For example, high-intensity LED lighting has been found to significantly enhance leaf photosynthesis compared to traditional fluorescent lamps (Hidaka et al., 2013). Furthermore, research on the short-day cultivar 'Fukuoka S6' demonstrated that a 12 h photoperiod using supplemental lighting produced the highest fruit yield (Hidaka et al., 2014). These findings highlight the potential of light supplementation to improve both the productivity and quality of strawberry cultivation.

Strawberry plants (*Fragaria* × *ananassa* Duch.) exhibit varied responses to environmental conditions, particularly in relation to photoperiod sensitivity, as seen in short-day cultivars. According to previous studies (Ito and Saito, 1962; Taylor, 2002), strawberry cultivars require a specific critical day length to trigger flower bud differentiation. When the photoperiod exceeds this threshold, flower bud formation may be inhibited, resulting in delayed flowering and reduced yield. This response is further influenced by the interaction between temperature and photoperiod (Samad et al., 2021).

Since strawberry growth and development are strongly influenced by photoperiod, it plays a crucial role in regulating both the vegetative and reproductive phases of the plant (Garcia and Kubota, 2017). The effectiveness of supplemental lighting in improving yield may vary depending on the cultivar's genetic characteristics. Therefore, understanding how different cultivars respond to light supplementation is essential for optimizing production in tropical environments.

This research was designed to assess the impact of supplemental lighting on cultivar-specific responses by applying white LED lighting in a tropical greenhouse environment and comparing the results with those under natural (non-LED) lighting conditions. Three Japanese strawberry cultivars with distinct characteristics were selected to evaluate the potential for developing targeted lighting management strategies suitable for each genotype grown in tropical climates.

Materials and Methods

Plant materials and growth conditions

This study utilized two short-day strawberry cultivars obtained from Miyoshi F1 seeds (Yamanashi, Japan): F1 'Berry Pop Haruhi' (Lot code 54984) and F1 'Berry Pop Sakura' (priming; Lot code 54760). In addition, an everbearing (day-neutral) cultivar, 'KS75', developed through tissue culture by Nii Bio (Tokushima, Japan), was included.

The F1 hybrid strawberry seedlings, certified by the Japanese Government and commercially available, were first grown into young plantlets in a nursery room. The nursery conditions were adjusted to mimic the native growing environment of Yamanashi, Japan, with a controlled temperature of approximately 23 ± 2 °C, relative humidity between 60–69%, and CO_2 concentration ranging from 600 to 700 ppm. During the nursery stage, the seedlings were exposed to 12 h of artificial light using LED T8 Tube RoHS IP65 lamps (23 watts, model T8-1200-23, CCT 4000K), which emit cool white light suitable for plant growth.

At four weeks of age, or when the seedlings had developed 5–6 leaves, they were transferred to a greenhouse. Transplanting was conducted in the morning at 9 a.m., with the root balls and growing media carefully removed from the nursery net pots. The seedlings were then planted using a hydroponic system with planting beds set inside the greenhouse.

Each seedling was positioned at an angle of approximately ± 5 degrees from the bed surface.

The planting beds measured 75 cm × 35 cm × 15 cm externally and 70 cm × 25 cm × 10 cm internally. Before covering the roots with the growing medium, each plant's crown was placed between heat exchange pipes containing a water circulation system set at 19 °C, while the roots were positioned adjacent to the irrigation pipes. Plants were spaced at 15 cm intervals within each bed, with seven plants per bed, resulting in a planting density of 42 plants per cultivar per treatment.

Both the nursery and greenhouse experiments were conducted at the experimental field of Padjadjaran University, Jatinangor campus, West Java, Indonesia. Under typical outdoor conditions at this site, the average temperature was 27 ± 3 °C, and relative humidity ranged between 35–40%. The growth medium was a combination of peat moss (10%), cocopeat (45%), and ash husk (45%). Fertilization and watering were carried out using a drip irrigation system (Brand; Dosatron International S.A.S France; Type; D3GL2VL S/N 23260870; Operating flow rate 10 L h^{-1} – 3 m^3 h^{-1}; Injection rate 0.2 – 2%; Operating pressure 0.3 – 6 bar; Max temperature 40 ºC) with a watering frequency of 5 min every hour, using a concentrated mix of nutrient solutions A and B, consisting of Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca), Magnesium (Mg), Sulfur (S), and micronutrients, in a ratio of (5 L (A/B) per 20 L of water), and solution C (Citric Acid) at 1 kg 35 L^{-1} of water as a nutrient solution stabiliser to maintain stability (EC ± 600 ppm, pH ± 5.5).

Lighting system and experimental conditions

This study employed a two-factor experimental design involving three strawberry cultivars and two lighting treatments: supplemental Light-Emitting Diodes (LED) and conventional (natural, non-LED) lighting. Each treatment combination was replicated four times, resulting in a total of 24 experimental units. Each unit consisted of seven plants per cultivar, yielding a total sample size of 168 plants (n = 168).

Preliminary observations revealed that the natural photoperiod in the tropical study area averaged less than 12 h. This observation was a key consideration in the experimental design. For the LED treatment, the photoperiod was extended to 12 h, while the natural lighting treatment maintained the average ambient photoperiod of approximately 10 h. Supplemental LED lighting was programmed to operate from 6:00 to 8:00 a.m. and from 4:00 to 6:00 p.m.

The supplemental lighting setup used two white LED T8 tube lights (23 watts, model T8-1200-23, AC input 100–240 V, CCT 4000K, RoHS IP65) per bed. These LEDs were installed horizontally above the planting beds at a height of approximately 60 cm from the bed surface, ensuring even light distribution across the plants.

To monitor lighting conditions during the cultivation period, Photosynthetically Active Radiation (PAR) was measured using a pyranometer (Apogee Instruments, USA; spectral range: 360–1120 nm; accuracy: ± 5%; resolution: 1 W m^{-2}; measurement range: 0–1,750 W m^{-2} / 0–350 mV; field of view: 180° hemispherical; sensor dimensions: 2.4 cm × 2.75 cm). Data were logged using a Decagon EM50 Data Logger (Decagon Devices Inc., USA; 7.5 VDC, 5 × AA or LR6 batteries; address: 2365 NE Hopkins Ct., Pullman, WA, USA).

Light data were collected using two PAR sensors placed among the three cultivars under the supplemental LED treatment and two additional sensors placed among the same cultivars under natural lighting conditions. This setup enabled accurate, real-time monitoring of the light environment experienced by the plants across both treatments.

The cultivation was conducted in a greenhouse unit measuring 19 × 20 × 10 m, equipped with a comprehensive set of environmental control systems. These included a temperature and humidity monitoring device (Fujita 295u Watch Logger, made in Japan), two large exhaust fans for removing hot air from the greenhouse, and a combined heating and cooling unit (model NGP109T-N, 220V-50Hz indoor; NGP109TQ-G5, 380V-50Hz outdoor; Nepon Inc., manufactured in Thailand), which provided an air output capacity of at least 90 m^3 min^{-1}.

To regulate temperature and humidity, the greenhouse was fitted with a cooling and humidification system that generated fine mist (Semi-Dry Fog), using equipment from Kirinoikeuchi (H. Ikeuchi & Co., Ltd., Japan). Additionally, a Daikin-brand water-based air cooler (A/C water) was used to maintain the plant crown temperature at a constant 19 °C throughout the cultivation period.

Light management within the greenhouse was further supported by an automated shading curtain system (S&H brand) with a mesh density of approximately 30, allowing an average light transmission of about 60%. The system operated automatically in response to incoming light intensity, using sensors and motorized controls (series 22096966 SCM1-620, 34 W, DC 24V, 2 A, 3.95 r min^{-1}; Sigma-Giken, Shanghai).

Analysis of growth

Growth analysis was conducted on the three cultivars to assess the effects of supplemental lighting. Plant growth analysis was divided into several stages:

Growth before and after fruit formation

Plant responses to supplemental lighting during cultivation were assessed on a weekly basis. Observed parameters included plant height, crown height, number of leaves, and number of stolons. These measurements were recorded from the time of transplanting up to the pre-fruiting stage. Following fruit formation, further growth assessments were conducted using destructive sampling, where plants were separated into distinct components: leaves, flowers, petioles, stolons, crowns, and roots.

Each plant part was weighed to obtain fresh weight data prior to drying. The drying process was carried out in a closed plastic drying chamber, which maintained a consistent temperature of 40 ± 3 °C using sunlight as the heat source. The drying period lasted for 14 d, after which the plant parts were reweighed to determine dry weight. The growth parameters analyzed included fresh and dry weights of the entire plant, roots, crown, leaves, and other vegetative parts (stolons and petioles), as well as crown diameter, root length, number of leaves, and plant height. Growth characteristics were evaluated for both the vegetative and post-fruiting stages and subjected to statistical analysis to assess treatment effects.

Measurement of chlorophyll content, transpiration rate, stomatal conductance, and leaf temperature

Leaf physiological activity under supplemental LED lighting and natural (non-LED) lighting was assessed across the three strawberry cultivars using a portable gas exchange system (LI-600, Li-Cor Inc., USA). Measurements included transpiration rate, stomatal conductance, and leaf temperature. To collect data, a fully expanded leaf was clamped into the instrument's head chamber, positioned horizontally approximately 15 cm above the plant base. Once secured, the leaf was scanned and data were recorded automatically, following the method described by (Lemoine, 2022). Measurements were conducted at 10:00 a.m. on plants five weeks post-transplanting, corresponding to the flowering stage.

Chlorophyll content was also analyzed by sampling 0.5 g of fresh leaf tissue, which was ground and extracted using a solvent mixture of 40% acetone and 60% n-hexane. The extract was then analyzed by a spectrophotometer at absorbance wavelengths of 663 nm and 645 nm to determine chlorophyll concentration, applying the Lambert-Beer law in accordance with (Daniel I., 1949; Lichtenthaler, 1987; Porra et al., 1989). Leaf samples for all physiological analyses were collected from fully developed, fully expanded young leaves (specifically the third and fourth leaves from the apex), between 08:00 and 10:00 a.m. on cool days, four weeks after transplanting. All sampled plants were cultivated under greenhouse conditions.

Analyses of flowering and yield

To evaluate the impact of supplemental lighting on flowering, we analyzed 12 plants per cultivar and treatment, across the three different cultivars. Flowering date was recorded by calculating the time from the appearance of the first flower to the point at which 50% of the plants had flowers, starting from the transplanting date. This duration was used to determine the flowering age (in days). Additional measurements included the number of flowers per plant, number of flowers per bunch, and fruit set percentage.

To assess the effect of supplemental lighting on yield, samples from each cultivar and treatment were harvested, and several yield parameters were measured. These included total yield weight (g), which refers to the total fruit obtained from the plants of each cultivar; average fruit weight (g); number of fruits per plant per period (plant.month^{-1}); fruit length (mm); fruit diameter (mm); fruit hardness (kgf); number of fruits per plant; number of fruits per bunch; and harvest age (days). Harvest age was determined by calculating the time from the first fruit harvest that met the standard of physiological maturity (approximately 80%) after transplanting.

Statistical analysis

Statistical analysis was conducted using a factorial split-plot design. Differences between means were evaluated using Duncan's Multiple Range Test (DMRT) at a significance level of $P \leq 0.05$. Data were processed with the DSAASTAT statistical software (Version 1.514, Dipartimento di Scienze Agrarie ed Ambientali, Perugia, Italy).

Results

Photoperiod, light intensity, and environmental conditions during cultivation

During the strawberry cultivation period, the average photoperiod under LED lighting was approximately 12 h, while the conventional (non-LED) treatment resulted in an average of 10 h. The inclusion of LED lighting significantly affected the Photosynthetic Photon Flux Density (PPFD) values. Figures 1 and 2 present the PPFD graph and the environmental conditions observed during the cultivation of the three strawberry cultivars from September 2023 to January 2024. Based on the obtained data, the highest average Photosynthetic Photon Flux Density (PPFD) values for both LED light supplementation and non-LED treatments occurred in September and October 2023, reaching 358.8 and 353.6 µmol m^{-2} s^{-1} for the LED treatment, and 425.8 and 370.2 µmol m^{-2} s^{-1} for the non-LED treatment, respectively. These values corresponded with the increased Daily

Light Integral (DLI) values for September and October 2023, which were 15.9 and 15.8 mol m^{-2} d^{-1} for the LED treatment and 18.5 and 16.3 mol $m^{-2}d^{-1}$ for the non-LED treatment (Fig. 1).

Measurements were conducted using four light sensors, placed in different environments—specifically between plants with LED lighting and those without. The placement of the sensors was designed to ensure equal optimization for measuring light intensity in each treatment. Seasonal factors, such as the transition between the rainy and dry seasons, also significantly influenced plant conditions and the ability of the light sensors to capture light intensity. During the dry season (September to October 2023), extreme sunlight resulted in very high light intensity. However, as the rainy season began in November 2023, the light intensity decreased significantly due to overcast outdoor conditions and the misting system inside the greenhouse, which often obstructed the light. In contrast, from December 2023 to January 2024, the rainy season stabilized, leading to more consistent light intensity inside the greenhouse.

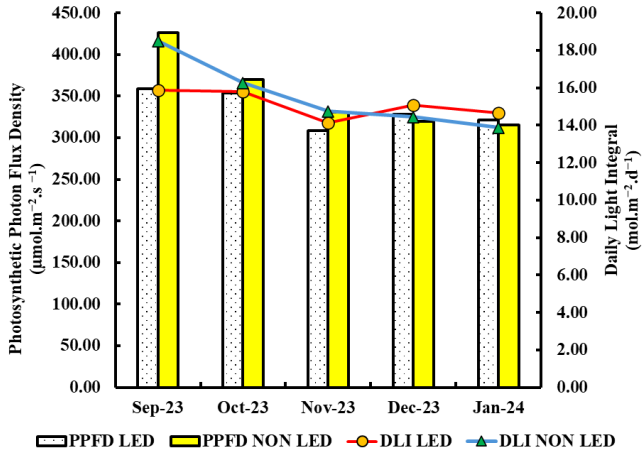

Fig. 1. Average values of photosynthetic photon flux density (PPFD; µmol m^{-2} s^{-1}) and daily light integral (DLI; mol m^{-2} d^{-1}) during the cultivation period from September 2023 to January 2024.

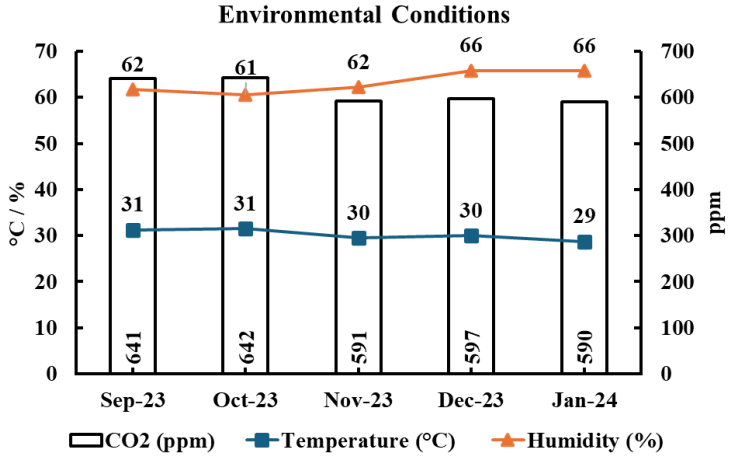

Fig. 2. The average values of environmental conditions measured inside the greenhouse during strawberry cultivation.

The recorded data revealed that light intensity was higher in the non-LED treatment compared to the LED treatment. This pattern was influenced by the prolonged dry season, which resulted in extremely high sunlight intensity outside the greenhouse. Furthermore, environmental conditions during September (31 °C, 62% humidity, 641 ppm CO_2) and October (31 °C, 61% humidity, 642 ppm CO_2) were notably extreme in terms of temperature, humidity, and CO_2 levels compared to the subsequent months (Fig. 2).

Effect of supplemental LED lighting on growth

Growth observations were conducted weekly for 49 d after transplanting (DAP) during the pre-fruit

formation phase, on the three strawberry cultivars used in the study. The parameters measured included plant height, crown height, number of leaves per plant, and number of stolons per plant. The resulting data were statistically analyzed.

Overall, plant height, crown height, and the number of leaves increased from 7 DAP to 49 DAP. However, significant interactions between cultivar and lighting treatment only affected plant height at 49 DAP and crown height at 7, 35, 42, and 49 DAP. There were no cultivar × lighting interaction effects on the number of leaves or stolons (Fig. 3).

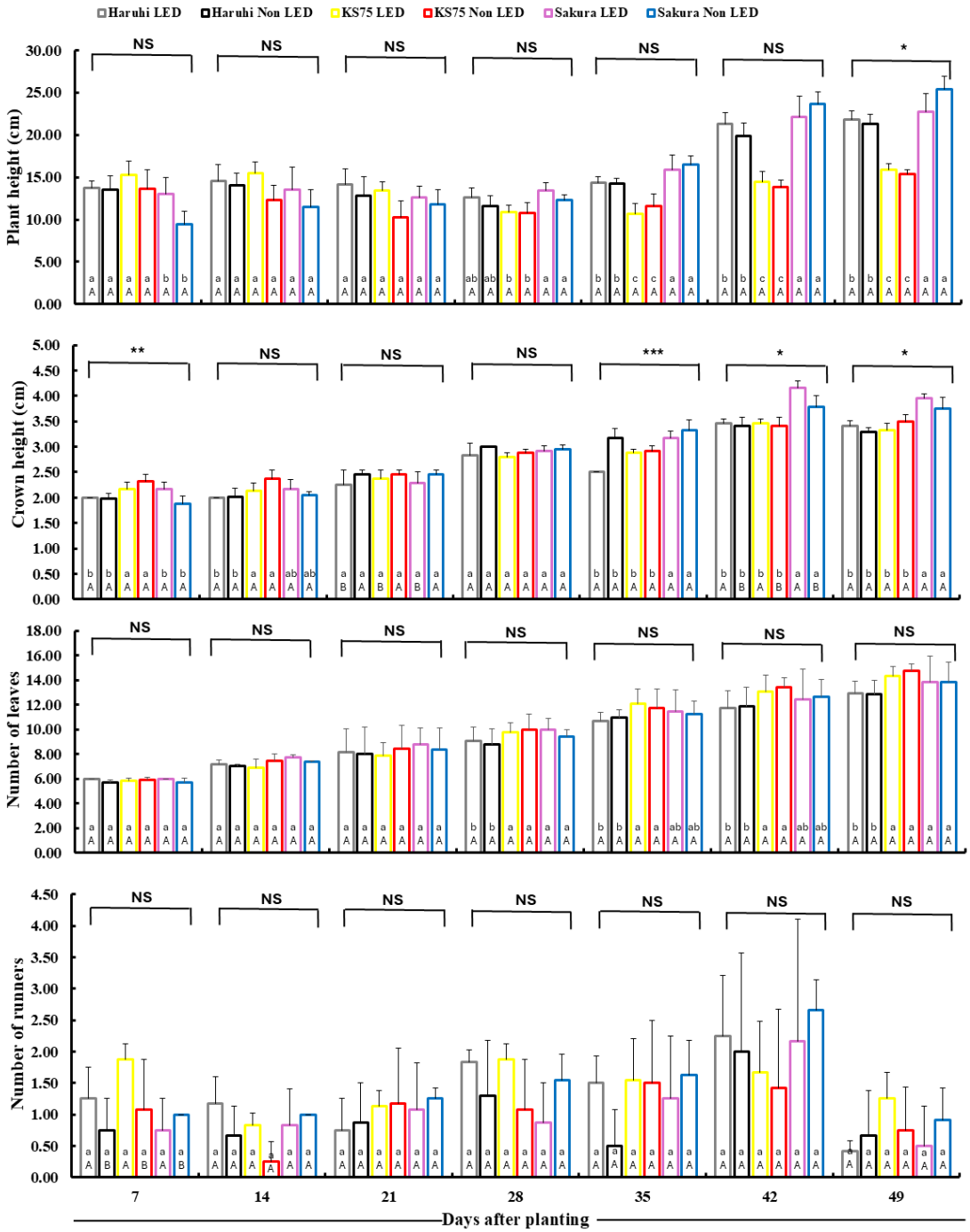

Fig. 3. Independent Effect and Cultivar × Lighting Interaction on Growth Parameters Before Fruit Formation (Plant Height, Crown Height, Number of Leaves, Number of Stolons). Note: Mean values ± SE, followed by an asterisk, significantly indicate the cultivar × lighting interaction based on the LSD post hoc test; (*) significant difference at $P \leq 0.05$, (**). significant difference at $P \leq 0.01$, (***) significant difference at $P \leq 0.001$. Lowercase letters compare the three cultivars ('Haruhi', 'KS75', and 'Sakura') that differ. Uppercase letters compare the two lighting treatments, LED and non-LED. Different letters on each treatment indicate a significant difference based on the independent LSD test.

The data presented in Tables 1 and 2 reflect plant growth observations taken after fruit formation, followed by measurements conducted post-harvest, once plant parts had been separated. Stomatal conductance, leaf temperature, and transpiration rates were recorded using a portable Li-Cor device (LI-600), while total chlorophyll content was measured via spectrophotometry. The results revealed a highly significant interaction between cultivar and lighting treatments for leaf temperature. A similar interaction was also observed in strawberry crown diameter, where both factors showed significant effects based on the LSD post hoc test ($P \leq 0.05$) (Table 1).

Table 1. The effect of lighting on crown diameter, root height, total chlorophyll content, stomatal conductance, leaf temperature, and transpiration of strawberry plants.

Treatment	Crown diameter	Root height	Total chlorophyll	Stomatal conductance	Temperature leaf	Transpiration
	mm	cm	mg g^{-1}	mol^{+1} m^{-2} s^{-1}	°C	$mmol^{+1}$ m^{-2} s^{-1}
			Cultivar			
Haruhi (H)	16.18 ± 1.21^{a}	34.12 ± 0.88^{a}	0.26 ± 0.03^{a}	0.27 ± 0.01^{a}	27.82 ± 1.08^{b}	2.88 ± 0.42^{a}
KS75 (K)	15.52 ± 2.33^{a}	27.81 ± 1.67^{b}	0.21 ± 0.01^{a}	0.03 ± 0.00^{b}	27.20 ± 0.16^{c}	0.39 ± 0.04^{b}
Sakura (S)	15.82 ± 0.21^{a}	30.37 ± 0.17^{ab}	0.22 ± 0.06^{a}	0.24 ± 0.01^{a}	28.91 ± 0.96^{a}	2.97 ± 0.69^{a}
Probability	ns	*	ns	***	***	***
***P*-value**	**0.708**	**0.021**	**0.149**	**< 0.001**	**< 0.001**	**< 0.001**
			Lighting			
LED (L)	16.15 ± 0.93^{a}	30.54 ± 4.07^{a}	0.20 ± 0.03^{b}	0.18 ± 0.13^{a}	27.53 ± 0.61^{b}	1.80 ± 1.25^{b}
Non-LED (N)	15.53 ± 1.59^{a}	31.00 ± 2.29^{a}	0.26 ± 0.03^{a}	0.18 ± 0.12^{a}	28.42 ± 1.26^{a}	2.35 ± 1.68^{a}
Probability	**ns**	**ns**	*****	**ns**	**	***
P-value	**0.463**	**0.772**	**0.048**	**0.968**	**0.003**	**< 0.001**
Interaction			**Cultivar × Lighting**			
HL	15.32 ± 0.80^{ab}	34.75 ± 2.32^{a}	0.24 ± 0.03^{a}	0.28 ± 0.02^{a}	27.05 ± 0.13^{c}	2.57 ± 0.15^{a}
HN	17.05 ± 2.56^{a}	33.50 ± 2.51^{a}	0.29 ± 0.11^{a}	0.25 ± 0.02^{a}	28.59 ± 0.22^{b}	3.18 ± 0.45^{a}
KL	17.17 ± 1.05^{a}	26.62 ± 2.86^{a}	0.20 ± 0.01^{a}	0.03 ± 0.01^{a}	27.32 ± 0.09^{c}	0.36 ± 0.17^{a}
KN	13.87 ± 1.19^{b}	29.00 ± 3.71^{a}	0.22 ± 0.02^{a}	0.04 ± 0.03^{a}	27.08 ± 0.32^{c}	0.41 ± 0.28^{a}
SL	15.97 ± 1.85^{ab}	30.25 ± 6.39^{a}	0.17 ± 0.02^{a}	0.23 ± 0.03^{a}	28.22 ± 0.34^{b}	2.48 ± 0.36^{a}
SN	15.67 ± 0.86^{ab}	30.50 ± 4.43^{a}	0.26 ± 0.02^{a}	0.25 ± 0.04^{a}	29.59 ± 0.52^{a}	3.47 ± 0.78^{a}
Probability	*	ns	ns	ns	***	ns
P-value	**0.024**	**0.652**	**0.383**	**0.360**	**< 0.001**	**0.216**

Note: Mean values ± SE, with different letters following each treatment, indicate significant differences based on independent LSD post-hoc test. Asterisks on each parameter indicate significant differences from the independent LSD post-hoc test or the interaction between cultivar and lighting based on the LSD test; (*) significant difference at $P \leq 0.05$, (**) significant difference at $P \leq 0.01$, (***) significant difference at $P \leq 0.001$.

Additional parameters, including total chlorophyll, stomatal conductance, and transpiration, also demonstrated significant effects for each treatment factor when analyzed independently using the LSD test ($P \leq 0.05$) (Table 1). Likewise, Table 2 indicates significant differences in root dry weight, crown fresh weight, and crown dry weight. The LSD results further revealed that the non-LED lighting treatment elicited a stronger physiological response compared to the LED treatment across all three cultivars (Fig. 4).

Table 2. The effect of lighting on the fresh and dry weight of strawberry plants (destruction).

Treatment	Root fresh weight	Root dry weight	Crown fresh weight	Crown dry weight	Leaf fresh weight	Leaf dry weight	Plant fresh weight	Plant dry weight	Other fresh weights	Other dry weights
	g	g	g	g	g	g	g	g	g	g
Cultivar										
Haruhi (H)	48.63 ± 18.88^{a}	9.18 ± 2.80^{a}	5.19 ± 0.18^{b}	0.95 ± 0.09^{b}	45.93 ± 0.91^{a}	11.32 ± 0.09^{a}	128.41 ± 12.76^{a}	25.06 ± 2.94^{a}	23.01 ± 3.66^{a}	3.83 ± 0.06^{a}
KS75 (K)	46.95 ± 15.95^{a}	9.00 ± 2.39^{a}	8.29 ± 0.92^{a}	0.93 ± 0.02^{b}	62.04 ± 12.30^{a}	16.18 ± 4.20^{a}	154.33 ± 40.83^{a}	30.34 ± 9.17^{a}	16.86 ± 4.12^{a}	2.83 ± 0.77^{a}
Sakura (S)	31.82 ± 12.10^{a}	5.54 ± 1.66^{a}	7.07 ± 0.09^{ab}	1.33 ± 0.12^{a}	41.84 ± 2.94^{a}	10.22 ± 0.89^{a}	118.27 ± 12.61a	22.40 ± 4.08^{a}	33.75 ± 2.99^{a}	5.4 ± 1.25^{a}
Probability	ns	*	*	*	ns	ns	ns	ns	ns	ns
P-value	**0.059**	**0.019**	**0.026**	**0.017**	**0.085**	**0.073**	**0.361**	**0.130**	**0.159**	**0.149**
Lighting										
LED (L)	53.53 ± 11.54^{a}	9.52 ± 2.43^{a}	6.65 ± 1.19^{a}	1.13 ± 0.25^{a}	53.31 ± 15.10^{a}	13.80 ± 4.64^{a}	149.28 ± 29.82^{a}	29.75 ± 6.19^{a}	25.35 ± 9.11^{a}	4.48 ± 1.57^{a}
Non-LED (N)	31.40 ± 7.05^{a}	6.29 ± 1.66^{a}	7.05 ± 1.94^{a}	1.01 ± 0.19^{a}	46.56 ± 6.79^{a}	11.35 ± 1.81^{a}	118.06 ± 8.13^{a}	22.11 ± 2.29^{a}	23.73 ± 8.99^{a}	3.55 ± 1.14^{a}
Probability	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
P-value	**0.172**	**0.247**	**0.755**	**0.650**	**0.516**	**0.466**	**0.345**	**0.346**	**0.864**	**0.569**
Interaction	**Cultivar x Lighting**									
HL	61.98 ± 14.75^{a}	11.16 ± 2.61^{a}	5.32 ± 0.34^{a}	1.02 ± 0.06^{a}	45.28 ± 10.84^{a}	11.39 ± 3.14^{a}	137.43 ± 16.07^{a}	27.14 ± 4.36^{a}	20.41 ± 5.35^{a}	3.79 ± 1.04^{a}
HN	35.28 ± 11.13^{a}	7.20 ± 2.38^{a}	5.06 ± 2.00^{a}	0.88 ± 0.56^{a}	46.58 ± 4.48^{a}	11.26 ± 1.99^{a}	119.38 ± 18.67^{a}	22.98 ± 5.51^{a}	25.60 ± 2.60^{a}	3.88 ± 0.80^{a}
KL	58.23 ± 31.22^{a}	10.69 ± 5.92^{a}	7.64 ± 1.68^{a}	0.95 ± 0.26^{a}	70.74 ± 17.76^{a}	19.16 ± 8.66^{a}	183.20 ± 70.56^{a}	36.83 ± 14.26^{a}	19.78 ± 3.39^{a}	3.37 ± 0.54^{a}
KN	35.67 ± 7.44^{a}	7.30 ± 1.39^{a}	8.94 ± 2.86^{a}	0.92 ± 0.41^{a}	53.34 ± 14.43^{a}	13.20 ± 3.74^{a}	125.46 ± 28.44^{a}	23.85 ± 5.94^{a}	13.94 ± 6.04^{a}	2.28 ± 0.77^{a}
SL	40.38 ± 18.52^{a}	6.72 ± 3.10^{a}	7.01 ± 2.04^{a}	1.42 ± 0.32^{a}	43.93 ± 19.39^{a}	10.85 ± 4.22^{a}	127.20 ± 65.82^{a}	25.29 ± 12.01^{a}	35.87 ± 31.61^{a}	6.28 ± 5.41^{a}
SN	23.26 ± 5.60^{a}	4.37 ± 0.77^{a}	7.14 ± 3.15^{a}	1.24 ± 0.46^{a}	39.76 ± 26.95^{a}	9.59 ± 6.18^{a}	109.35 ± 63.49^{a}	19.51 ± 9.87^{a}	31.64 ± 22.68^{a}	4.51 ± 2.70^{a}
Probability	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
P-value	**0.873**	**0.804**	**0.719**	**0.859**	**0.556**	**0.073**	**0.664**	**0.464**	**0.774**	**0.749**

Note: Mean values ± SE, with different letters following each treatment, indicate significant differences based on independent LSD post-hoc test. Asterisks on each parameter indicate significant differences from the independent LSD post-hoc test or the interaction between cultivar and lighting based on the LSD test; (*) significant difference at $P \leq 0.05$, (**) significant difference at $P \leq 0.01$, (***) significant difference at $P \leq 0.001$.

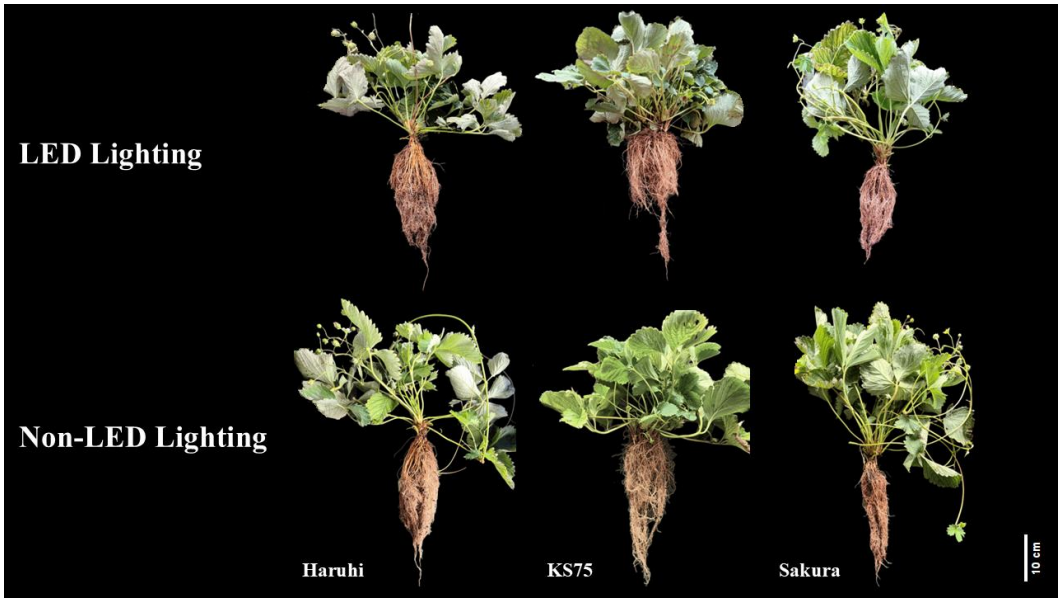

Fig. 4. Visual differences in strawberry plant conditions under LED and non-LED lighting treatments at 19 weeks of growth.

Effect of supplemental LED lighting on the flowering and yield

This study investigated the differences in flowering and fruit formation among three Japanese strawberry cultivars under supplementary lighting. A highly significant interaction between cultivar and lighting treatments was observed. The interaction was primarily driven by the addition of LED lighting, which positively influenced all three cultivars, 'Haruhi,' 'KS75,' and 'Sakura,' in terms of the number of flowers per plant and per inflorescence during the cultivation period. Conversely, the absence of supplemental lighting (non-LED) produced a favorable response in terms of reduced days to flowering, indicating earlier floral initiation compared to the LED treatment. This trend was supported by the independent LSD test, which showed significant differences among cultivars, 'Haruhi' (59.41 d), 'KS75' (76.54 d), and 'Sakura' (60.29 d), as well as between lighting treatments, non-LED (60.29 d) and LED (70.88 d) (Table 3).

This study found no significant interaction between cultivar and lighting treatments for the measured fruit yield parameters. However, results from independent LSD tests indicated that supplemental lighting had a significant effect on fruit length. In contrast, fruit diameter, number of fruits per plant per month, and average fruit weight, all key contributors to total yield, exhibited significant differences among cultivars throughout the cultivation period (Table 4). Among the three cultivars tested, 'KS75' displayed the highest yield potential, significantly outperforming 'Haruhi' and 'Sakura.'

Statistical analysis revealed a highly significant linear relationship among the yield-related parameters. Specifically, the differences observed between 'Haruhi' and 'Sakura' compared to 'KS75' were evident in fruit diameter (3.58 and 6.53 mm), average fruit weight (3.1 and 4.67 g), and total yield (47.1 and 77.88 g, respectively). Similarly, the average number of fruits produced per plant per month varied across the cultivars, with 'KS75' yielding 14.5 fruits, compared to 11.23 and 8.55 for 'Haruhi' and 'Sakura,' respectively.

Discussion

Pre-fruit set growth

The cultivar × lighting interaction led to different responses in the strawberry cultivars' ability to capture light for growth metabolism. These variations are closely related to the plants' photoperiodic requirements. Photoperiod (day length) is a reliable and predictable indicator of the optimal timing for flowering in various plants and is used to classify plants as short-day (SD) or long-day (LD) species. In this study, the strawberry cultivars used, 'Haruhi' and 'Sakura,' are classified as short-day (SD), while 'KS75' is a day-neutral (DN) cultivar. This classification resulted in different morphological growth responses across cultivars.

During the early growth phase (before fruit formation), significant cultivar × lighting interactions were observed, particularly affecting plant height at 49 DAP, with notable differences in the 'Haruhi' and 'KS75' cultivars. The lighting treatment influenced strawberry plant morphology, especially in the leaf petioles (Nadalini et al., 2017). However, cultivar had a more significant impact on plant height at 7 DAP ('Haruhi' and 'KS75'), 28 DAP ('Haruhi' and 'Sakura'), and 42 DAP ('Haruhi'

and 'KS75'). These effects were evaluated using analysis of variance (ANOVA), followed by post hoc testing using the Least Significant Difference (LSD) at a 5% significance level (Fig. 3).

Table 3. The effect of lighting on flowering and fruit formation in strawberry plants.

Treatment	Number of flowers	Number of fruits			Fruit set	Flowering age	Harvesting age
	plant^{-1}	bunch^{-1}	plant^{-1}	bunch^{-1}	%	day	day
				Cultivar			
Haruhi (H)	32.83 ± 0.23^{b}	16.41 ± 0.11^{b}	21.41 ± 5.65^{a}	10.70 ± 2.82^{a}	63.34 ± 19.34^{b}	59.41 ± 0.23^{b}	20.00 ± 0.94^{ab}
KS75 (K)	12.00 ± 0.35^{c}	6.00 ± 0.17^{c}	10.87 ± 0.05^{b}	5.43 ± 0.02^{b}	92.34 ± 1.75^{a}	76.54 ± 19.38^{a}	22.66 ± 0.47^{a}
Sakura (S)	40.37 ± 8.30^{a}	20.18 ± 4.15^{a}	25.08 ± 0.82^{a}	12.54 ± 0.41^{a}	61.80 ± 13.67^{b}	60.29 ± 3.59^{b}	18.91 ± 1.41^{b}
Probability	***	***	**	**	***	***	*
P-value	**< 0.001**	**< 0.001**	**0.002**	**0.002**	**0.001**	**< 0.001**	**0.030**
				Lighting			
LED (L)	30.50 ± 17.13^{a}	15.25 ± 8.56^{a}	17.61 ± 6.79^{a}	8.80 ± 3.39^{a}	64.29 ± 23.24^{a}	59.94 ± 2.61^{b}	21.19 ± 1.60^{a}
Non-LED (N)	26.30 ± 12.63^{a}	13.15 ± 6.31^{a}	20.63 ± 8.49^{a}	10.31 ± 4.24^{a}	80.69 ± 11.50^{a}	70.88 ± 16.84^{a}	19.86 ± 2.25^{b}
Probability	ns	ns	ns	ns	ns	**	*
P-value	**0.235**	**0.235**	**0.425**	**0.425**	**0.082**	**0.002**	**0.030**
Interaction				**Cultivar X Lighting**			
HL	33.00 ± 5.84^{b}	16.50 ± 2.92^{b}	17.41 ± 7.51^{a}	8.70 ± 3.75^{a}	49.66 ± 18.87^{a}	59.25 ± 4.95^{b}	20.66 ± 2.22^{a}
HN	32.66 ± 2.27^{b}	16.33 ± 1.13^{b}	25.41 ± 6.06^{a}	12.70 ± 3.03^{a}	77.01 ± 17.51^{a}	59.58 ± 4.34^{b}	19.33 ± 1.12^{a}
KL	12.25 ± 3.43^{c}	6.12 ± 1.71^{c}	10.91 ± 2.37^{a}	5.45 ± 1.18^{a}	91.10 ± 2.94^{a}	62.83 ± 4.22^{b}	23.00 ± 2.01^{a}
KN	11.75 ± 2.64^{c}	5.87 ± 1.32^{c}	10.83 ± 2.44^{a}	5.41 ± 1.22^{a}	93.58 ± 1.89^{a}	90.25 ± 0.50^{a}	22.33 ± 1.05^{a}
SL	46.25 ± 7.75^{a}	23.12 ± 3.87^{a}	24.50 ± 9.35^{a}	12.25 ± 4.67^{a}	52.13 ± 16.69^{a}	57.75 ± 7.54^{b}	19.91 ± 3.61^{a}
SN	34.5 ± 8.87^{b}	17.25 ± 4.43^{b}	25.66 ± 5.96^{a}	12.83 ± 2.98^{a}	71.47 ± 9.70^{a}	62.83 ± 10.19^{b}	17.91 ± 1.68^{a}
Probability	*	*	ns	ns	ns	***	ns
P-value	**0.041**	**0.041**	**0.402**	**0.402**	**0.199**	**0.001**	**0.869**

Note: Mean values ± SE, with different letters following each treatment, indicate significant differences based on independent LSD post-hoc test. Asterisks on each parameter indicate significant differences from the independent LSD post-hoc test or the interaction between cultivar and lighting based on the LSD test; (*) significant difference at $P \leq 0.05$, (**) significant difference at $P \leq 0.01$, (***) significant difference at $P \leq 0.001$.

A significant interaction between cultivar and lighting was observed, influencing crown height at 7, 35, 42, and 49 d after planting (DAP), with the addition of light enhancing growth across all three cultivars during the early greenhouse phase (Fig. 3). This effect was attributed to increased plant biomass, supported by a photoperiod ranging from 308.78 to 425.78 µmol m^{-2} s^{-1} and the prevailing environmental conditions in the greenhouse (Fig. 1). These findings align with (Park et al., 2023), which reported a 10–11 mm increase in crown height in 'Albion' strawberries grown under single light sources, with crown height rising linearly by 18–64% as PPFD increased from 200 to 450 µmol m^{-2} s^{-1}.

Although no interaction was detected at 14 and 21 DAP, an independent LSD test ($P \leq 0.05$) revealed a significant effect on crown height for the 'KS75' and 'Sakura' cultivars at 14 DAP, with the non-LED treatment producing higher average values. A similar trend was observed at 21 DAP, where non-LED treatment had a significantly greater impact than LED supplementation across all three cultivars.

Table 4. The effect of lighting on the fruit yield of strawberry introduction.

Treatment	Total yield	Average fruit weight	Number of fruits	Fruit length	Fruit diameter	Fruit fresh weight	Fruit dry weight	Fruit hardness
	g	g	Plant month^{-1}	mm	mm	g	g	kgf
Cultivar								
Haruhi (H)	209.44 ± 36.16^{b}	6.78 ± 0.58^{b}	9.65 ± 0.46^{b}	26.40 ± 0.02^{a}	22.42 ± 0.29^{b}	51.91 ± 8.56^{a}	11.23 ± 0.95^{ab}	2.08 ± 0.23^{a}
KS75 (K)	256.54 ± 16.47^{a}	9.88 ± 0.28^{a}	7.09 ± 0.90^{c}	29.62 ± 0.65^{a}	26.00 ± 0.34^{a}	70.71 ± 6.29^{a}	14.50 ± 0.47^{a}	1.86 ± 0.17^{a}
Sakura (S)	178.66 ± 39.22^{b}	5.21 ± 0.52^{b}	11.52 ± 0.02^{a}	25.80 ± 1.05^{a}	19.47 ± 0.82^{c}	60.25 ± 7.02^{a}	8.55 ± 2.78^{b}	2.12 ± 0.07^{a}
Probability	**	***	***	ns	***	ns	*	ns
P-value	**0.007**	**0.001**	**< 0.001**	**0.064**	**< 0.001**	**0.134**	**0.037**	**0.158**
Lighting								
LED (L)	200.99 ± 60.48^{a}	6.96 ± 2.47^{a}	9.75 ± 1.91^{a}	26.88 ± 2.09^{b}	22.29 ± 3.44^{a}	62.07 ± 14.90^{a}	11.74 ± 2.09^{a}	2.02 ± 0.25^{a}
Non-LED (N)	228.77 ± 19.99^{a}	7.62 ± 2.28^{a}	9.09 ± 2.53^{a}	27.67 ± 2.09^{a}	22.97 ± 3.11^{a}	59.84 ± 5.71^{a}	11.11 ± 4.18^{a}	2.02 ± 0.13^{a}
Probability	ns	ns	ns	*	ns	ns	ns	ns
P-value	**0.238**	**0.187**	**0.390**	**0.023**	**0.183**	**0.723**	**0.316**	**0.969**
Interaction	**Cultivar X Lighting**							
HL	183.87 ± 18.41^{a}	6.37 ± 1.08^{a}	9.98 ± 2.27^{a}	26.42 ± 1.82^{a}	22.21 ± 0.90^{a}	45.85 ± 8.79^{a}	10.55 ± 4.52^{a}	2.25 ± 0.43^{a}
HN	235.01 ± 43.04^{a}	7.19 ± 1.26^{a}	9.32 ± 0.62^{a}	26.39 ± 1.74^{a}	22.63 ± 1.38^{a}	57.97 ± 17.31^{a}	11.91 ± 3.40^{a}	1.91 ± 0.15^{a}
KL	268.19 ± 32.47^{a}	9.68 ± 0.82^{a}	7.73 ± 0.59^{a}	29.16 ± 0.76^{a}	25.76 ± 0.75^{a}	75.16 ± 23.71^{a}	14.16 ± 1.88^{a}	1.74 ± 0.11^{a}
KN	244.89 ± 46.72^{a}	10.08 ± 1.27^{a}	6.45 ± 0.83^{a}	30.09 ± 2.05^{a}	26.25 ± 1.29^{a}	66.26 ± 11.92^{a}	14.84 ± 4.07^{a}	1.98 ± 0.12^{a}
SL	150.92 ± 41.80^{a}	4.83 ± 2.85^{a}	11.54 ± 1.62^{a}	25.05 ± 5.10^{a}	18.88 ± 2.56^{a}	65.21 ± 23.48^{a}	10.52 ± 4.75^{a}	2.06 ± 0.22^{a}
SN	206.40 ± 46.63^{a}	5.58 ± 1.58^{a}	11.51 ± 1.87^{a}	26.55 ± 3.11^{a}	20.05 ± 1.34^{a}	55.29 ± 19.85^{a}	6.58 ± 2.72^{a}	2.17 ± 0.37^{a}
Probability	ns	ns	ns	ns	ns	ns	ns	ns
P-value	**0.130**	**0.968**	**0.632**	**0.885**	**0.880**	**0.383**	**0.389**	**0.115**

Note: Mean values ± SE, with different letters following each treatment, indicate significant differences based on independent LSD post-hoc test. Asterisks on each parameter indicate significant differences from the independent LSD post-hoc test or the interaction between cultivar and lighting based on the LSD test; (*) significant difference at $P \leq 0.05$, (**) significant difference at $P \leq 0.01$, (***) significant difference at $P \leq 0.001$.

Regarding leaf number, all cultivars showed an increasing trend with age; however, no significant interaction was observed between cultivar and lighting in response to LED supplementation. Nonetheless, the LSD test ($P \leq 0.05$) indicated a significant cultivar effect on leaf number at 28, 35, 42, and 49 DAP for 'KS75' and 'Sakura'. This was influenced by the differing photoperiods, 12 h for LED and 10 h for non-LED treatments, and the greenhouse temperature, which reached approximately 30 °C.

Leaf production in both day-neutral and short-day strawberries continues throughout the season but is generally more robust under long-day conditions. Optimal temperatures for leaf growth range between 15–26 °C, depending on the cultivar (Hancock, 2000; Zarei et al., 2019). According to (Arney, 1953; Hancock, 2000), leaf initiation in 'Royal Sovereign' declines significantly at temperatures above 35 °C, and plant growth ceases between 35–38 °C, though leaves were not damaged even after six weeks of exposure to elevated temperatures.

For stolon production, the average number varied based on lighting treatment and cultivar. However, no significant interaction was observed between cultivar and lighting, suggesting that cultivar traits respond more strongly to environmental variables—particularly temperature and humidity—than to lighting alone. These environmental factors, in turn, influence stolon formation as part of the plant's developmental cycle. Still, LED supplementation significantly affected stolon number at 7 DAP in the dominant cultivars 'KS75' and 'Sakura', as confirmed by the LSD test at the 5% level. This agrees with (Bradford et al., 2010), who reported that stolon production in 'Tribute' and 'Honeoye' cultivars is influenced by temperature, photoperiod, and genotype. Stolon number increased as temperature rose from 20 °C to 26 °C, but decreased beyond 26 °C.

Stolon formation in day-neutral cultivars tends to be irregular, whereas short-day cultivars show more consistent stolon production under the same conditions (Durner et al., 1984; Hancock, 2000, 2020). Both cultivar types are capable of producing high stolon numbers under photoperiods longer than 10 h, particularly following new leaf formation after flowering, and when temperatures range between 21–30 °C (Durner, 2015; Heide, 1977). Under a 16 h photoperiod, stolon production was found to triple at 21 °C compared to cooler temperatures of 12.8 °C or 15.6 °C (Hancock, 2000, 2020). High temperatures combined with short days often favor stolon formation, though the plant's photoperiodic response may vary depending on additional experimental factors, leading to inconsistent stolon development (Sønsteby and Heide, 2009). Environmental factors, particularly temperature, played a critical role throughout the study in shaping plant growth responses.

Post-fruit set growth

However, not all cultivar-specific responses were statistically significant. For example, differences in total chlorophyll content were not significant among the cultivars, a result that may be attributed to the environmental temperature conditions within the greenhouse during the experimental period (Fig. 2). As noted by (Kadir et al., 2006), chlorophyll content in strawberry plants tends to decline under high-temperature stress. Similar trends have been reported in other crops; for instance, (Chaitaya et al., 2001) observed chlorophyll reduction in mulberry plants (Morus spp. L.) under elevated temperatures, while (Fukuda and Matsumoto, 1988) found higher chlorophyll levels in grapevines cultivated in open-field conditions.

No overall interaction was observed between cultivar and lighting treatments for the fresh and dry biomass parameters (Table 2). This lack of interaction is likely attributable to the elevated temperature conditions in the greenhouse (Fig. 2), which may have interfered with the plant's metabolic processes, particularly those related to photosynthesis. Nevertheless, for root dry weight, crown fresh weight, crown dry weight, and stomatal conductance, the different cultivars exhibited distinct physiological responses, although these were not significantly influenced by lighting treatments.

In contrast, transpiration showed no significant interaction between cultivar and lighting. However, significant individual effects were identified for both factors, as determined by the independent LSD post hoc test ($P \leq 0.05$). The cultivars 'Haruhi' and 'Sakura,' as well as the non-LED lighting treatment, demonstrated more pronounced effects. These differences are attributed to the genetic variability among cultivars, each possessing unique physiological traits that influence yield-related characteristics.

Lighting had a significant effect on each strawberry cultivar during the cultivation period. Several parameters, such as leaf temperature, demonstrated notable interactions between cultivar and lighting treatments. The average leaf temperature under non-LED lighting was higher (28.42 ± 1.26 °C) than under LED lighting (27.53 ± 0.61 °C). This interaction was particularly evident in the 'Sakura' (29.59 ± 0.52 °C) and 'Haruhi' (28.59 ± 0.22 °C) cultivars, which displayed greater sensitivity compared to 'KS75' (27.08 ± 0.32 °C). Environmental data collected during cultivation (Fig. 2) indicated average greenhouse temperatures ranging between 29–31 °C, which contributed to the observed plant responses. 'Sakura' and 'Haruhi' were more sensitive to these elevated temperatures and exhibited higher responsiveness to non-LED

lighting. These two cultivars, classified as short-day types, are photoperiod-dependent and thus respond differently to light quality.

It can therefore be inferred that 'Sakura' and 'Haruhi' are well adapted to tropical climates, where natural lighting conditions are generally sufficient for their growth without the need for LED supplementation (Fig. 4). Short-day strawberry cultivars are suitable for cultivation in tropical and subtropical regions, though they typically require a chilling period to achieve optimal productivity (Hancock, 2000).

A similar interaction was observed in crown diameter, particularly in the 'Haruhi' cultivar, which exhibited significantly greater crown growth under non-LED conditions (17.05 ± 2.56 mm). Conversely, the 'KS75' cultivar showed improved crown diameter under LED supplementation (17.17 ± 1.05 mm) compared to non-LED treatment. This difference is explained by the fact that 'KS75' is a day-neutral cultivar, which is less influenced by photoperiod and more responsive to temperature variations within the greenhouse environment. As noted by (Hancock, 2020; Rowley et al., 2011), day-neutral strawberries are bred for temperate climates and initiate flowering approximately three months after planting, regardless of day length. They thrive within a temperature range of 4.4–29.4 °C and thus show optimal adaptability when provided with suitable environmental conditions.

During the experiment, cooling water was circulated through pipes to maintain the crown zone at approximately 19 °C, further emphasizing 'KS75' sensitivity to ambient temperature fluctuations. As reported by (Al-madhagi et al., 2014), adequate cooling is essential in temperate environments to enhance plant growth. The strawberry crown, a short and thick stem structure, plays a vital role in plant development, as it serves as the central reservoir of carbohydrates essential for fruit formation and overall plant vigor (Macías-Rodríguez et al., 2002; Morgan, 2006; Torres-Quezada et al., 2015). Carbohydrate reserves stored in the crown and root systems support early floral and fruit development (Costa et al., 2016; Eshghi et al., 2007). During the early stages of growth, carbohydrate accumulation in vegetative tissues is critical for determining the potential yield and fruit production capacity of the plant (Eshghi et al., 2007; Goldschmidt et al., 1985).

Flowering in strawberries

These differences can be attributed to the intrinsic photoperiod sensitivity of the cultivars, which affects their flowering behavior. Strawberries are classified into short-day (SD), long-day or everbearing (LD), and day-neutral (DN) types based on their flowering responses to photoperiod. SD cultivars initiate flowering under short-day conditions, while LD cultivars flower under long-day conditions. DN cultivars, in contrast, are relatively insensitive to photoperiod, initiating flowers across a range of day lengths (Darnell et al., 2003).

However, both temperature and photoperiod modulate these responses, particularly in everbearing and day-neutral types. Everbearing cultivars behave as qualitative long-day plants at high temperatures, requiring specific day lengths to flower. Meanwhile, DN cultivars act as quantitative long-day plants at lower temperatures, responding gradually to increasing day length (Nishiyama and Kanahama, 2002).

The variability in flowering behavior among genotypes under different temperature and photoperiod regimes arises from three main factors: (1) the temperature range over which flowering becomes photoperiod-insensitive, (2) the specific photoperiod requirements at temperatures above this range, and (3) the developmental stage of the axillary meristems, which influences floral induction (Bradford et al., 2010).

In this study, although the shorter photoperiod conditions under the non-LED treatment were sufficient to induce flowering in all three cultivars, other environmental factors, particularly those within the greenhouse (Fig. 2), also influenced flowering and fruit development. Among these, temperature and day length (photoperiod) are the primary environmental cues regulating floral initiation in strawberries (Durner, 2015). The 'KS75' cultivar exhibited a longer period before flowering compared to the 'Haruhi' and 'Sakura' cultivars, which flowered at similar times. This is consistent with their classification as short-day (SD) cultivars, which require reduced photoperiods to induce flowering. In contrast, 'KS75' is a day-neutral (DN) cultivar, which can flower under a wide range of day lengths, albeit often with delayed response under suboptimal thermal conditions. These differences in flowering time also impacted harvest age, as statistical analysis indicated significant effects of flowering time among the cultivars.

This finding aligns with earlier studies (Garcia and Kubota, 2017; Heide, 1977; Heide et al., 2013), which showed that flower initiation in SD cultivars is significantly reduced at 24 °C compared to 18 °C, due to the requirement for photoperiods below a critical threshold (critical photoperiod). Furthermore, day/night temperature regimes of 26 °C/22 °C significantly inhibited flowering in both DN and SD cultivars compared to cooler conditions of 18 °C/14 °C or 22 °C/18 °C (Durner et al., 1984). At even higher temperatures, such as 27 °C, flowering was only observed under long-day conditions (Sønsteby and Heide, 2009).

The most notable difference between treatments was the effect of lighting on flowering and harvest timing. The addition of LED lighting tended to delay harvest compared to the non-LED treatment, as

indicated in the flowering and harvest age data (Table 3). For instance, the 'KS75' cultivar had a longer time to flowering under the 12 h LED photoperiod (62.83 ± 4.22 d) compared to the 10 h non-LED photoperiod (90.25 ± 0.50 d). However, no significant difference in harvest time was observed between LED (23.00 ± 2.01 d) and non-LED (22.33 ± 1.05 d) treatments for 'KS75,' which supports its classification as a day-neutral cultivar, less influenced by photoperiod and more responsive to other environmental factors (Durner et al., 1984).

Modern research has highlighted that flowering in contemporary strawberry cultivars is increasingly influenced by temperature sensitivity rather than photoperiod alone, with SD cultivars generally exhibiting greater sensitivity to elevated temperatures than DN types (Palha, 2005). This explains why the 'Haruhi' and 'Sakura' cultivars flowered more rapidly than 'KS75,' as supported by the flowering data presented in Table 3.

Fruit development in strawberries

In Table 4, significant variation underscores the higher productivity of 'KS75,' which can be attributed to its classification as a day-neutral (DN) cultivar. These results are in line with previous findings by (Soønsteby and Heide, 2007), which noted that DN and long-day strawberry cultivars, deriving their flowering traits from *Fragaria virginiana* subsp. glauca, exhibit continuous flowering and fruiting in contrast to the seasonal pattern observed in short-day (SD) cultivars. The enhanced fruit production observed in 'KS75' is therefore likely due to a combination of its genetic predisposition and the influence of environmental factors such as temperature and light, which affect both flower induction and fruit development.

Fruit formation in strawberries is intrinsically linked to the flowering process, which in turn impacts harvest timing and overall yield. Successful fruit development relies on optimal physiological and metabolic activity during the flowering and fruit-setting phases. This is particularly critical for achieving high-quality and high-quantity yields. However, the physiological mechanisms underlying flowering in most strawberry cultivars remain only partially understood, due to the sensitivity of both vegetative growth and flower initiation to environmental variables such as temperature, photoperiod, and their interactions (Heide et al., 2013).

In tropical (equatorial) regions, where photoperiods are consistently short, temperature becomes the dominant factor influencing the flowering response in strawberries. Temperatures above 28°C have been shown to inhibit flowering in both SD and DN cultivars of *Fragaria* × *ananassa* and *F. vesca* (Darnell et al., 2003; Durner et al., 1986; Ito and Saito, 1962). Supporting this, studies by (Durner et al., 1984; Nishiyama and Kanahama, 2002) demonstrated that DN cultivars such as 'Hecker' and 'Summerberry' failed to initiate inflorescences at day/night temperatures of 26/22 °C or 30/26 °C under a 9 h photoperiod. Flower Bud Initiation (FBI) resumed only when the temperature dropped to 20/15 °C or when a continuous 24 h photoperiod was applied at 30/25 °C, suggesting that DN strawberries can bypass photoperiod sensitivity under specific thermal conditions.

Conclusions

A significant interaction between cultivar and lighting was observed across various growth and yield parameters for the three Japanese strawberry cultivars studied. Prior to fruiting, plant height at 49 d after planting (DAP) was notably greater in the 'Sakura' and 'Haruhi' cultivars, while crown height at 7, 35, 42, and 49 DAP was more pronounced in 'Sakura' and 'KS75'. These interactions extended to several other traits, including crown diameter (in 'Haruhi' and 'KS75'), leaf temperature (in 'Haruhi' and 'Sakura'), number of flowers per plant and per bunch (in 'Sakura'), and flowering age (in 'KS75'). These differences were observed both during the vegetative phase and the reproductive phase of plant development.

Post-hoc LSD analysis ($P \leq 0.05$) confirmed statistically significant differences among the cultivars for a wide range of growth and yield characteristics, including root height, stomatal conductance, transpiration rate, root dry weight, crown fresh weight, crown dry weight, number of fruits per plant, fruit set percentage, harvest timing, total yield, average fruit weight, fruit diameter, and fruit dry weight. Of the three cultivars, 'KS75' consistently demonstrated superior performance across most parameters, exhibiting statistically significant dominance.

Regarding the lighting factor, post-hoc LSD analysis revealed that traits such as total chlorophyll content, transpiration rate, harvest age, and fruit length were affected by supplemental lighting. However, the addition of LED light in tropical conditions did not elicit a markedly superior response compared to the non-LED treatment. In fact, strawberry plants grown under non-LED conditions reached harvest age more quickly, likely due to the influence of natural photoperiod conditions, which were already sufficient for flower induction and fruit development. The observed light intensity ranged from 308.7 to 358.8 μmol m^{-2} s^{-1} for the LED treatment and 330.8 to 425.8 μmol m^{-2} s^{-1} for the non-LED treatment, indicating that non-LED lighting provided a broader and potentially more effective light spectrum under tropical conditions.

Furthermore, the internal greenhouse temperature during the cultivation period averaged

approximately 30 °C, a level that may have influenced several physiological responses. This is supported by the relatively elevated values for leaf temperature, transpiration, and total chlorophyll content under both lighting regimes, with non-LED conditions showing slightly higher values. These findings suggest that in tropical environments, natural light combined with ambient high temperatures may sufficiently support strawberry plant development without the need for additional LED supplementation.

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Author Contributions
Conceptualisation, SM, and ES; methodology, SM; validation, SM, ES, RH, MN, KE, and YM; formal analysis and investigation, ES; resources, SM; data curation, SM, NW, NS, ES; writing—original draft preparation, ES; writing—review and editing, SM, ES, RH, MN, KE, IY, and YM; visualisation, SM, ES; supervision, SM, NW, and NS. All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest
The authors indicate no conflict of interest in this work.

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