HortScience 59(3):394–399. 2024. https://doi.org/10.21273/HORTSCI17587-23

Yield and Photosynthesis Related to Growth Forms of Two Strawberry Cultivars in a Plant Factory with Artificial Lighting

Asaya Takahashi
Graduate School of Bioresource and Bioenvironment Sciences, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan

Daisuke Yasutake
Faculty of Agriculture, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan; and IoP Collaborative Creation Center, Kochi University, B200, Monobe, Nankoku, Kochi 783-8502, Japan

Kota Hidaka
NARO Kyushu Okinawa Agricultural Research Center, National Agriculture and Food Research Organization (NARO), Kurume, Fukuoka 839-8503, Japan

Shintaro Ono
Graduate School of Bioresource and Bioenvironment Sciences, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan; and Research Fellow of Japan Society for the Promotion of Science

Masaharu Kitano
IoP Collaborative Creation Center, Kochi University, B200, Monobe, Nankoku, Kochi 783-8502, Japan

Tomoyoshi Hirota and Gaku Yokoyama
Faculty of Agriculture, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan

Takeshi Nakamura and Minami Toro
OREC Co Ltd, 548 Hiyoshi, Hirokawa-cho, Yame-gun, Fukuoka 834-0195, Japan

Keywords. dry weight, leaf area, photosynthetic capacity, photosynthetic rate, plant height

Abstract. **Appropriate growth forms for strawberry production in a plant factory with artificial lighting (PFAL), which is a recently developed production system, remain undetermined. Improving strawberry productivity in a PFAL requires insights into the interplay between production characteristics (growth and photosynthesis) and growth forms, such as plant height and leaf area (*LA*), which are major determinants of crop yield. Growth status, yield, and photosynthetic characteristics of the two cultivars of strawberries (*Fragaria ×ananassa* Duch. Tochiotome and Koiminori) with different growth forms were examined. 'Koiminori' exhibited a 1.9-fold higher yield and a 2.0-fold greater total dry weight of respective organs compared with 'Tochiotome'. The single-plant photosynthetic rate (A_P), serving as an index for both cultivars, was 2.2-times higher for Koiminori than for Tochiotome. The photosynthetic rates of a single leaf (A_L) and *LA* were also analyzed as important factors that influence the A_P. The A_L for 'Koiminori' surpassed that of 'Tochiotome' by 1.4 times. This was attributed to the elevated photosynthetic photon flux density received by the upper leaves of Koiminori, which is a consequence of its higher plant height in proximity to the light source. Evaluation of four photosynthetic capacities, maximum rate of carboxylation, maximum rate of electron transport, photosynthetic rate under saturating light, and light utilization efficiency, which are potential factors that affect A_L, revealed no differences in these capacities between cultivars. 'Koiminori' exhibited a significantly larger *LA* (2.3- to 3.1-times) than 'Tochiotome', indicating that the former's higher A_P resulted mainly from its higher A_L and larger *LA*. Thus, strawberry production in a PFAL can be improved by growing cultivars with growth forms such as higher plant height and larger *LA*.**

A plant factory with artificial lighting (PFAL) is expected to serve as a stable food production system and is designed to consistently and systematically yield crops throughout the year. The PFAL overcomes the limitations imposed by seasonal variations and climate-related disasters (e.g., typhoons or sudden heavy rainfall) on crop production because the entire environment surrounding the crop can be protected and controlled (Beacham et al. 2019). Additionally, proper management can enable pesticide-free cultivation of crops in closed crop production, thus effectively discouraging pathogen invasion (Kozai 2021). Furthermore, the PFAL enables multitier cultivation, enhances land use efficiency, and fosters urban agriculture, consequently lowering transport costs (Avgoustaki and Xydis 2020).

Despite its advantages, the PFAL also has disadvantages, such as the high cost of cultivation (Kalantari et al. 2018). In particular, the costs of controlling environmental conditions to optimize crop growth are the major problem. Approximately 25% of operational expenses are attributed to electricity costs, with lighting constituting 75% of this expenditure (Kozai 2021). Therefore, to reduce electricity costs, the traditional crops cultivated in the PFAL are typically leafy vegetables, which can be grown at relatively low light levels (Armanda et al. 2019). Additionally, they can be easily applied to multitier cultivation because of their low plant height. However, addressing the challenge of high electricity costs requires the identification of more profitable crops. Therefore, strawberry cultivation in the PFAL is attracting attention because of its high market value (Wortman et al. 2016). Compared with other fruits and vegetables (e.g., tomatoes and cucumbers), strawberries can be grown under relatively low light intensity (Maeda and Ito 2020).

However, the implementation of strawberry cultivation in a PFAL is limited, and basic long-term data such as growth status [e.g., plant height and leaf area (*LA*)] and yield are lacking. Consequently, assessing the viability of strawberries as suitable PFAL crops and adopting a scientific approach for improved optimization are hindered. This research gap highlights the need to explore the growth status and yield characteristics of strawberries in a PFAL to obtain and accumulate data regarding their long-term variation. The growth status and yield depend on the canopy photosynthetic rate (Nomura et al. 2020; Parry et al. 2011), which depends on the *LA* and photosynthetic rate of a single leaf (Kaneko et al. 2022). Furthermore, the photosynthetic rate of a single leaf also depends on the maximum rate of carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}), photosynthetic rate under saturating light (A_{max}), and light utilization efficiency (Φ), which are important parameters for examining the biochemical and light response processes of photosynthesis. Therefore, to assess crop growth and yields, the photosynthetic rate and capacity of a canopy and a single leaf should be evaluated.

Strawberry cultivation in a PFAL requires a larger space above the cultivation bed for crop management (removing leaves and fruits and harvesting) during long-term cultivation compared with that needed for leafy vegetable cultivation. Under such space conditions, cultivars with higher plant heights should be advantageous because they receive higher light intensity because of the attenuation of the intensity of artificial light with increasing distance from the light source. Thus, plant height should be a main factor that determines the crop yield in the PFAL. Investigations of the growth status, yield, and photosynthetic characteristics of strawberry cultivars and the incorporation of growth forms (plant height and *LA*) into the PFAL are required.

The objective of this study was to clarify the characteristics of strawberry production (yield, growth, and photosynthesis) in relation to growth forms in the PFAL. In the present study, we measured the growth status as the growth forms, yields, and photosynthetic rates of a single plant and a single leaf and the photosynthetic capacities (V_{cmax}, J_{max}, A_{max}, Φ) of two cultivars with different growth forms throughout the long-term cultivation period.

Materials and Methods

Plant materials and cultivation. Two strawberry cultivars (*Fragaria ×ananassa* Duch. "Tochiotome" and "Koiminori') were grown in a PFAL located at the Joshima Factory of OREC Co., Ltd. (Kurume City, Fukuoka, Japan; 33°25.8′N, 130°43.2′E). On 22 Feb 2021, young plants were transplanted to cultivation beds [1.22 m (length) × 0.34 m (width) × 0.17 m (height)] filled with porous grains of diatomaceous earth (ISOLITE CG; Isolite Insulating Products Co., Ltd., Osaka, Japan), with 0.2 m between plants and 0.15 m between rows to ensure growth conditions (Fig. 1). The distance from the top of the cultivation beds to the light source was 0.3 m for daily cultivation management, such as removing leaves and fruits and harvesting (Fig. 2). A nutrient solution (OAT House No. 1:OAT House No. 2:OAT House No. 5 = 60:40:1; OAT Agrio Co., Ltd., Tokyo, Japan) with electrical conductivity (EC) of 0.6 $dS \cdot m^{-1}$ was supplied at a rate of 385 mL per day per plant every 30 min from 8:00 HR to 16:00 HR. Four light-emitting diode (LED) lamps (LT8018AP0104; 18W, Hansen Japan Co., Ltd., Tokyo, Japan) were used as the light source and fixed 30 cm above the cultivation bed. Figure 3 presents the spectral distributions of the lamps. The air temperature was maintained at 25 °C/20 °C during the photoperiod and dark period from 23 Jun 2021 to 31 Aug 2021, and at 22 °C/17 °C from 1 Sep 2021 to 24 Jan 2022. Although the relative humidity (RH) was controlled at 80% ± 5%, the CO_2 concentration was controlled at 800 $\mu mol \cdot mol^{-1}$ during the photoperiod without a control dark period.

Received for publication 2 Nov 2023. Accepted for publication 28 Dec 2023.
Published online 16 Feb 2024.
This study was conducted as a joint research project by OREC Co. Ltd., Kyushu University, and NARO Kyushu Okinawa Agricultural Research Center. It was partially supported by Grants in Aid for Scientific Research (No. 21H02318 and 22KJ2433) from the Japan Society for the Promotion of Science and the Cabinet Office grant-in-aid, the Advanced Next-Generation Greenhouse Horticulture by IoP (Internet of Plants), Japan.
We are grateful to the former and current students of the Laboratory of Agricultural Meteorology, Faculty of Agriculture, Kyushu University, for cooperation with our study.
D.Y. is the corresponding author. E-mail: yasutake@bpes.kyushu-u.ac.jp.

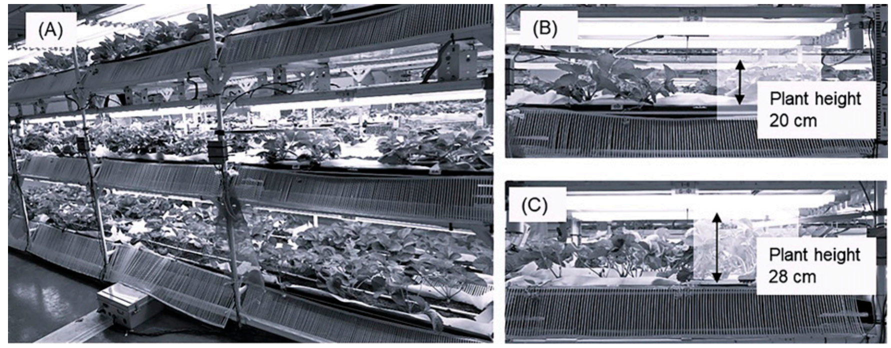

Fig. 1. Photographs of overview of the plant factory (**A**) and cultivation beds of Tochiotome (**B**) and Koiminori (**C**).

Environmental measurements. To investigate the cultivation environment, we introduced sensors near each strawberry plant cultivar. The photosynthetic photon flux density (PPFD) was measured using photon quantum sensors (PAR-02D; Prede Co., Ltd., Tokyo, Japan) placed at a point corresponding to plant height and changed by plant growth during the experiment. The air temperature and RH were measured using a temperature and humidity sensor (HMP110; VAISALA Co., Ltd., Tokyo, Japan) inside a forced ventilator (RSVH01A1203; CSE Inc., Sapporo, Japan), and the air CO_2 concentration was measured using a CO_2 sensor (GMP222; VAISALA Co., Ltd., Tokyo, Japan). Data were recorded at 5-min intervals using a data logger (GL240; GRAPHTEC Co., Ltd., Kanagawa, Japan).

Measurements of plant height, leaf area, soil plant analysis development, and fruit yield. The plant height and leaf area (*LA*) of single plants were measured monthly. The leaf area per leaf was estimated by measuring the leaflet length (L_L) and leaflet width (W_L) using Eq. [1]. This equation was obtained based on the relationship between the products of the L_L multiplied by the W_L and the leaf areas of individual leaves, as described by Hidaka et al. (2013).

$$LA = a \ (L_L \times W_L) + b \qquad [1]$$

where *a* and *b* represent constant values for the two cultivars (*a* = 1.647 and *b* = 11.666 for Tochiotome; *a* = 2.157 and *b* = 3.572 for Koiminori). The coefficients of determination were 0.7928 for Tochiotome and 0.8924 for Koiminori.

The soil plant analysis development (SPAD) value that correlated with the leaf chlorophyll concentration was measured monthly using a chlorophyll meter (SPAD-502; Konica Minolta, Inc., Tokyo, Japan). Fully ripe fruits were harvested daily from Jul 2021 to Dec 2021 to determine the yield of the cultivars.

Measurements of dry matter in strawberries. Removed leaves were dried for 72 h at 80 °C in a circulation dryer and weighed every month. On the last day of the experiment (24 Jan 2022), eight Tochiotome and Koiminori plants were harvested and separated into their respective organs (leaves, fruits, crowns, and roots). Each part was dried for 72 h at 80 °C in a circulation dryer and weighed.

Photosynthetic characteristics. The photosynthetic rates of a single plant (A_P) of Tochiotome and Koiminori were measured using a closed chamber measuring 25, 17, and 24 cm in height, width, and length,

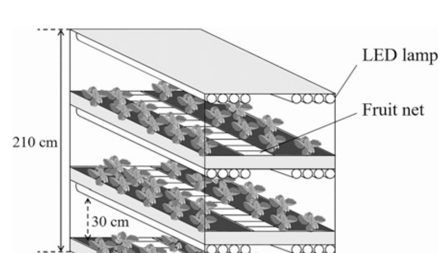

Fig. 2. Schematic diagram of a multitier strawberry cultivation system in a plant factory with artificial lighting.

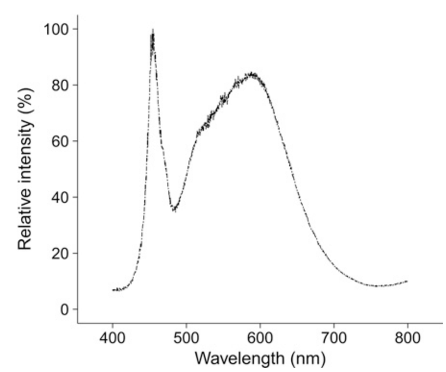

Fig. 3. Spectral distribution of light emitted from the light-emitting diode light source used in the plant factory. The spectrum is shown as the value relative to the maximum intensity at 454 nm.

respectively. The chamber system mainly consisted of a closed PVC chamber, an infrared CO_2 gas analyzer (GMP343; VAISALA Co., Ltd., Tokyo, Japan), and an air pump (CM-15-24; Enomoto Micro Pump Mfg. Co., Ltd., Tokyo, Japan). The system used to measure the time change in the CO_2 concentration and the method used to calculate A_P (CO_2 exchange rate of a single plant) followed those described by Ono et al. (2022). The A_P was calculated using the following equation:

$$A_P = V \times \frac{\Delta C}{t} \quad [2]$$

where V represents the volume of the chamber (m^3), t represents the elapsed time since the chamber (s) was closed, and C represents the CO_2 density ($\mu mol \cdot m^{-3}$). C was calculated using the following equation:

$$C = [CO_2] \times \frac{1}{0.0224 \times \frac{273+T}{273}} \quad [3]$$

where $[CO_2]$ represents the CO_2 concentration ($\mu mol \cdot mol^{-1}$) and T represents the air temperature inside the chamber.

The single-leaf photosynthetic rates of Tochiotome and Koiminori (A_L) were measured using a portable open gas exchange system (LI-6400XT; LI-COR, Inc., Lincoln, NE, USA) with a transparent top chamber (standard leaf chamber; LI-COR) on 24 Nov 2021 and 28 Dec 2021. The environmental conditions controlled inside the chamber were as follows: air temperature, RH, and CO_2 concentration of $\sim$25 °C, 50% to 60%, and 800 $\mu mol \cdot mol^{-1}$, respectively.

To evaluate the leaf photosynthetic ability of Tochiotome and Koiminori, the maximum rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) were estimated using the A-C_i curve method or one-point method (De Kauwe et al. 2016) using the LI-6400XT with an LED light source chamber (6400–02B; LI-COR). The A-C_i curve was obtained under saturating light (1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and a leaf temperature of 25 °C; the CO_2 concentration was changed stepwise (400, 300, 200, 100, 50, 0, 400, 600, 800, 1000, and 1500 $\mu mol \cdot mol^{-1}$). Using the one-point method, A was measured at CO_2 concentrations of 300 and 800 $\mu mol \cdot mol^{-1}$. The A-C_i curve was analyzed using the plantecophys package in R (Duursma 2015), which considers the biochemical photosynthesis model (Farquhar et al. 1980). Then, V_{cmax} and J_{max} were evaluated.

Photosynthetic rates under saturating light (A_{max}) and light utilization efficiency (Φ) were evaluated by obtaining the A-PPFD curve and then fitting the measured A and PPFD to Eq. [4] formulated by Thornley (1998). The A-PPFD curve was obtained at a concentration of 800 $\mu mol \cdot mol^{-1}$ CO_2 and leaf temperature of 25 °C, and the light intensity changed stepwise (400, 700, 1200, 400, 300, 200, 100, 50, and 0 $\mu mol \cdot mol^{-1}$) using the LI-6400XT with an LED light source chamber. Then, A_{max} and Φ were evaluated.

$$A = \frac{\phi PPFD + A_{max} - \sqrt{(\phi PPFD + A_{max})^2 - 4\phi PPFD A_{max}\theta}}{2\theta} \quad [4]$$

where θ represents the convexity of the A-PPFD curve.

Statistical analysis. Experimental data obtained from the plant height ($n = 5$), LA ($n = 5$), SPAD ($n = 5$), fruit yield ($n = 4$), dry weight (DW) of respective organs ($n = 8$), $PPFD$ ($n = 16$), A_P ($n = 3$), A_L ($n = 16$), V_{cmax} ($n = 19$), J_{max} ($n = 19$), A_{max} ($n = 5$), and Φ ($n = 5$) were subjected to the Student t test using R software (version 1.4.1717; R Development Core Team, Vienna Austria). $P < 0.05$ was considered statistically significant.

Results

Cultivation environments. Figure 4 shows the daily changes in the integrated PPFD (I) (Fig. 1A), average air temperature (T_a) (Fig. 1B), average RH (Fig. 1C), and average CO_2 concentration (C_a) (Fig. 1D) for the two strawberry cultivars (Tochiotome and Koiminori) during the entire experimental period from 25 Jun 2021 to 23 Jan 2022. The I values observed at the tops of the canopies of Tochiotome and Koiminori were $\sim$10 and 15 $mol \cdot m^{-2} \cdot d^{-1}$ from Jun 2021 to Oct 2021 and $\sim$13 and 16 $mol \cdot m^{-2} \cdot d^{-1}$ from Nov 2021 to Jan 2022, respectively. The intensity of the artificial light decreased with the increasing distance from the light source. Therefore, this difference between Tochiotome and Koiminori can be attributed to the installation of photon quantum sensors in accordance with each plant height, but not to the changing light intensity of the light source. Tochiotome and Koiminori had similar T_a, RH, and C_a values; T_a values were approximately 24 °C from Jun 2021 to Aug 2021 and approximately 22 °C from Sep 2021 to Jan 2022, the RH was approximately 80% ± 5% throughout the experiment, and C_a gradually increased from June to September and then were maintained at approximately 700 ± 50 $\mu mol \cdot mol^{-1}$.

Plant growth dynamics. Figure 5 shows the time change for plant height, LA, and SPAD values of the plants of the two strawberry cultivars (Tochiotome and Koiminori) during the entire experimental period. The plant heights of Tochiotome and Koiminori were approximately 15.1 ± 2.2 cm and approximately 22.9 ± 2.9 cm, respectively. The LA of Tochiotome varied from 500 to 1000 cm^2/plant throughout the experimental period, and that of Koiminori varied from 500 to 1000 cm^2/plant during the first 2 months; thereafter, they varied from 1500 to 3000 cm^2/plant. The SPAD values varied from 50 to 55 and from 43 to 52 for Tochiotome and Koiminori, respectively. Koiminori exhibited a significantly higher plant height and LA than those of Tochiotome during the experimental period, except for those during the first 2 months. Koiminori exhibited markedly lower SPAD values (which are correlated with leaf chlorophyll contents) than Tochiotome throughout the experimental period.

Yield and dry weights of the respective organs of crops. Figure 6 shows the monthly accumulations of Tochiotome and Koiminori fruit yields per plant. Koiminori exhibited a significantly higher yield (321.5 g/plant) than Tochiotome (168.7 g/plant) throughout the experimental period. Table 1 shows the DW of the respective plant organs (removed leaf, leaf, fruit, crown, and root) and their ratios to those of the entire plant body of the two

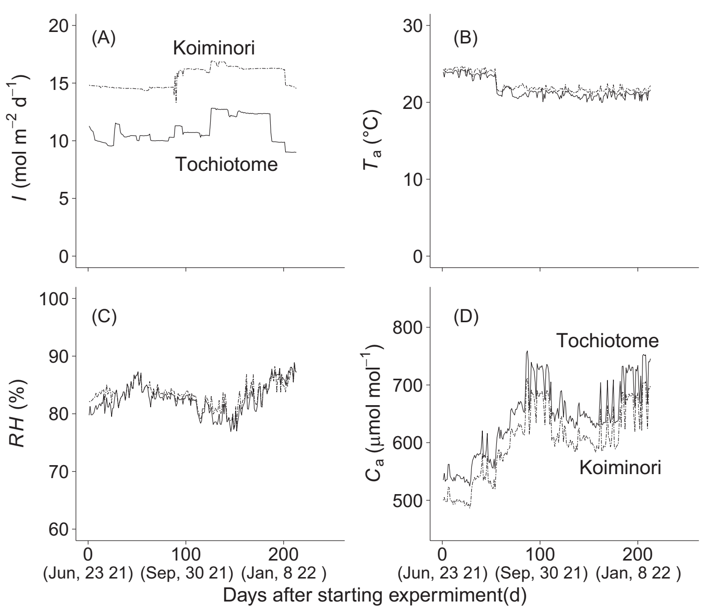

Fig. 4. Daily changes in integrated photosynthetic photon flux density (I) (**A**), average air temperature (T_a) (**B**), average relative humidity (RH) (**C**), and average CO_2 concentration (C_a) (**D**) as a function of time for the two strawberry cultivars (Tochiotome and Koiminori) during the entire experimental period from 25 Jun 2021 to 23 Jan 2022. The solid and dashed lines represent the data of Tochiotome and Koiminori, respectively.

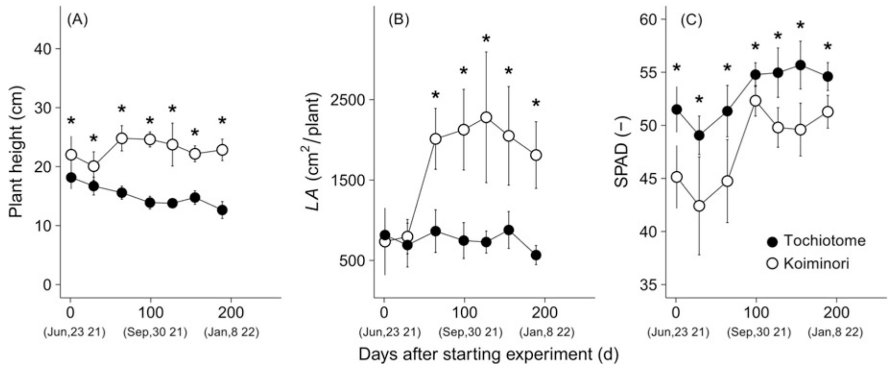

Fig. 5. Plant height (**A**), leaf area (**B**), and soil plant analysis development (SPAD) value (**C**) of the plants of the two strawberry cultivars (Tochiotome and Koiminori) as a function of time during the entire experimental period from 23 Jun 2021 to 23 Jan 2022. Closed and open circles represent the values of Tochiotome and Koiminori, respectively. Values are presented as mean ± *SD* (n = 5). *A significant difference between the cultivars at $P < 0.05$ according to Student's *t* test.

strawberry cultivars (Tochiotome and Koiminori) at the end of the cultivation experiment. The value for Koiminori was approximately twice that of Tochiotome. No differences in the relative DWs of the respective organs were observed between Tochiotome and Koiminori.

Photosynthetic characteristics. Figure 7 shows the PPFD on the surface of upper leaves of Tochiotome and Koiminori, A_P, and A_L. Koiminori had a higher PPFD (400 μmol·m^{-2}·s^{-1}) than Tochiotome (300 μmol·m^{-2}·s^{-1}). This difference occurred because Koiminori had greater plant heights than Tochiotome, and its leaves in the upper part of the canopy were closer to the light source than those of Tochiotome. Koiminori also had significantly higher A_L and A_P than Tochiotome. Koiminori had 1.4-times higher PPFD and A_L values and 2.2-times higher A_P values than Tochiotome. The differences in A_L and A_P were attributed to differences in PPFD because both parameters are known to increase until the PPFD reaches ~500 μmol·m^{-2}·s^{-1} in strawberries (Mochizuki et al. 2019; Trong et al. 2021). Table 2 shows the V_{cmax}, J_{max}, A_{max}, and Φ of Tochiotome and Koiminori; no significant differences in the parameters for either cultivars were observed.

Discussion

Factors affecting the yield of PFAL. The yield and DW of plant organs are often correlated with the total photosynthetic content during the cultivation period (Heuvelink 2005; Yoneda et al. 2020). During this study, the yield of Koiminori was 1.9-times higher than that of Tochiotome at the end of cultivation (Fig. 6), and the total DW of the plant organs of Koiminori was twice that of Tochiotome (Table 1).

The A_P of Koiminori was 2.2-times higher than that of Tochiotome (Fig. 7), indicating that the differences in the yields and dry weights between cultivars are attributable to differences in their A_P. The A_P should be strongly affected by the A_L and *LA*. The A_L was 1.4-times higher for Koiminori than for Tochiotome (Fig. 7). The difference in A_L between cultivars can be attributed to the difference in the PPFD at the upper position of the canopy (Tochiotome, 280 μmol·m^{-2}·s^{-1}; Koiminori, 400 μmol·m^{-2}·s^{-1}) because light intensity is the major factor that amplifies photosynthesis (Fig. 7) (Choi et al. 2016; Hidaka et al. 2013; Iwao et al. 2021). This difference in PPFD should be attributable to the difference in their plant height because that of Koiminori was 1.2- to 1.8-times higher than that of Tochiotome, and the upper leaves of its canopy received more light because they were closer to the light source during the cultivation (Figs. 5 and 7).

Other factors that strongly affect A_L include V_{cmax}, J_{max}, A_{max}, and Φ, which represent the photosynthetic capacity based on the biochemical and light response processes of photosynthesis (Chen et al. 2014; Wilson et al. 2000). During this study, four parameters, V_{cmax}, J_{max}, A_{max}, and Φ, were examined to investigate whether differences in the photosynthetic capacities of a single leaf existed between cultivars; however, no significant differences between cultivars were observed in these parameters (Table 2), indicating that photosynthetic capacities did not induce a difference in A_L between cultivars. Therefore, the difference in PPFD caused by plant height should cause a difference in the A_L in the PFAL.

For Koiminori, a higher *LA* should contribute to a higher A_P because it had 2.3-times to 3.1-times higher *LA* than Tochiotome, except for that during the first 2 months (Fig. 5). Furthermore, a positive feedback loop seemed to exist between photosynthesis and growth; the leaf growth should induce increased A_P, which is expected to accelerate leaf growth (Nomura et al. 2021). Thus, growth forms (plant height and *LA*) of the two cultivars are expected to result in differences in their yield based on the DW, A_P, and A_L of the respective cultivars within the PFAL. Therefore, we concluded that a higher plant height (leading to the receipt of more light from light sources) and larger *LA* lead to higher yields.

Limitations of this study and implications for future research. Although the results of this study indicate that strawberry cultivars with higher plant height and *LA* are well-suited for PFAL cultivation, the applicability of these results to other cultivars within the PFAL is not guaranteed because only two cultivars were considered during this study. Because some strawberry cultivars may have different levels of photosynthetic capacity

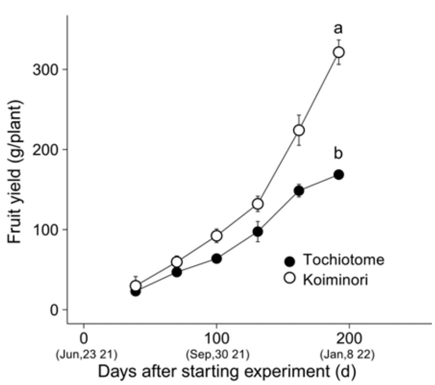

Fig. 6. Time change in the monthly accumulated fruit yield of the two strawberry cultivars (Tochiotome and Koiminori) from 1 Jul 2021 to 31 Dec 2022. Values are presented as the mean ± *SD* (*n* = 4). Different letters indicate significant differences ($P < 0.05$) according to Student's *t* test.

Table 1. Dry weight (DW) of the respective plant organs (leaf, removed leaf, fruit, harvested fruit, crown, and root) and its ratio to that of the entire plant body (values in parentheses) for the two strawberry cultivars (Tochiotome and Koiminori) at the end of the cultivation experiment (24 Jan 2022).

Organ	Tochiotome	Koiminori
Leaf (g)	3.39 ± 1.13 a (6)	9.25 ± 4.25 b (9)
Removed leaf (g)	16.05 (30)	32.07 (31)
Fruit (g)	0.86 ± 0.56 a (2)	1.98 ± 1.26 a (2)
Harvested fruit (g)	21.07 ± 1.26 a (40)	39.35 ± 3.12 b (38)
Crown (g)	4.14 ± 1.87 a (14)	10.48 ± 2.07 b (10)
Root (g)	7.16 ± 4.34 a (8)	10.86 ± 6.25 a (10)
Total (g)	52.66 ± 5.86 a (100)	103.98 ± 10.24 b (100)

Values are presented as the means ± *SD* (n = 8). Different letters indicate significant differences in DW between cultivars ($P < 0.05$, Student's *t* test).

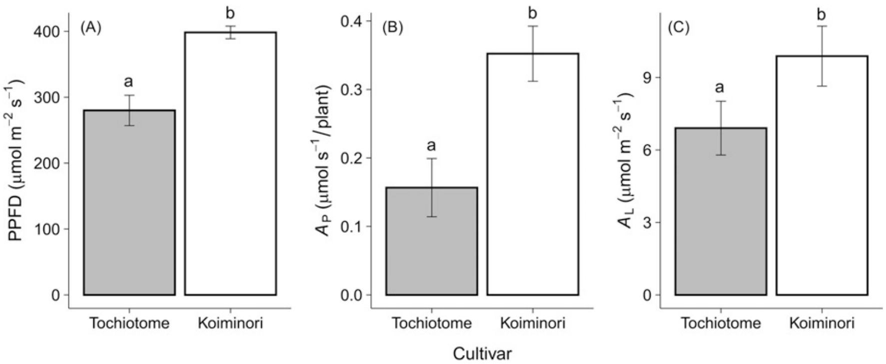

Fig. 7. Photosynthetic photon flux density on the surface of upper leaves (**A**) and photosynthetic rates of a whole plant (A_P) (**B**) and a single leaf (A_L) (**C**) of two strawberry cultivars (Tochiotome and Koiminori). Values are presented as mean ± *SD* [n = 3 (A_P) and n = 16 (A_L)]. Different letters indicate significant differences ($P < 0.05$) according to Student's *t* test.

Table 2. Maximum rate of carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}), photosynthetic rate at light saturation (A_{max}), and initial slope of the *A*-PPFD curve (Φ) for the two strawberry cultivars (Tochiotome and Koiminori).

Photosynthetic capacity	Tochiotome	Koiminori
V_{cmax} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	67.63 ± 7.89 a	63.28 ± 8.63 a
J_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	150.33 ± 21.26 a	155.98 ± 24.35 a
A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	32.76 ± 6.47 a	38.62 ± 6.15 a
Φ	0.11 ± 0.02 a	0.13 ± 0.01 a

Values represent mean ± *SD* (V_{cmax}, J_{max}: n = 19; A_{max}, Φ: n = 5). Different letters indicate significant differences between cultivars ($P < 0.05$, Student's *t* test).

(Kanno et al. 2022), further research is warranted to investigate whether the findings of this study are common to strawberry cultivation in a PFAL.

Furthermore, many leaves can be shaded within the canopy in the PFAL because of the fixed light source located at the upper position of the canopy and the light intensity is stable at the lower levels. Because shaded leaves may cause a reduced photosynthetic rate at the canopy scale (Brouwer et al. 2012; Velerskov 1987), this could induce a decrease in productivity. Therefore, several studies have investigated cultivation with multiple light directions to reduce shaded leaves in the PFAL (Zhang et al. 2015). Saito and Goto (2023) reported that the canopy photosynthetic rate was increased by combining upward and downward lighting compared with the use of only downward lighting in the PFAL. Thus, studies considering light directions as well as growth forms of cultivars are necessary to improve canopy photosynthesis and yield in PFALs.

Conclusions

Koiminori exhibited a greater yield and total DW than Tochiotome in their respective organs, which was attributed to a higher A_P of Koiminori. The A_L of Koiminori was 1.4-times higher than that of Tochiotome; this was induced by the higher PPFD of upper leaves of Koiminori caused by its higher plant height in proximity to the light source, not by the photosynthetic capacities. Koiminori exhibited a significantly larger *LA* that was 2.3-times to 3.1-times that of Tochiotome. Therefore, a higher A_L and larger *LA* for Koiminori led to a higher A_P. Thus, growing cultivars with growth forms such as higher plant height and larger *LA* can lead to improved strawberry production in the PFALs in which the light intensity decreases with the increasing distance from the light source.

References Cited

Armanda DT, Guinée JB, Tukker A. 2019. The second green revolution: Innovative urban agriculture's contribution to food security and sustainability – a review. Glob Food Secur. 22:13–24. https://doi.org/10.1016/j.gfs.2019.08.002.

Avgoustaki DD, Xydis G. 2020. Indoor vertical farming in the urban nexus context: Business growth and resource savings. Sustainability. 12(5):1–18. https://doi.org/10.3390/su12051965.

Beacham AM, Vickers LH, Monaghan JM. 2019. Vertical farming: A summary of approaches to growing skywards. J Hortic Sci Biotechnol. 94(3):277–283. https://doi.org/10.1080/14620316.2019.1574214.

Brouwer B, Ziolkowska A, Bagard M, Keech O, Gardeström P. 2012. The impact of light intensity on shade-induced leaf senescence. Plant Cell Environ. 35(6):1084–1098. https://doi.org/10.1111/j.1365-3040.2011.02474.x.

Chen TW, Henke M, De Visser PHB, Buck-Sorlin G, Wiechers D, Kahlen K, Stützel H. 2014. What is the most prominent factor limiting photosynthesis in different layers of a greenhouse cucumber canopy? Ann Bot. 114(4):677–688. https://doi.org/10.1093/aob/mcu100.

Choi HG, Moon BY, Kang NJ. 2016. Correlation between strawberry (*Fragaria ananassa* Duch.) productivity and photosynthesis-related parameters under various growth conditions. Front Plant Sci. 7:1607. https://doi.org/10.3389/fpls.2016.01607.

Duursma RA. 2015. Plantecophys - An R package for analysing and modelling leaf gas exchange data. PLoS One. 10(11):1–13. https://doi.org/10.1371/journal.pone.0143346.

Farquhar GD, Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta. 149(1):78–90.

Heuvelink E. 2005. Tomatoes. CABI Publishing, Trowbridge, UK.

Hidaka K, Dan K, Imamura H, Miyoshi Y, Takayama T, Sameshima K, Kitano M, Okimura M. 2013. Effect of supplemental lighting from different light sources on growth and yield of strawberry. Environ Control Biol. 51(1):41–47. https://doi.org/10.2525/ecb.51.41l.

Iwao T, Murakami T, Akaboshi O, Cho HY, Yamada M, Takahashi S, Kato M, Horiuchi N, Ogiwara I. 2021. Possibility of harvesting june-bearing strawberries in a plant factory with artificial light during summer and autumn by re-using plants cultivated by forcing culture. Environ Control Biol. 59(2):99–105. https://doi.org/10.2525/ecb.59.99.

Kalantari F, Tahir OM, Joni RA, Fatemi E. 2018. Opportunities and challenges in sustainability of vertical farming: A review. J Landsc Ecol. 11(1):35–60. https://doi.org/10.1515/jlecol-2017-0016.

Kaneko T, Nomura K, Yasutake D, Iwao T, Okayasu T, Ozaki Y, Mori M, Hirota T, Kitano M. 2022. A canopy photosynthesis model based on a highly generalizable artificial neural network incorporated with a mechanistic understanding of single-leaf photosynthesis. Agr For Meteorol. 323:109036. https://doi.org/10.1016/j.agrformet.2022.109036.

Kanno K, Sugiyama T, Eguchi M, Iwasaki Y, Higashide T. 2022. Leaf photosynthesis characteristics of seven Japanese strawberry cultivars grown in a greenhouse. Hortic J. 91(1):8–15. https://doi.org/10.2503/hortj.UTD-237.

De Kauwe MG, Lin YS, Wright IJ, Medlyn BE, Crous KY, Ellsworth DS, Maire V, Prentice IC, Atkin OK, Rogers A, Niinemets Ü, Serbin SP, Meir P, Uddling J, Togashi HF, Tarvainen L, Weerasinghe LK, Evans BJ, Ishida FY, Domingues TF. 2016. A test of the "one-point method" for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis. New Phytol. 210(3):1130–1144. https://doi.org/10.1111/nph.13815.

Kozai T. 2021. Contribution of PFALs to the sustainable development goals and beyond, p 57–79. In: Kozai T, Niu G, Masabni J (eds). Plant factory basics, applications and advances. Elsevier, Amsterdam. https://doi.org/10.1016/B978-0-323-85152-7.00016-1.

Maeda K, Ito Y. 2020. Effect of different PPFDs and photoperiods on growth and yield of everbearing strawberry "elan" in plant factory with white LED lighting. Environ Control Biol. 58(4):99–104. https://doi.org/10.2525/ECB.58.99.

Mochizuki Y, Sekiguchi S, Horiuchi N, Aung T, Ogiwara I. 2019. Photosynthetic characteristics of individual strawberry (*Fragaria ×ananassa* Duch.) leaves under short-distance lightning with blue, green, and red led lights. HortScience. 54(3):452–458. https://doi.org/10.21273/HORTSCI13560-18.

Nomura K, Takada A, Kunishige H, Ozaki Y, Okayasu T, Yasutake D, Kitano M. 2020. Long-term and continuous measurement of canopy photosynthesis and growth of spinach.

Environ Control Biol. 58(2):21–29. https://doi.org/10.2525/ecb.58.21.
Nomura K, Yasutake D, Kaneko T, Takada A, Okayasu T, Ozaki Y, Mori M, Kitano M. 2021. Long-term compound interest effect of CO_2 enrichment on the carbon balance and growth of a leafy vegetable canopy. Scientia Hortic. 283:110060. https://doi.org/10.1016/j.scienta.2021.110060.
Ono S, Yasutake D, Yokoyama G, Teruya Y, Hidaka K, Okayasu T, Nomura K, Kitano M. 2022. Closed chamber system for easily measuring the respiration rate of intact fruits. Environ Control Biol. 60(1):33–37. https://doi.org/10.2525/ecb.60.33.
Parry MAJ, Reynolds M, Salvucci ME, Raines C, Andralojc PJ, Zhu XG, Price GD, Condon AG, Furbank RT. 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J Expt Bot. 62(2):453–467. https://doi.org/10.1093/jxb/erq304.
Saito K, Goto E. 2023. Evaluation of the enhancement of photosynthetic rate in a komatsuna (*Brassica rapa* L. var. *perviridis*) canopy with upward lighting using an optical simulation in a plant factory with artificial light. Front Plant Sci. 14:1–17. https://doi.org/10.3389/fpls.2023.1111338.
Thornley JHM. 1998. Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. Ann Bot. 81(3):421–430. https://doi.org/10.1006/anbo.1997.0575.
Trong LL, Dinh HT, Takaragawa H, Watanabe K, Kawamitsu Y. 2021. Whole-plant and single-leaf photosynthesis of strawberry under various environmental conditions. Environ Control Biol. 59(4):173–180. https://doi.org/10.2525/ecb.59.173.
Velerskov B. 1987. Irradiance-dependent senescence of isolated leaves. Physiol Plant. 71(3): 316–320. https://doi.org/10.1111/j.1399-3054.1987.tb04349.x.
Wilson KB, Baldocchi DD, Hanson PJ. 2000. Quantifying stomatal and non-stomatal limitations to carbon assimilation resulting from leaf aging and drought in mature deciduous tree species. Tree Physiol. 20(12):787–797. https://doi.org/10.1093/treephys/20.12.787.
Wortman SE, Douglass MS, Kindhart JD. 2016. Cultivar, growing media, and nutrient source influence strawberry yield in a vertical, hydroponic, high tunnel system. HortTechnology. 26(4):466–473. https://doi.org/10.21273/horttech.26.4.466.
Yoneda A, Yasutake D, Hidaka K, Muztahidin NI, Miyoshi Y, Kitano M, Okayasu T. 2020. Effects of supplemental lighting during the period of rapid fruit development on the growth, yield, and energy use efficiency in strawberry plant production. Int Agrophys. 34(2):233–239. https://doi.org/10.31545/INTAGR/117623.
Zhang G, Shen S, Takagaki M, Kozai T, Yamori W. 2015. Supplemental upward lighting from underneath to obtain higher marketable lettuce (*Lactuca sativa*) leaf fresh weight by retarding senescence of outer leaves. Front Plant Sci. 6:1–9. https://doi.org/10.3389/fpls.2015.01110.