Local CO₂ Application within Strawberry Plant Canopy Increased Dry Matter Production and Fruit Yield in Summer and Autumn Culture

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ABSTRACT
June-bearing strawberry cultivars have been widely grown in Japan. Since they are harvested in winter and spring, little produce is available in summer and autumn. To achieve stable year-round supply, we need to expand the production area of ever-bearing cultivars. Here, we examined whether it is possible to increase dry matter (DM) production and fruit yield by increasing the CO₂ concentration within the plant canopy through local application to promote photosynthesis in summer and autumn protected culture. We investigated the CO₂ concentration in the plant canopy, DM production characteristics, yield characteristics, fruit quality, projected leaf area, cumulative light interception, and light use efficiency. We confirmed that the CO₂ concentration within the plant canopy could be increased in summer and autumn (Control; 398 ppm, CO₂; 1280 ppm), significantly increasing DM production and total yield (Control; 349 g, CO₂; 447.5 g). We consider that local application of CO₂ increased the projected leaf area and thus cumulative light interception. This method may help to increase fruit yield in summer and autumn protected culture.

KEYWORDS
Fragaria × ananassa; local CO₂ application; ever-bearing strawberry; destructive measurement; light interception

Introduction
Strawberry (Fragaria × ananassa Duch.) is popular worldwide. The main method of growing strawberry in Japan is forcing culture of June-bearing cultivars transplanted at the end of September and kept warm from mid-October to develop flowers; the fruit is harvested from December to the following May. This method accounts for >90% of strawberry production in Japan. Since strawberries are in constant demand year-round (Yanagi, 2017), most of the supply during summer and autumn is covered by imports. However, since strawberries are soft and their quality deteriorates during transportation (Hikawa-Endo, 2019; Hikawa-Endo and Sone, 2017), it is desirable to increase the domestic production of summer and autumn strawberries. Ever-bearing strawberries, which bloom and set fruit under long-day conditions, are grown, but their production is limited to cooler areas such as the northern Tohoku and Hokkaido regions (Ohta and Yasuba, 2019; Yamazaki, 2015).

Cultivation of ever-bearing strawberries in summer and autumn faces problems such as reduced photosynthesis (Balasooriya et al., 2018) and heavy fruit loads (Hikawa-Endo et al., 2017) due to high temperatures. Since these problems reduce yields, it is necessary to maintain plant vigor by fruit thinning (Khanizadeh et al., 1992), and promoting photosynthesis under high temperatures. Various environmental factors are involved in plant photosynthesis, including CO₂. Many effects of CO₂ supplementation have been reported, including increased photosynthetic rate of strawberry in...
winter and spring (Mizukami et al., 2011), increased yield of strawberry (Itani et al., 1999), improved citrus plant vigor (Fujsawa et al., 2001). It is known that increasing the total dry weight is important for increasing the yield of tomatoes (Higashide and Heuvelink, 2009) and strawberries (Mochizuki et al., 2014, 2013). Total dry weight is affected by light use efficiency and cumulative light interception. Light use efficiency is most affected by the CO₂ concentration (Higashide and Heuvelink, 2009). Therefore, we speculate that the yield of ever-bearing strawberries may be increased by using supplemental CO₂ to alleviate the decrease in plant vigor caused by high temperatures.

Generally, CO₂ is supplied to winter–spring strawberries in greenhouses by the combustion of kerosene and liquefied petroleum gas (LPG). However, most of the CO₂ is dissipated to the outside if the greenhouse is ventilated (Kuroyanagi, 2014), so the combustion method is not realistic in summer and autumn. Furthermore, unlike tomatoes and cucumbers, strawberries plants are short, and full-scale application of CO₂ within the greenhouse is not efficient. So far, local application of CO₂ from an air duct has been tried in June-bearing strawberries (Miyoshi et al., 2017) in winter, but no studies have applied CO₂ in summer and autumn, when the inside temperatures become high, and no long-term yield survey using destructive measurements has been done. Therefore, here, we examined whether it is possible to increase the DM production and fruit yield of ever-bearing strawberries by increasing the CO₂ concentration within the plant canopy by using a local application method to promote photosynthesis in summer–autumn cultivation.

**Materials and Methods**

**Plant Materials and Cultivation Method**

We grew the ever-bearing strawberry ‘Suzuakane’ (Hokusan Co., Ltd., Hokkaido, Japan). On 19 April 2020, 6 frigo bareroot plants (crown size was about 1.0 cm) were planted in a polystyrene container (35.5 cm × 75.0 cm × 14.5 cm deep; 24 L) filled with a 1:1:1 (vol.) mixture of Kanuma soil, peat moss, and vermiculite. The frigo bareroot plants were grown from May to November 2019, and dug up from the greenhouse, and they were kept in plastic bag at −2°C until transplanting. Fungicide treatment was done before storage. The frigo bareroot plants were planted in a 30-cm between plants and 10-cm between rows. Plant density was 7.0 m⁻². There were 72 plants (12 containers) for each treatment and assigned completely randomized. The guard plants were placed between the control and the CO₂ treatment to avoid the effects of CO₂ application. The plants were grown on a high bench in a plastic house of the Faculty of Agriculture, Ibaraki University (elevation of experiment site is 21.8 m), until 17 November 2020. They were irrigated via an automatic drip-irrigation system (Aqua-touch, Sunhope-Aqua Co., Ltd., Chiba, Japan) with −30 mL per plant at 06:00 every morning and again after every 3.0 MJ.m⁻² of cumulative solar radiation. The solar radiation sensor was set in greenhouse. Fertilization was prepared from OAT-A nutrient solution (OAT Aglio Co., Ltd, Tokyo, Japan) with EC adjusted to 0.3–0.5 dS.m⁻² and pH to 5.5–6.0. The nutrient solution contained 2.2 to 3.7 mM NO₃⁻, 1.0 to 1.7 mM K⁺, 1.0 to 1.7 mM Ca²⁺, 0.4 to 0.7 mM Mg²⁺, 0.6 to 1.0 mM H₂PO₄⁻, 0.3 to 0.5 mg.L⁻¹ Fe, 0.2 to 0.3 mg.L⁻¹ Mn, 0.2 to 0.3 mg.L⁻¹ B, 0.01 to 0.02 mg.L⁻¹ Zn, 0.003 to 0.005 mg.L⁻¹ Cu, and 0.003 to 0.005 mg.L⁻¹ Mo. In August to October, senescent leaves were removed once a month. The temperature inside the greenhouse was measured at 10-min intervals (Figure 1) with a TR-76Ui CO₂ Recorder (T&D Co. Ltd., Tokyo, Japan). CO₂ was supplied from a gas cylinder to the plants through porous tubes laid within the canopy under the control of a controller (Omnia Concerto Co. Ltd., Tokyo, Japan; Figure 2). From 9 May, CO₂ was supplied daily from sunrise to 6 h before sunset at a pressure of 0.2 MPa and a flow rate of 15 L.min⁻¹, as determined in preliminary experiments. To measure the diurnal change of CO₂ concentration, we installed a TR-76Ui CO₂ Recorder within the canopy of each treatment on 18 September, which recorded measurements at 10-s intervals. The average of CO₂ concentration was calculated every 15 minutes.
Dry Matter Production

Destructive measurements were conducted on 9 May, 25 June, 19 July, 24 August, 21 September, 20 October, and 17 November 2020. Six plants were harvested from each treatment and were separated into roots, crowns, petioles, leaves, fruits, and peduncles, which were dried at 80°C for 72 h in a circulation drier, cooled, and weighed. The harvest index and cumulative dry weight of fruits were calculated as:

\[
\text{Harvest index} = \frac{\text{fruit DW} + \text{peduncle DW}}{\text{total DW}} \quad (1)
\]

\[
\text{Cumulative DW of fruits} = (\text{Cumulative fresh weight of fruits harvested by the day of destructive measurement date} + \text{fresh weight of fruits that had set on the day of destructive measurement}) \times 0.1 \text{ (pre – measured DM ratio)} \quad (2)
\]
To measure the total leaf area, we used the leaves of the destructively measured plants. The leaves were photographed, and the leaf area was calculated from the photos in lia32 leaf area analysis software (https://www.flatworld.jp/soft/142711.html). Fruits with ≥80% of the skin colored were harvested, and those >4 g were counted. Harvesting period was from 2 July to 18 November. Artificial pollination was conducted to set the fruits.

**Growth Analysis**

The cultivation period was divided into 6 periods from May to November. The values of relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) during each period were calculated as:

\[
RGR = \frac{\ln (W2) - \ln (W1)}{(t2 - t1)} \tag{3}
\]

\[
NAR = \frac{(W2 - W1)}{(A2 - A1)} \times \left\{ \frac{[\ln (A2) - \ln (A1)]}{(t2 - t1)} \right\} \tag{4}
\]

\[
LAR = \frac{RGR}{NAR} \tag{5}
\]

where \(W1\) and \(W2\) are the DW (g) and \(A1\) and \(A2\) are the leaf area (m\(^2\)) at \(t1\) and \(t2\), respectively.

**Projected Leaf Area (PLA) Cumulative Light Interception, and Light Use Efficiency (LUE)**

On 26 May, 22 June, 6 July, 30 July, 13 August, 27 August, 17 September, 5 October, 31 October, and 18 November, the upper part of the plant canopy was photographed with a smartphone (iPhone 8, Apple Inc., California, USA). After the leaves were extracted from the photograph in Microsoft PowerPoint software, the light-receiving leaf area was calculated in lia32 software. This was used to calculate projected leaf area. Daily PLA was estimated by linear interpolation. Daily light reception was calculated as (Monsi and Saeki, 1953):

\[
\text{Daily light reception} = \text{total daily solar radiation} \times \text{photosynthetically active radiation coefficient} [0.5] \times \text{greenhouse light transmittance} [0.8] \times \text{light receiving leaf area} \times \text{planting density} [7.0\text{m}^{-2}] \tag{6}
\]

Total solar radiation was sourced from AMEDAS Tateno (Tsukuba City, Ibaraki Prefecture, Japan). Daily light reception during the cultivation period was totaled. LUE was calculated by a linear regression between the total DM and the cumulative light reception on the dates of the destructive measurements.

**Fruit Quality**

The Brix content and acidity of fruit were measured with a pocket sugar acidity meter (PAL-BX | Acid F5, Atago Co. Ltd., Tokyo, Japan). Brix content was measured in the juice of crushed fully colored fruit. Acidity was measured in 1:50-diluted juice. Fruit hardness was measured with a fruit hardness meter (KM-1, Fujiwara Scientific Co., Ltd., Tokyo, Japan), with the plunger inserted between the achenes.

**Statistical Analysis**

All data were tested by F-test and then t-test. LUEs were compared among treatments by analysis of covariance. All statistical analyses were performed using Excel Analysis (Social Survey Research Information Co., Ltd., Tokyo, Japan).
Results

Changes in CO₂ Concentration

The average of CO₂ concentration every 15 minutes in the plant canopy of the CO₂ treatment ranged from 806 to 1440 ppm, with an average of 1280 ppm. That in the control ranged from 379 to 405 ppm and averaged 398 ppm (Figure 3).

Dry Matter Production and Growth Analysis

The CO₂ treatment had significantly higher total DW than the control in June, July, October, and November; lower harvest index in September and October; higher leaf weight in June, petiole weight in June, October, and November, crown weight in June and September, and root weight in July, September, and October (Table 1). The RGR was larger in the CO₂ treatment from May to June and from August to November. The NAR was larger in the CO₂ treatment from May to June and from October to November. The LAR was larger in the CO₂ treatment (Table 2).

Fruit Yield and Quality

Total fruit yield was significantly higher in the CO₂ treatment (447.5 g per plant) than in the control (349.0 g per plant) (Figure 4A). Monthly fruit yield was higher in the CO₂ treatment in July and August. Total fruit number was higher in the CO₂ treatment (57.4 per plant) than in the control (42.3 per plant) (Figure 4B). There was no significant difference in single fruit weight between treatments throughout the growing period (Figure 5A). The Brix content of fruit was higher in the CO₂ treatment in September (Figure 5B), but there was no significant difference in acidity (Figure 5C) or firmness (Figure 5D) between treatments.

Projected Leaf Area (PLA) Cumulative Light Interception, and Light Use Efficiency (LUE)

The PLA of the CO₂ treatment was significantly larger than that of the control on 22 June, 6 July, 13 and 27 August, and 17 September (Figure 6A). The total amount of light received was larger in the CO₂ treatment throughout the growing period (Figure 6B). LUE was 1.89 g.MJ⁻¹ in the CO₂ treatment and 2.01 g.MJ⁻¹ in the control, with no significant difference (Figure 6C).

Figure 3. Diurnal changes in CO₂ concentration. CO₂ concentration was measured on 18 September. The average of CO₂ concentration was calculated every 15 minutes.
Table 1. Changes in total dry weight and in dry weights of each plant part.

| Date     | Treatment | Leaf (g DW) | Petiole (g DW) | Crown (g DW) | Root (g DW) | Peduncle (g DW) | Fruit (g DW) | Total (g DW) | Harvest index |
|----------|-----------|-------------|----------------|-------------|-------------|-----------------|--------------|--------------|---------------|
| 9 May    | —         | 0.30        | 0.06           | 0.24        | 0.51        | ND              | ND           | 1.11         | ND            |
| 25 Jun   | Control   | 6.33        | 0.96           | 1.15        | 3.98        | 0.42            | 0.63         | 13.2         | 0.08          |
|          | CO₂       | 11.4        | 1.01           | 2.22        | 4.49        | 0.59            | 0.97         | 20.7         | 0.07          |
|          | t-test    | *           | *              | *           | NS          | NS              | NS           | NS           | NS            |
| 19 Jul   | Control   | 6.37        | 0.71           | 1.24        | 3.55        | 1.25            | 7.51         | 20.6         | 0.43          |
|          | CO₂       | 8.87        | 1.15           | 1.60        | 4.37        | 2.13            | 9.05         | 27.2         | 0.41          |
|          | t-test    | NS          | NS             | *           | NS          | NS              | *            | NS           | NS            |
| 24 Aug   | Control   | 12.6        | 1.95           | 2.39        | 5.91        | 2.65            | 23.0         | 47.2         | 0.52          |
|          | CO₂       | 13.7        | 2.37           | 2.94        | 7.00        | 2.17            | 23.1         | 51.3         | 0.51          |
|          | t-test    | NS          | NS             | NS          | NS          | NS              | NS           | NS           | NS            |
| 21 Sep   | Control   | 12.7        | 1.76           | 2.12        | 3.84        | 2.85            | 28.9         | 52.2         | 0.61          |
|          | CO₂       | 17.4        | 3.40           | 4.02        | 6.86        | 2.87            | 21.9         | 59.3         | 0.43          |
|          | t-test    | NS          | NS             | *           | NS          | NS              | *            | NS           | NS            |
| 20 Oct   | Control   | 15.2        | 2.14           | 3.11        | 5.69        | 2.50            | 33.2         | 61.8         | 0.58          |
|          | CO₂       | 17.2        | 3.19           | 4.33        | 8.74        | 7.36            | 30.0         | 70.4         | 0.49          |
|          | t-test    | NS          | NS             | *           | NS          | NS              | *            | NS           | NS            |
| 18 Nov   | Control   | 23.7        | 4.03           | 7.17        | 8.26        | 3.12            | 38.9         | 85.1         | 0.50          |
|          | CO₂       | 29.5        | 7.19           | 10.1        | 8.52        | 4.04            | 53.2         | 112.3        | 0.48          |
|          | t-test    | NS          | *              | NS          | NS          | NS              | NS           | NS           | NS            |

1ND: not detected.
2*Significant at the 5% level by t-test; NS, not significant.

Table 2. Comparison of growth analysis between treatments.

| Date     | Treatment | RGR (g g⁻¹ day⁻¹) | NAR (g m⁻² day⁻¹) | LAR (m² g⁻¹) |
|----------|-----------|-------------------|-------------------|--------------|
| 9 May – 25 Jun | Control | 0.053             | 10.78             | 0.0049       |
|          | CO₂      | 0.062             | 11.04             | 0.0056       |
| 25 Jun – 19 Jul | Control | 0.021             | 5.08              | 0.0041       |
|          | CO₂      | 0.011             | 2.77              | 0.0041       |
| 19 Jul – 24 Aug | Control | 0.022             | 7.38              | 0.0030       |
|          | CO₂      | 0.018             | 5.90              | 0.0030       |
| 24 Aug – 21 Sep | Control | 0.003             | 1.24              | 0.0027       |
|          | CO₂      | 0.004             | 1.09              | 0.0035       |
| 21 Sep – 20 Oct | Control | 0.006             | 2.21              | 0.0026       |
|          | CO₂      | 0.010             | 1.47              | 0.0065       |
| 20 Oct – 18 Nov | Control | 0.009             | 3.88              | 0.0024       |
|          | CO₂      | 0.016             | 6.22              | 0.0026       |

Figure 4. Comparison of (A) fruit yield and (B) fruit number between treatment. *Significant at the 5% level by t-test; NS, not significant.
**Figure 5.** Comparison of (A) individual fruit weight, (B) Brix, (C) acidity, and (D) firmness between treatment. *Significant at the 5% level by t-test; NS, not significant.

**Figure 6.** Effects of local CO2 application on (A) projected leaf area, (B) cumulative light interception, and (C) light use efficiency. *Significant at the 5% level by t-test; NS, not significant.
Discussion

Our results confirm that supplementary CO$_2$ significantly increased the total DW and the DW of the vegetative organs throughout the growing season (Table 1). The same treatment increased the DW of tomato (Takahashi et al., 2012) and June-bearing strawberry (Matsugaki et al., 1998) by enhancing photosynthesis, creating a surplus of assimilation products (Matsugaki et al., 1998). Most of the photosynthetic products of strawberries are distributed to fruits as they mature, and little is distributed to roots and leaves (Nishizawa and Hori, 1988), thus decreasing plant vigor. Therefore, the application of CO$_2$ strengthened the vigor of the strawberry plants.

The RGR was larger in the CO$_2$ treatment except in June to August (Table 2). CO$_2$ application increases DM production rate (Ushio et al., 2014). In general, NAR increases with the magnitude of net photosynthetic rate, so it should be larger in the CO$_2$ treatment, as reported in grapes (Azukizawa and Yamamoto, 2005) and Eustoma grandiflorum (Ushio et al., 2014). However, CO$_2$ application reduced LAR in rice (Makino et al., 1997) and June-bearing strawberry (Deng and Woodward, 1998). Self-shading of leaves decreased the net photosynthetic rate in some woody plants (Reich et al., 2009). In this study, we removed only senescent leaves. Therefore, the NAR was smaller in the CO$_2$ treatment from 25 June to 20 October (Table 2), because the area of self-shading increased with the LAR owing to the application of CO$_2$. To maximize the effect of CO$_2$, it is necessary to estimate the optimal leaf area index for ever-bearing strawberry by using a growth model (Saito et al., 2020).

Total fruit yield and fruit number were significantly higher in the CO$_2$ treatment (Figure 4). On the other hand, there was no significant difference in individual fruit weight (Figure 5A). Therefore, the total yield increased owing to the increase in the number of fruits. This result is inconsistent with studies that reported that the application of CO$_2$ increased the fruit weight of June-bearing strawberries (Kawashima, 1991; Takahashi et al., 2006). It is known that the maturation period of strawberries shortens, and the weight of fruit lessens as the temperature rises (Kumakura and Shishido, 1994). Therefore, the absence of a significant difference in the fruit weight here was likely due to the shortened maturation period, in turn due to high temperatures, and the fruit was colored before it was sufficiently enlarged. In contrast, there was no significant difference in fruit yield after September. The leaf photosynthetic rate of strawberry is affected by temperature under high light intensity (Choi et al., 2016). Generally, the leaf photosynthetic rate of strawberry June-bearing strawberry is decreased under high temperature (Choi et al., 2016; Kadir et al., 2006; Sun et al., 2012), however, that of ever-bearing strawberry is decreased under cold temperature (Rivero et al., 2021). Furthermore, ever-bearing strawberry is qualitative long day plants at high temperatures (Samad et al., 2021). Therefore, the reason why fruit yield did not increase after September may be due to the lower temperature.

In general, when CO$_2$ is applied to crops, the sugar content of the fruits is increased owing to the promotion of translocation of photosynthetic products, as in grapes (Kurooka et al., 1990) and June-bearing strawberry (Takahashi et al., 2006). However, we found no significant difference in Brix content of fruit except in September (Figure 5B), largely inconsistent with those cited results. The sugar content of strawberries decreases in hot weather because the high temperatures promote the coloring of the fruits, which are harvested without enough sugar (Kawanobu et al., 2011), as happened here. In addition, there was no significant difference in fruit acidity or firmness (Figure 5C, D), as in previous research (Klieber et al., 1996; Matsugaki et al., 1998; Takahashi et al., 2006). Therefore, local CO$_2$ application might not affect fruit quality.

CO$_2$ application increased PLA (Figure 6A) and therefore cumulative light interception (Figure 6B). On the other hand, there was no significant difference in LUE (Figure 6C). Although CO$_2$ application increased LUE in tomato (Higashide et al., 2015) and poplar (Tomimatsu et al., 2019), it did not do so here because the application of CO$_2$ increased the leaf expansion rate (Matsugaki et al., 1998; Mizukami et al., 2011). Leaf tip trimming increased LUE in tomato (Higashide et al., 2017).
Therefore, further study is needed to focus on the optimal leaf area with CO₂ application. Our results suggest that the total DW of ever-bearing strawberries increased because the increased PLA increased cumulative light interception.

**Conclusions**

We confirmed that local CO₂ application can increase the CO₂ concentration within the plant canopy even when the greenhouse is ventilated in summer and autumn. It significantly increased DM production and total yield and marginally increased leaf area. On the other hand, it did not increase the NAR for a long period. These results show that the photosynthetic rate per leaf area did not increase on account of self-shading, but the photosynthetic production of the whole plant increased owing to the increase in the leaf area due to the application of CO₂ and the increase in the cumulative light interception. Therefore, we suggest that the local application of CO₂ can be an effective measure for increasing the production of ever-bearing strawberries in summer and autumn culture. This technique may help growers increase fruit yield of ever-bearing strawberries under summer and autumn protected culture.

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