Leaf Photosynthesis Characteristics of Seven Japanese Strawberry Cultivars Grown in a Greenhouse

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Many strawberry cultivars are developed in Japan each year; however, the characterization of each cultivar, including yield, is insufficient. As they may affect strawberry yield, leaf photosynthesis characteristics were determined for seven Japanese strawberry cultivars (‘Akihime’, ‘Benihoppe’, ‘Ibarakiss’, ‘Oi C berry’, ‘Sachinoka’, ‘Suzuakane’, and ‘Yotsuboshi’) and evaluated with reference to a C₃ photosynthesis model. Plants were grown hydroponically with a substrate-filled elevated-bed system in a glass greenhouse. Leaf gas-exchange rates were assessed at different photosynthetic photon fluxes and CO₂ partial pressures using full-expanded leaves of plants 130–150 days after transplanting (DAT). We found that the net photosynthetic rate (Pn) was higher in ‘Yotsuboshi’ and ‘Sachinoka’ than in other cultivars both under light-limited and light-saturated conditions. The difference in Pn was correlated with stomatal conductance (gs), irrespective of light conditions. We also measured leaf Pn under both CO₂-limited and CO₂-saturated conditions; however, there were only a slight differences in either capacity of ribulose-1,5-bisphosphate carboxylation or regeneration among cultivars. Our results suggest that a difference in gs contributed to variations in leaf Pn among Japanese strawberry cultivars.

Key Words: CO₂ concentration, photosynthesis, photosynthetic photon flux density (PPFD), stomatal conductance, strawberry (Fragaria × ananassa Duch).

Introduction

Strawberry (Fragaria × ananassa Duch.) is one of the most important vegetable plants in Japan and annual strawberry production has accounted for a large amount of domestic fruit production for many years (Ministry of Agriculture Forestry and Fisheries, 2018a). However, total production of strawberry has slowly decreased over the last two decades, declining by 3–4% every year since 2000. In contrast, the amount of strawberry exports have increased, with the amount exported in 2016 being almost five times that in 2010 (Ministry of Agriculture Forestry and Fisheries, 2018b). More recently, strawberry export projects have been addressed by growers nationwide to supply high-quality fruit to meet both domestic and foreign demand. Given this background, to improve the productivity of horticulture including strawberry, the “Large-Scale Greenhouses and Equipment in Japan” initiative was launched (Ministry of Agriculture Forestry and Fisheries, 2014). According to a progress report published in 2018, it was noted that the introduction of these greenhouses and equipment gradually improved productivity in terms of both crop yield and labor efficiency in Japan (Higashide, 2018). For instance, an agricultural company in Miyagi involved in long-term cultivation of tomato achieved a 40% increase in yield and reduced labor time by 20% per season. Sweet pepper growers in Oita also improved not only crop yield, but also labor efficiency. Thus, this project has contributed to enhanced productivity of Japanese growers. However, while the crop productivity of tomato, sweet pepper, and cucumber increased steadily, the yield of strawberry hardly improved. There are several possible reasons, one of which is that it may be difficult to optimize cultivation according to the varietal characteristics of strawberries due to different requirements from traditional cultivation methods. In the above project, some strawberry cultivars were cultivated in larger-scale
greenhouses than had been used previously. Additionally, large-scale greenhouses can optimize the CO₂ and light environment for crops, maintain optimal leaf photosynthesis, and increase productivity. To improve cultivation using such sophisticated greenhouses requires an understanding of the leaf photosynthesis of the target crop. Accordingly, we need to understand the physiological mechanisms and morphological behavior of strawberries, and to clarify the characteristics of the responses to the environment of each cultivar in order to improve strawberry productivity.

Some reports have concluded that it is important to increase the activity of photosynthesis to achieve high-yield strawberry production. Hidaka et al. (2013) reported that the higher strawberry yields achieved with supplemental lighting were associated with not only greater leaf area per plant, but also a higher rate of net photosynthesis (Pn) of their leaves. In their subsequent report (Hidaka et al., 2015), they found a significant difference in the effect of supplemental lighting on yield and dry matter production depending on the strawberry cultivar. They compared the effects of supplemental lighting on the net photosynthetic rate using four different varieties: ‘Sagahonoka’, ‘Ookimi’, ‘Akihime’, and ‘Benihoppe’. The extent of Pn enhancement differed depending on the cultivar, with ‘Akihime’ the highest and ‘Sagahonoka’ the lowest. These observations suggested that leaf photosynthetic capacity differs among cultivars, and that a wide survey of more cultivars is necessary to comprehensively compare cultivar characteristics, especially when new cultivars are developed.

According to a biochemical model of C₃ photosynthesis rates, known as the FvCB model (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982; Sharkey, 1985), Pn is limited either by RuBP carboxylation, which is determined by the capacity of ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) to consume RuBP, including the conductance of CO₂ diffusion from the leaf surface to chloroplasts, or by the capacity of electron transport determined by Calvin cycle enzymes other than Rubisco, and/or Pi regeneration depending on the capacity for sucrose and starch synthesis, to regenerate RuBP (RuBP regeneration) (Matsuda et al., 2013). For instance, Pn is limited by the CO₂ concentration when it is measured under conditions of optimal temperature and saturating photosynthetic photon flux density (PPFD). Consequently, leaf Pn is limited by RuBP carboxylation at the current ambient level or a lower atmospheric CO₂ partial pressure (pCa), whereas it is limited by RuBP regeneration in a range above the current level of pCa (Sudo et al., 2003; Hikosaka et al., 2006; Makino and Sage, 2007; Sage and Kubien, 2007). However, leaf Pn is limited by RuBP regeneration under conditions of insufficient PPFD. This is because low PPFD limits the rates of light harvesting and electron transport (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982; Weber et al., 1987; von Caemmerer, 2000). Many reports have suggested that the balance between the capacities for RuBP carboxylation and regeneration is not generally uniform, even within the same species (Sudo et al., 2003; Onoda et al., 2005; Yamori et al., 2010). In addition, there have been many reports concerning variations in Pn within the same species, including differences in stomatal conductance (gs) (Qu et al., 2017). Taking these reports into consideration, we need to carefully compare Pn and other photosynthetic parameters. However, there have been few comparisons of Pn among strawberry cultivars in Japan. Hidaka et al. (2013) reported differences in leaf Pn among four strawberry cultivars. Unfortunately, no analysis has been carried out focusing on how the balance between capacities for RuBP carboxylation and regeneration affect the difference in Pn. In the case of tomato cultivars, Matsuda et al. (2013) suggested that leaf Pn differed between Dutch and Japanese cultivars. They also reported that there was no difference in the balance between capacities for RuBP carboxylation and regeneration among the cultivars used in their experiment, and that cultivars with high Pn also had higher gs and LMA. Based on these results, it is considered that the cause of the difference in Pn can be clarified not only by analyzing C₃ photosynthesis to investigate the balance between capacities of RuBP carboxylation and regeneration, but also by evaluating the physiological and ecological traits related to stomata and leaves. Therefore, we need to carry out detailed analysis and evaluation of the difference in photosynthetic capacity among strawberry cultivars, for example, leaf Pn measurements at different PPFD and CO₂ partial pressures.

The aim of this study was to evaluate the leaf gas-exchange for modern strawberry cultivars in Japan and provide fundamental knowledge to improve crop productivity. A previous study by Matsuda et al. (2013) conducted a detailed analysis of Pn in modern tomato cultivars. The format of this experiment was applied to strawberries with reference to their study. To determine the difference in Pn and analyze the relationships among Pn and other parameters such as gs, intercellular CO₂ partial pressure (pCi), and leaf mass area (LMA) among seven cultivars, we first measured leaf Pn under light-limiting and light-saturated conditions. Second, we analyzed leaf Pn at different pCi values to evaluate the capacities for RuBP carboxylation/regeneration among cultivars. Finally, we discuss the results of the analysis of the seven cultivars in this experiment.

Materials and Methods

Plant material and growth conditions

Seven strawberry (Fragaria × ananassa Duch.) cultivars that are typically used in commercial production were grown and analyzed in this experiment: ‘Oi Cberry’, ‘Benihoppe’, ‘Sachinoka’, ‘Suzuakane’,
‘Yotsuboshi’, ‘Ibarakiss’, and ‘Akihime’. ‘Suzuakane’ and ‘Yotsuboshi’ are everbearing cultivars. Plants were grown by forcing culture in a Venlo-type greenhouse (162 m²) in Tsukuba, Ibaraki, Japan (141°43'E, 38°56'N) from the end of September 2018. We transplanted 5–7 plants of each cultivar. At the end of September, young plants were transplanted to substrate-filled beds (75 cm long, 30 cm wide, and 20 cm high) with approximately 3 L of substrate per plant. The beds were filled with coconut coir substrate (BVB Substrates, Co., Ltd., Maasland, the Netherlands). These plants were spaced 18 cm apart with 90 cm between rows. They were supplied with Otsuka A nutrient solution (OAT Agrio Co., Ltd., Tokyo, Japan); electrical conductivity of the nutrient solution was adjusted to 0.7 dS·m⁻¹ from transplanting to the end of cultivation, and pH ranged within 6.0–7.0. The solution consisted of 4.3–8.6 mM NO₃⁻, 2.0–4.0 mM K⁺, 1.9–3.8 mM Ca²⁺, 0.7–1.4 mM Mg²⁺, 1.2–2.4 mM H₂PO₄⁻, 0.6–1.2 mg·L⁻¹ Fe, 0.35–0.70 mg·L⁻¹ Mn, 0.006–0.012 mg·L⁻¹ Cu, and 0.006–0.012 mg·L⁻¹ Mo. Flower pollination was performed by bees. Fruit thinning was not conducted. Mature fruit were harvested once or twice a week from all cultivars. Daily means of air temperature inside the greenhouse and outside solar radiation throughout the experiment were within the ranges of 13.0–21.3°C and 0.3–6.9 MJ·m⁻²·d⁻¹, respectively. Ducted warm air was provided at floor level when the inside air temperature was lower than 8°C. Roof and greenhouse side windows were opened for natural ventilation when the inside air temperature exceeded 25°C. Supplemental lighting was not used, and the CO₂ concentration inside the greenhouse was not regulated.

Gas-exchange measurements and leaf sampling
Leaf Pn, gs, and pCi were measured on mature leaves (fifth or sixth leaf from the youngest leaf of the crown) inside the greenhouse from 8–31 March 2019. Measurements were made on 1–3 leaves per day; the leaves used for gas exchange measurements were randomly selected from well-grown plants in the bed. We measured steady-state rates of photosynthesis under four conditions consisting of different light conditions and

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Fig. 1. Schematic diagrams of processes limiting C₃ photosynthesis. Under conditions of limiting light (a) and saturated-light (b), CO₂ assimilation changes depending on light intensity and is limited by both stomatal conductance (gs) and internal CO₂ partial pressures (pCi). Under conditions of saturating light, CO₂ assimilation is limited by the capacity of RuBP carboxylation at low pCi (c) and the capacity of RuBP regeneration at high pCi (d). The dotted line in the figure shows the steps that limit the overall reaction. The line thickness in the figure shows the relative capacity of each reaction. The thicker line indicates that the step is sufficient.
pCi around the target leaf. Details of the conditions of this experiment are shown in Figure 1 as follows: (a) low-light condition, PPFD of 500 μmol m⁻² s⁻¹ at pCa of 40 Pa; (b) high-light condition, PPFD of 1800 μmol m⁻² s⁻¹ at pCa of 40 Pa; (c) low-CO₂ condition, saturating PPFD of 1800 μmol m⁻² s⁻¹ with limiting CO₂ partial pressure at a pCi of 20 Pa; and (d) high-CO₂ condition, saturating PPFD of 1800 μmol m⁻² s⁻¹ with a saturating CO₂ partial pressure at a pCi of 70 Pa. We evaluated the effect of light condition on Pn through (a) and (b) including the influence of the stomatal opening and pCi (Fig. 1a, b). In addition, examination of (c) indicated the capacity for RuBP carboxylation, and (d) reflected the performance in terms of RuBP regeneration (Makino et al., 1994; Matsuda et al., 2008; Kanno et al., 2017), removing the effect of the extent of stomatal opening (Fig. 1c, d). The leaf temperature was set at 25°C and a leaf-to-air vapor pressure deficit of 1.1–1.3 kPa using a portable gas-exchange measurement system (LI-6800; Li-Cor Inc., Lincoln, NE, USA) for all measurements. The pCi was controlled by manipulating pCa inside the leaf chamber for each measurement. Light was provided from red (peak wavelength: 660 nm) and blue (453 nm) light-emitting diodes (6800-02; Li-Cor).

After completing leaf gas-exchange measurements, the leaf blade used for the gas-exchange measurements was sampled and its leaf area measured using a leaf area meter (Li-3100C; Li-Cor). Thereafter, the leaves were dried in an oven at 80°C for at least 72 h, after which they were weighed to obtain their dry mass. The LMA was calculated using the leaf area and dry weight data.

**Statistical analysis**

All experimental data were used for analysis of variance by standard procedures using R (R Development Core Team, 2013). The correlation matrixes for Pn, gs, pCi, and LMA for low and high light conditions were generated with R using Pearson’s correlation as the statistical metric.

**Results**

The leaf Pn, gs, and pCi under the light-limited condition with an ambient CO₂ concentration of 40 Pa pCa are shown in Table 1. The Pn differed among the cultivars (Table 1). It was lowest for ‘Akihime’ and ‘Ibarakiss’ and was relatively high for ‘Sachinoka’ and ‘Yotsuboshi’. The same trend was observed in gs, being lowest for ‘Akihime’ and ‘Ibarakiss’ and highest for ‘Yotsuboshi’. The differences in pCi between cultivars were not significant. Therefore, these results suggest that there were varietal differences in Pn in strawberry leaves under the light-limiting condition.

Table 2 shows the Pn, gs, and pCi under the light-saturated condition with an ambient CO₂ concentration of 40 Pa pCa. The Pn was lower for ‘Akihime’, ‘Ibarakiss’, and ‘Suzuakane’, and was highest for ‘Yotsuboshi’ among all cultivars. There were significant differences in gs, being highest for ‘Yotsuboshi’.

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**Table 1.** Rate of net photosynthesis (Pn), stomatal conductance (gs), and intercellular CO₂ partial pressure (pCi) in leaves of seven strawberry cultivars analyzed under PPFD = 500 μmol m⁻² s⁻¹ and pCa = 40 Pa.

| Cultivar    | Pn (μmol CO₂·m⁻²·s⁻¹) | gs (mol H₂O·m⁻²·s⁻¹) | pCi (Pa) |
|-------------|------------------------|-----------------------|----------|
| ‘Akihime’   | 15.9±0.6 b             | 0.209±0.006 c         | 26.0±0.2 a|
| ‘Benihoppe’ | 17.3±0.3 ab            | 0.227±0.009 bc        | 25.9±0.3 a|
| ‘Ibarakiss’ | 16.1±0.1 b             | 0.207±0.003 c         | 25.6±0.3 a|
| ‘Oi C berry’| 17.5±0.7 ab            | 0.247±0.029 abc       | 26.5±1.0 a|
| ‘Sachinoka’ | 18.8±0.4 a             | 0.281±0.001 ab        | 26.1±1.4 a|
| ‘Suzuakane’ | 16.5±0.6 ab            | 0.227±0.011 bc        | 26.6±0.8 a|
| ‘Yotsuboshi’| 18.9±0.5 a             | 0.301±0.016 a         | 28.0±0.4 a|

Means±standard errors (n = 3). Different small letters represent significant differences by LSD among cultivars in each column (P<0.05).

**Table 2.** Rate of net photosynthesis (Pn), stomatal conductance (gs), and intercellular CO₂ partial pressure (pCi) in leaves of seven strawberry cultivars analyzed under PPFD = 1800 μmol m⁻² s⁻¹ and pCa = 40 Pa.

| Cultivar    | Pn (μmol CO₂·m⁻²·s⁻¹) | gs (mol H₂O·m⁻²·s⁻¹) | pCi (Pa) |
|-------------|------------------------|-----------------------|----------|
| ‘Akihime’   | 20.4±0.5 c             | 0.244±0.007 b         | 24.8±0.3 ab|
| ‘Benihoppe’ | 22.0±0.7 abc           | 0.259±0.014 b         | 24.1±0.4 ab|
| ‘Ibarakiss’ | 20.3±0.3 c             | 0.241±0.011 b         | 24.6±0.8 ab|
| ‘Oi C berry’| 22.7±1.3 abc           | 0.259±0.023 b         | 23.6±0.4 b |
| ‘Sachinoka’ | 24.6±0.7 ab            | 0.296±0.009 ab        | 24.1±0.5 ab|
| ‘Suzuakane’ | 21.4±0.8 bc            | 0.242±0.012 b         | 23.8±0.2 b |
| ‘Yotsuboshi’| 25.4±0.3 a             | 0.345±0.005 a         | 26.0±0.1 a |

Means±standard errors (n = 3). Different small letters represent significant differences by LSD among cultivars in each column (P<0.05).
the case of ‘Yotsuboshi’, the gs level was also highest. Thus, there were varietal differences in Pn among the cultivars irrespective of light conditions, and the overall trends for Pn and gs were similar regardless of light intensity under ambient CO2 conditions.

Table 3 indicates Pn under both CO2-limiting (20 Pa pCi) and CO2-saturating (70 Pa pCi) conditions. It has been reported that Pn at 20 Pa pCi reflects the capacity of RuBP carboxylation, and that Pn at 70 Pa pCi shows the level of RuBP regeneration. The Pn at 20 Pa pCi was significantly lower for ‘Akihime’ than ‘Sachinoka’ and ‘Yotsuboshi’; and Pn at 70 Pa pCi, and was significantly lower for ‘Akihime’ and ‘Ibarakiss’ than ‘Sachinoka’ and ‘Yotsuboshi’. However, there was no significant difference in the ratio of Pn at 20 Pa pCi to that at 70 Pa pCi among cultivars. Considering these results, the balance between the capacity for RuBP carboxylation and regeneration did not significantly differ among cultivars. We also found no significant difference in LMA among cultivars (Table 3).

We then assessed the relationships among Pn, gs, pCi, and LMA using Pearson’s correlations under light-limited and light-saturated conditions for all seven cultivars (Table 4). There was a positive correlation between Pn and gs regardless of light conditions (P < 0.01). Additionally, there was also a significant negative correlation between Pn and LMA, but this was weak under both light conditions. These results suggested that gs was closely associated with leaf Pn among the tested strawberry cultivars.

Pn and gs were positively correlated under both low and high light conditions (Fig. 2), suggesting that an increase in Pn was accompanied by an increase in gs in all cultivars.

**Discussion**

The mean Pn was highest for ‘Yotsuboshi’ and ‘Sachinoka’ under both low and high light conditions, but was lowest for ‘Akihime’ and ‘Ibarakiss’ among the seven cultivars (Tables 1 and 2). We also compared the balance between the capacities for RuBP carboxylation and regeneration; however, there were no significant differences in the ratio of Pn at 70 Pa pCi to that at 20 Pa pCi among cultivars. Considering these results, the balance between the capacity for RuBP carboxylation and regeneration did not significantly differ among cultivars. We also found no significant difference in LMA among cultivars (Table 3).

**Table 3.** Rate of net photosynthesis (Pn) in leaves of seven strawberry cultivars analyzed under PPFD = 1800 μmol·m−2·s−1 and pCi = 20 or 70 Pa, and the ratio of Pn at pCi = 70 Pa to that at pCi = 20 Pa.

| Cultivar       | Pn (μmol CO2·m−2·s−1) | Ratio (70 Pa/20 Pa) | LMA (m2·g−1) |
|----------------|-----------------------|---------------------|--------------|
|                | pCi = 20 Pa           | pCi = 70 Pa         |              |
| ‘Akihime’      | 15.9 ± 1.1 c          | 36.4 ± 1.9 c        | 2.44 ± 0.07 ab | 76.0 ± 0.5 a |
| ‘Benihoppe’    | 16.9 ± 0.5 abc        | 39.7 ± 0.8 abc      | 2.35 ± 0.06 ab | 73.0 ± 2.1 a |
| ‘Ibarakiss’    | 15.7 ± 0.4 bc         | 35.5 ± 0.4 bc       | 2.26 ± 0.04 ab | 82.2 ± 2.8 a |
| ‘Oi C berry’   | 18.5 ± 0.8 ac         | 42.3 ± 1.2 abc      | 2.29 ± 0.04 ab | 70.1 ± 2.7 a |
| ‘Sachinoka’    | 19.6 ± 0.7 a          | 42.5 ± 2.5 ab       | 2.17 ± 0.06 a  | 66.7 ± 5.7 a |
| ‘Suzuakane’    | 16.8 ± 0.5 abc        | 42.1 ± 1.3 abc      | 2.50 ± 0.02 b  | 74.6 ± 2.1 a |
| ‘Yotsuboshi’   | 19.6 ± 0.4 a          | 44.0 ± 1.0 a        | 2.25 ± 0.10 ab | 71.7 ± 3.2 a |

Means ± standard errors (n = 3). Different small letters represent significant differences by LSD among cultivars in each column (P < 0.05).

**Table 4.** Pearson correlations between the rate of net photosynthesis (Pn), stomatal conductance (gs), intercellular CO2 partial pressure (pCi), and leaf mass area (LMA) for all cultivars used in this study.

| Variables | PPFD = 1800 μmol·m−2·s−1 | PPFD = 500 μmol·m−2·s−1 |
|-----------|--------------------------|--------------------------|
|           | 1                        | 2                        | 3                        | 4                        |
| Pn        | —                        | —                        | —                        | —                        |
| gs        | 0.89 **                  | —                        | —                        | —                        |
| pCi       | 0.27                     | 0.66                     | —                        | —                        |
| LMA       | −0.36 **                 | −0.33 **                 | −0.12                    | —                        |

Pearson correlations were calculated based on the data in Tables 1 and 2. Photosynthesis measurement was performed at PPFD = 500 or 1800 μmol·m−2·s−1 and pCa = 40 Pa. *, ** mean P < 0.05 and P < 0.01, respectively.
differences in the ratio of $P_n$ at $p_{Ci} = 70\, \text{Pa}$ to that at $p_{Ci} = 20\, \text{Pa}$ (Table 3). These results suggest that there was no difference in the balance between the capacity of RuBP carboxylation and regeneration among cultivars. On the other hand, our results showed that higher $P_n$ was associated with a higher $g_s$ for all seven cultivars (Fig. 2), meaning that increased $g_s$ resulted in lower limitations on $P_n$, that is, $g_s$ plays an important role in determining $P_n$ under both light-limited and light-saturated conditions. Therefore, our results suggest that the natural variation in leaf $P_n$ in strawberry leaves is associated with the difference in $g_s$ among cultivars.

Choi et al. (2016) pointed out that $P_n$ was well correlated with $g_s$ and chlorophyll fluorescence parameters, which were both positively related to strawberry yield. They investigated $P_n$ and photosynthesis-related parameters, including fruit yield, for plants grown under different light and temperature combinations during winter. Their correlation analysis showed that an increase in $P_n$ was accompanied by an increase in $g_s$. The same phenomenon was reported by Keutgen et al. (1998), who investigated $P_n$ in the leaflets of two different strawberry cultivars, ‘Elsanta’ and ‘Korona’, and evaluated $P_n$ and photosynthesis-related parameters under equal light and $\text{CO}_2$ conditions (PPFD; 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $p_{Ca}$; 36 Pa). They reported that $g_s$ differed between the two investigated cultivars; regardless of the cultivar differences, there was a tendency for a positive correlation between $P_n$ and $g_s$. These results are consistent with the relationship between $P_n$ and $g_s$ that we found in this experiment indicating that correlation between $P_n$ and $g_s$ was significant and leaf $P_n$ was limited by the extent of $g_s$. Thus, the phenomenon of $P_n$ and $g_s$ being positively correlated seems to be common among strawberry cultivars, including Japanese cultivars.

However, the mechanisms responsible for the difference in $g_s$ during the steady state among strawberry cultivars remain unclear. The control mechanism of stomata reaction is complicated. Adjustments in stomatal aperture are affected by not only internal, but also external leaf conditions, including light conditions, the water potential of the leaf itself, and the photosynthetic status of guard cells. Recently, hormonal signals were also found to contribute to stomatal action (Flexas et al., 2008; Lawson and Vialet-Chabrand, 2019). Our data suggest that light intensity affects $g_s$, with increased irradiance contributing to enhanced $g_s$ under ambient $\text{CO}_2$ conditions. Unfortunately, the other factors related to stomatal action in strawberry leaves are still unknown, and this will require intensive investigation of not only $P_n$, but also photosynthesis-related parameters that may limit the rate of leaf photosynthesis, including $g_s$. Additionally, the data produced in this experiment represent differences among cultivars with this in mind. In our experiments, we evaluated only the steady state of $P_n$ and related parameters under different light and internal $\text{CO}_2$ conditions by using 130–150 DAT plants. We selected and measured fully expanded mature leaves at similar growth stages. In the present study, we assumed that all strawberry cultivars must have been growing steadily because they continued to produce fruit from early winter and maintained vegetative growth. Taking into consideration the plant conditions, our results provide limited information.

$g_s$ is determined by the rate of passage of $\text{CO}_2$ entering, or water vapor leaving through the stomata, of a leaf, and so it also plays an important role in the efficient use of water (Wang et al., 2014). It has been sug-
gested that photosynthetic rates were associated with gs when other photosynthesis steps were not limited (Wong et al., 1979). Additionally, Fischer et al. (1998) found a positive correlation between gs and yield in different wheat (Triticum aestivum) cultivars. Based on the above observations, some successful examples of efficiency improvement of dry matter production using differences in the photosynthetic trait of gs have been reported. Qu et al. (2017) found that variations of Pn in rice were strongly associated with gs, even if plants were grown under different environmental conditions. They cultivated 204 accessions of U.S. Department of Agriculture a collected minicore rice (Oryza sativa) diversity panel in Beijing and Shanghai and investigated the photosynthetic traits related to biomass production. Their results showed good correlations between Pn in a single leaf and gs, even under light-limited conditions. They concluded that gs could be a good indicator for use in rice breeding, especially for Pn under low light conditions, because improvement in Pn under low light conditions may help to increase overall canopy photosynthesis. In fact, at the International Maize and Wheat Improvement Center (CIMMYT), wheat breeding projects have already been done based on physiological differences in gs (Rajaram et al., 1994). This means that there is substantial natural variation in gs among cultivars of some plant species and potential to improve plant productivity by making good use of these differences.

Previous experiments have suggested that gs in leaves shows genetic diversity, and utilizing this will be effective for improving crop yields by enhancing Pn in leaves. However, research on the relationship between gs and dry matter production in strawberry has not been strongly pursued, and we may be missing opportunities to improve productivity. There are already over 300 strawberry cultivars in Japan, and many cultivars are developed each year. There were 21 new cultivars registered on the Japan plant variety registration system database in 2017 and 11 in 2018 (Ministry of Agriculture, Forestry and Fisheries). Unfortunately, few of these have been quantitatively analyzed for dry matter production (Mochizuki et al., 2013; Kanno et al., 2019). To break the yield barrier in Japanese strawberries, we need to identify traits related to photosynthetic capacity and characterize changes in biomass production and yield in response to the environment. It is important to breed not only high yielding, but also good quality, varieties, so improved Pn capacity could contribute to establishing new varieties. We also need to investigate the relationship between dry matter production and Pn capacity, including other photosynthesis-related traits, in order to break the yield barrier in strawberry production.

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