Whole-plant and Single-leaf Photosynthesis of Strawberry under Various Environmental Conditions

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Photosynthesis is a crucial process for the existence, development, and productivity of crops. Appropriate measurements should be met to evaluate and control the photosynthesis quality accurately. In this study, we presented advantages and compared the results from two measurement methods used on strawberry plants, namely, the single-leaf method (SL), and the whole-plant method (WP). The leaf age of 12-15 days, optimal in the area and photosynthetic potential, were suitable to measure a representative leaf by the single-leaf method. The WP showed the complete patterns and trends of whole-plant photosynthesis under different environmental conditions while this was a restriction in the SL. However, the light response curve patterns showed no differences regardless of measurement methods. The photosynthetic values between the two methods were only significant differences under low CO2 and PPFD. The limitations of SL were mainly from the manners and measurement conditions, which led to significant differences with the WP. In conclusion, we believe that the whole-plant method may be the most suitable, nonetheless, the single-leaf method is still high valid if there are appropriate manners.

Keywords : diurnal photosynthesis, environmental factors, leaf age, light response curve, open-chamber method, plant factory

INTRODUCTION

Photosynthesis is a crucial process for the existence, development, and productivity of crops, which directly impacts the world food security (Amthor, 2000; Simkin, 2019). Hence, the photosynthesis of plants has been meticulously studied. One of the concerned research directions is to build plant growth models based on the photosynthesis process (Fourcaud et al., 2008; Wu et al., 2019; Amitrano et al., 2020). Therefore, to build accurate models, the photosynthetic measurement methods should be suitable and engender the most accurate results possible.

Currently, two popular photosynthesis measurement methods are available which are, namely, the single-leaf measurement method and the whole-plant measurement method (for short, single-leaf, and whole-plant method, respectively). The application of the whole-plant method will overcome deviations in photosynthesis of plants introduced by differences in canopy structure, leaf ages, mutual shading, and leaf orientation (Lanoue et al., 2017; Nomura et al., 2020). The single-leaf method may not overcome those deviations without applying a proper practice. On the contrary, the advantage of the single-leaf method is its convenience and ease of measurement, and it can be flexibly moved in the measurement site. Therefore, in this study, we compare measurements of the whole-plant and single-leaf method on strawberry plants (Fragaria × ananassa Duch.) grown under plant factory conditions to provide an overview of measurement methods for this plant species. The strawberry is a small herbaceous species with high economic values and convenient for the cultivation and measurement of photosynthesis.

MATERIALS AND METHODS

Plant materials

'Sachinoka' variety of strawberry (Fragaria × ananassa Duch.) was used as materials. The plants were grown on a vertical-shelf system using the circulation hydroponics method in a plant factory with artificial light (PFAL) at the University of the Ryukyus, Okinawa, Japan (26°15′N, 127°45′E).

Cultivation conditions

The environmental conditions in the PFAL were established as a CO2 concentration of 1,000 μmol mol-1, PPFD of 150 μmol m-2 s-1, photoperiod of 10 hours day-1, a temperature of 23°C, and humidity 70±10%. The light source was white light-emitting diode (LED) (LED FL40 AX-120AD, 19W, Ryukyu Kougaku Kenkyu Unit, Japan). The nutrient solution was modified Hoagland and Arnon solution (1950), and renewed every seven days. Nutrient solution composition (macronutrients in mM, micronutrients in μM): 12 N-NO3, 2 P, 10 K, 4 Ca, 2 Mg, 46 B, 15 Mn, 2 Zn, 5 Cu, 0.5 Mo and 100 Fe-FeEDTA with an EC of 2.1 mS cm-1, and pH of 6.0–6.2.

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The strawberries were used for two investigations, namely, (1) evaluating leaf area, SPAD values, and the maximum photosynthetic potential \( \text{A}_{\text{max}} \) at different leaf ages, (2) measuring whole-plant diurnal photosynthesis, light response curves and single leaf photosynthesis.

Under this cultivation conditions, after the 12 day of age, leaves expressed small superficial necrotic lesions. However, the individuals still exhibited normal growth appearance. The necrotic lesions strongly reduced on the leaves when growing under higher PPFD (from 250 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) upward, data not shown).

**Data collection**

The leaf age was determined in terms of days (1, 3, 6, 9, 12, 15, 18, and 21 days) after the three leaflets of each trifoliate leaf (hereafter called leaf) were fully opened. Leaf areas were calculated using the formula \( \text{area} = \frac{1}{2} \cdot \text{length} \cdot \text{width} \) (Fig. 1). The leaf area was the sum of the three leaflet areas, and SPAD values measured by a SPAD meter (SPAD-502, Minolta, Japan) were the mean values of the three leaflet values.

**Gas exchange measurement**

The photosynthesis of strawberries was measured using the single-leaf method and whole-plant methods. In the single-leaf method, the leaflets were measured using a portable photosynthesis system (Li-6400; Li-COR, Lincoln, Nebraska, USA). In the whole-plant method (Wp method), an open-chamber measurement system described in Fig. 2.1 was applied. The system consists of two assimilation chambers (A and B) made of transparent acryl resin (ø 30 cm, H 14.5 cm, thickness 3 mm, Fig. 2.2A), which were set up in the same conditions to measured simultaneously. The assimilation chambers were placed in a container chamber; the temperature of the container chamber was controlled at 23°C by a radiator connected to a constant water temperature circulator (MTC-1500, As One, Japan). Firstly, an air compressor pumped atmospheric air passed through a low-range pressure regulator (PR) and then through a mass flow controller to a pipe column (ø 10 cm, length 100 cm) of Soda-lime (No. 2, Wako Co., Ltd., Japan) to remove CO2. This air (zero CO2) passed through a dew point control system connected to a constant water temperature circulator (CTW802, Komatsu-Yamato, Japan). The airflow was then mixed with 10% CO2 (N2 balance) in an air mixing box to make 400, 1,000, 1,200, 1,500, 1,800, 1,100, 1,500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), CO2 concentration of 1,500 \( \mu \text{mol mol}^{-1} \), and PPFD of 2,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Data were recorded after 5 minutes when the photosynthesis was stable.

Whole-plant diurnal photosynthesis measurement conditions: using the whole-plant method, relative humidity of 85±5%, airflow rate of 14 L min\(^{-1}\); photoperiod of 12 hours (6:00–18:00 light on, 18:00–6:00 light off), PPFD (chamber temperature day/night time of 23/23°C), and 1,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) with 1,000 \( \mu \text{mol mol}^{-1} \) (chamber temperature day/night time of 27/23°C). The high temperature of the chamber in the day time (27°C) was the result of high PPFD established (1,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)).

**Gas exchange measurement**

The CO2 concentration in the reference airflow, inlet, and outlet airflow of the assimilation chamber A and B were monitored by an IRGA (LI-840A, Shimadzu, Japan) and three solenoid valves. Signals from IRGA and thermal sensors were converted by analog to digital converter (DA100, Yokogawa) and linked to the computer by a LAN system. The system automatically recorded data with an interval of 3 minutes 20 seconds for each assimilation chamber. The light source was a 600W LED system (model PFQ-600DT, NK System Ltd., Japan). The maximum PPFD of this system was 1,500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The whole plant of strawberries with seven leaves were placed into the assimilation chamber as Fig. 2.2B to conduct the measurement.

\[ \text{A}_{\text{max}} \] measurement conditions: applying the single-leaf method, chamber temperature of 23°C, vapor pressure deficit (VPD) value of 1.2±0.2 kPa, and airflow rate of 400 \( \mu \text{mol s}^{-1} \), CO2 concentration of 1,500 \( \mu \text{mol mol}^{-1} \), and PPFD of 2,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Data were recorded after 5 minutes when the photosynthesis was stable.

Whole-plant diurnal photosynthesis measurement conditions: using the whole-plant method, relative humidity of 85±5%, airflow rate of 14 L min\(^{-1}\); photoperiod of 12 hours (6:00–18:00 light on, 18:00–6:00 light off), PPFD (chamber temperature day/night time of 23/23°C), and 1,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) with 1,000 \( \mu \text{mol mol}^{-1} \) (chamber temperature day/night time of 27/23°C). The high temperature of the chamber in the day time (27°C) was the result of high PPFD established (1,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)).

Whole-plant light response curves measurement conditions: using the whole-plant method, chamber temperature of 23°C, relative humidity of 80±10%; airflow rate of 14 L min\(^{-1}\); PPFD of 200, 400, 600, 800, 1,000, 1,200, 1,500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Each PPFD level was changed after 30 minutes; data were manually recorded after 30 minutes respectively. The measurement was fulfilled under three CO2 levels of 400, 1,000, and 1,500 \( \mu \text{mol mol}^{-1} \).

**Gas exchange measurement**

Single-leaf photosynthesis measurement conditions: using the single-leaf method, chamber temperature of 23°C, VPD value of 1.2±2 kPa, and airflow rate of 400 \( \mu \text{mol s}^{-1} \). The CO2 and PPFD conditions were same as in whole-plant diurnal photosynthesis measurement conditions. This measurement was used to compare with the photosynthesis values obtained from the whole-plant values. The single-leaf photosynthesis was measured in two manners, specifically, (1) measuring all the leaves, then calculating the mean value (averaged single-leaf method, ASL method), and (2) measuring only the 4th leaf (the 4th full-open leaf from the top of the plant, L4 method). The same plants used in the whole-plant diurnal photosynthesis measurements were used for this measurement to make the comp-
The water use efficiency (WUE) was calculated following the formula reported by Dinh et al. (2017): for the single-leaf method: \( \text{WUE} = \frac{\text{Photosynthetic rate (A)}}{\text{transpiration rate (E)}} \); for the whole-plant method \( \text{WUE} = \frac{\text{CO}_2 \text{exchange rate (CER)}}{\text{transpiration rate (E)}} \).

Statistical analyses

All data were prepared using Microsoft Excel 2016 software and statistically analyzed using STAGRAPHIC software. The mean values were compared using the least significant difference (LSD) test with a significance level of \( P < 0.01 \), or \( P < 0.05 \).

RESULTS

Photosynthetic potential for single leaves at different ages

We found that the strawberry leaf area rapidly and continuously increased from the leaf opening point on day 1 to day 9 (Fig. 3A). The increasing rate gradually decreased from 19.1 to 12.6 \( \text{cm}^2 \text{leaf}^{-1} \text{day}^{-1} \) for the first nine days and reduced to 0.8 \( \text{cm}^2 \text{leaf}^{-1} \text{day}^{-1} \) until day 12. From day 12, the leaf area remained constant; the mean leaf area (included three leaflets) at the steady stage reached 208.2 \( \text{cm}^2 \text{leaf}^{-1} \).

In growing leaves, after the leaf opening point, SPAD values continuously and simultaneously increased with the
The increase of leaf area (Fig. 3B). However, a rapid rise only occurred in the first nine days with an increasing rate of 1.2–2.3 leaf⁻¹ day⁻¹. Afterward, the increment was slowed down from 0.7 to 0.3 leaf⁻¹ day⁻¹ and tended to stabilize until the 21st day. The mean SPAD values of leaves from day 12 to day 21 were around 48.4.

The stability of leaf area and SPAD values are one of the criteria to evaluate leaf maturity in terms of its structure and function. However, a determination of leaf photosynthetic potential using specific ages can provide more accurate clues for the complete leaf function.

Figure 3C shows the variation in maximum photosynthetic potential (Amax) of strawberry leaves at different ages (ranged with a six-day interval for each measurement time). Amax values (25.4 μmol m⁻² s⁻¹) increased from leaves at three days of age and peaked (29.7 μmol m⁻² s⁻¹) at day 15, then sharply decreased (24.3 μmol m⁻² s⁻¹) at day 21.

The stomatal conductance (gs) and transpiration rate (E) indicated the same trend as in Amax (Fig. 3D, E). However, both gs and E values were not different in leaves between 9 and 15 days of age.

Water use efficiency (WUE) of leaves tended to be stable in magnitude between different leaf ages despite a slight increase in leaves of 21 days of age (Fig. 3F).

From these results, for strawberry plants grown under plant factory conditions, we recommend that the leaves at 12–15 days of age (equivalent to the 4th full-open leaf from the top of the plant) are the best options to measure photosynthesis in case of only one leaf measurement.

Diurnal changes in CO₂ exchange rate (CER), E, gs, and WUE of the whole plant

Under the low condition of CO₂ and PPFD (400 μmol mol⁻¹ and 200 μmol m⁻² s⁻¹, respectively), the whole plant CER remained stable at 5.0 μmol m⁻² s⁻¹ during the photoperiod (Fig. 4A). Whereas, under elevated CO₂ and PPFD conditions (1,000 μmol mol⁻¹ and 1,000 μmol m⁻² s⁻¹, respectively), the whole plant CER increased approximately 18.5% (equivalent to a 5.4-fold increase) compared with that under low CO₂ and PPFD conditions. On the other hand, under high CO₂ and PPFD conditions, the whole plant CER slightly decreased during the photoperiod. Specifically, the whole plant CER increased rapidly and reached a maximum (27.4 μmol m⁻² s⁻¹) about an hour after the light was on, then slightly decreased (from 27.4 to 25.4 μmol m⁻² s⁻¹) in the next hours until the light was off again. Regardless of CO₂ and PPFD conditions, the whole plant CER pattern was the same as in the dark period; suggesting that the differences in CO₂ and PPFD in this study did not affect the respiration pattern in our model plant.

The whole-plant transpiration rates were significantly higher (approximately 40%) in photoperiod and the dark period when CO₂ and PPFD increased to 1,000 μmol mol⁻¹ and 1,000 μmol m⁻² s⁻¹, respectively (Fig. 4B). A higher-level transpiration rate during the nighttime suggested that elevated CO₂ and PPFD conditions control the respiration intensity of the plants.

Figure 4C shows the same diurnal pattern and magnitude of the whole-plant gs regardless of CO₂ and PPFD conditions. Interestingly, during the dark period, the stomata of the strawberry plants were not completely closed. Therefore, both E and gs values were nonzero (Fig. 4B, C).

Elevated CO₂ and PPFD conditions were factors driv-
ing the increase in WUE of the whole-plant diurnal photosynthesis (Fig. 4D). WUE increased by approximately 61% compared with that under low CO2 and PPFD. In this measurement, the stomata activity did not play a dominant role in E and CER values of the whole plant (Fig. 4C).

The results of the whole-plant methods show an overview of the trends and the magnitude of CER, E, gs, and WUE of the whole-plant diurnal pattern, which is difficult to observe using the single-leaf method.

Whole-plant light response curve patterns

The whole-plant light response curve proportionally increased with CO2 and PPFD (Fig. 5A). One important result was that the fully-functioning of CO2 concentration only occurred apparently when PPFDs were at high levels. Specifically, under a PPFD of 200 μmol m⁻² s⁻¹, the photosynthesis rate slightly differed at three levels of CO2. When the PPFD increased from 400 to 600 μmol m⁻² s⁻¹, the photosynthesis rate was divided into two distinctive groups (i.e., high and low). The high group was under 1,000–1,500 μmol mol⁻¹ of CO2, and the low group was under 400 μmol mol⁻¹ of CO2. Finally, when the PPFD was at a higher level (from 800 to 1,500 μmol m⁻² s⁻¹), the photosynthetic rate difference between three levels of CO2 became apparent.

Our results confirm the dependence of CO2 concentration on PPFD in controlling the trend and magnitude of the photosynthesis rate. Moreover, these results may also be a basis to assess the CO2 use efficiency in a plant factory operation.
In contrast with the photosynthetic rate, the transpiration rate (Fig. 5B) between CO2 levels had no difference and tended to slightly increase when PPFD increases. The whole-plant stomata activities widely varied under low PPFD under three CO2 levels (Fig. 5C). However, when the PPFD was close to the highest PPFD (1,500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)), the gs did not differ between the CO2 levels.

WUE of the whole plant proportionally increased with the rise of PPFD (Fig. 5D). Interestingly, under high PPFD, A and WUE distinctly increased (Fig. 5A, E) across CO2 levels, while the E and gs (Fig. 5B, C) were not different. These results proved the role of high CO2 concentration in the water use efficiency to fasten the photosynthetic rate.

In Fig. 5, the A, E, gs, and WUE of the single leaves were added (identified by the black arrows) to compare trends of these parameters between the whole plant and single-leaf measurement methods. All parameters indicated the same trend except for gs. An evaluation of the magnitude of these parameters is presented in Table 1.

| Treatment code | CO2 of 400 \( \mu \text{mol mol}^{-1} \) PPFD of 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) | CO2 of 1,000 \( \mu \text{mol mol}^{-1} \) PPFD of 1,000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) |
|----------------|---------------------------------|---------------------------------|
| ASL            | A: 7.5 \( a \), 215 b, 2.4 a    | A: 26.1                          |
|                | g: 8.1 a, 280 ab, 2.9 a          | g: 28.5                         |
|                | E: 3.5 b                         | E: 421                          |
|                | WUE: 3.0 b                       | WUE: 4.4 a                      |
| L4             | 5.0 b                            | 6.2 a                           |
|                | 347 a                            | 26.4                            |
|                | 1.0 b                            | 351                             |
|                |                                 | 1.7 b                           |
|                |                                 | 15.9 a                          |

ANOVA: ** * NS ** ** NS

Values within a column followed by the same letter are not significant different by LSD test.

** or * denote the significant different at \( P < 0.01 \), \( P < 0.05 \) or non-significant.

**DISCUSSION**

*Photosynthetic potential for single leaves at different ages*

The photosynthetic capacity of leaves noticeably depended on their growth features (Fig. 3). However, the selection of suitable leaves to measure photosynthesis has not been consistent in previous studies (Paul and Pellny, 2003; Hidaka et al., 2013; Choi and Kang, 2019). We supposed that the photosynthesis measured from a single leaf at a particular age to represent the whole plant should be carefully considered to its accuracy because different-aged leaves can photosynthesize and contribute differently to the total capacity of the whole plant (Fig. 3, Table 1). The single-leaf method remains undeniably valid when the whole-plant method is impossible to fulfill. Therefore, the number of leaves as well as their age or position and the measurement conditions needs to be considered when measuring a plant using the single-leaf method. On the other hand, the photosynthesis capacity of leaves can also be the cornerstone for reverse predictions of the physiological state and development of leaves (Fig. 3).

*Diurnal changes in CER, E, gs, and WUE of the whole plant*

CO2 and PPFD were determinants of the equilibrium or a slight decrease in the photosynthesis rate (Fig. 4A). The photosynthetic reduction might be due to an imbalance in the synthesis and translocation of photoassimilates. Specifically, under elevated CO2 and PPFD, the synthetic rate of photoassimilates was faster than their translocation rate. Consequently, it caused feedback inhibitions, which led to a photosynthetic rate decrease (Upmeyer and Koller, 1973; Paul and Pellny, 2003; Figueroa et al., 2016). On the contrary, under low CO2 and PPFD, the balance between the two processes were maintained, resulting in a constant rate of photosynthesis throughout the photoperiod (Fig. 4A). We recommend that the time-period to measure photosynthesis of strawberries under plant factory conditions should not be fixed during the photoperiod because the light intensity is always kept steady at a low level (typically below 300 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) in a plant factory. In case the PPFD reaches 1,500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), a slight change of photosynthetic rate may not lead to a large error in the photosynthetic capacity of leaves.

The increase of A, E, and WUE (Fig. 4A, B, D) shows that these trends were typical responses of plants under elevated CO2 and PPFD. Similar results were observed in previous studies (Chandra et al., 2008; Baligar et al., 2012).

During the dark periods, gs values were nonzero (Fig. 4C), and the dark transpiration rates were approximately 40% higher in the plants measured under elevated CO2 and PPFD (Fig. 4B). These results can be explained by three factors. Firstly, the stomata are not completely closed at night due to the need for the plant respiration (Caird et al., 2007). Secondly, plants grown under elevated CO2...
increase their respiration (Wang et al., 2001), and leaf transpiration linearly correlates with the respiratory process (Stoyanova, 1996). Finally, the leaf transpiration drives the mineral absorption, responding to the growth during nighttime (Tanner and Beaver, 2001).

**Whole-plant light response curve patterns**

The light response pattern of A, E, and WUE did not differ when the whole-plant and single-leaf light response curve were compared (Fig. 5). Mochizuki et al. (2019) also reported similar patterns when using the single-leaf method.

The gs patterns of the whole-plant and single-leaf measurements were dissimilar (Fig. 5C). This difference is because, in our Wp measurement system, high power LEDs caused a rise of temperature (from 23 to 27°C) in the assimilation chambers when the PPFD was in the range of 1000–1500 μmol m−2 s−1. Consequently, the relative humidity in the chambers was reduced leading the VPD to increase from ~4 kPa to ~10 kPa (data not shown). Therefore, the response of the plants to the increase of VPD was that the gs decreased (Merilo et al., 2017).

**Comparison between whole-plant and single-leaf photosynthesis measurement methods**

The A and E from the two measurement methods only differed under low CO2 and PPFD (Table 1). The A and E reductions of the whole plant may emerge from (1) mutual shading and (2) different leaf age. The effect of mutual shading on plants is reducing the PPFD received by the leaves at the lower position within a plant canopy. As a result, the low PPFD directly reduces photosynthetic rate (A) of lower leaves. Kitano et al. (2007) and Chandra et al. (2008) reported that the changes in leaf transpiration rate were PPFD-dependent and were coordinated with the changes of photosynthetic rate. Whereas, in the single-leaf method, a small leaf area was measured with adequate light intensity provided; hence the mutual shading effect was removed. Consequently, the A and E values of ASL and L4 were significantly higher than that of Wp.

In contrast, under 1000 μmol mol−1 CO2 combined with a PPFD of 1000 μmol m−2 s−1, the interleaf mutual shading may be noticeably reduced. Moreover, elevated CO2 can enhance the leaves reaching close to the Amax values. Therefore, the variation in A caused by PPFD and leaf ages may also be reduced. As a result, the difference in photosynthetic rate values of the two methods becomes negligible (Table 1).

The Wp may be the most suitable measure, however, if there are appropriate manners, the single-leaf method is still valid. Based on the results presented in Figs. 3A, 5A, and Table 1, we believe that the ASL method can be used instead of the Wp under high CO2 and PPFD conditions. Also, measuring only the 4th leaf (L4 method) to represent the whole plant seems to be acceptable. Otherwise, under low PPFD (regardless of CO2 concentrations), the ASL and L4 methods still need to be further considered to achieve better results in terms of accuracy.

**REFERENCES**

Amiratano, C., Chirico, G. B., De Pascale, S., Roupahel, Y., De Micco, V. 2020. Crop management in controlled environment agriculture (CEA) systems using predictive mathematical models. Sensors 20 : 3110.

Amthor, J. S. 2000. The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. Ann. Bot. 86 : 1–20.

Baligar, V. C., Bunce, J. A., Elson, M. K., Fageria, N. K. 2012. Photosynthetic photon flux density, carbon dioxide concentration and temperature influence photosynthesis in crotalaria species. Open Plant Sci. J. 6 : 1–7.

Caird, M. A., Richards, J. H., Donovan, L. A. 2007. Nighttime stomatal conductance and transpiration in C3 and C4 plants. Plant Physiol. 143 : 4–10.

Chandra, S., Lata, H., Khan, I. A., Elshoby, M. A. 2008. Photosynthetic response of Cannabis sativa L. to variations in photosynthetic photon flux densities, temperature and CO2 conditions. Physiol. Mol. Biol. Plants. 14 : 299–306.

Choi, H. G., Kang, N. J. 2019. Effect of light and carbon dioxide on photosynthesis, chlorophyll fluorescence, and fruit yield in strawberry (Fragaria ×ananassa Duch.) plants. J. Berry Res. 9 : 51–61.

Dinh, T. H., Watanabe, K., Takaragawa, H., Nakabaru, M., Kawanami, Y. 2017. Photosynthetic response and nitrogen use efficiency of sugarcane under drought stress conditions with different nitrogen application levels. Plant Prod. Sci. 20 : 412–422.

Figueroa, M. C., Pattoni, C. V., Tripsidi, K. E. J., Podestà, F. E., Iglesias, A. S. 2016. Role of phosphorus in photosynthetic carbon assimilation and partitioning. In “Handbook of Photosynthesis” (ed. by Pessarakli, M.). CRC Press, Boca Raton, p 603–607.

Fourseau, T., Zhang, X., Stokes, A., Lambers, H., Köhner, C. 2008. Plant growth modelling and applications: the increasing importance of plant architecture in growth models. Ann. Bot. 101 : 1053–1063.

Huldak, K., Dan, K., Imamura, H., Miyoshi, Y., Takayama, T., Sameishima, K., Kitano, M., Okumura, M. 2013. Effect of supplemental lighting from different light sources on growth and yield of strawberry. Environ. Control Biol. 51 : 41–47.

Hoagland, D. R., Arnon, D. I. 1950. The water-culture method for growing plants without soil. Calif. Agric. Exp. Stn. Cir. 347 : 30–32.

Kitano, M., Yasutake, D., Araki, T. 2007. Measurement of transpiration streams in plants. Environ. Control Biol. 45 : 223–239.

Lanoose, J., Leonardos, E. D., Ma, X., Grodzinski, B. 2017. The effect of spectral quality on daily patterns of gas exchange, biomass gain, and water-use-efficiency in tomatoes and lisianthus: an assessment of whole plant measurements. Front. Plant Sci. 8 : 1076.

Merilo, E., Yarmolinsky, D., Jalakas, P., Patik, H., Tulva, I., Rasulov, B., Kilk, K., Kollist, H. 2017. Stomatal VPD response: there is more to the story than ABA. Plant Physiol. 176 : 851–864.

Mochizuki, Y., Sekiguchi, S., Horiiuchi, N., Aung, T., Ogiwara, I. 2019. Photosynthetic characteristics of individual strawberry (Fragaria ×ananassa Duch.) leaves under short-distance lighting with blue, green, and red LED lights. HortScience 54 : 452–458.

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.
Paul, M. J., Pellny, T. K. 2003. Carbon metabolite feedback regulation of leaf photosynthesis and development. J. Exp. Bot. 54: 539–547.

Simkin, A. J. 2019. Genetic engineering for global food security: photosynthesis and biofortification. Plants (Basel) 8: 586.

Stoyanova, J. 1996. Relationship between transpiration and respiration in plants during the dark period. Biol. Plant 38: 77.

Tanner, W., Beevers, H. 2001. Transpiration, a prerequisite for long-distance transport of minerals in plants? Proc. Natl. Acad. Sci. USA 98: 9443–9447.

Upmeyer, D. J., Koller, H. R. 1973. Diurnal trends in net photosynthetic rate and carbohydrate levels of soybean leaves. Plant Physiol. 51: 871–874.

Wang, X., Lewis, J. D., Tissue, D. T., Seemann, J. R., Griffin, K. L. 2001. Effects of elevated atmospheric CO$_2$ concentration on leaf dark respiration of Xanthium strumarium in light and in darkness. Proc. Natl. Acad. Sci. USA 98: 2479–2484.

Wu, A., Hammer, G. L., Doherty, A., Caemmerer, S. V., Farquhar, G. D. 2019. Quantifying impacts of enhancing photosynthesis on crop yield. Nat. Plants 5: 380–388.