Modeling and Prediction of Dry Matter Production by Tomato Plants in Year-round Production Based on Short-term, Low-truss Crop Management

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We investigated dry matter (DM) and fruit production of tomato plants, the effects of CO₂ levels on DM production, and light-use efficiency (LUE) in a tomato production system based on short-term, low-truss crop management during six consecutive periods over one year in a commercial greenhouse. The CO₂ concentration, total dry matter production (TDM), and LUE differed significantly among the periods. Since LUE was significantly correlated with the mean daytime CO₂ concentration, we modeled LUE empirically from that. We developed a model to predict LUE and DM production of tomato plants and validated the model using data from the six periods. We accurately predicted LUE and TDM within a range of ca. 400 to 650 µmol·mol⁻¹ daytime CO₂ concentration. However, when daytime CO₂ concentration was beyond this range, or when a management failure such as inadequate irrigation occurred, predicted values differed significantly from observed values.

Key Words: CO₂ concentration, empirical model, light-use efficiency, validation, yield.

Introduction

Although tomatoes are produced in long-term, multi-truss production systems around the world, some Japanese growers in commercial greenhouses produce tomatoes year-round using a short-term, low-truss crop management system. In short-term production, tomato plants are typically pinched above the 1st to 3rd truss and are then grown at high density, with renewal using transplants three or four times a year in the same greenhouse (Araki et al., 2009; Johkan et al., 2014; Ohkubo et al., 2019). Long-term production needs a tall greenhouse, a high wiring system, and special trolleys, but short-term production does not. Growers who adopt short-term cultivation can reduce their workload by scheduling and combining the cultivation of different tomato crops. In short-term production, tomatoes with a high Brix value are often produced by imposing water or salinity stress, which is acceptable because the growers do not need to maintain the plants for the long term (Araki et al., 2009; Johkan et al., 2014).

Light-use efficiency (LUE) indicates the dry matter (DM) production per unit of intercepted photosynthetically active radiation (PAR), and determines the crop yield together with several other factors. LUE of tomato plants differed among cultivars (Higashide and Heuvelink, 2009; Higashide et al., 2012). Previous research investigated the effects of planting stage and plant density (Kaneko et al., 2015), and of the number of leaves (Ohkubo et al., 2019), on yield and LUE in short-term production. Although the yields differed among planting stages, plant densities, and numbers of leaves, LUE did not. The authors concluded that the differences in yield and DM production were determined mainly by differences in light interception by the plants.

To improve the yield of greenhouse crops such as tomatoes, cucumbers, and sweet peppers, growers use elevated carbon dioxide (CO₂) concentrations in many greenhouses in Japan (Takahashi et al., 2012; Yasuba et al., 2011). Several reports showed that the CO₂ level affected the LUE level (de Koning, 1997; Higashide et al., 2015; Nederhoff, 1994). These reports implied that LUE could be predicted from the CO₂ level. Since greenhouse temperature is controlled by ventilation, it
can be difficult to maintain high CO$_2$ levels, which vary between seasons in response to changes in the amount of ventilation required. Thus, in short-term production, the CO$_2$ level and LUE differ depending on the cultivated season. It is more important for growers using short-term production to arrange a planting and selling schedule than those involved in long-term production. If we can predict LUE from the CO$_2$ level, DM production could also be calculated. Eventually, this will enable growers to evaluate yield during cultivation or predict the effect of CO$_2$ elevation on yield. These predictions will aid in the management of short-term production.

In this study, we investigated DM and fruit production by tomato plants in short-term, low-truss production in a commercial greenhouse. We also investigated the effects of the CO$_2$ level on LUE and DM production, and developed a model for the relationship among these factors. Using the model, we predicted (postdicted; prediction after the experiment) both LUE and DM production by the tomato plants and validated these in experiments conducted during six consecutive, but partially overlapping, periods of the year.

**Materials and Methods**

Plants, experimental conditions, and sampling

We investigated the effects of intercepted PAR and the CO$_2$ level on DM production and LUE in year-round short-term production, with the tomato plants pinched above the 3rd inflorescence. We conducted experiments during consecutive, but partially overlapping periods, over one year in a commercial greenhouse (1730 m$^2$) in Miyagi Prefecture, Japan. The transplanting, pinching, and harvest dates and the environmental conditions during each experiment are shown in Table 1.

In all experiments, tomato seeds (Solanum lycopersicum L. ‘Momotaro York’; Takii & Co., Ltd., Kyoto, Japan) were sown in seed trays filled with nursery soil and germinated in the dark at 30°C. Two days later, the trays were placed in a seedling growth chamber (Nae Terrace; Mitsubishi Chemical Agri Dream Co., Ltd., Tokyo, Japan), where they were illuminated with fluorescent lamps under a 16-h day length and were exposed to air temperatures of 23°C (daytime) and 17°C (nighttime). The plants were grown at 1000 μmol·mol$^{-1}$ CO$_2$. Seedlings were fertilized every day with a commercial nutrient solution (HighTempo; Sumitomo Chemical, Tokyo, Japan) consisting of 10.7 mM NO$_3^-$, 6.3 mM K$^+$, 5.4 mM Ca$^{2+}$, 1.9 mM Mg$^{2+}$, 2.4 mM H$_2$PO$_4^-$, 3.8 mg·L$^{-1}$ Fe, 0.38 mg·L$^{-1}$ Mn, 0.26 mg·L$^{-1}$ B, 0.15 mg·L$^{-1}$ Zn, 0.05 mg·L$^{-1}$ Cu, and 0.07 mg·L$^{-1}$ Mo, and adjusted to an electrical conductivity of 1.8 dS·m$^{-1}$. After three weeks, the seedlings were transplanted into 9-cm-diameter plastic pots (2 per pot) filled with commercial soil (IkubyouBaido; Takii). The pots were then placed in the greenhouse for one to two weeks and grown under supplemental lighting (where necessary) to provide the same photoperiod. Seedlings were then transplanted into coconut fiber slabs (Coco Bag; Toyotane Co., Ltd., Toyohashi, Japan) in 10 double rows that covered 580 m$^2$ in each experiment. Each row was 28 m long, with a spacing of 1.6 m between rows and 25 cm between pots within a row. We transplanted 224 seedlings per double row (for a total of 2240 plants per experiment), and the plant density was 5.0·m$^{-2}$.

The plants were supplied with a mixture of TF Noushuku tomato S (Toyotane; 241.9 mM NO$_3^-$, 616.9 mM K$^+$, 71.8 mM Mg$^{2+}$, 140.0 mM H$_2$PO$_4^-$, 500 mg·L$^{-1}$ Fe, 200 mg·L$^{-1}$ Mn, 200 mg·L$^{-1}$ B, 18 mg·L$^{-1}$ Zn, 6 mg·L$^{-1}$ Cu, and 6 mg·L$^{-1}$ Mo) and TF Mix B (Toyotane; 387.1 mM NO$_3^-$, 52.9 mM K$^+$, 420.5 mM Ca$^{2+}$, and 157.1 mM Mg$^{2+}$). The mixture was diluted with water and then adjusted to an electrical conductivity of 0.6 to 2.0 dS·m$^{-1}$ as the plants grew. The rate of nutrient solution supply was based on the rate of drainage. The daily rate of drainage was maintained at 20% of the total quantity of nutrient solution supplied, and the drainage solution was not reused in any experiment. We did not impose water stress to increase the Brix value of fruits. Irrigation appears to have been inadequate and deficient at the beginning of experiment Ex1 because of the grower’s lack of familiarity with the proposed irrigation system.

**Table 1.** Dates of transplanting, pinching, sampling, and the end of the experiment (days after transplanting in parentheses), and the associated environmental conditions: daily average air temperature and cumulative photosynthetically active radiation (PAR) inside the greenhouse.

| Experiment | Transplanting; (sample 1) | Pinching; (sample 2) | Sample 3 | End | Daily air temperature (°C) | Cumulative PAR (MJ·m$^{-2}$·d$^{-1}$) |
|------------|--------------------------|---------------------|----------|-----|---------------------------|--------------------------------------|
| Ex1        | 16 Apr. 2014             | 5 June 2014         | (50)     | 11 July 2014               | (86)          | 15 July 2014               | (90)                                 |
|            |                          |                     |          |                              | 22.8 b        | 570.1                    |
| Ex2        | 16 July 2014             | 19 Aug. 2014        | (34)     | 8 Oct. 2014                 | (84)          | 11 Oct. 2014               | (87)                                 |
|            |                          |                     |          |                              | 24.6 a        | 380.6                    |
| Ex3        | 12 Aug. 2014             | 24 Sept. 2014       | (43)     | 29 Nov. 2014                | (109)         | 30 Nov. 2014               | (110)                                 |
|            |                          |                     |          |                              | 21.4 c        | 440.3                    |
| Ex4        | 2 Sept. 2014             | 22 Oct. 2014        | (50)     | 7 Jan. 2015                 | (127)         | 14 Jan. 2015               | (134)                                 |
|            |                          |                     |          |                              | 19.5 d        | 457.3                    |
| Ex5        | 15 Oct. 2014             | 25 Nov. 2014        | (41)     | 3 Mar. 2015                 | (139)         | 4 Mar. 2015                | (140)                                 |
|            |                          |                     |          |                              | 17.6 e        | 389.6                    |
| Ex6        | 1 Dec. 2014              | 27 Jan. 2015        | (57)     | 16 Apr. 2015                | (136)         | 20 Apr. 2015               | (140)                                 |
|            |                          |                     |          |                              | 17.5 e        | 438.5                    |

$^z$ Values within a column followed by the same letter are not significantly different (P<0.05; Steel–Dwass test; n=90, 87, 110, 128, 140, and 140 in experiments 1 to 6, respectively).
All plants were pinched at two leaves above the 3rd inflorescence. Old leaves were not pruned. The number of fruits per truss was not adjusted by pruning. Flowers were pollinated by bumblebees (Bombus ignitus Smith). The greenhouse environmental system was set to begin ventilation at > 28°C and heating at < 13°C. CO₂ levels were set at 1000 μmol·mol⁻¹ when the ventilation windows were closed and were allowed to decrease to 400 μmol·mol⁻¹ when they were open. Air temperature, CO₂ concentration, and solar radiation inside the greenhouse were measured at 1-min intervals by an automatic monitoring device (Shisetsu-engei SaaS; Fujitsu Limited, Kawasaki, Japan). Table 1 summarizes the 24-time of transplanting, pinching, and the end of the experiment. LAI was obtained as the sum of leaf, stem, and fruit DWs at the end of the experiment. The sampled LAI was obtained on 20 May 2015 using the method of Higashide et al. (2012). LAI on each date was obtained by interpolation between the values determined by destructive sampling on the previous and current sampling dates.

Modeling of DM production and LUE
PAR was assumed to equal 50% of the global radiation (Ohtani, 1997). The daily PAR intercepted by the plants (IL₀, MJ·m⁻²·d⁻¹) was calculated from the leaf area index (LAI; m²·m⁻²) and daily cumulative PAR inside the greenhouse (PARₑ, MJ·m⁻²·d⁻¹) on each date and the light-extinction coefficient (k) as:

$$IL₀ = (1 - e^{-k·LAI})·PAR$$

The light-extinction coefficient (k = 0.90) was obtained on 20 May 2015 using the method of Higashide et al. (2012). LAI on each date was obtained by interpolation between the values determined by destructive sampling on the previous and current sampling dates.

$$LUE₀ = \frac{g·MJ·PAR}{g·MJ·PAR}$$

was obtained as the slope of the linear regression of TDM (g·m⁻²) as a function of the cumulative plant-intercepted PAR (IL₀; MJ·m⁻²) using the method of Higashide and Heuvelink (2009). IL₀ at pinching and the end of the experiment were obtained by summing ILₑ: TDM was then expressed as:

$$TDM = LUE₀ × ILₑ$$

where LUE₀ is the observed LUE.

Since the CO₂-photosynthetic curve appeared to be a saturation curve, we assumed that the relationship between CO₂ and LUE also showed a saturation curve. We performed logarithmic regression of the relationship between LUE and the daytime CO₂ concentration across all experiments. The predicted LUE (LUEₚ) was based on the daytime (08:00 to 16:00) mean CO₂ concentration (C) in each experiment:

$$LUEₚ = a·\lnC + b$$

where a and b are regression coefficients. To validate this regression model, the regression was based on the independent datasets (cross-validation) defined in Table 2 as:

$$LUEₚₑₙ = aₑₙ·\lnCₑₙ + bₑₙ$$

where LUEₚₑₙ is LUEₚ, Cₑₙ is the daytime mean CO₂ concentration, and aₑₙ and bₑₙ are the regression coefficients for Experiment n.

Prediction and validation of DM production
To validate the model, we predicted (post-dicted; prediction after the experiment) LUE and DM production in each experiment on the pinching date and at the end of the experiment. LUEₚₑₙ on these dates was obtained using Eq. 4 with Cₑₙ for both the period until pinching and for the whole experimental period. We compared LUEₑₙ with the observed LUE (LUEₑₛₙ) in each experiment. ILₑ on each day was based on Eq. 1. We then predicted daily DM production (DMₚ, g·m⁻²·d⁻¹) using Eq. 5 with LUEₑₙ and ILₑ:

$$DMₚ = LUEₑₙ × ILₑ$$

Predicted TDM (TDMₚ, g·m⁻²) was obtained as the
cumulative \( DM_p \) in each experiment. For validation in each experiment, we obtained \( TDM_p \) on the pinching date and at the end of the experiment and compared the values with the observed \( TDM \) (\( TDM_o \)).

All statistical analyses were performed using EZR software (Saitama Medical Center, Jichi Medical University, Saitama, Japan, http://www.jichi.ac.jp/saitama-set/SaitamaHP.files/manual.html; Kanda, 2013), which is a graphical user interface for R software (R Foundation for Statistical Computing, Vienna, Austria). EZR is a modified version of R commander (https://www.rcommander.com/) that adds statistical functions frequently used in biostatistics. Data were tested for normality using the Kolmogorov–Smirnov test and for heterogeneity of variance using Bartlett’s test. When the data were not normally distributed and the variances were heterogeneous, data were analyzed by one-way ANOVA followed by the Tukey–Kramer test. When the data were not normally distributed or the variances were heterogeneous, data were analyzed by the Kruskal–Wallis test. For validation, we tested for a significant difference between the observed and predicted \( TDM \) in each experiment using the Student’s \( t \)-test. When the variances of the data were not homogeneous, we analyzed the data using Welch’s \( t \)-test; when the variances were not homogeneous, we analyzed the data using Wilcoxon’s rank-sum test. For \( LUE \), we identified significant differences using 95% confidence intervals.

**Results**

Table 3 shows the \( LAI \) and cumulative plant-intercepted \( PAR \) on the pinching date and at the end of the experiment, as well as the fruit FW and the \( TDM \). \( LAI \) values on the pinching date and at the end of the experiment were significantly higher in Ex4 than in the other experiments, except on the pinching date in Ex2 and Ex6, and at the end of the experiment in Ex2 and Ex5. Because of irrigation failure at the start of Ex1, \( LAI \) on the pinching date was significantly lower than that in the other experiments. \( LAI \) at the end of the experiment was also significantly lower in Ex6 than in the other experiments. The cumulative plant-intercepted \( PAR \) was significantly higher at the end of Ex4 than in the other experiments. Total fruit FW differed significantly among the experiments. Fruit FW was significantly higher in Ex6 than in Ex1 to Ex3, whereas Ex2 produced a significantly lower fruit FW than in the other experiments. There was no significant difference in fruit FW in Ex4 Ex 5 or Ex6, or among Ex1, Ex3, Ex4, and Ex5. \( TDM \) differed significantly among the experiments. \( TDM \) was significantly higher in Ex6 than in the other experiments, whereas Ex1 and Ex2 had sig-

| Experiment | Dataset for the regression | \( R^2 \) | \( P \) | \( n \) | \( a_{\text{Ex}} \) | \( b_{\text{Ex}} \) |
|------------|---------------------------|-----------|--------|-------|----------------|----------------|
| Ex1        | Ex2–Ex6                   | 0.78      | <0.001 | 46    | 1.34           | −6.02          |
| Ex2        | Ex1, Ex3–Ex6              | 0.85      | <0.001 | 58    | 2.06           | −10.66         |
| Ex3        | Ex1–Ex2, Ex4–Ex6          | 0.69      | <0.001 | 58    | 1.52           | −7.23          |
| Ex4        | Ex1–Ex3, Ex5–Ex6          | 0.71      | <0.001 | 62    | 1.56           | −7.48          |
| Ex5        | Ex1–Ex4, Ex6              | 0.55      | <0.001 | 62    | 1.29           | −5.82          |
| Ex6        | Ex1–Ex5                   | 0.59      | <0.001 | 64    | 1.35           | −6.21          |

\( LUE_{\text{dpi}} = a_{\text{dpi}} \ln(C_{\text{dpi}}) + b_{\text{dpi}} \), where \( C_{\text{dpi}} \) represents the average daytime CO\textsubscript{2} concentration and \( En \) represents the experiment number in Ex1–Ex6. \( a_{\text{dpi}} \) and \( b_{\text{dpi}} \), regression coefficients based on the independent dataset in each experiment.

| Experiment | \( LAI \) (m\(^2\)·m\(^−2\)) | Cumulative intercepted \( PAR \) (MJ·m\(^−2\)) | Total fruit FW\(^\ast\) (kg·m\(^−2\)) | \( TDM \) (g·m\(^−2\)) |
|------------|-------------------------------|-----------------------------------------------|--------------------------------------|------------------------|
| Pinching   | End                           | Pinching End                                  |                                      |                        |
| Ex1        | 1.51 \( d^\prime \)          | 2.34 \( c \)                                 | 204.9 \( a \)                        | 326.2 \( b \)          | 8.7 \( b \)          | 626.2 \( d \)       |
| Ex2        | 2.44 \( abc \)               | 3.04 \( ab \)                                | 78.8 \( de \)                       | 292.3 \( c \)          | 5.4 \( c \)          | 576.9 \( d \)       |
| Ex3        | 2.48 \( b \)                | 2.51 \( bcd \)                               | 133.3 \( c \)                       | 344.4 \( a \)          | 8.4 \( b \)          | 709.5 \( c \)       |
| Ex4        | 3.52 \( a \)               | 3.48 \( a \)                                | 170.7 \( b \)                       | 381.0 \( a \)          | 9.3 \( ab \)         | 847.1 \( b \)       |
| Ex5        | 2.00 \( e \)             | 2.91 \( abc \)                              | 82.2 \( e \)                        | 297.1 \( c \)          | 9.0 \( ab \)         | 822.7 \( b \)       |
| Ex6        | 2.71 \( abc \)           | 1.72 \( d \)                                | 95.5 \( d \)                        | 334.8 \( b \)          | 11.0 \( a \)         | 931.5 \( a \)       |

\( \ast \) Including both marketable and unmarketable fruits.

\( \ast \) Values within a column followed by the same letter are not significantly different (\( P < 0.05 \)) by Kruskal–Wallis test followed by Steel–Dwass test (italics), or by ANOVA followed by Tukey–Kramer test (roman type). For \( LAI \) and intercepted \( PAR \) on the pinching date, \( n = 24, 12, 8, 12, 12, \) and 8 in experiments Ex1 to Ex6, respectively; for \( LAI \) and intercepted \( PAR \) at the end of the experiment and for \( TDM \), \( n = 24, 12, 8, 8, 6, 8, 10, 8, 6, 5, 5, \) and 5, respectively; for fruit FW, \( n = 5 \).
Light-use efficiency (LUE) differed significantly among the experiments (Fig. 1). LUE was significantly positively correlated with the average daytime CO₂ concentration ($R^2 = 0.69$, $P < 0.001$). This relationship followed a natural logarithmic function.

Table 4 shows the $LUE_{pE}$ values for the period until pinching and for the whole experimental period, and the 95% confidence interval for $LUE_o$. Only $LUE_{pE}$ for the whole period fell within the 95% confidential interval for $LUE_o$. $LUE_{pE4}$, $LUE_{pE5}$, and $LUE_{pE6}$ for the whole period were close to the confidence intervals for $LUE_o$ in Ex4, Ex5, and Ex6. However, $LUE_{pE1}$ and $LUE_{pE2}$ for the whole period differed greatly from $LUE_o$.

Figure 2 shows the mean daytime CO₂ concentrations in each experiment. The mean daytime CO₂ concentration during the whole period in each experiment was at almost the same level or higher than that before pinching, except in Ex1 (Fig. 2A, B). The mean CO₂ concentrations in Ex5 and Ex6 both before pinching and for the whole period were significantly higher than those in the other experiments. The CO₂ concentration in Ex2 was significantly lower than that in the other experiments. $TDM_o$ and $TDM_p$ did not differ significantly in Ex4, Ex5, and Ex6 on the pinching date (Fig. 2C), or between Ex3 and Ex4 at the end of the experiment (Fig. 2D). $TDM_p$ was significantly lower than $TDM_o$ on the pinching date in Ex2 and Ex3, and at the end of the experiment in Ex2, Ex5, and Ex6 (Fig. 2C, D). $TDM_p$ in Ex1 was significantly higher than $TDM_o$ at both time points.

**Discussion**

Elevation of CO₂ concentration has been shown to improve the yield of greenhouse crops such as tomatoes, cucumbers, and sweet peppers (de Gelder et al., 2005; Fierro et al., 1994; Heuvelink et al., 2008; Hicklenton and Jolliffe, 1978; Tripp et al., 1991). Several studies reported a relationship between CO₂ concentration and LUE that agree with the present results. de Koning (1997) used crop models to show that LUE was increased by elevated CO₂. Nederhoff (1994) reported that elevated CO₂ increased LUE by 15% per 100 μmol·mol⁻¹ increase in concentration. Higashide et al. (2015) reported that with elevated CO₂ in a greenhouse with humidity controlled by a fogging system, LUE was ca. 1.5 times the LUE in an ambient CO₂ greenhouse non-controlled for humidity. Our results support these reports: CO₂ and TDM differed significantly among the experiments, and LUE increased significantly (from 1.77 g MJ⁻¹ PAR at 364 μmol·mol⁻¹ to 2.75 g MJ⁻¹ PAR at 692 μmol·mol⁻¹) with increasing CO₂ (Fig. 1).

We modeled LUE on the basis of the mean daytime CO₂ concentration and DM production (Eq. 1 to 4), and predicted LUE and TDM (Table 4). There was no significant difference between $TDM_o$ and $TDM_p$ on the pinching date in Ex4, Ex5, and Ex6 (Fig. 2C) or at the end of the experiment in Ex3 and Ex4 (Fig. 2D). However, $TDM_o$ differed significantly from $TDM_p$ on the pinching date in Ex1 to Ex3 (Fig. 2C) and at the end of the experiment in Ex1, Ex2, Ex5, and Ex6 (Fig. 2D). When the 25%-to-75% interval for the average daytime

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**Table 4.** Predicted $LUE_p$ in experiment $n$ ($LUE_{pE}$) for the period before pinching and for the whole experimental period, and the corresponding 95% confidential intervals for the observed $LUE (LUE_o)$ for the whole experimental period.

| Experiment | $LUE_{pE}$ for | 95% confidence interval for $LUE_o$ for the whole period |
|------------|----------------|---------------------------------------------------------|
|            | Before pinching | Whole period                                            |
| Ex1        | 2.23           | 2.14                                                    | 1.72–1.83 |
| Ex2        | 1.40           | 1.50                                                    | 1.92–2.07 |
| Ex3        | 1.67           | 2.08                                                    | 2.03–2.12 |
| Ex4        | 1.94           | 2.31                                                    | 2.09–2.24 |
| Ex5        | 2.34           | 2.51                                                    | 2.66–2.85 |
| Ex6        | 2.48           | 2.62                                                    | 2.64–2.82 |

$LUE_{pE}$ was obtained using Eq. 4 ($LUE_{pE} = a_{E} \cdot \ln(C_{E}) + b_{E}$) with $C_{E}$ representing the mean daytime CO₂ concentration for the period before pinching and for the whole experimental period, and $a_{E}$ and $b_{E}$ as regression coefficients based on the independent dataset in each experiment.
CO₂ concentration ranged from about 400 µmol·mol⁻¹ to 650 µmol·mol⁻¹, which represented the conditions in Ex4, Ex5, and Ex6 on the pinching date and during Ex3 and Ex4 at the end of the experiment (Fig. 2A, B), we successfully predicted TDM (Fig. 2C, D). In contrast, at daytime CO₂ concentrations outside this range, which represent the conditions during Ex2 and Ex3 on the pinching date and during Ex2, Ex5, and Ex6 at the end of the experiment (Fig. 2A, B), we did not successfully predict TDM (Fig. 2C, D). We obtained Eq. 4 from the regression for CO₂ concentrations ranging from 364 to 692 µmol·mol⁻¹ CO₂ (Fig. 1). Eq. 4 then predicted LUE, and therefore was inaccurate beyond the range of CO₂ that we studied and near the lower and higher limits of that range. To improve prediction accuracy, it will be necessary to repeat the regression for Eq. 4 using a wider range of CO₂ values.

Owing to the irrigation problem at the beginning of Ex1, plant growth may have been restricted. In Ex1, although the CO₂ concentration at both pinching and the end of the experiment ranged from about 400 µmol·mol⁻¹ to 650 µmol·mol⁻¹, TDM, was significantly lower than TDMp (Table 3). De Pascale et al. (2015) reported that salinity reduced not only LAI, but also LUE. Although cause was not salinity, but rather an irrigation problem in Ex1, incorrect irrigation may have induced plant growth restriction and resulted in reductions in LAI and LUE. It may be difficult to predict LUE and DM production using our model if crops are not managed consistently, as in the case of this irrigation failure.

The LUE of ‘Momotaro York’ has been reported in several studies. In short-term, low-truss tomato production, LUE of plants pinched at two leaves above the third truss was 1.93 g·MJ⁻¹PAR (Kaneko et al., 2015); in contrast, that of plants pinched at two leaves above the first truss was 2.69 g·MJ⁻¹PAR (Ohkubo et al., 2019). Although these authors did not report CO₂ concentrations in their studies, their LUE values were within our range. In contrast, in long-term, multi-truss production, Higashide et al. (2015) reported that LUE values at ca. 500 and 950 µmol·mol⁻¹ CO₂ were 2.85 and 4.16 g·MJ⁻¹PAR, respectively, considerably higher than ours. When plants are pinched at a low truss, the period after pinching accounts for a larger proportion of the whole crop period than in multi-truss cultivation. Since the number of leaves and fruits did not increase after pinching, the sink strength did not increase either. Although the leaves and fruits increased in size, these sizes, especially fruit size, were limited (Matsuda et al., 2011); therefore, the sink strength (fruits per plant) may decrease after pinching. LUE and then DM production may also decrease relative to non-pinched cultivation because of this reduction in sink strength per plant.

Matsuda et al. (2011) reported that ‘Momotaro York’ appeared to have a lower sink strength than that of a Dutch cultivar, and that this may limit fruit production under high CO₂ conditions. Accordingly, choosing a cultivar with a high fruit sink strength like this Dutch cultivar increased the sink capacity at high CO₂. At high CO₂, an increase in plant or stem density (Heuvelink et al., 2008) also increased the sink capaci-
ty. Since a low-truss production system terminates the cultivation after a much shorter period than in high-truss production, it is possible to choose cultivars, as well as the plant density. This could improve the sink capacity, depending on the CO\(_2\) concentration.

Vanthoor et al. (2011) reported that growth inhibition of tomato plants began at a 24-h average temperature higher than around 23°C. The high number of days with a temperature above this threshold in Ex1, Ex2, and Ex3 induced the growth inhibition and reduced DM production and LUE. Additionally, Sato et al. (2000) reported that stress from high temperatures reduced the percentage of fruit set because pollen release and pollen viability both decreased. Adams et al. (2001) reported that plants grown at 26°C showed a lower growth rate, a reduced number of fruit set per truss, fruit size, and TDM. Although these reports did not mention LUE, the reduction in the number of fruits due to high temperatures may lead to a decrease in sink capacity and then in LUE.

We conclude that LUE was significantly correlated with the mean daytime CO\(_2\) concentration. We modeled LUE on the basis of this concentration and used the model to predict LUE and TDM in short-term tomato production for one year. At ca. 400 to 650 mol mol\(^{-1}\) mean daytime CO\(_2\), we were able to predict LUE and TDM with high accuracy. However, the predicted values differed significantly from the observed values when the mean daytime CO\(_2\) was beyond this range or when a management failure such as the irrigation failure in Ex1 happened during the cultivation period.

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