



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

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can be difficult to maintain high CO₂ levels, which vary between seasons in response to changes in the amount of ventilation required. Thus, in short-term production, the CO₂ 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 CO₂ level, DM production could also be calculated. Eventually, this will enable growers to evaluate yield during cultivation or predict the effect of CO₂ 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 CO₂ 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 CO₂ 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 m²) 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 CO₂. Seedlings were fertilized every day with a commercial nutrient solution (HighTempo; Sumitomo Chemical, Tokyo, Japan) consisting of 10.7 mM NO₃⁻, 6.3 mM K⁺, 5.4 mM Ca²⁺, 1.9 mM Mg²⁺, 2.4 mM H₂PO₄⁻, 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 (IkubyoBaido; 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 m² 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 NO₃⁻, 616.9 mM K⁺, 71.8 mM Mg²⁺, 140.0 mM H₂PO₄⁻, 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 NO₃⁻, 52.9 mM K⁺, 420.5 mM Ca²⁺, and 157.1 mM Mg²⁺). 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) ^z	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 $> 28^{\circ}\text{C}$ and heating at $< 13^{\circ}\text{C}$. CO_2 levels were set at $1000 \mu\text{mol}\cdot\text{mol}^{-1}$ when the ventilation windows were closed and were allowed to decrease to $400 \mu\text{mol}\cdot\text{mol}^{-1}$ when they were open. Air temperature, CO_2 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-h mean air temperature and the cumulative PAR inside the greenhouse during each experiment. The air temperature differed significantly among the experiments, being significantly lower during the experiments that began in September or later. Cumulative PAR throughout the experiments was highest in Ex1 and lowest in Ex2, which differed by $190 \text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. The experimental period was shortest in Ex1 and Ex2 (90 and 87 days after transplanting, respectively) and longest in Ex5 and Ex6 (140 days after transplanting).

In each experiment, the plants in the 1st, 5th, 6th, and 10th rows and the plants in three coconut fiber slabs placed at both ends of the rows were considered guard plants and were excluded from the measurements. We measured the leaf area (leaf blade + petiole) with an area meter (LI-3100C; Li-Cor, Lincoln, NE, USA) and obtained the fresh weight (FW) and dry weight (DW) of leaves, stems, and fruits by destructive sampling at the time of transplanting, pinching, and the end of the experiment (Table 1). The leaf area index (LAI) was calculated by multiplying the measured leaf area by the plant density. DW was determined by oven-drying the sample at 105°C to a constant weight. The sampled plants were chosen randomly ($n = 5$ to 24) from the plants in the 2nd to 4th and 7th to 9th rows in the greenhouse. At the end of the experiment, mature and immature fruits from the sampled plants were weighed separately. We harvested mature fruits three to seven times a week and measured the number and FW of fruits harvested from small spots planted with 8–12 plants and from entire rows in the greenhouse. Because of the business needs of the greenhouse, the number of measured spots and rows differed among the experiments. We sampled three spots and two rows in Ex1, six and four in Ex2, four and four in Ex3, three and three in Ex4, and three and two in Ex5 and Ex6. We measured the FWs of marketable fruits separately from those of unmarketable fruits. Fruit DW was calculated by multiplying the FW by the average DM content of fruit that we measured at the end of the experiment. Total aboveground DM production (TDM) of each plant was obtained as the sum of leaf, stem, and fruit DWs at the sampling date, with the cumulative fruit DW harvested from the beginning to the sampling added.

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 (IL_d , $\text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) was calculated from the leaf area index (LAI ; $\text{m}^2 \text{m}^{-2}$) and daily cumulative PAR inside the greenhouse (PAR_i , $\text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) on each date and the light-extinction coefficient (k) as:

$$IL_d = (1 - e^{-k\cdot LAI})\cdot PAR_i \quad \text{Eq. 1}$$

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.

LUE_o ($\text{g}\cdot\text{MJ}^{-1}\text{PAR}$) was obtained as the slope of the linear regression of TDM ($\text{g}\cdot\text{m}^{-2}$) as a function of the cumulative plant-intercepted PAR (IL_c , $\text{MJ}\cdot\text{m}^{-2}$) using the method of Higashide and Heuvelink (2009). IL_c at pinching and the end of the experiment were obtained by summing IL_d . TDM was then expressed as:

$$TDM = LUE_o \times IL_c \quad \text{Eq. 2}$$

where LUE_o is the observed LUE .

Since the CO_2 -photosynthetic curve appeared to be a saturation curve, we assumed that the relationship between CO_2 and LUE also showed a saturation curve. We performed logarithmic regression of the relationship between LUE and the daytime CO_2 concentration across all experiments. The predicted LUE (LUE_p) was based on the daytime (08:00 to 16:00) mean CO_2 concentration (C) in each experiment:

$$LUE_p = a \cdot \ln C + b \quad \text{Eq. 3}$$

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:

$$LUE_{pEn} = a_{En} \cdot \ln C_{En} + b_{En} \quad \text{Eq. 4}$$

where LUE_{pEn} is LUE_p , C_{En} is the daytime mean CO_2 concentration, and a_{En} and b_{En} 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. LUE_{pEn} on these dates was obtained using Eq. 4 with C_{En} for both the period until pinching and for the whole experimental period. We compared LUE_{pEn} with the observed LUE (LUE_{oEn}) in each experiment. IL_d on each day was based on Eq. 1. We then predicted daily DM production (DM_p , $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) using Eq. 5 with LUE_{pEn} and IL_d :

$$DM_p = LUE_{pEn} \times IL_d \quad \text{Eq. 5}$$

Predicted TDM (TDM_p , $\text{g}\cdot\text{m}^{-2}$) 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-sct/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 normally distributed and the variances were homogeneous, 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, the data were analyzed by the Kruskal–Wallis test followed by the Steel–Dwass 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 data were not normally distributed and 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-

Table 2. Regressions used to obtain the parameters for Eq. 4^z, and its coefficients.

Experiment	Dataset for the regression	R^2	P	n	a_{En}	b_{En}
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

^z $LUE_{pEn} = a_{En} \ln C_{En} + b_{En}$, where C_{En} represents the average daytime CO_2 concentration and En represents the experiment number in Ex1–Ex6. a_{En} and b_{En} , regression coefficients based on the independent dataset in each experiment.

Table 3. Leaf area index (LAI) and cumulative plant-intercepted PAR on the pinching date and at the end of the experiment, as well as total fruit fresh weight (FW) and total dry matter (TDM) in each experiment.

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

^z Including both marketable and unmarketable fruits.

^y 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, $n = 24, 12, 8, 12, 12, 12$, and 8 in experiments Ex1 to Ex6, respectively; for LAI and intercepted PAR at the end of the experiment and for TDM , $n = 24, 12, 12, 8, 8, 6$, respectively; for fruit FW, $n = 5, 10, 8, 6, 5, 5$, respectively.

nificantly lower *TDM* than in the other experiments.

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_{pEn} values for the period until pinching and for the whole experimental period, and the 95% confidence interval for LUE_o . Only LUE_{pE3} 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

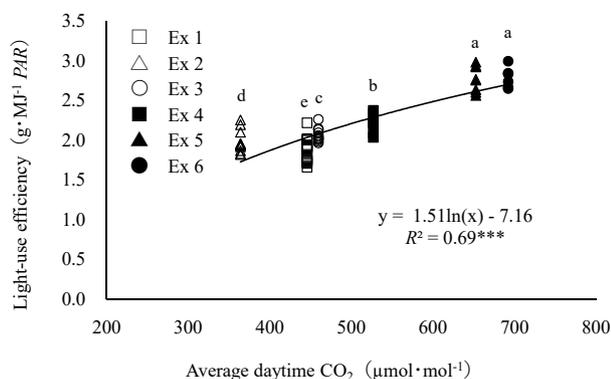


Fig. 1. Observed light-use efficiency (*PAR*, photosynthetically active radiation) as a function of the average daytime (08:00 to 16:00) CO₂ concentration by tomato plants grown in the six experiments described in Table 1 (Ex1 to Ex6). *** $P < 0.001$. Clusters of data labeled with different letters differed significantly (95% confidence intervals) among the experiments.

in Ex2 was significantly lower than that in the other experiments. TDM_p and TDM_o 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⁻¹PAR at 364 μmol·mol⁻¹ to 2.75 g·MJ⁻¹PAR 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, Ex 5, 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

Table 4. Predicted *LUE* in experiment *n* (LUE_{pEn}) 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_{pEn} ^z 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

^z LUE_{pEn} was obtained using Eq. 4 ($LUE_{pEn} = a_{En} \cdot \ln C_{En} + b_{En}$) with C_{En} representing the mean daytime CO₂ concentration for the period before pinching and for the whole experimental period, and a_{En} and b_{En} as regression coefficients based on the independent dataset in each experiment.

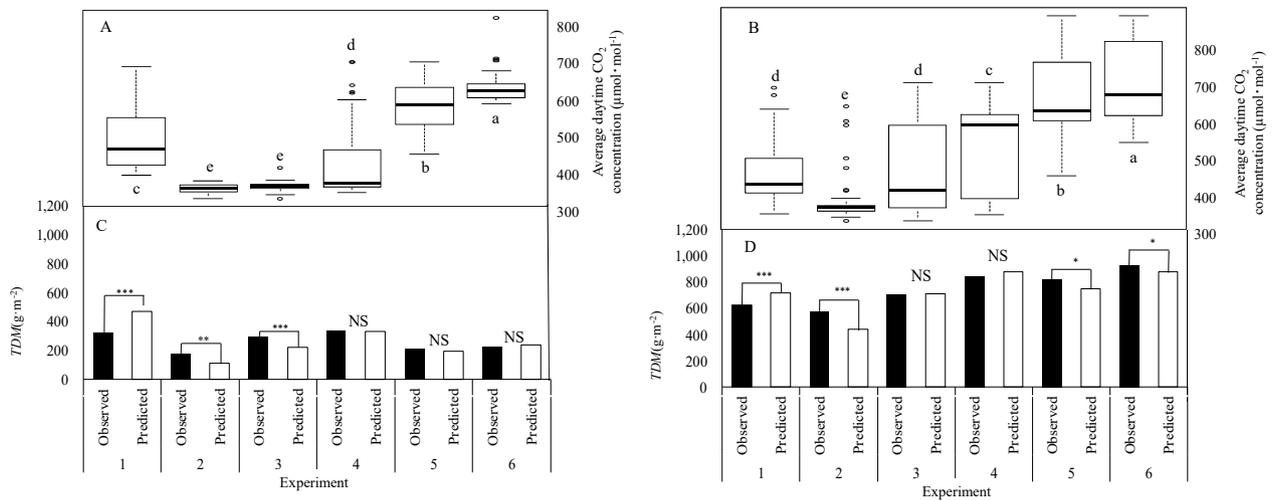


Fig. 2. (A, B) Mean daytime CO_2 concentrations in experiments Ex1 to Ex6 (A) before pinching and (B) for the whole experimental period. (C, D) Observed and predicted total aboveground DM production (TDM) (C) on the pinching date and (D) at the end of the experiment. In A and B, the bottom and top of each box represent the 25th and 75th percentiles, respectively. The heavy horizontal line represents the median. The whiskers above and below the boxes represent the minimum and maximum values, and the small circles outside this range represent outliers (values outside the range of median $\pm 1.5 \times$ the interquartile range). Boxes labeled with the same letter are not significantly different ($P < 0.05$) by the Kruskal–Wallis test followed by the Steel–Dwass test. In C and D, pairs of bars for observed and predicted TDM differed significantly as follows: NS, no significant difference; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, by Student's *t*-test (*italics*) and Welch's *t*-test (roman type). Sample sizes on the pinching date: $n = 48, 24, 16, 22, 24,$ and 16 in experiments Ex1 to Ex6, respectively; at the end of the experiment, $n = 48, 24, 24, 16, 16,$ and 12 , respectively.

CO_2 concentration ranged from about $400 \mu\text{mol}\cdot\text{mol}^{-1}$ to $650 \mu\text{mol}\cdot\text{mol}^{-1}$, which represented the conditions in Ex4, Ex 5, 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 CO_2 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 CO_2 concentrations ranging from 364 to $692 \mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ (Fig. 1). Eq. 4 then predicted LUE , and therefore was inaccurate beyond the range of CO_2 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 CO_2 values.

Owing to the irrigation problem at the beginning of Ex1, plant growth may have been restricted. In Ex1, although the CO_2 concentration at both pinching and the end of the experiment ranged from about $400 \mu\text{mol}\cdot\text{mol}^{-1}$ to $650 \mu\text{mol}\cdot\text{mol}^{-1}$, TDM_o was significantly lower than TDM_p (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 $1.93 \text{ g}\cdot\text{MJ}^{-1}\text{PAR}$ (Kaneko et al., 2015); in contrast, that of plants pinched at two leaves above the first truss was $2.69 \text{ g}\cdot\text{MJ}^{-1}\text{PAR}$ (Ohkubo et al., 2019). Although these authors did not report CO_2 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 $950 \mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ were 2.85 and $4.16 \text{ g}\cdot\text{MJ}^{-1} \text{PAR}$, 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 CO_2 conditions. Accordingly, choosing a cultivar with a high fruit sink strength like this Dutch cultivar increased the sink capacity at high CO_2 . At high CO_2 , 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 CO₂ 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 CO₂ 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 CO₂, 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 CO₂ 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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Literature Cited

- Adams, S. R., K. E. Cockshulland and C. R. J. Cave. 2001. Effect of Temperature on the Growth and Development of Tomato Fruits. *Ann. Bot.* 88: 869–877.
- Araki, T., S. Watanabe, T. Wajima, M. Kitano, Y. Nakano and K. Okano. 2009. Short-term application of the concentrated deep seawater for production of high quality tomatoes by single-truss and high density cultivation. *Environ. Control. Biol.* 47: 37–46.
- de Gelder, A., E. Heuvelink and J. J. G. Opdam. 2005. Tomato yield in a closed greenhouse and comparison with simulated yields in closed and conventional greenhouses. *Acta Hortic.* 691: 549–552.
- de Koning, J. C. M. 1997. Modeling the effects of supplementary lighting on production and light utilization efficiency of greenhouse crops. *Acta Hortic.* 418: 65–71.
- De Pascale, S., A. Maggio, F. Orsini, C. Stanghellini and E. Heuvelink. 2015. Growth response and radiation use efficiency in tomato exposed to short-term and long-term salinized soils. *Sci. Hort.* 189: 139–149.
- Fierro, A., N. Tremblay and A. Gosselin. 1994. Supplemental carbon dioxide and light improved tomato and pepper seedling growth and yield. *HortScience* 29: 152–154.
- Heuvelink, E., M. Bakker, L. F. M. Malcelis and M. Raaphoes. 2008. Climate and yield in a closed greenhouse. *Acta Hortic.* 801: 1083–1092.
- Hicklenton, P. R. and P. A. Jolliffe. 1978. Effects of greenhouse CO₂ enrichment on the yield and photosynthetic physiology of tomato plants. *Can. J. Plant Sci.* 58: 801–817.
- Higashide, T. and E. Heuvelink. 2009. Physiological and morphological changes over the past 50 years in yield components in tomato. *J. Amer. Soc. Hort. Sci.* 134: 460–465.
- Higashide, T., K. Yasuba, T. Kuroyanagi and A. Nakano. 2015. Decreasing or non-decreasing allocation of DM to fruit in Japanese tomato cultivars in spite of the increase in total DM of plants by CO₂ elevation and fogging. *Hort. J.* 84: 111–121.
- Higashide, T., K. Yasuba, K. Suzuki, A. Nakano and H. Ohmori. 2012. Yield of Japanese tomato cultivars has been hampered by a breeding focus on flavor. *HortScience* 47: 1408–1410.
- Johkan, M., A. Nagatsuka, A. Yoshitomi, T. Nakagawa, T. Maruo, S. Tsukagoshi, M. Hohjo, N. Lu, A. Nakaminami, K. Tsuchiya and Y. Shinohara. 2014. Effect of moderate salinity stress on the sugar concentration and fruit yield in single-truss, high-density tomato production system. *J. Japan. Soc. Hort. Sci.* 83: 229–234.
- Kanda, Y. 2013. Investigation of the freely-available easy-to-use software “EZR” (Easy R) for medical statistics. *Bone Marrow Transplant.* 48: 452–458.
- Kaneko, S., T. Higashide, K. Yasuba, H. Ohmori and A. Nakano. 2015. Effects of planting stage and density of tomato seedlings on growth and yield component in low-truss cultivation. *Hort. Res. (Japan)* 14: 163–170 (In Japanese with English abstract).
- Matsuda, R., A. Nakano, D. Ahn, K. Suzuki, K. Yasuba and M. Takaichi. 2011. Growth characteristic and sink strength of fruit at different CO₂ concentrations in a Japanese and a Dutch tomato cultivar. *Sci. Hort.* 127: 528–534.
- Nederhoff, E. M. 1994. Effects of CO₂ concentration on photosynthesis, transpiration and production of greenhouse fruit vegetable crops. *Landbouwniversiteit Wageningen (PhD Thesis, Wageningen Agricultural University), Wageningen, The Netherlands.*
- Ohkubo, S., T. Higashide, S. Kaneko, K. Yasuba, H. Ohmori and A. Nakano. 2019. Effect of number of leaves per truss on yield and yield components in single truss tomato production. *Bulletin of Hokkaido Research Organization Agricultural Experiment Station* 103: 7–12 (In Japanese with English abstract).
- Ohtani, Y. 1997. Effective radiation, micrometeorological phenomena. p. 106–107. In: T. Maki, S. Iwata, Z. Uchijima, T. Oikawa, K. Omasa, K. Kurata, T. Kozai, E. Goto, H. Kon, I. Nouchi, Y. Harazono, T. Hoshi, H. Honjo and S. Yamakawa (eds.). *Agricultural meteorology glossary (In Japanese).* Society for Agricultural Meteorology of Japan, Tokyo.
- Sato, S., M. M. Peet and J. F. Thomas. 2000. Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic, mild heat stress. *Plant Cell Environ.* 23: 719–726.
- Takahashi, T., Y. Ishigami, E. Goto, K. Niibori and K. Goto. 2012. Effect of CO₂ enrichment on the growth and yield of tomato plants cultivated in a large-scale greenhouse with a high-ventilation rate. *J. SHITA* 24: 110–115 (In Japanese

- with English abstract).
- Tripp, K. E., M. M. Peet, D. M. Pharr, D. H. Willits and P. V. Nelson. 1991. CO₂-enhanced yield and foliar deformation among tomato genotypes in elevated CO₂ environments. *Plant Physiol.* 96: 713–719.
- Vanthoor, B. H. E., P. H. B. de Visser, C. Stanghellini and E. J. van Henten. 2011. A methodology for model-based greenhouse design: Part 2, description and validation of a tomato yield model. *Biosystems Engineering* 110: 378–395.
- Yasuba, K., K. Suzuki, H. Sasaki, T. Higashide and M. Takaichi. 2011. Fruit yield and environmental condition under integrative environment control for high yielding production at long-time culture of tomato. *Bull. Natl. Inst. Veg. Tea Sci.* 10: 85–93 (In Japanese with English abstract).