



# Prediction and Improvement of Yield and Dry Matter Production Based on Modeling and Non-destructive Measurement in Year-round Greenhouse Tomatoes

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We validated a model for predicting dry matter (DM) production in growing plants without the need for destructive sampling with three tomato cultivars in a one-year experiment. In an attempt to improve DM, we managed the temperature and CO<sub>2</sub> concentration in the greenhouse as well as the leaf area index (LAI) of the tomato plants to meet targets determined based on model predictions. In the model, leaf area and thus the intercepted light is obtained by non-destructive, manual measurements of leaf width and length and the number of leaves. Light-use efficiency is expressed as a function of daytime CO<sub>2</sub> concentration. Although the model generally successfully predicted LAI in two of the cultivars, the observed LAI differed from the predicted value in the third cultivar. DM production, however, was predicted with high accuracy in all three cultivars from photosynthetically active radiation, temperature, CO<sub>2</sub>, and manual measurements of leaves; the predicted total DM in all cultivars at three sampling times fell within the range of observed DM ± standard deviation. By controlling temperature, daytime CO<sub>2</sub>, and LAI according to targets determined by simulations run on the model, we were able to improve yield to > 50 kg·m<sup>-2</sup> per year. Therefore, the model was useful for improving tomato yield.

**Key Words:** environmental control, leaf area index (LAI), light use efficiency, simulation, yield improvement.

## Introduction

The average yield of greenhouse tomatoes in Japan is ca. 12 kg·m<sup>-2</sup>, and less than 20% of that in the Netherlands; 65 kg·m<sup>-2</sup> (KWIN, 2017; MAFF, 2018). In 2015, 44% of greenhouse growers in Japan were aged over 65 years (MAFF, 2018), so the number of greenhouse growers is expected to decrease drastically in the near future. Although the total population in Japan is decreasing, the number of greenhouse growers may decrease faster, which could lead to a lack of greenhouse-grown vegetables in Japan. To produce enough

greenhouse vegetables in Japan for Japanese consumers, yield and labor efficiency must be drastically improved. Recently, there has been a rapid increase in the installation of computer-controlled environmental control systems in Japanese greenhouses. However, it is not easy for the growers to manage these systems to improve their yields.

Higashide (2018) reported in his review paper that continuous monitoring of growth and dry matter (DM) could provide data to support crop management by environmental control systems. If it were possible to accurately simulate growth and DM production at various settings, simulations could help to improve crop production. Tomato yield is a function of DM production, which in turn is determined by the product of light intercepted by plants and light-use efficiency (LUE) (Higashide, 2015; Higashide and Heuvelink, 2009). Intercepted light is determined by photosynthetically active radiation (PAR), leaf area index (LAI), and light extinction coefficients in the plant canopy. Kaneko et al. (2015) reported that in one cultivar there was no difference in LUE even if planting density and seedling

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stage at transplanting differed. As a result, Higashide (2018) suggested that dry matter production and yield could be predicted from cumulative intercepted light and LUE.

We have developed an empirical growth model that describes DM production and yield of greenhouse tomatoes continuously without destructive sampling. Leaf area, and thus intercepted light, was obtained by non-destructive, manual measurements of leaf width and length and the number of leaves; LUE was expressed as a function of daytime CO<sub>2</sub> concentration.

Using the model, we succeeded in estimating continuous DM production of growing plants without destructive sampling, and in simulating growth under different conditions. The model and simulations can support the search for appropriate settings for environmental control systems and appropriate crop management practices to boost yields. In this paper, we confirmed that the model accurately predicted DM production on the basis of long-term cultivation experiments for one year with three tomato cultivars, and we attempted to improve the yield by managing LAI and environmental settings based on the model and simulations.

### Materials and Methods

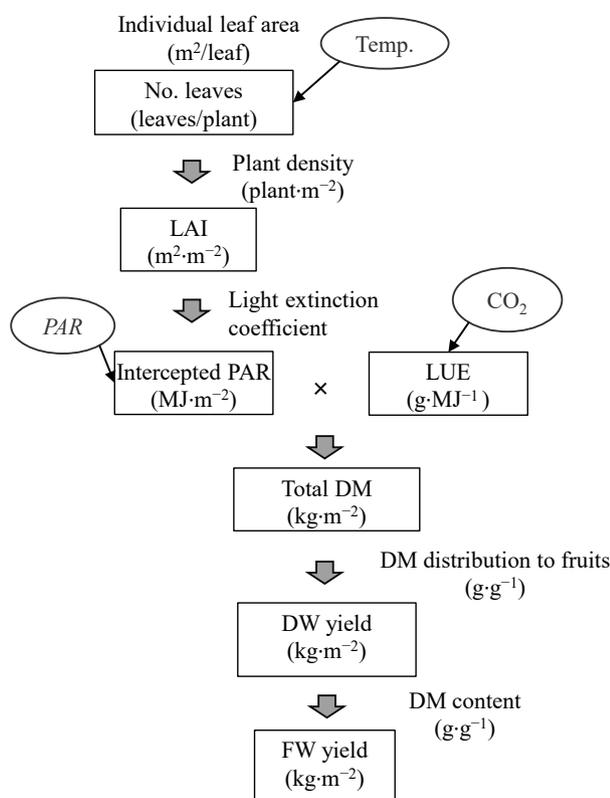
Three tomato cultivars (*Solanum lycopersicum* L.), ‘Ringyoku’ (Rn; NARO, Japan; Matsunaga and Saito, 2017), ‘CF Momotaro York’ (My; Takii & Co., Ltd., Kyoto, Japan), and ‘Managua EZ F1’ (Mn; Rijk Zwaan, The Netherlands) were compared over one year in a long-term experiment. We sowed seeds of Rn, Mn, and rootstock ‘Maxifort’ (De Ruiter Seeds, The Netherlands) in seed trays filled with nursery soil on 21 March 2017, and seeds of My on 28 March 2017. The seed trays were placed in a seedling growth chamber (Seedling Terrace; Mitsubishi chemical Agri Dream Co., Ltd., Tokyo, Japan). The seedlings were fertilized every day from below with a commercial nutrient solution (High-Tempo; Sumitomo Chemical Co., Ltd., Tokyo, Japan) consisting of 10.7 mM NO<sub>3</sub><sup>-</sup>, 6.3 mM K<sup>+</sup>, 5.4 mM Ca<sup>2+</sup>, 1.9 mM Mg<sup>2+</sup>, 2.4 mM H<sub>2</sub>PO<sub>4</sub><sup>-</sup>, 3.8 mg·L<sup>-1</sup> Fe, 0.38 mg·L<sup>-1</sup> Mn, 0.26 mg·L<sup>-1</sup> B, 0.15 mg·L<sup>-1</sup> Zn, 0.05 mg·L<sup>-1</sup> Cu, and 0.07 mg·L<sup>-1</sup> Mo, adjusted to an electrical conductivity of 1.6 dS·m<sup>-1</sup>. The seedlings were illuminated with fluorescent lamps with a 16-h day length and a photosynthetic photon flux density (PPFD) of 250–350 μmol·m<sup>-2</sup>·s<sup>-1</sup>, and were grown at 1000 μmol·mol<sup>-1</sup> CO<sub>2</sub> with air temperatures of 25°C (day) and 18°C (night). At 14 days after sowing, the seedlings of Rn and Mn were grafted onto the rootstock ‘Maxifort’. The seedlings of My were not grafted.

On 17 April 2017, the plants were transplanted into six rows of a rockwool system in a greenhouse (9 m width, 18 m length, 4.75 m gutter-height) at the NARO Institute of Vegetable and Floriculture Science, Tsukuba, Japan. The greenhouse was divided into four areas, with Rn plants in two of them and My and Mn

plants in one area each, and 105 plants in each area. The spacings were about 60 cm between rows within double rows, and 160 cm between the double rows. Planting density was 3.3 plants per m<sup>2</sup>. The 40 Rn plants and 20 My and Mn plants in the border rows were excluded from measurements. Plants were trained, and in accordance with standard Dutch practice, their axillary buds and leaves were pruned; the pruned buds were excluded from the measurements of DM production. To promote fruit set, 15 mg·L<sup>-1</sup> of 4-chlorophenoxyacetic acid was sprayed on inflorescences. The number of fruits per truss was not adjusted by pruning, since it does not influence fruit size in these cultivars. We supplied the plants with a nutrient solution consisting of 16.2 me·L<sup>-1</sup> NO<sub>3</sub>, 4.5 me·L<sup>-1</sup> P, 9.8 me·L<sup>-1</sup> K, 9.3 me·L<sup>-1</sup> Ca, 4.6 me·L<sup>-1</sup> Mg, 0.07 me·L<sup>-1</sup> Fe, 0.103 me·L<sup>-1</sup> B, 0.017 me·L<sup>-1</sup> Mn, 0.076 me·L<sup>-1</sup> Zn, 0.00120 me·L<sup>-1</sup> Cu, and 0.00083 me·L<sup>-1</sup> Mo, adjusted to an electrical conductivity of 3.4 dS·m<sup>-1</sup> up to 17 days after transplanting (DAT) and 2.6 dS·m<sup>-1</sup> from 18 DAT.

In the greenhouse, the air temperatures for natural ventilation were set at 30°C at 0–77 DAT, 25°C at 78–141 DAT, and 27°C at 142–344 DAT. Heating was set to turn on once temperatures fell to 14°C from 133 to 185 DAT and to 16°C from 186 to 255 DAT. To maintain a daily average temperature of 25°C, a heat pump (Green Package; Nepon Inc., Tokyo, Japan) was turned on at night (20:00–05:00) for cooling. The heat pump was also turned on at 07:00–15:00 from 126 to 248 DAT for heating once temperatures fell to 18°C, and at 10:00–16:00 at 249 to 283 DAT for cooling once temperatures reached 27°C. A fogging system (Tokita, Chiba, Japan) was used during the daytime to maintain 75% relative humidity from 0 to 7 DAT and 70% from 8 to 344 DAT. Air temperature, relative humidity, and CO<sub>2</sub> concentration in the greenhouse were recorded every 5 min by a Ubiquitous Environmental Control System (Akisai; Fujitsu Limited, Tokyo, Japan), and solar radiation outside the greenhouse was recorded once a minute by another Ubiquitous Environmental Control System (Stella Green, Osaka, Japan). Daily average temperature was 21.6 (± 3.2) °C (± SD), daytime (8:00–16:00) CO<sub>2</sub> concentration was 572 (± 180) μmol·mol<sup>-1</sup>, and cumulative outdoor solar radiation was 11.5 (± 5.8) MJ·m<sup>-2</sup>·day<sup>-1</sup>. Light transmissivity of the greenhouse was 0.55, and was measured before this experiment. The ratio of PAR to solar radiation was assumed to be 0.5 (Ohtani, 1997).

A flow diagram of how DM production was calculated in the model is shown in Figure 1. The equations used in the model are shown in Table 1. We first calculated the leaf appearance rate per day on the basis of daily average temperature and Eq. 1 (Table 1) and then obtained the number of leaves. To obtain individual leaf areas, we manually measured leaf width and length of all leaves on six plants in each cultivar every month.



**Fig. 1.** Flow diagram for calculation of yield and dry matter production. Temp., daily average air temperature; LAI, leaf area index; PAR, photosynthetically active radiation; LUE, light-use efficiency; DM, dry matter; DW, dry weight; FW, fresh weight.

From the leaf width and length and Eq. 2 (Table 2), individual leaf areas were obtained. We also measured the number of leaves on plants every week. LAI was based on the number of leaves, individual leaf areas, and Eqs. 3–9. Light intercepted by plants was obtained by LAI and Eq. 10. LUE was obtained by daytime (08:00–16:00) CO<sub>2</sub> concentration and Eq. 11. Daily DM production was obtained by light intercepted by plants and LUE (Eq. 12), and total DM was obtained by Eq. 13. Yield of dry fruit weight was obtained by total DM and DM distribution to fruit (Eq. 14), and fresh fruit yield was obtained by dry weight yield and dry matter content (Eq. 15).

To improve DM production, we optimized LAI by pruning the lower leaves every week. The optimum LAI in each cultivar was determined by Eq. 16 from solar radiation. Since future solar radiation is unpredictable, we used past data on solar radiation and determined the target LAI monthly. The target LAI at 50–130 DAT was 4.0–4.5, that at 130–280 DAT was 3.5–4.0, while that at 281–344 DAT was 4.0–4.5. We measured the fresh weight of the pruned leaves, and estimated the dry weights from the fresh weights and the corresponding dry matter content of leaves determined by sampling measurements as described later. We also controlled daytime CO<sub>2</sub> concentration to improve DM

production by using liquid CO<sub>2</sub>. Daytime (06:00–16:00) CO<sub>2</sub> at 0–53, 54–165, 166–202, 203–227, and 228–344 DAT was enriched to 500, 400, 500, 600, and 800 μmol·mol<sup>-1</sup>, respectively. We could not provide CO<sub>2</sub> at 261 DAT because we ran out of liquid CO<sub>2</sub>.

To validate the model, we randomly chose six plants of each cultivar to record leaf appearance and yield: we measured the appearance of leaves longer than 7 cm every week; we harvested fruits from 60 to 344 DAT and recorded their fresh weights and numbers. There were some physiological disorders on the fruits such as fruit cracking and blossom end-rot but these occurred at a low rate. We included all fruits as FW yield. To measure LAI and total DM, we sampled four plants from each cultivar at 38 DAT, four at 206 DAT, and six at 325 DAT, and measured the leaf area and the fresh and dry weights of leaves, stems, and fruits. Total DM was obtained by adding the DM at the sampling measurement to the DM of the pruned leaves and the harvested fruit that was calculated from the fresh weight and dry matter content.

## Results

The daytime CO<sub>2</sub> concentration was ~500 μmol·mol<sup>-1</sup> at 0–50 DAT, ~400 μmol·mol<sup>-1</sup> at 51–170 DAT, increased to ~800 μmol·mol<sup>-1</sup> from 171 to 230 DAT, and ~800 μmol·mol<sup>-1</sup> at 231–344 DAT (Fig. 2). As with the daytime CO<sub>2</sub> concentration, the daily LUE values obtained from the model fluctuated in the range of 4.0–8.0 for Rn and Mn, and in the range of 2.5–7 for My.

The predicted number of leaves was almost the same as the average of the observed number of leaves in all cultivars, and was within the range of one standard error (SE) of the observed numbers (Fig. 3). The largest difference in number was observed at 77 DAT in Rn (2.7 leaves/plant), 35 DAT in My (3.2 leaves/plant), and 175 DAT in Mn (3.6 leaves/plant). The average difference in number between the prediction and observation was 1.1 leaves/plant in Rn, 1.5 in My, and 2.8 in Mn.

The daily LAI as estimated by the model fluctuated as shown in Figure 4. At 38 DAT, the observed LAIs for Rn and Mn were slightly higher than the estimated LAI, but the estimated LAI was within the range of observed LAI ± SE for My. At 206 DAT, the estimated LAIs for Rn and Mn were within the range of observed LAI ± SE, but the observed LAI was lower than the estimation for My. At 325 DAT, the estimated LAIs for Rn and Mn were also within the range of the observed LAI ± SE, but the observed LAI was higher than the estimation for My.

Predicted and observed total DMs are shown in Figure 5. At 38 DAT, the predicted total DMs for Rn, My, and Mn (474, 347, and 501 g·m<sup>-2</sup>, respectively) were within the range of the observed DM ± SE. At 206 DAT, the predicted total DMs for My and Mn (2064 and 3024 g·m<sup>-2</sup>, respectively) were within the range of the observed DM ± SE, but the prediction for Rn

**Table 1.** Equations, parameters, coefficients, and values for each cultivar in the model for dry matter production.

No.	Equation	Parameters and coefficients (source)
1	$dNl_n/dt = a \cdot \ln(T_n) - b$	$dNl_n/dt$ : rate of leaf appearance at $n$ DAT (leaves/plant/day) $T_n$ : daily average temperature at $n$ DAT ( $^{\circ}\text{C}$ ) $a$ (coefficient): Rn, 0.40; My, 0.44; Mn, 0.35 $b$ (coefficient): Rn, 0.89; My, 1.03; Mn, 0.72 (Saito et al., 2020)
2	$ai = c \cdot Ll \cdot Lw$	$ai$ , individual leaf area ( $\text{m}^2/\text{leaf}$ ) $Ll$ , leaf length (m/leaf) $Lw$ , leaf width (m/leaf) $c$ : coefficient; Rn: 0.3348, My: 0.2456, Mn: 0.3646 (Saito et al., 2020)
3	$Mai = \sum_{n=Lpl+1}^{Lpu-1} ai / (Nrl - Nlu - Nll)$	$Mai$ , average individual leaf area without upper and lower leaves ( $\text{m}^2/\text{leaf}$ ) $Nrl$ , number of remaining leaves (leaves/plant) $Nlu$ , number of upper leaves (leaves/plant) $Nll$ , number of lower leaves (leaves/plant) $Lpu$ , leaf position from the highest leaf ( $1 \leq Lpu \leq Nlu$ ) $Lpl$ , leaf position from the first true leaf ( $1 \leq Lpl \leq Nll$ )
4	$Ai_n = (Nrl_n - Nlu - Nll) \cdot Mai + Aiu_n + Ail_n$	$Ai_n$ , leaf area per plant at $n$ DAT ( $\text{m}^2/\text{plant}$ ) $Nrl_n$ , $Nrl$ at $n$ DAT (leaves/plant) $Aiu_n$ and $Ail_n$ , upper and lower leaf area, respectively, at $n$ DAT ( $\text{m}^2/\text{plant}$ )
5	$Aiu = \Sigma((f \cdot e^{g \cdot Lpu}) \cdot Mai)$	$Aiu$ , upper leaf area ( $\text{m}^2/\text{plant}$ ) $f$ (coefficient): Rn, 0.0265; My, 0.034; Mn, 0.0245 $g$ (coefficient): Rn, 0.6451; My, 0.6651; Mn, 0.6871 (Saito et al., 2020)
6	$Ail = \Sigma((h \cdot e^{i \cdot Lpl}) \cdot Mai)$	$Ail$ , lower leaf area ( $\text{m}^2/\text{plant}$ ) $h$ (coefficient): Rn, 0.0063; My, 0.0109; Mn, 0.0151 $i$ (coefficient): Rn, 0.9603; My, 0.6651; Mn, 0.5215 (Saito et al., 2020)
7	$Ai_e = \Sigma ai$	$Ai_e$ , leaf area per plant at early stage; i.e., < 16 leaves ( $\text{m}^2/\text{plant}$ )
8	$Ai_{e_n} = j \cdot e^{l \cdot Nln}$	$Ai_{e_n}$ , leaf area per plant at an early stage; i.e., < 16 leaves at $n$ DAT ( $\text{m}^2/\text{plant}$ ) $j$ (coefficient): Rn, 0.0036; My, 0.0023; Mn, 0.0044 $l$ (coefficient): Rn, 0.3692; My, 0.375; Mn, 0.3519 (Saito et al., 2020)
9	$LAI_n = Ai_n \cdot Pd$	$LAI_n$ , LAI at $n$ DAT ( $\text{m}^2 \cdot \text{m}^{-2}$ ) $Pd$ , plant density ( $\text{plants} \cdot \text{m}^{-2}$ )
10	$IL_n = (1 - e^{-k \cdot LAIn}) \cdot T_g \cdot R_p \cdot Sr_n$	$IL_n$ , cumulative intercepted light ( $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) at $n$ DAT $k$ , light extinction coefficient in plant canopy: Rn, 0.72; My, 0.99; Mn, 0.77 (Saito et al., 2020) $Sr_n$ , solar radiation outside at $n$ DAT ( $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) $T_g$ , light transmissivity of the greenhouse: 0.55 (measured before this experiment) $R_p$ , ratio of PAR to solar radiation: 0.5 (Ohtani, 1997)
11	$LUE_n = m \cdot \ln(\text{CO}_{2n}) - o$	$LUE_n$ , light-use efficiency at $n$ DAT ( $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) $\text{CO}_{2n}$ , daytime $\text{CO}_2$ concentration at $n$ DAT ( $\mu\text{mol} \cdot \text{mol}^{-1}$ ) $m$ (coefficient): Rn, 4.9166; My, 4.5124; Mn, 4.5217 $o$ (coefficient): Rn, -25.434; My, -24.168; Mn, -22.74 (Saito et al., 2020)
12	$DM_n = LUE_n \cdot IL_n$	$DM_n$ , dry matter production per day at $n$ DAT ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ )
13	$TDM_n = \Sigma_0^n DM_n$	$TDM_n$ , total dry matter production at 0– $n$ DAT ( $\text{g} \cdot \text{m}^{-2}$ )
14	$Y_{d_n} = TDM_n \cdot F_f$	$Y_{d_n}$ , dry fruit yield ( $\text{g} \cdot \text{m}^{-2}$ ) $F_f$ , fraction of dry matter distribution to fruits ( $\text{g} \cdot \text{g}^{-1}$ ): Rn, 0.53; My, 0.62; Mn, 0.48 (Saito et al., 2020)
15	$Y_{f_n} = Y_{d_n} / C_d$	$Y_{f_n}$ , fresh fruit yield ( $\text{g} \cdot \text{m}^{-2}$ ) $C_d$ , fruit dry matter content ( $\text{g} \cdot \text{g}^{-1}$ ): Rn, 0.046; My, 0.046; Mn, 0.044 (Saito et al., 2020)
16	$LAI_{op} = p \cdot \ln(Sr) + q$	$LAI_{op}$ , Optimal LAI ( $\text{m}^2 \cdot \text{m}^{-2}$ ) $Sr$ , solar radiation ( $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) $p$ (coefficient): Rn, 1.43; My, 1.00; Mn, 1.28 $q$ (coefficient): Rn, 0.81; My, 1.69; Mn, 1.61 (Saito et al., 2020)

Rn, Ringyoku; My, Momotaro York; Mn, Managua.

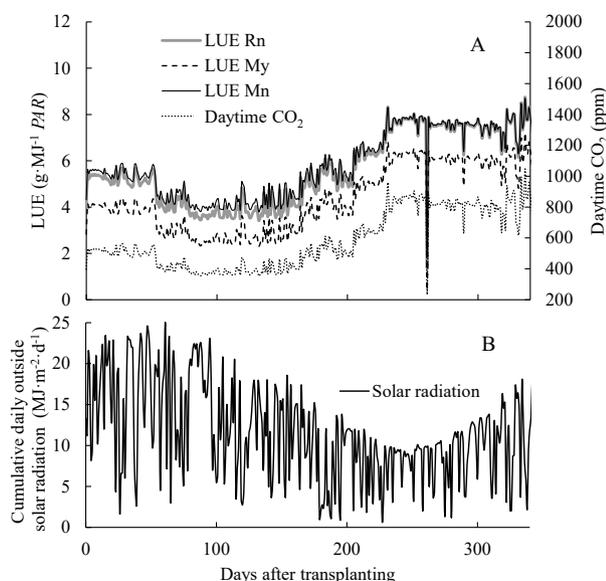
**Table 2.** Estimated intercepted light, predicted total dry matter (DM), predicted fresh fruit yield, observed fresh fruit yield, fraction of DM distribution to fruit, and light-use efficiency (LUE) obtained from three destructive measurements in three tomato cultivars (Rn, Ringyoku; My, Momotaro York; Mn, Managua) at 345 DAT.

Cultivar	Estimated intercepted light (MJ·m <sup>-2</sup> )	Predicted total DM production (kg·m <sup>-2</sup> )	Predicted fresh fruit yield <sup>z</sup> (kg·m <sup>-2</sup> )	Observed fresh fruit yield <sup>y</sup> (kg·m <sup>-2</sup> )	Fraction of DM distribution to fruits <sup>x</sup> (g·g <sup>-1</sup> )	LUE by destructive measurements (g·MJ <sup>-1</sup> )
Rn	976	5.18	59.7	55.3±2.8	0.47	4.70
My	987	3.99	53.8	50.6±4.3	0.57	3.99
Mn	981	5.43	59.2	60.7±5.5	0.47	5.23

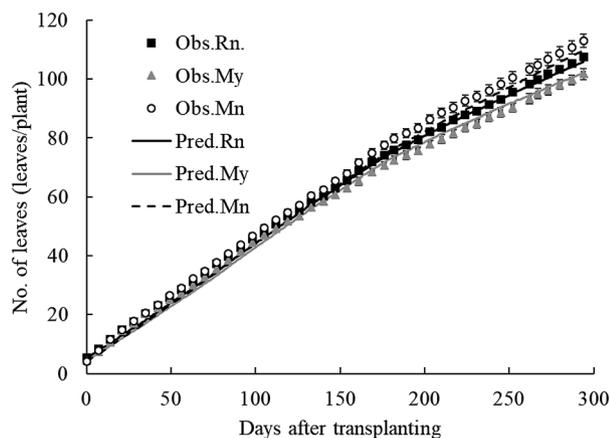
<sup>z</sup> Based on Eqn. 14 and 15 in Table 1.

<sup>y</sup> mean±SD (n=6).

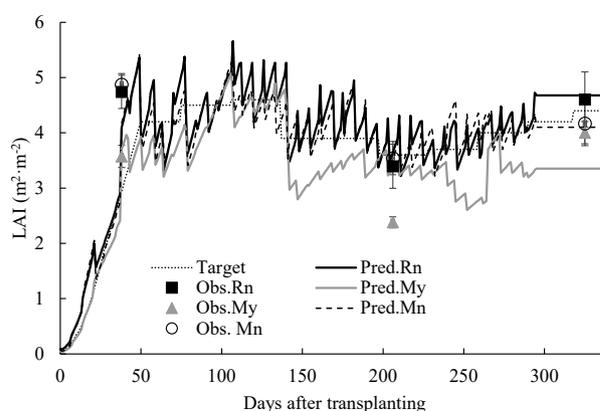
<sup>x</sup> observed dry fruit yield/predicted total DM production.



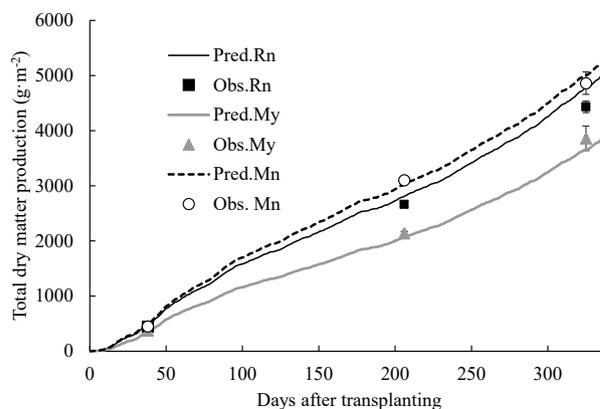
**Fig. 2.** Change in observed daytime CO<sub>2</sub> concentration and in daily light-use efficiency (LUE) estimated by the model for three tomato cultivars (Rn, Ringyoku; My, Momotaro York; Mn, Managua) (A) and cumulative daily outside solar radiation (B) during the experimental term. CO<sub>2</sub> at 261 DAT was not provided.



**Fig. 3.** Predicted and observed number of leaves in three tomato cultivars. Rn, Ringyoku; My, Momotaro York; Mn, Managua. Observed number of leaves indicates the average ± SE (bars) (n = 6).



**Fig. 4.** Target, predicted, and observed leaf area index (LAI) for three tomato cultivars. Rn, Ringyoku; My, Momotaro York; Mn, Managua. Observed LAIs show the average ± SE (bars) (38 and 206 DAT: n = 4; 325 DAT: n = 6).



**Fig. 5.** Predicted and observed total DM in three tomato cultivars. Rn, Ringyoku; My, Momotaro York; Mn, Managua. Observed total DM shows the average ± SE (bars) (38 and 206 DAT, n = 4; 325 DAT, n = 6).

(2809 g·m<sup>-2</sup>) was higher than the observation. At 325 DAT, the predicted total DMs for My and Mn were also within the range of the observed DM ± SE, but the prediction for Rn was higher than the observation. The predicted total DMs for all cultivars at all sampling times were within the range of the observed DM ± SD (data not shown).

Table 2 shows the estimated light interception by plants, predicted total DM, predicted fresh fruit yield, observed fresh fruit yield, fraction of DM distribution to fruit, and LUE determined by destructive sampling at 345 DAT (the end of the experiment). The estimated light interception was almost the same for each of the three cultivars. The predicted DM production and the predicted fresh fruit yield were lower in My than in Rn and Mn. The observed fresh fruit yields were  $55.3 \text{ kg}\cdot\text{m}^{-2}$  in Rn,  $50.6 \text{ kg}\cdot\text{m}^{-2}$  in My, and  $60.7 \text{ kg}\cdot\text{m}^{-2}$  in Mn. The predicted yields of My and Mn were within the range of the observed fresh fruit yield  $\pm$  SD, but the predicted yield of Rn was higher than that observed. As with the predicted total DM and the observed yield, LUE assessed by destructive measurements was highest in Mn and lowest in My.

### Discussion

As the yield of greenhouse tomatoes in Japan is currently far lower than in the Netherlands, it needs to be improved. Several recent reports have explored approaches to improving yields of Japanese greenhouse tomatoes such as using environmental control, selecting high-yielding cultivars, and grafting onto rootstock (Higashide et al., 2012, 2014, 2015). As reported in the review paper by Higashide (2018), eco-physiological research into dry matter production, light interception by the plant canopy, and environmental conditions such as light and  $\text{CO}_2$  concentration has been advancing rapidly. Based on this accumulated knowledge, we developed a growth model to predict DM production and yield. Here, we validated the model and attempted to improve yields in a long-term experiment. From the model and simulation, we determined targets for temperature,  $\text{CO}_2$  concentration, and LAI, and managed these parameters in accordance with the targets. We succeeded reasonably well in our ability to predict total DM in the three cultivars (Fig. 5), and the total actual yields were considerable:  $55.3 \text{ kg}\cdot\text{m}^{-2}$  in Rn,  $50.6 \text{ kg}\cdot\text{m}^{-2}$  in My, and  $60.7 \text{ kg}\cdot\text{m}^{-2}$  in Mn (Table 2).

These very high yields may be the result of two main factors. Firstly, controlling the daytime  $\text{CO}_2$  concentration had a role in these very high yields. Since the photosynthetic rate is promoted at high  $\text{CO}_2$  concentrations, LUE is improved at high  $\text{CO}_2$  concentrations (Higashide et al., 2015), and high LUE improves DM production and yield (Higashide and Heuvelink, 2009; Higashide et al., 2012, 2014, 2015). Since the daytime  $\text{CO}_2$  concentration in a greenhouse is influenced by ventilation, it increased mainly during winter in our experiment (Fig. 2). Accordingly, the predicted daily LUE ranged from 4.0 to 8.0 for Rn and Mn, and between 2.5 and 7 for My (Fig. 2), and the LUE indicated by the destructive sampling ranged from 3.99 to 5.23 (Table 2). These high LUE values helped to improve DM production and therefore yield. Secondly, we managed LAI every week in accordance with the target LAI (Fig. 4),

which was determined to maximize DM production based on Eq. 16 and from past solar radiation data. We roughly succeeded in controlling LAI by pruning the lower leaves (Fig. 4). A value of LAI that is too low may decrease the amount of light intercepted by plants and thus decrease DM production. In contrast, a value that is too high may also decrease DM production since the respiration will be higher than the photosynthetic rate in the lower leaves. Our LAI management adjusted according to monthly PAR also likely improved DM production and yield.

We considered the accuracy of the predictions made by the model. Firstly, we used the model to predict leaf appearance from the temperature (Fig. 3). The relationship between leaf appearance and temperature is well known, and leaf appearance is not influenced by other factors such as  $\text{CO}_2$  concentration, plant density, or number of fruits per plant. We used the model and predicted leaf appearance with high accuracy (Fig. 3). Accordingly, we could also predict the appearance of inflorescences, since an inflorescence appears at every three leaves in tomato plants. Secondly, we used the model to predict leaf area and LAI. Leaf area and LAI are determined by individual leaf area and the number of leaves. Although measurement of LAI by destructive sampling can include errors, it is more difficult to measure individual leaf areas without destructive sampling. We measured leaf width and length to obtain individual leaf areas (Eq. 2, Table 1). This method has been reported for tomatoes and cucumbers (Ahn et al., 2015; Cho et al., 2007; Higashide and Heuvelink, 2009; Higashide et al., 2015). We predicted LAI throughout the experiment without destructive sampling. Although we partially succeeded in predicting approximate LAI for Rn and Mn, the observed LAI for My at 206 and 325 DAT differed substantially from the prediction (Fig. 4). LAI directly influences light intercepted by plants and therefore DM production (Higashide and Heuvelink, 2009). At low LAI, differences in LAI directly influence intercepted light and DM production (Kaneko et al., 2015); however, when the LAI exceeds approximately 3, differences in LAI only slightly influence intercepted light (Higashide, 2013; Monsi and Saeki, 2005). At the end of our long-term experiment (345 DAT), the intercepted light did not differ between cultivars (Table 2).

Several studies of tomatoes have reported LUE obtained by destructive measurements (Higashide and Heuvelink, 2009; Higashide et al., 2012, 2014, 2015; Kaneko et al., 2015; van der Ploeg et al., 2007). However, daily LUE cannot be obtained by daily destructive sampling. Therefore, we calculated daily LUE for each cultivar from daytime  $\text{CO}_2$  and Eq. 11 (Table 1). Equation 11 and the accompanying parameters were obtained from another experiment that determined LUE for two weeks by destructive sampling of plants grown at different  $\text{CO}_2$  concentrations (Saito et al., 2020). However, they reported the relationship between LUE

and CO<sub>2</sub> in only three cultivars, and the parameters differed among cultivars; to improve the accuracy of the model, we need to collect more data on LUE under different CO<sub>2</sub> conditions and for many more cultivars.

Although predicted LAI often differed from the observed LAI, the total DM was predicted with high accuracy in our long-term experiment (Fig. 5); total DMs for all cultivars at 38, 206, and 325 DAT were within the range of the observed DM ± SD. We estimated fresh fruit yield from total DM and Eq. 14 (Table 1). The predicted fractions of DM distribution to fruit (parameter Ff) for Rn, My, and Mn (0.53, 0.62, and 0.48, respectively) were slightly larger than the observed fractions of DM distribution to fruit (0.47, 0.57, and 0.47, respectively) (Table 2). Accordingly, the observed yield was smaller than the predicted yield (Table 2). To improve the accuracy of the model, we should also collect data on the fraction of DM distribution to fruit. Fresh fruit yield was given by Eq. 15. Although we did not measure fruit dry matter content, it may fluctuate seasonally depending on soluble solids.

### Conclusion

By using the model and inputting parameters based on environmental conditions such as PAR, temperature, and CO<sub>2</sub> and manual measurement of leaves, we predicted DM production with high accuracy in three tomato cultivars. By controlling temperature and daytime CO<sub>2</sub> in the greenhouse and the LAI of tomato plants according to targets determined by the model and simulations, we improved yields to > 50 kg·m<sup>-2</sup> per year. Therefore, we demonstrated that the model is useful for improving tomato yields.

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