

# Dry Matter Production and Fruit Sink Strength Affect Fruit Set Ratio of Greenhouse Sweet Pepper

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**ABSTRACT.** We investigated the relationships among the fruit set, dry matter production, and source-to-sink ratio of sweet pepper (*Capsicum annuum*) plants grown in a greenhouse. We quantified daily fruit sink strength per stem (st) at  $m$  days after transplanting ( $SST_{m\_st}$ ) by modeling the fruit growth curve. The daily total dry matter production ( $TDM_{m\_st}$ ) was calculated and defined as the source strength. During an experiment lasting  $\approx 250$  days, the fruit set ratio [number of fruit harvested/number of flowers ( $FSR_m$ )] decreased significantly with increases in both the weekly average  $SST_{m\_st}$  from 9 days before anthesis (DBA) to 13 days after anthesis (DAA) and the weekly average fruit number ( $FRN_{m\_st}$ ) from 9 to 1 DBA.  $FSR_m$  increased significantly with increases in both the weekly average  $TDM_{m\_st}$  from 1 to 13 DAA and the weekly average source-to-sink ratio [source strength/fruit sink strength ( $SSR_{m\_st}$ )] from 5 DBA to 13 DAA. During the whole experimental period, significant positive correlations with  $FSR_m$  were observed for  $TDM_{m\_st}$  and  $SSR_{m\_st}$ , and significant negative correlations with  $FSR_m$  were observed for  $SST_{m\_st}$  and  $FRN_{m\_st}$ .  $FSR_m$  increased until approximately the time when the weekly average  $SSR_{m\_st}$  at 1 to 7 DAA (anthesis to  $156^\circ\text{C}\cdot\text{d}^{-1}$ ) ranged from 1.0 to 4.0; then, it showed a saturation curve at  $SSR_{m\_st}$  values more than 4.0 ( $R^2 = 0.81$ ). These results suggest that it is possible to moderate the fluctuations in sweet pepper yield by monitoring the  $SSR_{m\_st}$  and the number of fruit set.

Sweet pepper (*Capsicum annuum*) production increased considerably across more than 100 countries from 17 to 36 million tons during 1997 to 2017 (Tripodi and Kumar, 2019), and the global demand for sweet pepper is still increasing. Yields of greenhouse sweet pepper differ dramatically among countries (Kleijbeuker and Lee, 2019; Kwantitatieve Informatie voor de Glastuinbouw, 2017; Marcelis et al., 2019; Ministry of Agriculture Forestry and Fisheries of Japan, 2018), and yield fluctuation is inevitable for greenhouse sweet pepper.

This crop shows a clear pattern of fluctuation: periods of high fruit set alternate with periods of low fruit set; eventually, the numbers of harvestable fruit differ on a weekly and monthly basis (Heuvelink et al., 2016). A high-yield period caused by high fruit set is called “flushing.” Because of this irregular fluctuation, the fresh yield and the labor demand over short periods are difficult to predict, resulting in a lack or excess of labor (Heuvelink and Körner, 2001; Heuvelink et al., 2004). In addition, the yield fluctuation results in periods of high market supply with low prices, followed by periods of low market supply with high prices (Heuvelink and Körner, 2001; Heuvelink et al., 2004). Flushing can make it difficult for sweet pepper growers to maintain market reliability because it is associated with the unstable production and supply of sweet pepper. Therefore, avoiding and mitigating irregular fruit setting patterns is an advantageous production strategy. To establish stable and efficient production of sweet peppers, we need to clarify the factors associated with fruit set and predict and mitigate yield fluctuations.

Fluctuating fruit set in sweet pepper is caused mainly by environmental conditions of plants and the competition for assimilates between the fruit and vegetative organs (Wubs et al., 2009a). During studies of the effects of environmental conditions on fruit set, flower abortion rates have been higher under severe conditions, such as high temperatures (Bakker, 1989a; Erickson and Markhart, 2001; Marcelis et al., 2004), low temperatures (Bosland and Votava, 2012), low nighttime relative humidity (Bakker, 1989b), short fertigation intervals (Ćosić et al., 2015; de Souza et al., 2019), and high electric conductivity (EC) of a nutrient solution (Bosland and Votava, 2012; Chartzoulakis and Klapaki, 2000), than under mild conditions. Tadesse et al. (1999) and Rubio et al. (2011) also reported that the fresh weight yield was decreased by the high EC of a nutrient solution; however, they did not provide data regarding fruit numbers.

Even when sweet pepper plants are grown under apparently optimal conditions, fluctuation of the fruit set occurs during production (Ma et al., 2011; Wien et al., 1989). Several studies (Heuvelink et al., 2004, 2016; Kleijbeuker and Lee, 2019; Ma et al., 2011; Marcelis et al., 2004; Wubs, 2010; Wubs et al., 2009a, 2009b) have revealed factors related to flushing by pointing out reasons why flushing occurs, namely, the interaction of source and sink strengths. Additionally, the number of seeds in fruit are positively correlated to the fruit size, which may affect the fruit sink strength (Rylski, 1973). Flushing is mitigated in seedless fruit (Heuvelink and Körner, 2001; Heuvelink et al., 2016); however, parthenocarpic sweet pepper is not currently commercially available. Some studies of the effects of source and fruit sink strength on flushing have found that an increase in dry matter production increases fruit set; in contrast, other studies found that an increase in the fruit load on the stem has decreased the fruit set (Heuvelink et al., 2004; Kleijbeuker and Lee, 2019; Marcelis et al., 2004; Wubs et al., 2009a). However, the effects of the source and fruit sink strength on the fruit set have not yet been sufficiently validated quantitatively.

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To determine how to produce sweet pepper in a stable manner, we investigated the quantitative effects of the source and fruit sink strength on the fruit set and developed a model for predicting the fruit set in sweet pepper. We attempted to elucidate the most dominant fruit set factors. To avoid the effects of environmental stress on fruit set, we grew sweet pepper plants in a mild climate. Nutrient solution was used to fertigate at frequent and adequate intervals according to the growth stage.

## Materials and Methods

Sweet pepper [cultivar Artega (Enza Zadan, Enkhuizen, the Netherlands)] plants were grown hydroponically in a rockwool system in a greenhouse (width, 9 m; length, 18 m; gutter height, 4.75 m) at Tsukuba, Japan (lat. 36°26'N, long. 140°10'E). Seeds were sown in seed trays on 4 June 2019 and incubated in a germination chamber under dark conditions for 3 d at 28 °C. After germination, the seed trays were placed in a seedling growth chamber (Nae-Terrace; Mitsubishi Chemical Agri Dream, Tokyo, Japan) and raised for 3 weeks. In the growing chamber, the seedlings were illuminated with fluorescent lamps at a photosynthetic photon flux density (PPFD) of 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  with a 16-h day (25 °C)/8-h night (20 °C) cycle at 1000  $\mu\text{mol}\cdot\text{mol}^{-1}$  CO<sub>2</sub>. The seedlings were fertilized every day with a commercial nutrient solution (High-Tempo; Sumitomo Chemicals, Tokyo, Japan) adjusted to an EC of 1.8 dS·m<sup>-1</sup>. According to manufacturer's instructions, this solution consisted of 10.07 mmol nitrogen (consisting of NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>; ratio of total nitrates to NH<sub>4</sub><sup>+</sup> = 0.09), 3.07 mmol phosphorus, 5.61 mmol potassium, 4.96 mmol calcium, 1.67 mmol magnesium, 0.34 mg·L<sup>-1</sup> manganese, 0.23 mg·L<sup>-1</sup> boron, 3.39 mg·L<sup>-1</sup> iron (Fe-EDTA), 0.13 mg·L<sup>-1</sup> zinc (Zn-EDTA), 0.04 mg·L<sup>-1</sup> copper (Cu-EDTA), and 0.06 mg·L<sup>-1</sup> molybdenum [(NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>·4H<sub>2</sub>O].

After the seedling period, plants in their seed trays were moved to the greenhouse as a secondary nursery until the transplanting date. On 10 July 2019, the plants were transplanted onto rockwool slab (Grotop Expert; Grodan, Roermond, the Netherlands) in the greenhouse. The greenhouse was divided into six rows. The interrow width was ≈1.6 m. The plants were transplanted in the six rows. However, the plants in the outside rows were excluded from our measurements because the plants in outside rows received more light than those in the central four rows. Plants were planted with 96 plants in each row (3.75 plants/m<sup>2</sup>). The six plants at the north and south ends were excluded from measurements. Plants were trained with two main stems per plant. All flowers were removed at nodes 0 to 2 of the main stem. On each main stem with dichotomous branching, the weaker lateral stem was pruned just above the second leaf at 0 to 36 d after transplanting (DAT), and just above the first leaf at 37 to 246 DAT. The experiment ended at 246 DAT.

We supplied plants with a commercial nutrient solution (OAT-SA; OAT Agrio, Tokyo, Japan) adjusted to EC of 1.5 dS·m<sup>-1</sup> at 0 to 47 DAT, 2.0 dS·m<sup>-1</sup> at 48 to 70 DAT, and 2.5 dS·m<sup>-1</sup> at 71 to 246 DAT. The OAT-SA solution adjusted to an EC of 2.6 dS·m<sup>-1</sup> (including clear water with an EC of 0.3 dS·m<sup>-1</sup>), which is the value recorded for a standard solution made in accordance with the manufacturer's instructions, consisted of 21.5 mmol nitrogen (consisting of NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>; ratio of total nitrates to NH<sub>4</sub><sup>+</sup> = 0.02), 4.4 mmol phosphorus (P<sub>2</sub>O<sub>5</sub>), 10.2 mmol K (K<sub>2</sub>O), 4.1 mmol calcium [CaO and Ca(NO<sub>3</sub>)<sub>2</sub>], 1.5 mmol magnesium (MgO), 2.75 mg·L<sup>-1</sup> manganese (MnO), 3.05 mg·L<sup>-1</sup> boron

Table 1. Operating setpoints of ventilation windows, heat pump, CO<sub>2</sub> gas regulator, and shade curtain in the greenhouse for growing and examining sweet pepper 'Artega' from 0 to 246 d after transplanting.

Days after transplanting	Setpoints for operating environmental equipment			
	Ventilation windows (°C)	Heat pump (°C)	CO <sub>2</sub> gas regulator ( $\mu\text{mol}\cdot\text{mol}^{-1}$ )	Shade curtain (kW·m <sup>-2</sup> )
0–37	25–28	30 (0800–1800 HR), 20–25 (1800–0800 HR)	—	0.69
38–57	25–28	20–25 (1800–0800 HR)	—	0.80
58–71	25–28	20–25 (1800–0800 HR)	—	1.00
72–82	25–28	— <sup>i</sup>	—	1.00
83–84	29	—	—	1.00
85–103	29	—	400	1.00
104–118	29	—	400	1.00
119–160	33–36	—	800	1.00
161–165	33–36	—	400	1.00
166–184	27	—	400	1.00
185–198	36	—	1600	1.00
199–211	36	—	1200	1.00
212–246	27	—	400	1.00

<sup>i</sup> Without operation.

(B<sub>2</sub>O<sub>3</sub>), 7.95 mg·L<sup>-1</sup> iron (Fe-EDTA), 0.07 mg·L<sup>-1</sup> copper (Cu-EDTA), 0.17 mg·L<sup>-1</sup> zinc (Zn-EDTA), and 0.07 mg·L<sup>-1</sup> molybdenum [(NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>·4H<sub>2</sub>O]. A drainage rate (drainage volume/volume of nutrient solution supplied) of ≈30% to 40% per day was maintained. Fertigation was performed every 30 min during the day (0700–1700 HR) from 0 to 52 DAT, and from sunrise to 1 h before sunset from 53 to 246 DAT; during the latter period, the frequency of application was determined by the amount of solar radiation.

Operating setpoints of the ventilation windows, heat pump, CO<sub>2</sub> gas regulator, and shade curtain are shown to Table 1. Setpoints of ventilation windows were mainly determined based on the periods of highly concentrated CO<sub>2</sub> application in the greenhouse. During the daytime at 85 to 246 DAT, the concentration of CO<sub>2</sub> gas was supplied from a liquid CO<sub>2</sub> source, and it was controlled when the ventilation windows were closed. A heat pump (Green Package; Nepon, Tokyo, Japan) was turned on for cooling during the early growing period (0–71 DAT). A shade screen (SLS50 Harmony; Svensson, Kinna, Sweden) was extended across the whole roof of the greenhouse during daytime when the outside solar radiation reached the setpoints (Table 1). To maintain a daily average temperature of 20 °C, a heater (House Kaonki; Nepon) was set to turn on at 104 to 246 DAT when the air temperature decreased 18 °C at night (1600–0800 HR) and 23 °C during the daytime (0800–1600 HR). From 0 to 246 DAT, a fogging system was operated during the daytime when the humidity deficit exceeded 8.0 g·m<sup>-3</sup>.

Air temperature, humidity deficit, solar radiation, and CO<sub>2</sub> concentration in the greenhouse were recorded every 1 min by a Ubiquitous Environmental Control System (YoshiMax; SANKI KEISO, Tokyo, Japan). Drainage and the amount of nutrient solution supplied were also recorded every 1 min by the system. We plotted the daily average air temperature (°C) and daytime and nighttime average air temperatures (°C) in the greenhouse during the whole experimental period (Fig. 1).

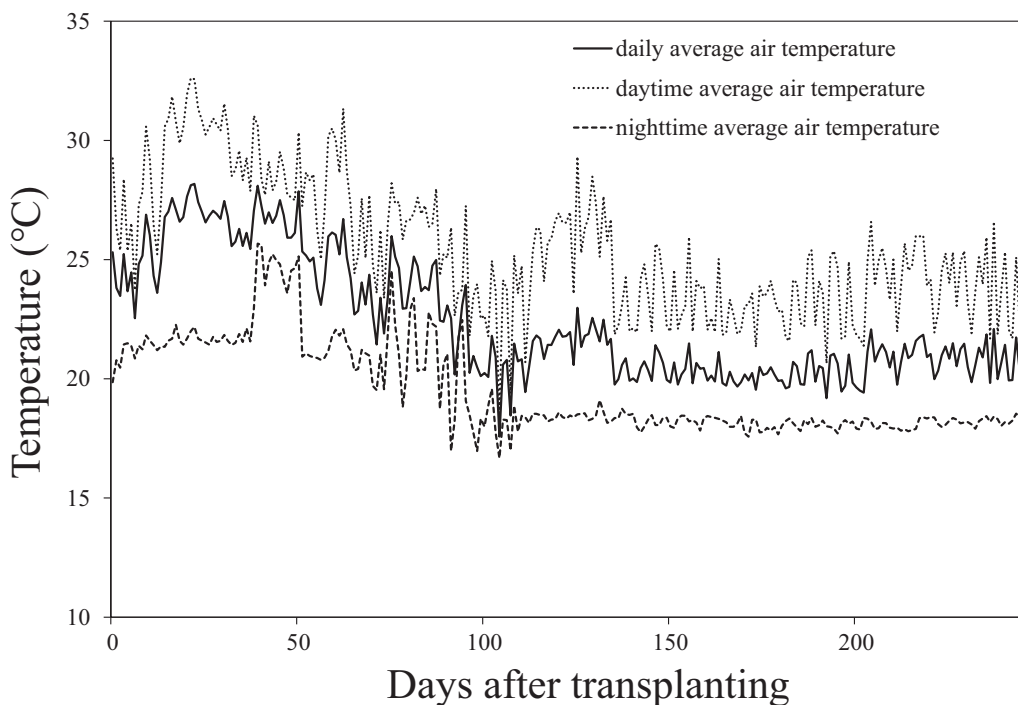


Fig. 1. Changes in the observed air temperature in the greenhouse for growing sweet pepper 'Artega' from 0 to 246 d after transplanting. The solid line (—), dotted line (···), and dashed line (- -) represent the daily average air temperature, daytime average air temperature, and nighttime average air temperature, respectively.

During this experiment, the anthesis date was defined as the date when the petals had completely opened and pollen was considered to be produced (Wubs et al., 2011). Anthesis dates at each node of the main stem were investigated two or three times per week from 42 to 83 DAT. Flowers were selected randomly from plants in each row. To plot a fruit growth curve, 33 fruit were harvested at 78 DAT, 25 fruit were harvested at 84 DAT, 22 fruit were harvested at 90 DAT, and 34 fruit were harvested at 97 DAT from any plants in each row; 1 fruit was harvested between the age of 0 to 9 d after anthesis (DAA), 15 fruit were harvested between the age of 10 to 19 DAA, 36 fruit were harvested between the age of 20 to 29 DAA, 26 fruit were harvested between the age of 30 to 39 DAA, 34 fruit were harvested between the age of 40 to 49 DAA, and 2 fruit were harvested between the age of more than 50 DAA. Fresh fruit were assessed for fresh weight (grams per fruit) and dry matter weight (grams per fruit). Fruit were dried for at least 72 h at 105 °C before dry matter weight was measured (large forced ventilation drier; Maruto Testing Machine; Tokyo, Japan).

For three randomly selected plants in each row (a total of 12 plants), the anthesis and abortion dates at each node on the main stem at 0 to 246 DAT were recorded twice per week. At the time of each measurement, if the flowers had fallen, then the abortion date of each node was recorded. Anthesis and abortion dates of all flowers on the 12 plants were recorded, and all fruit were harvested at the fully mature stage.

Each main stem had 40 to 50 nodes (80–100 flowers per plant) at the end of the experiment. Twenty-nine flowers dropped before anthesis from 12 plants; therefore, we excluded them from the analyses. A total of 1035 data points were recorded for the anthesis and abortion dates from 12 plants. Flowers observed at 233 to 246 DAT were excluded from our analyses because it was possible that they would abort after the end of the experiment.

Hence, the anthesis and abortion dates of 952 flowers at 0 to 232 DAT were used for the statistical analyses.

Daily total dry matter (TDM) production per unit area (grams per m<sup>2</sup>) was defined as the source strength that day. TDM<sub>m</sub> at *m* DAT was estimated based on Eqs. [1] to [3] using the calculations presented by Higashide (2018) and Watabe et al. (2021):

$$\text{TDM}_m = \text{LUE}_m \times \text{IL}_m \quad [1]$$

$$\text{LUE}_m = a \times \ln(\text{CO}_{2m}) + o \quad [2]$$

$$\text{IL}_m = (1 - e^{-k \times \text{LAI}_m}) \times T_g \times R_p \times \text{Sr}_m \quad [3]$$

where LUE<sub>m</sub> (grams per megajoule) is the light use efficiency at *m* DAT (Table 2). LUE<sub>m</sub> is a function of daytime mean CO<sub>2</sub> concentration in the greenhouse. IL<sub>m</sub> (megajoules per m<sup>2</sup>) is the cumulative amount of light intercepted by the plant at *m* DAT; this amount is a function of outside solar radiation at *m* DAT (Sr<sub>m</sub>; megajoules per m<sup>2</sup>), light transmissivity of the greenhouse (T<sub>g</sub> = 0.65 MJ·MJ<sup>-1</sup>) (Watabe et al. 2021), ratio of photosynthetically active radiation (PAR) to outside solar radiation (R<sub>p</sub> = 0.5 MJ·MJ<sup>-1</sup>) (Ohtani 1997), leaf area index at *m* DAT (LAI<sub>m</sub>; m<sup>2</sup> per m<sup>2</sup>), and light extinction coefficient (*k*) (Monsi and Saeki, 2005; Watabe et al., 2021). Coefficients for estimating LUE<sub>m</sub> and light extinction coefficients were cited by Watabe et al. (2021). Details of the methodology for estimating light extinction coefficients were reported by Monsi and Saeki (2005) and Watabe et al. (2021). During this experiment, PPFD and LAI in each plant were measured at 196 and 198 DAT and at 210 or 211 and 212 DAT, respectively. During the PPFD measurements at 196 and 210 or 211 DAT, the plant canopy was segmented into four and five layers, respectively, and the PPFD in each layer was measured by using a line quantum sensor (LI-191R; LI-COR, Lincoln, NE) and light meter (LI-250A; LI-COR). Each leaf area in each layer was measured individually to estimate the LAI. During the destructive measurement, the leaf

Table 2. All abbreviations and units considered in the model used for estimating the effects of source and sink strength on the fruit set ratio of sweet pepper 'Artega' from different days before and after the anthesis date.

Abbreviated name	Description	Units
DAT	Days after transplanting date	d
DBA	Days before anthesis date	d
DAA	Days after anthesis date	d
TDM <sub>m</sub>	Total dry matter production per unit area at <i>m</i> DAT	g·m <sup>-2</sup> ·d <sup>-1</sup>
LUE <sub>m</sub>	Light use efficiency at <i>m</i> DAT	g·MJ <sup>-1</sup> ·d <sup>-1</sup>
IL <sub>m</sub>	Light intercepted by plants per unit area at <i>m</i> DAT	MJ·m <sup>-2</sup> ·d <sup>-1</sup>
LAI <sub>m</sub>	Leaf area index at <i>m</i> DAT	m <sup>2</sup> ·m <sup>-2</sup> ·d <sup>-1</sup>
T <sub>g</sub>	Light transmittivity in the greenhouse	MJ·MJ <sup>-1</sup>
R <sub>p</sub>	Ratio of photosynthetically active radiation to the outside solar radiation	MJ·MJ <sup>-1</sup>
Rr <sub>m</sub>	Outside solar radiation per unit area at <i>m</i> DAT	MJ·m <sup>-2</sup> ·d <sup>-1</sup>
TDM <sub>m,st</sub>	Total dry matter production per stem <i>st</i> at <i>m</i> DAT	g/stem per day
STD	Stem density per unit area set at cultivation	stem/m <sup>2</sup>
DWF	Dry matter weight per fruit	g/fruit
SSF <sub>m,n</sub>	Fruit sink strength of fruit number <i>n</i> at <i>m</i> DAT	g/fruit per day
SST <sub>m,st</sub>	Fruit sink strength per stem <i>st</i> at <i>m</i> DAT	g/stem per day
SSR <sub>m,st</sub>	Source-to-sink ratio per stem <i>st</i> at <i>m</i> DAT	g·g <sup>-1</sup> ·d <sup>-1</sup>
FRN <sub>m,st</sub>	Fruit number per stem <i>st</i> at <i>m</i> DAT	fruit/stem per day
FSR <sub>m</sub>	Fruit set ratio at <i>m</i> DAT	fruit/flowers per day
BFL <sub>m</sub>	Quantity of flowers at <i>m</i> DAT	flowers/d
AFL <sub>m</sub>	Quantity of aborted flowers at <i>m</i> DAT	flowers/d

area was measured using an automatic leaf area meter (AAC-400; Hayashi Denko, Tokyo, Japan). The daily LAI was obtained by linear interpolation of the averaged data of destructively measured plants. Eight plants were measured destructively at 0, 15, 30, 49, 84, 118, 160, 184, 198, and 212 DAT. Approximately two leaves grew in each node, and the node numbers eventually reached 37 to 42 at 212 DAT. Therefore, ≈74 to 84 leaves per stem were measured at 212 DAT.

The daily total dry matter production per stem (TDM<sub>m,st</sub>; grams per stem) was obtained using Eq. [4] by dividing the TDM<sub>m</sub> by the stem density:

$$TDM_{m,st} = \frac{TDM_m}{STD} \quad [4]$$

where STD is the stem density in this experiment (7.5 stems/m<sup>2</sup>) and *st* is the number of stems per plant.

We used the Gompertz function in Eq. [5] based on the method of Wubs et al. (2012), to express the relationship between the cumulative temperature after anthesis and dry matter weight per fruit (DWF):

$$DWF = K \times b^{e^{-c \times x}} \quad [5]$$

where DWF is the dry matter weight per fruit (grams per fruit) at time *x* (cumulative temperature from 0 DAA; °C·d<sup>-1</sup>), *K* is the asymptote line, *b* is the intercept of the function, and *c* is a constant determining the curvature.

Fruit sink strength per fruit (SSF<sub>m,n</sub>; grams per fruit) at *m* DAT was calculated using Eq. [6] according to Wubs (2010) and Wubs et al. (2012). Eq. [6] is a derivative of Eq. [5]:

$$SSF_{m,n} = -[(K \times b^{e^{-c \times x}}) \times \ln(b) \times (c \times e^{-c \times x})]_m \quad [6]$$

where *n* is the number of fruit per stem at *m* DAT. The explanatory variable *x* and the coefficients (*K*, *c*, and *b*) are the same as those in Eq. [5]. By accumulating SSF<sub>m,n</sub> (grams per fruit) for each fruit at *m* DAT, the daily fruit sink strength per stem

(SST<sub>m,st</sub>; grams per stem) can be estimated using Eq. [7]. The source-to-sink ratio (SSR<sub>m,st</sub>; grams per gram) per stem at *m* DAT was calculated using Eq. [8]:

$$SST_{m,st} = \sum_0^n (SSF_{m,n}) \quad [7]$$

$$SSR_{m,st} = \frac{TDM_{m,st}}{SST_{m,st}} \quad [8]$$

Wubs et al. (2007, 2009a, 2011) reported that flowers were most susceptible to abortion just before anthesis and at 0 to 14 DAA. During this experiment, we investigated the anthesis and abortion dates of 952 flowers at 0 to 232 DAT. An abortion rate of 78.1% occurred between 0 and 7 DAA, and a rate of 91.4% occurred between 0 and 14 DAA. Therefore, by using the method of Higashide (2009), we investigated the average TDM<sub>m,st</sub>, SST<sub>m,st</sub>, SSR<sub>m,st</sub>, and fruit number (FRN<sub>m,st</sub>; fruit per stem) at *m* DAT at different periods before and after anthesis. Then, we determined Pearson's correlation coefficients (*r*) of TDM<sub>m,st</sub>, SST<sub>m,st</sub>, SSR<sub>m,st</sub>, and FRN<sub>m,st</sub> with the fruit set ratio (FSR) every 7 d from 25 to 232 DAT to determine the period with the highest correlation with the FSR. During the calculation of FSR, data from 0 to 24 DAT were excluded because we could not measure the first flower of 12 investigated plants until 24 DAT. The FSR<sub>m</sub> at *m* DAT was defined using Eq. [9]:

$$FSR_m = \frac{BFL_m - AFL_m}{BFL_m} \quad [9]$$

where BFL<sub>m</sub> is the number of flowers at *m* DAT and AFL<sub>m</sub> is the number of aborted flowers at *m* DAT. We counted BFL<sub>m</sub> and AFL<sub>m</sub> once to twice per week in the greenhouse.

After identifying the factors affecting FSR<sub>m</sub> and the effective period for FSR<sub>m</sub>, we analyzed the quantitative effects of these factors within an effective period on FSR<sub>m</sub> by applying a regression analysis. We used statistical software (R version 3.6.3; R Foundation for Statistical Computing, Vienna, Austria) for all analyses.

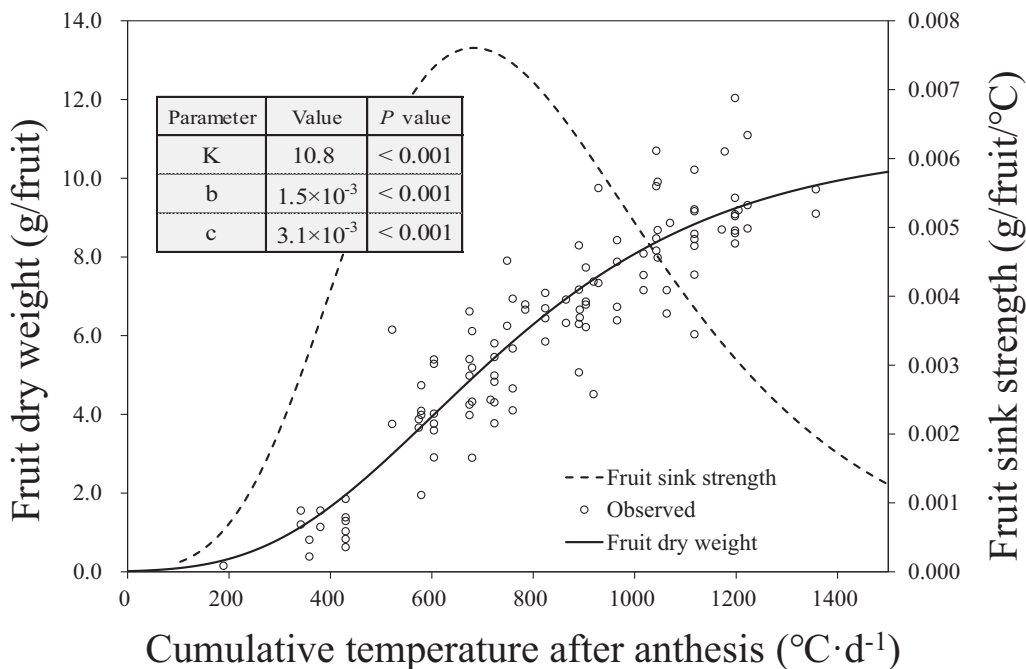


Fig. 2. Estimated fruit dry weight (solid line: —), estimated fruit sink strength (dashed line: - -), and observed fruit dry weight (open circle: ○) of sweet pepper ‘Artega’ grown in the greenhouse at different cumulative temperatures after anthesis ( $^{\circ}\text{C}\cdot\text{d}^{-1}$ ). Estimated parameters K, b, and c of the Gompertz function were statistically significant ( $P < 0.001$ ) based on the observed fruit samples with different fruit sizes harvested at 78, 84, 90, and 97 d after transplanting ( $n = 114$ ).

## Results

The observed DWF (grams per fruit) increased gradually with the cumulative temperature after anthesis (Fig. 2). The Gompertz function was applied to estimate the relationship between cumulative temperature after anthesis and DWF. We plotted the estimated DWF values (solid line in Fig. 2). We chose the Gompertz function for expressing fruit growth based on previous studies (Adams et al., 2001; Wubs, et al., 2012). All estimated parameters (K, b, c) of the Gompertz function were statistically significant ( $P < 0.001$ ); therefore, this function could describe fruit growth with statistical validity during this experiment. We also plotted a differential curve of the Gompertz function (dashed line in Fig. 2) and treated it as the  $\text{SSF}_{m,n}$ . The estimated DWF values (solid line in Fig. 2) showed increasing cumulative fruit weight corresponding to the cumulative temperature. The differential curve of the Gompertz function (dashed line in Fig. 2) showed the instantaneous fruit weight increase with each cumulative temperature.  $\text{SSF}_{m,n}$  increased rapidly from anthesis ( $0^{\circ}\text{C}\cdot\text{d}^{-1}$ ) to the vertex of the regression curve (at a cumulative temperature of  $\approx 622^{\circ}\text{C}\cdot\text{d}^{-1}$ ); then, it decreased gradually from the vertex to the harvestable period ( $1200^{\circ}\text{C}\cdot\text{d}^{-1}$  to  $1400^{\circ}\text{C}\cdot\text{d}^{-1}$ ). In other words, the fruit growth rate reaches its maximum at  $622^{\circ}\text{C}\cdot\text{d}^{-1}$ , which indicates a half time  $x$  temperature period for the fruit to reach its final size. At this point, the fruit has not started to change its color.

The estimated  $\text{TDM}_{m,st}$  fluctuated from 0.2 to 3.1 g/stem per day with the changes in solar radiation and daily  $\text{CO}_2$  concentration in the greenhouse (Fig. 3A and B). Estimated and observed cumulative  $\text{TDM}_{m,st}$  are shown in Fig. 3C. We examined the  $\text{SST}_{m,st}$  and  $\text{SSR}_{m,st}$  of weekly moving averages from 0 to 232 DAT (Fig. 4A). The daily  $\text{SST}_{m,st}$  had an inverse relationship with  $\text{SSR}_{m,st}$ ; a high  $\text{SST}_{m,st}$  with a low  $\text{SSR}_{m,st}$  alternated with a low  $\text{SST}_{m,st}$  with a high  $\text{SSR}_{m,st}$ . The daily  $\text{SST}_{m,st}$  at 73 to

94 DAT, 135 to 150 DAT, and 207 to 234 DAT exceeded  $0.7$  g/stem. We plotted the change in the mean  $\text{FSR}_m$  of 10-d moving averages from 0 to 232 DAT (Fig. 4B). High values ( $>0.50$ ) were observed at  $\approx 20, 60, 120,$  and  $180$  DAT (Fig. 4B). The values fluctuated cyclically; the mean  $\text{FSR}_m$  over the whole period was  $\approx 0.37$  (Fig. 4B).  $\text{SSR}_{m,st}$  at 0 to 26 DAT, 110 to 123 DAT, and 170 to 192 DAT exceeded 3.0; these periods corresponded to periods of high  $\text{FSR}_m$  (exceeding 0.50) (Fig. 4A and B). High  $\text{SST}_{m,st}$  periods corresponded to periods of low  $\text{FSR}_m$  ( $<0.20$ ) (Fig. 4A and B). Additionally,  $\text{SST}_{m,st}$  increased and  $\text{FSR}_m$  decreased  $\approx 30$  d ( $\approx 622^{\circ}\text{C}\cdot\text{d}^{-1}$  from anthesis) after each flush period.

Harvested fruit fresh yields of 10-d moving averages fluctuated cyclically through cultivation (Fig. 4C). Before  $\approx 2$  months from harvest,  $\text{FSR}_m$  also fluctuated with the same tendency (Fig. 4B and C). From 25 to 232 DAT, the average daily  $\text{TDM}_{m,st}$  was 1.16 g/stem, the average daily  $\text{SST}_{m,st}$  was 0.59 g/stem, and the average daily  $\text{SSR}_{m,st}$  was  $2.18 \text{ g}\cdot\text{g}^{-1}$  (data not shown).

Table 3 shows Pearson’s correlation coefficients ( $r$ ) of the  $\text{FSR}_m$  and weekly average  $\text{TDM}_{m,st}$ ,  $\text{SST}_{m,st}$ ,  $\text{SSR}_{m,st}$ , and  $\text{FRN}_{m,st}$  during different 7-d periods before and after anthesis during the period from 25 to 232 DAT.  $\text{FSR}_m$  was correlated positively and significantly with  $\text{TDM}_{m,st}$  and  $\text{SSR}_{m,st}$ , except during the periods from 9 DBA to 5 DAA and from 9 DBA to 1 DBA, respectively.  $\text{FSR}_m$  was correlated negatively and significantly with  $\text{SST}_{m,st}$  and  $\text{FRN}_{m,st}$ , except during the period from 5 DBA to 13 DAA for  $\text{FRN}_{m,st}$  (Table 3). The  $r$  values in the case of  $\text{SST}_{m,st}$  during the period 3 DBA to 5 DAA were more than 0.60; in the case of  $\text{SSR}_{m,st}$ , the  $r$  values during the period 1 DBA to 13 DAA were also more than 0.60 (Table 3).

We examined the relationships between  $\text{FSR}_m$  calculated using 30-sample moving averages and the average  $\text{TDM}_{m,st}$  (Fig. 5A),  $\text{SST}_{m,st}$  (Fig. 5B),  $\text{SSR}_{m,st}$  (Fig. 5C), and  $\text{FRN}_{m,st}$  (Fig. 5D) of these samples. Explanatory factors were sorted in ascending order

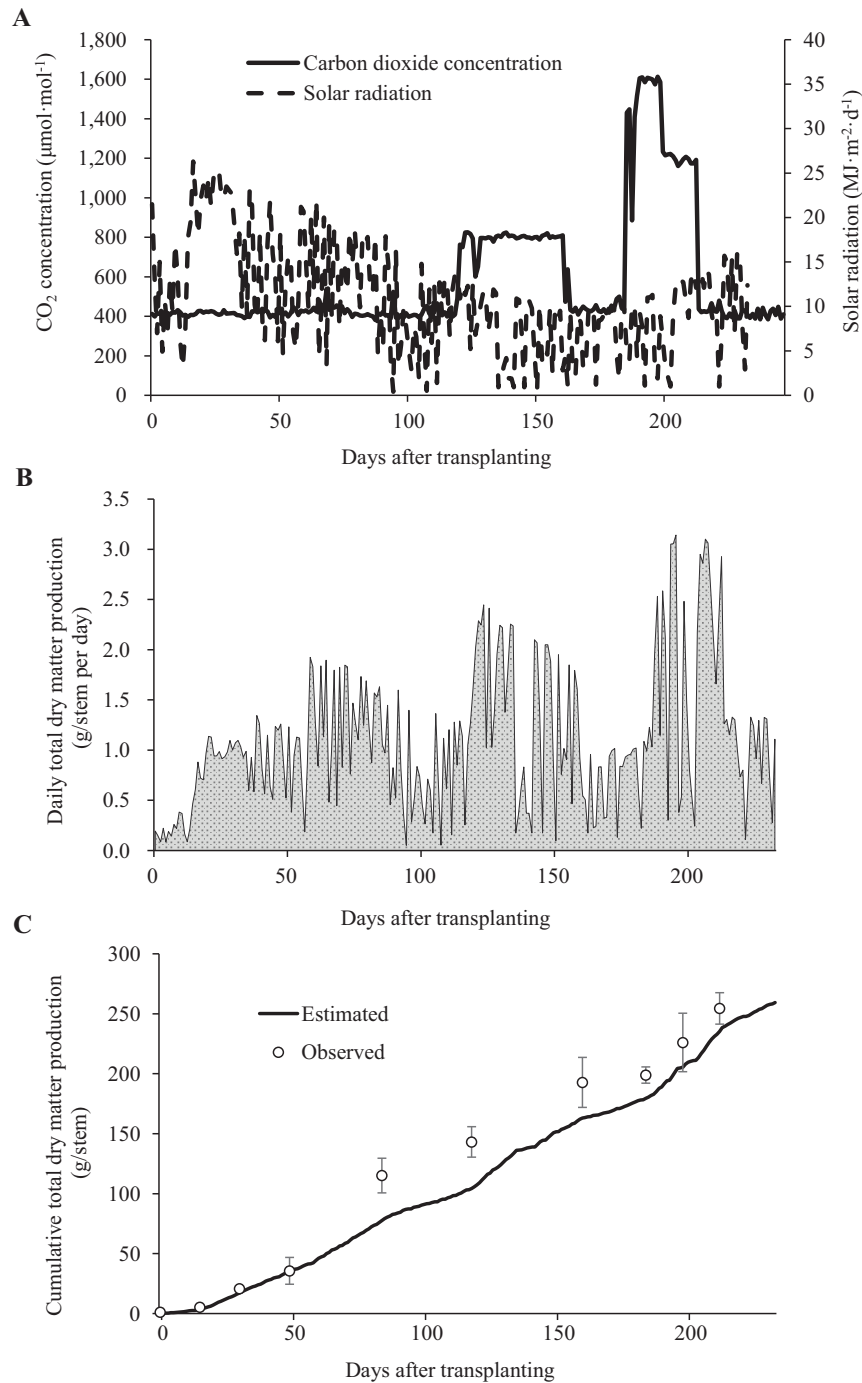


Fig. 3. Changes in the cumulative outside solar radiation (dashed line: - -) and daytime CO<sub>2</sub> concentration in the greenhouse (solid line: —) from 0 to 232 d after transplanting (A), in the calculated daily total dry matter production of sweet pepper ‘Artega’ grown in the greenhouse from 0 to 232 d after transplanting (B), and in the estimated (solid line: —) and observed (open circle: ○) cumulative total dry matter production of sweet pepper ‘Artega’ grown in the greenhouse from 0 to 232 d after transplanting (C). Error bars indicate mean ± SD (n = 8). Data were recorded 0, 15, 30, 49, 84, 118, 160, 184, 198, and 212 d after transplanting.

and averaged during the period 1 to 7 DAA. This period was chosen because the  $r$  value for the correlation between  $FSR_m$  and  $SSR_{m_{st}}$  was highest (Table 3), and the relationships between  $FSR_m$  and  $TDM_{m_{st}}$ ,  $SST_{m_{st}}$  and  $SSR_{m_{st}}$  during this period were all statistically significant. The  $R^2$  value of the regression curves for the correlation of  $FSR_m$  with  $TDM_{m_{st}}$  was 0.41 (Fig. 5A). The  $R^2$  value of the regression curves for the correlation of  $FSR_m$  with  $SST_{m_{st}}$  was 0.80 (Fig. 5B). The  $R^2$  value of the

regression curves for the correlation of  $FSR_m$  with  $SSR_{m_{st}}$  was 0.81 (Fig. 5C). The  $R^2$  value of the regression curves for the correlation of  $FSR_m$  with  $FRN_{m_{st}}$  was 0.14 (Fig. 5D).  $FSR_m$  increased as  $TDM_{m_{st}}$  increased within the range of 0.5 to 2.0 g/stem per day (Fig. 5A).  $FSR_m$  decreased as  $SST_{m_{st}}$  increased; then, it tended toward saturation at values  $\geq 0.1$  (Fig. 5B).  $FSR_m$  increased when  $SSR_{m_{st}}$  was within the range of 1.0 to 4.0; then, it tended toward saturation at values  $\leq 1.0$  (Fig. 5C).

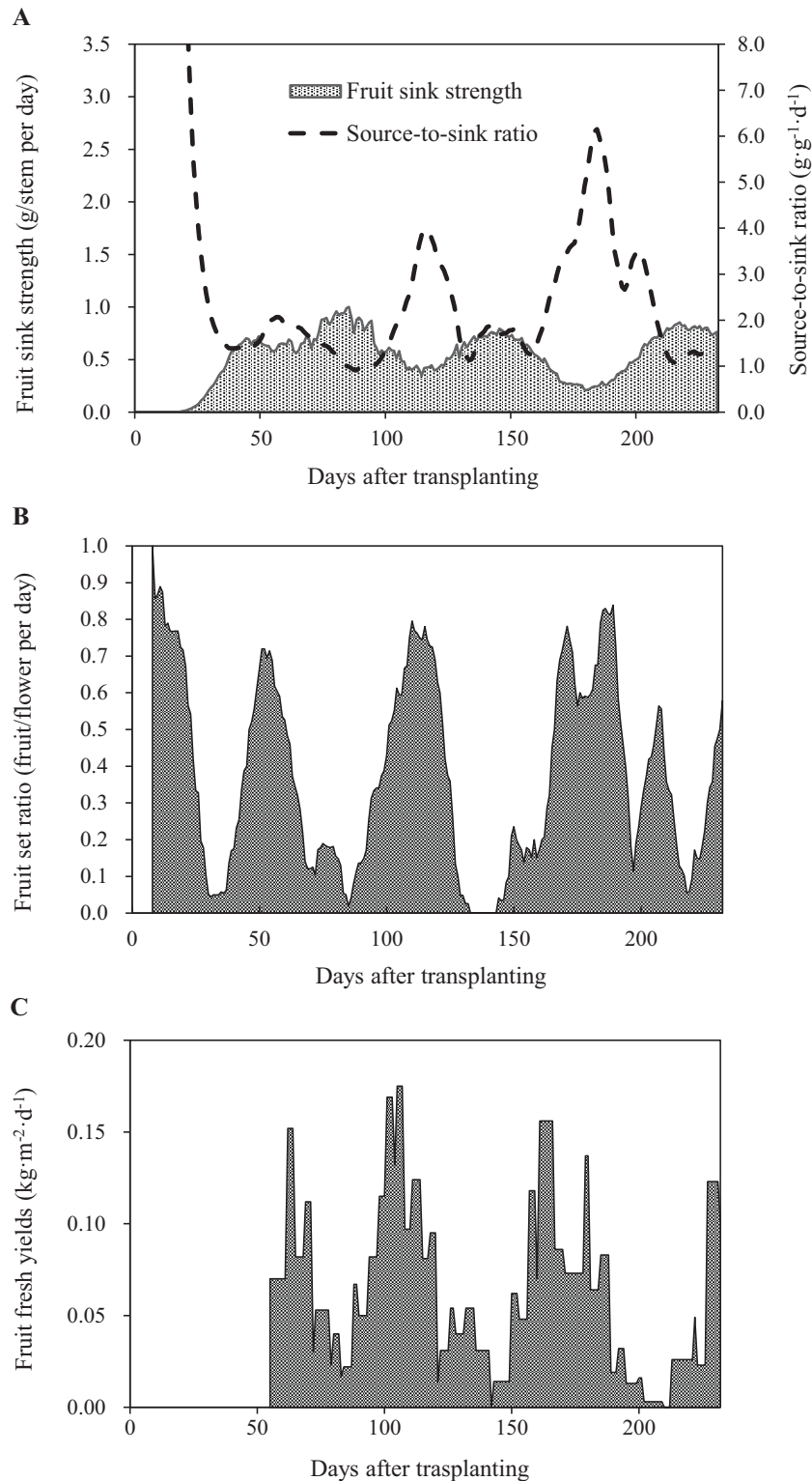


Fig. 4. Changes in the daily fruit sink strength and weekly moving averages source-to-sink ratio (A), 10-d moving averages fruit set ratio (B), and 10-d moving averages fruit fresh yields (C) of sweet pepper 'Artega' grown in the greenhouse from 0 to 246 d after transplanting. Fruit sink strength, source-to-sink ratio, and fruit fresh yields of 12 plants were calculated, and the fruit set ratios were calculated using 952 flower samples from 12 plants.

### Discussion

We defined fruit sink strength based on fruit growth (Eqs. [5] and [6]) according to the method of Wubs (2010) and Wubs et al. (2012). During some studies, fruit sink strength was

calculated on a daily basis (Kleijbeuker and Lee, 2019; Wubs et al., 2009b). However, fruit growth is closely related to the daily mean temperature (de Koning, 1994). For example, the growth rate of tomato (*Solanum lycopersicum*) fruit grown in high temperatures was significantly increased compared to

Table 3. Pearson's correlation coefficients ( $r$ ) of the relationships between weekly average fruit set ratio ( $FSR_m$ ) and daily average total dry matter production per stem ( $TDM_{m\_st}$ ), fruit sink strength per stem ( $SST_{m\_st}$ ), source-to-sink ratio per stem ( $SSR_{m\_st}$ ), and fruit number per stem ( $FRN_{m\_st}$ ) of sweet pepper 'Artega' grown in the greenhouse from 25 to 232 d after transplanting. Weekly average  $FSR_m$  for 7-d periods ( $n = 30$ ) were calculated using 909 flower samples from 12 plants, and the corresponding  $TDM_{m\_st}$ ,  $SST_{m\_st}$ ,  $SSR_{m\_st}$ , and  $FRN_{m\_st}$  were calculated for 7-d periods from 9 d before anthesis (DBA) to 13 d after anthesis (DAA).

Period	Correlation ( $r$ ) between $FSR_m$ calculated every 7 d from 25 to 232 DAT and averaged							
	$TDM_{m\_st}$ <sup>i</sup>		$SST_{m\_st}$		$SSR_{m\_st}$		$FRN_{m\_st}$	
9 to 3 DBA <sup>ii</sup>	-0.24 <sup>iii</sup>	NS	-0.45	**	0.14	NS	-0.33	*
7 to 1 DBA	-0.06	NS	-0.52	***	0.24	NS	-0.32	*
5 DBA to 1 DAA	0.12	NS	-0.57	***	0.41	**	-0.27	NS
3 DBA to 3 DAA	0.24	NS	-0.61	***	0.56	***	-0.19	NS
1 DBA to 5 DAA	0.30	NS	-0.61	***	0.63	***	-0.12	NS
1 DAA to 7 DAA	0.42	**	-0.58	***	0.64	***	-0.01	NS
3 DAA to 9 DAA	0.42	**	-0.52	***	0.61	***	0.02	NS
5 DAA to 11 DAA	0.48	**	-0.45	**	0.61	***	0.06	NS
7 DAA to 13 DAA	0.57	***	-0.34	*	0.60	***	0.08	NS

<sup>i</sup> DAT = days after transplanting;  $FRN_{m\_st}$  = fruit number;  $FSR_m$  = fruit set ratio at  $m$  DAT;  $SSR_{m\_st}$  = source-to-sink ratio;  $SST_{m\_st}$  = fruit sink strength;  $TDM_{m\_st}$  = total dry matter production per stem (st) at  $m$  DAT.

<sup>ii</sup> DAA = days after anthesis; DBA = days before anthesis.

<sup>iii</sup> Pearson's correlation coefficient excluding data between 0 to 24 and 233 to 246 d after transplanting.

The average weekly  $FSR_m$  ( $n = 30$ ) was calculated using the anthesis and abortion dates of 909 flowers at 25 to 232 DAT.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; NS = not significant.

tomato fruit grown in low temperatures (Adams et al., 2001). Therefore, we calculated the fruit sink strength based on the cumulative temperature (Fig. 2). Adams et al. (2001) indicated that

the tomato fruit weight decreased when grown under high temperatures. This implies that the fruit sink strength of each fruit also fluctuates during the seasons. During this experiment, the

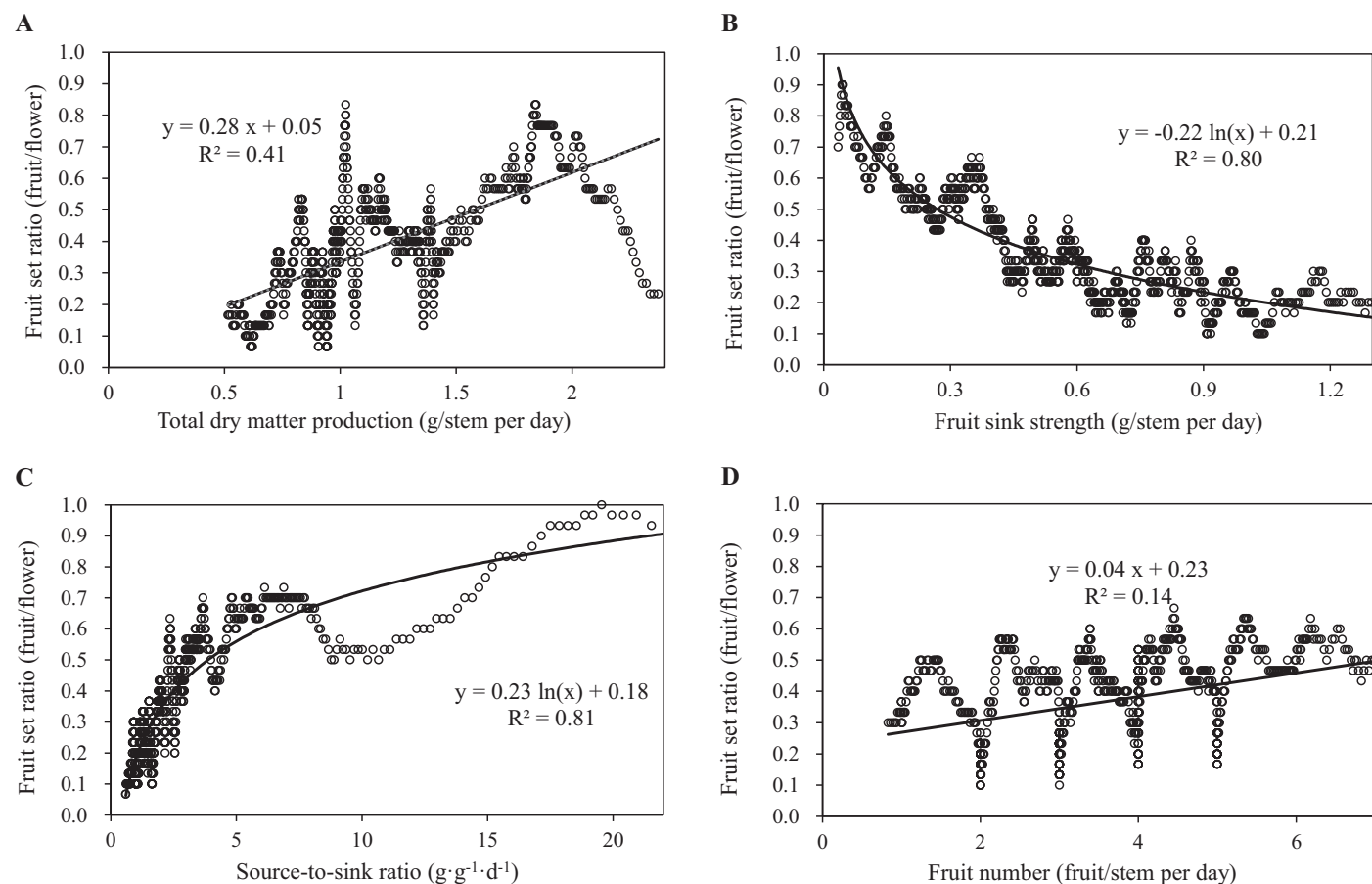


Fig. 5. Effects of daily average total dry matter production (A), fruit sink strength (B), source-to-sink ratio (C), and fruit number (D) at 1 to 7 d after anthesis on the fruit set ratio of sweet pepper 'Artega' grown in the greenhouse. The data of 952 flower samples from 12 plants were recorded from 0 to 232 d after transplanting. The fruit set ratio is shown as an open circle (○) calculated using the 30-sample moving average ( $n = 922$ ).



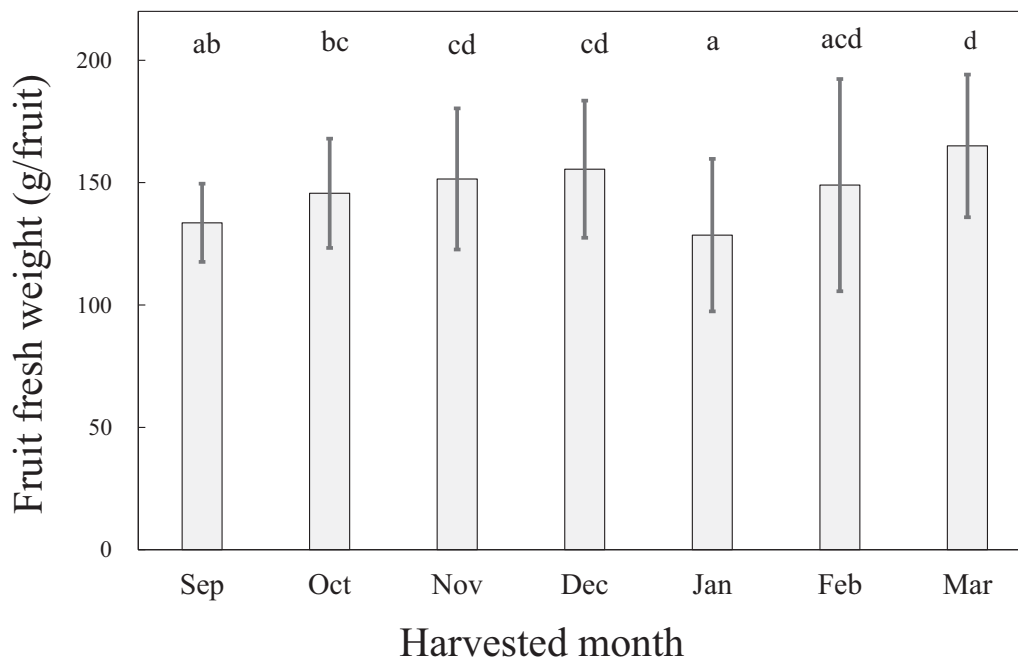


Fig. 6. The fluctuation of the monthly average individual fruit fresh weight of sweet pepper 'Artega' grown in the greenhouse. Fruit was harvested from 12 plants during cultivation. Error bars indicate mean  $\pm$  SD (Sept.,  $n = 49$ ; Oct.,  $n = 52$ ; Nov.,  $n = 44$ ; Dec.,  $n = 45$ ; Jan.,  $n = 42$ ; Feb.,  $n = 11$ ; Mar.,  $n = 43$ ). Different small letters represent significant differences at  $P < 0.05$  as determined by Tukey's test.

monthly averaged fruit fresh weight throughout cultivation also slightly fluctuated ( $P < 0.05$ ), but all values were within the SD (Fig. 6). Therefore, during this experiment, we could calculate the fruit sink strength without considering the seasonal variation of the fruit weight.

Crop parameters for estimating  $TDM_{m, st}$  [ $IL_m$  (k),  $LUE_m$  (a and o)] have statistical validity according to Watabe et al. (2021). During this study, we used  $TDM_{m, st}$  calculated using these crop parameters, but there were differences between the observed and calculated  $TDM_{m, st}$  at 84 and 118 DAT (observed  $TDM_{m, st} >$  calculated  $TDM_{m, st}$ ); these differences decreased after 118 DAT (Fig. 3C). During our experiment, we enhanced the EC of the nutrient solution from 2.0 to 2.5  $dS \cdot m^{-1}$  at 71 DAT. Yasuor et al. (2013) reported that the EC of the nutrient solution was closely related to the photosynthesis ability of sweet peppers. The enhancement of the EC of the nutrient solution at 71 DAT might improve photosynthesis and  $TDM_{m, st}$ .

By using models of dry matter production (Higashide, 2018, 2022; Watabe et al., 2021) and fruit growth based on Eqs. [5] and [6], we investigated the quantitative conditions associated with fruit set and abortion. As a result, the fruit set ratio was significantly and positively correlated with the total dry matter production and negatively correlated with the fruit sink strength (Table 3, Figs. 4 and 5). We represented the source-to-sink ratio using Eq. [8] as a function of total dry matter production and fruit sink strength. The fruit set ratio was also significantly and positively correlated with the source-to-sink ratio (Table 3, Fig. 5C). Based on these results, we propose that yield fluctuation of sweet pepper could be closely related to source-to-sink ratio fluctuation, which was determined by the change in total dry matter production and fruit sink strength. In other words, yield fluctuations are caused by both weather conditions and the quantity of fruit the plant is producing at the moment and the growth phase of those fruit.

Rapid increases in the source-to-sink ratio throughout the experimental period (Fig. 4A) were closely related to the occurrence of flushing, as reported previously (Heuvelink et al., 2004; Kleijbeuker and Lee, 2019; Wubs et al., 2009a, 2009b). Several studies have already presented models of the source-to-sink ratio and have evaluated its effects on the fruit set (Kleijbeuker and Lee, 2019; Wubs et al., 2009b, 2011). Our results showed that the fruit set ratio was significantly correlated with the source-to-sink ratio (Fig. 5C) when considering both the source-to-sink ratio and the most critical period for the fruit set (Table 3). From 1 DBA to 7 DAA, positive correlations between the source-to-sink ratio and fruit set ratio were observed (Table 3). Our results show an obvious relationship between flowering/pollination and fruit set. This period comprised anthesis to  $156 \pm 15^\circ C \cdot d^{-1}$  and represented the cumulative temperature. That is, the source-to-sink ratio from anthesis to  $\approx 156^\circ C \cdot d^{-1}$  was most closely related to the fruit set ratio results reported by Wubs et al. (2011). Because there was no difference between the source-to-sink ratio from anthesis to  $\approx 156^\circ C \cdot d^{-1}$  and the source-to-sink ratio from 1 DBA to 7 DAA during our experiments, we described the source-to-sink ratio on a daily basis during this study.

The fruit set ratio increased when the source-to-sink ratio at 1 to 7 DAA (from anthesis to  $156^\circ C \cdot d^{-1}$ ) was within the range of  $\approx 1.0$  to 4.0; the increment in the fruit set ratio decreased when the source-to-sink ratio increased to more than  $\approx 4.0$  (Fig. 5C). The fruit set ratio was  $\approx 0.5$  when the source-to-sink ratio was within the range of 3.0 to 4.0. In other words, it will be possible for growers to harvest constant fruit quantities by supplying three- to four-times the surplus photosynthates compared with that of fruit growth. Therefore, controlling and maintaining the source-to-sink ratio within this range might mitigate yield fluctuations. However, source and fruit sink manipulation may affect the dry matter distribution to each organ; therefore, further experimental studies are needed. Also, we investigated the

relationship between the fruit set ratio and the source-to-sink ratio within the following environments: daily average temperature,  $\approx 20$  to  $27^\circ\text{C}$  (Fig. 1); daytime  $\text{CO}_2$  concentration in the greenhouse,  $\approx 400$  to  $1600 \mu\text{mol}\cdot\mu\text{mol}^{-1}$  (Fig. 3); and daily drainage rate, 30% to 40%. However, not only the source-to-sink conditions within plants but also the high and low temperatures ( $<16$  or  $<32^\circ\text{C}$ ) (Bosland and Votava, 2012), lack of fertigation (positive correlation between irrigation level and fresh yields) (de Souza et al., 2019), and  $\text{CO}_2$  application during the winter season (Nederhoff and van Uffelen, 1988) considerably change the amount of fruit set as well. Therefore, we consider that our presented hypothesis has validity within the range of the environments used during this experiment. Overall, based on the relationship between the fruit set ratio and source-to-sink ratio at 1 to 7 DAA, it would be possible to predict the fruit set ratio. Prediction of the fruit set will help to moderate flushing and promises to help growers and retailers of sweet peppers.

In conclusion, we revealed the quantitative effects of the source-to-sink ratio and its critical period on the fruit set ratio. The fruit set ratio was positively correlated with  $\text{SSR}_{\text{m-st}}$  ( $R^2 = 0.81$ ) from 1 to 7 DAA (from anthesis to  $156^\circ\text{C}\cdot\text{d}^{-1}$ ). Therefore, the change in the source-to-sink ratio is similar to the fluctuation of the fruit set ratio, and the yield fluctuation occurred because the quantity of harvestable fruit could be determined by the fruit set ratio. Hence, the yield fluctuation of sweet pepper could be partly explained by this relationship. Knowledge of this relationship should be helpful for managing sweet pepper production and planning the harvest and labor distribution.

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