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Abstract: Osmotic stress enhances fruit quality, including the dry matter content, in tomatoes (Solanum lycopersicum L.). This study aimed at providing further insight into the precision control of fruit yield and quality on the long-term moderate osmotic stress conditions in tomato fruit production. We compared the growth pattern between fruits of two cultivars, typical Japanese and Dutch cultivars, under two different nutrient concentrations (2.3 and 5.0 dS m$^{-1}$) to understand the effect of electrical conductivity (EC) on dry mass and water content of fruits. The experiment was performed with a rockwool bag culture system in a controlled greenhouse. Increasing EC resulted in an approximately 20% decrease in fruit yield and a 0.5–1% increase in fruit dry matter content in both cultivars. This yield reduction was not caused by the fruit number, but by an approximately 25% decrease in individual fresh fruit weight. Non-linear models were used to describe the changes in dry matter content, water content, and dry weight of tomato fruit as a function of cumulative temperature. The decay rate of dry matter content in the fruit decreased with high EC treatments in the Japanese cultivar. The points at which the rates of changes in water and dry weight increased in the fruit were around 585 and 480 °C-days after anthesis, respectively, under the low EC condition. Rates of water increase in the fruit were changed by high EC treatment, while the shifts were opposite with respect to the cultivars. Dry weight increase in the fruit was not affected by EC treatment. Collectively, our findings clarify the effect of EC on the fruit growth characteristics of Japanese and Dutch tomato cultivars, and provide new insights into the yield of high-Brix tomato cultivation.

Keywords: cumulative temperature; dry mass; growth curve; osmotic stress; water flux

1. Introduction

Japanese consumers have long preferred high-quality and sweet-flavored tomato (Solanum lycopersicum L.) fruits. In hydroponically grown tomatoes, fruit quality is accomplished by irrigation strategies, including restricted irrigation frequency, increased electrical conductivity (EC) by adding saline to the nutrient solution, and using a highly concentrated nutrient solution [1–5]. These irrigation strategies trigger osmotic stress, and the detailed biological processes have been discussed elsewhere [6–11]. Osmotic stress increases the fruit quality characteristics, including soluble solid concentration (i.e., Brix%) and titratable acidity in fruits, and it also affects the water and carbon flux to fruits [12]. It is well known that Brix% and dry matter content are highly correlated with each other in tomatoes [13]. The literature indicates that there is a trade-off between yield and Brix% [14–17]. Severe osmotic stress causes growth and developmental defects throughout the shoot and root systems, and results in lower fruit yield [18–20]. Developmental defects caused by osmotic stress, for example, decreased leaf area, can accompany the inhibition of photosynthetic
performance. Therefore, understanding dry matter production and allocation to fruits under stress conditions is crucial [17,21]. At the actual production sites, previous studies attempting to produce high-Brix tomatoes conducted short-term low-truss crop management due to difficulty in maintaining plant vigor [14–17]. Thus, in this study, we aimed to achieve both slightly higher quality and long-term stable production of tomato fruits.

During tomato fruit growth, synthesized carbohydrate is accumulated at the early developmental stage [22]. Thus, starch accumulation at the early growth stage acts as a key of the final soluble solid content in the fruit [23,24]. Several studies have been reported regarding the sugar metabolism and related enzyme activities [25]. Furthermore, the water and carbon transport to fruits is affected by the fruit fresh and dry weight, and the osmotic potential triggers water inflow to the fruit by degradation of stored starch at the late cell expansion stage [22]. Osmotic stress could disturb water transport; however, few quantitative descriptions of water and dry matter accumulation exist [26]. Fruit growth is defined as an increase in fruit size and weight, and is of particular importance in crop production management, and growth curve analysis is a powerful technique for describing growth trajectories. Non-linear asymptotic models provide parameters for biological explanations, such as harvestable size and growth rate, to understand and estimate the growth pattern. The growth curves of tomato fruits have been reported in several studies [27–30]. The growth rate of tomatoes is responsive to temperature [31]. However, in the above studies, growth curves were calculated chronologically (i.e., growth per day), and no thermal time-adjusted approach (i.e., cumulative temperature (°C-days)) was conducted. Moreover, growth patterns under osmotic stress conditions remain elusive.

The prioritized breeding goal for Japanese tomato cultivars is to improve fruit quality, whereas in recent years, it has focused on the yield increase for Dutch cultivars [32]. Thus, attempts to clarify the difference between fruit yield and quality characteristics of Japanese and Dutch cultivars were made. For instance, a previous study reported that under a low-EC condition (1.5 dS·m⁻¹), the Dutch cultivar ‘Endeavour RZ F1’ had a higher yield and lower free sugar concentration than the Japanese cultivar ‘CF Momotaro York’ [33]. As mentioned above, several studies previously evaluated the yield and fruit quality under high-EC conditions (at least 3 dS·m⁻¹) [1–5]. In contrast, no studies have reported the differences in temporal patterns of weight changes during fruit growth under osmotic stress. Soilless culture in a controlled environment allows for the high production of tomatoes of consistent quality and quantity. Representative Japanese and Dutch tomato cultivars with different phenotypes were cultivated on a rockwool system, and the fruit size was non-destructively and continuously measured from anthesis to harvest. We constructed non-linear regression models of fruit size and compared the model parameters among cultivars and EC treatments to dissect the differences in growth patterns.

2. Materials and Methods
2.1. Growth Conditions
2.1.1. Greenhouse Environment

The experiments were conducted in a greenhouse at the Institute of Vegetable and Floriculture Science, National Agriculture and Food Research Organization, Tsukuba, Japan (36°26' N, 140°10' E). One compartment (width, 9 m; length, 18 m; gutter height, 5 m) was used to cultivate the tomato plants. The environmental conditions in the greenhouse were controlled and recorded every five minutes using an environmental control system (Maximizer; Priva, South Holland, The Netherlands). Natural ventilation began at 25 °C. Heating was achieved through a liquefied petroleum gas heating system (House Kaonki; Nepon, Tokyo, Japan), and heating initiation was set at 15 °C (day)/15 °C (night) from 17 days after transplanting (DAT), and then at 16 °C (day)/13 °C (night) from 48 DAT. A fogging system (LYOHM System; H. Ikeuchi, Tokyo, Japan) was used during the daytime for humidification, and relative humidity of >70% was maintained. The plants were shaded using a plastic sheet (28% shading rate) in the greenhouse when the temperature rose above 29 °C and with outdoor radiation above 0.6 kW·m⁻². The CO₂ concentration in the
greenhouse was maintained by applying liquid CO$_2$ to improve dry matter production. Lower limits of daytime CO$_2$ levels were set at 350 µmol·mol$^{-1}$ when ventilation windows were opened, and at 400 µmol·mol$^{-1}$ when they were closed. Nighttime CO$_2$ concentrations were not controlled. The daily environmental conditions during the experimental period are summarized in Figure 1a–c.

Figure 1. Changes in daily mean temperature (a), day-time mean CO$_2$ concentration (b), daily cumulative outdoor solar radiation (c), and day-time mean drainage EC (d) during the experiment. The dashed vertical lines indicate the start date of anthesis in the first truss (14 days after transplanting (DAT), 25 October 2019) and the start date of the investigation (76 DAT, 26 December 2019). Labels and symbols in (d) denote the cultivars (CF Momotaro York (My, black lines), Endeavour (En, gray lines)), and the treatments (low-EC (solid lines), high-EC (dashed lines)).

2.1.2. Plant Materials

Commercial tomato cultivar ‘CF Momotaro York’ (My) (Takii, Kyoto, Japan) and ‘Endeavour RZ F1’ (En) (Rijk Zwaan, South Holland, The Netherlands) were grown in open soilless culture on rockwool slabs.

Seeds were sown in 72-well plug trays filled with nursery soil (Tane Baido 1; Sumitomo Forestry Landscaping, Tokyo, Japan) on 10 September 2019 (En) or 11 September 2019 (My), and incubated in a germination chamber in the dark at 29 °C. Seedlings were placed in a growth chamber (Nae-terrace; Mitsubishi Chemical Agri Dream, Tokyo, Japan) on 13 September 2019 and grown under constant illumination on a 16-h day (25 °C)/8-h night (20 °C) cycle at 1000 µmol·mol$^{-1}$ CO$_2$. The seedlings were fertilized daily with a commercial nutrient solution mix (High-Tempo Ar and High-Tempo Cu; Sumitomo Chemical, Tokyo, Japan) at an adjusted EC of 2.0 dS·m$^{-1}$. The composition of the mixture was as follows: 7.74 mEq·L$^{-1}$ P, 11.04 mEq·L$^{-1}$ NO$_3$-N, 1.62 mEq·L$^{-1}$ S, 1.04 mEq·L$^{-1}$ NH$_4$-N, 6.73 mEq·L$^{-1}$ K, 2.00 mEq·L$^{-1}$ Mg, 5.95 mEq·L$^{-1}$ Ca, 4.07 mg·L$^{-1}$ Fe, 0.28 mg·L$^{-1}$ B, 0.41 mg·L$^{-1}$ Mn, 0.16 mg·L$^{-1}$ Zn, 0.05 mg·L$^{-1}$ Cu, and 0.07 mg·L$^{-1}$ Mo. On 4 October 2019, the seedlings were transplanted into rockwool cubes (width, 7.5 cm; length, 7.5 cm; height, 6.5 cm, Grodan Delta Block; Rockwool B.V., Limburg, The Netherlands), and incubated in the greenhouse for a week.

On 11 October 2019, the seedlings were transplanted into rockwool slabs (width, 20 cm; length, 100 cm; height, 7.5 cm, Grodan Expert; Rockwool B.V.). Planting beds were arranged in six rows and were 13.0 m long with 1.5 m between rows. Two rows beside the wall were used as guard plants, and the plant density was 2 plants·m$^{-2}$ (three plants per
slab), and aboveground parts of plants were arranged at 0.33-m intervals. The experimental area was placed within the four middle rows, and these four rows were prescribed with any combination of two cultivars and two nutritional supplements. The plant density was 3.3 plants m\(^{-2}\) (five plants per slab), and plants were arranged into 0.2-m intervals. Each four middle row contained 65 plants per experimental combination, and two border rows contained 39 plants per row. On 14 November 2019, plants were thinned out to 2.7 plants m\(^{-2}\) (four plants per slab), and plants were rearranged at 0.25 m intervals. Plants were trained on a single main stem in a V-shaped training system [34]. Plant lowering was continued along the entire length of the bed as they grew taller to balance their growth by exposing plants to the north-to-south direction of environmental deviation by turns. The older leaves were pruned to maintain the number at approximately 25 leaves per plant.

2.1.3. Nutrient Solution Treatment

The plants were supplied a mixture of commercial fertilizer solution (OAT House; OAT Agrio, Tokyo, Japan) with a modified SA prescription. Two concentrated stock solutions (Solution A: 1.5 g·L\(^{-1}\) OAT-S1 and 0.05 g·L\(^{-1}\) OAT-5, Solution B: 1.0 g·L\(^{-1}\) OAT-2) were mixed in a ratio of Solution A:Solution B = 1:1 using a diaphragm pump (RAKU-RAKU 3; CEM Corporation, Tokyo, Japan), and diluted with raw water to adjust the EC value. According to the manufacturer’s instruction, the nutrient contents at the standard dilution rate of concentrated stock solutions (100-fold) were as follows: 17.1 mEq·L\(^{-1}\) NO\(_3\)-N, 0.4 mEq·L\(^{-1}\) NH\(_4\)-N, 4.4 mEq·L\(^{-1}\) P, 10.2 mEq·L\(^{-1}\) K, 8.2 mEq·L\(^{-1}\) Ca, 3.0 mEq·L\(^{-1}\) Mg, 2.75 mg·L\(^{-1}\) Mn, 3.05 mg·L\(^{-1}\) B, 7.95 mg·L\(^{-1}\) Fe, 0.07 mg·L\(^{-1}\) Cu, 0.17 mg·L\(^{-1}\) Zn, 0.07 mg·L\(^{-1}\) Mo, and EC was 2.6 dS·m\(^{-1}\). Mineral concentrations in raw water were 0.73 mEq·L\(^{-1}\) NO\(_3\)-N, 0.12 mEq·L\(^{-1}\) K, 0.12 mEq·L\(^{-1}\) Ca, and 0.21 mEq·L\(^{-1}\) Mg, respectively. Two levels of nutritional supplementation were administered: low-EC, high-EC. The nutrient solution was maintained at a constant EC of 2.3 dS·m\(^{-1}\) in the low-EC treatment. In the high-EC treatment, the target value of the nutrient solution was gradually increased from 3.7 dS·m\(^{-1}\) (2 DAT) to 5.0 dS·m\(^{-1}\) (21 DAT), and then maintained until the end of the experiment (15 April 2020, 187 DAT). The nutrient solution application was controlled based on outdoor solar radiation, and its frequency was 1 MJ m\(^{-2}\). A daily drainage rate was maintained above 25% of the total nutrient solution applied, and the drainage was discarded. Continuous measurement of the volume and EC of the drainage was performed with a tipping-bucket-type meter (Agrilog, ITKOBO-Z, Nagoya, Japan) at five-minute intervals. The drainage EC when drainage was discharged, was averaged to obtain the daytime mean drainage ECs during the experimental period, and these are summarized in Figure 1d.

2.2. Sampling and Measurement

2.2.1. Continuous Measurement

Flowers were sprayed with a 1/150 dilution of ‘Tomato Tone’ (containing 0.15% 4-chlorophenoxyacetic acid; ISK Biosciences K.K., Tokyo, Japan) at anthesis of the third flower in each truss. The treatment date was time zero for the subsequent investigation. To measure temporal changes in fruit size, three diameters (length of longitudinal axis, major horizontal axis, and minor axis (cm)) of the second or third fruit in each truss were measured once or twice a week with a caliper from when the horizontal diameter of the fruit exceeded 15 mm until harvest. To consider the effect of fruit load on the competition for fruit growth, the measurement was started from the beginning of the harvest of the undermost fruits (26 December 2019, 76 DAT (My) or 29 December 2019, 79 DAT (En)), when it was presumed that the amount of bearing fruit became constant. The measurement target was the fruit after the seventh truss (My) or eighth truss (En). Throughout the experiment, fruits up to the 11th truss reached harvestable color. The measurement values were obtained for at least ten fruits in each truss, and the two highest and two lowest values were excluded from the calculation procedures. The number of fruits and measuring times per treatment that were included in the analyses were as follows: 48 and 344 for My, low-EC;
44 and 335 for My, high-EC; 42 and 345 for En, low-EC; and 48 and 393 for En, high-EC. When the fruits reached the harvestable stage, continuous measurement was finished and the fruits were harvested. The harvest was conducted with a calyx with a peduncle attached. The criteria for fruit maturity and harvesting point was based on color change to light red (60–90% of fruit surface being red) [35]. After harvesting, individual fruit fresh weight (g) and dry weight (g) were measured, and the ratio of dry weight to fresh weight (i.e., dry matter content (%)) was determined. Dry weight was measured after drying at 80 °C for 72 h. Except for the temporal change measurements, harvested fruits were discarded after measuring their fresh weight. The remaining immature to near-harvestable fruits upward from the 12th truss were sampled at the end of the experiment (15 April 2020, 187 DAT). The number of immature fruits per treatment was as follows: 92 for My, low-EC; 88 for My, high-EC; 105 for En, low-EC; and 108 for En, high-EC. After sampling, individual fruit diameters and fresh weights were measured to estimate the allometric relationships of fruit size and fresh weight, and individual fruit dry matter content was determined to estimate the temporal changes during fruit growth.

2.2.2. Destructive Measurement

The aboveground portion of the plants (n = 8 for each sample) was sampled at the end of the experiment (15 April 2020, 187 DAT). The sampled plants were divided into leaves (including petioles), stems, and fruits. The leaf area and dry weight of each part were determined. The leaf area (cm²) was measured using a leaf area meter (LI-3100; LI-COR, Lincoln, NE, USA). Pruned older leaves were included in the measurement of leaf dry weight but were not included in the leaf area. Fresh and dry weight yields were calculated as the sum of harvested and remaining immature fruits. The actual fresh weight of all fruits was measured and summed to obtain the fresh weight yield. Except for the above-described temporal change experiment, the individual dry weight of the harvested fruits was estimated by multiplying the individual fresh weight and mean dry matter content. The dry weights of the remaining immature fruits were measured individually to obtain the dry matter content for each growth duration. The dry weight yield was obtained as the sum of the actual harvested dry weight of the temporal change experiment, estimated dry weight of other harvested fruits, and actual dry weight of immature fruits.

2.3. Statistics

All statistical and regression analyses were performed using statistical software including Excel (Microsoft, Redmond, WA, USA) and R (ver. 4.0.4; https://www.R-project.org/ accessed on 20 February 2021).

The non-destructive estimation of fresh fruit weight from measured diameters was assessed using the allometric power law relationship:

\[ F_w = A(Vol)^B \] (1)

where \( F_w \) is the fresh fruit weight (g), \( Vol \) is the estimated fruit volume calculated by ellipsoidal approximation (cm³), and \( A \) and \( B \) are the coefficients of the allometric scaling factor estimated by ANCOVA. Coefficient \( A \) was 1.093 (My, low-EC), 1.108 (My, high-EC), 1.078 (En, low-EC), and 1.074 (En, high-EC). Coefficient \( B \) was 1.003 for each sample.

For the growth curve analyses of fruit weight, the Gompertz function [36] was applied to determine the curve parameters:

\[ W_t = C e^{-De^{-Et}} \] (2)

where \( W_t \) is the estimated fruit weight characteristics, \( C_t \) is the cumulative temperature after anthesis (°C-days), and \( C, D, \) and \( E \) are coefficients of the function that are biologically interpreted as asymptotic \( W_t \), integrated constant related to initial \( W_t \), and growth rate, respectively. \( W_t \) includes the fresh weight (g), relative dry mass (g g⁻¹), and relative water content (g g⁻¹). Before fitting the model, the initial fresh weight at anthesis (0 °C-days)
was set at 0.1 g. Estimated dry weight was calculated by the multiplication of fresh weight and fruit dry matter content at each sampling point, and estimated water content was calculated by subtracting the fresh and dry weights. The values at harvest were rescaled to 1 to obtain the relative dry mass and relative amount of water.

To estimate the dry weight growth curve, the non-destructively estimated fresh fruit weight at each time point was multiplied by the fruit dry matter content to obtain the estimated fruit dry weight. Destructively obtained individual fruit dry matter contents upward from the 12th truss were arranged in order of the cumulative temperature after anthesis and considered this order as the pseudo-time series of the fruit growth. Temporal changes in dry matter content were then modeled using the exponential decay curve. The following equation was used to determine the dry matter content:

\[
Dmc = F + (G - F)e^{-H \cdot t}
\]

where \(Dmc\) is the dry matter content (%), and \(F, G, \) and \(H\) are the coefficients of the function that are biologically interpreted as asymptotic \(Dmc\), initial \(Dmc\), and decay rate, respectively.

The fitness of each model was evaluated using the degree of freedom adjusted quasi-coefficient of determination (\(adj-R^2\)). The significance of the regression coefficients (\(p\)-value) was obtained using the \(t\)-distribution under the null hypothesis that the coefficient was equal to zero. To compare the estimated regression models among cultivars and EC treatments, 95% confidence intervals of regression coefficients were examined for the presence of overlap.

3. Results

3.1. Greenhouse Environment and Treatment

To avoid environmental effects on tomato plant growth, we maintained the average daily mean temperature and average daytime mean CO\(_2\) concentration at 18.7 ± 1.7 °C and 449 ± 29 \(\mu\)mol·mol\(^{-1}\), respectively, throughout the experiment (Figure 1a,b). On the premise that the daily cumulative solar radiation could not be controlled in the natural lighting greenhouse, the effect of fluctuation of solar radiation was not removed in this study (Figure 1c). The daily drainage EC ranged approximately 2–4 dS·m\(^{-1}\) in the low-EC treatment, whereas it reached 5–6 dS·m\(^{-1}\) before the beginning of the investigation in the high-EC treatment (Figure 1d).

3.2. Plant Growth

The destructive measurements at the end of the experiment (187 DAT) are summarized in Table 1. Fresh fruit weight yield significantly decreased (by approximately 20%) under high-EC conditions in both cultivars. However, fruit dry weight yield and the fraction of dry matter distributed in the fruit were not significantly different among the EC treatments. Moreover, there was no clear change in the number of emerged trusses when the leaf area index and weight of non-edible parts significantly decreased in the high-EC-treated En.

Table 1. Effect of EC treatment and cultivar on growth characteristics.

| Group       | Leaf Area Index \(\text{m}^2\cdot\text{m}^{-2}\) | No. of Trusses Reaching Anthesis per Plant | No. of Fruits per Plant | Fruit Fresh Weight Yield \(\text{kg} \cdot \text{m}^{-2}\) | Fruit Dry Weight Yield \(\text{kg} \cdot \text{m}^{-2}\) | Total Dry Matter Production \(\text{kg} \cdot \text{m}^{-2}\) | Dry Matter Distributed to Fruit \(\%\) |
|-------------|---------------------------------------------|------------------------------------------|-------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|
| My, low-EC  | 3.66 ± 0.62 \(^{ab}\)                      | 19.3 ± 0.7 \(^a\)                       | 58.4 ± 3.7 \(^b\)      | 15.46 ± 2.15 \(^ab\)                       | 0.71 ± 0.09 \(^a\)                        | 1.34 ± 0.14 \(^bc\)                         | 53.1 ± 3.0 \(^a\)                           |
| My, high-EC | 3.65 ± 0.61 \(^ab\)                       | 18.8 ± 1.0 \(^a\)                       | 62.9 ± 3.5 \(^b\)      | 11.90 ± 0.82 \(^ab\)                       | 0.67 ± 0.05 \(^a\)                        | 1.25 ± 0.10 \(^c\)                         | 53.4 ± 3.3 \(^a\)                           |
| En, low-EC  | 4.40 ± 0.66 \(^a\)                       | 19.8 ± 0.5 \(^a\)                       | 76.0 ± 2.8 \(^b\)      | 16.18 ± 1.52 \(^a\)                       | 0.72 ± 0.07 \(^a\)                        | 1.61 ± 0.17 \(^a\)                         | 44.9 ± 1.8 \(^b\)                           |
| En, high-EC | 3.41 ± 0.38 \(^b\)                       | 19.5 ± 0.9 \(^a\)                       | 75.5 ± 3.0 \(^b\)      | 12.92 ± 0.63 \(^b\)                       | 0.66 ± 0.03 \(^a\)                        | 1.39 ± 0.07 \(^b\)                         | 47.5 ± 1.9 \(^b\)                           |

Values are presented as mean ± SD (\(n=8\), acquired at the end of the experiment (187 days after transplanting). Means followed by the same letter are not significantly different from each other (Bonferroni-corrected Welch’s \(t\)-test, \(p<0.05\)). Group: My, CF Momotaro York; En, Endeavour. \(^{a}\) Summation of leaf, stem and fruit dry weight per unit area obtained by destructive measurement. \(^{b}\) Quotient of fruit dry weight yield divided by total dry matter production, then multiplied 100 to rescale percentage values.
3.3. Fruit Weight

The average individual fruit weight and growth duration of the harvested fruits are shown in Figure 2. There were no differences in the mean fresh fruit weight, dry weight, or dry matter content between the two cultivars under the low-EC treatment. In comparison, the high-EC treatment caused a significant decrease in fruit fresh weight and dry weight, with a significant increase in dry matter content in both cultivars. The period from anthesis to harvest was around 1200 °C-days. It was significantly shortened in high-EC-treated En, while it was slightly, but insignificantly, lengthened in the high-EC-treated My (Figure 2d). These results suggest that the decrease in fruit yield was caused not by the fruit number, but by the decrease in individual fruit size.

![Figure 2](image)

**Figure 2.** Fresh weight (a), dry weight (b), dry matter content (c), and cumulative temperature after anthesis (d) of the harvested mature fruits. Open circles indicate mean values. Bonferroni-corrected significant levels are shown (**; *p* < 0.01, ***; *p* < 0.001, n.s.; not significant). Labels denote the cultivar (CF Momotaro York (My), Endeavour (En)), and the treatment (low-EC, high-EC).

The Gompertz curves of fresh fruit weight revealed different growth patterns for each treatment (Equation (2); Figure 3). Parameters that were represented as asymptotic fresh weights of growth curves (coefficient C) were 111.5 g (My, low-EC), 81.5 g (My, high-EC), 122.5 g (En, low-EC), and 95.9 g (En, high-EC), and these were comparable to Figure 2a. The decrease in asymptote in the high-EC treatment was approximately 27% in My and 22% in En. Differences in the fresh weight growth in high- and low-EC treatment were greater prior to 500 °C-days after anthesis in My, and after 500 °C-days in En.

3.4. Fruit Dry Matter Content

Throughout fruit development, dry matter content gradually decreased (Figure 4). Measured values varied from 8.5–3.8% (My, low-EC), 9.7–4.7% (My, high-EC), 7.6–3.6% (En, low-EC), and 8.2–4.4% (En, high-EC). Temporal changes in dry matter content were fitted by a three-parameter exponential decay function, and adj-\(R^2\) values ranged from 0.88–0.94 (Equation (3); Figure 4; Table 2). Estimated parameters, coefficient \(G\), interpreted as initial dry matter content, significantly differed between the low-EC-treated My and En. No significant difference was observed between the EC treatments, but there was a slight increase in the high-EC-treated My and En groups. The estimated asymptotic dry matter content, coefficient \(F\), did not differ significantly between low-EC-treated My and En groups. Between EC treatments, the high-EC-treated En was significantly higher.
than the low-EC-treated En, while it was not applicable between My because of the lack of significance of the estimated coefficient in high-EC-treated My. The estimated decay rates, coefficient $H$, were significantly different between low- and high-EC in My. No significant differences were observed between low- and high-EC in En, or between the cultivars under the low-EC. These results suggest that the dry matter content gradually decreased throughout fruit growth and was affected at the harvestable stage by the EC treatment. Furthermore, the curvature of the decay curve was altered by EC treatment in My, whereas the curve was shifted in parallel in En.

![Figure 3](image3.png)

**Figure 3.** Comparison of non-destructively estimated fresh weight growth of tomato fruit as a function of cumulative temperature after anthesis. Regression curves based on Gompertz model are shown. Arrows indicate the mean harvest time. Labels and symbols denote the cultivar (CF Momotaro York (My, black lines, black arrows), Endeavour (En, gray lines, gray arrows)), and the treatment (low-EC (solid lines, closed arrows), high-EC (dashed lines, open arrows)).

![Figure 4](image4.png)

**Figure 4.** Changes in dry matter content of tomato fruit as a function of cumulative temperature after anthesis. Destructively obtained discrete fruit dry matter contents were arranged for growth duration. Regression curves based on the 3-parameter exponential decay model are shown. Arrows indicate the mean harvest time. Labels and symbols denote the cultivar (CF Momotaro York (My, black lines, black arrows), Endeavour (En, gray lines, gray arrows)), and the treatment (low-EC (solid lines, closed arrows), high-EC (dashed lines, open arrows)).
Table 2. Estimated parameters for tomato fruit dry matter content.

| Model                  | Group        | $F$       | 95% CI (Lower–Upper) | $G$       | 95% CI (Lower–Upper) | $H$       | 95% CI (Lower–Upper) |
|------------------------|--------------|-----------|----------------------|-----------|----------------------|-----------|----------------------|
| 3-parameter exponential decay | My, low-EC   | 3.03 ***  | 2.32–3.75            | 9.89 ***  | 9.10–10.67           | 1.38 × 10^{-3} ***  | 9.33 × 10^{-3}–1.82 × 10^{-3} |
|                        | My, high-EC  | −1.75 n.s. | −9.75–6.25           | 10.93 *** | 10.17–11.69          | 4.75 × 10^{-4} ***  | 2.47 × 10^{-3}–9.26 × 10^{-4} |
| $D_{mc} = F + (G − F) e^{−H t}$ | En, low-EC   | 3.12 ***  | 2.56–3.68            | 8.20 ***  | 7.77–8.64            | 1.23 × 10^{-3} ***  | 8.60 × 10^{-3}–1.59 × 10^{-3} |
|                        | En, high-EC  | 4.14 ***  | 3.69–4.58            | 9.20 ***  | 8.50–9.90            | 1.59 × 10^{-3} ***  | 1.09 × 10^{-3}–2.10 × 10^{-3} |

Significant levels—***; $p < 0.001$, n.s.; not significant. Variables—$D_{mc}$; dry matter content (%), $C_t$; cumulative temperature from anthesis (°C-days). Coefficients—$F$; asymptotic dry matter content, $G$; initial dry matter content, $H$; decay rate. Group: My, CF Momotaro York; En, Endeavour.

3.5. Normalized Fruit Weight Growth

The distribution of the measured fresh and dry weights of the fruit spread as the cumulative temperature elapsed (data not shown). To confirm the heterogeneity of the distribution, we aligned the scale of the measured values to compare the rates (coefficient $F$) of water and dry mass accumulation (Figure 5; Table 3). Adj-$R^2$ values in the regression models of relative water content and dry mass ranged from 0.98–1.00 and 0.97–0.99, respectively. Comparing the relative water content between cultivars, the growth rate in low-EC-treated My was significantly slower than that in En. Among EC treatments, the growth rate declined significantly in high-EC-treated My, while it was inclined significantly in high-EC-treated En. In contrast, the growth rates of relative dry mass were significantly different between low-EC-treated My and En, but there was no clear change between the high-EC-treated My and En. Cumulative temperatures at the inflection point of the growth curves can be derived by solving the Gompertz equation (Figure 6). The inflection points of relative water content occurred at 585 °C-days (My, low-EC), 630 °C-days (My, high-EC), 585 °C-days (En, low-EC), and 556 °C-days (En, high-EC). The inflection points of dry mass growth were narrowly ranged and occurred at 479 °C-days (My, low-EC), 496 °C-days (My, high-EC), 482 °C-days (En, low-EC), and 474 °C-days (En, high-EC). These results suggest that water flux to the fruit, but not dry mass growth, was affected by EC treatment.

Figure 5. Comparison of relative water content (a) and relative dry mass (b) growth of tomato fruit as a function of cumulative temperature after anthesis. Regression curves based on Gompertz model are shown. Arrows indicate the mean harvest time. Labels and symbols denote the cultivar (CF Momotaro York (My, black lines, black arrows), Endeavour (En, gray lines, gray arrows)) and the treatment (low-EC (solid lines, closed arrows), high-EC (dashed lines, open arrows)).
Table 3. Estimated parameters for normalized tomato fruit fresh and dry weight.

| Model          | Response Variable | Group       | C          | 95% CI (Lower–Upper) | D          | 95% CI (Lower–Upper) | E          | 95% CI (Lower–Upper) |
|----------------|-------------------|-------------|------------|----------------------|------------|----------------------|------------|---------------------|
| Gompertz       | rW                | My, low-EC  | 1.07 ***   | 1.05–1.10            | 10.1 ***   | 9.0–11.1             | 3.95 × 10^{-3} *** | 3.74 × 10^{-3}–4.15 × 10^{-3} |
|                |                   | My, high-EC | 1.11 ***   | 1.08–1.15            | 8.7 ***    | 7.6–9.7              | 3.44 × 10^{-3} *** | 3.24 × 10^{-3}–3.65 × 10^{-3} |
|                |                   | En, low-EC  | 1.08 ***   | 1.06–1.09            | 8.0 ***    | 7.6–8.3              | 3.55 × 10^{-3} *** | 3.46 × 10^{-3}–3.64 × 10^{-3} |
|                |                   | En, high-EC | 1.08 ***   | 1.06–1.09            | 8.4 ***    | 8.0–8.8              | 3.82 × 10^{-3} *** | 3.72 × 10^{-3}–3.93 × 10^{-3} |

Significant levels—***; p < 0.001. Variables: rW, relative fruit water content (g·g^{-1}); rD, relative fruit dry mass (g·g^{-1}); Ct, cumulative temperature from anthesis (°C-days). Coefficients: C, asymptotic Wt; D, integrated constant related to initial Wt; and E, growth rate. Group: My, CF Momotaro York; En, Endeavour.

Figure 6. Changes in growth rates of tomato fruit as a function of cumulative temperature after anthesis in CF Momotaro York (a) and Endeavour (b). Differential of regression curves based on the Gompertz model are shown. Arrows indicate the inflection point. Labels and symbols denote the accumulation of water (black lines), dry mass (gray line), and the treatment (low-EC (solid lines, closed arrows), high-EC (dashed lines, open arrows)).

4. Discussion

Tomato fruit quality can be improved by osmotic stress, although this is accompanied by a decrease in yield [37]. Various studies aimed at clarifying the relationship between yield and quality under osmotic stress treatment have been conducted in Japan [14–17]. In this study, there were two differences in the experimental conditions compared to previous studies. We carried out long-term cultivation (approximately until the 20th truss appeared) compared to short-term cultivation (single-truss in most cases, or no longer than the eighth truss), and the target EC level of irrigation was relatively lower (5 dS·m^{-1}) than that reported in the literature (more than 6 dS·m^{-1}) (Table 1; Figure 1). Excessive stress could trigger severe yield loss, such as fruit abortion and damaged fruits (e.g., blossom-end rot), caused by various physiological defects. Low-truss pinching tomato cultivation can specify the timing of appropriate stress treatment and improve and homogenize fruit quality [14,16]. In contrast, long-term tomato cultivation is generally difficult to achieve while maintaining fruit quality and plant vigor. The literature proposed that osmotic stress could be applied to the last two to three trusses in long-term cultivation to avoid growth defects [38]. We observed a similar trend about the fruit production under the high-EC treatment, with decreased individual fruit size, and increased dry matter content (Table 1; Figure 2). Even though the fresh weight yield was also decreased, the plant growth was not obviously affected except for the decreased leaf area index in high-EC-treated En, and long-term cultivation attained the yield of >10 kg·m^{-2} (Table 1). Our study achieved both
long-term stability and even slightly improved fruit dry matter content under moderate stress conditions.

The harvest periods were reached at around cumulative temperature from anthesis of 1200 °C-days and were close to those previously reported [31,39]. The harvestable point shifted in opposite directions, depending on the cultivar (Figure 2d). Thus, this study introduced thermal time to the model. In the dry matter content decay curve, high adj-$R^2$ values were observed in all models. However, in high-EC-treated My, the coefficient $F$ (asymptotic dry matter content) was not significantly estimated, indicating that the estimated curve was not flattened at the harvestable point (Figure 4). Studies have shown that increased pigment deposition and inhibited expression of cell wall modification enzymes in the fruit pericarp are caused by salinity [40–43]. This implies that whereas the harvestable point was decided by fruit color, water flux to the fruit and pericarp softening might still have been ongoing in high-EC-treated My.

The Gompertz curves for dry mass and water content represented a high adj-$R^2$ value (>0.97), indicating that our models showed a good fit in predicting fruit weight (Figure 5). Considering the growth rates and inflection points of growth curves, it was suggested that the peak of dry matter accumulation (approximately 480 °C-days) preceded the peak of water flux (approximately 585 °C-days) (Figure 6). The water increase rates were affected by osmotic stress, and the high-EC treatment in the Japanese and Dutch cultivars showed contrasting trends. The peak of water flux was delayed (630 °C-days) in Japanese cultivar owing to the high-EC treatment, whereas it shifted earlier (556 °C-days) in Dutch cultivar. In contrast, the EC conditions did not affect dry mass growth rates. These shifts in growth rate and the inflection point of water flux to fruit were comparable with the trend at the harvestable point (Figures 2d and 6; Table 3). This study focused only on fruit size under stress conditions. In previous studies on fruit growth, although growth stages were finely classified and contained detailed molecular, physiological, and anatomical information, these studies were conducted in a stress-free environment [25–27,44]. Further studies integrating the model and biological characterization under stress conditions are required.

Taken together, the model-based approach revealed differences in the fruit growth patterns of two representative tomato cultivars under osmotic stress. Compared with conventional time units (e.g., days after anthesis) for growth curve analyses, the thermal time approach can provide more precise fruit weight and dry matter content. Recently, a yield prediction model based on dry matter production and partitioning in the fruit has been proposed for tomato production [45]. Based on the dry weight growth rate in this study, it was suggested that dry matter partitioning in the fruit was not affected by moderate osmotic stress, and we expect that the yield prediction would apply to high-Brix tomato cultivation. The fruit growth curve may be helpful for improving the model accuracy by contributing to the estimation of dry matter partitioned to fruit.

5. Conclusions

In this study, we performed tomato cultivation under moderate osmotic stress conditions. We successfully produced tomato fruits exhibiting the coexistence of long-term stability and improved fruit quality. We found that the effect of osmotic stress on water accumulation in the fruit differed in terms of shift patterns depending on cultivar, while dry weight growth was not affected. Collectively, our findings may be useful for the stable and efficient production of high-Brix tomatoes.

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