Yield of Japanese Tomato Cultivars Has Been Hampered by a Breeding Focus on Flavor

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Abstract. The yield of greenhouse tomatoes in Japan has not increased since the 1980s and remains much less than 30 kg·m⁻² per year. To investigate the cause of this low yield, we compared six Japanese tomato cultivars that were commonly grown or released during the past 80 years to see whether fruit yield (fruit fresh weight per area) and dry matter (DM) content per fruit improved under current cultivation conditions. Fruit yield in ‘Momotaro’ (released in 1985) was lower than that in older cultivars. Total DM was determined mainly by light use efficiency and photosynthetic rate, and light use efficiency was correlated with maximum photosynthetic rate. The more modern cultivars did not show improved DM content per fruit. The DM content per fruit was strongly correlated with the soluble solids content in fruits except in ‘Momotaro’ and ‘Momotaro colt’, but soluble solids in fruits of the ‘Momotaro’-type cultivars were higher than in other cultivars for a given DM content per fruit. Thus, tomato breeding in Japan appears to have focused on fruit soluble solids content per unit DM rather than fruit yield or DM content; as a result, only the former parameter has improved greatly.

The yield of greenhouse tomatoes (Solanum lycopersicum) in The Netherlands has doubled from ≈30 kg·m⁻² per year in the 1980s to 60 kg·m⁻² per year in 2005 (Kwantitatieve Informatie voor de Glastuinbouw, 2005). Breeding for higher-yielding cultivars undoubtedly played a role in this yield increase: the yield of modern tomato cultivars under current cultivation conditions was 40% higher than that of old cultivars under the same conditions (Van der Ploeg et al., 2007). Higashide and Heuvelink (2009) showed that the yield increase over the past 50 years in Dutch tomatoes resulted from increased total DM production, which resulted from high light use efficiency (LUE).

In Japan, tomato is the most important crop placed in the vegetable category with the highest total value of production for many years (MAFF, 2007). However, although cultivation techniques and breeding of new cultivars have been improved in Japan, the yield of greenhouse tomatoes has not increased since the 1980s, remaining much less than ≈30 kg·m⁻² per year. Although temperatures are higher in Japanese summer than in The Netherlands, little research supports the belief that this low yield is caused by high summer temperatures. To determine the cause and to find ways to improve yield, the Super Horticulture Project was launched, and several studies have recently been conducted under it.

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Materials and Methods

Relying on the data of Aoki (1998) and Sumida et al. (2008), we selected six Japanese tomato cultivars that were released and that had been commonly grown during the past 80 years: ‘Sekai-ichi’ (commonly used in the 1930s), ‘Fukujyu 2’ (1940s to the 1950s), ‘Aiichi fast’ (1950s to the 1960s), ‘Koryoku-beijyu’ (1950s to the 1960s), ‘Momotaro’ (released in 1985), and ‘Momotaro colt’ (2003). ‘Sekai-ichi’ is a true-breeding cultivar; ‘Fukujyu 2’ is one of the earliest F1 hybrids. ‘Momotaro’ inherited Japanese cultivars and ‘Florida MH-1’ and was the most popular cultivar in Japan. After release of ‘Momotaro’, 26 sister cultivars have been released until now and ‘Momotaro colt’ is one of them. We compared their fruit and other characteristics in a short-term experiment. All six cultivars are indeterminate-growth types with large, round fruits.

The seeds were sown in seed trays on 15 Jan. 2010, and 20 d later, the seedlings were transplanted into rockwool cubes. On 18 Feb. 2010, we transplanted the plants (60 plants per row, 2.5 plants/m²) into seven rows in a rockwool system in a greenhouse compartment (14 m × 12 m) at the National Agriculture and Food Research Organization Institute of Vegetable and Tea Science in Taketoyo, Japan. The temperatures at which ventilation and heating began were set at 25 and 13 °C, respectively. The experiment was conducted from 18 Feb. to 20 June 2010. Otsuka-A nutrient solution (Otsuka Agrotechno, Tokyo, Japan; it consisted of 9.3 mM NO₃⁻, 4.3 mM K⁺, 4.1 mM Ca²⁺, 1.5 mM Mg²⁺, 0.9 mM H₂PO₄⁻, 2.7 mg·L⁻¹ iron, 1.2 mg·L⁻¹ manganese, 0.51 mg·L⁻¹ boron, 0.09 mg·L⁻¹ zinc, 0.03 mg·L⁻¹ copper, and 0.03 mg·L⁻¹ molybdenum) adjusted to 1.2 to 2.5 dS·m⁻¹ was provided to the plants. The interval of the nutrient solution supply was controlled based on outdoor solar radiation. The daily drain percentage was maintained at 20% to 30% of the total supply of nutrient solution. Plants were trained and leaves were pruned following standard modern Dutch practices because tomato yields are usually higher in the Dutch practices than in Japanese practices (Kanai et al., 2001; Suzuki, 2006). Flowers were pollinated by bumblebees, and the number of fruits per truss was not adjusted by pruning because fruit size in each cultivar was not decreased depending on number of fruits per truss. All plants were pinched...
above the sixth to eighth truss on 28 Apr. 2010, when they had reached the top of the training wire. The experiment was conducted in three blocks by a complete randomized block design with two double rows per block and one border row on each side of the blocks. The spacing was 60 cm between rows within the double rows and 190 cm between double rows. We planted 20 plants per cultivar in each block (three cultivars per double row × two double rows). We planted 10 plants per cultivar in the border rows and did not measure these plants.

We harvested all mature fruits from eight plants per cultivar in each block three days a week and measured their fresh and dry weights. We also measured leaf (leaf blade + petiole) area (using a LI-3100C leaf area meter; LI-COR, Lincoln, NE) and the fresh and dry weights of leaves, stems, and all fruits of two or four plants per cultivar per block by destructive sampling at 34, 61, and 116 d after transplanting. Mature and immature fruits were measured separately. To avoid the influence of this harvesting on the remaining plants and their light interception, we harvested two plants and two guard plants per cultivar per block remained in each measurement during the first two destructive samples. We also measured the SS content (percent of fresh weight) in fruits from the fourth to the seventh trusses (n = 25 to 39) using a refractometer (PR-101; Atago, Tokyo, Japan).

We measured the individual-leaf maximum photosynthetic rate of mature upper leaves twice, at 54 and 55 d after transplanting, using one leaf from each of four plants in each cultivar per block with a portable photosynthesis system (LI-6400; LI-COR) at 1500 μmol·m⁻²·s⁻¹ photosynthetic photon flux density [PPFD; red (630 nm) + 10% blue (470 nm)] light-emitting diodes and at 1000 μmol·mol⁻¹ CO₂. To obtain a photosynthetic light-response curve, we chose four cultivars, Sekai-ichi, Aichi fast, Momotaro, and Momotaro colt, that covered the full range of cultivar ages, and we measured photosynthetic rate of mature upper leaves twice using one leaf from each of two plants in each cultivar at 56 and 57 d after transplanting. The photosynthetic rate of the leaves was measured at light intensities of 0, 10, 20, 40, 60, 200, 300, 500, 800, 1000, and 1500 μmol·m⁻²·s⁻¹ PPFD and the ambient CO₂ level (370 μmol·mol⁻¹).

Light extinction in the plant canopy can be described using the following equation (Monsi and Saeki, 1953):

\[
 I = I_0 e^{-kL}
\]

where \( I \) represents the light intensity at a given point in the plant canopy, \( I_0 \) represents the light intensity above the canopy, \( k \) represents the light-extinction coefficient, and \( L \) represents the cumulative leaf area index (LAI) at that point in the canopy. To obtain the light-extinction coefficient for each cultivar, we measured PPFD using a 1-m-long PPFD sensor (LI-1915A; LI-COR) at six different heights in the closed plant canopy of each cultivar at 67 to 69 d after transplanting: LAI ranged from 4.2 to 5.5, and plant height ranged from 180 to 230 cm. PPFD above the plant canopy was also measured with a PPFD sensor (LI-190SA; LI-COR) and recorded using a data logger (NR-600; Keyence, Tokyo, Japan). The individual leaf area of each cultivar was obtained using the following regression equation:

\[
 A_l = a \cdot L^1 \cdot W^1
\]

where \( A_l \) represents the leaf area (cm²), \( a \) represents a proportionality factor for each cultivar (0.31, ‘Sekai-ichi’; 0.38, ‘Fukuyuu’ 2; 0.38, ‘Aichi fast’; 0.31, ‘Kyoryoku-Bei’; 0.38, ‘Momotaro’; 0.35, ‘Momotaro colt’), \( L \) represents the leaf length (cm), and \( W \) represents the leaf width (cm). The regression equations \((R^2 = 0.76 to 0.90, P < 0.05 for all regressions) were obtained by destructive sampling at 61 d after transplanting. The cumulative LAI at each of the six heights was calculated from the individual leaf area and the number of leaves at that height. The light-extinction coefficient was obtained as the slope of a logarithmic regression of PPFD against cumulative LAI at the six heights. LUE was calculated as the slope of a linear regression of the total cumulative DM production as a function of the integral intercepted photosynthetically active radiation (PAR) at the three sample dates. Greenhouse transmissivity and the fraction of PAR were assumed to be 60% and 50% of global radiation, respectively (Kurata, 1994; Society of Agricultural Meteorology of Japan, 1997). Daily PAR intercepted by the plants of each cultivar was calculated from LAI and the light-extinction coefficient in each cultivar.

Results and Discussion

Table 1 presents the fruit data. Fruit yields were significantly higher in ‘Aichi fast’ and ‘Kyoryoku-Bei’ than in the more recent ‘Momotaro’. Fruit yield was higher in ‘Aichi fast’ than in all other cultivars, and the difference was significant except for ‘Kyoryoku-Bei’ and ‘Sekai-ichi’. Fruit numbers per truss and per plant were also significantly higher in ‘Aichi fast’ than in all other cultivars. Total DM production in ‘Momotaro colt’ was also significantly lower than in all other cultivars except ‘Kyoryoku-Bei’. DM allocation to the fruits was significantly higher in ‘Aichi fast’ than in all other cultivars except ‘Sekai-ichi’ and ‘Kyoryoku-Bei’, and it was significantly lower in ‘Momotaro’ and ‘Momotaro colt’ than in ‘Kyoryoku-Bei’ and ‘Aichi fast’.

Table 3 presents the growth and morphological data of the canopy. The light-extinction coefficient represents how steeply light is diminished by light interception of leaves with increasing depth in the canopy. This coefficient was significantly lower in ‘Sekai-ichi’ than in all other cultivars. The coefficients in ‘Aichi fast’ and ‘Momotaro colt’ were significantly lower than those in ‘Kyoryoku-Bei’ and ‘Fukuyuu’ 2’. There was no difference...
in specific leaf area among the cultivars. LAI at 116 d after transplanting was significantly lower in ‘Aichi fast’ than in ‘Sekai-ichi’, ‘Fukujyu 2’, and ‘Momotaro colt’. Average LAI during the experimental period was significantly lower in ‘Aichi fast’ than in ‘Fukujyu 2’ and ‘Momotaro Colt’. LUE was significantly lower in ‘Momotaro’ than in all other cultivars except ‘Kyoryoku-beijyu’. LUE was significantly higher in ‘Sekai-ichi’, ‘Aichi fast’, and ‘Momotaro colt’ than in the other cultivars.

The maximum photosynthetic rate per leaf measured at 1500 μmol·m⁻²·s⁻¹ and 1000 μmol·mol⁻¹ CO₂ was significantly lower in ‘Momotaro’ than in ‘Momotaro colt’ and ‘Sekai-ichi’ (data not shown). However, no other cultivars differed significantly. The photosynthetic rate per leaf was significantly lower in ‘Momotaro’ than in ‘Sekai-ichi’, ‘Aichi fast’, and ‘Momotaro colt’ at almost all PPFD levels (Fig. 1).

There was no significant correlation between the period when a cultivar was commonly grown and the fruit yield or dry weight yield per area (data not shown). We therefore saw no increase in fresh fruit yield in the Japanese cultivars during the period when the yield of Dutch cultivars increased rapidly (Higashide and Heuvelink, 2009). In fact, the yield of ‘Momotaro’ (released in 1985) was less than those of the cultivars that were grown before the 1950s. There was also no significant correlation between the period when a cultivar was commonly used and the DM content per fruit (data not shown). We therefore did not find evidence of an improvement in DM content per fruit. Although the yield in processing tomato increased drastically, there was only a slight increase in the DM content per fruit (Stevens, 1994; Zamir et al., 1999). Improving the DM content per fruit may be challenging for breeders.

There was no significant correlation between the period when a cultivar was commonly used and any of the other yield and fruit characteristics (data not shown). These results suggest that tomato breeders in Japan have not attempted to develop improved high-yielding cultivars and have not focused on specific characteristics such as total DM production and its allocation to the fruits.

Table 4 shows the correlations between the yield components and the growth and photosynthetic characteristics. Fresh fruit yield was significantly positively correlated with the fruit dry weight per area, although there was no significant correlation between fresh fruit yield and the DM content per fruit. Accordingly, the difference in fresh fruit yield among the cultivars is mainly explained by the difference in fruit dry weight per area rather than the DM content per fruit. Dry weight yield per area may be determined by the total DM and by the DM allocation to the fruits. There was no significant correlation between fruit dry weight per area and total DM or its allocation to the fruits (P = 0.078 and 0.094, respectively). Total DM was strongly and significantly positively correlated with LUE and maximum photosynthetic rate but not with the fraction of intercepted light. LUE was significantly correlated with the maximum photosynthetic rate but not with LAI or the light-extinction coefficient. The difference in LUE among cultivars therefore is mainly explained by the difference in leaf photosynthetic rate. DM allocation to the fruits was significantly correlated with the number of fruits per plant (r = 0.84) and per truss (data not shown). There was no correlation between DM allocation to the fruits and fruit weight per fruit (data not shown). Thus, the difference in DM allocation to the fruits is explained by the difference in the number of fruits. DM allocation to the fruits was significantly negatively correlated with LAI. This suggests that DM allocation to the fruits restricted the growth of the leaf area.

The lack of any significant correlation between the period when a cultivar was commonly used and the DM content per fruit suggests that breeding for the latter parameter was not a goal of Japanese breeders. However, there was no correlation between the DM content per fruit and the SS content of the fruits of all six cultivars combined, but there was a strong and significant positive correlation when ‘Momotaro’ and ‘Momotaro colt’ were excluded (Fig. 2). The SS content in fruits of ‘Momotaro’ and ‘Momotaro colt’ were much higher than the values predicted by the regression for the four other cultivars. Because low DM content indicates high water content, the low DM content and high SS in ‘Momotaro colt’ accordingly implied juicy and sweet fruits. Although there is generally a correlation between the DM content per fruit and the SS content in tomatoes, Kawahata et al. (2002) observed that changes in the SS concentration were inconsistent with changes in DM content per fruit under conditions that restricted growth: the carbohydrates transported to the fruits were preferentially allocated to SS rather than insoluble carbohydrates. We

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**Table 2. Leaf, stem, and fruit dry weight (DW) per plant, total dry matter production, and dry matter allocation to fruits of six Japanese tomato cultivars at 116 d after transplanting.**

| Cultivar         | Period | Leaf DW (g/plant) | Stem DW (g/plant) | Fruit DW* (g/plant) | Total dry matter (g·m⁻²) | Dry matter allocation to the fruits (g·g⁻¹) |
|------------------|--------|------------------|------------------|--------------------|-------------------------|------------------------------------------|
| Sekai-ichi       | 1930   | 147 ab           | 87 ab            | 291 b              | 1267 b                  | 0.57 abc                                 |
|                  | 1940   | 147 ab           | 81 ab            | 286 b              | 1260 b                  | 0.56 ab                                  |
|                  | 1950   | 118 ab           | 70 a             | 283 b              | 1164 ab                 | 0.60 bc                                  |
| Aichi fast       | 1985   | 112 a            | 75 a             | 313 b              | 1237 b                  | 0.63 c                                   |
| Momotaro         | 1985   | 129 a            | 69 a             | 217 a              | 1026 a                  | 0.52 a                                   |
| Momotaro colt    | 2003   | 153 c            | 104 b            | 274 b              | 1311 b                  | 0.52 a                                   |

*Period when the four old cultivars were commonly used and the year when the ‘Momotaro’-type cultivars were released.*

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**Table 3. Light-extinction coefficient at 67 to 69 d after transplanting of six Japanese tomato cultivars, specific leaf area (SLA) and leaf area index (LAI) at 116 d after transplanting, and average LAI and light-use efficiency (LUE) during the experiment.**

| Cultivar         | Period | Light-extinction coefficient (m² g⁻¹) | SLA (m² m⁻²) | LAI (m² m⁻²) | Avg LAI (m² m⁻²) | LUE (g MJ⁻¹) |
|------------------|--------|--------------------------------------|--------------|-------------|-----------------|--------------|
| Sekai-ichi       | 1930   | 0.69 ab                              | 0.016 a      | 5.9 bc      | 3.3 ab          | 3.1 c        |
|                  | 1940   | 0.83 cd                              | 0.018 a      | 6.3 c       | 3.4 b           | 2.9 b        |
|                  | 1950   | 0.89 d                               | 0.017 a      | 4.9 ab      | 2.8 ab          | 2.7 ab       |
| Aichi fast       | 1950   | 0.74 b                               | 0.016 a      | 4.5 a       | 2.7 a           | 3.1 c        |
| Momotaro         | 1985   | 0.75 bc                              | 0.016 a      | 5.1 ab      | 3.2 ab          | 2.4 a        |
| Momotaro colt    | 2003   | 0.76 bc                              | 0.017 a      | 6.3 c       | 3.5 b           | 3.1 c        |

*Period when the four old cultivars were commonly used and the year when the ‘Momotaro’-type cultivars were released.*

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**Fig. 1. Photosynthetic light-response curves for individual leaves of four Japanese tomato cultivars. Values are means ± sds (n = 4 to 8).**
Because the total DM was strongly correlated with LUE and photosynthetic rate (Table 4), like in Dutch cultivars (Higashide and Heuvelink, 2009), then breeders who want to develop high-yielding Japanese cultivars should select cultivars with a high LUE. High DM allocation to the fruits may also improve yield. Among the six cultivars we tested, ‘Aichi fast’ seems likely to have traits that might be used in breeding for high yield, because it had higher LUE (Table 3) and DM allocation to fruits (Table 2) than the other cultivars. However, it is not easy to measure LUE in a large segregating population. If the molecular markers linked to LUE can be found, the breeders could use them to improve high-yielding cultivars. We do not recommend trying to improve the increase DM allocation to the fruits more than ‘Aichi fast’, because increasing DM allocation to the fruits will decrease LAI (based on the negative correlation between the two parameters; Table 4), and this may decrease whole-plant photosynthesis sufficiently to decrease fruit yield.

We conclude that high-yielding cultivars have not been a priority for Japanese tomato breeders. Similarly, breeders have not tried to improve the DM content per fruit. However, the SS content per unit of DM content has increased in ‘Momotaro’ (released in 1985) and further in ‘Momotaro colt’ (released in 2003) compared with several of the older cultivars, which suggests that Japanese breeders have improved fruit quality. We believe that Japanese consumers and retailers have demanded improvements in fruit taste more strongly than in yield, and Japanese breeders have therefore focused on fruit quality such as SS rather than quantity.

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