Original Paper

An investigation of differences in fruit yield and components contributing to increased fruit yield in Japanese and Dutch tomato cultivars

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Abstract   Tomato fruit yield per area in Japan is 88% lower than that in The Netherlands, because higher-yielding tomato cultivars are bred and cultivated in The Netherlands. In this study, we investigated differences between the Japanese common cultivar 'Reiyou' and the Dutch high-yielding cultivar 'Levanzo' in fruit yield and components contributing to an increase in fruit yield using the low-node-order pinching and high-density plant training system used in Japan. Fresh and dry fruit yield of 'Levanzo' were significantly higher than those of 'Reiyou'. Estimated leaf blade area of the whole plant and solar radiation on individual leaves were higher in the 'Levanzo' canopy than in that of 'Reiyou'. Although transpiration rate and stomatal conductance were similar in the two cultivars during the latter half of the fruit development period, the photosynthetic rate in 'Levanzo' was higher than that in 'Reiyou' during the fruit development period. The difference in photosynthetic rate was because chlorophyll *a* and *b* content had not decreased in 'Levanzo' compared with that in 'Reiyou' at 50 days after flowering, corresponding to the latter half of the fruit development period. Transcriptional levels of *LeSUT1*, which determines sucrose loading activity in source leaves, did not differ between the two cultivars. The higher tomato fruit yield of 'Levanzo' compared with that of 'Reiyou' was caused by a higher photosynthetic rate, increased solar radiation on individual leaves, and the large sink size due to numerous fruits, but not by sucrose loading activity.

Key words: Chlorophyll, fruit yield, photosynthetic rate, sucrose transporter, tomato.

Tomato (*Solanum lycopersicum*) is one of the most important fresh vegetable crops in the world. China has recently become one of the largest tomato producers in the world. However, the leading tomato fruit–producing country is The Netherlands. The average tomato fruit yield per unit area in the world was $34,818 \, \text{kg ha}^{-1}$ in 2009, but tomato fruit yield per area in The Netherlands was $500,000 \, \text{kg ha}^{-1}$, according to FAOSTAT (http://faostat.fao.org/site/567/default.aspx#ancor, July 27, 2011). In Japan, the total yield of tomato fruit was highest among all vegetables, but tomato fruit yield per area in 2009 ($57,815 \, \text{kg ha}^{-1}$) was 88% lower than that of The Netherlands. This difference in tomato fruit yield per area is caused by many factors, including improvements in greenhouse transmissivity and developments in cultivation techniques, such as a long-period cropping system, a high-wire training system, computerized environmental control, and the successful breeding of higher-yielding cultivars in The Netherlands (van der Ploeg et al. 2007; Higashide and Heuvelink 2009). Improvements in fruit quality in Japanese tomato cultivars may be more important than increased yield for tomato breeding (Higashide and Heuvelink, 2009). In contrast, breeding has increased yields in modern Dutch tomato cultivars (van der Ploeg et al. 2007; Higashide and Heuvelink 2009).

Some researchers have investigated physiological differences between Japanese and Dutch tomato cultivars (Higashide and Heuvelink 2009; Matsuda et al. 2011a, b). Higashide and Heuvelink (2009) reported that the increased tomato fruit yield of Dutch modern tomato cultivars was achieved by an increase in light-use

efficiency (LUE) resulting from morphological and physiological changes through breeding. Matsuda et al. (2011a) investigated the effects of altered source/sink ratio following leaf or fruit pruning on leaf photosynthetic characteristics and whole plant growth in Japanese and Dutch cultivars. Matsuda et al. (2011b) found that fruit growth was limited by sink strength in Japanese and Dutch tomato cultivars under enhanced source conditions, and reported that the Japanese cultivar 'Momotaro York' had a lower sink strength relative to source strength than did the Dutch cultivar 'Dundee'. However, these investigations were conducted under a high-wire training system and constant planting density in a Dutch-style greenhouse. Investigations using both the Dutch and Japanese systems are required to determine the difference in productivity between Japanese and Dutch tomato cultivars.

In this study, we evaluated photosynthetic rate, leaf parameters, and sucrose loading capacity at the source leaves to clarify the difference in fruit yield between the Japanese and Dutch tomato cultivars and to identify the components contributing to an increase in fruit yield, particularly from the aspect of source capacity under the low-node-order pinching and high-density plant training system of Japan. In order to evaluate the difference in fruit yield, we use 'Reiyou' as Japanese cultivar, and 'Levanzo' as Dutch cultivar. Both cultivars are known as high yielding cultivars and are grown widely in their respective country.

Materials and methods
Plant materials and growing conditions
The tomato cultivars (Japanese cultivar 'Reiyou'; Sakata Seed Corporation, Kanagawa, Japan; Dutch cultivar 'Levanzo'; Rijk Zwaan, De Lier, the Netherland) were grown hydroponically using the low-node-order pinching and high-density plant training system. In this training system, main stems are pinched after the third truss to allow high-density production and easy handling.

Tomato seeds were sown in pots filled with a substrate comprised of coconut husks (Cocobed; Kaneko Seeds Company Ltd., Gunma, Japan) and germinated in a 30°C temperature-controlled chamber. Seedlings were transplanted into an ebb and flow system and irrigated with a commercial nutrient solution (Otsuka-A; Otsuka AgriTechno Co. Ltd., Tokyo, Japan). The electrical conductivity (EC) level was 1.2 dS m^{-1}, and pH was adjusted to 6.0–7.0. After 2 weeks, 20 seedlings of each cultivar were transplanted into a nutrient film technique system in a greenhouse at the Agricultural and Forestry Research Center of the University of Tsukuba in Japan. The planting density was six plants m^{-2} (150-cm ridge widths, 11-cm plant spacing). All measurement data were shown as average of three to four plants and nine fruits as replication. When the first flower of the first truss on each plant bloomed, each flower was treated with a vibrator and sprayed with an A4-chlorophenoxy acetate-containing solution (Tomato

Tone; ISK Biosciences K. K., Tokyo, Japan) to promote pollination. All lateral shoots were removed as they appeared, and the plants were pinched above the third truss, leaving two true leaves above the truss. After the first flower of the first truss appeared, another commercial nutrient solution (Otsuka-B nutrient solution; Otsuka AgriTechno Co. Ltd.), set at an EC of 2.4 dS m^{-1} and a pH of 6.5–7.0 and containing 20 ppm NH_4^+, 210 ppm NO_3^-, 93 ppm PO_4^{3-}, 377 ppm K^+, 219 ppm Ca^{2+}, 89 ppm Mg^{2+}, 1.0 ppm Mn^{2+}, 1.0 ppm B^-, 2.9 ppm Fe^{3+}, 0.02 ppm Cu^{2+}, 0.04 ppm Zn^{2+}, and 0.02 ppm Mo^+, was irrigated for 15 min/h from 6:00 until 17:00. Air temperature in the greenhouse was controlled by ventilation and maintained at >10°C by heating during winter.

Experiments 1 and 2 were conducted in a greenhouse in Tsukuba, Ibaraki, Japan, from March 27 to August 12, 2009 and from February 12 to June 10, 2010, respectively.

Fruit yield and quality analysis
Fruits were harvested at the red stage, and the total weight and number of fruits were recorded. The harvested fruits were classified as marketable or unmarketable; the unmarketable fruit was characterized by blossom-end rot and cracking. Approximately 10 g of homogenized fruit was dried in an electric oven at 80°C for 48 h to determine its dry matter content. The total soluble solid content of fruit was also determined using a digital refractometer (BRX-242; Erma Inc., Tokyo, Japan).

In Experiment 2, the leaves just below the second truss were sampled from tomato plants at 10, 30, and 50 days after flowering (DAF) of the first flower of the second truss, and the sampled leaves were frozen at −80°C until use. The sampled leaves were used to measure chlorophyll (Chl) content and to perform a *Le SUT1* transcriptional analysis.

Measurement of leaf area and dry weight
All leaves were sampled from the entire plant during the fruit enlargement period of the second truss. Leaf blade area of representative leaves just below each truss was measured using the Leaf Profile Analysis System (Tanabata et al. 2010). Then, all leaf blades were dried in an electric oven at 80°C for 48 h, and dry weights were measured. Leaf blade area of the entire plant was calculated using the following formula:

Leaf blade area of whole plant=leaf blade area of representative leaves×leaf blade dry weight of entire plant/leaf blade dry weight of representative leaves.

Measurement of solar radiation on individual leaves in a colony
In Experiment 1, the solar radiation at the individual leaf level was recorded with integrated solarimeter film (R-2D; Taisei Environment and Landscape Corp., Tokyo, Japan) (Watanabe et al. 2003). A 2×3-cm piece of integrated solarimeter film was attached to the apical and central part of each compound leaf just below the second truss on three plants of each cultivar for 14 days, from June 28 to August 11, corresponding to 112–126 DAF of the second truss. The optical transmittance (T) of the film was determined using a portable photometer (THS470; Taisei Environment and Landscape Corp.). The absorbance (A) of the film was calculated from T as follows:

$A = -Log_{10}(T/100)$.

Table 1. Fruit yield, yield component and total soluble solid content in Experiment 1.

Cultivar	Fruit yield (gFW* plant^{-1})	Fruit number (Number plant^{-1})	Fruit weight (gFW fruit^{-1})	Estimated dry matter yield (gDW plant^{-1})	Total soluble solid content (Brix %)
Reiyou	1666.8 ± 41.22** a***	11.3 ± 0.41 a	149.5 ± 9.44 b	96.9 ± 2.40 a	5.4 ± 0.13 a
Levanzo	2106.0 ± 128.50 b	19.8 ± 0.95 b	106.6 ± 3.48 a	125.6 ± 7.66 b	5.1 ± 0.15 a

* FW, fresh weight; DW, dry weight. ** Means ± standard errors ($n=3$ for fruit yield, fruit number and estimated dry matter yield per plant; $n=9$ for fruit weight and total soluble solid content). *** Different letters in each column significant differences by Student's *t*-test ($P=0.05$).

The amount of solar radiation per leaf (R) was calculated from the absorbance of the film before use (D_0) and after exposure (D) using the following formula:

$$R = -0.0101(D/D_0 \times 100)^2 - 0.5419(D/D_0 \times 100) + 167.59$$

Measurement of photosynthetic rate

In Experiment 2, photosynthesis and respiration rates of fully expanded young leaves just below the second truss were measured between 10:00 and 12:00 am with a LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA). Measurements were made at photosynthetic photon flux densities (PPFD) of 0, 500, and 4000 μmol m^{-2} s^{-1} to obtain the net photosynthesis rate for the photosynthesis curve. Each measurement was repeated two times. Measurements were conducted once every 2 weeks from May 2 to July 10, corresponding to 1–64 DAF of the first flower on the second truss.

Measurement of chlorophyll content in leaves

In Experiment 2, the total Chl content in developing leaf tissues was measured according to Porra et al. (1989). Leaf sections (20 mg) were placed in glass tubes containing 2 ml of N, N-dimethylformamide and incubated overnight at 4°C under absolute dark conditions. Absorbance was measured at 663.8 and 646.8 nm, respectively, and the Chl concentrations were calculated using the following formula:

Chl *a* concentration (μM) = 13.43 × $A_{663.8}$ − 3.47 × $A_{646.8}$
Chl *b* concentration (μM) = 22.90 × $A_{646.8}$ − 5.38 × $A_{663.8}$

RNA isolation, cDNA synthesis, and quantitative RT-PCR

Total RNA was extracted from frozen samples with the RNeasy Plant Mini kit (Qiagen, Valencia, CA, USA). The extracted RNA was dissolved in RNase-free water and stored at −80°C until use. For cDNA synthesis, 1 μg of total RNA was reverse-transcribed with the First Strand cDNA Synthesis kit (Takara Bio Inc., Otsu, Japan). The gene-specific primers (forward: aactcccggagaaagaagag, reverse: tacagtttcgcatcaccgac) were designed with Amplify software (ver.3.1.4; B. Engels, University of Wisconsin, USA; http://engels.genetics. wisc.edu/amplify/), based on published sequences (see Supplementary Table 1 at JXB online; Yin et al. 2010). Quantitative RT-PCR (qRT-PCR) reactions were conducted on an Mx 3000P qRT-PCR system (Stratagene, San Diego, CA, USA). The endogenous actin gene was used as an internal standard to normalize the qRT-PCR reaction (accession no. U60482; forward primer: aactcccggagaaagaagag, reverse primer: tacagtttcgcatcaccgac; Moniz and Drouin 1996). The reaction cycles were as follows: for the *LeSUT1* genes, initial denaturation at 95°C for 10 min; 40 cycles of 95°C for 20 s, 50°C for 30 s, 72°C for 20 s; and one cycle of 95°C for 30 s, 55°C for 30 s, and 95°C for 30 s. Specific amplifications were
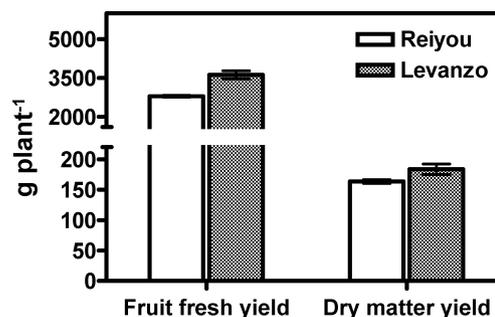

Figure 1. Fruit yield and estimated dry matter yield of 'Reiyou' and 'Levanzo' in Experiment 2. Bars indicate standard errors ($n=4$). Different letters in each bar indicate significant differences by Student's *t*-test ($P=0.05$).

confirmed by single transcript amplification on agarose gels, single dissociation peaks, and calibration curves. Gene expression was calculated in relation to the level of actin gene expression, according to the instructions provided by Stratagene and based on the method reported by Pfaffl (2001).

Results

Yield, dry matter, and soluble solids of fruits

In Experiment 1, fruit yield and fruit number were 26% and 75% higher, respectively, in the Dutch cultivar 'Levanzo' than in the Japanese cultivar 'Reiyou' (Table 1). In contrast, average fruit fresh weight was significantly (40%) higher in 'Reiyou' than in 'Levanzo'. Total soluble fruit solids showed similar trends in both cultivars. Estimated dry matter yield, which was calculated by fruit yield and dry matter fruit content, was significantly (30%) higher in 'Levanzo' than in 'Reiyou'.

In Experiment 2, fruit yield in 'Levanzo' (3622.5 g plant^{-1}) was significantly (30%) higher than that in 'Reiyou' (2794 g plant^{-1}; Figure 1). Dry matter yield in 'Levanzo' (183.7 gDW plant^{-1}) was 12% higher than that in 'Reiyou' (163.6 gDW plant^{-1}).

Leaf parameters and solar radiation in canopy

'Levanzo' tended to show 10% larger leaf area than 'Reiyou', but the difference was not significant (Table 2). However, the specific leaf area (SLA) that was used as a leaf thickness index in 'Levanzo' was significantly (16%) smaller than that in 'Reiyou'. Solar radiation on individual leaves in the canopy was measured at the apices and centers of compound leaves. Solar radiation at the center was higher than that at the apex in both

Table 2.   Leaf area, SLA and solar radiation on individual leaf in canopy in Experiment 1.

Cultivar	Leaf area (cm^2)	SLA ($cm^2 gDW^{-1}$*)	Solar radiation on individual leaf in canopy ($MJ cm^{-2} d^{-1}$)	
			Center	Apical
Reiyou	8541.2 ± 768.77** a ***	355.0 ± 14.04 b	23.9 ± 2.84 a	20.0 ± 2.81 a
Levanzo	9357.1 ± 1132.16 a	299.7 ± 2.09 a	33.3 ± 7.32 a	24.7 ± 4.70 a

* DW, dry weight. ** Means±standard errors ($n=3$). *** Different letters in each column significant differences by Student's t-test ($P=0.05$).
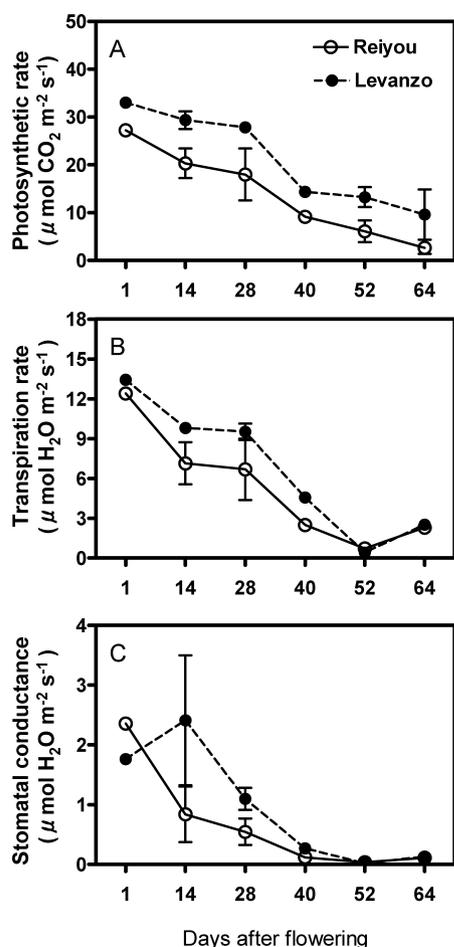

Figure 2.   Photosynthetic rate (A), transpiration rate (B), and stomatal conductance of leaves just below the second truss during the fruit development period of the second truss. Bars indicate standard errors ($n=3$).

Figure 3.   Chlorophyll a (A) and b (B) content in leaves. Bars indicate standard errors ($n=3$). Different letters indicate significant differences on the same day (Student's t-test).

cultivars. 'Levanzo' tended to show 39% and 23% higher solar radiation at the center and apex of compound leaves, respectively, but the result was not significant.

Photosynthetic rate

The photosynthetic rate, transpiration rate, and stomatal conductance of fully expanded young leaves just below the second truss were saturated at a PPFD of 4000 μmol $m^{-2} s^{-1}$ in both cultivars. During the fruit developing period, the photosynthetic rate, transpiration rate, and stomatal conductance decreased gradually (Figure 2). The photosynthetic rate decreased 29% in 'Levanzo' and 10% in 'Reiyou' at 1–64 DAF (Figure 2A). These results were higher for 'Levanzo' than for 'Reiyou'; however, a significant difference occurred only at 40 DAF.
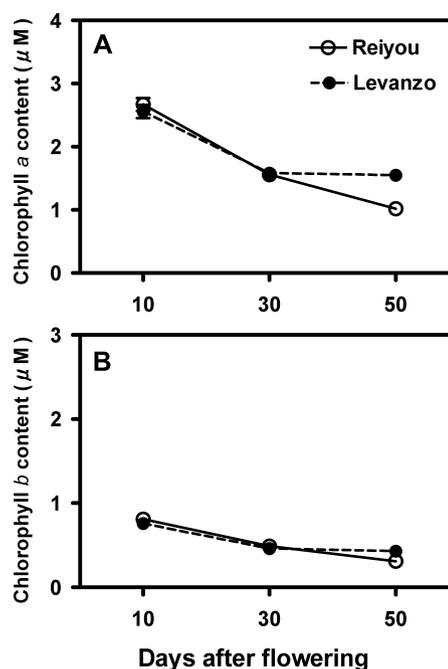
Transpiration rate and stomatal conductance in 'Levanzo' were higher than those in 'Reiyou' until 40 DAF; however, the cultivars showed similar trends after 52 DAF (Figure 2B, C).

Chlorophyll content

In the Japanese cultivar 'Reiyou', leaf Chl a and b contents gradually decreased during the measurement period (Figure 3A, B). In the Dutch cultivar 'Levanzo', both Chl contents decreased at 10–30 DAF, and these values were unchanged at 30–50 DAF. Thus, Chl a and b contents of the leaves in 'Levanzo' were 52% and 40% higher, respectively, than those in 'Reiyou' at 50 DAF, although no significant difference in Chl a or b content was observed at 10 or 30 DAF between the cultivars.

Expression of the sucrose transporter in source leaves

LeSUT1 transcriptional levels were investigated to elucidate the difference in sugar loading activity in source leaves between the two cultivars (Figure 4). This gene encodes the major isoform of the sucrose transporter in photosynthetic source leaves, which
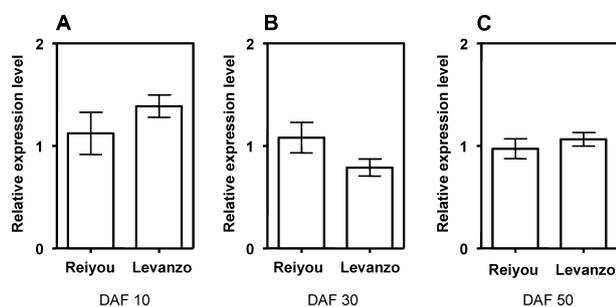
Figure 4. Relative *LeSUT1* gene expression levels in leaves just below the second truss at 10 (A), 30 (B) and 50 (C) days after flowering. Bars indicate standard errors ($n=3$).

functions in phloem loading of sucrose in tomato plants (Kühn et al. 1997; Hackel et al. 2006; Yin et al. 2010). No significant difference in *LeSUT1* transcriptional level was observed between the cultivars at 10, 30, or 50 DAF.

Discussion

Solar radiation on compound leaves was higher in the 'Levanzo' canopy than in the 'Reiyou' canopy (Table 2). This result indicates that the light extinction coefficient, the index of the light competition in the canopy, of 'Levanzo' was lower than that of 'Reiyou'. Cultivar differences in canopy development and radiation interception have been reported in sugarcane (Singels et al. 2005). Higashide and Heuvelink (2009) reported that an increase in LUE, which determines the increase in yield, is caused by a decrease in the light extinction coefficient and an increase in the leaf photosynthetic rate. Additionally, the increase in total dry matter production is caused by higher LUE in the high-yielding modern Dutch tomato cultivars (van der Ploeg et al. 2007). We did not determine LUE, but our results strongly suggest that the LUE of 'Levanzo' may have been higher than that of 'Reiyou'.

Leaf blade area and leaf dry weight were higher and SLA was lower in 'Levanzo' than in 'Reiyou' (Table 2). These results indicate that leaves of 'Levanzo' were thicker than those of 'Reiyou', and that not only fruit yield but also vegetative growth may be greater in 'Levanzo' than in 'Reiyou'. Increases in fruit dry yield are determined by an increase in total dry matter production in the aboveground parts (Higashide and Heuvelink 2009), and a high photosynthetic rate is required for high accumulation of dry matter in the plant body. Total plant productivity depends on the appropriate export of carbon from source leaves, which, in turn, depends on the carbon assimilation rate (Komor 2000). Some researchers have recently reported cultivar differences in photosynthetic rates, and a positive correlation has been observed between photosynthetic rate and yield among cultivars in some crops, such as tomato (Higashide and Heuvelink 2009; Matsuda et al.

2011a; van der Ploeg et al. 2007), asparagus (Bai and Kelly 1999; Faville et al. 1999), potato (Tekalign and Hmmes 2005), rice (Sasaki and Ishii 1992; Sasaki et al. 1996), and cotton (Stiller et al. 2005). Transpiration rates of both cultivars decreased drastically from 40 DAF, caused by a decrease in stomatal conductance (Figure 2B, C). The photosynthetic rate of 'Levanzo' was always higher than that of 'Reiyou' during the fruit enlarging period (Figure 2A). In 'Reiyou', photosynthetic rate decreased rapidly from 40 DAF to 9.6% of the peak value at 64 DAF, which was the last measurement day before the end of the harvesting period (90 DAF). This may have been caused by a decrease in stomatal conductance and Chl content (Figure 2C, 3). In contrast, 'Levanzo' maintained 29.1% of the peak photosynthetic rate at 64 DAF (the end of harvesting period was 86 DAF) because Chl content had not decreased, although stomatal conductance decreased. Downregulation of the photosynthetic components in tomato and soybean, such as Chl and RuBPcase, have been reported under high source/sink conditions (Matsuda et al. 2011a; Wittenbach 1982, 1983). However, the exact response to the source/sink ratio depends on the cultivar and probably on environmental conditions in other monocarpic plants (Crafts-Brandner and Egli 1987; Crafts-Brandner et al. 1984; Feller 1979; Patterson and Brun 1980). In 'Reiyou', the increase in the source/sink ratio caused by harvesting fruit may have had a greater influence on the decrease in Chl around the harvested truss. The source/sink ratio in 'Levanzo' may have been maintained by the stem, which works as a sink organ instead of fruit. As in de-podded soybean plants, additional starch may accumulate in the leaves and stems (Derman et al. 1978; Mondal et al. 1978). In contrast, *LeSUT1* transcriptional levels, which determine sugar loading activity in source leaves, did not differ between the cultivars. This result may have been due to the lack of difference in the capacity of sucrose loading from leaves to the phloem in the two cultivars. Therefore, the difference in translocation to fruit may have been based on the difference in sink capacity.

Under low-node-order pinching and high-density planting conditions, fresh and dry fruit weights of 'Levanzo' were higher than those of 'Reiyou' in the two experiments conducted during different years. The main factor affecting the difference in fruit yield per plant was the increase in fruit set in 'Levanzo' (Table 1, Figure 1). Matsuda et al. (2011b) reported that increasing fruit number per truss may improve the yields of Japanese tomato cultivars under high source/sink conditions such as high CO_2. Average fruit weight in 'Reiyou' was larger than that in 'Levanzo'; however, a significant difference in fruit weight was observed between proximal and distal fruit on the same truss in 'Reiyou' (data not shown). Thus, the distribution rate of assimilates among fruits in

the same truss varied widely in 'Reiyou', and most of the assimilate was translocated to a proximal fruit during early fruit development. This result is contrary to the observations of Bangerth and Ho (1984) and Bertin (1995), who found that the ability to attract assimilates is lower in distal fruit, and that distal fruits are disadvantaged when competing for assimilates. No significant difference in fruit weight among fruit positions on the same truss was observed in 'Levanzo'. This means that the sink activity of all fruits on the same truss was equal, and abundant photosynthate was efficiently and uniformly translocated to all fruits, due to the simultaneous enlargement of the fruits on the same truss. However, it is necessary to conduct a more detailed experiment to elucidate the difference in fruit growth between two cultivars because Matsuda et al. (2011b) reported that fruit growth rate were changed with environmental factor such as CO_2 concentration.

In conclusion, fruit yield of the Dutch cultivar 'Levanzo' was significantly higher than that of the Japanese cultivar 'Reiyou' under the low-node-order pinching and high-density planting conditions of Japan. This was caused by high source capacity due to higher photosynthetic rate and solar radiation on individual leaves in the canopy, although the leaf area was large and many sink fruit accepted abundant photosynthates, but not by sucrose loading at source leaves. We expected a larger difference in yield between the two cultivars under high-wire training. It is necessary to promote the photosynthetic rate by applying CO_2 and to improve solar radiation on canopy leaves using appropriate defoliation based on the analysis of tomato plant structure to improve fruit yield in Japanese tomato cultivars.

References

Bai Y, Kelly JF (1999) A study of photosynthetic activities of eight asparagus genotypes under field conditions. *J Am Soc Hort Sci* 124: 61–66

Bangerth F, Ho LC (1984) Fruit position and fruit sequence in a truss as factors determining final fruit size of tomato fruits. *Ann Bot* 53: 315–319

Bertin N (1995) Competition for assimilates and fruit position affect fruit set in indeterminate greenhouse tomato. *Ann Bot* 75: 55–65

Crafts-Brandner SJ, Below FE, Harper JE, Hageman RH (1984) Differential senescence of maize hybrids following ear removal. I. Whole plant. *Plant Physiol* 74: 360–367

Crafts-Brandner SJ, Egli DB (1987) Sink removal and leaf senescence in soybean. Cultivar effects. *Plant Physiol* 85: 662–666

Derman BD, Rupp DC, Nooden LD (1978) Mineral deitribution in relation to fruit development and monocarpic senescence in Anoka soybeans. *Am J Bot* 65: 205–213

Faville MJ, Silvester WB, Green TGA, Jermyn WA (1999) Photosynthetic characteristics of three asparagus cultivars differing in yield. *Crop Sci* 39: 1070–1077

Feller U (1979) Effect of changed source/sink relations on proteolytic activity and on nitrogen mobilization in field-grown wheat (*Triticum aestivum* L.). *Plant Cell Physiol* 20: 1577–1583

Hackel A, Schauer N, Carrari F. Fernie AR, Grimm B, Kühn C (2006) Sucrose transporter LeSUT1 and LeSUT2 inhibition affects tomato fruit development in different ways. *Plant J* 45: 180–192

Higashide T, Heuvelinka EP (2009) Physiological and morphological changes over the past 50 years in yield components in tomato. *J Am Soc Hort Sci* 134: 460–465

Komor E (2000) Source physiology and assimilate transport: the interaction of sucrose metabolism, starch storage and phloem export in source leaves and the effects on sugar status in phloem. *Aust J Plant Physiol* 27: 497–505

Kühn C, Franceschi VR, Schulz A, Lemoine R, Frommer WB (1997) Macromolecular trafficking indicated by localization and turnover of sucrose transporters in enucleate sieve elements. *Science* 275: 1298–1300

Matsuda R, Suzuki K, Nakano A, Higashide T, Takaichi M (2011a) Responses of leaf photosynthesis and plant growth to altered source-sink balance in a Japanese and Dutch tomato cultivar. *Sci Hort* 127: 520–527

Matsuda R, Nakano A, Ahn DH, Suzuki K, Yasuba K, Takaichi M (2011b) Growth characteristic and sink strength of fruit at different CO_2 concentrations in a Japanese and a Dutch tomato cultivar. *Sci Hort* 528–534

Mondal MH, Brun WA, Brenner ML (1978) Effects of sink removal on photosynthesis and senescence in leaves of soybean (*Glycine max* L.) plants. *Plant Physiol* 61: 394–397

Moniz SM, Drouin G (1996) Phylogeny and substitution rates of angiosperm actin genes. *Mol Biol Evol* 13: 1198–1212

Patterson TG, Brun WA (1980) Influence of sink removal in the senescence pattern of wheat. *Crop Sci* 20: 19–23

Pfaffl MW (2001) A new mathematical model for relative quantification in real-time RT-PCR. *Nucleic Acids Res* 29: e45

Porra RJ, Thompson WA, Kriedemann PE (1989) Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochim Biophys Acta* 975: 384–394

Tanabata T, Yamada T, Shimizu Y, Shinozaki Y, Kanekatsu M, Takano M (2010) Development of automatic segmentation software for efficient measurement of area on the digital images of plant organ. *Hort Res* 9: 501–506 (in Japanese)

Sasaki H and Ishii R (1992) Cultivar differences in leaf photosynthesis of rice (*Oryza sativa* L.) bred in Japan. *Photosynth Res* 32: 139–146

Sasaki H, Samejima M, Ishii R (1996) Analysis by $\delta^{13}C$ measurement on mechanism of cultivar difference in leaf photosynthesis of Rice (*Oryza sativa* L.). *Plant Cell Physiol* 37: 1161–1166

Singels A, Smit MA, Redshaw KA, Donaldson RA (2005) The effect of crop start date, crop class and cultivar on sugarcane canopy development and radiation interception. *Field Crop Res* 92: 249–260

Stiller WN, Read JJ, Constable GA, Reid PE (2005) Selection for water use efficiency traits in a cotton breeding program: cultivar differences. *Crop Sci* 45: 1107–1113

Tekalign T, Hmmes PS (2005) Growth and productivity of potato as influenced by cultivar and reproductive growth I. Stomatal

conductance, rate of transpiration, net photosynthesis, and dry matter production and allocation. *Sci Hort* 105: 13–27

van der Ploeg A, van der Meer M, Heuvelink E (2007) Breeding for more energy efficient greenhouse tomato: Past and future perspectives. *Euphytica* 158: 129–138

Watanabe S, Nakano Y, Okano K (2003) Effect of planting density on fruit size, light—interception and photosynthetic activity of vertically trained watermelon (Citrullus lanatus (Thunb.) Masum. et Nakai) plants. *J Jpn Soc Hort Sci* 72: 497–503

Wittenbach VA (1982) Effect of pod removal on leaf senescence in soybeans. *Plant Physiol* 70: 1544–1548

Wittenbach VA (1983) Effect of pod removal on leaf photosynthesis and soluble protein composition of field-grown soybeans. *Plant Physiol* 73: 121–124

Yin YG, Kobayashi Y, Sanuki A, Kondo S, Fukuda N, Ezura H, Sugaya S, Matsukura C (2010) Salinity induces carbohydrate accumulation and sugar-regulated starch biosynthetic genes in tomato (*Solanum Lycopersicum* L. cv. 'Micro-Tom') fruits in an ABA- and osmotic stress- independent manner. *J Exp Bot* 61: 563–574