Hybrid Vigor Induced by Cross-breeding Enhances Canopy Photosynthesis and Fruit Yield of Japanese Sweet Pepper

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The effect of hybrid vigor on the fruit yield in Japanese sweet pepper (*Capsicum annuum* L.) was investigated by comparing dry matter production, canopy light-intercepting characteristics and canopy photosynthesis of F1 cultivars to those of their parent lines. The greater yields in the F1 cultivars were caused by both higher dry matter partitioning rate into fruits and total dry matter production. There was no difference in the leaf photosynthetic capacity between the F1 cultivars and their parent lines. The canopy photosynthetic rate, total dry matter production, and yield showed significantly positive correlations with the photosynthetic photon flux absorbed within the plant canopy. The hybrid vigor caused higher plant statures with richer foliage, which led to more effective vertical profiles of leaf area, light absorption, and photosynthesis within the respective canopies. These factors caused a sufficiently higher canopy photosynthesis to produce greater dry matter production and maintain a higher dry matter partitioning rate into fruits, which resulted in higher yields. These results suggest that the vertical profiles of light-intercepting characteristics and photosynthesis within the canopies, which are evaluated by agro-meteorological methodology, are effective selection indices for breeding plants with higher yields.

Keywords : breeding, *Capsicum annuum* L., dry matter production, growth analysis, photosynthetic vertical profile

INTRODUCTION

First filial generation (F1) hybrids, created by crossing two inbred lines (i.e., parent lines), are well known to bring different characteristics to those of their parent lines, and become superior in terms of size, vigor, fertility and productivity, which is known as hybrid vigor (heterosis) (Shull, 1908; Harrington, 2007). Furthermore, F1 hybrids are not only beneficial in terms of higher yields, but also higher resistances to pests, and varieties of F1 have been introduced as commercial cultivars in many crops, including peppers (*Capsicum*).

Except for the yield and growth characteristics, there is little understandings of hybrid vigor in peppers (Geleta and Labuschagne, 2004a; 2004b; Rego et al., 2009; Marame et al., 2009). Selecting superior F1 hybrids and parent lines for cross-breeding plants with higher yields requires an enormous amount of time and effort; it is necessary to judge the effects of hybrid vigor on the growth characteristics and yield based on comparative analyses with field cultivation tests using a large number of F1 combinations. On the other hand, the mechanism of hybrid vigor is known for dry matter production, such as total dry matter production or dry matter partition rate into fruits in Arabidopsis (Meyer et al., 2004), maize (Tollenaar et al., 2004), and rice (Yang et al., 2002; Peng et al., 2008); and for genetic analysis, such as the elucidation of the gene related to yield and the development of molecular markers in maize (Stuber et al., 1992), rice (Yu et al., 1997) and, tomato (Semel et al., 2006; Krieger et al., 2010; Yamamoto et al., 2015) to find a shortcut to selecting superior F1 and parent lines. Furthermore, morphological traits, such as the form, size, and the number of each organ are expected to contribute to finding the shortcut for selection in rice (Peng et al., 2008) and tomato (Krieger et al., 2010). In the cross-breeding of pepper for higher yields, it is expected that elucidating the mechanism of hybrid vigor for yield and determination of the reasonable selection index can produce more efficient breeding with a smaller amount of time and effort. In this study, the effect of hybrid vigor on the fruit yield in Japanese sweet pepper was investigated by comparing the F1 cultivars to their parent lines in terms of dry matter production and canopy photosynthesis, determined by both the leaf photosynthetic capacity and the light-intercepting characteristics depending on foliage structure.

MATERIALS AND METHODS

Plant materials and growth conditions

Four F1 cultivars of typical Japanese sweet pepper (*Capsicum annuum* L.) and their seed and pollen parent lines bred at the Kochi Agricultural Research Center were used as plant materials: two seed parent lines, Shosuke (S1) and 95S1-4 (S2), two pollen parent lines, MK18-3-1 and 58S1-429, vol. 57, no. 2 (2019), Environ. Control Biol., 57 (2), 29-38, 2019
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(P1) and 99B2-11-7-4 (P2); and their four F1 cultivars, ‘Tosahime’ (S1×P1), ‘Tosahime R’ (S2×P1), ‘Tosa P red’ (S1×P2), and ‘Tosamidorii’ (S2×P2), were examined.

The seeds were sown in trays filled with a nursery soil on August 10, 2016. Just before the transplantation in the greenhouse at 0 day after transplantation (DAT), the initial leaf areas in four seedlings of the respective four F1 cultivars and their parent lines were measured using an automatic leaf area meter (AAC-400; Hayashi Denko; Tokyo, Japan). The leaves with their petioles and stems were dried at 80°C for more than 96 hours, and the dry weight was measured. On the same day, the seedlings were transplanted into a greenhouse located in the Kochi Agricultural Research Center (Nankoku-city, Japan; 33.59°N, 133.64°E). Figure 1 shows the schematic diagram of the experimental greenhouse used in this study. The greenhouse was a N-S oriented plastic house (height, 3.6 m; width, 7.6 m; length, 20 m), where four ridges with a width of 1.8 m and a length of 16 m were set in a N-S orientation, and two ridges in the middle were used for the experiment (two ridges on the east and west sides were for protection). The planting density was 3.7 plants m$^{-2}$, with a stock distance of 30 cm and a distance between rows of 50 cm. Two ridges in the middle were separated into four plots: two plots were for destructive analyses of dry matter production, leaf area, and the other two plots were for non-destructive analyses of growth characteristics and yield, using statistical tests, until the end of cultivation. Each plot was surrounded by guard plants which were not sampled. Four plants of the respective four F1 cultivars and their parent lines were planted in each plot. Ventilation in the greenhouse was provided through roof vents when the air temperature was higher than 27°C. The air temperature during the nighttime was maintained at higher than 18°C by operating an oil heater. Biological pest control was also applied during the experiment. Fertilizer (N = 31, P = 37, K = 27 g m$^{-2}$) was applied to all of the ridges. Plants were irrigated every day at a rate of 208–1,226 mL d$^{-1}$ per plant depending on the growth and the weather condition, so that the soil moisture tension (pF) value was maintained at 2.0 to 2.5. Once a week, 300–500 fold diluted liquid fertilizer was applied (N = 0.8, P = 1.3, K = 0.5 g m$^{-2}$), and consequently, the soil chemical condition was maintained at around pH = 5.8 and EC = 0.8.

Each plant was pruned into two main branches on the main stem, and the side shoots on the main branches were pinched leaving one leaf and one flower. Furthermore, old leaves that had completely yellowed on the shoot were removed. The dry weight of the pinched side shoots and old yellow leaves were measured. Three times a week, fully matured red fruits were harvested, together with their pedicles, from every 30 cm canopy layer above the ground, and their fresh and dry weights were measured. At 40 and 75 DAT, the leaf area and dry weights of leaves, stems and fruits from every 30 cm canopy layer in four plants of the respective F1 cultivars and their parent lines on each plot for destructive analyses were measured. At the end of the cultivation (114 DAT), eight plants of the respective four F1 cultivars and their parent lines on two plots left for non-destructive analyses were sampled from every 30 cm canopy layer. In these sampled plant materials from the respective 30 cm canopy layers, the leaf areas, fresh and dry weights of fruits, and dry weights of the stem and leaves were measured. The total dry matter production above ground ($TDM$) was evaluated.

**Growth characteristics**

At 0, 16, 40, 56, 75, 96, and 114 (DAT), the plant height (from the ground surface to the growing point of the higher main branch), lengths of the two main branches, maximum diameter of the main stem (at the middle point between the first and second nodes), and number of nodes in the main branch were measured in eight plants of the respective four F1 cultivars and their parent lines in the two plots for non-destructive analyses.

**Growth analysis**

The daily rate of dry matter production of the aboveground shoots (Crop growth rate; [CGR]) was evaluated as follows:

$$CGR = \frac{[W(t_{2})-W(t_{1})]}{t_{2}-t_{1}} \text{ (g m}^{-2} \text{ d}^{-1})$$

where $W(t)$ is total dry matter weight of aboveground shoot per unit ground area and $t$ is the time (days) (Saeki, 1965). The daily rate of dry matter production of aboveground shoot per unit leaf area (net assimilation rate; [NAR]) was evaluated as follows:

$$NAR = \frac{[W(t_{2})-W(t_{1})] \times [\ln LA(t_{2})-\ln LA(t_{1})]}{t_{2}-t_{1}} \times [\ln LA(t_{2})-\ln LA(t_{1})] \text{ (g m}^{-2} \text{ d}^{-1})$$

where $LA$ is the leaf area at time ($t$) (Saeki, 1965). Watson (1956; 1958) reported that $NAR$ decreased nearly linearly with an increase in the mean leaf area index ($mLAI$); hence, the $mLAI$ values at two dates were evaluated as follows:

![Fig. 1 Schematic diagram of the experimental greenhouse used in this study. (A) Destructive analysis at 40 days after transplanting (DAT), (B) destructive analysis at 75 DAT, and (C and D) non-destructive analyses of the growth characteristics and yield for destructive analyses at 114 DAT (the end of cultivation). Black dots (●) are shows as plants. Black parts were used for the guard.](image-url)
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mLAI = \[LA(t_i) - LA(t_i)\] / \[lnLA(t_i) - lnLA(t_i)\] (3)

From Eqs. (1), (2), and (3), the NAR was also estimated by dividing CGR by mLAI

\[NAR = \frac{CGR}{mLAI}\] (4)

Measurements of photosynthetic rate and light condition

The leaf photosynthetic rate was measured in matured leaves of the four F1 cultivars and their parent lines by using a portable photosynthesis system (LI-6400XT; LI-COR, Lincoln, NE, USA). The measurement was conducted on a single upper leaf (fifth or sixth leaf from the growing point) and the single lower leaf (second or third leaf from the base of main branches, 30–60 cm from the ground) under photosynthetic photon flux densities (PPFDs) of 0, 100, 250, 500, and 1,000 μmol m⁻² s⁻¹ using a light source (Li-6400-02B; LI-COR, Lincoln, NE, USA) at a CO₂ concentration of 400 μmol mol⁻¹. The relationship between the photosynthetic rate (A) and PPFD was fitted by a hyperbolic equation:

\[A = \frac{b\times PPFD}{1 + (b\times A_{max})\times PPFD}\]

\[-R = (\mu \text{mol m}^{-2} s^{-1})\] (5)

where \(b\) is the initial slope, \(A_{max}\) is the maximum photosynthetic rate, and \(R\) is the respiration rate.

To obtain the vertical profile of light intensity within the respective plant canopies of the F1 cultivars and their parent lines, we measured the PPFD at height intervals of 30 cm using a line-PPFD sensor (ACCUPAR LP-80; Meter Group, Inc., Hopkins Court, NE, USA). The relative light intensity (RLI) of the 30 cm height (0, 30, 60, 90, 120, 150, 180, 210, and 240 cm) from the bottom of plant canopy was evaluated as follows:

\[RLI = \frac{PPFD}{PPFD_{100}}\] (6)

where \(PPFD\) is the PPFD of the 30 cm height (0, 30, 60, 90, 120, 150, 180, 210, and 240 cm) from the bottom of the plant canopy, and \(PPFD_{100}\) is the PPFD at the top of the plant canopy (240 cm height from the bottom of plant canopy). The light extinction coefficient (K) within the respective plant canopies can be also evaluated based on the Monsi and Saeki theory (1953) by using the PPFD and leaf area index (LAI):

\[PPFD_i = PPFD_{100} \times e^{-k \cdot \text{LAI}}\] (7)

Furthermore, we approximated the photosynthetic photon flux (PPF_{Ai}) absorbed by leaves within the ith 30 cm canopy layer from the bottom of the plant canopy (0–30, 30–60, 60–90, 90–120, 120–150, 150–180, 180–210, and 210–240 cm) as follows:

\[PPF_{Ai} = RLI_{i} / 100 \times PPFD_{i} / LA_i\] (8)

where \(LA_i\) is the leaf area within the ith 30 cm canopy layer (0–30, 30–60, 60–90, 90–120, 120–150, 150–180, 180–210, and 210–240 cm).

The photosynthetic rate (\(A_i\)) with the ith 30 cm canopy layer from the bottom of the plant canopy was evaluated based on the photosynthetic curve of Eq. (5) by using PPFD_{i-1} and LA_i:

\[A_i = A_{PPFD_{i-1}} / LA_i\] (9)

The photosynthetic rate within the whole plant canopy (\(AC\)) (0–240 cm) was evaluated by accumulating the \(A_i\) of each 30 cm canopy layer:

\[AC = \sum A_i\] (10)

RESULTS

Growth, yield, and dry matter

Table 1 shows the growth characteristics of the four F1 cultivars and their parent lines. The plant heights of the F1 cultivars were higher than those of their parent lines. The diameters of the main stems of the F1 cultivars were thinner than those of their parent lines. The length and node numbers of the main branches were smaller in the pollen parent lines than in the seed parent lines and F1 cultivars. The leaf areas were also smaller in the pollen parent lines than those in the seed parent lines and F1 cultivars.

Table 2 shows the yield and number of fruits, average fruit weight, dry matter ratio of ripe fruits, aboveground TDM, and dry matter partitioning ratios into the respective organs of fruits, stems and leaves. The fruit yields were

| Cultivar     | Plant height | Main stem | Main branch | Leaf area |
|--------------|--------------|-----------|-------------|-----------|
|              | (cm)         | Diameter  | Length      | Node number | (cm²)    |
| Shosuke      | 203 a        | 11.8 ab   | 161 a       | 29.5 a     | 7,506 bc |
| 95S1-4       | 170 c        | 11.6 abc  | 132 c       | 28.5 a     | 9,342 a  |
| MK18-3-1     | 177 bc       | 12.5 a    | 129 c       | 23.8 b     | 5,823 de |
| 99B2-11-7-4  | 117 d        | 10.9 bcd  | 71 d        | 19.8 c     | 4,874 e  |
| Tosahime     | 189 ab       | 10.4 d    | 152 ab      | 26.8 ab    | 6,641 cd |
| Tosahime R   | 193 ab       | 10.9 bcd  | 158 a       | 28.6 a     | 7,861 b  |
| Tosa P red   | 204 a        | 10.6 cd   | 162 a       | 28.9 a     | 8,066 b  |
| Tosamidori   | 178 bc       | 10.3 d    | 137 bc      | 27.6 a     | 7,871 b  |

* The survey date: January 13, 2017, at the end of the cultivation.

† Values within a column followed by different letters differ significantly for the same environmental conditions (P<0.05; by Turkey’s multiple comparison test).

‡ Diameter of the main axis: the middle point between the first and second node of the main axis.
larger in the F1 cultivars than those in their parent lines. ‘Tosa P red’ showed the largest fruit yield among the four F1 cultivars, although its pollen parent line, 99B2-11-7-4, showed the smallest fruit yield. The fruit numbers in the four F1 cultivars were significantly larger than those in their pollen parent lines, while the largest fruit number was found in the seed parent line Shosuke. The average fruit weights in the four F1 cultivars were larger than those in their seed parent lines, but smaller than those in their pollen parent lines. The dry matter ratios of ripe fruits of the four F1 cultivars were higher than those of their pollen parent lines and the same as those of their seed parent lines. The aboveground TDM value were larger in the four F1 cultivars than those of their parent lines; moreover, the TDM in the F1 cultivar of ‘Tosa P red’ was also larger than that of the other F1 cultivars. The dry matter partitioning rate into fruits were significantly higher in the four F1 cultivars than those in their parent lines. On the other hand, the dry matter partitioning rates into the stems and leaves in the F1 cultivars were lower than those in their parent lines.

**Table 2** Fruit yield, fruit number, average fruit weight, dry matter ratio of ripe fruits, total dry matter production (above ground) (TDM; fruits, stems, leaves, and pruned shoot) and dry matter partitioning rate to each organ (fruits, stems, and leaves) of four F1 cultivars (‘Tosahime’, ‘Tosahime R’, ‘Tosa P red’, and ‘Tosamidori’), and their two seed parent lines (Shosuke and 95S1-4) and two pollen parent lines (MK18-3-1 and 99B2-11-7-4).a

| Cultivar          | Fruit yield | Fruit number | Fruit average weight | Dry matter ratiob of ripe fruits | TDM (above ground) | Dry matter partitioning rate to | % | % | % |
|------------------|-------------|--------------|----------------------|----------------------------------|-------------------|------------------------------|----|----|----|
|                  | g FW        |              | g FW                 | g DW × g−1FW                     | g DW              | fruits                      | stems | leaves |
| Shosuke (S1)     | 1.096 cd    | 42 a         | 31 d                 | 0.10 ab                          | 190 bc            | 52 b                        | 20 b  | 17 b |
| 95S1-4 (S2)      | 741 ef      | 29 bc        | 32 d                 | 0.10 ab                          | 167 cd            | 42 c                        | 20 b  | 25 a |
| MK18-3-1 (P1)    | 983 de      | 15 d         | 83 b                 | 0.08 e                           | 153 d             | 50 b                        | 24 a  | 19 b |
| 99B2-11-7-4 (P2) | 610 f       | 6 e          | 136 a                | 0.09 bc                          | 99 e              | 52 b                        | 20 b  | 23 a |
| Tosahime (S1×P1) | 1,270 bc    | 28 bc        | 56 c                 | 0.11 a                           | 199 ab            | 62 a                        | 16 d  | 14 d |
| Tosahime R (S2×P1) | 1,355 ab    | 30 b         | 55 c                 | 0.10 ab                          | 209 ab            | 58 a                        | 17 cd | 16 cd |
| Tosa P red (S1×P2) | 1,581 bc   | 30 b         | 67 c                 | 0.09 abc                         | 224 a             | 60 a                        | 17 d  | 16 cd |
| Tosamidori (S2×P2) | 1,239 bc  | 24 c         | 59 c                 | 0.10 ab                          | 192 bc            | 58 a                        | 16 d  | 18 bc |

a Survey date: January 13, 2017.
y Values within a column followed by different letters differ significantly under the same environmental conditions (P<0.05; by Turkey’s multiple comparison test).
x Dry matter ratio of ripe-fruits: dry weight of ripe fruits/fresh weight of ripe fruits.

**Fig. 2** Mean leaf area index (mLAI), net assimilation rate (NAR) and crop growth rate (CGR; mLAI×NAR) during three different periods of (A) 0–40 days after transplanting (DAT), (B) 40–75 DAT and (C) 75–114 DAT in two seed parent lines (Shosuke [S1] and 95S1-4 [S2]), two pollen parent lines (MK18-3-1 [P1] and 99B2-11-7-4 [P2]) and their four F1 cultivars (‘Tosahime’ [S1×P1], ‘Tosahime R’ [S2×P1], ‘Tosa P red’ [S1×P2], and ‘Tosamidori’ [S2×P2]).
Figure 2 shows mLAI, NAR, and CGR during the three periods of 0–40, 40–75, and 75–156 DAT. During all periods, the CGRs of the four F₁ cultivars remained at a higher level than those of their parent lines, because the seed parent lines had low NAR value and the pollen parent lines had low mLAI values compared to those of their F₁ cultivars.

Photosynthesis and light condition in plant canopies

Figure 3 shows the relationships between the PPFD and photosynthetic rate in single upper and lower leaves of the four F₁ cultivars and their parent lines. In both the upper and lower leaves, there was no significant difference in the photosynthetic rate at each PPFD between the four F₁ cultivars and their parent lines. Figure 4 shows the vertical profiles of the leaf area per plant, relative light intensity, and photosynthetic photon flux (PPF) absorbed by leaves in each 30 cm canopy layer within the respective plant canopies of the four F₁ cultivars and their parent lines, where the light extinction coefficient (K) through each canopy was also shown. The leaf area, light intensity, and, consequently, the absorbed PPF appeared in different vertical profiles among the four F₁ cultivars and their parent lines, and in particular, the leaf area and the absorbed PPF within each plant canopy showed different vertical profiles because of the vertical extinction of light intensity. Furthermore, there are no clear relationships in each vertical profile between the F₁ cultivars and their parent lines. In the four F₁ cultivars, the PPF absorbed by the leaves in the upper three layers was large compared to that of their parent lines. Figure 5 shows vertical profiles of the leaf area and photosynthetic rate (A) in each 30 cm layer within the respective plant canopies of the four F₁ cultivars and their parent lines. The vertical profile of A was different to that of the leaf area. As found in the profile of PPF (Fig. 4), the total A within the upper three or four canopy layers was larger in the four F₁ cultivars than in their parent lines.

Figure 6 shows vertical profiles of the photosynthetic rates and dry weights of the respective organs of leaves, fruits, and stems in each 30 cm layer within the respective plant canopies of the four F₁ cultivars and their parent lines. In all of the F₁ cultivars and their parent lines, most of the dry weights was localized to the fruits. The vertical profile of the fruit dry weight was quite different to that of A, and the fruit dry weight was distributed much more in the lower layers than A, the bulk fruit dry weight was localized to several decimeters below that of A. In the four F₁ cultivars, the bulk fruit dry weight was much larger than that of their parent lines, as found in A.

Figure 7 shows the relationships of the canopy photosynthetic rate, TDM, and fruit yield with the canopy-absorbed PPF. There are significant positive correlations among them (e.g., r = 0.99 and P<0.01 between the canopy photosynthetic rate and canopy absorbed PPF; r = 0.95 and P<0.01 between the TDM and canopy-absorbed PPF; r = 0.81 and P<0.05 between the fruit yield and canopy-absorbed PPF). Figure 8 shows the distribution of the fruit number and fruit fresh weight at each node along the main branches in a whole plant of the four F₁ cultivars and their parent lines. In all of the F₁ cultivars and their parent lines, all flowers appeared at each node, at the main branches and side shoot (data not shown), and the fruit number and fruit fresh weight on the middle nodes (from the 10th to 15th) were greatly reduced compared to those on the lower nodes (below the 10th) and higher nodes.
Fig. 4 Vertical profiles of leaf area, relative light intensity, absorbed photosynthetic photon flux of leaves (PPFₐ), and the extinction coefficient (K) evaluated from the relationship between the leaf area and relative light intensity in a whole plant of four F₁ cultivars and their two seed parent lines (S) and two pollen parent lines (P).

Fig. 5 Vertical profiles of leaf area and photosynthetic rate (A) in a whole plant of four F₁ cultivars and their two seed parent lines (S) and two pollen parent lines (P).
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Fig. 6  Vertical profiles of photosynthetic rate (\(A\)), dry weights (DW) of leaves, fruits and stems in a whole plant of four F1 cultivars and their two seed parent lines (S) and two pollen parent lines (P).

Fig. 7  The relationship between the canopy absorbed photosynthetic photon flux (PPF), canopy photosynthetic rate, and total dry matter production (above ground) and fruit yield of four F1 cultivars and their two seed parent lines (S) and two pollen parent lines (P). ***, * significant correlations at \(P<0.01\) and \(<0.05\).
DISCUSSION

The effects of the hybrid vigor induced in the four F₁ cultivars were investigated by comparative analyses with their parent lines, where the higher fruit yields induced in the F₁ cultivars were related to the dry matter production, growth characteristics, and vertical profiles of light absorption and photosynthesis in each plant canopy.

The larger fruit yield in the four F₁ cultivars were caused by the higher fruit numbers than those of their pollen parent lines (Table 2). The increase in the fruit yield of the F₁ cultivars was attributed to the increase in dry matter accumulation in fruits (i.e., a higher total fruit dry weight) rather than the increase in water accumulation in fruits (i.e., a lower dry matter ratio of ripe fruits). The higher dry matter partitioning rates to grains have been reported to contribute to the higher yields in rice (Saitoh et al., 1991; Saitoh et al., 1993; Ying et al., 1998) and durum wheat (Giunta et al., 2007). Furthermore, the larger total dry weights of a whole plant (TDM) have been reported to relate to the higher yields in tomato (Higashide and Heuvelink, 2009), rice (Saitoh et al., 1993; Ying et al., 1998), buckwheat (Morishita and Tetsuka, 2001), strawberry (Mochizuki et al., 2013), and soybean (Ookawa et al., 1999; Liu et al., 2005; De Bruin and Pedersen, 2009), and the larger TDMs induced by hybrid vigor have been found in Arabidopsis (Meyer et al., 2004), rice (Yang et al., 2002) and maize (Tollenaar et al., 2004). In this study, the hybrid vigor on fruit yield in the F₁ cultivars was significantly correlated with the higher dry matter partitioning rates into fruits and the increase in TDM (Table 2). The larger TDMs in the F₁ cultivars were caused by the higher CGRs (increasing rates of daily dry matter production in whole plants), and the higher CGRs in the F₁ cultivars were caused by a high mLAI and the high NAR compared.
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to those in their pollen parent lines and seed parent lines, respectively (Fig. 2).

The N4R of Eq. (2) has been used as the photosynthetic efficiency for plant canopy, which depends on the leaf photosynthetic capacity and the light-intercepting characteristics within the canopy (Lambers and Poorter, 1992). A higher leaf photosynthetic capacity has been reported to contribute to higher yields in tomato (Higashide and Heuvelink, 2009), spring wheat (Fischer et al., 1998) and rice (Jiang et al., 1988; Takai et al., 2013), but has not been related to higher yields in strawberry (Mochizuki et al., 2013) and soybean (Kokubun et al., 1988). In this study, there was no difference in the leaf photosynthetic capacity (in both the upper and lower leaves) between the F1 cultivars and their parent lines (Fig. 3). In addition, the PPF absorbed within the canopy of the F1 cultivars was larger than that of the parent lines (Figs. 4, 5, and 7). Therefore, the N4R can be considered to depend more significantly on the light-intercepting characteristics within the canopy rather than on the leaf photosynthetic capacity, as reported in rice (Saitoh et al., 1990). In pepper, the higher plant height is one of the morphological effects induced by the hybrid vigor (Geleta and Labuschagne, 2004a; Singh et al., 2014). The higher plant height induced in the four F1 cultivars was considered to develop richer foliage vertically, with leaf-layers effectively absorbing PPF.

The larger PPF absorption by the rich foliage through the higher canopy of the F1 cultivars caused a higher canopy photosynthetic rate, larger TDM, and consequently, a greater fruit yield. In Japanese sweet pepper, because of the characteristic of one flower and one leaf appearing at each node, all flowers (four flowers) were set per one node in a whole plant and the physiological abscission of flowers or fruits after active fruit set was occurred in each F1 cultivar and parent line, but recoveries from abscission in the F1 cultivars were more rapid than in their parent lines (Fig. 8). In pepper, the cyclic pattern in the yield caused by the physiological abscission of flowers or fruit depends on not only the source strength (i.e., the photosynthetic efficiency of the plant canopy) but also on the sink strength of each competing sink organ (Marcelis., 1996; Marcelis et al., 2004; Wubs et al., 2009a; Wubs et al., 2009b; Lin and Frey, 2009). The more rapid recoveries from physiological abscission in the F1 cultivars derives from the higher canopy photosynthetic rate (i.e., the source strength). Furthermore, the higher canopy photosynthetic rate in the F1 cultivars produced a greater TDM to supply sufficient dry matter to fruits as one of the main sink organs.

Long et al. (2006) has reported that plant breeding for a larger grain yields has mainly been performed though greater dry matter partitioning to grains and increased light-intercepting characteristics within plant canopies with poor leaf photosynthetic capacity. In this study, the hybrid vigor induced in the four F1 cultivars of Japanese sweet pepper caused higher plant statures with richer vertically developing foliage, which led to more effective vertical profiles of leaf area, light absorption, and photosynthesis within the plant canopies. These effective vertical profiles caused higher canopy photosynthetic levels, greater dry matter production, and higher dry matter partitioning rates to fruits, which resulted in higher fruit yields. This suggests that canopy photosynthesis depends on the vertical profiles of leaf area, light absorption, and photosynthesis within the plant canopies. These profiles, quantified by agro-meteorological methods, can be used as effective selection indices in breeding plants for higher yields.

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