Analysis of a High-yielding Strawberry (*Fragaria × ananassa* Duch.) Cultivar ‘Benihoppe’ with Focus on Dry Matter Production and Leaf Photosynthetic Rate

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This study was conducted to clarify the ecophysiological traits of high-yielding ‘Benihoppe’ with focus on its dry matter production, plant growth analysis, and leaf photosynthetic rate in comparison with those of ‘Toyonoka’ and ‘Sachinoka’. Total dry matter of ‘Benihoppe’ was higher than that of ‘Toyonoka’, while no difference was found between their harvest indices. In ‘Benihoppe’, the crop growth rate (CGR) and leaf area index (LAI) were higher than those of ‘Toyonoka’ and ‘Sachinoka’. The large LAI of ‘Benihoppe’ was attributed to its ability to bear larger leaves than other cultivars, while ‘Benihoppe’ demonstrated a superior net assimilation rate (NAR) to that of ‘Toyonoka’. NAR is affected by leaf photosynthetic activity; however, no difference was observed between the leaf photosynthetic rates of ‘Benihoppe’ and ‘Toyonoka’. Petioles in ‘Benihoppe’ that supported large leaves were longer and upright, and NAR might be affected by their trait, which allow solar radiation to penetrate the plant canopy. Thus, the outstanding CGR in ‘Benihoppe’ may be a result of the large LAI and upright petioles which allow solar radiation to penetrate the plant canopy.

Key Words: cultivars, dry matter accumulation, growth analysis, leaf area index, upright petiole.

Introduction

While the area planted with strawberry (*Fragaria × ananassa*) in Japan decreased from 13,000 ha in 1970 to 6,500 ha in 2007, fruit yield increased from 100,000 MT to 190,000 MT in the same period, which may be attributed to breeding of new cultivars and development of cultivation techniques (Morishita, 2011); however, during the past five years, strawberry yield per unit area has remained steady, while the planted area has continued to decrease. Furthermore, due to oil price hikes, farmers could not sufficiently heat their greenhouses in winter, which disadvantaged their strawberry production; therefore, it is necessary to breed new cultivars with higher-yielding capacity under unfavorable conditions.

High-yielding rice (*Oryza sativa*) and soybean (*Glycine max*) cultivars have been determined by their dry matter production, growth characteristics and leaf photosynthetic rate, compared to those of conventional cultivars (Asanuma et al., 2008; Fukushima et al., 2011; Ookawa et al., 1999; Xu et al., 1997; Wang et al., 1997). Regarding strawberry, however, recent studies have focused on product quality such as high sugar content and transportation tolerance (Ogiwara et al., 1998a, b; Sone et al., 2002). Under today’s socioeconomic circumstances as mentioned above, it has become necessary to investigate high-yielding characteristics of strawberry. To this end, modifications of the cultivation environment, e.g., carbon dioxide (CO2) applications (Shigeno et al., 2001), and warming of the rhizosphere (Fukumoto et al., 2003) and crown (Sato and Kitajima, 2010) have been examined. On the other hand, few ecophysiological studies have been conducted on the difference in fruit productivity between the recent high-yielding strawberry cultivars and the more traditional cultivars.

A strawberry cultivar, ‘Benihoppe’, was bred in Shizuoka Prefecture in 2002. This cultivar possesses the special trait of producing more than 600 grams of fruit per plant per season (Takeuchi et al., 1999) and has become one of the leading cultivars in the Japanese strawberry industry. Therefore, it may be useful breeding material for future variety improvement programs; however, so far there has been no report on the ecophysiological analysis of the high-yielding capacity...
of ‘Benihoppe’, which may facilitate the breeding of high-yielding strawberry in the future.

To increase fruit yield, it is necessary to increase the ability of leaf photosynthesis, product assimilation and partition of a larger portion of the assimilation products to fruit; therefore, it is important to know the relationships among these ecophysiological characteristics and fruit yield. In rice, high-yielding cultivars have special traits, such as a higher photosynthetic rate (Xu et al., 1997) and partitioning of a larger amount of assimilation products to ears (Saitoh et al., 1991). Furthermore, leaf positioning affects light-intercepting characteristics and CO₂ diffusion (Kuroda et al., 1989).

This study thus intends to clarify the ecophysiological traits of high-yielding ‘Benihoppe’ with focus on its dry matter production, plant growth, and leaf photosynthetic rate in comparison with those of ‘Toyonoka’ and ‘Sachinoka’.

Materials and Methods

In this study, three strawberry cultivars were used, namely the high-yielding ‘Benihoppe’, and ‘Toyonoka’ and ‘Sachinoka’ as contrast cultivars. Their growing season is 6 months from the end of September to the end of March the following year. This research was conducted for 4 years from 2007 through 2010. Firstly, ‘Benihoppe’ and ‘Toyonoka’ were studied in 2007 and 2008 growing seasons, followed by ‘Benihoppe’ and ‘Toyonoka’ were studied in 2007 and 2010 growing seasons. At the end of August, plantlets were cut from mother stocks ‘Sachinoka’ in 2009 and 2010 growing seasons. At the end of March the following year. This research was conducted for 4 years from 2007 through 2010. Firstly, ‘Benihoppe’ and ‘Sachinoka’ as contrast cultivars. Their growing season, two to five plants each of the two cultivars were investigated. In the 2007 growing season, three plants each of ‘Benihoppe’ and ‘Toyonoka’ in the 2007 growing season. Three plants each of ‘Benihoppe’ and ‘Toyonoka’ were harvested on December 1, 27, January 19, February 4, 23, and March 17. Plants were separated into root, crown, petiole, leaf, peduncle, and fruit. Therefore, they were dried at 80°C for 72 hours with a circulation drier and weighed after exposing to room temperature in a desiccator. Dry matter accumulation, partitioning and harvest index were calculated for each date and period. Harvest index is the ratio of strawberry fruit dry matter to total dry matter.

2. Growth analysis

Three plants each of ‘Benihoppe’ and ‘Toyonoka’ in the 2007 growing season, and five plants each of ‘Benihoppe’ and ‘Sachinoka’ in the 2010 growing season were sampled, respectively. The 2007 growing season was divided into three periods: December 1 to 27, December 27 to February 4, and February 4 to March 17. The 2010 growing season was divided into two periods: November 28 to December 23 and December 23 to February 13.

Crop growth rate (CGR), net assimilation rate (NAR), and leaf area index (LAI) were calculated by assigning the measurements of total dry matter and leaf area on each investigation date to the following formulae:

\[
\text{CGR} = \frac{(W_2 - W_1)}{G_A/(t_2 - t_1)}
\]

\[
\text{NAR} = \frac{(W_2 - W_1)}{(t_2 - t_1) \cdot [(\ln(L_{A2}) - \ln(L_{A1}))/(L_{A2} - L_{A1})]}
\]

\[
\text{LAI} = \frac{\text{CGR}}{\text{NAR}}
\]

where \(W_1\) and \(W_2\) indicate dry matter weights per plant on investigation dates \(t_1\) and \(t_2\), where growing area per plant was \(G_A\) and leaf areas were \(L_{A1}\) and \(L_{A2}\), respectively.

3. Changes in total leaf area, average of single leaf area, and leaf number

The sample plants measured for dry matter were used. Before drying the plants, their leaf areas were measured by an automatic area meter (AMM-9; Hayashidenko Co., Ltd., Tokyo, Japan). Average of a single leaf area was calculated by dividing total leaf area by leaf number. The studied plants were adjusted to bear 4 fully expanded leaves each as of October 29, 2007, by removing extra leaves, and leaf development was recorded thereafter during the study period.

4. Leaf photosynthetic rate under different environmental conditions

In the 2007 growing season, three plants each of ‘Benihoppe’ and ‘Toyonoka’ were measured for comparison of their leaf photosynthetic rates on October 13, November 7, and February 26. In the 2008 growing season, two to five plants each of the two cultivars were measured likewise on October 14, 31, November 15, December 13, and February 5.
The photosynthetic rates under different temperatures, light intensities, and intercellular CO$_2$ concentrations were measured for three plants each of ‘Benihoppe’ and ‘Toyonoka’ on May 2, 2008. The photosynthetic rates at different leaf positions, from the second to fifth of five fully expanded leaves, were measured for four plants each of ‘Benihoppe’ and ‘Toyonoka’ on November 7, 2007.

The photosynthetic rate and intercellular CO$_2$ concentrations were measured using a portable photosynthesis system (LI-6400; LI-COR, NE, USA) with an LED light source (LI-6400-02B; LI-COR). The photosynthetic rate was measured under base conditions of humidity 60±5%, leaf temperature 25°C, light intensity 2,000 µmol·m$^{-2}$·s$^{-1}$, CO$_2$ concentration 350 µmol·mol$^{-1}$, and air flow 500 µmol·s$^{-1}$.

5. Comparison of integrated solar radiation of each leaf

Three plants each of ‘Benihoppe’ and ‘Toyonoka’ were measured for integrated solar radiation of individual leaves with a simple integrated solarimeter (Taisei Environment & Landscape Corp., Tokyo, Japan) adopted by Watanabe et al. (2001). The film solarimeter was placed at the center of leaflets for four days from December 19 to 23, 2008, and integrated solar radiation was calculated by color degradation of the film. The following standard curve developed by Taisei Environment & Landscape Corp. based on the measurements in Tokyo at an average maximum temperature of 29°C was used for calculating integrated solar radiation;

$$\text{Integrated solar radiation} = 409.5 - 204.1 \cdot \log_{10}(D/D_0 \cdot 100)$$

where $D_0$ and D indicate absorbance before and after exposure at 521 nm wavelength.

### Results

1. Changes in total dry matter and dry matter partitioning in strawberry plants

There was no difference in total dry matter between ‘Benihoppe’ and ‘Toyonoka’ on December 1 and 27, while total dry matter of ‘Benihoppe’ was about twice as high as that of ‘Toyonoka’ on March 17 (Table 1). On and after January 19, 2008, total dry matter and fruit of ‘Benihoppe’ were higher than those of ‘Toyonoka’; however, there was no difference in the harvest index (Table 1). The dry matter accumulation of ‘Benihoppe’ was higher than that of ‘Toyonoka’ except from January 19 to February 4 (Fig. 1A, B). Dry matter accumulation in the root and crown of ‘Benihoppe’ decreased during 16 days from January 19 to February 4, and that in the root, crown petiole and leaf of ‘Toyonoka’ decreased during 58 days from December 27 to February 23; however, the total decrease in weight of ‘Benihoppe’ was less than that of ‘Toyonoka’. Focusing on dry matter partitioning, leaves and roots were more partitioned than other organs in December, but fruits were partitioned preferentially after the end of December. In particular,

<table>
<thead>
<tr>
<th>Date</th>
<th>Cultivar</th>
<th>Total dry matter*</th>
<th>Leaf (%)</th>
<th>Petiole (%)</th>
<th>Fruit (%)</th>
<th>Peduncle (%)</th>
<th>Crown (%)</th>
<th>Root (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec. 1</td>
<td>Toyonoka</td>
<td>11.22 (100)</td>
<td>6.11 (54.5)</td>
<td>1.39 (12.4)</td>
<td>0.04 (0.4)</td>
<td>0 (0)</td>
<td>0.82 (7.3)</td>
<td>2.86 (25.5)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>12.84 (100)</td>
<td>5.71 (44.5)</td>
<td>1.85 (14.4)</td>
<td>1.59 (12.4)</td>
<td>0.57 (4.5)</td>
<td>0.75 (5.8)</td>
<td>2.36 (18.4)</td>
</tr>
<tr>
<td></td>
<td>**</td>
<td>**</td>
<td>*</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Dec. 27</td>
<td>Toyonoka</td>
<td>18.94 (100)</td>
<td>9.05 (47.8)</td>
<td>1.91 (10.1)</td>
<td>1.38 (7.3)</td>
<td>0 (0)</td>
<td>1.56 (8.2)</td>
<td>5.05 (26.7)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>24.89 (100)</td>
<td>9.35 (37.6)</td>
<td>3.00 (12.1)</td>
<td>5.36 (21.5)</td>
<td>1.16 (4.7)</td>
<td>1.53 (6.1)</td>
<td>4.49 (18.0)</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>NS</td>
<td>NS</td>
<td>**</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Jan. 19</td>
<td>Toyonoka</td>
<td>23.33 (100)</td>
<td>7.38 (31.6)</td>
<td>1.91 (8.2)</td>
<td>6.58 (28.2)</td>
<td>0.98 (4.2)</td>
<td>1.56 (6.7)</td>
<td>4.93 (21.1)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>37.07 (100)</td>
<td>8.80 (23.7)</td>
<td>3.39 (9.1)</td>
<td>16.31 (44.0)</td>
<td>2.50 (6.7)</td>
<td>1.68 (4.5)</td>
<td>4.39 (11.8)</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>**</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Feb. 4</td>
<td>Toyonoka</td>
<td>26.33 (100)</td>
<td>7.48 (28.4)</td>
<td>1.64 (6.2)</td>
<td>10.24 (38.9)</td>
<td>0.97 (3.7)</td>
<td>1.62 (6.2)</td>
<td>4.39 (16.7)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>39.88 (100)</td>
<td>9.44 (23.7)</td>
<td>3.46 (8.7)</td>
<td>19.89 (49.9)</td>
<td>2.50 (6.3)</td>
<td>1.37 (3.4)</td>
<td>3.23 (8.1)</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>**</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Feb. 23</td>
<td>Toyonoka</td>
<td>28.02 (100)</td>
<td>6.32 (22.6)</td>
<td>1.33 (4.7)</td>
<td>14.2 (50.7)</td>
<td>1.22 (4.35)</td>
<td>1.08 (3.85)</td>
<td>3.88 (13.8)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>57.19 (100)</td>
<td>14.19 (24.8)</td>
<td>5.11 (8.9)</td>
<td>24.80 (43.4)</td>
<td>3.32 (5.8)</td>
<td>2.83 (4.9)</td>
<td>6.93 (12.1)</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>*</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Mar. 17</td>
<td>Toyonoka</td>
<td>35.39 (100)</td>
<td>8.78 (24.8)</td>
<td>2.15 (6.1)</td>
<td>16.42 (46.4)</td>
<td>1.69 (4.8)</td>
<td>1.99 (5.6)</td>
<td>4.36 (12.3)</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>72.00 (100)</td>
<td>15.89 (22.1)</td>
<td>6.22 (8.6)</td>
<td>37.63 (52.3)</td>
<td>3.56 (4.9)</td>
<td>2.57 (3.6)</td>
<td>6.13 (8.5)</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>*</td>
<td>NS</td>
<td>**</td>
<td>*</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>

* Percentage of total dry matter in each plant part.
** * NS: significance at $P = 0.01$, 0.05, and non-significance by t-test (n = 3).
partitioning dry matter to fruits was higher from December 27 to February 23 in ‘Toyonoka’ and from December 27 to February 4 in ‘Benihoppe’.

2. Growth analysis

In the study of 2007, the results of growth analysis showed higher CGR of ‘Benihoppe’ than ‘Toyonoka’ (Table 2), and the difference between ‘Benihoppe’ and ‘Toyonoka’ amplified as they grew older (Table 2). For ‘Toyonoka’, LAI did not increase from December 1, 2007 to March 17, 2008, and NAR decreased during the same period. For ‘Benihoppe’ LAI increased throughout the study period, while NAR decreased from December 27, 2007 to February 4, 2008, with subsequent rapid recovery.

In the study of 2010, CGR and LAI showed a similar tendency to the study in 2007 (Table 3); however, from December 23, 2010 to February 13, 2011, NAR of ‘Benihoppe’ was a little lower than that of ‘Sachinoka’ (Table 3).

![Fig. 1](image)

**Fig. 1.** Changes in total dry matter accumulation in each plant part (A, B) and partitioning (C, D) in ‘Benihoppe’ (B, D) and ‘Toyonoka’ (A, C).

**Table 2.** Comparison of growth analysis in ‘Benihoppe’ and ‘Toyonoka’ in the study in 2007.

<table>
<thead>
<tr>
<th>Period</th>
<th>Cultivars</th>
<th>CGR (g·m⁻²·d⁻¹)</th>
<th>LAI (m²·m⁻²)</th>
<th>NAR (g·m⁻²·d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>12/1–12/27</td>
<td>Toyonoka</td>
<td>16.83</td>
<td>7.36</td>
<td>2.29</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>26.25</td>
<td>7.66</td>
<td>3.43</td>
</tr>
<tr>
<td>12/27–2/4</td>
<td>Toyonoka</td>
<td>10.72</td>
<td>7.67</td>
<td>1.40</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>21.76</td>
<td>9.13</td>
<td>2.38</td>
</tr>
<tr>
<td>2/4–3/17</td>
<td>Toyonoka</td>
<td>11.77</td>
<td>7.37</td>
<td>1.60</td>
</tr>
<tr>
<td></td>
<td>Benihoppe</td>
<td>43.27</td>
<td>11.22</td>
<td>3.86</td>
</tr>
</tbody>
</table>

*Percentage value of ‘Toyonoka’ was set as supposed 100.*
3. Changes in total leaf area, average of single leaf area, and leaf number

Total leaf area per plant of ‘Benihoppe’ was larger than that of ‘Toyonoka’ after January 19, 2008, and especially so after February 23 (Fig. 2A). The single leaf area of ‘Toyonoka’ decreased from 180 cm$^2$ on December 1, 2007 to 100 cm$^2$ on February 23, 2008, while that of ‘Benihoppe’ maintained 200 cm$^2$ throughout the study period (Fig. 2B). Leaf number in ‘Toyonoka’ was larger than that of ‘Benihoppe’ from December 27, 2007 to January 19, 2008, but there was no subsequent difference in both cultivars (Fig. 2C).

4. Leaf photosynthetic rate under different environmental conditions

There was no difference in leaf photosynthetic rates of ‘Benihoppe’ and ‘Toyonoka’ under different conditions, such as period (Fig. 3A, B), temperature (Fig. 4A), light intensity (Fig. 4B), intercellular CO$_2$ concentrations in leaves (Fig. 4C) and leaf position (Fig. 5).

5. Comparison of integrated solar radiation of each leaf and plant form

The integrated solar radiation of ‘Benihoppe’ was higher than that of ‘Toyonoka’ at the upper 4th and 5th
leaves (Fig. 6). The petiole in ‘Benihoppe’ that supported large leaves was longer and upright (Fig. 7).

Discussion

In a study of a high-yielding rice cultivar, the harvest index was reportedly more important than total dry matter for its high-yielding ability (Asanuma et al., 2008), while in the case of Dutch tomato cultivars, fruit

Fig. 4. Comparison of leaf photosynthetic rate in ‘Benihoppe’ and ‘Toyonoka’ under different environmental conditions: temperature (A), light intensity (B) and leaf internal carbon dioxide (C). Data are the mean (±SD) of three independent measurements. NS: non-significance by t-test.

Fig. 5. Comparison of leaf photosynthetic rate in different leaf positions in ‘Benihoppe’ and ‘Toyonoka’. Data are the mean (±SD) of three independent measurements. NS: non-significance by t-test.

Fig. 6. Comparison of integrated solar radiation of each leaf in ‘Benihoppe’ and ‘Toyonoka’. Data are the mean (±SD) of three independent measurements. * and NS: significance at $P=0.05$ and non-significance by t-test.

yield is not correlated with harvest index but total dry matter (Higashide and Heuvelink, 2009). In this study, however, no difference in harvest index was observed between the cultivars ‘Benihoppe’ and ‘Toyonoka’ (Table 1), while the difference in total dry matter between ‘Benihoppe’ and ‘Toyonoka’ (Table 1) was marked large, showing similar results to Higashide and Heuvelink (2009); therefore, in strawberry, total dry matter influences fruit yield more effectively than harvest index.

It is known that assimilation products stored in the vegetative organs are retranslocated to fruits, and if this happens excessively, subsequent plant growth becomes poor (Nishizawa, 1995). In this study, ‘Benihoppe’ produced more dry matter than ‘Toyonoka’ after January 19 in the winter season (Table 1), and partitioned and stored it in the vegetative organs (Fig. 1).

The authors thus conducted growth analysis to examine why ‘Benihoppe’ can produce higher total dry matter than the contrast cultivars. It was assumed that the outstanding CGR of ‘Benihoppe’ was influenced by vigorous LAI and high NAR (Tables 2 and 3). In general, LAI is influenced by increasing leaf number and leaf area. A strawberry leaf commonly develops every eight days at 20°C, but the leaf emergence rate differs by cultivar and growth period, and lower leaf emergence rates may be observed in cold weather or under heavy fruit load (Takeuchi, 1997); however, in this study there was no difference between ‘Benihoppe’ and ‘Toyonoka’ in leaf emergence rate from December 27, 2007 to February 4, 2008 (Fig. 2C). On the other hand, it is generally held that leaves developing under cold weather are smaller (Nishizawa and Hori, 1989). In this study, ‘Benihoppe’ produced large leaves throughout the whole growing season, while leaves of ‘Toyonoka’ were small during the cold winter season (Fig. 2A, B); therefore, the enhanced LAI of ‘Benihoppe’ contributed to its augmented CGR.

NAR is affected by leaf photosynthetic activity. In this study, no difference was observed between the leaf photosynthetic rates of ‘Benihoppe’ and ‘Toyonoka’ under various environmental conditions (Figs. 3, 4, and 5). A previous paper reported no difference among Japanese, American and European strawberry cultivars in leaf photosynthetic rate (Oda and Yanagi, 1990). In addition, in Japan, a limited number of cultivars including ‘Fukuba’ have been repeatedly used for strawberry breeding (Inaba and Yoshida, 2006), and therefore, little difference in leaf photosynthetic rate is expected among the new strawberry cultivars.

In wild strawberry (F. virginiana), expanded leaf area was observed under high light intensity (Jurik et al., 1982). As the growing point of strawberry is covered by leaves, leaf position may affect the light interception of new leaves. The 4th and 5th leaves of ‘Benihoppe’, having longer and upright petioles, demonstrated higher integrated solar radiation than those of ‘Toyonoka’ (Fig. 6), and ‘Benihoppe’ produced larger leaves in the cold weather season. In addition, the petiole in ‘Benihoppe’, which supported large leaves, was longer and upright (Fig. 7). NAR might be affected by traits that allow solar radiation to penetrate the plant canopy. Therefore, leaf position is associated with leaf expansion and further studies are needed on the formative factors of favorable light-intercepting and strong petiole characteristics of ‘Benihoppe’.

In conclusion, this study shows that total dry matter is more important than the harvest index for the high-yielding ability of ‘Benihoppe’. Efficient dry matter production in the critical short-day and cold-weather season is associated with large LAI and its upright petioles, which allow solar radiation to penetrate the plant canopy.

**Literature Cited**


