Effects of Flag Leaves and Panicles on Light Interception and Canopy Photosynthesis in High-Yielding Rice Cultivars

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Abstract: The effects of flag leaves and panicles on canopy photosynthesis in a leading cultivar (Nipponbare) and two high-yielding rice cultivars (Takanari and Chugoku 117) bred in Japan were compared. The total dry matter production was in the order of Takanari > Chugoku 117 > Nipponbare. Canopy photosynthesis was highest in Takanari throughout the growth season, and was higher in Chugoku 117 than in Nipponbare during the ripening period. The photosynthetic rate in the flag leaf was in the order of Nipponbare > Takanari > Chugoku 117. The light extinction coefficient of canopy was higher in Takanari than in the others. At the middle ripening stage, canopy photosynthesis increased 35 and 17% in Nipponbare and Takanari, respectively, by the removal of panicles and decreased 37 and 48%, respectively, by the removal of flag leaves. In Chugoku 117, canopy photosynthesis was hardly influenced by these treatments. Clearly, the panicles intercept more radiation at the upper layer of the canopy in Nipponbare than in Takanari and flag leaves contribute more to canopy photosynthesis in Takanari than in Nipponbare. However, these effects were small in Chugoku 117. In conclusion, Takanari produces more dry matter than the others due to larger, wider, longer and more erect 1st (flag) and 2nd leaves above the panicles, which intercept more radiation. Chugoku 117 had erect panicles which allowed more radiation to penetrate into the deeper layer of the canopy, resulting in a high dry matter production. The lower panicle height relative to leaf layer and erect panicles are important characteristics for higher yield in rice.

Key words: Canopy photosynthesis, Dry matter production, Flag leaf, High-yielding, Light interception, Panicles, Rice.

Increase in yield potential of crops is a basic necessity for breeding programs facing the increased demand of food in the 21st century. Yield potential of rice in Japan has doubled from the 1950s to 1990s (Evans, 1993). These have resulted from the breeding of cultivars with a short culm and erect leaves (Takeda, 1984; Saitoh et al., 1993).

It is important to understand the eco-physiological characteristics directly responsible for high yield. Saitoh (1994) considered that the favorable agronomic characteristics of high-yielding rice are large sink size due to heavy panicle type, the large, wide and erect leaves above the panicles and high photosynthetic rate in the upper leaves during ripening period.

Recently a new plant type having greater light interception by the leaves during ripening and greater lodging tolerance has been proposed by International Rice Research Institute (Peng et al., 1994, Khush 1996). The plants of this type have a lower panicle height in the canopy. In Japan, a superior high yield breeding program was started during 1981, and a semi dwarf indica cultivar Takanari was bred. Its yield exceeded 9 t ha⁻¹ in brown rice under favorable conditions (Hiraoka et al., 1992; Xu et al., 1997a).

The effects of the lowering panicle height were examined by measuring the canopy photosynthesis after removal and without removal of panicles (Setter et al., 1995), and by comparison of the canopy photosynthesis and yield of isogenic lines with low and high panicle heights (Setter et al., 1996). The results showed that canopy photosynthesis increased by 42–52% following removal of panicles and the lines with low panicle height had 15–40% greater yields than isogenic lines with high panicle height. Saitoh et al. (1990) also reported that higher panicle position affected the light penetration into the canopy. However, no quantitative estimation has been done for the effect of panicles on canopy photosynthesis.

The experiments presented here were conducted with a leading cultivar Nipponbare and two high-yielding cultivars bred in Japan, Takanari and Chugoku 117, by quantifying the effects of the removal of flag leaves and panicles on the canopy photosynthesis.

Materials and Methods

1. Plant cultivation

The experiments were carried out at the paddy field of Okayama Univ. in 1997. Young seedlings of the rice cultivars Nipponbare, Takanari and Chugoku 117 (Fig. 1) were transplanted to the field on 11 June at a hill

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Abbreviations: PAR, photosynthetically active radiation; CGR, crop growth rate; NAR, net assimilation rate; LAI, leaf area index; CER, carbon dioxide exchange rate.
the light extinction coefficients of canopy were calculated. After the harvest, yield and yield components of brown rice were examined.

3. Photosynthetic measurement
The carbon dioxide (CO₂) exchange rate (CER) of flag leaf blade was measured in the field by using a portable photosynthesis measurement system (SPB-H4, Shimadzu, Kyoto, Japan) from 65 to 108 days after planting at about 10-day intervals. The measurement was replicated three times for each cultivar at a relative humidity of 60%, a CO₂ concentration of 350 μL L⁻¹ under a PAR of higher than 1500 μE m⁻² s⁻¹.

The canopy CER was measured by the closed air-flow chamber method under a PAR of higher than 1700 μE m⁻² s⁻¹. After the open-top frame (40×40×60, 40×40×120 cm) covered with plastic film was installed into the canopy and 6 hills were enclosed into the frame carefully not to disrupt the canopy architecture, gas circulation was provided using two electric fans for stabilizing the CO₂ concentration in the frame. Then the top of the canopy frame was closed with a transparent plastic plate and the canopy CER on a land area basis (g m⁻² hr⁻¹) was obtained by measuring the decreasing rate of CO₂ concentration inside the frame from the start (350~380 μL L⁻¹) for two minutes. The measurement was replicated three times for each cultivar between 11 a.m. and 1 p.m. Atmospheric temperature rising and high humidity in the assimilation frame was prevented by putting a cold-agent package near the fan, but the temperature ranged from 30 to 35°C and although relative humidity was maintained lower than 90%.

4. Removal of panicles and flag leaves
To examine the effect of the removal of panicles and flag leaves on the canopy CER, we removed all of the panicles and flag leaves in the area of 1.8 m² (1.2×1.5 m) at each neck node and lamina joint, respectively, in the evening at the early and middle ripening stages. Between 11 a.m. and 1 p.m. on the next day, we measured canopy CER three times for each treatment under a PAR of higher than 1700 μE m⁻² s⁻¹.

5. ¹³CO₂ feeding experiments
At the stage of internode elongation, heading and middle ripening, ¹³CO₂ (0.5g of barium carbonate) was generated by applying 5% lactic acid solution for 10 minutes inside the canopy frame (40×40×120 cm) covered with plastic film under a PAR of higher than 1700 μE m⁻² s⁻¹ between 11 a.m. and 13 p.m. (Okano et al., 1995). The six hills of rice plant were enclosed into the frame. Immediately after the generation of ¹³CO₂, the concentration of ¹³CO₂+¹²CO₂ became higher than 500 μL L⁻¹, then decreased to lower than 50 μL L⁻¹ after 10 minutes. Gas circulation was provided and temperature rising and high-humidity was prevented by the same method as in the canopy CER measurement.
Immediately after the feeding, plants were cut into the leaves at each node positions, stems and panicles, then air-dried at 80°C. Feeding of $^{13}$CO$_2$ was carried out with two replications for each cultivar and $^{13}$C contents of the samples were determined using the mass spectrometer and CN–Corder (MSI-150–MT–700NC, YANACO, Kyoto, Japan). Then percent distribution of fixed $^{13}$C at each leaf position was calculated.

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>No. of panicles (m$^2$)</th>
<th>No. of spikelets /panicle</th>
<th>No. of spikelets of ripened 10$^3$ m$^{-2}$ grains</th>
<th>Percentage 1000-grain weight (g)</th>
<th>Brown rice yield (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nipponbare*</td>
<td>340a</td>
<td>69.6c</td>
<td>23.7c</td>
<td>90.9a</td>
<td>499.27c</td>
</tr>
<tr>
<td>Takanari</td>
<td>235b</td>
<td>164.3a</td>
<td>38.6a</td>
<td>81.2b</td>
<td>715.25a</td>
</tr>
<tr>
<td>Chugoku 117</td>
<td>210b</td>
<td>132.5b</td>
<td>27.8b</td>
<td>92.3a</td>
<td>578.25b</td>
</tr>
</tbody>
</table>

*: Leading cultivar in Japan. Means followed by the same letter are not significantly different at 0.05 level according to Fisher's LSD.

1. Yield and dry-matter production
Grain yield (Table 1) was in the order of Takanari (715 g m$^{-2}$) > Chugoku 117 (578 g m$^{-2}$) > Nipponbare (499 g m$^{-2}$). Yield was the highest in Takanari owing to the larger sink size due to the heavy panicles. Yield and sink size in Chugoku 117 was medium owing to the fewer number of panicles. The total dry matter production was in the order of Takanari > Chugoku 117 > Nipponbare (Fig. 2). A large amount of dry matter was translocated from the leaves and stems to the panicles, resulting in the decrease in the dry weight, especially in Takanari. Nipponbare showed a marked increase in the stem dry weight at the late ripening stage. This indicates that the sink capacity restricts the yield in Nipponbare. CGR was higher in Takanari and Chugoku 117 than in Nipponbare from 60 to 80 days after transplanting owing to both higher LAI and higher NAR (Fig. 3).

2. Canopy structure and CER
The light extinction coefficient of canopy was the lowest at the panicle formation stage in all three cultivars.
and was the highest in Takanari at each stage as compared with the other two cultivars (Table 2). Takanari had more erect leaves than Nipponbare and Chugoku 117 during ripening period (Fig. 4). Takanari had a large leaf area above the panicle layer due to large, long and erect flag leaves (Fig. 1, 5). Chugoku 117 had erect panicles that occupied more space in the upper layer of the canopy (Fig. 1, 5). Although the flag leaf CER was in the order of Nipponbare > Takanari > Chugoku 117 (Fig. 6), canopy CER in Takanari was higher than that in Nipponbare and Chugoku 117 throughout the growth period (Fig. 6).

3. Effects of the removal of flag leaves and panicles

The removal of panicles increased the canopy CER whereas the removal of flag leaves significantly reduced it (Fig. 7). At the middle ripening stage, canopy CER

![Relative light intensity (%)](image)

**Fig. 4.** Percent distribution of leaf area with different inclination angles of whole canopy foliage at the middle ripening stage.

![Canopy CER (g m⁻² hr⁻¹)](image)

**Fig. 5.** Canopy structures of rice stand at the middle ripening stage.

![Flag leaf CER (µmol m⁻² s⁻¹)](image)

**Fig. 6.** Changes in canopy and flag leaf CER during ontogeny. Bars indicate mean SD (n=3).

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Tillering stage</th>
<th>Panicle formation stage</th>
<th>Middle ripening stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nipponbare</td>
<td>0.36</td>
<td>0.25</td>
<td>0.46</td>
</tr>
<tr>
<td>Takanari</td>
<td>0.38</td>
<td>0.33</td>
<td>0.59</td>
</tr>
<tr>
<td>Chugoku 117</td>
<td>0.31</td>
<td>0.24</td>
<td>0.53</td>
</tr>
</tbody>
</table>
was increased to 135 and 117% of the control in Nipponbare and Takanari, respectively, by the removal of panicles and was decreased to 63 and 52% of the control, respectively, by the removal of flag leaves. In Chugoku 117, canopy CER was hardly influenced by these treatments. These results indicate that the panicles intercept more radiation at the upper layer of the canopy in Nipponbare than in Takanari and flag leaves contribute more to canopy CER in Takanari than in Nipponbare. However, these effects are slight in Chugoku 117.

4. Percent contribution of leaf position to the canopy CER ($^{14}$CO$_2$ feeding experiment)

With the senescence of leaves, the contribution of flag and the 2nd leaves to canopy CER became large in Takanari than in Nipponbare (Fig. 8). This means that the upper leaves contribute more to the higher canopy CER in Takanari.

Discussion

Takanari, a semi-dwarf Indica high-yielding cultivar, easily produce more than 50,000 spikelets per m$^2$, and its yield exceeds 800 g per m$^2$ in brown rice under favorable climate (Hiraoka et al., 1992; Xu et al., 1997) owing to higher dry matter production throughout the growth season and higher harvest indexes (Ishikawa et al., 1999; Xu et al., 1997). In our experiments Takanari showed higher CGR than Nipponbare for 30 days after transplanting and during the ripening period, which resulted from the higher rate of leaf area enlargement at the early growth stage and the higher net assimilation rate during the ripening period, respectively (Xu et al., 1997a; Saitoh et al., 2000). Ishikawa et al. (1999) also reported that the higher the atmospheric temperature, the higher the leaf expansion rate at the early growth stage.

Takanari showed a lower flag leaf CER (Fig. 6) and higher light extinction coefficient (Table 2) than Nipponbare. These results contradict to the findings that Takanari had a higher leaf CER and lower light extinction coefficient than Nipponbare reported by Xu et al. (1997a, b). Although the rate of fertilization was slightly higher than that in their experiment, LAI was considerably small in the present experiment. It was considered that the photosynthetic capacity and light extinction coefficient were not stable characteristics and vary with the climate and cultural condition.

To clarify the factors that contribute to the highest canopy CER in Takanari, we examined the effect of removal of panicles and flag leaves on canopy CER. The removal of flag leaves at the middle-ripening stage decreased canopy CER by 48% in Takanari but only 37% in Nipponbare. The $^{14}$CO$_2$ feeding experiment provided the evidence that flag leaves contributed about 38% of the total canopy CER. These results indicated that Takanari had the longer, wider, larger, and more erect flag leaves than Nipponbare (Fig. 1) allowing higher canopy photosynthesis. The neck node of Takanari did not appear from the flag leaf sheath during heading so that the distance from the neck node to flag leaf auricle in Takanari was $-32$ mm as compared with $+91$ mm in Nipponbare. This is an important morphological characteristic for lowering panicle height relative to flag leaf.

Chugoku 117, a lodging-tolerant high-yielding cultivar despite its long culm (Ookawa and Ishihara, 1992), showed 16% higher grain yield than Nipponbare due to the larger sink size but the grain yield was lower than that in Takanari (Table 1). It also showed higher CGR (Fig. 3) and higher canopy CER (Fig. 6) during the ripening period than Nipponbare inspite of the
having higher panicle height (Fig. 5). The panicles removal affected canopy CER only slightly (4%) at the middle ripening stage in Chugoku 117 but increased 35% in Nipponbare. Chugoku 117 has erect panicles (Fig. 1), which allow more radiation penetrates into the middle layer of the canopy, i.e., panicles intercept less radiation.

Setter et al. (1995) reported that the leaves above the panicles intercepted only 4–12% incident radiation in two tropical rice cultivars (IR72 and IR36). When panicles were removed at 11 and 15–19 days after flowering, the canopy CER increased by 42–52% and 75%, respectively. In the present study, panicle removal increased canopy CER by 16–23% at 10 days after flowering and by 4–35% at 22 days after flowering (Fig. 7). The rate of the increase was higher in the experiment of Setter et al. (1995) as compared with that in our experiment. This might have resulted from the difference in LAI, which was larger in their experiment (5.0–6.9) than that in this study (3.3–4.5). When panicles were removed from the canopy with high LAI, the leaves in the lower layer intercept more radiation, so that canopy CER increases more than that with a low LAI.

In conclusion, Takanari is medium in flag leaf CER, but produces more dry matter than the others because large, wide, long and erect 1st (flag) and 2nd leaves intercept more radiation. Chugoku 117 had erect panicles, which allowed more radiation to penetrate into the deeper layer of the canopy, resulting in high dry matter production. The lower panicle height relative to leaf layer within canopy and erect panicles are important characteristics for high yield in rice cultivars.

References


*In Japanese with English abstract.

**In Japanese.