Enhancement of Rice Leaf Photosynthesis by Crossing between Cultivated Rice, *Oryza sativa* and Wild Rice Species, *Oryza rufipogon*

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**Abstract**: To study whether wild rice species have genes that may increase potential photosynthetic capacities of rice cultivars, we generated BC$_2$ populations by reciprocally backcrossing *Oryza rufipogon* (W630) with *O. sativa* cv. Nipponbare and IR36; N-BC$_2$ populations and IR-BC$_2$ populations, respectively. We measured the oxygen evolution rates (OER) of single leaves under saturating light and CO$_2$ as the maximum photosynthetic rates and the contents of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and Rubisco activase. Several lines in each BC$_2$ population had significantly higher OERs than parental cultivars, and 14~25% of plants in BC$_2$ populations had higher OERs than the highest values in parental cultivars. The highest OERs in BC$_2$ populations were about 60% higher than average OERs in parental cultivars. The BC$_2$ populations contained 30~40% more Rubisco than parental cultivars. Cytoplasms derived from *O. rufipogon* and *O. sativa* had different effects on the contents of Rubisco and Rubisco activase particularly in N-BC$_2$ populations. In several lines of each BC$_2$ population the OERs had positive correlations with the contents of Rubisco and/or Rubisco activase. These results suggest that *O. rufipogon* can be used as a source of germplasm to enhance the photosynthetic capacity of *O. sativa*.

**Key words**: Leaf photosynthesis, *Oryza rufipogon*, *Oryza sativa*, Rice, Rubisco, Rubisco activase, Wild rice species.

Global grain production has been increased largely by generation of high-yielding cultivars, expansion of planted areas, establishment of irrigation facilities and widespread use of chemical fertilizers, insecticides and pesticides. However, the rate of increase in grain production in 1982~1994 decreased to 1.5%, which might be lower than that in demand, and the maximum yield of rice per unit area has not changed for past 30 years (Mann, 1999). Thus, new methods are needed to increase the grain yield. One of them is to improve photosynthetic capacities of single leaves and raise potential yields (Army and Greer, 1967).

In C$_3$ plants including rice, Rubisco is considered as a target enzyme for enhancing the photosynthetic capacity. Rubisco localizes in chloroplast stroma, where it catalyses the first step of CO$_2$ fixation. It is considered to be one of the factors limiting the photosynthetic rate because its catalytic capacity is very low compared with other photosynthetic enzymes and it reacts competitively with O$_2$ at the same site as CO$_2$. The kinetic properties of Rubisco in rice AA genome species are nearly the same, thus it is difficult to improve the kinetic efficiency of Rubisco by cross breeding among these species (Makino et al., 1987). However, differences in leaf gas exchange rates among AA genome species were observed. Sasaki and Ishii (1992) reported that the photosynthetic rate in the flag leaf at heading were 19.3-25.7 µmol CO$_2$ m$^{-2}$ s$^{-1}$ in 32 cultivars bred in Japan. The difference in photosynthetic rates at vegetative stage among AA genome species was 19.1-27.6 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (Cook and Evans, 1983a), or 10.6-19.1 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (Yeo et al., 1994). These results suggest that they either differ in the content or in vivo activity of Rubisco. Moreover, recent reports on rice photosynthesis indicate a close correlation between the amount of Rubisco activase and in vivo Rubisco activity or carboxylation efficiency (Fukayama et al., 1996; Uchida et al., 1995). The major role of Rubisco activase is promoting dissociation of sugar phosphate inhibitors from Rubisco, thus freeing active sites for activation by CO$_2$ and/or catalysis (Portis et al., 1986; Robinson and Portis, 1988; Edmondson et al., 1990). It is also considered to function as a molecular chaperone (Sánchez de Jiménez et al., 1995). It is worth investigating how genes from wild species closest to *Oryza sativa* influence the photosynthetic capacities of rice cultivars.

Wild rice species are generally inferior to cultivated species in agricultural traits, but the majority of genetic variations in the genus *Oryza* still remain untapped (Wang et al., 1992). In actual breeding, they...
have been used to improve qualitative traits, such as resistance to diseases or insects and cytoplasmic male sterility (Khush, 1977; Shin-Cheng and Yuan, 1980), but rarely used for quantitative traits, because superior quantitative alleles are often masked by the effects of deleterious alleles and could not be identified phenotypically in wild species. Xiao et al. (1996) identified that *O. rufipogon* has some alleles associated with an increase in grain yield per plant by quantitative trait loci (QTL) analysis, although its yield was lower than that of *O. sativa*. This indicates a possibility that introduction of genes from wild rice species raises the yield of cultivars. Among many factors associated with yield, photosynthesis is a fundamental process and has significant influences on yield throughout vegetative and reproductive stages. Therefore, it is thought that genes that enhance photosynthetic capacity exist in wild species, although they have lower photosynthetic rates than cultivated species (Cook and Evans, 1983a; Yeo et al., 1994).

In this study, we investigated variations in leaf photosynthetic rates, and the contents of Rubisco and Rubisco activase in BC2 populations derived by crossing between *O. rufipogon* and *O. sativa* as a basis to increase the yield of rice by changing the photosynthetic capacities. We discuss the changes in photosynthetic characteristics due to crossing with *O. rufipogon* and relationship between photosynthetic capacity and Rubisco or Rubisco activase contents.

**Materials and Methods**

1. **Plant materials and growth**

   *O. rufipogon* (W630) was chosen for this study because it grows vigorously and blooms without photoperiodic treatment under natural conditions in Japan. This wild rice species can be crossed easily with *O. sativa*. W630 was crossed as a female parent with *O. sativa* cv. Nipponbare or IR36. The F1 plants were backcrossed as females with *O. sativa*. Sixteen BC1 plants were reciprocally backcrossed with *O. sativa* Nipponbare (N) and IR36 (IR) to investigate the effects of cytoplasm. Two alternative BC2 populations whose cytoplasmic genome was derived from *O. rufipogon* (W), N(W) and IR(W), or *O. sativa* (C), N(C) and IR(C) were obtained. Seeds of BC2, W630, Nipponbare and IR36 were sown on 30 April 1998, and seedlings were transplanted at a planting density of 25 cm×25 cm in a paddy field on 22 May. The field was fertilized with 40 kg ha⁻¹ of N, P and K using commercially available fertilizers before transplanting. The ninth leaf blades on the main stems were sampled at the 10.5 leaf stage at about one month after transplanting. About ten plants were sampled from each line, namely, N(C), N(W), IR(C) and IR(W) populations, which consisted of 158, 154, 159 and 159 BC2 plants, respectively.

2. **Measurement of photosynthetic rate**

   In this experiment, the photosynthetic rate was determined as a maximum O2 evolution rate (OER) using a gas-phase oxygen electrode (CB1D, LS2, LD-1; Hansatech, King's Lynn, UK). This method is suitable for measuring a number of samples because the measurement time is short. A piece of about 5 cm² was cut from the center of the 9th leaf blade. The leaf piece was floated on deionized water overnight to

| Variety or line | OER (µmol m⁻² s⁻¹) |
|-----------------|-------------------|
|                 | N(C)              | N(W)              |
| *O. sativa* cv. Nipponbare (N) | 46.1 ± 4.5       | 50.8 ± 4.2        |
| IR36 (IR)       | 50.8 ± 4.2        | 50.8 ± 4.2        |
| *O. rufipogon* (W630) | 37.1 ± 4.4       |                   |

Table 1. Photosynthetic oxygen evolution rate (OER) in *O. rufipogon* (W630), *O. sativa* (Nipponbare and IR36) and their BC2 lines.

Mean ± standard deviation. The bold and underlined figures represent significantly higher and lower values compared with parental cultivars, respectively (P<0.05).

* indicates a significant difference between the average of (C) line and that of (W) line (P<0.05).
obtain a higher and stable O₂ evolution rate (Fukayama et al., 1996). Photosynthetic measurements were conducted under the following conditions: air temperature of 25°C, gas mixture of 5% CO₂, 20% O₂ and 75% N₂, saturated water vapor, and irradiation at 2,000 µmol photon m⁻² s⁻¹. The measurement started after pre irradiation for 5 min in air stream under the conditions described above. Then the leaf piece was frozen in liquid nitrogen and stored at −80°C until chemical analysis.

3. Determination of Rubisco and Rubisco activase contents

The frozen leaf piece was homogenated in 4 mL of extraction buffer (50 mM Na-phosphate, 5 mM DTT, 0.1 mM EDTA, 12.5% glycerol, pH 7.5) in a small amount of polyvinylpolypyrrolidion and acid-washed quartz sand in a chilled mortar with a pestle. The homogenate was centrifuged at 30,000×g for 10 min at 4°C. The supernatant was used to determine the amounts of Rubisco and Rubisco activase.

The amounts of Rubisco and Rubisco activase were measured by enzyme-linked immunosorbent assay (ELISA) according to Fukayama et al. (1996) with some modifications. Leaf extracts were diluted at 1:500 with 10 mM Na-phosphate buffer, pH 7.2, and then applied to wells of a polystyrene microtiter plate for ELISA in duplicate. After incubation at 4°C for 16 hr, non specific protein-binding sites were blocked with T-PBS (10 mM Na-phosphate, 0.5 mM NaCl, 0.05% Tween20, pH 7.2) containing 3% BSA for 16 hr at 4°C. Then, a rabbit polyclonal antibody against rice Rubisco or Rubisco activase diluted at 1 : 250 or 1 : 1000, respectively, with antibody dilution buffer (10 mM Na-phosphate, 1M NaCl, 0.05% Tween20, pH 7.2) was added to the plate and the plate was incubated at 25°C for 1 hr. Peroxidase-conjugated rabbit IgG (H+L)-goat antibody was applied to each well and the plate was incubated at 25°C for 1 hr. After each process described above, the plate was washed with T-PBS completely. A substrate solution (0.1 M citrate, 0.2 M Na-phosphate, 1 mM 2,2-azinobis(3-ethylbenzothiazoline-6-sulfonic acid), and 150 µl L⁻¹ H₂O₂ at pH 5.0) was applied to the plate to start a reaction. After incubation at 25°C for about 1 hr, the reaction was stopped with 0.25 M citric acid solution. The optical absorbance at 415 nm was measured using a micro plate reader (A4; Tosoh, Tokyo, Japan) and the absorbance obtained was compared with that of purified rice Rubisco (0-100 ng) and Rubisco activase (0-20 ng) in duplicate.

Results and Discussion

1. Oxygen evolution rate (OER)

Table 1 shows the averages of OER in parental rice species and BC₂ lines. The average OER of W630 was 19% and 27% lower than that of Nipponbare and IR36, respectively. This result is consistent with the gas exchange rates under ambient conditions of various Oryza species (Cook and Evans, 1983a; Yeo et al., 1996).
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The N(C) and N(W) populations had about the same average OER as Nipponbare. The average OERs in 2 lines of N(C) and 4 lines of N(W) were significantly higher than that of Nipponbare (P<0.05). IR(C) population and IR(W) population had about the same average OER as IR36. Four lines of both IR(C) and IR(W) had significantly higher average OERs than IR36 (P<0.05).

Fig. 1 shows the frequency distributions of OER in the N-BC2 populations and the IR-BC2 populations. Fourteen percent of BC2 plants in the N(C) population and 25% in the N(W) population had higher OERs than the maximum OER in Nipponbare, 52.5 μmol m⁻² s⁻¹. The highest value in the N(C) population was 60.4 μmol m⁻² s⁻¹ and was 31% higher than the average in Nipponbare. In N(W) population, the highest value was 74.7 μmol m⁻² s⁻¹ and was 62% higher than the average in Nipponbare. Twenty-two percent of BC2 plants in the IR(C) population and 18% in the IR(W) population had higher OERs than the maximum OER in IR36, 40.5 μmol m⁻² s⁻¹. The highest value in the IR(C) population was 48.6 μmol m⁻² s⁻¹ and was 21% higher than the average in IR36. In IR(W) population, the highest value was 55.4 μmol m⁻² s⁻¹ and was 38% higher than the average in IR36.

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### Table 2: The content of Rubisco in *O. rufipogon* (W630), *O. sativa* (Nipponbare and IR36) and their BC2 lines.

| Variety or line | Rubisco (g m⁻²) |
|----------------|----------------|
| *O. sativa* cv. Nipponbare (N) | 2.65 ± 0.46 |
| IR36 (IR) | 2.34 ± 0.60 |
| *O. rufipogon* (W630) | 1.64 ± 0.30 |
| BC2 line | Rubisco (g m⁻²) |
| A * | 3.50 ± 0.81 |
| B * | 3.98 ± 0.26 |
| C * | 3.62 ± 0.46 |
| D * | 3.64 ± 0.72 |
| E * | 4.17 ± 0.34 |
| F * | 3.98 ± 0.34 |
| G * | 4.26 ± 0.47 |
| H * | 3.28 ± 0.57 |
| K | 3.54 ± 0.59 |
| L | 3.32 ± 0.59 |
| M | 3.66 ± 0.31 |
| N | 3.71 ± 0.46 |
| O * | 3.80 ± 0.41 |
| P * | 2.97 ± 0.33 |
| Q | 4.10 ± 0.48 |
| R | 3.24 ± 0.60 |
| Total * | 3.67 ± 0.60 |

Mean±standard deviation. The bold and underlined figures represent significantly higher and lower values compared with parental cultivars, respectively (P<0.05).

### Table 3: The content of Rubisco activase in *O. rufipogon* (W630), *O. sativa* (Nipponbare and IR36) and their BC2 lines.

| Variety or line | Rubisco activase (g m⁻²) |
|----------------|--------------------------|
| *O. sativa* cv. Nipponbare (N) | 0.241 ± 0.021 |
| IR36 (IR) | 0.157 ± 0.029 |
| *O. rufipogon* (W630) | 0.146 ± 0.029 |
| BC2 line | Rubisco activase (g m⁻²) |
| A * | 0.182 ± 0.046 |
| B * | 0.148 ± 0.023 |
| C | 0.185 ± 0.028 |
| D | 0.188 ± 0.033 |
| E | 0.174 ± 0.049 |
| F | 0.150 ± 0.026 |
| G * | 0.159 ± 0.045 |
| H | 0.228 ± 0.049 |
| L * | 0.159 ± 0.036 |
| M | 0.216 ± 0.030 |
| N * | 0.196 ± 0.036 |
| O | 0.155 ± 0.043 |
| P | 0.120 ± 0.020 |
| Q | 0.150 ± 0.042 |
| R | 0.138 ± 0.027 |
| Total | 0.174 ± 0.047 |

Mean±standard deviation. The bold and underlined figures represent significantly higher and lower values compared with parental cultivars, respectively (P<0.05).

* indicate there was a significant difference between the average of (C) line and that of (W) line (P<0.05).
population had higher OERs than the maximum OER in IR36, 59.0 µmol m\(^{-2}\) s\(^{-1}\). The highest value in the IR(C) population was 83.8 µmol m\(^{-2}\) s\(^{-1}\), which was 65% higher than the average OER in IR36. In the IR(W) population, the highest value was 74.4 µmol m\(^{-2}\) s\(^{-1}\), which was 46% higher than the average in IR36.

With respect to the difference in function of the cytoplasm, the averages of OER in the N(C) population significantly differed from that in the N(W) population (P<0.05), but the latter had only 4% higher OER than the former (Table 1). The average OER in the IR(C) population did not differ from that in IR(W) population. In several lines with significantly higher OER than the parental cultivars, (C) lines had the same OER as the (W) lines (Table 1, N-E, N-P, IR-H, IR-J and IR-N). These results indicate that the cytoplasmic genomes of *O. rufipogon* and *O. sativa* did not have different effects on the photosynthetic rate and that nuclear genes from *O. rufipogon* could enhance the photosynthetic capacity of *O. sativa*.

Xiao et al. (1996) reported that backcrossed plants derived from *O. sativa* and *O. rufipogon* gave a higher yield than high-yielding hybrid rice, although the yield of *O. rufipogon* was low. These results indicate that genes related to enhance photosynthetic capacity might be masked by the effect of deleterious alleles in *O. rufipogon*, but unmasked in BC\(_2\) plants by crossing with *O. sativa*.

**2. Rubisco and Rubisco activase contents**

We measured the amount of Rubisco, a key enzyme in photosynthesis (Table 2). The content of Rubisco in W630 was 38% and 30% lower than that in Nipponbare and IR36, respectively. The average contents of Rubisco in BC\(_2\) populations were higher than those in parental cultivars; 38% higher in N(C), 32% higher in N(W), 38% higher in IR(C) and 33% higher in IR(W). Fifteen lines of N(C), 14 lines of N(W), 10 lines of IR(C) and 11 lines of IR(W) contained significantly more Rubisco than the parental cultivars (P<0.05). About 90% of plants in both N- and IR-BC\(_2\) populations had more Rubisco than Nipponbare and IR36 (Fig. 2). In rice leaves, the amount of Rubisco increases with N contents (Makino et al., 1984). *O. rufipogon* tends to have the same or more N in leaves and heavier specific leaf weight, which indicates leaf thickness, than *O. sativa* (Cook and Evans, 1983b). Thus, the leaf N and leaf thickness might be involved in the increases of Rubisco content in BC\(_2\) plants.

N(C) population contained significantly more Rubisco than a N(W) population (P<0.05), the average Rubisco content in the former was 5% higher than those in the latter (Table 2). The IR(C) population also contained 3% more Rubisco than the IR(W) population, but the difference was not significant. In higher plants, the small subunit (SS) of Rubisco is encoded in the nuclear genome and the large subunit (LS) in the chloroplast genome (for review refer to Gutteridge and Gatenby, 1995). The present result indicates that the cytoplasmic genomes of *O. rufipogon* and *O. sativa* had different effects on the Rubisco content but the difference is slight. The Rubisco contents in the BC\(_2\) populations might be increased mainly by nuclear genes of W630.

We determined the amount of Rubisco activase (Table 3). The content of Rubisco activase in W630 was 40% lower than that in Nipponbare. The average Rubisco activase contents in N-BC\(_2\) populations were lower than that in Nipponbare. Many N-BC\(_2\) lines contained significantly less Rubisco activase compared with Nipponbare (P<0.05). About 80% of N-BC\(_2\) plants had less Rubisco activase than Nipponbare (Fig. 3A). The content of Rubisco activase in W630 was considerably lower than that in Nipponbare. Thus, genes from W630 might lead the Rubisco activase in N-BC\(_2\) plants to decrease. The content of Rubisco activase in IR36 was 8% higher than that in W630 (Table 3). IR-BC\(_2\) populations contained a slightly
larger amount of Rubisco activase than IR36. The Rubisco activase contents in 3 lines of IR(C) and 6 lines of IR(W) were significantly higher than that in IR36 (P<0.05). The negative effect of W630 as in N lines was not observed and genes from W630 might cause Rubisco activase in several IR lines to increase.

With respect to the difference in functions of cytoplasm, the Rubisco activase content in N(W) population was 17% higher than that in N(C) population and there was a significant difference between them (P<0.01) (Table 3). IR(W) population contained 4% more Rubisco than IR(C) population, but the difference was not significant. These results suggest that the cytoplasms inherited from O. rufipogon and O. sativa have some different effect on the Rubisco activase content in N populations. Rubisco activase is encoded in the nuclear genome and its protein level is regulated posttranscriptionally in rice (Zhang and Komatsu, 2000). The cytoplasm genome might influence the posttranscriptional regulation of Rubisco activase and change conditions in chloroplast stroma that affect the turnover of Rubisco activase in our study.

The chloroplast genome in W630 is classified into Japonica type by the absence of deletion of the 69-bp sequences in open reading frame 100 (Sun et al., 2002). However, the difference of cytoplasm influenced the contents of Rubisco and Rubisco activase in N population in our study. Why the effect of cytoplasm on the contents of these enzymes appeared particularly in the N population remains unknown.

3. Correlations between OER and Rubisco or Rubisco activase content

We examined the correlations of OER with the content of Rubisco and Rubisco activase to determine the effects of these enzymes on the photosynthetic rates in BC2 lines (Table 4). Three lines in N(C) population, 6 lines in N(W), 2 lines in IR(C) and 1 line in IR(W) had positive correlations between OER and the content of Rubisco (P<0.05). Four lines in the N(C) population, 5 lines in N(W), 6 lines in IR(C) and 5 lines in IR(W) had positive correlations between OER and the Rubisco activase content (P<0.05). The other lines did not have any correlations between them.

In rice, the photosynthetic capacity is associated with the amount of Rubisco activase rather than with that of Rubisco (Fukayama et al., 1996). There were several BC2 lines consistent with this report, and it was thought that the photosynthetic rates in these lines were regulated mainly by the content of Rubisco activase. There were several BC2 lines that had positive correlations between OER and the Rubisco content although these lines contained more than 3 g m^-2 Rubisco is thought to exceed its photosynthetic capacity (Fukayama et al., 1996). It was reported that inhibitors other than 2-Carboxy-D-arabinitol-1-phosphate regulated the activity of Rubisco in the light (Parry et al., 1997). These inhibitors and other factors might decrease the in vivo Rubisco activity, so Rubisco in excess of 3 g m^-2 was correlated with OER in these lines.

Photosynthesis is not controlled by merely one enzyme or reaction. Stitt (1986) suggested that OERs in spinach leaves under saturated light and CO2 were limited by a capacity for sucrose synthesis, by restricting the rate at which inorganic phosphate can be recycled. A biochemical model also shows that the photosynthetic rate under a saturated light intensity and CO2 concentration is regulated by the inorganic phosphate regeneration capacity (Sharkey, 1985). The capacities involving sucrose synthesis might affect the photosynthetic rates in the BC2 lines in which OER did not correlate with the amount of Rubisco and Rubisco activase.

Fig. 3. Frequency distributions of the content of Rubisco activase in BC2 populations. A. N-BC2 populations, B. IR-BC2 populations. The solid lines and the dotted lines represent frequency distributions of (C) population and (W) population, respectively. Arrows indicate the averages of parental rice species. The average values are shown in Table 3.
The present findings suggest that *O. rufipogon* can be used as a source of germplasm to enhance the photosynthetic capacity of *O. sativa*. Many plants in BC2 populations derived from *O. rufipogon* and *O. sativa* had higher photosynthetic rates than parental cultivars. It was thought that the photosynthetic rates were limited by Rubisco contents or Rubisco activase contents in several BC2 lines. We are now carrying out QTL analysis and experiments to clarify how the photosynthetic capacity was increased in progenies.

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