

Photosynthesis and Dry-Matter Production during Ripening Stage in a Female-Sterile Line of Rice

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Abstract : The relation between the source capacity of leaves and the sink capacity of panicles affects dry-matter production and determines grain yield in rice. The source-sink relation has so far been studied on rice plants from which panicles were artificially removed. We examined the source-sink relation using a female-sterile line FS1 with intact panicles each having a few fertile grains instead of panicle removal. The leaf photosynthetic rate during the ripening stage in FS1 was measured, in comparison with a normal counterpart Fujisaka 5, and the effect of losing sink function on dry-matter production in the rice plant was characterized. The photosynthetic rate in flag leaves was maintained at a slightly higher rate in FS1 than in Fujisaka 5 in the late ripening stage, though panicles did not function as a sink organ in FS1, and dry-matter production in this line was not lower than that in Fujisaka 5. In the early ripening stage of FS1, culms and leaf sheaths fulfilled the sink function instead of panicles, and the tillers that appeared in the late ripening stage became a new sink organ. Roots also functioned as a possible sink of photosynthates. Owing to the unique character of dry-matter production after heading, FS1 may be useful as a forage crop.

Key words : Dry-matter production, Female sterility, Panicle, Photosynthesis, Rice, Sink, Source.

Photosynthates translocate to and accumulate in various organs in the rice plant throughout the vegetative and reproductive growth periods. Leaves and panicles function as the major source and sink organs of photosynthates, respectively in the panicle ripening stage after heading. Panicles accumulate 60 to 80% of the total photosynthetic carbon after heading (Hoshikawa, 1983). Therefore, the relation between the source capacity of active upper leaves and the sink capacity of panicles affects dry-matter production and determines rice yield. The sink capacity of the panicle has been studied on rice plants from which panicles were artificially removed. Some researchers reported that panicle removal did not affect the photosynthetic activity of flag leaves (Cho et al., 1981), and retarded the decrease in photosynthesis in flag leaves during plant senescence (Nakano et al., 1995). In other monocot plants such as wheat and barley, panicle removal had no significant effect on photosynthesis in the flag-leaf or total dry-matter production (Koide and Ishihara, 1992a,b). In these studies, reproductive organs were artificially removed, and the source functions of panicles in barley and wheat, and rachis-branches in rice were neglected. In rice, however, the role of panicle photosynthesis in matter production is not negligible (Ishihara et al., 1990); in addition, hulls play an important role as a pool for nutrient translocation, although there is a significant difference in the hull dry weight between fertile and sterile grains (Seo and Ota, 1981). We planned to analyze

the source-sink relation, and the translocation and accumulation of photosynthates in intact plants such as male or female sterile lines.

A female sterile line FS1 of rice has panicles with a few ripened grains; this sterility can be maintained through these ripened grains in the progeny (Yokoo, 1984). Under the assumption that the sink capacity of panicles in FS1 is negligible, we measured the photosynthetic rate of the flag and the 2nd leaves during the ripening stage in both FS1 and the control variety Fujisaka 5, and characterized the effects of losing the sink function of panicle on dry-matter production in rice plant.

Materials and Methods

1. Plant materials and culture

A female sterile line FS1 and a normal fertile line Fujisaka 5 of rice (*Oryza sativa* L.) were used. The breeding process of FS1 and genetics of female sterility have been reported by Yokoo (1984). The control variety Fujisaka 5 was the recurrent parent in the backcross breeding of FS1 from the cross between a Japanese variety Fujisaka 5 and an Indonesian variety Tjina.

Germinated seeds were sown on April 21 in a plastic box containing rice nursery soil (Kumiai Ryujou-baido K, Kureha Co. Ltd., Tokyo) in a vinyl house. Twenty-eight days after sowing, two seedlings at the 6-leaf stage were transplanted to a 1/5000 a Wagner pot containing 2.5kg of nursery soil with 0.8g N,

Table 1. Growth characteristics of FS1 and Fujisaka 5.

Line	Number of days from sowing to heading	Culm length at maturity (cm)	Panicle number (plant ⁻¹)	Panicle length (cm)	Number of late tillers (plant ⁻¹)
FS1	88	89.7 **	13.2	20.4 **	28.2 **
Fujisaka 5	89	73.6	14.0	16.5	4.0

** indicates significant difference between FS1 and Fujisaka 5 at 1% level by student's T-test.

3.8g P₂O₅, and 1.2g K₂O. Plants were placed under natural conditions in a vinyl house from April to September 2000 at the Agriculture Research Center, University of Tsukuba. Pots were kept submerged in a pool throughout the growing period. Each pot was topdressed with 3g compound fertilizer (N : P : K=14) 45 days after transplanting.

2. Measurements

Plant length, stem number, plant age in leaf number, and the SPAD value of an uppermost leaf were measured for 20 plants every seven days until panicle heading. The chlorophyll meter (SPAD-502, Minolta Co. Ltd., Tokyo) was used for the SPAD value measurement. Every seven days from heading to maturity, the photosynthetic rate and stomatal conductance of the flag leaf and 2nd leaf were measured by an open gas-exchange method using a portable photosynthesis and transpiration measurement system (LI-6400, LI-COR, USA) equipped with an artificially illuminated leaf-chamber. The photosynthetic rate was measured in a leaf chamber where photosynthetic active radiation was 1,400 μmol m⁻² s⁻¹ and temperature and humidity were maintained at the same levels as the surrounding air. The SPAD value was also determined for the leaves used for the gas exchange measurement.

On the day following the measurement of photosynthesis, the bleeding rate of 4 plants from which the aboveground parts were removed was measured in the manner suggested by Morita and Abe (1999).

At heading and maturity time six plants were harvested and divided into six parts, namely : roots, culms plus leaf sheaths, leaf blades, dead leaves, panicles, and tillers that appeared in the last half of the ripening stage (late tillers). All the samples were oven-dried at 80°C for 72 hours and their dry weight was determined.

Results

1. Vegetative growth

Plant age in leaf number progressed slightly earlier in FS1 than in Fujisaka 5, but the total number of leaves on the main stem at heading was 15 in both lines. The heading date of FS1 was July 18, which was 88 days after sowing and 1 day earlier than that of

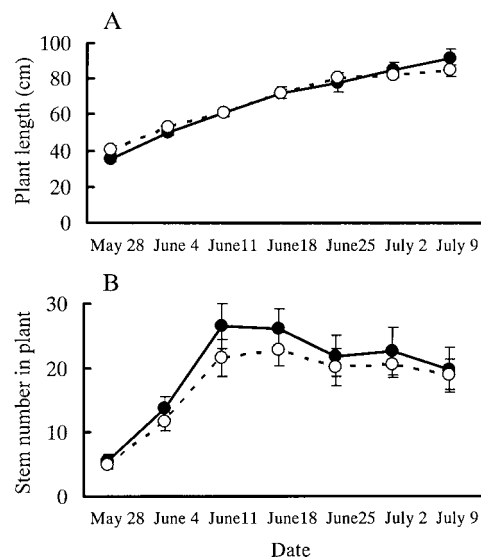


Fig. 1. Changes in plant length (A) and stem number (B) of FS1 (●) and Fujisaka 5 (○) during the vegetative growth phase. Vertical bars represent standard deviations (n=20).

Fujisaka 5 (Table 1). Plant length increased almost equally in both lines during the vegetative growth stage (Fig. 1), but FS1 was about 20 cm taller than Fujisaka 5 due to longer culm and panicle lengths (Table 1). Though FS1 had slightly more stems than Fujisaka 5 during the earlier growth stage, they had a similar number of stems by the heading time (Fig. 1). There was no difference in the number of ordinary panicles between the two lines, but the total number of panicles in FS1 increased because tillers appeared from almost all culms in the last half of the ripening stage (late tillers) in this line.

2. Changes in photosynthetic rate, stomatal conductance and the SPAD value of upper leaves during the ripening stage

The photosynthetic rate in the flag leaf and 2nd leaf decreased rapidly as leaf senescence proceeded after heading (Fig. 2), although the value in the flag leaf of FS1 decreased slowly and FS1 maintained a significantly higher rate than Fujisaka 5 at 28, 35 and 42 days after heading. On the other hand, the 2nd leaf of Fujisaka 5 maintained a higher photosynthetic rate after heading, but withered and died a week before maturity.

The SPAD value in the flag leaf and 2nd leaf decreased gradually during the ripening stage (Fig. 3). The decrease in the flag leaf of FS1 in the later ripening stage was slower than that of Fujisaka 5.

The stomatal conductance of the flag leaf also showed a gradual decrease in both rice varieties. The photosynthetic rate showed significantly positive correlations with the stomatal conductance (Fig. 4A) and with the SPAD value (Fig. 4B) in both FS1 and

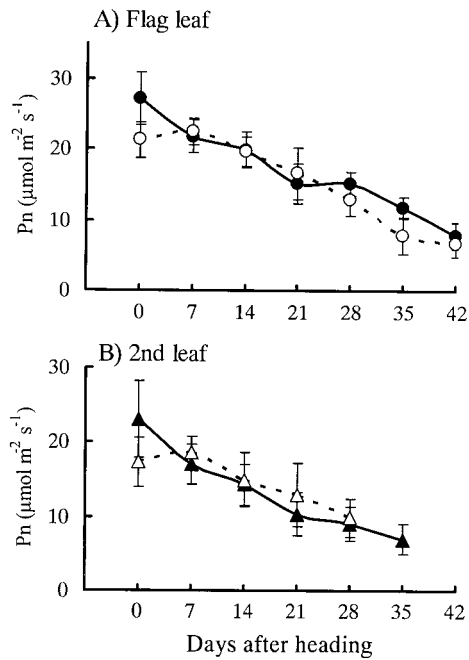


Fig. 2. Changes in the apparent photosynthetic rate (Pn) of the flag (A) and 2nd (B) leaves of FS1 (●, ▲) and Fujisaka 5 (○, △) during the ripening stage. Measurements were made for leaves on the main culm and 2 to 4 tillers in each of 6 plants at $1,400 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Vertical bars represent standard deviations ($n=17-30$).

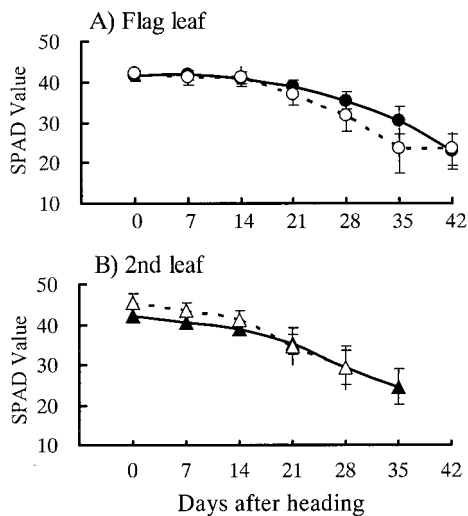


Fig. 3. Changes in the SPAD value of the flag (A) and 2nd (B) leaves of FS1 (●, ▲) and Fujisaka 5 (○, △) during the ripening stage. Vertical bars represent standard deviations ($n=17-30$).

Fujisaka 5. The rapid decrease of the photosynthetic rate in Fujisaka 5 caused a relatively lower correlation with the stomatal conductance in the late ripening stage.

3. Leaf characteristics and dry matter production

FS1 had a larger and heavier flag leaf than Fujisaka

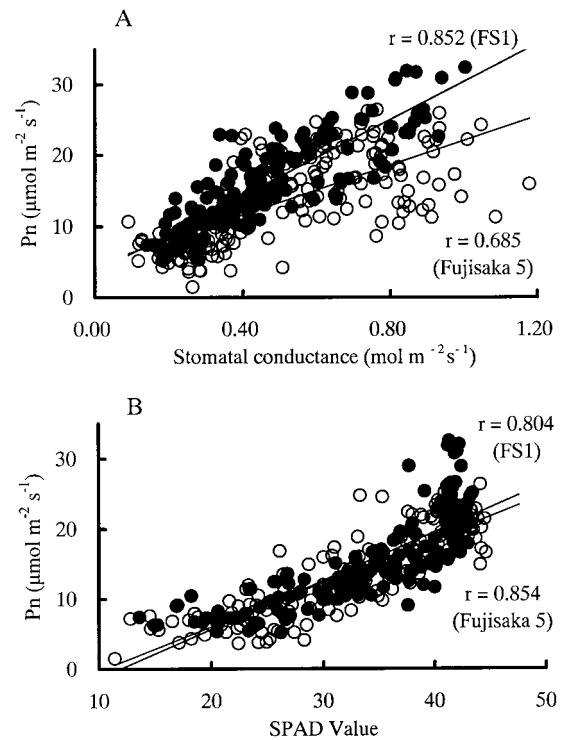


Fig. 4. Relations between the apparent photosynthetic rate (Pn) and the stomatal conductance (A) and the SPAD value (B) of the flag leaf in FS1 (●) and Fujisaka 5 (○) during the ripening stage.

5, and there was no difference in specific leaf area (SLA) between the two lines in the mid-ripening stage (Table 2).

Total dry weights were 48.5 and $40.4 \text{ g plant}^{-1}$ at heading time and 75.3 and $58.8 \text{ g plant}^{-1}$ at maturity in FS1 and Fujisaka 5, respectively. The relative increase in total dry weight during the ripening stage was 55% in FS1 and 46% in Fujisaka 5 (Fig. 5). The distribution of dry weight to each organ differed between FS1 and Fujisaka 5 during the period from heading to maturity. The dry weights of panicles increased markedly in Fujisaka 5 but remained unchanged in FS1 during maturity. Late tillers and roots occupied 24% and 11%, respectively, of the total dry weight at maturity in FS1 but only 5% and 7% in Fujisaka 5. Increases in dry weight of those organs in the late ripening stage were unique in FS1, differing from normal rice plants such as Fujisaka 5.

4. Bleeding rate and root biomass

Bleeding rates in FS1 and Fujisaka 5 were 1.3 and $1.7 \text{ mg plant}^{-1}$ at heading time and 0.8 and $0.4 \text{ mg plant}^{-1}$ at maturity, respectively. The rate decreased more slowly in FS1 than in Fujisaka 5 (Fig. 6). Dry weights of roots of FS1 and Fujisaka 5 were 6.7 and 5.5 g plant^{-1} respectively, at heading time and 8.1 and 3.9 g plant^{-1} respectively, at maturity. The weight decreased in Fujisaka 5 but increased in FS1 during ripening, and

Table 2. Leaf characteristics of upper leaves in FS1 and Fujisaka 5 on 21 days after heading.

Leaf	Line	Length (cm)	Width (cm)	Area (cm ² leaf ⁻¹)	Dry weight (g leaf ⁻¹)	Specific leaf area (cm ² g ⁻¹)	SPAD
Flag leaf	FS1	32.6 *	1.48 ***	36.1 ***	0.16 ***	220	39.1 *
	Fujisaka 5	27.7	1.37	26.5	0.12	225	37.2
2nd leaf	FS1	38.4 **	1.27 **	34.1 **	0.15 **	230	34.9
	Fujisaka 5	34.3	1.20	28.9	0.12	234	35.5

Values represent the means for leaves from a main culm and 2 tillers in each of 6 plants.

*, **, *** indicate significant difference between FS1 and Fujisaka 5 at 5%, 1% and 0.1% levels, respectively.

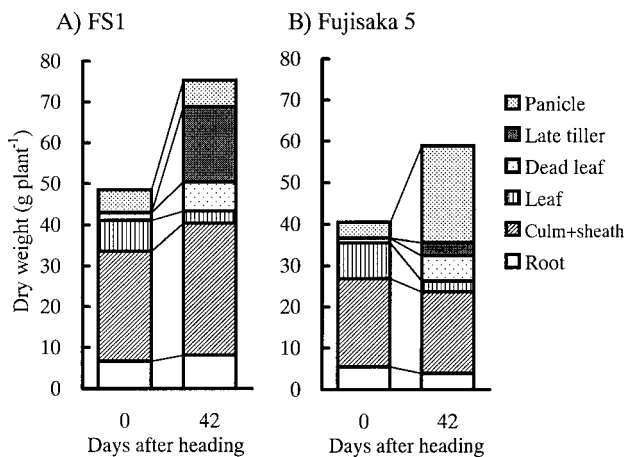


Fig. 5. Dry weight of each organ of FS1 (A) and Fujisaka 5 (B) measured at heading and maturity.

FS1 had significantly heavier roots than Fujisaka 5 at maturity.

Discussion

Higher yield and better grain quality in rice production require the maintenance of active photosynthesis during the ripening stage of rice plants. Source-sink relations have been studied on rice plants with panicles damaged or removed. Panicle removal had no effect on the photosynthetic ability of the flag leaf (Cho et al., 1981) and retarded the decrease of photosynthetic ability in the flag leaf during plant senescence (Nakano et al., 1995). Spikelet removal or emasculation delayed leaf senescence of the main, secondary, and tertiary branches in rice (Khan and Choudhuri, 1991). In rice, however, the panicle photosynthesis is not negligible (Ishihara et al., 1990) and panicle removal reduced light interception and increased net canopy photosynthesis after flowering (Setter et al., 1995). In the present study, we used a female sterile line FS1 with intact panicles each having a few fertile grains, instead of the artificial removal of panicles or spikelets, and revealed that FS1 maintained a slightly higher photosynthetic rate of flag leaves than

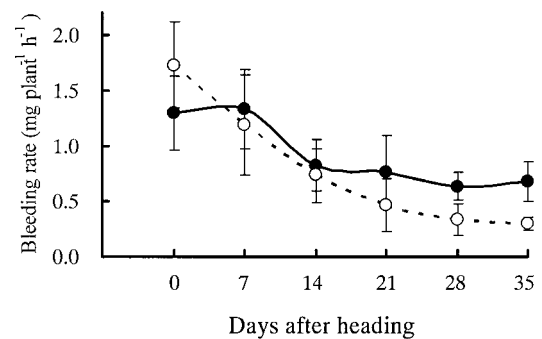


Fig. 6. Changes in the bleeding rate of FS1 (●) and Fujisaka 5 (○) during the ripening stage. Vertical bars represent standard deviations (n=4).

a normal counterpart Fujisaka 5 in the late ripening stage. The change in leaf photosynthetic rate and its relationship to stomatal conductance or SPAD in FS1 during the ripening stage were similar to those in normal rice (Kuroda and Kumura, 1990; Saitoh et al., 1991). A large sink size promoted flag leaf senescence (Wada et al., 1993). Although the flag leaf and 2nd leaf were significantly larger in FS1 than in Fujisaka 5, SLA in the mid-ripening stage was not different between the two lines (Table 2). It could be said that there was no feedback inhibition of photosynthates on leaf photosynthesis. The maintenance of higher photosynthetic activity due to the probable delay of leaf senescence particularly at the late ripening stage resulted in the significantly larger dry-matter production at maturity in FS1 than in Fujisaka 5.

Panicles and vegetative organs such as culms, leaves and roots are the sinks of photosynthates in rice. In FS1, culms and leaf sheaths were the largest sink organs through ripening period and late tillers became a new sink organ in the late ripening stage. The ratio of dry-matter partitioning to culms plus leaf sheaths changed from 55.5% at heading to 42.8% at maturity, while the weight of late tillers rapidly increased after heading and occupied 24.3% of the total dry-weight at maturity (Fig. 5). Active photosynthesis even at the later ripening stage in FS1 whose panicles

have a lower sink function might cause the rapid development of late tillers at this stage. These late tillers developed from both upper and based lateral buds. However, the development of late tillers or high node tillers has not been studied in relation to dry-matter distribution to respective organs (Cho et al., 1981; Oritani and Yoshida, 1971; Takahashi, 1992), though the development of upper lateral buds was related to starch and nitrogen concentrations in stems and leaves (Sato, 1959). Since root dry weight of FS1 increased during the ripening period, we suppose that new roots appeared along with the development of late tillers and worked as a sink of photosynthates. A higher bleeding rate of sap is a useful index of root activity (Yamaguchi et al., 1995). Jiang et al. (1988) reported a close relationship between root development and maintenance of photosynthetic activity in a high yielding rice variety. A higher bleeding rate of sap in the later stage may be related to the large root biomass in FS1. Prolonged root activity may have contributed to the delay of leaf senescence and to the final dry-matter production.

In FS1, vegetative organs such as culms, leaf sheaths, late tillers and roots substituted for panicles as photosynthate sinks, and contributed to the delay of leaf senescence and to the increase of dry-matter production during the ripening stage. Owing to these characteristics FS1 may be useful for biological production as a forage crop, since it may have a large amount of carbon in stems and produce vigorous ratoons, and such traits depend largely on the stem weights and the total available carbohydrate (Ichii and Sumi, 1983). The present results were obtained from the limited conditions for root growth in pots. Further field experiments under the higher nitrogen nutrition levels are needed to evaluate the potential biomass productivity of this female sterile line of rice.

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