Dry-Matter Partitioning and Accumulation of Carbon and Nitrogen during Ripening in a Female-Sterile Line of Rice

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Abstract: To evaluate the effect of sink restriction on dry-matter partitioning to rice plant organs during ripening, we observed the dry-weight partitioning and accumulation of carbon and nitrogen in a female-sterile line, FS1, which has intact panicles with only a few fertile grains, in comparison with those in a normal counterpart, Fujisaka 5. In spite of the loss of sink function in the panicles, FS1 produced a larger amount of dry-matter than Fujisaka 5. Without a change of panicle dry weight throughout the ripening period, FS1 increased dry weights of culms and leaf sheaths at the early stage and of late tillers at the late stage. The amounts of dry-matter partitioned to panicles, culms plus leaf sheaths and late tillers in FS1 were comparable to those amounts in Fujisaka 5 at maturity, indicating that the latter two organs function as a sink of dry matter to substitute for panicles. Carbon partitioning to plant organs was basically similar to the dry-matter partitioning. Since the amount of nitrogen in a plant hardly increased during the ripening period in FS1 and Fujisaka 5, nitrogen partitioning to plant organs was different from the partitioning of dry matter and that of carbon. Culms, leaf sheaths and late tillers function as a sink of nitrogen partly to substitute for panicles, but the sum of nitrogen partitioned to these organs and panicles in FS1 was markedly smaller than in Fujisaka 5 at maturity, suggesting that other organs do not substitute for panicles in the sink function for nitrogen partitioning. FS1 developed late tillers rapidly at the late stage and had a carbon-nitrogen ratio in the stems different from that in Fujisaka 5.

Key words: Carbon, C-N ratio, Dry-matter partitioning, Female sterility, Nitrogen, Panicle, Rice.

Leaves function as major sources of photosynthate and panicles function as sink organs of photosynthate in the ripening period in rice. Photosynthate after heading contributes to 60–80% of carbon accumulation in panicles (Hoshikawa, 1983). Therefore, the functional relations between the source capacity of leaves and the sink capacity of panicles affect dry-matter production that determines rice yield. To clarify this relationship, many researchers have studied the effects of sink restriction on source activity by removing panicles manually in rice (Murayama et al., 1957a, b; Cho et al., 1981). In rice, however, the panicle photosynthesis is not negligible (Ishihara, et al., 1990) and panicle removal reduced light interception and increased net canopy photosynthesis (Setter et al., 1995); in addition, hulls play an important role as a pool for nutrient translocation (Seo and Ota, 1981).

A female-sterile rice line, FSI, is the progeny of the cross Fujisaka 5 × Tjina backcrossed with pollen of Fujisaka 5 four times. Before heading, leaf number increased almost similarly in FSI and Fujisaka 5, and the heading date was 1 day earlier in FSI. Plant length increased almost equally in both genotypes during the vegetative growth stage (Kato et al., 2004). Under the assumption that the growth characteristics are similar until heading and the sink capacity of panicles in FSI is negligible, we characterized the effects of losing the sink function of panicles on dry-matter production in rice plants. Our previous study (Kato et al., 2004) revealed that the loss of sink function of panicles does not reduce the photosynthetic rate or dry-matter production. Our results also suggested that culms and leaf sheaths substitute for panicles in the sink function at the early stage of ripening, and late tillers function as a sink at the late stage. It remains to be clarified, however, how the sink function of different plant organs changes during the ripening period. Panicles serve as sink organs not only for carbohydrates but also for nitrogen, since rice grains contain 1.0–1.5% nitrogen, and 70–90% of the nitrogen in panicles is transferred from vegetative organs (Mae, 1997). Thus, sink restriction of panicles could affect nitrogen accumulation as well as dry-matter partitioning.

We here report the effect of the loss of sink function of panicles on dry-matter partitioning and carbon and nitrogen accumulations in a female-sterile line, FSI, and discuss the possible replacement of sink functions of panicles by other organs in dry-matter, carbon, and nitrogen partitioning.

Materials and Methods

1. Plant materials and culture
A female-sterile line, FSI, and a normal variety,
Fujisaka 5, of rice (*Oryza sativa* L.) were used. FS1 bears a few matured grains in a panicle, and its breeding process and genetics of female sterility were reported by Yokoo (1984). The control variety, Fujisaka 5, was the recurrent parent in the backcross breeding of FS1 (BC4F1) from the cross between a Japanese variety, Fujisaka 5, and an Indonesian variety, Tjina.

A pot experiment was conducted in a vinyl-covered house at the Agricultural and Forestry Research Center, University of Tsukuba, in 2000. Germinated seeds were sown in a plastic box containing nursery soil (Kumiai Ryujou-baido K, Kureha Co. Ltd., Japan) on April 21. Two seedlings at the 6-leaf stage were transplanted into a Wagner pot of 1/5000 filled with 2.5 kg of nursery soil on May 18. The soil in the pot contained 0.8 g N, 3.8 g P2O5, and 1.2 g K2O and was topdressed with 0.4 g of N, P2O5, and K2O at the panicle development stage on July 3. A total of 70 pots for each variety were placed randomly with a spacing 30 cm × 30 cm and rotated every two weeks until heading time. The pots were submerged in a pool throughout the experiment. The heading dates were July 18 for FS1 and July 19 for Fujisaka 5.

### Table 1. Statistical analysis of the difference in dry weight of plant parts between Fujisaka 5 and FS1.

| Plant part             | DAH |  |  |  |  |  |  |  |
|------------------------|-----|---|---|---|---|---|---|---|
|                        | −10 | 0 | 7 | 14| 21| 28| 35| 42|
| Total                  | ** | * | * | **| **| **| **| **|
| Panicle                | −  | **| ns| **| **| **| **| **|
| Dead leaf              | ns | **| * | ns| ns| ns| ns| ns|
| Leaf blade             | ns | ns| ns| ns| * | * | * | ns|
| Late tiller            | −  | − | − | − | − | − | − | **|
| Culm+Leaf sheath       | ns | **| * | **| **| **| **| **|
| Root                   | ** | * | ns| ns| * | * | * | **|

*, ** and ns indicate significant difference at the 5%, 1% and no significant difference, respectively (Student’s t test, n=3).

### 2. Measurement of dry weight of each plant part

Six plants for each variety were harvested from 3 pots 10 days before heading and every seven days after heading (0 DAH) to maturity (42 DAH). Plants were divided into 6 parts: roots, culms plus leaf sheaths (stems), leaf blades (leaves), dead leaves, panicles, and late tillers which appeared in the last 14 days of the ripening stage (28 to 42 DAH). All the samples were oven-dried at 80°C for 72 hours, and their dry weights were determined.

### 3. Determination of carbon and nitrogen contents

The dried plant parts were ground in a mill (Cyclone Sample Mill, UDY, USA). Carbon and nitrogen contents in about 100 mg of sample were determined with a CN-corder (MT-600, Yanaco, Japan). The amounts of carbon and nitrogen in plant parts were calculated by multiplying dry weight by each content.

### Results

#### 1. Dry-matter partitioning

Fig. 1 shows the changes in the dry weight of plant parts during the ripening period in Fujisaka 5 and FS1. FS1 increased its total dry weight more rapidly and
greatly than Fujisaka 5 during the ripening period.

From 0 to 21 DAH, normal variety Fujisaka 5 showed a rapid increase in panicle dry weight and a slight decrease in stem dry weight, but the values were unchanged thereafter (Fig. 1A). Fujisaka 5 showed decreases in dry weights of the leaves and roots during the ripening period, but it produced a few late tillers after 35 DAH. In contrast, FS1 maintained an unchanged dry weight of the panicles throughout the ripening period, and markedly increased dry weight of stems from 0 to 21 DAH, then decreasing it from 28 to 42 DAH (Fig. 1B). Late tillers appeared from both upper and lower lateral buds in FS1 in this period, and their dry weight increased until maturity. FS1 showed a slight decrease in dry weight of the leaves but increased dry weight of the roots during the ripening period.

At maturity, 8.7, 4.0, 9.4, 42.8, 24.3 and 10.7% of the dry matter was partitioned to panicles, leaves, dead leaves, stems, late tillers, and roots, respectively, in FS1 and 39.5, 4.3, 10.5, 33.7, 6.5 and 6.7%, respectively, in Fujisaka 5. FS1 accumulated less dry matter in the panicles but more in the stems and late tillers. Dry weights of stems, late tillers and roots were significantly heavier in FS1 than in Fujisaka 5 (Table 1).

2. Carbon and nitrogen contents

Fig. 2 shows the changes in carbon and nitrogen contents of plant parts during the ripening period. Carbon contents of the leaves, stems, and panicles during the ripening period in FS1 were in the range of 44–46, 40–44, and 42–46%, respectively, and those in Fujisaka 5 were in the range of 42–45, 38–42, and 44–46%, respectively (Fig. 2A). Although FS1 had values similar to Fujisaka 5 at heading, FS1 contained more carbon in the leaves and stems and less in the panicles than did Fujisaka 5 at maturity.

The nitrogen content of leaves in FS1 decreased from 2.5 to 1.8% and that in Fujisaka 5 from 2.7 to 1.4% during the ripening period (Fig. 2B). Nitrogen contents of stems and panicles in FS1 were in the range of 0.3–0.6 and 0.8–1.1%, respectively, and those in Fujisaka 5 were in the range of 0.4–0.7 and 1.3–1.4%, respectively. The nitrogen contents of plant parts in FS1 were slightly lower than those in Fujisaka 5 at heading, although the differences were not significant at the 5% level by t-test. FS1 contained more nitrogen in the leaves and less in the stems and panicles than Fujisaka 5 at maturity.

3. Carbon and nitrogen partitioning

Fig. 3 and 4 show the changes in carbon and nitrogen accumulations in plant parts during the ripening period in FS1 and Fujisaka 5, respectively. The carbon accumulation in plant parts was basically similar to their dry weight in both genotypes (Fig. 3 and Table 2).

The amount of nitrogen hardly increased during the ripening period in FS1 and Fujisaka 5: the amounts were 0.44–0.46 g plant⁻¹ in FS1 and 0.49–0.50 g plant⁻¹ in Fujisaka 5. In Fujisaka 5, the amount of nitrogen in panicles increased rapidly, that in leaves decreased markedly from 0 to 21 DAH, and slowly thereafter, and that in stems slightly decreased during the ripening period (Fig. 4A). In contrast, the amount of nitrogen in panicles hardly increased during the ripening period in FS1, but that in stems gradually increased from 0 to 28 DAH (Fig. 4B). It decreased in stems rapidly after 28 DAH and increased in late tillers during this period. It decreased in leaves gradually during the ripening period.

At maturity, the rates of nitrogen partitioned to panicles, leaves, dead leaves, stems, late tillers, and roots, respectively, were 11.9, 12.5, 9.7, 20.6, 32.4 and 12.9% in FS1, and 54.9, 7.2, 8.5, 17.2, 6.4 and 6.8%, respectively, in Fujisaka 5. FS1 accumulated less nitrogen in the panicles but more in the leaves, stems, late tillers, and roots than did Fujisaka 5. The differences were significant only for late tillers and roots at maturity (Table 3).

Fig. 5 shows the changes in the carbon-nitrogen (C-N) ratio in stems, leaves, and panicles in FS1 and Fujisaka 5. FS1 increased the C-N ratio in stems from...
74 to 151, while Fujisaka 5 increased it from 62 to 92. In particular, FS1 increased the value in stems markedly after 28 DAH. The C-N ratios of leaves and panicles were in the range of 18–25 and 44–53, respectively, in FS1, and 17–31 and 34–37 in Fujisaka 5. FS1 had a higher value in the stems and panicles than did Fujisaka 5 at maturity.

**Discussion**

In a normal variety, Fujisaka 5, panicles occupied about 40% of the total dry weight, 44% of total accumulated carbon and 55% of total accumulated nitrogen. A female-sterile rice line, FS1, showed a unique pattern of changes in dry weights for plant parts during the ripening period. FS1 had a heavier total dry weight than Fujisaka 5 before heading. In spite of the loss of sink function of panicles, the total dry weight was significantly heavier in FS1 than in Fujisaka 5 at maturity. A decrease or a lack of change in total dry weight due to sink restriction has been reported in rice (Murayama et al., 1957a; Cho et al., 1981) and in wheat and barley (Koide and Ishihara, 1992a). Koide and Ishihara (1992a) suggested that the response of dry-matter production to sink restriction was different among crops. In rice, the dry weight increase of other organs compensated for the dry-matter production loss by the removal of spikelets (Murayama et al., 1957a). The dry-matter production and distribution in FS1 were almost the same as in the normal plants with panicles removed in those reports. In fact, FS1 accumulated 76% and Fujisaka 5 accumulated 80% of their total dry matter in panicles, stems and late tillers. These results suggest that stems and late tillers function as a sink of dry-matter substituting for panicles.

Partitioning of carbon to plant parts was similar to that of dry-matter in both genotypes. This is because the difference of carbon contents among plant parts was relatively small, and was almost constant during the ripening period. Nevertheless, the carbon contents of leaves and stems were significantly higher, and those of panicles were lower in FS1 than in Fujisaka 5 at maturity. Contents of cell wall constituents such as lignin and cellulose in stems were relatively higher in panicle-removed plants than in control plants (Murayama et al., 1957b). The types of carbon...
compounds in each plant organ may be different in the two genotypes.

Nitrogen partitioning to plant parts was different from the partitioning of dry-matter and carbon. Nitrogen contents were higher in the order of leaves, panicles and stems; a large amount of nitrogen was partitioned to leaves and panicles as compared with dry matter and carbon. FS1 kept the amount of nitrogen in panicles almost unchanged throughout the ripening period. Stems and late tillers functioned as a sink of nitrogen substituting for panicles. However, FS1 had a lower nitrogen content in the stems than Fujisaka 5. In FS1, 65% of the total accumulated nitrogen was partitioned to the panicles, stems and late tillers at maturity, while in Fujisaka 5, 79% of the total accumulated nitrogen was partitioned to those organs. These results suggested that stems and late tillers do not substitute for the sink functions of panicles in nitrogen partitioning. The large dry-matter production in FS1 was attributed to the high level of leaf photosynthesis maintained due to the delay of leaf senescence, particularly at the late ripening stage, as we reported previously (Kato et al., 2004). Panicle removal did not affect the photosynthetic ability of the flag leaf (Cho et al., 1981), or retard the decrease of photosynthetic ability of the flag leaf during plant senescence (Nakano et al., 1995). Manual removal of panicles delayed leaf senescence and maintained the ability of photosynthesis in wheat (Koide and

Fig. 4. Changes in nitrogen accumulation in plant parts in Fujisaka 5 (A) and FS1 (B) during the ripening period.

Table 3. Statistical analysis of the difference in nitrogen accumulation in plant parts between Fujisaka 5 and FS1.

| Plant part  | DAH |  |  |  |  |  |  |  |
|------------|-----|---|---|---|---|---|---|---|
|            | -10 | 0 | 7 | 14 | 21 | 28 | 35 | 42 |
| Total      | ns  | ns | ns | ns | ns | ns | ns | ns |
| Panicle    | -   | **| ns | **| **| **| **| **|
| Dead leaf  | ns  | **| ns | ns | ns | ns | ns | ns |
| Leaf blade | ns  | ns | ns | ns | * | * | **| ns |
| Late tiller| -   | - | - | - | - | - | - | **|
| Culm+Leaf sheath | ns | ns | ns | **| **| **| **| ns |
| Root       | ** | ns | ns | ns | ns | * | * | **|

*, ** and ns indicate significant difference at the 5%, 1% and no significant difference, respectively (Student’s t test, n=3).

*Fig. 5. Changes in the carbon (C)-nitrogen (N) ratio in culms + leaf sheaths, leaf blades and panicles in Fujisaka 5 (open symbols) and FS1 (solid symbols) during the ripening period. The vertical bar indicates standard error from 3 pots.
Ishihara, 1992b). Wada et al. (1993) suggested that the difference in leaf senescence was associated with the different rates of nitrogen withdrawal from leaf blades to grains. In this experiment, the total amount of nitrogen hardly increased during the ripening period in FS1 and Fujisaka 5. This can be due to the insufficient nitrogen supply and limited root growth in a potted condition.

FS1 developed late tillers rapidly after 28 DAH from both upper and basal lateral buds. The development of late tillers was generally found in panicle-removed rice plants (Oritani and Yoshida, 1971; Cho et al., 1981). High nodal-position tillers are usually in dormancy, and they start to grow when the panicles are cut off (Takahashi, 1992). The development of upper lateral buds was related to starch and nitrogen contents of stems and leaves (Sato, 1959). The amount of nitrogen in stems decreased after 28 DAH in FS1. The sharp increase in the C-N ratio in stems after 28 DAH in FS1 reflected the fact that the nitrogen accumulated in stems rapidly translocated to late tillers but not to panicles. The rapid development of late tillers after 28 DAH may be related to the dormancy awakening and/or the end of the sink capacity of stems for carbon and nitrogen.

FS1 is considered to have a larger amount of carbon and nitrogen in the stems than Fujisaka 5, which might be used for ratoon production. Ratoon traits, such as ratoon number, height and weight, depend largely on the weights of the stem base and total available carbohydrate (Ichii and Sumi, 1983). Total dry-matter production and nitrogen accumulation would have to be evaluated before use of FS1 for biological production.

In conclusion, vegetative organs such as culms, leaf sheaths and late tillers play an alternative role as a sink instead of panicles in FS1. However, those organs could not fulfill the sink capacity for nitrogen. The growth of FS1 after heading is characterized by a higher nitrogen level in leaves and the rapid development of late tillers as a new sink organ in the late ripening stage. However, the present results were obtained under the limited conditions in pots with the standard nitrogen nutrition supply. Additional field experiments under sufficient nitrogen supply are needed to evaluate the potential productivity of this female-sterile rice line.

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