Effects of Assimilate Supply and High Temperature during Grain-Filling Period on the Occurrence of Various Types of Chalky Kernels in Rice Plants (Oryza sativa L.)

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Abstract: The objective of this study was to clarify the effect of assimilate supply and high temperature on the occurrence of chalky kernels, i.e. milky white, white back, basal white and white belly kernels. Rice cultivars Koshihikari and Takanari, contrasting in number of spikelets in a panicle were used. After heading, sink-source manipulation was imposed on plants, through changing supply of assimilates to spikelets by shading or panicle clipping. Plants with each sink-source manipulation were subjected to temperature treatments, i.e., high temperature and ambient temperature, using a temperature-gradient chamber. Percentage of various types of chalky kernels was examined with the treatment for each cultivar. High temperature treatment increased milky white and white back kernels while no significant effect of temperature was observed on the percentage of white belly and basal white kernels. Effects of sink-source manipulation on the occurrence of chalky kernels varied with the type of chalky kernels. Although sink-source manipulation had no effect on white back and basal white kernels, it had a significant effect on the percentage of milky white and white belly kernels, which indicates the association of assimilate supply with the occurrence of these types of chalky kernels. A close hyperbolic relation was observed between the rate of assimilate supply and the percentage of milky white kernels, suggesting that milky white kernels are caused by assimilate deficit during the initial half period of grain filling. The higher percentage of milky white kernels at a given rate of assimilate supply at a high temperature implied that the high temperature during the grain-filling period increases the assimilate demand to avoid the occurrence of milky white kernels. This is presumably because the high temperature during the grain-filling period accelerates grain growth especially in inferior spikelets.

Key words: Assimilate supply, Chalky kernels, Grain filling, High temperature, Milky white kernels, Rice.
Milky white kernels increased when flag leaves were removed or decreased in plants in which light environment was improved by thinning half of the population at heading (Kobata et al., 2004; Nakagawa et al., 2006). Tashiro and Ebata (1975) reported that the occurrence of white belly kernels is affected by the sink-source status during the grain-filling period, although there is also an observation which showed no effect of sink-source manipulation on the occurrence of this type of chalky kernels (Nakagawa et al., 2006). On the other hand, the effects of assimilate supply on the occurrence of basal white and white back kernels seem to be much smaller than those on milky white or white belly kernels (Morita et al., 2005b; Nakagawa et al., 2006). These previous results imply the association between assimilate supply and the occurrence of some types of chalky kernels. However, the combined effects of assimilate supply and high temperature on the occurrence of each type of chalky kernels have not been studied. The objective of this study was to clarify the combined effects of sink-source status and high temperature on the occurrence of each type of chalky kernels and further discussed the reason why an assimilate deficit occur under high temperature conditions.

Materials and Methods

Rice cultivars Koshihikari and Takanari were used in this study. On 2 May 2005, 20 plants were directly sown in Wagner pots, 16.0 cm in diameter and 19.0 cm in depth, with a basal dressing of 1.0 g of N as ammonium sulfate, 1.5 g of P₂O₅ as superphosphate and 1.5 g of K₂O as potassium chloride, and with a top dressing of 1.0 g of N as ammonium sulfate 20 days before heading. Tillers were removed every week until heading. Plants were grown under an outdoor condition until the start of temperature treatment. Plants headed on 2 August in Koshihikari and 6 August in Takanari were tagged and used for the measurement.

Three days after heading, the tagged plants were divided into three groups and sink-source manipulation was imposed on the plants in each group, i.e., shading treatment, panicle-clipping treatment and control. Shading treatment was conducted by covering leaf blades except the flag leaf with aluminum foil and panicle-clipping treatment by removing every second primary rachis branches from the top of the panicles. The plants for each treatment were then divided into two groups and subjected to temperature treatments. Temperature treatments consisted of high temperature and ambient temperature treatment. At 6 days after heading, the temperature treatments were commenced using a temperature gradient chamber (TGC). The TGC is a greenhouse covered with vinyl sheet, 4.5 m in width, 24 m in length, 2 m in maximum height, with exhaust fans placed at one end so that a constant air flow arose from the other open end to the outlet, which generated temperature gradient in a daytime. Three oscillating fans were placed at intervals of 6 m on each side of the house. High temperature
treatment was conducted by placing pots between 18 and 22 m from the inlet and ambient temperature treatment by placing pots between 2 and 6 m from the inlet. At 4 points in each temperature treatment, air temperature was measured at a height of 1 m, just above panicles. Difference in mean daily temperature measured at 4 points for each temperature treatment was within 0.2ºC. Fig. 1 shows the changes in daily mean temperature for each temperature treatment. The temperature difference between high and ambient temperature treatments between 6 and 20 days after heading was 0.9ºC in Koshihikari, and 1.0ºC in Takanari, respectively.

At 3, 20 and 40 days after heading, 10 tagged plants were harvested in each treatment. Plants were separated into panicles, leaf blades, and culms plus leaf sheaths (stems), oven dried at 80ºC for 72 hours and dry weight was measured. Dried samples of stems were ground and used for measurement of non-structural-carbohydrate (stem-NSC). The stem-NSC content was determined as the sum of total soluble sugar and starch content as described by Thongbai et al. (1995). Total soluble sugar was extracted with hot ethanol and assayed with anthrone reagent. Starch in the residue was hydrolyzed to glucose with amyloglucosidase and the glucose content was assayed with anthrone reagent. Starch content was determined by multiplying the glucose content by 0.9.

At 3- to 5-day intervals after heading, panicles were harvested from the five tagged control plants of both temperature treatments in both cultivars. Immediately after the harvest, the panicles were frozen with liquid nitrogen and freeze-dried. From each dried panicle, superior and inferior spikelets were collected and hulled. The superior and the inferior spikelets were defined as the fifth spikelets from the top of the apical three primary rachis branches and the second spikelets from the top of the secondary rachis branches attached to the basal three primary rachis branches, respectively. Starch content of grain in superior and inferior spikelets was determined as described above.

At 43 days after heading, 10 tagged panicles were harvested. All the hulled grains with a thickness of more than 1.7 mm were classified into perfect grains, milky white kernels, basal white kernels, white back kernels, white belly kernels and opaque rice kernels visually. Table 1 shows the number of grains investigated in each treatment for each cultivar. Percentage of each kind of chalky kernels was calculated from the number of spikelet.

Analysis of variance of the data was performed in a factorial design by considering three factors; cultivar, temperature and sink-source status with 10 replicate plants.

**Results**

The amount of dry matter production per spikelet is shown in Fig. 2. Dry matter production was reduced by shading treatment and increased by spikelet clipping treatment in both cultivars and both temperature conditions. High temperature treatment did not reduce the dry matter production in both cultivars. The dry matter production per spikelet was larger in Koshihikari due to much smaller number of spikelets than in Takanari.

Table 2 shows the percentage of each type of chalky kernels with temperature and sink-source manipulation in Koshihikari and Takanari.

| Cultivar | Temperature | Sink-source manipulation | Number of kernels |
|----------|-------------|--------------------------|-------------------|
| Koshihikari | A | S | 72.5 ± 4.8 |
| | | P | 40.3 ± 1.3 |
| | | C | 79.1 ± 7.6 |
| | H | S | 70.1 ± 5.0 |
| | | P | 44.4 ± 2.9 |
| | | C | 80.6 ± 5.1 |
| Takanari | A | S | 124.6 ± 5.8 |
| | | P | 73.5 ± 6.0 |
| | | C | 146.0 ± 12.1 |
| | H | S | 128.4 ± 13.7 |
| | | P | 74.1 ± 4.3 |
| | | C | 134.1 ± 9.5 |

1) A and H denote ambient and high temperature conditions during grain-filling period, respectively.
2) S, P and C denote treatments of shading, panicle-clipping and control, respectively.
3) mean ± standard error.
Significant differences were observed between the cultivars in the percentage of all the types of chalky kernels. The percentage of basal white and white back kernels was higher, while that of milky white, white belly and opaque kernels was lower in Koshihikari than in Takanari.

Temperature affected the percentage of milky white and white back kernels \((P < 0.01\) for each). The high temperature treatment increased milky white kernels in both cultivars, but increased white back kernels only in Koshihikari. No significant difference was observed in the percentage of white belly, basal white and opaque kernels between the temperature treatments.

Sink-source manipulation did not affect the percentage of white back, basal white and opaque kernels. There were significant differences \((P < 0.01\) for each) in the percentage of milky white and white belly kernels among treatments of sink-source manipulation. Shading treatment increased and panicle-clipping treatment decreased these types of chalky kernels. While the effect of sink-source manipulation was observed on the percentage of milky white kernels in both cultivars, its effect on the percentage of white belly kernels was observed only in Koshihikari. In the percentage of milky white kernels and white back kernels, significant interaction \((P < 0.01)\) was observed between cultivar and sink-source manipulation treatment and between temperature and

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**Table 2. Percentage (%) of each type of chalky kernels with temperature and sink-source manipulation in Koshihikari and Takanari.**

| Cultivar | Temperature \(^1\) Sink-source manipulation \(^2\) | Milky white kernels \(^3\) | White back kernels | Basal white kernels | White belly kernels | Opaque kernels |
|----------|-----------------------------------------------|-------------------------------|-------------------|--------------------|-------------------|---------------|
| Koshihikari | A S | 5.9 ± 0.9 | 20.6 ± 3.1 | 6.7 ± 1.3 | 25.3 ± 5.8 | 3.1 ± 1.3 |
| | P | 0.9 ± 0.6 | 7.7 ± 1.5 | 8.8 ± 1.3 | 11.1 ± 2.9 | 1.1 ± 0.8 |
| | C | 0.2 ± 0.2 | 10.7 ± 1.7 | 8.8 ± 1.5 | 12.2 ± 1.9 | 1.3 ± 0.8 |
| | H S | 21.0 ± 3.0 | 13.4 ± 1.1 | 4.4 ± 1.2 | 30.6 ± 2.4 | 2.4 ± 0.8 |
| | P | 3.9 ± 1.7 | 24.5 ± 3.8 | 6.6 ± 1.4 | 14.6 ± 2.1 | 1.9 ± 1.2 |
| | C | 20.8 ± 4.5 | 18.0 ± 2.0 | 8.0 ± 1.4 | 19.4 ± 2.3 | 3.2 ± 2.2 |
| Takanari | A S | 28.9 ± 2.2 | 4.4 ± 0.8 | 0.3 ± 0.2 | 35.8 ± 3.4 | 3.8 ± 1.9 |
| | P | 7.6 ± 2.5 | 4.1 ± 0.9 | 0.3 ± 0.3 | 34.2 ± 3.7 | 2.8 ± 0.8 |
| | C | 9.8 ± 2.7 | 5.0 ± 1.2 | 1.3 ± 0.3 | 38.8 ± 4.8 | 2.4 ± 1.4 |
| | H S | 46.7 ± 3.0 | 4.6 ± 0.8 | 0.2 ± 0.1 | 37.3 ± 2.8 | 3.3 ± 1.4 |
| | P | 17.3 ± 2.3 | 4.7 ± 1.2 | 0.0 ± 0.0 | 38.2 ± 2.2 | 3.2 ± 2.6 |
| | C | 35.0 ± 4.7 | 5.1 ± 1.6 | 0.3 ± 0.2 | 32.4 ± 4.1 | 4.2 ± 2.2 |

**Result of ANOVA test (Factorial effects)**

| Cultivar | Treatments | mean |
|----------|-------------|------|
| Koshihikari | A | 8.9 | 15.9 | 7.1 | 19.1 | 2.2 |
| | H | 24.2 | 4.7 | 0.4 | 36.1 | 3.3 |
| Takanari | A | 9.0 | 8.8 | 4.2 | 26.6 | 2.4 |
| | H | 24.1 | 11.7 | 3.3 | 28.7 | 3.0 |

Temperature, Sink-source manipulation, Cultivar × Temperature, Cultivar × Sink-source manipulation, Temperature × Sink-source manipulation, Cultivar × Temperature × Sink-source manipulation

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1) A and H denote ambient and high temperature conditions during grain-filling period, respectively.
2) S, P and C denote treatments of shading, panicle clipping and control, respectively.
3) mean ± standard error.
4) *, ** and ns indicate significant difference at 5%, 1% levels and no significant difference, respectively.
5) different alphabet letters within a factor indicate significant difference at 5% level (Fisher’s LSD).
sink-source manipulation treatment.

Fig. 3 shows the amount of stem-NSC in plants. In the control and the shaded plants, stem-NSC rapidly decreased for 20 days after heading and thereafter re-accumulated except for shaded plants of Takanari. The rate of stem-NSC decrease after heading was higher under the high temperature condition than under the ambient temperature condition and this trend was clear in the shaded plants. In control plants, re-accumulation of NSC during the latter half of the grain-filling period was larger under high temperature conditions.

In superior spikelets, starch content of endosperm rapidly increased after heading (Fig. 4). The rate of starch accumulation was lower in inferior spikelets than in superior spikelets during the initial half of the grain-filling period. While high temperature treatment enhanced starch accumulation in endosperm in both superior and inferior spikelets, starch accumulation in inferior spikelets was more accelerated than in superior spikelets in both cultivars. Under the high temperature condition, starch accumulation in the endosperm leveled off earlier than in ambient temperature conditions in both superior and inferior spikelets in both cultivars.

Discussion
A significant difference was observed between the
cultivars in the percentage of each type of chalky kernel (Tables 1 and 2). The percentage of milky white and white belly kernels was higher in Takanari than in Koshihikari, whereas the percentage of basal white and white back kernels was higher in Koshihikari. This result suggests that the types of chalky kernels with a high frequency of occurrence are various among cultivars as suggested by Nagahata and Yamamoto (2005).

A high temperature significantly affected the percentage of milky white kernels and white back kernels ($P<0.01$), but not on basal white kernels and white belly kernels. Previously, a high temperature was reported to increase basal white kernels and white belly kernels (Nagato and Ebata, 1965; Tashiro and Ebata, 1975; Omoteno et al., 2003; Nagahata and Yamamoto, 2005), which is contrary to our results. The effects of high temperature on each type of chalky kernels were various in this study, possibly for the following reason.

Although each type of chalky kernel is induced by a high temperature at the specific stage of grain-filling, the temperature difference between the temperature treatments was not constant during the grain-filling period, since the temperature difference in the TGC used in this study largely depended on the intensity of solar radiation.

Significant effects of sink-source manipulation were not observed on the percentage of the basal white and white back kernels, which is in agreement with the previous studies (Morita et al., 2005b; Nakagawa et al., 2006). On the other hand, sink-source manipulation significantly affected the percentage of milky white and white belly kernels. Tashiro and Ebata (1975) reported that the percentage of white belly kernels is affected by the sink-source manipulation. In this study, sink-source manipulation affected the percentage of white belly kernels in Koshihikari but not in Takanari. Nakagawa et al. (2006) observed no effect of sink-source manipulation on the percentage of white belly kernels. The effect of assimilate supply on the occurrence of white belly kernels seems inconsistent depending on the cultivar or experiment. Tashiro and Ebata (1975) observed that white belly kernels were sharply increased by shading between 20 and 30 days after heading while those were rather decreased by shading between 0 and 10 days or between 10 and 20 days after heading. The occurrence of white belly kernels is assumed to be more associated with assimilate supply during the latter half of the grain-filling period than that in the initial half, which might result in the inconsistent effects of assimilate supply on the occurrence of white belly kernels with the cultivar or experiment. The effect of sink-source manipulation on the percentage of milky white kernels in both cultivars suggests a strong association between assimilate supply and the occurrence of milky white kernels, which agrees well with the previous studies (Inoue, 2003; Tsukimori, 2003; Kobata et al., 2004). The varietal difference in milky white kernels under field conditions was not expressed by temperature treatments during the grain-filling period, but that in white back and basal white kernels was well represented (Iida et al., 2002; Nagahata and Yamamoto, 2005). The association of assimilate supply with the occurrence of milky white kernels might cause difficulty in expressing varietal difference only by temperature treatment. Furthermore, the significant interaction ($P<0.01$) between temperature and sink-source manipulation indicates that the effect of sink-source status on the occurrence of milky white kernels depends on temperature conditions during the grain-filling period (Table 2). A significant interaction between temperature and sink-source manipulation was also observed on the occurrence of white back kernels. In this case, however, under a high temperature condition, the percentage of white
In both temperature regimes (Fig. 5). The higher percentage of milky white kernels in both cultivars was well explained by the rate of assimilate supply during the initial half of the grain-filling period. The higher percentage of milky white kernels was associated with an assimilate deficit during this period (Hoshikawa, 1968). The amount of assimilate available for grain growth in the initial half of the grain-filling period is considered to be the sum of concurrent photosynthetic products and stem-NSC stored prior to heading. Therefore rate of assimilate supply can be shown by \( \frac{dW}{dt}(20) + \frac{d\text{NSC}}{dt}(20) \)/n, where \( \frac{dW}{dt}(20) \) is plant growth rate on average for 20 days after heading, \( \frac{d\text{NSC}}{dt}(20) \) is rate of stem-NSC decrease and n is the number of spikelets of a plant. Close hyperbolic relations were observed between the rate of assimilate supply and the percentage of milky white kernels in both cultivars in both temperature regimes (Fig. 5). The higher percentage of milky white kernels in Takanari can be attributed to a lower rate of assimilate supply due to larger number of spikelets than in Koshihikari. Milky white kernels increased as the rate of assimilate supply decreased. Under the high temperature condition, the occurrence of milky white kernels was higher at a given rate of assimilate supply and was more affected by the rate of assimilate supply than under the ambient temperature condition. This suggests that assimilate demand to avoid the occurrence of milky white kernels is larger under a high temperature condition than under an ambient temperature.

Then, why does a high temperature during the grain-filling period increase assimilate demand? One reason may be the acceleration of grain growth by the high temperature. Under a high temperature condition, starch accumulation in grains was accelerated during the initial half of the grain-filling period especially in inferior spikelets and it leveled off earlier than under ambient temperature condition (Fig. 4). This result agreed with previous studies that under high temperature conditions the grain growth rate increased and its peak appeared earlier than those under optimum temperature, whereas the duration of grain growth was shortened (Sato and Inaba, 1976; Yoshida and Hara, 1977; Morita et al., 2005a). Inaba and Sato (1976) observed that enzyme activity of grain declined earlier at a high temperature than at an optimal temperature. The dry weight increase and development of spikelets delayed in inferior spikelets compared with those in superior spikelets, and those of inferior and superior spikelets were in parallel with the expression of genes related carbohydrates metabolism (Ishimaru et al., 2005). In this study, starch accumulation was accelerated in inferior spikelets during the initial half of the grain-filling period under a high temperature condition, which indicated an increase in assimilate demand in the whole panicle during this period. This increment of assimilate demand under a high temperature condition is assumed to be met by increased NSC translocation from the stem and leaf sheath, as shown by the higher rate of NSC decrease under a high temperature condition. However, the higher rate of NSC translocation under a high temperature condition resulted in earlier NSC depletion especially in the shading treatment, which might lead to insufficient assimilate supply for panicle demand.

We conclude that sink-source manipulation significantly affected the percentage of milky white and white belly kernels but not that of the basal white and white back kernels. Close hyperbolic relations between the rate of assimilate supply and the percentage of milky white kernels show that the occurrence of milky white kernels was well explained by the rate of assimilate supply during the initial half of the grain-filling period. The higher percentage of milky white kernels in the shading treatment was smaller than that in the panicle-clipping treatment or the control indicating that the occurrence of white back kernels does not reflect the amount of assimilate supply. These results suggest that the effects of assimilate supply on the occurrence of each type of chalky kernel are various and that assimilate supply is strongly associated with the occurrence of milky white kernels, partly associated with the occurrence of white belly kernels and is hardly associated with the occurrence of basal white and white back kernels. Although the opaque kernels seem to have occurred regardless of assimilate supply, many opaque kernels were observed among grains with a thickness of less than 1.7 mm (data not obtained), which were marked in the shaded plants. Further study is needed to clarify the effect of assimilate supply on the occurrence of opaque kernels.

Poor starch accumulation at the center of the endosperm in milky white kernels suggest that milky white kernels are associated with an assimilate deficit during the initial half of the grain-filling period since starch accumulates in the center of endosperm during this period (Hoshikawa, 1968). The amount of assimilate available for grain growth in the initial half of the grain-filling period is considered to be the sum of concurrent photosynthetic products and stem-NSC stored prior to heading. Therefore rate of assimilate supply can be shown by \( \frac{dW}{dt}(20) + \frac{d\text{NSC}}{dt}(20) \)/n, where \( \frac{dW}{dt}(20) \) is plant growth rate on average for 20 days after heading, \( \frac{d\text{NSC}}{dt}(20) \) is rate of stem-NSC decrease and n is the number of spikelets of a plant. Close hyperbolic relations were observed between the rate of assimilate supply and the percentage of milky white kernels in both cultivars in both temperature regimes (Fig. 5). The higher
kernels at a given rate of assimilate supply under a high temperature condition suggests that a high temperature during the grain-filling period increases the assimilate demand to avoid the occurrence of milky white kernels. The larger demand for assimilate under a high temperature is presumably due to the acceleration of starch accumulation in grains especially in inferior spikelets. The higher percentage of milky white kernels in Takanari is attributed to the lower rate of assimilate supply per spikelet than in Koshihikari.

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