



## Characterization of high-yielding rice cultivars with different grain-filling properties to clarify limiting factors for improving grain yield



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### ABSTRACT

Recently developed high-yielding rice varieties with extra-large sink capacity often have unstable grain filling. Therefore, understanding the factors that limit grain filling is essential for further improvement of rice grain yield. Because grain-filling is determined by the complex sink–source balance, grain-filling ability is very difficult to evaluate. In this study, we compared grain-filling-related traits of three high-yielding cultivars with high sink capacity. We found that the translocation of non-structural carbohydrates (NSC) from stem to panicle during early ripening and grain filling was significantly lower in Momiroman than in Hokuriku 193 and Teqing, whereas dry matter accumulation of the whole plant did not differ among the cultivars throughout ripening. The NSC-components, sucrose and starch were both remained higher in stems of Momiroman than other cultivars. ADP-glucose pyrophosphorylase (AGPase; EC 2.7.7.27) activity was not enhanced and  $\alpha$ -Amylase (EC 3.2.1.1) and  $\beta$ -Amylase (EC 3.2.1.2) activities were not impeded in the stems. These data suggested lower sucrose translocation is responsible for lower NSC translocation in Momiroman, rather than too high starch synthesis and too low starch degradation activities. At early ripening, grain growth of the superior spikelets was slow in Momiroman even if carbon supply was increased by spikelet-thinning treatments. These results raise the possibility that low sink strength determines low grain filling in Momiroman, which delays grain growth and decreases sucking force of NSC from the stem.

### 1. Introduction

Rice (*Oryza sativa* L.) is one of the world's most important crops, and its yield must be improved to feed the increasing global population. In Japan, the demand for high-yielding rice for animal feed has increased; to match it, many high-yielding cultivars have been developed. Although they commonly have extra-large sink capacity (total number of spikelets per unit area  $\times$  filled grain weight), the grain-filling ability of different cultivars varies considerably (Yoshinaga et al., 2013). Chinese high-yielding cultivars, called 'super rice', also have unstable grain filling (Yang and Zhang, 2010).

The poor grain filling of high-yielding rice often occurs in inferior spikelets, which are located on the secondary branches in the lower part of a panicle (Yang and Zhang, 2010; Yoshinaga et al., 2013). Some

studies showed that removing superior spikelets of large-panicle cultivars improves grain filling of the inferior ones, suggesting that grain filling of the inferior spikelets is restricted by the supply of assimilated carbon (Kato, 2004; Kobata et al., 2013; You et al., 2016). Other studies suggested that the low starch-synthesis rate of inferior spikelets, caused by low enzyme activity or hormone imbalances, leads to poor grain filling (Yang et al., 2006; Wang et al., 2015; Zhang et al., 2012). Whether the carbohydrate supply (source ability) or starch-synthesis rate (sink strength) restricts grain filling may depend on the cultivar, location and field conditions. To understand the grain-filling properties and factors that limit rice cultivars with high yield potential, it is essential to analyse them in the same environment for further improvement of rice grain yield.

Grain-filling ratio is determined by the complex sink–source

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balance. High sink capacity requires high source ability for stable grain filling. Because translocation of non-structural carbohydrates (NSC) from stem to panicle is indispensable for stable grain filling (Yoshida 1972; Okamura et al., 2013), source ability for grain-filling is affected not only by the ability of carbon assimilation in leaves, but also by that of carbon translocation from stems to panicles. Therefore, to evaluate differences in grain filling, we must understand the differences and relationships of many traits such as sink size, dry matter accumulation and stem-carbon metabolism.

Momiroman is a Japanese high-yielding cultivar that showed one of the highest sink capacities but low grain-filling ratio in Tsukubamirai, Ibaraki, in the Kanto region of Japan (Hirabayashi et al., 2010; Yoshinaga et al., 2013). Another Japanese high-yielding cultivar Hokuriku 193 (H193) showed the highest yield with a relatively high grain-filling ratio at the same location (Goto et al., 2009; Yoshinaga et al., 2013). We compared the grain-filling properties and stem-carbon metabolism of Momiroman and H193 in terms of the sink–source balance. We also tested a Chinese high-yielding *indica* cultivar, Teqing. Based on these analyses, we deduced the possible factors limiting grain filling of high-yielding cultivars, which could be a target trait for achieving high yield potential.

## 2. Materials and methods

### 2.1. Plant materials and growth conditions

The rice cultivar Momiroman, H193 and Teqing were planted in the Yawara experimental paddy field of the National Agriculture and Food Research Organization (NARO) at Tsukubamirai, Ibaraki, Japan (36°00'N, 140°02'E, altitude above sea level: 10 m) in 2014–2016. The climate condition was shown in Supplementary Fig. S1. Momiroman and H193 are Japanese *indica-japonica* hybrid high-yielding cultivars and their major genetic backgrounds are assumed to be *japonica* and *indica*, respectively (Yonemaru et al., 2014). Teqing is a Chinese high-yielding *indica* cultivar. Seedlings (20–24 days old) were transplanted on 15 May 2014, 21 May 2015 and 19 May 2016. The plants were grown at a density of 22.2 hills m<sup>-2</sup> (spacing of 15 cm × 30 cm), with one plant per hill. The plot size was 6.50 m<sup>2</sup> in 2014, 47.25 m<sup>2</sup> in 2015 and 10.80 m<sup>2</sup> in 2016. The plots were arranged in a randomized block design with three replicates, except for two replicates of Teqing in 2014. Controlled-release fertilizer (equal parts LP40, LPs100 and LP140; JCAM Agri, Tokyo, Japan) containing 16 g N m<sup>-2</sup> was applied as a basal nitrogen dressing. LP40, LPs100 and LP140 release 80% of their total nitrogen content within 40, 100 and 140 days, respectively, after application, at 25 °C. Inorganic fertilizers containing 15 g P<sub>2</sub>O<sub>5</sub> m<sup>-2</sup> and 15 g K<sub>2</sub>O m<sup>-2</sup> in 2014 and 2015 and 20 g P<sub>2</sub>O<sub>5</sub> m<sup>-2</sup> and 15 g K<sub>2</sub>O m<sup>-2</sup> in 2016 were applied as a basal phosphorus and potassium dressing.

### 2.2. Yield and yield components

At maturity, when approximately 85% of grains became yellow, 20 plants were harvested in 2014 and 40 in 2015 and 2016; plants were air-dried for more than 2 weeks. The panicles were counted and then threshed; paddy (whole grains with hull) were weighed. A 30–60 g aliquot of paddy was separated using a Sample Divider (Fujikinzoku, Tokyo, Japan) for spikelet counting. Grains were counted on an auto-counter. Half of the paddy were hulled and weighed to rough (whole) brown rice yield. Then the rough brown rice was sieved with a grain sorter with a sieve size of 1.6 mm and retained grains were weighed to calculate actual brown rice yield. A 20–40 g aliquot of retained grains was counted to calculate 1000-g weight, number of filled spikelets, and the moisture content was measured using a grain moisture tester (Riceter f, Kett, Tokyo, Japan). Rough paddy yield, rough brown rice yield, brown rice yield and 1000-grain weight were adjusted to 15% (w/w) moisture content. Sink capacity was estimated by multiplying

single grain yield by the number of spikelets per area, assuming all the spikelets were completely filled (Yoshinaga et al., 2013). Harvest index was calculated by dividing dry weight of sieved brown rice by shoot dry weight measured as described below.

### 2.3. Dry weight and non-structural carbohydrate content

At full heading, at about 20 days after heading (DAH) and at maturity, 10 plants per plot were harvested. The heading date and full-heading date were defined as the dates when about 50% and 80%, respectively, of panicles had emerged. The sampling dates for each cultivar and stage are shown in Supplementary Table S1. Two representative plants among 10 harvested plants with an average number of panicles were separated into panicles, leaf sheaths + culms (stems), and leaf blades. Those and the other 8 plants were dried on the same day at 80 °C for at least a week and the dry weights were determined. The total shoot weight per m<sup>2</sup> of the 10 plants was calculated. The weight of each part was calculated from that of the entire shoot multiplied by the ratio of the part in the 2 representative plants. These stems were powdered in a vibrating sample mill (TI-1001, CMT Co., Tokyo, Japan) for measurement of stem NSC content. The contents of starch, sucrose, glucose and fructose in the powdered samples were measured according to Okamura et al. (2016) with glucoamylase (Toyobo, Osaka, Japan), an F-kit #716260 (J.K. International, Tokyo, Japan) and a microplate reader (Sunrise, Tecan, Männedorf, Switzerland, or Epoch 2, BioTek, Winooski, VT, USA). The NSC content was calculated as the sum of the contents of these carbohydrates. The apparent NSC translocation ( $\Delta$ NSC) is estimated from the difference of NSC content between full heading and 20 DAH. Apparent translocation ratio of NSC (Ratio of  $\Delta$ NSC) was estimated by dividing  $\Delta$ NSC by NSC content at Full heading.

### 2.4. Heading and flower-opening days, and spikelet thinning

We classified spikelets into six groups by their position within a panicle as follows (see also Supplementary Fig. S2a). First, panicles were divided into upper and lower parts so that the number of primary branches was the same (the middle branch was placed in the upper part when the number of primary branches was odd). Thereafter, spikelets in each part were divided into (A) those on the primary branch, (B) those on the secondary branch except its tip and (C) those on tip of the secondary branch. On 9–13 August 2015, the panicles that had just started heading were labelled. Immediately after labelling or the next day, at least five opening spikelets of the upper A group of H193 and Teqing were marked with colour markers. Two days after labelling, those of Momiroman were marked. Four days after labelling, the opening spikelets of the lower B group in the labelled panicles of H193 and Teqing were marked. Six days after labelling, those of Momiroman were marked. In addition, spikelets in some panicles were thinned out (Supplementary Fig. S2b, c) by marking three upper A or lower B opening spikelets on the same primary branch of a labelled panicle and removing all other spikelets on the same primary branch (spikelets on the other primary branches remained intact). The numbers of harvested panicles and grains are shown in Supplementary Table S2.

### 2.5. Carbohydrate contents and AGPase and amylase activities in stems

On 31 July 2015 (11 days before anthesis) and at 0, 7, 14, 21 and 28 days after spikelet marking (days after anthesis, DAA), the third internodes from the uppermost internodes and the sheaths of the third leaves from the flag leaves, which had the highest NSC contents among elongating internodes in Momiroman and H193 (our unpublished observations), were harvested, immediately frozen in liquid N<sub>2</sub> and ground under cryogenic conditions in a ShakeMaster Auto (Bio Medical Science, Tokyo, Japan). Starch, sucrose, glucose and fructose contents of the ground samples were measured as described in 2.3. ADP-glucose

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