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## Genetic analysis of sugar-related traits in rice grain

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#### 1. Introduction

Biochemical, molecular, and genetic experiments have supported a central role of sugars in the control of plant metabolism, growth, and development and have revealed interactions that integrate light, stress, and hormone signaling (Rolland et al., 2002). As the major product of photosynthesis in higher plants, sucrose is transported from leaf to grain in rice (Cho et al., 2011). The formation, transport, and storage of sucrose are necessary to support normal development of rice (Lim et al., 2006). To maintain an optimal functioning photosynthetic system, the synthesis of sucrose and starch needs to be subtly regulated (Stitt, 2004). The products can be stored as starch granules in chloroplast or transported to where they are needed by sucrose transporter, or assimilated.

The purpose of starch biosynthesis in plants is to provide a store of energy. Many plants have evolved to store large quantities of starch. For example, near 90% of the dry weight consists of starch in rice grain (Tian et al., 2009). The detail of starch biosynthesis is, however, more complicated than this – involving a number of enzymes – but can be summarized as follows. The process starts with combining of glucose-1-phosphate with adenosine triphosphate (ATP) to form adenosine diphosphate glucose (ADP-glucose), catalyzed by the enzyme AGPase.

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#### ABSTRACT

Sugar is the primary product of photosynthesis in plant and plays a critical role in regulating plant growth and development. In this study, quantitative trait loci (QTLs) for total soluble sugar, sucrose, and fructose contents in rice grain were identified using a double haploid population derived from a cross between *japonica* CJ06 and *indica* TN1. A total of 17 QTLs, including four QTLs for total soluble sugar content, seven QTLs for sucrose content, and six QTLs for fructose content, were detected on chromosome 1, 3, 4, 5, 6, and 8, with the LOD ranges from 2.61 to 3.85. Furthermore, among the determined varieties, we found that the total soluble sugar content in *japonica* showed higher than that in *indica*. Comparative genetic analysis showed that starch synthesis related gene is presumably involved in sugar-related metabolic activity in rice grain.

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> The synthesis of amylose is catalyzed by a starch granule-bound form of starch synthase (GBSS). While amylopectin is synthesized by the coordinated actions of AGPase, starch synthase (SS), starch branching enzyme (SBE), and starch debranching enzyme (DBE) (Ohdan et al., 2005). Each enzyme plays a distinct role, but presumably functions as part of a network (Tian et al., 2009). Disproportionating enzyme (DPE) and phosphorylase (PHO) are generally considered to be involved in starch degradation, but some studies suggest that both DPE and PHO may play some parts in starch biosynthesis, although the precise mechanisms of their roles are unclear (Ball and Morell, 2003; Tetlow et al., 2004).

> In rice, the major storage tissues named as endosperm consist primarily of starch and a minor pool of soluble sugar which represents an alternative storage form for incoming photosynthate (Smyth and Prescott, 1989). Soluble sugar, especially the sucrose, is the primary product of photosynthesis in plant and plays a critical role for plant growth and development (Smeekens, 2000). Some rice endosperm mutations are known which increase soluble sugar content of cereal grain (Nakamura et al., 1997). The increasing soluble sugar in mutant usually results from a blockage in starch biosynthesis, and consequently, grain weight is reduced (Kubo et al., 2005). The content of soluble sugar in rice grain is minor; however, the pool of soluble sugar may affect the flavor and color reactions that take place during cooking or processing (Smyth and Henry, 1989).

> QTL analysis on sugar-related traits has been carried out on some plants, such as sugarcane, tomato, and sorghum (Ming et al., 2001; Jia et al., 2010; Shiringani et al., 2010), whereas similar study on rice

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grain is rarely reported. Ishimaru et al. (2007) reported QTLs for sucrose, hexose and starch accumulation in the milking stage. They reckoned that *sucrosephosphate synthase 1* (*SPS1*) may play an essential role in the conversion of starch to sucrose before heading (Ishimaru et al., 2007). Nevertheless, little has been reported on the genetic base of sugar-related traits in rice grain. Here, we demonstrated the inheritance of sugar-related traits in rice grain.

#### 2. Materials and methods

#### 2.1. Materials

A DH population comprising 120 DH lines, which was established in our laboratory, was used in this study. This population was developed by anther culture of an F1 hybrid between the typical *japonica* CJ06 and the typical *indica* TN1 (Sogawa et al., 2004). And 35 conventional rice varieties were used to evaluate the soluble sugar content in grain. All materials were planted at the experimental farm of China National Rice Research Institute (Hangzhou, China) in 2012. Each line was planted in four rows, with six plants in each row. After harvesting, the grains of each line with three replicates were sampled for evaluation of soluble sugar, sucrose and fructose.

#### 2.2. The evaluation of soluble sugar, sucrose and fructose

The polished grains were used to ground flour for the evaluation of sugar-related properties. The ground flour was oven-dried at 110 °C for 15 min, then stayed at 70 °C overnight. 50 mg flour was transferred into a centrifuge tube with 4 ml 80% ethanol solution. The tube was placed in 80 °C water bath with continuous stirring for 40 min. After centrifugating at 8000 g for 20 min, the supernatant was collected and decolorized by activated carbon. The extract was diluted with water to 10 ml for further assay.

The content of total soluble sugar was measured as described by Scott and Melvin (1953) with a slight modification. 3 ml 0.15% anthrone solution was added in a new tube carrying 0.5 ml extract, and then the tube stayed at 90 °C water bath for 15 min. The solution was used to determine the OD (optical density) value under the 620 nm wavelength. The total soluble sugar content was measured according to a standard curve, which was obtained by the concentration of a series of glucose solution against its corresponding OD value.

To evaluate the sucrose content, 0.1 ml extract was mixed with  $50 \,\mu$ l 2 N NaOH in a tube. At the boiling water bath for 5 min, and then added 0.7 ml 30% HCl, 0.2 ml 0.1% resorcinol. The tube with the above mixture was put in 80 °C water bath for 10 min to accomplish the chromogenic reaction. The solution was used to determine the OD (optical density) value under the 480 nm wavelength. The sucrose content was measured according to a standard curve, which was generated by the concentration of a series of sucrose solution against its corresponding OD value.

To evaluate the fructose content in rice grain, 0.1 ml extract was mixed with 0.2 ml 0.1% resorcinol and 0.7 ml water in a tube under 80 °C water bath for 10 min. The solution was used to determine the OD (optical density) value under the 480 nm wavelength. The fructose content was measured according to a standard curve, which was generated by the concentration of a series of fructose solution against its corresponding OD value.

### 2.3. Data and QTL analysis

Population distribution and correlation analysis were performed using the SAS8.0 statistical software. A linkage map containing a total of 178 SSR and STS markers, distributed evenly on 12 chromosomes of rice, was selected to construct a rice linkage map using Mapmaker/ EXP version 3.0 (Zeng et al., 2009). The map spanned approximately 1674.8 cM, with an average interval of 9.4 cM between markers. Interval QTL mapping was conducted using the software Mapmaker/QTL version

#### Table 1

The content of rice grain total soluble sugar, sucrose and fructose in the DH population and their parents.

Traits	Parents		DH population	
	CJ06	TN1	$\text{Mean} \pm \text{SD}$	Range
Total soluble sugar (%) Sucrose (%) Fructose (%)	$\begin{array}{c} 2.27 \pm 0.08 \\ 1.33 \pm 0.07 \\ 0.31 \pm 0.008 \end{array}$	$\begin{array}{c} 1.50 \pm 0.23 \\ 0.94 \pm 0.02 \\ 0.16 \pm 0.004 \end{array}$	$\begin{array}{c} 1.51  \pm  0.31 \\ 0.93  \pm  0.21 \\ 0.19  \pm  0.088 \end{array}$	1.04–2.54 0.66–1.55 0.05–0.44

1.1 to analyze the QTLs. A likelihood of odds (LOD) threshold of 2.5 was used to declare the presence of a putative QTL in a given genomic region. The contribution to the phenotypic variance and additive effect of each QTL for relative traits were also calculated. The QTL nomenclature followed was that of McCouch et al. (1997).



**Fig. 1.** The distribution of sugar-related traits in DH population. A. The total soluble sugar content in rice grain; B. THE sucrose in rice grain; C. The fructose content in rice grain.

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