The promoter activities of sucrose phosphate synthase genes in rice, OsSPS1 and OsSPS11, are controlled by light and circadian clock, but not by sucrose

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INTRODUCTION
Sucrose is the major photosynthetic product and plays a central role in plant metabolism. Many plant species utilize sucrose as the main sugar for translocation of carbohydrate from source leaves to sink tissues. Sucrose is also reported to be a signal molecule that regulates gene expression in plants (Chiou and Bush, 1998; Lunn and MacRae, 2003). SPS activity is regulated by allosteric effectors, glucose-6-phosphate (activator) and inorganic phosphate (inhibitor), and by environmental factors such as light and osmotic stress via the phosphorylation of several serine residues. In particular, light–dark modulation of SPS activity via reversible phosphorylation is well established in several plant species (see Winter and Huber, 2000, for review). In addition, the expression of SPS genes can be regulated by light and cold stress at the transcriptional level (Chávez-Bárcenas et al., 2000; Lutfiyya et al., 2007; Okamura et al., 2011).

Although sucrose plays a role in sugar sensing and its signaling pathway, little is known about the regulatory mechanisms of the expressions of plant sucrose-related genes. Our previous study on the expression of the sucrose phosphate synthase gene family in rice (OsSPSs) suggested the involvement of sucrose sensing and/or circadian rhythm in the transcriptional regulation of OsSPS. To examine whether the promoters of OsSPSs can be controlled by sugars and circadian clock, we produced transgenic rice plants harboring a promoter–luciferase construct for OsSPS1 or OsSPS11 and analyzed the changes in the promoter activities by monitoring bioluminescence from intact transgenic plants in real-time. Transgenic plants fed sucrose, glucose, or mannitol under continuous light conditions showed no changes in bioluminescence intensity; meanwhile, the addition of sucrose increased the concentration of sucrose in the plants, and the mRNA levels of OsSPS remained constant. These results suggest that these OsSPS promoters may not be regulated by sucrose levels in the tissues. Next, we investigated the changes in the promoter activities under 12-h light/12-h dark cycles and continuous light conditions. Under the light–dark cycle, both OsSPS1 and OsSPS11 promoter activities were low in the dark and increased rapidly after the beginning of the light period. When the transgenic rice plants were moved to the continuous light condition, both P<sub>OsSPS1</sub>-LUC and P<sub>OsSPS11</sub>-LUC reporter plants exhibited circadian bioluminescence rhythms; bioluminescence peaked during the subjective day with a 27-h period: in the early morning as for OsSPS1 promoter and midday for OsSPS11 promoter. These results indicate that these OsSPS promoters are controlled by both light illumination and circadian clock and that the regulatory mechanism of promoter activity differs between the two OsSPS genes.

Keywords: sucrose phosphate synthase, promoter–luciferase reporter, transcriptional regulation, circadian clock, sugar sensing, rice
Table 1 | Primer sequences used in this study.

| Primer | Nucleotide sequence (5'-3') | Purpose |
|--------|-----------------------------|---------|
| M13F   | GAAAAACGACGCGCAGGCG          | Amplification of the Gateway cassettes |
| M13R   | CAGAAAAACGACTGATG            |         |
| OsSPS1-F | GGCGAGGTTCGTGTTGCAGC        | Amplification of P<sub>OsSPS1</sub> |
| OsSPS1-R | GGCGAGGTTCGTGTTGCAGC        |         |
| LUC-F   | GGCGAGGATTTTTTACAAAGGAGGCTG | Amplification of LUC<sup>+</sup> |
| LUC-R   | GGCGAGGATTTTTTACAAAGGAGGCTG |         |
| Tnos-F  | GGCGAGTTTTCAGCTAAAGGTATG    | Amplification of T<sub>Tnos</sub> |
| Tnos-R  | GGCGAGTTTTCAGCTAAAGGTATG    |         |
| SP51-5' | TGGAGGATTTTTTACCAACGATTG    | RTPCR of OsSPS1 |
| SP51-3'R | ACCGAGGTTCGTGTTGCAGC        | RTPCR of OsSPS11 |
| SP51-5'QF | ACCGAGGTTCGTGTTGCAGC        | RTPCR of OsSPS11 |
| SP51-3'QR | ACCGAGGTTCGTGTTGCAGC        |         |

Materials and Methods

Growth Conditions of Rice Plants and Sampling

Surface-sterilized seeds (Oryza sativa L. cv. Nipponbare) were grown for 14 days in Milli-Q water (Millipore, Tokyo, Japan) under 18-h light/6-h dark cycles. The light intensity in the light period was 80 μmol m<sup>-2</sup> s<sup>-1</sup> emitted by halogen lamps. The temperature was maintained at 30°C in the light period and 25°C in the dark period. For RNA analysis and the measurement of sugar contents, detached aerial parts of plants were treated with each sugar, immediately frozen in liquid nitrogen, and stored at −80°C.

P<sub>OsSPS1</sub>:LUC and P<sub>OsSPS11</sub>:LUC Reporter Constructs

MultiSite Gateway cloning technology (Life Technologies, Tokyo, Japan) was employed to obtain promoter-reporter constructs containing either OsSPS1 (O01g0919400) or OsSPS11 (O11g12236100) promoters, modified firefly luciferase gene (LUC<sup>+</sup>) as a reporter gene, and nopaline synthase terminator (T<sub>OSG</sub>). PCR amplification of the elements required for the constructs was carried out with a high-fidelity DNA polymerase, PrimeSTAR GXL (Takara Bio, Shiga, Japan), according to the manufacturer’s instructions. The primers used to make the constructs are listed in Table 1.

A destination vector, pIG-R4R3, was constructed by introducing a Gateway cassette comprising attB1, cclf, chloramphenicol resistance gene (Cm<sup>+</sup>), and attR3 into the HindIII site of an ordinary binary vector, pGL212-Hm (AB449142). Entry clones harboring SPs promoters, the reporter, and the terminator were prepared as follows. The promoter regions of OsSPS2 and OsSPS11, P<sub>OsSPS1</sub> and P<sub>OsSPS11</sub>, respectively, were amplified from genomic DNA from a japonica rice cultivar, Nipponbare, as a template. P<sub>OsSPS1</sub> and P<sub>OsSPS11</sub> covered the genome regions from 6 to +6 and −2.830 to +6 nucleotides from the translation start point, respectively. These two promoter DNAs were cloned into
Onekura et al. Regulation of 3% (w/v) sucrose, 1% (w/v) glucose, 0.03% (w/v) casamino acids, (AF485783; Jefferson et al., 1987) and cloned into the pDONR line synthase terminator was amplified from binary vector pBI121 and cloned into the pDONR221 vector (Life Technologies). Nopa-designated either pSPS1 or pSPS11 vector, in which the initial two destination vector using LR Clonase II Plus (Life Technologies) and P2R-P3 vector (Invitrogen).

Finally, these entry clones were assembled into the pGL-R4R3 designation vector using LR Clonase II Plus (Life Technologies) and designated either pSPS1 or pSPS11 vector, in which the initial two amino acid residues of SPs were fused in frame with luciferase.

GENERATION OF TRANSGENIC RICE PLANTS

Five-week-old calli derived from a mature rice seed (cv. Nipponbare) were co-cultivated with Agrobacterium tumefaciens strain EHA105 harboring either pSPS1 or pSPS11 plasmid for 3 days in N6 (Chu et al., 1997) co-cultivation medium supplemented with 3% (w/v) sucrose, 1% (w/v) glucose, 0.03% (w/v) casamino acids, 2 mg L−1 2,4-dichlorophenoxyacetic acid (2,4-D), 10 mg L−1 acetylsyringone, and 0.4% (w/v) gelrite at 28°C in the dark. The calli were then transferred to N6 selection medium supplemented with 3% (w/v) sucrose, 1% (w/v) glucose, 0.03% (w/v) casamino acids, 2 mg L−1 2,4-D, 0.4% (w/v) gelrite, 500 mg L−1 carbenicillin, and 25 mg L−1 hygromycin B as selective antibiotics for 4 weeks (subcultured every 2 weeks) at 30°C under dark conditions. The resistant calli were transferred to MS (Murashige and Skoog, 1962) regeneration medium supplemented with 3% (w/v) sucrose, 3% (w/v) sorbitol, 2% (w/v) casamino acids, 2 mg L−1 kinetin, 2 μg L−1 naphthaleneacetic acid, 0.4% (w/v) gelrite, and 25 mg L−1 hygromycin B for 4 weeks (subcultured every 2 weeks) to regenerate the aerial parts of rice and then transferred to MS regeneration hormone-free medium for 2 weeks to regenerate the roots at 30°C under continuous light conditions. Regenerated plants (T0 plants) were transplanted into sterilized soil and grown in a greenhouse at 30°C under 12-h light/12-h dark cycles. Self-pollinated heterozygous progenies (T1 seeds and T2 plants) were used for the experiment. Several independent lines were described by Okamura et al. (2011). Self-pollinated heterozygous progenies (T1 seeds and T2 plants) were used for the experiment. Several independent lines were described by Okamura et al. (2011).

MEASUREMENT OF BIOLUMINESCENCE OF P

OsSPS1

reporter plants after 12-h light/12-h dark cycles. The bioluminescence data was represented as circadian time (CT) calculated by dividing the peak-phase value by the period length and multiplying by 24.

REAL-TIME QUANTITATIVE RT-PCR

Total RNA was extracted from sugar-treated wild-type (non-transgenic) plants as described by Okamura et al. (2011). Real-time quantitative RT-PCR analysis was performed using sets of gene-specific primers for OsSPS1 or OsSPS11 (Table 1; Okamura et al., 2011). Real-time quantitative RT-PCR using the One Step SYBR PrimeScript PLUS RT-PCR Kit (Takara Bio, Shiga, Japan) and SMART Cycler II System (Cepheid Inc., CA, USA) according to the manufacturers’ instructions. The results were normalized according to the transcript levels of a rice polyubiquitin gene, RUBIQ (Wang et al., 2000).

DETERMINATION OF SOLUBLE SUGAR CONTENT

Soluble sugars were extracted from sugar-treated non-transgenic plants with 80% (v/v) ethanol and determined enzymatically as described by Okamura et al. (2011).

RESULTS

EFFECTS OF SUGARS ON THE PROMOTER ACTIVITIES OF OsSPS1 AND OsSPS11

Several independent lines of transgenic rice plants carrying a promoter-luciferase reporter for OsSPS1 or OsSPS11 (P

OsSPS1

::LUC or P

OsSPS11

::LUC) were established. When D-luciferin was added to the medium, all reporter plants used exhibited bioluminescence and we found no significant differences among lines (data not shown). Therefore, both reporter sequences, P

OsSPS1

and P

OsSPS11

, were functional in the rice cells.

To examine whether the promoter activities of OsSPS1 and OsSPS11 are regulated by sugars, we measured the bioluminescence of the P

OsSPS1

::LUC and P

OsSPS11

::LUC reporter plants after exogenously supplying 3% (w/v) sucrose, 5% (w/v) glucose, or 5% (w/v) mannitol. In both of the reporter plants, bioluminescence levels did not fluctuate significantly during the 48-h continuous light, even without the sugar treatments (0%). We did not observe significant changes in bioluminescence with any treatment (Figures 1A,B).

To confirm if exogenous sugars added to the medium were successfully taken up into the plant cells, we examined concentrations of sucrose, glucose, and fructose in the plants after the
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FIGURE 1 | Promoter activities of OsSPS1 and OsSPS11 with the addition of sugars in continuous light. Fifteen-day-old plants were exposed to sugars added to the medium 24 h after the onset of illumination. (A) Bioluminescence of $P_{OsSPS1}::LUC$ reporter plants without resetting the circadian clock. Data points indicate the mean ± SD of four independent plants in each line. We obtained essentially the same results from three independent experiments. (B) Bioluminescence of $P_{OsSPS1}::LUC$ reporter plants. Data points indicate the mean ± SD of five independent plants in each line. We obtained essentially the same results from three independent experiments. (C) Endogenous sugar contents of wild-type (non-transgenic) plants after an exogenous supply of 5% sucrose, 5% glucose, 5% mannitol, or no sugar (0%, water). The y-axis represents sugar contents (nmol) per fresh weights of the plants (mg). Error bars indicate the SD of three independent plants. We obtained essentially the same results from three independent experiments. (D) mRNA levels of OsSPS1 in non-transgenic plants after an exogenous supply of 5% sucrose, 5% glucose, 5% mannitol, or no sugar (0%, water). Values were normalized to the expression level of a rice polyubiquitin gene ($RUBQ1$). Note that the data at time 0 indicate the relative expression levels before the supply of sugars. Error bars indicate the standard errors of three independent plants. We obtained essentially the same results from three independent experiments.

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addition of sugars (Figure 1C). When 5% sucrose was added to the medium, the amount of sucrose within the tissues increased 2.5-fold for 24 h whereas glucose and fructose levels remained unchanged. The addition of 5% glucose increased the amount of glucose twofold after 12 h of treatment. The amount of sucrose also increased twofold compared to the control after 6 h of treatment, but fructose levels remained unchanged. No changes in the amounts of these sugars were observed with the addition of 5% mannitol.

We also examined the mRNA levels of OsSPS1 and OsSPS11 during the sugar treatments and found no significant differences between OsSPS1 mRNA levels at any time point (Figure 1D). The result was consistent with those from P_{OsSPS11}::LUC reporter plants. In contrast, we did not detect any significant amounts of OsSPS11 mRNA under these experimental conditions, suggesting low levels of OsSPS11 mRNA.

These results indicated that sucrose and glucose did not affect the promoter activities of OsSPS1 or OsSPS11 even though exogenous sugars in the medium were taken up into the cells.

**DIURNAL CHANGES IN THE PROMOTER ACTIVITIES OF OsSPS1 AND OsSPS11**

Previously, we found that OsSPS1 and OsSPS11 mRNA levels changed within a day-night cycle (Okamura et al., 2011). We measured the diurnal changes of the promoter activities of OsSPS1 and OsSPS11 according to bioluminescence from the reporter plants under 12-h light/12-h dark cycles (Figure 2). The promoter activities of both OsSPS1 and OsSPS11 were low during the dark period and increased rapidly after the onset of the light period. While the promoter activity of OsSPS1 decreased gradually during the day and remained low throughout the night (Figure 2A), the OsSPS11 promoter remained active throughout the day and became inactive immediately after the onset of the dark period (Figure 2B).

These results indicated that the promoter activities of both OsSPSs were controlled by light but not in the same manner.

**REGULATION OF THE PROMOTER ACTIVITIES OF OsSPS1 AND OsSPS11 BY CIRCADIAN CLOCK**

Circadian rhythms are endogenous daily fluctuations in physiological activities sustained under constant conditions with a periodicity of nearly 1 day. As shown in Figure 1, neither P_{OsSPS1}::LUC nor P_{OsSPS11}::LUC reporter plants exhibited a significant fluctuation in bioluminescence under continuous light conditions. However, the sugar-feeding experiments were conducted without a pretreatment to synchronize the circadian clock of measured plants, which is a general procedure for measuring circadian rhythms. In fact, when the reporter plants were exposed to three 12-h light/12-h dark cycles prior to the transfer to continuous light conditions, a clear circadian rhythm in bioluminescence was observed in both P_{OsSPS1}::LUC and P_{OsSPS11}::LUC reporter plants (Figure 3). The period lengths, peak phases, and amplitudes of rhythms are shown in Table 2. Both reporters exhibited circadian bioluminescence rhythms for at least 3 days with period lengths of approximately 27 h. However, these two reporters exhibited different rhythm profiles with respect to their peak phases and amplitudes. The rhythmicity of the P_{OsSPS1}::LUC reporter plants peaked in the early morning (around CT1), whereas those of P_{OsSPS11}::LUC reporter plants peaked in midday (around CT9). The rhythms of the P_{OsSPS11}::LUC reporter plants were weak; their amplitudes were quarter those of P_{OsSPS1}::LUC reporter plants (0.13 and 0.10 for P_{OsSPS1}::LUC reporter and 0.03 and 0.02 for P_{OsSPS11}::LUC reporter). These results indicated that the promoter
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Table 2 | Bioluminescence rhythms of P_{OsSPS1}::LUC (A) and P_{OsSPS11}::LUC (B) reporter plants in continuous light. Fourteen-day-old plants were exposed to three 12-h light/12-h dark cycles to reset the circadian clock and transferred to continuous light conditions at 30°C for bioluminescence measurement. Data points indicate the mean ± SD of data obtained in the experiments. The results are summarized in Table 2. We obtained essentially the same results from three independent experiments.

| Reporter line | Period length (h) | Phase (CT) | Amplitude |
|---------------|-------------------|------------|-----------|
| P_{OsSPS1}::LUC-8 | 270 ± 0.2 | 16 ± 0.4 | 0.13 ± 0.02 |
| P_{OsSPS1}::LUC-10 | 25.9 ± 0.5 | 0.9 ± 1.0 | 0.10 ± 0.03 |
| P_{OsSPS1}::LUC-10 | 274 ± 0.8 | 9.3 ± 2.4 | 0.03 ± 0.02 |
| P_{OsSPS11}::LUC-18 | 277 ± 0.5 | 8.5 ± 1.5 | 0.02 ± 0.01 |

Values are expressed as the mean ± SD of data obtained in the experiments described in Figure 3.

activities of both OsSPSs were controlled by the circadian clock but their regulations by the clock were distinct.

DISCUSSION

Since sucrose is a signaling molecule as well as the major photosensitizer in plants, the transcriptional regulation of genes related to the synthesis, transport, and metabolism of sucrose may play roles in sugar sensing and its signaling pathway. However, little is known about the regulatory mechanisms of the expressions of plant sucrose-related genes except for a gene for a proton–sucrose symporter in sugar beet (Vaughn et al., 2002; Ransom-Hodgkins et al., 2003). In the present study, we examined whether genes for SPS can be transcriptionally regulated by sugars in rice plants using promoter–reporter assays for OsSPS and OsSPS11. However, neither sucrose nor glucose influenced the activities of the OsSPS1 and OsSPS11 promoters (Figures 1A, B). In addition, the sugar treatments did not alter OsSPS1 mRNA levels in rice plants (Figure 1D). These results suggest that the expressions of OsSPS1 and OsSPS11 are not regulated by sugar levels in rice plants. There is a possibility that the exogenously supplied sucrose is hydrolyzed by invertases in the apoplast and then taken up into cells in the form of glucose and fructose. If so, it would not be surprising that the effect of sucrose on gene expression looks similar to that of glucose.

It should be noted that feeding sucrose to rice plants induced an increase of sucrose level within the tissues whereas glucose and fructose levels remained unchanged (Figure 1C). It is also surprising that glucose feeding induced the accumulation of sucrose as well as glucose. Sucrose feeding in Arabidopsis thaliana results in the accumulation of glucose and fructose as well as sucrose (Mita et al., 1997; Sokolov et al., 1998); moreover, sucrose does not accumulate as a result of glucose feeding (Yonekura, Aoki, Hirose, and Onai, unpublished). These differential outcomes of sugar feeding between rice and Arabidopsis suggest that caution should be taken when assuming that these plants have the same regulation of sugar metabolism through sugar sensing and signaling.

We also investigated the involvement of light and circadian rhythms in the transcriptional regulation of the two OsSPSs. When bioluminescence from OsSPS1- and OsSPS11-transgenic plants was measured under a light–dark cycle, OsSPS1 and OsSPS11 promoter activities were low in the dark and increased rapidly after the beginning of the light period (Figure 2). These results indicate that light is an important cue for the expressions of the two OsSPSs at the transcriptional level as well as the post-translational regulation mechanism of SPS protein, which is well-established in several plant species (Winter and Huber, 2000). OsSPS1 is reported to possess a light-responsive element in its promoter region and...
that its expression is positively regulated by light (Argüello-Astorga and Herrera-Estrella, 1996; Chávez-Bárcenas et al., 2000). In the OsSPS1 promoter sequence, as well as OsSPS1, we found putative light-responsive cis-acting regulatory elements such as GATA-box and I-box core sequences, which were previously identified in light-regulated genes (Higo et al., 1999; Prestridge, 1991; Tera- ghi andCashmore, 1995). The existence of these cis-elements corroborates the present experimental data. However, another interpretation could be given for the diurnal pattern of promoter activities: light illumination may influence indirectly to the pro- moter activities of OsSPS1 and OsSPS11. It is generally known in plants that many metabolites fluctuate in response to light-dark transition. The OsSPS promoters could be regulated by metabolic changes. Even though sugar levels in tissues did not affect the activities of the two OsSPS promoters (Figure 1), the sugar lev- els measured with whole-tissue extracts may not reflect the levels within cells where the OsSPSs are able to be active.

The diurnal changes in the promoter activities of OsSPS1 and OsSPS11 (Figure 2) are inconsistent with our previous data on the day-night accumulation patterns of their mRNAs (Okamura et al., 2013; see Introduction). We can attribute this inconsistency in OsSPS expression to post-transcriptional regulation, which influences the stability of mRNAs. For example, in CIRCADIAN CLOVER ASSOCIATED1 (CCA1), one of the clock genes in Ara- bidopsis, the mRNA levels in the P_{CAM V}:CCA1 plants are constantly high in the dark; meanwhile, in the light, they rapidly decline to about 40% of the dark level. The rapid decrease in CCA1 transcript level is attributable to the light-modulated stability of the mRNA (Yakir et al., 2007). Likewise, the two OsSPS mRNAs might be unstable and degraded immediately in the light, although the transcription of the gene is activated by light. Therefore, it can be speculated that a decrease in the pool size of the transcripts during the daytime enables the sucrose biosynthesis system to respond quickly to rapidly changing environments, including light condition, by the de novo transcription of the gene and/or post-translational regulation of the enzyme. In this study, we only used the 5′-untranslated region (UTR). Since Newman et al. (1993) reported that 3′-UTR sequences contribute to mRNA stability like downstream elements, the lack of a 3′-UTR might account for the differences between the diurnal changes in promoter activity and RNA accumulation.

In the sugar-feeding experiments (Figure 1), both P_{OsSPS1}:LUC and P_{OsSPS11}:LUC reporter plants did not exhibit circadian rhythms in bioluminescence even under constant condition. However, clear circadian rhythms became detectable when bio- luminescence was monitored under constant condition after the reporter plants were exposed to three 12-h light/12-h dark cycles (Figure 3). Apparently, the circadian rhythms of promoter activ- ities were masked in the sugar-feeding experiments, probably because the rhythms of four individual plants used were not fully synchronized without the pretreatment before measurements. Although the reason why no circadian rhythms could be detectable without pretreatment still remains unclear, the different results between the two experiments indicate that the pretreatment for synchronization is important to assess the existence of circadian rhythm.

By monitoring bioluminescence in real-time, we found that the decay pattern of promoter activity during the dark period differed between OsSPS1 and OsSPS11 (Figure 2). We also dis- covered that both OsSPS1 and OsSPS11 promoters are controlled by the circadian clock at least under constant light condition, but their phases and amplitudes were distinct (Figure 3). These results clearly show that OsSPS1 and OsSPS11 are regulated differently at the transcriptional level, implying multiplicity in the transcrip- tional control mechanisms of the five OsSPSs. Further studies at the both transcriptional and post-transcriptional levels are ne- cessary to fully elucidate the complex regulatory mechanisms of the expressions of OsSPSs and characterize the roles of the five OsSPSs in sucrose metabolism and assimilate partitioning in rice plants.

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