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ARTICLE

Rice ASR1 regulates sugar levels and participates in sugar signaling in roots

Joungsu Joo · Sang Ik Song

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Abstract The *ASR* gene is found in various plant species. Although *ASR* is also expressed in sink tissues, most functional studies on this gene have been performed in source leaves. Here, we report that OsASR1 is involved in the abscisic acid (ABA) response via regulation of sugar levels in the roots. Overexpression of *OsASR1* altered root sugar content by increasing fructose levels and decreasing sucrose levels. Moreover, the transcript levels of sugar transporters and sucrose metabolism-related genes were altered in the roots of OsASR1-OX lines. Upon ABA treatment, an additional increase in the glucose and fructose levels was observed in the roots of OsASR1-OX lines compared with ABA-treated NT controls and untreated OsASR1-OX lines. Compared with NT control, the root growth of OsASR1-OX lines was more strongly inhibited by 10 % glucose. Our results suggest that OsASR1 plays an important role in the ABA response and sugar signaling in the roots.

Keywords ABA · ASR1 · Rice · Root · Sugar

Introduction

Abiotic stresses are key factors that determine crop yield. In particular, drought stress can significantly affect crop production and leads to an average yield loss of 50 % for most major crop plants (Boyer 1982). Until recently, most studies exploring drought stress have been focused on the source leaves rather than on the sink roots. The root system is increasingly being considered as an important target for enhanced drought tolerance. Rice is a notoriously drought sensitive crop due to its small root system, rapid stomatal closure, and reduced cuticular wax during mild water stress (Hirasawa 1999). The drought response of rice is different from that of other crops because rice is adapted to water-saturated soils. Accumulation of osmolytes and alteration of carbohydrate metabolism are physiological and biochemical responses to drought stress (Tabaeizadeh 1998). Sugar signaling and responses to biotic and abiotic stresses are tightly linked in plants (Wingler and Roitsch 2008). A number of genes are upregulated under drought, cold or high salinity stress (Seki et al. 2002). Many of these genes encode enzymes involved in carbohydrate metabolism. These findings indicate that the enzymes involved in sugar metabolism are critical in stress tolerance (Gupta and Kaur 2005). Therefore, it is important to identify the molecular players that may directly or indirectly control sugar levels in plants.

Abscisic acid (ABA) is a key regulator of the abiotic stress response, and numerous genes are regulated by ABA during this response. One of these, the *ASR* (abscisic acid-, stress- and ripening-induced) gene, was first described in tomato (Iusem et al. 1993). Various plant species encode ASR proteins, and the involvement of *ASR* genes in various abiotic and biotic stresses has been previously described in many of these species (Kalifa et al. 2004; Liu et al. 2010; Dai et al. 2011; Hsu et al. 2011; Arenhart et al. 2013; Hu et al. 2013). Moreover, several *ASR* genes are transcriptionally regulated by ABA and sugars (Cakir et al. 2003; Kalifa et al. 2004; Liu et al. 2010; Virlouvet et al. 2011).

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J. Joo · S. I. Song (✉)
Division of Bioscience and Bioinformatics, Myongji University, Yongin 449-728, Korea
e-mail: sisong@mju.ac.kr

Although ASR is involved in sugar, hormone, and stress responses, the physiological role of *ASR* genes is unclear.

Previously, we reported that the overexpression of rice *OsASR1* enhanced abiotic stress tolerance (Joo et al. 2013a, b). Moreover, *OsASR1* is differentially regulated by sugar and hormones in the source leaves and in the sink roots. In this study, we investigated the physiological role of the *OsASR1* gene in the roots. Our results suggest that OsASR1 plays an important role in root carbohydrate metabolism and glucose response.

Materials and methods

Plant materials and growth conditions

Transgenic and non-transgenic (NT) rice plants (*Oryza sativa* subsp. *japonica* cv. Nakdong) were used. The sterilized seeds were germinated in one-half-strength Murashige and Skoog (MS) solid medium in a growth chamber. After 3 days at 28 °C in darkness, the germinated seedlings were incubated under 16 h light/8 h dark cycles for 2 days at the same temperature. Finally, the seedlings were transplanted into soil pots and grown in the greenhouse until further use. For ABA or gibberellin treatment, 3-week-old plants grown on soil were hydroponically adapted in water (H_2O) for 3 days and subsequently transferred to a solution containing 100 μM ABA or 100 μM gibberellin in growth chambers (16 h light/8 h dark cycles) for 4 h (Joo et al. 2014).

Quantitative real-time PCR analysis

Total RNA was isolated from rice tissue samples using TRI REAGENT® (Molecular Research Center) according to the manufacturer's instructions. cDNA synthesis was performed using the RevertAid™ First Strand cDNA Synthesis Kit (Fermentas) according to the manufacturer's instructions. The 2X Real-Time PCR Pre-Mix with Evagreen (SolGent) was used. Thermocycling and fluorescence detection were performed using an Mx3000p Real-Time PCR Machine (Stratagene). Quantitative real-time PCR (qRT-PCR) reactions were performed in triplicate, and each experiment was repeated three times (Joo et al. 2013a, b). *Ubi* was used as a control to normalize the expression data. The primers used for qRT-PCR analyses are listed in Table S1.

Determination of soluble sugars

The soluble sugar concentrations of rice leaves and roots were assayed according to the enzymatic method (Stitt et al. 1989). Samples were harvested at the indicated times. Sucrose, glucose and fructose levels were then measured in the soluble fractions of water extracts. Briefly, rice samples (0.1 g) were ground in liquid nitrogen to a fine powder. Soluble sugars were extracted with boiling water for 10 min and subsequently separated by centrifugation (20,000 *g* for 5 min). The aqueous phase was used to determine soluble sugar content spectrophotometrically (Jelitto et al. 1992).

Results

Functional analysis of *OsASR1* in sink tissues

Although many *ASR* genes have been reported to be involved in sugar and various abiotic responses, the exact molecular mechanism of ASR function remains unclear. Previously, we showed that *OsASR1* transcripts were significantly upregulated in both the leaves and roots after drought treatment (Joo et al. 2013b). Transgenic plants overexpressing *OsASR1* (OsASR1-OX, Fig. 1a) exhibited an increase in drought tolerance (Joo et al. 2013a, b). However, the *OsASR1* gene showed a different response to hormones and sugar in the leaves and roots (Joo et al. 2013b). To investigate whether *OsASR1* plays a role in sugar response and metabolism in sink tissues, the glucose, fructose, and sucrose levels were measured in the roots of three independent T_5 OsASR1-OX plants and NT controls (Fig. 1b). The glucose level, which was relatively lower than the fructose level, was similar in the roots of OsASR1-OX plants and NT controls. The fructose level was increased approximately 1.3- to 1.8-fold, whereas the sucrose level was significantly decreased compared with that of the NT controls. The sucrose level in OsASR1-OX plants was approximately 0.6- to 0.5-fold lower than that in the NT controls. These results indicate that the overexpression of *OsASR1* alters the sugar content in the root tissues.

It is well known that transcript levels of *ASR* genes are regulated by ABA in many plants. Moreover, the *OsASR1* gene showed tissue-dependent ABA and gibberellin sensitivity (Joo et al. 2013a, b). We next investigated the effect of ABA and gibberellin on sugar content in the leaves and roots of OsASR1-OX plants (Fig. 2). To determine whether ABA and gibberellins have an effect on sugar content, 4-week-old NT and OsASR1-OX transgenic seedlings were treated with 100 μM ABA or 100 μM gibberellin for 4 h. The sampling time was 14:00. Under normal conditions, the sugar levels in the leaves of the OsASR1-OX plants were similar to those in the NT controls (Fig. 2a). The application of exogenous ABA caused increases in glucose and fructose levels and a decrease in the sucrose level in the leaves of the OsASR1-OX plants and NT controls. Unexpectedly, exogenous ABA and gibberellin

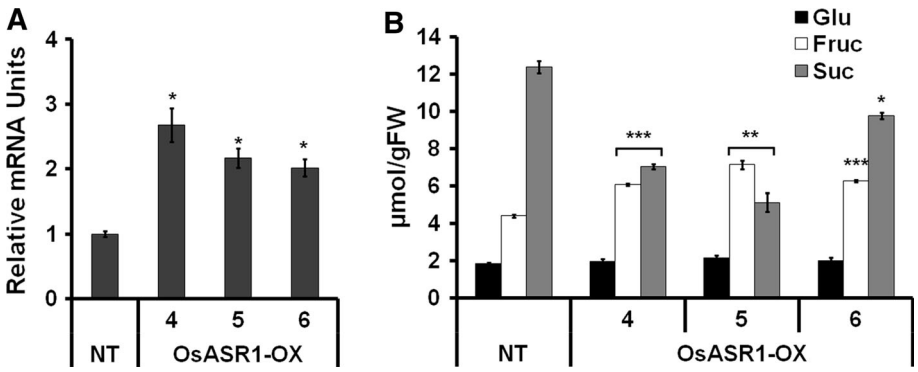

Fig. 1 Analysis of *OsASR1* transcript levels in the roots of OsASR1-OX plants (**a**). Soluble sugar content in the roots of OsASR1-OX plants (**b**)

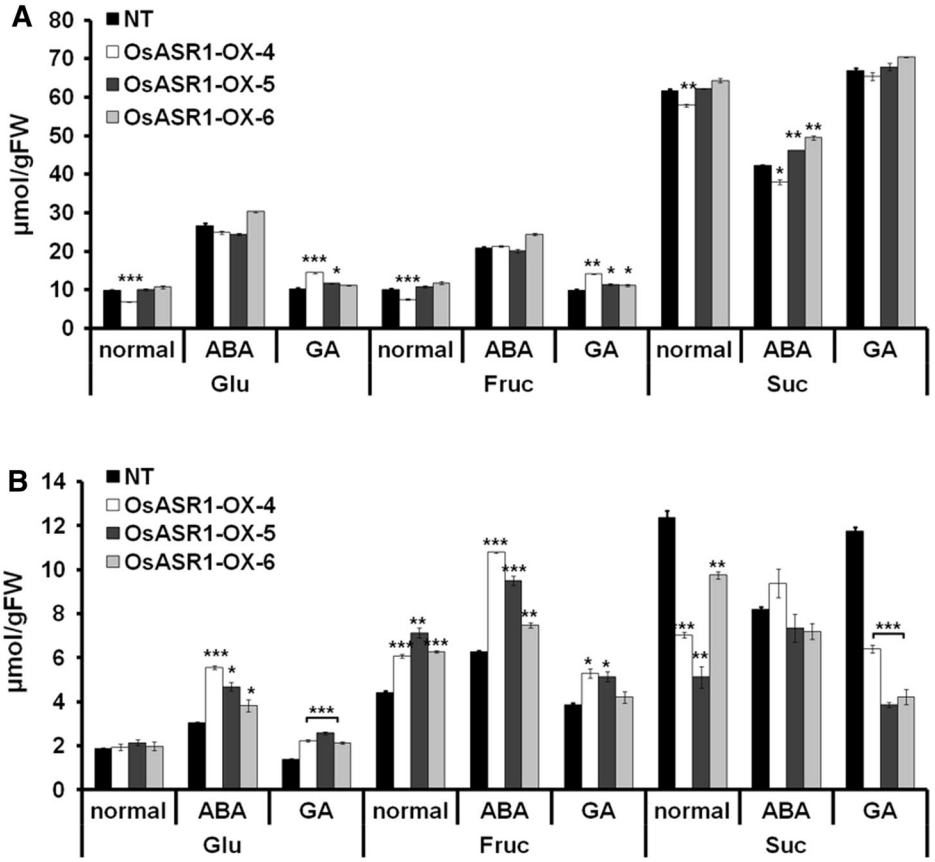

Fig. 2 The effects of ABA and gibberellin on soluble sugar content in the leaves and roots of OsASR1-OX plants. Changes in the soluble sugar content in the source leaves (**a**) and the sink roots (**b**) were determined under normal conditions and in the presence of ABA or gibberellin (GA). *Asterisks* indicate statistically significant differences based on the Student's *t* test (*$p < 0.05$; **$p < 0.005$; ***$p < 0.001$)

did not alter sugar levels in the leaves of the OsASR1-OX plants compared with the NT controls.

In the roots, exogenous gibberellin did not significantly alter the sugar levels in NT controls (Fig. 2b). Similar to the results obtained in the leaves, exogenous ABA increased glucose and fructose levels and decreased sucrose levels in the roots of NT controls. An additional increase in glucose and fructose levels was caused by ABA treatment in the roots of OsASR1-OX plants compared with ABA-treated NT controls and untreated OsASR1-OX plants. Treatment with exogenous ABA led to a decrease in sucrose levels in the roots of NT controls, whereas the sucrose concentration in treated OsASR1-OX plants was slightly increased compared with that in the untreated OsASR1-OX plants. Exogenous ABA upregulated *OsASR1* transcription markedly in the leaves and only slightly in the roots (Joo et al. 2013a, b); however, sugar levels of OsASR1-OX plants were significantly altered by ABA treatment only in the roots. These results suggest that ABA is required for the maximal effect of OsASR1 in the roots. OsASR1 may play a role in the ABA response through regulation of sugar levels in the roots.

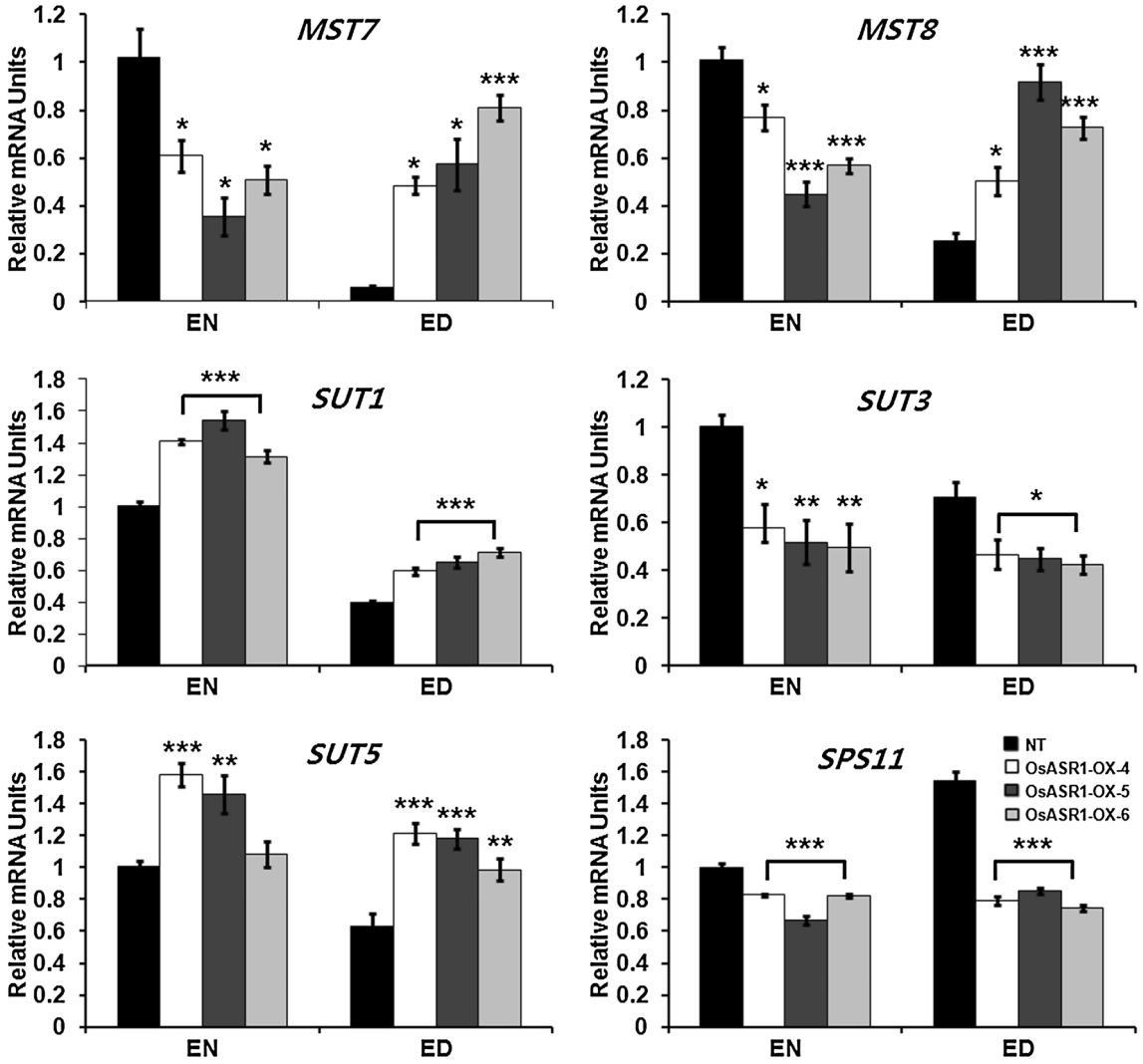

Fig. 3 Analysis of the transcript levels of genes related to sugar metabolism and partitioning in the roots. The transcript levels of genes related to sugar metabolism and partitioning were analyzed by qRT-PCR using the primers listed in Supplementary Table 1. All samples were harvested at 05:00 (EN, end of night) and 20:00 (ED, end of day). Total RNA was extracted from roots of 14-day-old OsASR1-OX lines and NT control plants. The GenBank accession numbers of sequences are MST7 (Os01g0567600), MST8 (Os01g0567500), SUT1 (Os03g0170900), SUT3 (Os10g0404500), SUT5 (Os02g0576600), SPS11 (Os11g0236100). *OsUbi1* was used as a reference gene, and the ratios were normalized against the control. The data presented are the mean ± SE ($n = 3$) of two independent experiments. *Asterisks* indicate statistically significant differences based on the Student's *t* test (*$p < 0.05$; **$p < 0.005$; ***$p < 0.001$)

OsASR1 alters expression of sugar metabolism and transport-related genes

OsASR1-OX plants exhibited changes in their root sugar content. To further understand the effects of OsASR1, the transcript levels of genes related to sugar metabolism and allocation were analyzed. Specifically, we analyzed the transcript levels of sucrose transporters (SUT), monosaccharide transporters (MST), sucrose phosphate synthases (SPS), sucrose synthases (RSus), and cell wall invertase (CIN). The transcript levels of these genes were measured by qRT-PCR in mature roots harvested at the end of the night (EN) and the end of the day (ED) (Fig. 3, Fig. S1).

Of the five *SUT* genes, the transcript levels of *SUT1* and *SUT5* were increased, whereas *SUT3* was decreased in the OsASR1-OX plants. The transcript levels of *SUT1*, *3* and *5* were higher at EN and lower at ED in the NT control. These daily expression patterns of *SUT1* and *SUT5*, which were upregulated by *OsASR1* overexpression, were maintained in the OsASR1-OX plants. Interestingly, the *SUT3* transcript level, which was decreased by *OsASR1* overexpression, was similar at EN and ED. In OsASR1-OX plants, the transcript levels of *MST7* and *MST8* were significantly altered at EN and ED compared with NT controls. Specifically, *MST7* and *MST8* were downregulated at EN but upregulated at ED when compared with NT controls. *MST7* and *MST8* showed the

same expression pattern as *SUTs* (higher at EN and lower at ED). However, *MST7* and *MST8* expression levels were constant between EN and ED in OsASR1-OX plants. The transcript levels of *SPS11* were significantly decreased (by approximately 50 %) at ED but only slightly decreased at EN. However, the transcript levels of *RSus* genes were unaltered in OsASR1-OX plants compared to NT controls (Fig. S1). The transcript levels of *CIN2* were slightly increased at ED, and the transcript levels of *CIN5* were increased at EN compared with the NT controls (Fig. S1). These results indicate that the expression levels of sugar transport and metabolism-related genes are altered by *OsASR1* overexpression in the roots. Interestingly, the diurnal oscillation pattern of *MST7*, *MST8*, *SUT3*, and *SPS11* was disturbed, and their transcript levels were unaltered between EN and ED.

OsASR1 is involved in sugar signaling in roots

The involvement of *ASR* genes in sugar signaling has been described in the leaves of various plant species. *OsASR1* overexpression affected the sugar levels in roots. To determine whether OsASR1 has an effect on sugar signaling, the seeds of NT and OsASR1-OX plants were germinated and etiolated on one-half-strength MS solid medium (without sucrose) containing 5 or 10 % glucose under constant dark conditions for 7 days, and the lengths of their shoots and roots were subsequently measured (Fig. 4). On the medium containing 5 % glucose, shoot growth was inhibited, whereas root growth was enhanced in both NT and OsASR1-OX plants compared with the same plants grown on one-half-strength MS. The growth rate of OsASR1-OX plants was similar to that of NT controls on 5 % glucose. However, on 10 % glucose, OsASR1-OX plants showed statistically significant root growth inhibition compared with NT control plants, although minimal differences were noted in shoot growth between OsASR1-OX plants and NT controls. Specifically, the root growth inhibition of OsASR1-OX plants was approximately 40 % greater than that of the NT controls. These results suggest that OsASR1 plays an important role in sugar signaling in the roots.

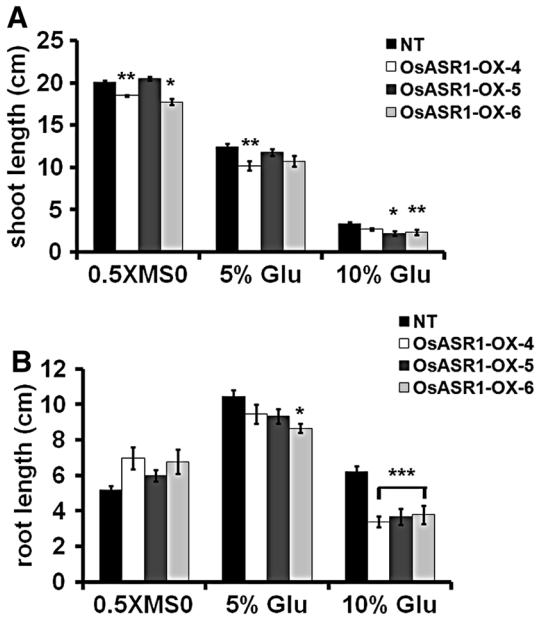

Fig. 4 OsASR1 is involved in sugar-mediated inhibition of early growth. Growth rate assays of OsASR1-OX transgenic seedlings on 5 or 10 % glucose under continuous dark conditions. Seeds from three independent homozygous T_4 OsASR1-OX transgenic lines and NT were germinated and etiolated on half-strength MS solid medium (without sucrose) containing 5 or 10 % glucose under continuous dark conditions for 7 days, and the lengths of shoots and roots were subsequently measured. The data presented are the mean ± SE ($n = 10$) of two replicate plate experiments. *Asterisks* indicate statistically significant differences compared with the NT controls (*$p < 0.05$; **$p < 0.005$; ***$p < 0.001$) based on the Student's *t* test

Discussion

Although the physiological roles of *ASR* genes remain unclear, these genes have been reported to play roles in plant responses to environmental and developmental signals including abiotic stress, biotic stress and sugar signals (Kalifa et al. 2004; Shkolnik and Bar-Zvi 2008; Liu et al. 2010; Dai et al. 2011; Hsu et al. 2011; Virlouvet et al. 2011; Arenhart et al. 2013). Moreover, *ASR* overexpression and silenced lines in different species exhibit diverse phenotypes. Although *ASR* genes are transcriptionally regulated by ABA, gibberellin, and sugars in the source and sink tissues, most studies examining ASR have been performed in the leaves. *Asr1*-silenced *Nicotiana tabacum* plants exhibited large phenotypic changes in the leaves; however, changes were not observed in the overexpression lines. This finding suggests that *ASR1* levels in wild-type plants are saturating with respect to their role in glucose metabolism (Dominguez et al. 2013). Interestingly, potatoes overexpressing *Asr1* exhibited reduced tuber number, and *Asr1*-silenced lines showed decreased tuber fresh weight (Frankel et al. 2007). The physiological role of *ASR* genes in the sink tissues is unknown. A previous study showed that the *OsASR1* gene is differentially regulated by hormones and sugar in the leaves and roots (Joo et al. 2013a, b). Thus, it can be postulated that *OsASR1* may differentially respond to hormones and sugar in the leaves and roots. To understand the function of OsASR1 in roots, the soluble sugar content as well as the sugar and hormone responses of OsASR1-OX plants were investigated. Under normal conditions, an increase in fructose and a decrease in sucrose were observed in the roots of OsASR1-OX plants compared with NT controls, whereas the same results were not observed in the leaves (Fig. 1). Exogenous ABA

dramatically increased the content of glucose and fructose while decreasing the sucrose content in leaves and roots; however, exogenous gibberellin did not cause similar effects (Fig. 2).

In the roots, the glucose and fructose contents were increased by ABA treatments (Fig. 2b). In contrast, sucrose content was decreased by ABA treatment. In addition, the fructose level was higher than glucose level in roots (Fig. 1b). This result indicated that fructose could play an important role in ABA response. It was reported that drought increased the content of hexose sugars (glucose and fructose) and decreased sucrose content in rice seedlings (Shu et al. 2011). The OsASR1-OX plants exhibited increased tolerance to drought and cold stress conditions (Kim et al. 2009; Joo et al. 2013a, b). A change in the soluble sugar content of the roots (i.e., an increase in hexose and a decrease in sucrose content) could promote the ability of the OsASR1-OX plants to adapt to drought and cold stress. These results indicate that OsASR1 plays an important role in controlling sugar status in the roots under ABA and abiotic stress conditions.

Intriguingly, an additional increase in glucose and fructose levels was observed in ABA-treated OsASR1-OX roots compared with ABA-treated NT controls and untreated OsASR1-OX plants. This result suggests that ABA-inducible factors may be necessary for the maximal activity of ASR1 in the roots. ASR proteins have been shown to possess zinc-dependent DNA binding activity, suggesting they may act as transcription factors (Carrari et al. 2004). Tomato ASR1 competed with ABI4 for DNA binding in Arabidopsis (Shkolnik and Bar-Zvi 2008). Furthermore, rice ASR5 (OsASR1 in this study) was found in the nuclear and cytosolic fractions (Arenhart et al. 2013). Therefore, OsASR1 could function as a transcription factor that directly or indirectly regulates sugar metabolism- and stress-related genes. Moreover, ABA is necessary for the maximal function of OsASR1.

The transcript levels of genes related to sugar metabolism and allocation were also altered in the roots of OsASR1-OX plants (Fig. 3). Grape ASR (*VvMsa*) recognized specific binding sites in the promoter/enhancer region of the hexose transporter *VvHt1* (Cakir et al. 2003). The overexpression of *Asr1* negatively regulated the transcript levels of the plasma membrane hexose transporter *Ht2* (Frankel et al. 2007). Similarly, the transcript levels of rice *MST* and *SUT* genes were altered in the roots of OsASR1-OX plants (Fig. 3). MST8 was reported as a key component of the anther apoplastic sugar transport pathway (Zhang et al. 2010). *OsSUT1* gene expression is involved in sucrose allocation to the root under salt stress (Siahpoosh et al. 2012). The fructose content of potato tubers overexpressing *OsSUT5Z* was significantly increased up to threefold (Sun et al. 2011). Compared with other SUTs, OsSUT5 has a higher affinity for substrate and decreased substrate specificity and is less dependent on pH. The unique properties of OsSUT5 may reflect its function in sink tissue (Sun et al. 2010). These results suggest that the increase in *SUT1* and *SUT5* could lead to a significant increase in fructose content in the roots of OsASR1-OX plants. The transcript levels of *SPS11*, *CIN2*, and *CIN5* genes were also altered. The transcript levels of sugar metabolic enzymes generally exhibit diurnal oscillations (Harmer et al. 2000). Interestingly, the diurnal oscillations of some of these genes were perturbed by *OsASR1* overexpression (Fig. 3). These results indicate that OsASR1 plays an important role in sugar metabolism and transport in the roots.

The constitutive overexpression of *OsASR1* resulted in a root phenotype of hypersensitivity to glucose (Fig. 4). These results indicate that OsASR1 is involved in the glucose signaling response in the roots. This study further highlights the molecular function of the *ASR1* gene in the roots. We present evidence that OsASR1 regulates soluble sugar content in the roots. Moreover, the expression levels of genes that are involved in sugar metabolism and allocation in sink tissues were altered by the overexpression of *OsASR1* in the roots. Based on these data, we suggest that OsASR1 plays an important role in root carbohydrate metabolism.

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