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Review

Transcription factors for sugar-inducible genes

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Abstract Expression of a variety of sink-related genes for the synthesis of storage compounds are up-regulated in response to increased levels of sugars, while expression of many genes involved in photosynthesis and the breakdown of storage compounds is repressed by sugars. Despite of extensive studies on sugar signaling in plants, only few transcription factors involved in the expression of sugar-inducible genes have been identified so far. A transgenic *Arabidopsis thaliana* line carrying luciferase gene under the control of a short sugar-inducible promoter derived from a sweet potato sporamin gene was used to screen for loss-of-function type as well as gain-of-function type mutants. These genetic screens resulted in the identification of novel transcription factors that are involved in the expression of at least a subset of sugar-inducible genes in *Arabidopsis*.

Key words: *Arabidopsis* mutants, enhancer activation tagging, LUC reporter gene, storage compound synthesis, transcription factor.

As in yeast and animals, expression of a number of plant genes is regulated in response to changes in sugar nutritional status of the cell. In general, expression of genes involved in source activities, such as photosynthesis and starch breakdown, are down-regulated by sugars, whereas expression of genes involved in sink activities, such as genes coding for storage proteins and enzymes involved in starch synthesis, are upregulated in response to elevated sugar availability. Sugar-dependent regulation of gene expression in plants occurs through multiple signal transduction pathways in close association with response to other signals such as light, nitrogen and phytohormones (reviewed in Koch 1996; Smeekens 2000; Rolland et al. 2002). Although many transcription factors are expected to be involved in such a complex regulation of a variety of genes, only few transcription factors involved in sugar-regulated gene expression have been identified in plants.

Transcription factors involved in sugar-modulated gene expression

Sweet potato SPF1, which is the first WRKY protein identified, was identified as a protein that binds to the sugar-responsible region of sporamin gene promoter (Ishiguro and Nakamura 1992). However, it was later shown that it actually binds to a W box-like sequence closely neighboring to an actual *cis*-element for the sugar-responsible expression (Maeo et al. 2001a). On the other hand, SUSIBA2 (sugar-signaling in barley) isolated as a homolog of SPF1 and other WRKY proteins was shown to bind to SURE (sugar response element; Grierson et al. 1994) and W-box elements in the promoter of barley *iso1* gene encoding starch debranching enzyme (Sun et al. 2003). Expression of *SUSIBA2* gene occurs temporally in developing endosperm and is inducible by sugars, thus a possible involvement of SUSIBA2 in sugar signaling in developing wheat endosperm is suggested.

STOREKEEPER (STK) of potato isolated by its ability to bind to the B-box element that participates in tuber-specific and sugar-inducible expression of class I patatin genes is a member of a novel family of DNA-binding proteins (Zourelidou et al. 2002). Expression of *STK* gene itself is tuber-specific and sugar-inducible. Three novel one-repeat MYB factors isolated from rice bind to TATCCA element important for the GA-induction and sugar-repression of α-amylase genes (Lu et al. 2002). Two of these MYBs transactivate a promoter

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Abbreviations: AP2, APETALA2; ASML1, Activator of *Spo^{min}::LUC1*; ASML2, Activator of *Spo^{min}::LUC2*; CaMV, Cauliflower Mosaic Virus; CCT, CONSTANS-CONSTANS-like-TOC1; EAR, ERF-associated amphiphilic repression; GUS, β-glucuronidase; LUC, luciferase; *Spo^{min}*, sporamin "minimal" promoter.

This article can be found at http://www.jspcmb.jp/

with the TATCCA element in the presence of sugar, while one of them represses the same promoter under sugar starvation.

Expression of an *Arabidopsis* gene for bZIP transcription factor ATB2 is inducible by light and sugars at the level of transcription, while the translation of its mRNA is repressed by sucrose (Rook et al. 1998) which occurs through a highly conserved upstream open reading frame (Wiese et al. 2004). Since the expression of ATB2 occurs predominantly in the vascular tissues of seedlings and young vegetative tissues, it might be involved in sugar signaling in newly established sinks. Constitutive high-level expression of *Arabidopsis* homeodomain leucine-zipper (HDZip) factor ATBH13 results in altered development of cotyledons and leaves when plants are grown on media containing metabolizable sugars (Hanson et al. 2001). In the ATBH13 transformants, expression of several sugar-inducible genes such as *Atβ-Amy* encoding the major β-amylase (Mita et al. 1995) and VSP encoding vegetative storage protein (Berger et al. 1995) in response to sucrose is elevated compared to the wild type, while the expression of other sugar-regulated genes such as genes coding for chalcone synthase, nitrate reductase, plastocyanin and light-harvesting chlorophyll *a*/*b*-binding protein is not affected (Hanson et al. 2001).

Many sugar-signaling mutants of *Arabidopsis* have been obtained by genetic screen based on inhibition of germination and early seedling development by sugars. Many of these mutants are due to mutations in genes involved in the production and response to ethylene and abscisic acid (ABA), indicating a close connection of sugar signaling pathways associated with seed germination with the production and perception of ethylene and ABA (reviewed in Gazzarrini and McCourt 2003; Rook and Bevan 2003). In particular, alleles of *abi3*, *abi4* and *abi5* with mutations in transcription factors containing B3, AP2 and bZIP DNA binding domains, respectively, were isolated as mutants with altered response of sugars. Among a small subfamily of ABRE (ABA responsive element)-binding bZIP factors designated ABFs, overexpression of ABF2 specifically promoted glucose-induced inhibition of seedling development and repressed the expression of genes such as *rbcS* and hexokinase genes (Kim et al. 2004).

Arabidopsis plant with sugar-inducible LUC reporter gene for mutant screening

Sporamin genes of sweet potato code for the most abundant protein in storage roots, and their expression is coordinately inducible in other vegetative tissues by metabolizable sugars such as sucrose and glucose (Hattori et al. 1990; Nakamura et al. 1991). Promoter analysis of sporamin A1 gene in tobacco using β-glucuronidase (GUS) reporter yielded a 210-bp sugar-inducible "minimal" promoter (*Spo^{min}*; Morikami et al. 2005). Expression of sporamin genes is also inducible by ABA (Ohto et al. 1992) and *Spo^{min}* directs sugar- and ABA-inducible expression of reporter genes in *Arabidopsis*.

A transgenic *Arabidopsis* line sGsL harboring a single copy of the S*po^{min}::GUS-Spo^{min}::LUC* dual reporter genes was characterized for the sugar- and ABA-inducible expression of GUS and LUC activities. Seeds of the sGsL line were mutagenized and used to screen for mutants, which show altered patterns of the sugar-inducible expression of LUC, by using a high-resolution photon counting camera. After screening for ca. 17,000 plants, 29 lines of *lsi*-type and 28 lines of *hsi*-type mutants showing lower levels of LUC expression under high-sugar conditions and showing higher levels of LUC expression under low-sugar conditions, respectively, compared to the sGsL line were obtained (Tsukagoshi et al. 2005; A. Morikami et al. manuscript in preparation). In addition, this screen identified 4 lines of putative mutants of LUC structural gene, which do not express LUC while showing normal expression of GUS, suggesting that mutant screening is extensive.

Phenotypes of *lsi* and *hsi* mutants were due to recessive mutation, suggesting that the sugar-inducible expression of *Spo^{min}::LUC* is under both positive and negative regulation, which is similar to mutants with altered sugar-inducible expression of *Atβ-Amy* (Mita et al. 1997a, b). Further analyses of the *lsi* and *hsi* mutants suggested that both ABA-mediated and -independent pathways operate in the sugar-regulated expression of *Spo^{min}::LUC* (A. Morikami et al. manuscript in preparation).

A novel B3 domain protein with EAR motif, HSI2, represses expression of Spo^{min}::LUC

Among 29 *hsi*-type mutants, *hsi2* mutant displayed highest levels of LUC and GUS activities under both low and high sugar conditions. Expression from the *Spo^{min}* promoter was not constitutive in the *hsi2* mutant, and *hsi2* mutation caused an enhancement of the expression of the *Spo^{min}* promoter without affecting the mode of regulation or the spatial pattern of expression.

Map-based cloning revealed that the *hsi2* mutation was due to a nonsense mutation in a gene encoding a protein with a plant-specific B3 DNA-binding domain (Tsukagoshi et al. 2005). Although the B3 domain of HSI2 and two other *Arabidopsis* proteins, HSI2-L1 and HSI2-L2, were similar to that of ABI3, FUS3 and LEC2 involved in seed development and ABA signaling, they constitute a novel subfamily distinct from other B3 domain proteins (Figure 1A). In particular, the C-terminal part of HSI2 subfamily proteins contains a

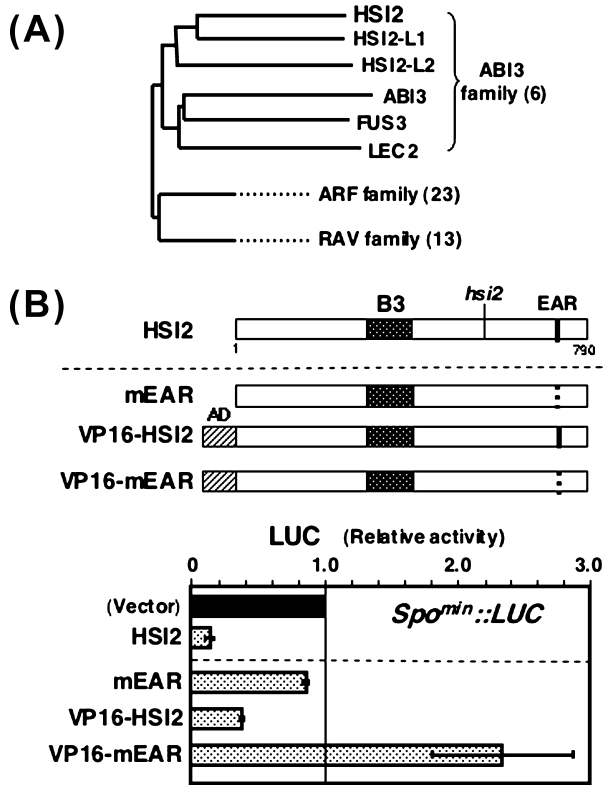

Figure 1. HSI2, a novel B3 DNA-binding domain protein with EAR motif, functions as an active transcriptional repressor of the sugar-inducible *Spo*^{min} promoter. (A) A phylogenetic tree of B3 domain proteins of *Arabidopsis*. (B) Effects of co-expression of HSI2, mEAR with mutations in the EAR motif, HSI2 or mEAR fused with the activation domain of VP16 (VP16-HSI2 or VP16-mEAR) on transient-expression of *Spo*^{min}*::LUC* in protoplasts. The LUC activity in each assay was normalized according to the level of expression of *35S::GUS* included in co-transfection. Figures are modified from Tsukagoshi et al. (2005).

sequence similar to the ERF-associated amphiphilic repression (EAR) motif (Ohta et al. 2001), and a null allele of *hsi2* due to T-DNA insertion in the *HSI2* gene showed even higher *Spo*^{min}*::LUC* expression than the *hsi2* mutant. On the other hand, constitutive overexpression of HSI2 cDNA under the Cauliflower Mosaic Virus (CaMV) 35S promoter reduced the LUC expression. Furthermore, transient co-expression of *35S::HSI2* with the *Spo*^{min}*::LUC* reporter in *Arabidopsis* protoplasts repressed the LUC expression (Figure 1B). Attachment of VP16 activation domain to HSI2 did not negate the repressor activity, while deletion or mutation of the EAR motif of HSI2 abolished the trans-repression. These results indicate that HSI2 functions as an active transcription repressor and it has negative effects on the basal transcription level from the *Spo*^{min} promoter (Tsukagoshi et al. 2005). Recombinant HSI2 protein showed specific binding to the *Spo*^{min} promoter fragment *in vitro*, and the DNA binding site sequence specificity of HSI2 is currently under analysis.

It is not known at present whether HSI2 is specifically involved in the sugar-dependent regulation of gene expression or it is involved in more general regulation. Although disruption of *HSI2* gene alone does not cause severe visible phenotypes, double mutant of *HSI2* and *HSI2-L1* genes is seedling lethal, suggesting that HSI2 and HSI2-L1 share some overlapping functions essential for growth.

Enhancer activation-tagging

In addition to screening of loss-of-function mutants, an enhancer activation-tagging approach (Kakimoto 1996; Weigel et al. 2000) was also taken to isolate gain-of-function type mutants for the sugar-inducible gene expression. The sGsL plants were transformed with a binary vector carrying four repeats of the 339-bp enhancer region of the CaMV 35S promoter near the right border of T-DNA (Kakimoto 1996), and screened for mutants exhibiting LUC expression under non-inducing low-sugar condition. After screening of 12,000 lines, four mutants exhibiting a dominant phenotype for the high-level LUC expression that is linked with T-DNA were obtained. In one of the mutant, enhancer T-DNA was integrated near the sGsL dual reporters. In the other three mutants, enhancer T-DNA was integrated near a gene for putative transcription factor. Two of these mutants were characterized (Masaki et al. 2005a, b).

Activator of Spo^{min}::LUC1 (ASML1)/ WRINKLED1 activates a subset of sugar-inducible genes and controls seed oil accumulation

One of the mutants obtained by the enhancer activation-tagging showed higher levels of expression of several endogenous sugar-inducible genes such as *At*β*-Amy* and *SUS2* encoding sucrose synthase 2 (Déjardin et al. 1999), in addition to LUC and GUS reporters, compared to the sGsL plants. Expression of other sugar-inducible genes such as *VSP2* and *ApL3* for the ADP-glucose pyrophosphorylase large subunit (Sokolov et al. 1998) was the same as in the sGsL plants.

In this mutant, the enhancer T-DNA was inserted in the lower arm of chromosome 3 near *APETALA3*, and a gene designated *ASML1* for Activator of *Spo*^{min}*::LUC1* located between the enhancer and *APETALA3* was significantly elevated compared to the sGsL plants (Masaki et al. 2005a). The sGsL plants that overexpress ASML1 cDNA under the CaMV 35S promoter mimicked phenotypes of the original mutant. ASML1 contains two copies of the plant-specific AP2 DNA-binding domain (Weigel 1995). Among the large family of AP2 domain proteins in *Arabidopsis* (Sakuma et al. 2002), 14 of them contain two AP2 domains (Figure 2A). This AP2 subfamily includes APETALA2 (AP2),

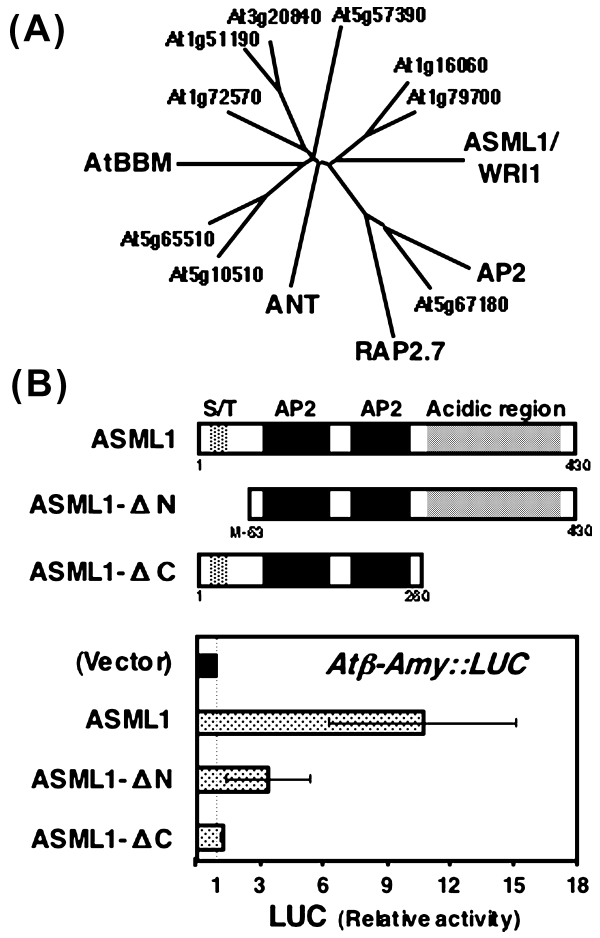

Figure 2. ASML1/WRI1 with two AP2 DNA-binding domains functions as a transcriptional activator of *Atβ-Amy*. (A) Unrooted N-J Tree for the 14 *Arabidopsis* proteins with two AP2 domains constructed by CLUSTAL W. (B) Protoplasts were co-transfected with the *Atβ-Amy::LUC* reporter plasmid, *35S::ASML1* effector plasmid and *35S::GUS* internal control plasmid. Deletion derivatives of ASML1, ASML1-ΔN and −ΔC, were also examined. The LUC activity in each assay was normalized according to the GUS activity. Figures are modified from Masaki et al. (2005a).

AINTEGUMENTA (ANT) and *Arabidopsis* BABY BOOM (AtBBM) that are involved in the control of flower and seed development (Bowman et al. 1989; Jofuku et al. 1994; Klucher et al. 1996; Boutilier et al. 2002) and in the control of seed size (Elliott et al. 1996; Ohto et al. 2005). *ASML1* turned out to be identical to a gene responsible for the *wrinkled1* (*wri1*) mutation of *Arabidopsis*, which causes reduced accumulation of seed oil (Focks and Benning 1998), recently identified by Cernac and Benning (2004).

Transient expression of *Spo^{min}::LUC* and *Atβ-Amy::LUC* in protoplasts was enhanced to about 9-fold by co-expression of *35S::ASML1* (Figure 2B). The C-terminal part of ASML1 is enriched with acidic amino acids, and co-expression of ASML1-ΔC with deletions in the C-terminal acidic region failed to show activation of *Spo^{min}::LUC*. These results suggest that ASML1 probably acts directly to *Spo^{min}* and *Atβ-Amy* promoters as a transcriptional activator and the C-terminal acidic region of ASML1 acts as an activation domain (Masaki et al. 2005a). The DNA-binding properties and the binding site sequence-specificity of ASML1 are currently under analysis.

Expression of *ASML1*/*WRI1* is high in reproductive organs such as flowers and siliques with developing seeds, although it can also be detected in stems, leaves and roots (Cernac and Benning 2004; Masaki et al. 2005a). Although expression of ASML1/WRI1 is not affected by ABA and other phytohormones, its mRNA in leaves showed transient accumulation after treatment with sucrose (Masaki et al. 2005a).

Seeds of the *wri1* mutant show an 80% reduction in oil content and an increased accumulation of soluble sugars (Focks and Benning 1998), and expression of genes encoding enzymes for glycolysis and triacylglycerol biosynthesis that share similar expression patterns during seed development are reduced in the *wri1* mutant compared to the wild-type (Ruuska et al. 2002). In addition, *Arabidopsis* plants expressing WRI1 cDNA under the control of the CaMV 35S promoter show not only increased seed oil content but also accumulation of triacylglycerols in seedlings (Cernac and Benning 2004). It is suggested that WRI1 plays a critical role in the control of the carbon flow from sucrose import to storage oil accumulation in developing seeds (Cernac and Benning 2004). The fact that ASML1/WRI1, which activates a subset of sugar-responsive genes, is involved in seed oil accumulation suggests a role for sugar signaling in the control of carbon flow to storage oil during seed development.

ASML2 with novel class of CCT-domain activates expression of a subset of sugar-inducible genes

Another enhancer activation-tagged mutant of sGsL showed higher levels of mRNAs for several endogenous sugar-inducible genes such as *Atβ-Amy*, *ApL3* and *VSP2*, in addition to LUC and GUS mRNAs, than in the sGsL plants under low-sugar conditions. In addition, this mutant showed severe growth defects and abnormal morphology. Although a large rearrangement of chromosome 3 occurred at the site of T-DNA integration in this mutant, expression of a gene designated as *ASML2* located immediately downstream of the enhancer was significantly higher in the mutant compared to the sGsL plants. Similar to the original mutant, sGsL plants that express ASML2 cDNA under the CaMV 35S promoter showed enhanced expression of not only LUC and GUS reporters but also endogenous *Atβ-Amy*, *ApL3*, and *VSP2* genes compared to the sGsL plants (Figure 3B; Masaki et al. 2005b). Unlike the original mutant, the *35S::ASML2* transformants did not show severe defects

in growth and development.

Constitutive overexpression of ASML2 alone does not cause expression of *Spo*^{min} and the tissue-specific expression pattern of *Spo*^{min} is not affected. Rather, it enhanced the level of expression of *Spo*^{min} in response to sugars (Figure 3c; Masaki et al. 2005b). Similar to *Spo*^{min}, expression of *Atβ-Amy*, *ApL3* and *VSP* that are enhanced in the *35S::ASML2* transformants are inducible by various metabolizable sugars. Although ABA induces expression of *VSP2* (Berger et al. 1995) or strongly enhances the sugar-inducible expression of *ApL3* (Rook et al. 2001), ABA does not induce the expression of *Atβ-Amy*. Expression of the cold stress- and ABA-inducible *COR15a* gene was not affected by the overexpression of ASML2. ASML2 mRNA showed small increase after treatment of seedlings with metabolizable sugars, while it did not respond to non-metabolizable sugar analogs and ABA. ASML2 seems to be involved in the expression of a subset of sugar metabolic signal-inducible genes independently from ABA-signaling, although it is possible that ASML2 is involved in the expression of more wide range of genes. Since ASML2 is strongly expressed in reproductive organs such as flowers and siliques with developing seeds, it could be involved in the expression of sugar-responsive genes in these organs.

ASML2 contains a 43 amino acid-long CCT (CONSTANS [CO], CONSTANS-like [COL], TOC1) domain (Strayer et al. 2000; Robson et al. 2001). In *Arabidopsis*, the CCT domain has been identified in CO and 16 COL proteins (Robson et al. 2001), TOC1 and 4 other pseudo-response regulators (APRRs; Strayer et al. 2000; Matsushika et al. 2000), and ZIM, a GATA-type zinc-finger protein expressed in inflorescence meristem, and two homologous proteins (Shikata et al. 2004). ASML2 does not belong to any of these groups and the ASML2 family represents a novel class of CCT domain proteins that has not been characterized previously (Figure 3A; Masaki et al. 2005b).

Although ASML2 does not contain sequences similar to typical DNA-binding motif and activation domain, transient co-expression of *35S::ASML2* activated the expression of *Spo*^{min}*::LUC* and *Atβ-Amy::LUC* reporters in protoplats. Deletion of the CCT domain from ASML2 abolished an activity to transactivate the *Spo*^{min} and *Atβ-Amy* promoters. It remains to be determined whether ASML2 functions as a DNA-binding transcription activator or ASML2 act through the interaction with a protein bound to the *Spo*^{min} and *Atβ-Amy* promoters in protoplasts. The CCT domain of CO and TOC1/APRR1 is required for nuclear localization (Robson et al. 2001; Makino et al. 2000) and it is also involved in protein-protein interactions. TOC1/APRR1 has been identified as one of the proteins that can interact with ABI3, and the CCT domain of CO also interacts with ABI3 (Kurup et al. 2000).

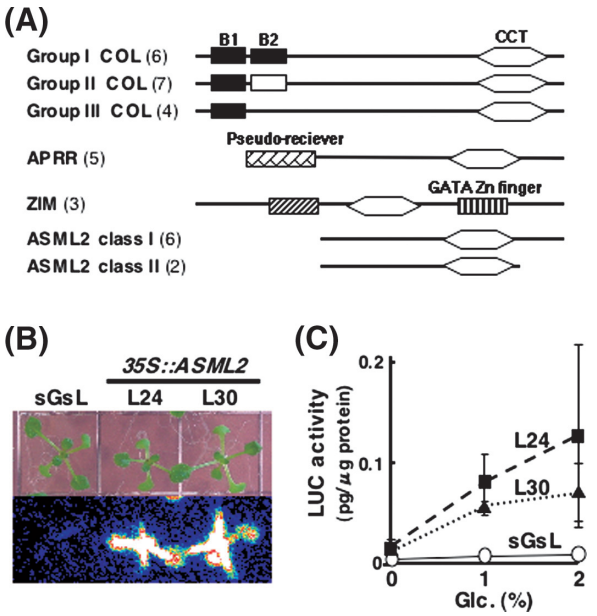

Figure 3. Overexpression of ASML2 with a novel class of CCT-domain promotes sugar-inducible expression of *Spo*^{min}*::LUC*. (A) Domain structures of CO/COL family, TOC1/APRR family, ZIM/ZML family, and ASML2 family proteins from *Arabidopsis*. Numbers in parenthesis indicate the number of predicted proteins. (B) Luminescence images of LUC activity in the sGsL plant and two representative lines transformed with *35S::ASML2*. Seedlings were grown on medium containing 1% sucrose for 12 days before detection of LUC activity. (C) LUC activities in seedlings of the sGsL plants and *35S::ASML2* transformants that were grown for 11 days on medium containing 0, 1 or 2% glucose. Figures are modified from Masaki et al. (2005b).

Multiple transcription factors involved in sugar-inducible gene expression

Expression of sugar-inducible *Spo*^{min} and other promoters apparently occurs downstream of a complex regulatory network. Both positive and negative regulation as well as both ABA-mediated and -independent pathways are involved in the sugar-inducible expression of *Spo*^{min} (A. Morikami et al., manuscript in preparation). Several regions of *Spo* promoter can function negatively on expression and even the short *Spo*^{min} and *β-Amy*^{min} promoters contain at least two separate positive *cis*-elements required for the maximum level of sugar-inducible expression (Maeo et al. 2001b; Morikami et al. 2005). Overexpression or mutation in ASML1/WRI1, ASML2 and HSI2 affects expression of *Spo*^{min} and these transcription factors either trans-activate or -repress transient expression of *Spo*^{min} in protoplasts (Figure 4; Tsukagoshi et al. 2005; Masaki et al. 2005a, b). We have recently identified another transcription factor that binds to and transactivates *Spo*^{min} (K. Maeo et al., unpublished data). Similarly, ATHB13, ASML1/WRI1 and ASML2 affects the expression of

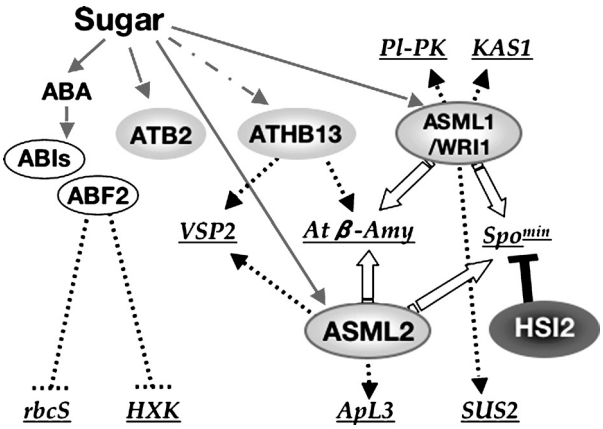

Figure 4. Transcription factors involved in the expression of sugar-regulated genes in *Arabidopsis*. Pl-PK, plastid pyruvate kinase; KAS1, 3-ketoacyl-ACP synthase I. See text for details and other abbreviations.

sugar-inducible *Atβ-Amy* and both ASML1/WRI1 and ASML2 can transactivate *Atβ-Amy* in protoplast transient assay (Masaki et al. 2005a, b). It is not established whether these transcription factors are inherent components of sugar signaling. Further analyses of their function and functional interactions among them are required to understand the mechanisms by which sugars regulate transcription in plants.

Future perspectives

Although regulation of gene expression in response to changes in carbohydrate nutritional status is crucial for all living organisms, sugar signaling in higher plants has unique features not shared with those in yeast and animals. In addition to regulation in response to glucose, regulation of many plant genes seems to occur in response to sucrose rather than glucose. The concentration of sucrose in the phloem often goes as high as ca 0.4 M that normally yeast and animal cells do not encounter. Transcription factors involved in the expression of sugar-regulated genes in plants identified so far often contain DNA-binding and related functional domains that are unique to plants such as WRKY, B3, AP2, and CCT domains. Further functional characterization of these transcription factors should reveal the mechanisms of sugar-dependent regulation of gene expression that are unique to plants.

Among the transcription factors characterized, ASML1/WRI1 plays an important role in the control of carbon flow from sucrose import to storage oil accumulation. Further identification and characterization of transcription factors involved in the sugar-regulated gene expression are expected to open a way not only to improve the sink storage activity but also to control the partitioning of carbohydrates to various storage compounds in the sink.

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