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Roles of cell-wall invertases and monosaccharide transporters in the growth and development of *Arabidopsis*

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Abstract

The hydrolysis of sucrose by cell-wall invertases (cwINV) and the subsequent import of hexoses into target cells appears to be crucial for appropriate metabolism, growth and differentiation in plants. Hexose uptake from the apoplast is catalysed by monosaccharide/H^+ symporters (Sugar Transport Proteins or STPs), which have the potential to sense sugars. Import of extracellular hexoses may generate signals to orchestrate cellular activities, or simply feed metabolic pathways distinct from those fed by sucrose. It is predicted that *Arabidopsis* has six *cwINV* genes and at least 14 *STP* genes. These genes show different spatial and temporal patterns of expression, and several knock-out mutants have been isolated for analysis. AtSTP1 transports glucose, galactose, xylose, and mannose, but not fructose. It accounts for the majority of the AtSTP activity in vegetative tissues and its activity is markedly repressed by treatment with exogenous sugars. These observations are consistent with a role in the retrieval of cell-wall-derived sugars, for example, during carbohydrate limitation or cell expansion. The *AtSTP1* gene is also expressed in developing seeds, where it might be responsible for the uptake of glucose derived from imported sucrose. The large number of *AtcwINV* and *AtSTP* genes, together with complex patterns of expression for each, and the possibility that each protein may have more than one physiological function, provides the plant with the potential for a multiplicity of patterns of monosaccharide utilization to direct growth and differentiation or to respond flexibly to changing environmental conditions.

Key words: *Arabidopsis thaliana,* cell wall, invertase, mutant, seed development, sugar sensing, sugar transport.

Sugars and the control of plant growth and development

In addition to serving as a source of carbon and energy, sugars are key signalling molecules which can potentially regulate cell division, growth, differentiation, metabolism, and resource allocation in plants (Koch, 1996; Smeekens, 2000). Sucrose is of central importance as a product of photosynthesis and the form in which most carbohydrate is transported between cells and throughout the plant. It is ideally suited to serve as a signalling molecule to co-ordinate source–sink relationships and resource utilization. Evidence for sucrose sensing is provided by the sucrose-induced expression of a sucrose transporter gene (Chiou and Bush, 1998) and repression of translation of ATB2 transcription factor mRNA (Rook *et al*., 1998). The regulation of metabolism and development by palatinose, a sucrose analogue, further suggests a regulatory role for sucrose (Fernie *et al*., 2001; Bornke *et al*., 2002).

In *Vicia faba* seed development there is a marked switch from hexose to sucrose provision to the embryo, which correlates with a switch from the cell division and morphogenesis phase to the cotyledon expansion and resource accumulation phase (Weber *et al*., 1997). When embryos at the cell division phase are isolated and incubated with sucrose, nuclear expansion and starch accumulation are promoted, whereas in the presence of hexoses, cell division activity is maintained (Weber *et al*., 1996). This observation provides strong evidence that these sugars are regulating cell division and differentiation.

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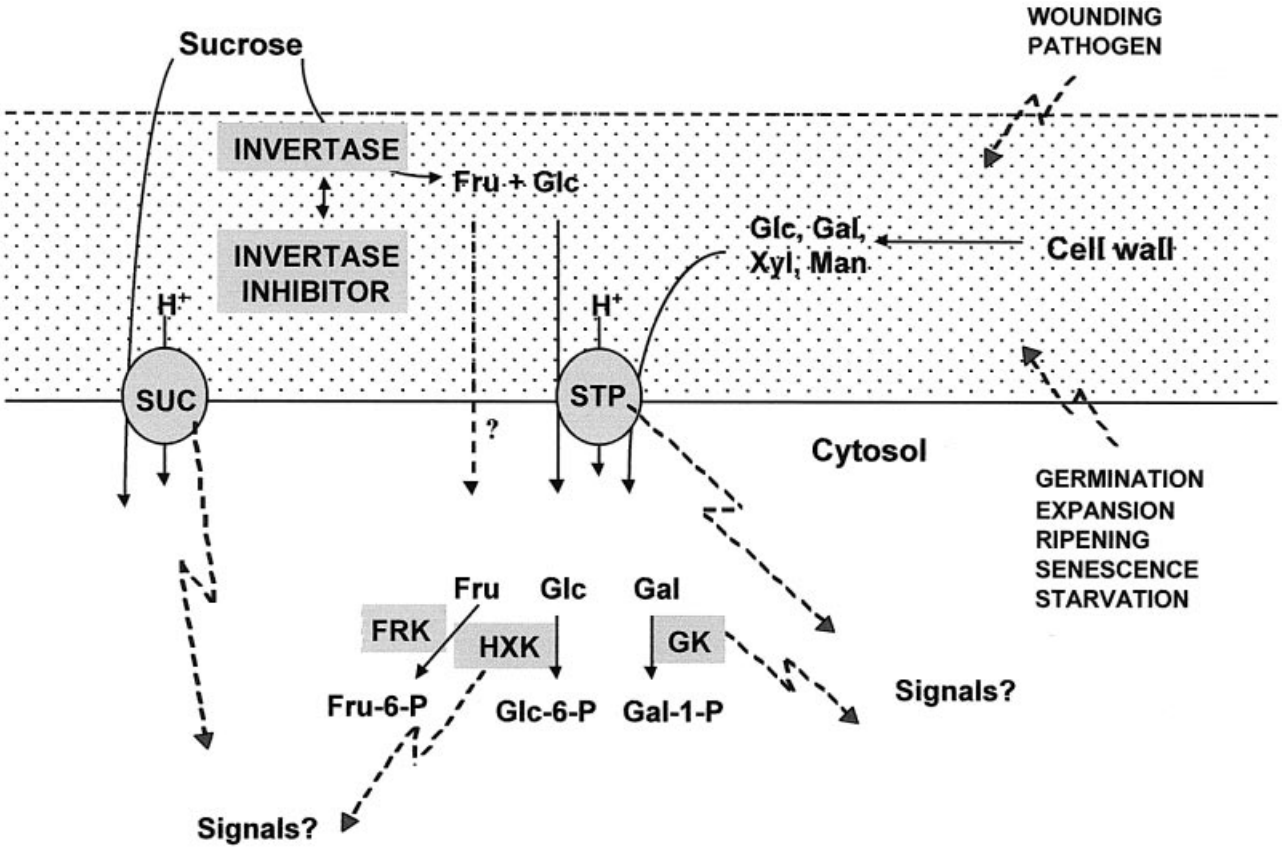

Fig. 1. Apoplastic sugar uptake and metabolism. Broken arrows represent potential signals. Uncertainty about the route of fructose uptake is indicated by a dashed arrow and question mark. Key: SUC, sucrose transporter; STP, sugar transport protein; FRK, fructokinase; HXK, hexokinase; GK, galactokinase.

A similar switch in sugar provision occurs in potato (*Solanum tuberosum*) as stolons undergo the transition to tuberization (Viola *et al*., 2001).

The activity of cell-wall invertase (cwINV) will determine whether a cell is provided with apoplastic sucrose or hexoses (Fig. 1). Therefore, cwINV plays a pivotal role in the control of many aspects of plant metabolism, growth and development. In developing *Vicia faba* seeds, a decline in cwINV activity is observed as the switch is made from hexose to sucrose provision to the embryo. However, the clearest demonstrations of the importance of cwINV come from analyses of the *miniature1* mutant of maize (*Zea mays*) and of antisense inhibition of cwINV synthesis in carrot (*Daucus carrota*). Seeds of the *miniature1* mutant are small because an endosperm-specific cwINV is absent and the endosperm fails to develop (Cheng *et al*., 1996). Antisense inhibition of cwINV synthesis in carrot roots abolishes tap root formation and leads to increased foliar growth (Tang *et al*., 1999). In both cases provision of apoplastic hexoses is apparently required for normal development.

Hexose sensing

In *Saccharomyces cerevisiae,* the plasma-membrane-localized, hexose-transporter-like proteins RGT2 and SNF3, sense glucose and relay a signal to a transduction pathway which ultimately leads to the regulation of expression of genes including those encoding functional hexose transporters (Ozcan *et al*., 1998). Thus extracellular glucose triggers the synthesis of the hexose transporters which catalyse its uptake. It is proposed that a similar glucose-transporter-like protein (RCO3) in *Neurospora crassa* functions as a sensor rather than a transporter (Madi *et al*., 1997). In mammals, the glucose transporter GLUT1 has been proposed to function in the sensing, transduction and amplification of a glucose signal without requiring the glucose to be transported (Bandyopadhyay *et al*., 2000). Furthermore, it has been proposed that a large cytoplasmic loop in the GLUT2 glucose transporter of hepatic cells is involved in glucose signalling (Guillemain *et al*., 2000). In plants, there are several reports that 3-*O*-methylglucose (3OMG) and 6-deoxyglucose (6DOG) can trigger changes in plant gene expression (Godt *et al*., 1995; Roitsch *et al*.,

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1995; Martin *et al*., 1997). These molecules can be transported into plant cells and it is generally believed that they are not metabolized (although this has not been confirmed in the experiments cited). One interpretation of these observations is that glucose (or 3OMG or 6DOG) is sensed by a cell-surface receptor such as a hexose-transporter-type protein (Fig. 1), but no sensor has yet been described.

There are many examples in which hexose metabolism is required for sensing (Rolland *et al*., 2001). Numerous reports show that substrates for hexokinase cause changes in gene expression, which has led to the proposal that hexokinase is a sugar sensor in yeast and plants (Rolland *et al*., 2001). While there is still no direct evidence for this (Halford *et al*., 1999), it is apparent that hexokinase is a key component in the sensing of its substrates (Fig. 1). In pancreatic beta cells it has been proposed that glucokinase may be a sensor, but current evidence suggests that it is simply a rate-limiting step in glucose metabolism, which in turn generates a signal (Rolland *et al*., 2001).

Galactokinase (GK) is another potential sugar-sensing molecule. In *Kluyveromyces lactis*, GK has been shown to be a bifunctional protein. In addition to its catalytic activity, in the presence of galactose and ATP it migrates to the nucleus and relieves transcriptional repression of genes required for galactose utilization (Zenke *et al*., 1996). In *Saccharomyces cerevisiae*, a protein (Gal3p) with homology to GK, carries out the same function instead of the enzymically-active GK. The plant and fungal GK enzymes are highly conserved (Kaplan *et al*., 1997). These observations raise the possibility that GK could be a sugar sensor in plants (Fig. 1). Much work is still required to establish how hexose metabolism generates signals in plants, but it is clear that hexoses have important roles to play in the control of growth and development.

Given the importance of cwINV and hexose transorters in plant metabolism, and the possibility that plant hexose transporters or transporter-like proteins might also function in sugar sensing (Lalonde *et al*., 1999), *Arabidopsis thaliana* has been adopted as a model to investigate the function of these proteins further.

Cell-wall invertases in *Arabidopsis*

In plant cells, invertases are found in the cell wall (cwINV), vacuole (vacINV) and cytosol (cytINV). cwINV and vacINV are both acid invertases and their amino acid sequences are more closely related to each other than to the cytINV (neutral) invertases (Sturm, 1999; Sturm and Tang, 1999). Six putative *cwINV* genes have been identified in the *Arabidopsis thaliana* genome (*AtcwINV* genes). Two of these genes have previously been studied and are referred to as β*FRUCT1* and β*FRUCT2* (Tymowska-Lalanne and Kreis, 1998). Since the putative vacINV genes were referred to as β*FRUCT3* and β*FRUCT4* (Tymowska-Lalanne and Kreis, 1998), a revised nomenclature has been adopted here specifically for the *AtcwINV* genes (Fig. 2). *AtcwINV1* has been reported to be expressed in stems, leaves and roots, but not in cotyledons or flowers, while *AtcwINV2* expression was flower-specific (Tymowska-Lalanne and Kreis, 1998). Gene-specific primers have been used in RT-PCR reactions to investigate expression of all six genes, and results were obtained for *AtcwINV1* and *ATcwINV2* that were broadly consistent with Tymowska-Lalanne and Kreis (1998) except that expression of *AtcwINV1* is detected in flowers (Fig. 2). All six genes show distinct levels and spatial patterns of expression (Fig. 2). Remarkably, five of the six *AtcwINV* genes are expressed in developing *Arabidopsis* seeds (Fig. 2), and of these, four appear to be expressed more strongly in the cell division stages (SM Sherson, unpublished results). While the precise temporal and spatial patterns of expression of these genes remain to be determined, these observations are consistent with the proposal that cwINVs have important roles in seed development.

To investigate the specific functions of AtcwINVs in growth and development, knock-out (KO) mutants (Thorneycroft *et al*., 2001) were sought for each gene. To date, KOs for four genes have been isolated and none show an abnormal growth phenotype, (SM Sherson, unpublished results). Detailed analysis of these mutants is expected to provide important information on the function of individual cwINV enzymes.

cwINV activity is potentially regulated by specifc inhibitor proteins (Greiner *et al*., 2000). Therefore, the presence of such proteins should be considered in the context of cwINV activity. The *Arabidopsis* genome contains approximately 15 genes encoding proteins with sequence similarity to tobacco and tomato cwINV inhibitor proteins. However, the expression patterns of these genes has not yet been investigated.

Arabidopsis plasma membrane monosaccharide/proton symporters

Hexose uptake across the plasma membrane is catalysed by monosaccharide/proton symporters, referred to as sugar transport proteins (STPs). The *Arabidopsis thaliana* genome contains 14 putative *AtSTP* genes within a family of at least 50 closely related genes. Most of these related genes are of unknown function, but several are similar to a mannitol transporter from celery (Noiraud *et al*., 2001). Four different AtSTP proteins have been expressed in heterologous cells (yeast and *Xenopus*) and shown to catalyse the uptake of exogenous sugars (reviewed by Büttner and Sauer, 2000), and a KO mutation in the *AtSTP1* gene results in a decrease in uptake of exogenous monosaccharides by *Arabidopsis* seedlings (Sherson *et al*., 2000). These observations are consistent with AtSTPs

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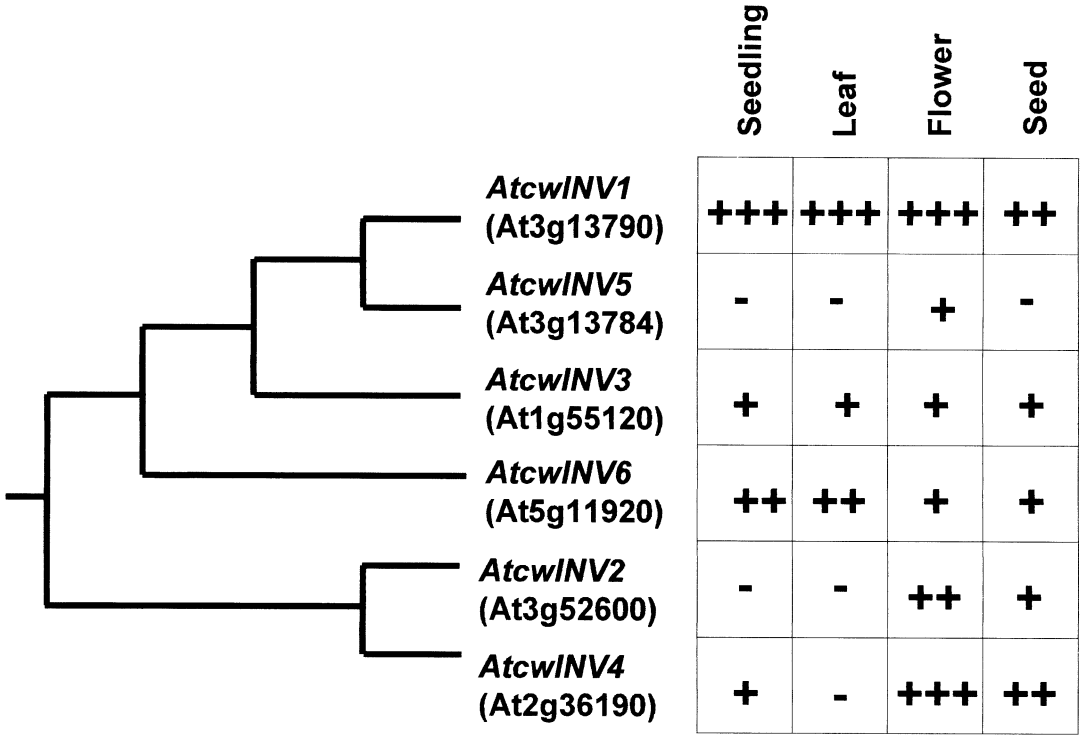

Fig. 2. The *Arabidopsis cwINV* gene family. Gene sequences were aligned using Clustal W and the phylogenetic tree derived using a PULP (Version 3.1) Heuristic search, with mid-point branching. The relative levels of expression of each gene were determined by RT-PCR using gene-specific primers and RNA from 3-d-old seedlings, expanding rosette leaves, flowers, and developing seeds removed from green siliques. (+) expression, (–) no expression detected (SM Sherson, unpublished results).

functioning in the plasma membrane to import monosaccharides from the apoplast. It remains to be determined whether all 14 putative AtSTPs catalyse monosccaharide transport, and what functions other related proteins have. Furthermore, the physiological functions of AtSTPs are unclear (Büttner and Sauer, 2000).

AtSTP1 is a high-affinity (K_m^{Glc} ~ 50 μM) symporter that transports several monosaccharides, but it transports fructose at a very low rate. The *AtSTP1* gene is expressed strongly in leaves, but also in roots, stems, flowers, siliques, and seedlings (Fig. 3; Sauer *et al*., 1990; Sherson *et al*., 2000). AtSTP1 is active during seed germination and accounts for approximately 60% of glucose uptake activity in *Arabidopsis* seedlings (Sherson *et al*., 2000). Despite these observations, the *Atstp1* KO mutant appears to grow and develop normally (Sherson *et al*., 2000). AtSTP2 is another high-affinity transporter but the *AtSTP2* gene is expressed specifically in developing pollen. It is hypothesized that it is responsible for the uptake of glucose derived from callose degradation during pollen maturation (Truernit *et al*., 1999). AtSTP3 is a low-affinity transporter (K_m^{Glc} ~ 2 mM Glc) and the *AtSTP3* gene is expressed in green tissues, and is induced slowly by wounding (Büttner *et al*., 2000). AtSTP4 is a high-affinity transporter expressed in root tips, pollen tubes, and leaves. The mRNA level increases appreciably in response to wounding and pathogen attack (Truernit *et al*., 1996).

Sequence comparisons (Büttner and Sauer, 2000) show that some *AtSTP* genes are closely related (eg *AtSTP1* and *12*; *6* and *8*; *9* and *10*), but in no cases are the closest relatives physically linked. Furthermore, the close relatives are not necessarily expressed co-ordinately. For example, while *AtSTP1* is expressed in many vegetative and reproductive tissues, *AtSTP12* is expressed predominantly in developing seeds (SM Sherson, unpublished results). In parallel with studies of *AtcwINV* gene expression, it was found that at least five *AtSTP* genes are expressed in developing seeds (SM Sherson, SM Forbes, unpublished results). The effects of KO mutations in *AtSTP1* and *AtSTP12* on seed development and resource acquisition are under investigation.

The specific case of AtSTP1

In order to investigate the physiological function of AtSTP1, the expression of the *AtSTP1* gene was examined in more detail. Extracellular glucose often controls the expression of hexose transporter genes in other eukaryotes in order to regulate its uptake (Boles and Hollenberg, 1997). To determine if the same is true in *Arabidopsis*,

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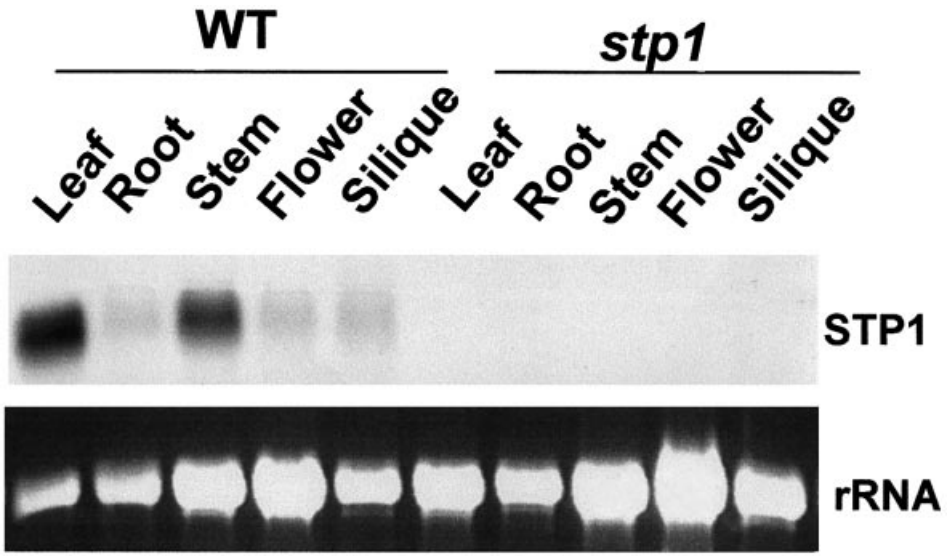

Fig. 3. Expression of the *AtSTP1* gene. Gel blot hybridization using RNA isolated from different organs of flowering plants and an *AtSTP1* cDNA probe. Wild-type and *Atstp1* mutant plants were analysed. Details of plant growth, gel blot analysis and description of the *Atstp1* mutant are given in Sherson *et al*. (2000).

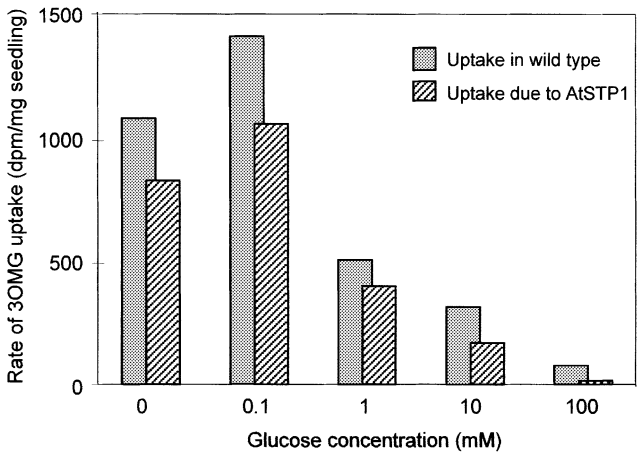

Fig. 4. Repression of STP activity by growth of *Arabidopsis* seedlings on glucose. Wild-type and *Atstp1* mutant seedlings were germinated on half-strength Murashige and Skoog medium and grown in the light in the presence of different concentrations of glucose, as described in Sherson *et al*. (2000). Rates of uptake of [^{14}C]3OMG were assayed as described in Sherson *et al*. (2000). The rates of uptake due to AtSTP1 activity were derived from the difference between rates of uptake for wild type and *Atstp1* mutant (G Wallace, unpublished results).

seeds were germinated and seedlings grown for 7 d on medium containing different concentrations of glucose. Total AtSTP activity in whole seedlings was then determined by assaying uptake of [^{14}C]3OMG (Sherson *et al*., 2000). The results show that AtSTP activity is markedly reduced by exogenous glucose at a concentration of 1 mM or greater (Fig. 4). By comparing results obtained from wild-type seedlings with those from the *Atstp1* KO mutant, it was deduced that AtSTP1 accounts for the majority of this transport activity, and that AtSTP1 and other AtSTPs active in seedlings are repressed by high concentrations of glucose (Fig. 4). These observations imply that AtSTP1 may function to acquire apoplastic sugars when other carbohydrate supplies are limiting. The low K_m of AtSTP1 is consistent with such a role. Furthermore, the substrate specificity of AtSTP1 is similar to the sugar composition of the primary cell wall (Reiter *et al*., 1997), consistent with a role in salvage of cell-wall-derived sugars (Sherson *et al*., 2000).

To extend this investigation on the role of AtSTP1, the *AtSTP1* promoter was linked to the luciferase reporter gene and introduced into *Arabidopsis* plants. Imaging of luciferase in 14-d-old plantlets shows that *AtSTP1* expression is strongest in young expanding leaves (Fig. 5a), but is also observed in roots (Fig. 5b). These observations are consistent with a role in the uptake of glucose derived from the hydrolysis of apoplastic sucrose in sink tissues. However, the rate of fructose uptake into *Arabidopsis* plantlets is very much slower than that of glucose (G Wallace, unpublished results), and none of the AtSTPs characterized so far, transports fructose. Therefore, the proposal that AtSTP1 functions in the uptake of monosaccharides released from the cell wall such as during cell expansion, and potentially in other circumstances (Fig. 1), is favoured.

Future research

No fructose transporters have yet been identified in *Arabidopsis*, and there is so far little evidence that the AtSTPs currently characterized are involved in the uptake

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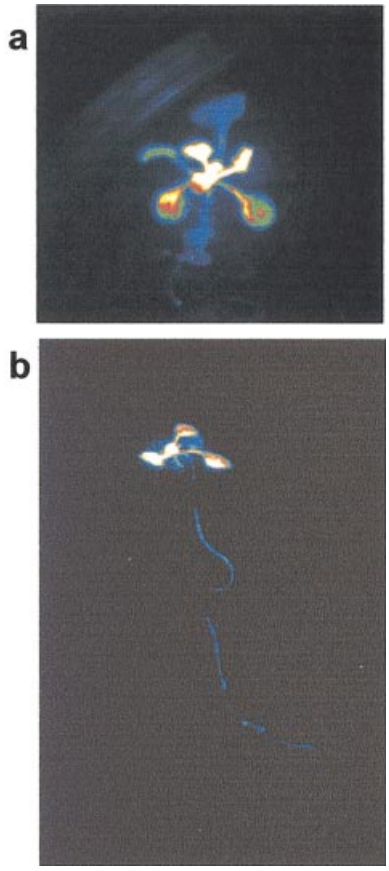

Fig. 5. Imaging of *AtSTP1* gene expressison with a *LUC* reporter gene. A 3 kbp *AtSTP1* gene promoter fragment was linked to the firefly luciferase gene and introduced into *Arabidopsis* plants using *Agrobacterium*-mediated transformation. Plants were grown on half-strength Murashige and Skoog medium in continuous light for 14 d as described in Sherson *et al*. (2000), then painted with 5 mM luciferin (in 0.01% Triton X-100), dark-incubated for 5 min to reduce chemiluminescence before imaging photon emission using an Andor CCD camera. Images are false-coloured such that increasing photon emission is represented progressively by blue, green, red, yellow, and white. (a) plant viewed from above showing emission predominantly from youngest leaves. (b) plant viewed longitudinally showing emission from shoot and root (HL Alford, unpublished results).

of hexoses derived from sucrose. Co-expression of specific *AtcwINV* and *AtSTP* genes would provide evidence for such a functional link, but so far none exists. Identification of AtSTPs which transport fructose will represent an important advance, and may then help to identify sink tissues in which extensive apoplastic sucrose hydrolysis and hexose uptake occur. The sensing of fructose uptake or phosphorylation would potentially provide the cell with a means to distinguish sucrose-derived hexoses from cell-wall- or callose-derived hexoses, and so to adjust to different physiological states. Whether fructose sensing occurs is speculative at this stage.

It is clear that cwINVs and STPs have very important roles in plant metabolism, growth and development, and that higher plants contain multiple genes encoding these proteins. *Arabidopsis* currently provides the best opportunity to determine the functions of these proteins through the application of functional genomics resources. KO mutants can not only be used to investigate the functions of individual genes systematically, but can be exploited as recipients for transgenes to engineer novel patterns of cwINV and STP synthesis in order to test the hypothesis that these proteins can direct growth and differentiation in plants.

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