Sugar transporters in higher plants – a diversity of roles and complex regulation

Lorraine E. Williams, Remi Lemoine and Norbert Sauer

Sugar-transport proteins play a crucial role in the cell-to-cell and long-distance distribution of sugars throughout the plant. In the past decade, genes encoding sugar transporters (or carriers) have been identified, functionally expressed in heterologous systems, and studied with respect to their spatial and temporal expression. Higher plants possess two distinct families of sugar carriers: the disaccharide transporters that primarily catalyse sucrose transport and the monosaccharide transporters that mediate the transport of a variable range of monosaccharides. The tissue and cellular expression pattern of the respective genes indicates their specific and sometimes unique physiological tasks. Some play a purely nutritional role and supply sugars to cells for growth and development, whereas others are involved in generating osmotic gradients required to drive mass flow or movement. Intriguingly, some carriers might be involved in signalling. Various levels of control regulate these sugar transporters during plant development and when the normal environment is perturbed. This article focuses on members of the monosaccharide transporter and disaccharide transporter families, providing details about their structure, function and regulation. The tissue and cellular distribution of these sugar transporters suggests that they have interesting physiological roles.

In higher plants, CO₂ fixation occurs predominantly in mesophyll cells of mature leaves. These are net exporters of sugars and are known as ‘carbon sources’. Heterotrophic cells in roots, reproductive structures, storage and developing organs rely on a supply of sugars for their nutrition; these are known as ‘carbon sinks’ (net importers). Mechanisms must exist to ensure that all sink tissues receive an adequate supply of sugars for growth and development, and sugar transporters play a pivotal role in the membrane transport of sugars and their distribution throughout the plant (Fig. 1).

Long-distance transport of carbohydrates between sources and sinks occurs in specific cells of the vascular system, the phloem sieve elements (Fig. 1). During their development, sieve elements extend longitudinally, degrade most of their organelles, including vacuoles, ribosomes and nuclei, and form large, plasma membrane-lined pores in their terminal cell walls, the sieve plates. The loss of organelar structures in sieve elements is paralleled by an extreme increase in organelle density in the phloem companion cells. Sieve elements and companion cells are intimately connected by numerous branched plasmodesmata and form the so-called sieve element–companion cell complex (SE–CCC). An important function of companion cells is the supply of energy and proteins to the sieve elements.

Phloem sap in sieve elements moves by bulk flow with rates of up to 1 m per h. At the source, accumulation of sugar inside the SE–CCC (at a concentration of several hundred mM to >1 M) results in the osmotic uptake of water, forcing sap to flow along the sieve tube. Unloading of sugar at the sink results in loss of water from the sieve tube and thus the gradient of pressure is maintained. Sucrose represents the main form of reduced carbon transported in sieve elements, although some plants can also transport raffinose, stachyose and polyols. These solutes are less subject to metabolism than glucose. After its synthesis, sucrose can pass the entire route from the mesophyll cells to the sieve element–companion cell in the symplast, moving from cell to cell via plasmodesmata (symplastic loading; Fig. 1). However, frequently, sucrose is released from the mesophyll cells and actively loaded from the apoplast into the SE–CCC (apoplastic loading). Plasma membrane sucrose–H⁺symporters are fundamental to this process. Unloading of sucrose at the sinks might also occur either symplastically or apoplastically. The route depends on species (both pathways might operate in the same organism), organ or tissue, and developmental stage. Sink cells either import sucrose from the apoplast directly via sucrose transporters or, alternatively, sucrose can be hydrolysed to glucose and fructose by cell-wall invertases and taken up via monosaccharide transporters.

Plants appear to have several monosaccharide and disaccharide transporters to coordinate sugar transport in diverse tissues, at different developmental stages and under varying environmental conditions. The nomenclature in the literature for plant sugar transporters has become rather confusing with SUT and SUC being used for disaccharide transporters, and STP, MST, HEX and ST being used for monosaccharide transporters. Here we will refer to disaccharide transporters as DSTs and refer to monosaccharide transporters as MSTs. Some of the physiological functions of these sugar transporters, as suggested from work at the molecular level, will be discussed. Other proteins that have been implicated in the transport of sugars [e.g. sugar-binding protein, SBP (Ref. 1)] will not be considered here.

**Multi-gene families for sugar transporters**

In *Arabidopsis*, 14 putative MST genes have been identified to date and at least seven DST genes can be found in *Arabidopsis* data libraries. Heterologous expression in yeast or *Xenopus* oocytes has been carried out for some of the family members, and evidence suggests that they function as proton symporters. Generally the DSTs are highly specific for sucrose, although some have been shown to transport maltose. Their *Kₘ* values are in the
Transporting a range of hexoses and pentoses with structural similarities (Fig. 2). They are thought to be members of DSTs share little homology at the amino acid level, although there preferred substrate being typically 10–100 M (Ref. 2). MSTs have broader substrate specificity, and this is related to impaired sucrose export. Phloem-localized SUT1 (DST) homologues might play an additional role in both the retrieval of sucrose leaking from sieve elements along the translocation pathway and possibly in catalysing the export of sucrose from the phloem in sinks (Fig. 1). Moreover, the same transporters are not always confined to the phloem but are also present at lower levels in other leaf cells where they might function in retrieval17,20.

Diverse locations for sugar transporters
Plant cells appear to possess sugar transporters tailored to meet their specific requirements at particular stages of development and this is related to impaired sucrose export. Phloem-localized SUT1 (DST) homologues might play an additional role in both the retrieval of sucrose leaking from sieve elements along the translocation pathway and possibly in catalysing the export of sucrose from the phloem in sinks (Fig. 1). Moreover, the same transporters are not always confined to the phloem but are also present at lower levels in other leaf cells where they might function in retrieval17,20.

Sugar transporters in roots
Roots represent heterotrophic carbon sinks and can be divided into zones of cell division, elongation and maturation. AtSTP4 (MST), a monosaccharide transporter from Arabidopsis, is found
only at the root tip, probably in the root meristem (Fig. 4). This indicates that part of the post-phloem transport in Arabidopsis roots occurs apoplastically and that the role of AtSTP4 (MST) is to import hexoses generated from sucrose hydrolysis by cell-wall invertase following phloem unloading. In Medicago truncatula, the gene for the monosaccharide transporter, Mtst1 (MST), is only expressed in cells immediately behind the root apical meristem, in cells within the elongation zone and possibly in the zone of cell division. Elongating cells have a high requirement for hexoses as precursors for macromolecular synthesis and to allow them to maintain osmotic pressure during elongation.Mtst1 (MST) is also expressed in primary phloem fibres where it might provide hexoses for cell wall biosynthesis and deposition.

Sucrose transporters have also been detected in particular cells of the root: DcSUT2 (DST) is expressed in storage parenchyma tissues of carrot tap-roots where it seems to import sucrose for storage. This and other DST homologues have also been detected in phloem cells of the root, where they might retrieve sucrose into the phloem or possibly catalyse the efflux of sucrose from the phloem.

A role for sugar transporters in developing and germinating seeds
The developing embryo is symplastically isolated from maternal tissues and is reliant on the import of sugars from the surrounding apoplastic space. Sugars are required for embryo development and for the deposition of storage compounds necessary for germination. DSTs and MSTs have been identified in Vicia faba, Pisum sativum and Hordeum vulgare (Refs 24–26). In Vicia, VfSTP1 (MST) is expressed in the embryo cotyledon epidermal cells. Expression is confined to epidermal regions covering the mitotically active parenchyma, indicating that this transporter serves to supply substrate for metabolism. During later stages of embryo development, VfSTP1 (MST) is replaced by the sucrose transporter VfSUT1 (DST) expression is highest in epidermal cells with transfer-cell morphology and with storage activity in the underlying parenchyma, indicating that the encoded transporter is responsible for providing substrate for the synthesis of storage compounds.

Certain seeds accumulate storage reserves in the endosperm during development. Upon germination, these are hydrolysed and the products, including sugars, are released into the apoplastic space (Fig. 5). In germinating seeds of Ricinus communis, a sucrose carrier, RcSUT1 (DST), is expressed at high levels in both the cotyledon epidermal cells that are situated adjacent to the endosperm and also in the phloem. This suggests that the epidermal cells initially accumulate sucrose from the apoplast and from here sucrose is transferred symplastically to the phloem region. The high expression of RcSUT1 (DST) in the phloem indicates that sugars are released into the apoplast before active loading by this transporter.

A variety of roles for sugar transporters in floral organs
Developing pollen grains are strong sinks that require carbohydrate import from the apoplast during maturation, germination and growth. The Arabidopsis monosaccharide transporter gene,
Fig. 3. Phylogenetic analysis for (a) monosaccharide transporters (MSTs) and (b) disaccharide transporters (DSTs). (a) Sugar-transport proteins homologous to lower and higher plant monosaccharide transporters are found in prokaryotes, fungi and mammals, indicating that the corresponding genes form an ancient gene family. Monosaccharide transporters from one species, such as the Arabidopsis AtSTPs, do not form a single subcluster within the higher plant subfamily, suggesting that several independent genes already existed at the beginning of or early in higher plant evolution. The less closely related Arabidopsis AtERD6 protein (Accession no. D89051), described as a putative sugar transporter, clusters with the human glucose facilitator. (b) Proteins closely related to higher plant sucrose transporters are not found in bacteria, fungi or mammals, indicating that plant sucrose-transporter genes evolved comparatively late. Sucrose transporters from Arabidopsis cluster together with sucrose transporters from monocots and from plants with symplastic phloem loading. A functionally uncharacterized transporter from Schizosaccharomyces pombe (Accession no. Z99165) shows some similarity, but only in the N-terminal half of the protein. EcMelB (the outgroup) is extremely distantly related to plant sucrose transporters. Bootstrap values given at internal nodes indicate the percentage of the occurrence of these nodes in 100 replicates (maximum parsimony) of the data set. The sequence of the E. coli xylose permease (EcXyIE; black) and of the E. coli melibiose transporter (EcMelB; black) were used as outgroups in (a) and (b), respectively. Accession numbers for nonplant monosaccharide transporter sequences are AmMS1T (Amanita muscaria monosaccharide transporter), X58282; EcAraE (E. coli arabinose transporter), J03732; EcGalP (E. coli galactose permease), AE00377; EcMelB (E. coli melibiose transporter), K01991; EcXyIE (E. coli xylose transporter), P90908; HsGlut1 (Homo sapiens glucose transporter), 75729; ScXyIE (Saccharomyces cerevisiae hexose transporter), M82963; ScHXT2 (S. cerevisiae hexose transporter), M33270; ScHXT3 (S. cerevisiae hexose transporter), L07080; ScRGT2 (S. cerevisiae hexose transporter-like glucose sensor), Z74186; ScSUT5 (S. cerevisiae hexose transporter-like glucose sensor), J03246; SspGTR (Synechocystis sp. glucose transporter), X16472. Maximum parsimony (MP) bootstrap analyses of aligned sequences were conducted with the PHYLIP package 3.572c. Addition of taxa was jumbled and repeated three times for each individual bootstrap replication in the MP analysis. Output treefiles were combined with the CONSENSE program and converted into a graphical representation by the TREEVIEW program. Accession numbers of plant sucrose transporters used in this tree are AbSUT1 (A. thaliana, X57382); AtSUT3 (A. thaliana, AC004138); AtSUC4 (A. thaliana, AC000132); AtSUC5 (A. thaliana, AC252133); AtSUC2 (A. thaliana, X75382); AtSUC3 (A. thaliana, AC004138); AtSUC4 (A. thaliana, AC000132); AtSUC5 (A. thaliana, AC252133); AtSUC2 (A. thaliana, AAC69375); AtSUC13 (A. thaliana, AB106875); BvSUT1 (Beta vulgaris, X38350); DcSUT1 (Daucus carota, Y16766); DcSUT2 (D. carota, AB036758); HvSUT1 (Hordeum vulgare; Accession no. not yet available); HvSUT2 (H. vulgare; Accession no. not yet available); NtSUT1 (Nicotiana tabacum, X82276); OsSUT1 (Oryza sativa, D87819); PmSUC1 (Plantago major, X75764); PmSUC2 (P. major, X75764); SoSUT1 (Spinacea oleracea, X76125); SiSUT1 (Solanum tuberosum, X69165); VisSUT1 (Vicia faba, 293774). Accession nos of plant monosaccharide transporters used in this tree are AtSTP1 (A. thaliana, X55350); AtSTP2 (A. thaliana, AJ001362); AtSTP3 (A. thaliana, AJ002399); AtSTP4 (A. thaliana, X66857); AtSTP6 (A. thaliana, AC013454); AtSTP7 (A. thaliana, AF001308); AtSTP8 (A. thaliana, AF077407); AtSTP9 (A. thaliana, AC007980); AtSTP10 (A. thaliana, AB025631); AtSTP11 (A. thaliana, AB007648); AtSTP12 (A. thaliana, AL022603); AtSTP13 (A. thaliana, AF077407); AtSTP14 (A. thaliana, AC004260); ChkHUP1 (Chlorella kessleri, Y07520); ChkHUP2 (C. kessleri, X66855); ChkHUP3 (C. kessleri, X75440); LeMST1 (Lycopersicon esculentum, AJ010942); MtMST1 (Medicago truncatula, U33651); PaMST1 (Picea abies, Z38329); PhPMT1 (Petunia hybrida, AF061106); RhX61 (Ricinus communis, L08197); RhX66 (R. communis, L08188); RcSTC (R. communis, L08196); SspGTR2 (Saccharum hybrid, L21753); VmST1 (V. faba, Z93775); VmST1 (Vitis vinifera, AJ001061).
AtSTP2 (MST), is expressed after meiosis of the pollen mother cell at the time when the uninucleate microspores are developing. This correlates with the time when callose surrounding the microspores is degraded. After this, AtSTP2 (MST) mRNA and protein are rapidly degraded. Thus, AtSTP2 (MST) could serve in the uptake of glucose (resulting from callose degradation) and also other monosaccharides such as xylose, mannose or galactose (from degradation of other cell-wall components) into the symplastically isolated, developing male gametophyte.

Carbohydrates are also required to supply energy for pollen germination and pollen-tube growth. PhPMT1 (MST), a putative hexose transporter gene in Petunia, is expressed specifically in mature anthers and pollen, and not in any other floral or vegetative tissues. Thus, in this species, sucrose might be hydrolysed to glucose and fructose by a cell-wall invertase before uptake by PhPMT1 (MST) in the growing pollen tube. A similar localization has been shown for the Arabidopsis AtSUC1 (DST) monosaccharide transporter (Fig. 4); however, its function is unclear because in this species (and in many others) sucrose is the preferred carbon source during pollen germination and growth in vitro. Recent studies describing the expression of the sucrose transporter genes, AtSUC1 (DST) in germinating Arabidopsis pollen (Fig. 4) and NtSUT3 (DST) in tobacco pollen, are consistent with this. Interestingly, AtSUC1 (DST) mRNA was detected in developing pollen whereas the protein was only found after pollen germination, indicating that expression might be translationally regulated and induced during germination.

AtSUC1 (DST) is also expressed in a ring of parenchymatic cells surrounding the transmitting tissue of the style and in the epidermal cell layers of the funiculi. This expression pattern is unlikely to reflect a higher requirement for carbohydrates by these cells; instead it might indicate that AtSUC1 (DST) modulates the availability of water in this region, which could establish a cue for pollen-tube guidance towards the ovule.

In anthers, AtSUC1 (DST) mRNA and protein were detected in parenchymatic cells surrounding the central vascular bundle of anther connective tissue just before anther opening by dehiscence (Fig. 4). Accumulation of sucrose by AtSUC1 (DST) could decrease the water potential and hence result in water uptake from the adjacent cells of the anther walls. This would result in dehydration of the endothecium and an increased tension of its wall thickenings, finally causing anther opening.

Fig. 4. Tissue and cellular distribution of various sugar transporters. The tissue or cell-specific expression of several sugar transporters indicates their specific physiological tasks. For example, sugar transporters have been implicated in processes as diverse as phloem loading and unloading, pollen development and germination, and pathogen interaction. (a) Expression of the sucrose transporter gene AtSUC2 (disaccharide transporter, DST) in the veins of Arabidopsis source leaves indicates a role in phloem loading. The expression is demonstrated by the activity of the reporter gene for β-glucuronidase (GUS) driven by the AtSUC2 promoter. In (b), the AtSUC2 (DST) protein was immunolocalized with fluorescent secondary antibodies in companion cells of leaf minor veins. Xylem vessels are identified by the yellow autofluorescence of lignin. (c) Expression of the monosaccharide transporter gene AtSTP4, from Arabidopsis in root tips is shown by GUS expression under the control of the AtSTP4 promoter. The expression of this carrier is also induced by wounding and pathogen attack. (d) In situ hybridization of AtSUC1 (DST) mRNA on an anther cross-section. At this stage, the AtSUC1 (DST) protein is detected in the connective tissue but not in the pollen, suggesting translational regulation. The sucrose carrier AtSUC1 (DST) mRNA from Arabidopsis has been identified in the connective tissue of mature anthers and also in pollen. In the connective tissue, AtSUC1 (DST) could be involved in the control of anther dehiscence. (e) The monosaccharide transporter AtSTP4 (MST) is detected in pollen tubes growing inside the transmitting tissue of the style (longitudinal section through a style). Specific antibodies were used and the fluorescence of the secondary antibodies appears in green. Interestingly, the sucrose transporter AtSUC1 (DST) is also present in germinating pollen.
approximately fourfold in Arabidopsis seedlings infected with Alternaria brassicicola or Fusarium oxysporum, and also in suspension-cultured cells of Arabidopsis treated with bacterial or fungal elicitors\(^\text{31}\). It has been concluded that AtSTP4 (MST) plays a role in the transportation of monosaccharides into the sink tissues and that it responds to an increased demand for carbohydrate by cells under stress conditions\(^\text{31}\). Induction of AtSTP4 (MST) expression is also observed during plant and fungal biotrophic interaction, for example, Arabidopsis infected with the powdery mildew Erysiphe cichoracearum\(^\text{31}\). Expression of AtSTP4 (MST) is induced dramatically in source leaves infected with mildew and, although the fungus is confined to epidermal cells, AtSTP4 (MST) expression is induced in many cell types within the leaf following infection (M. Gilbert et al., unpublished). The signalling pathway by which this occurs is unknown, and the role of this transporter in this interaction is unclear. It might help to increase carbohydrate import into infected tissues, in order to cope with the increased demand related to defence activities, or serve to recover sugars from the apoplast (particularly if host-cell permeability is increased) and thus reduce the loss of carbohydrate to the pathogen.

Sugar transporters are also important in carbon transfer to mycorrhizal fungi\(^\text{22}\). Colonization of Medicago truncatula roots with the mycorrhizal fungus Glomus versiforme, induces expression of the monosaccharide transporter gene, MtST1 (MST), in cortical cells of the root that correlates with regions that are heavily colonized by the fungus\(^\text{22}\). The effect is localized to cells within the immediate vicinity of the fungus, either in cells containing an arbuscle, or cells that are frequently in contact with intercellular hyphae. The nature of the signal for the induction of plant sugar-carriers during microorganism interactions is not yet clear.

**Role in sugar sensing**

 Sugars can act as regulatory signals that affect gene expression and hence plant development. In relation to resource allocation, the ability to sense altered sugar concentrations could have important advantages by allowing the plant to tailor its metabolism in source tissues to meet the demands in sinks. There is great interest in dissecting the signalling processes that are involved in sugar sensing and response pathways. There are three possible sugar-sensing systems in plants\(^\text{32}\):

- A hexokinase-sensing system.
- A sucrose-transport-associated sensor.
- A glucose-transport-associated sensor.

Based on sugar signal transduction processes in Saccharomyces, it has been proposed that members of the sugar transporter family in plants might play a role in sugar sensing\(^\text{31}\). In yeast, it has been shown that membrane-bound receptors closely related to sugar transporters are used to sense external sugar concentrations and activate a signal transduction pathway leading to the regulation of

---

**Fig. 5.** Localization of the sucrose carrier in a germinating Ricinus seedling. Seeds accumulate storage reserves in the endosperm during development. Upon germination, these are hydrolysed and the products, including sugars, are released into the apoplastic space. Seven-day-old dark-grown germinating Ricinus seedlings are shown in (a) with (left) and without (right) an endosperm. (b) Breakdown of lipids and protein in the endosperm and the release of sucrose and amino acids into the apoplast for uptake by the cotyledon. (c) Expression pattern of the sucrose transporter, RsSUT1 (DST)\(^\text{13,46}\), in the germinating Ricinus seedling (three-day-old). RsSUT1 transcripts were localized by in situ hybridization using an antisense RsSUT1 cRNA probe. Dark staining, indicating RsSUT1 expression, is seen in both the cotyledon lower epidermal cells (LE) that are situated adjacent to the endosperm (parts i–iii) and also in the phloem (red arrows in iii). No equivalent staining was observed in sections probed with the sense probe (results not shown). The expression pattern indicates that the epidermal cells initially accumulate sucrose from the apoplast and from here sucrose is transferred symplastically to the phloem region. The high level of expression of RsSUT1 in the phloem indicates that sugars are released into the apoplast before active loading by this transporter. Scale bars = 100 \(\mu\)m in (i) and (ii); 50 \(\mu\)m in (iii). (c) reproduced, with permission, from Ref. 13.
levels at which regulation might occur\textsuperscript{35,36}. As for all \(H^{+}\)-symporters, regulation of activity by the proton-motive force is clearly important. Thus, modulations in the activity of the \(H^{+}\)-ATPase would immediately affect their sugar transport kinetics.

There are numerous examples for transcriptional regulation of \textit{DST} or \textit{MST} gene expression, such as changes in \textit{DST} expression pattern in leaves undergoing sink-to-source transition\textsuperscript{19,37} during seed development (\textit{MST} and \textit{DST})\textsuperscript{24}, or during pollen maturation and germination (\textit{MST} and \textit{DST})\textsuperscript{25,26}. There is also evidence that biotic and abiotic factors (e.g. mechanical treatments, light, water and salt stress, phytohormones, and pathogen attack) have effects on the expression of certain sugar transporters\textsuperscript{21,30,36}. Post-transcriptional control mechanisms such as mRNA stability (turnover), mRNA translation and post-translational control have also been described for sugar transporters. Examples include the diurnal regulation of \textit{DSTs} (Refs 12,39), phosphorylation–dephosphorylation\textsuperscript{40}, and possible modification of activity by the lipid environment\textsuperscript{41}.

There is evidence that changing sugar levels might have an effect on sugar transporter expression and activity. Evidence has been provided that a putative sucrose-sensing pathway could modulate the expression levels and activity of a proton–sucrose transporter as a function of changing sucrose concentrations in the leaf (hexoses do not elicit the response)\textsuperscript{41}. This would have a direct impact on assimilate partitioning at the level of phloem translocation. Changes in transcriptional activity or mRNA turnover mediate this repression by sucrose but additional regulation by alterations in protein turnover or direct modification cannot be ruled out. The response is reversible, highlighting the dynamic nature of this signalling pathway.

Evidence for sugar regulation of transporters is variable. \textit{AtSUC2} (\textit{DST}) expression (analysed using a \textit{SUC2} promoter–\textit{GUS} construct) appears unaffected by sugars\textsuperscript{19}. However, down-regulation might not be seen in these experiments because of the stability of the \textit{GUS} protein. In addition, it is still possible that activity might be affected by other mechanisms, even if the promoter is insensitive to sugars. The expression of the \textit{Vicia faba} sucrose carrier gene, \textit{VfSUT1} (\textit{DST}), but not the glucose transporter, \textit{VfSTP1} (\textit{MST}), decreased in cotyledons following exposure to high concentrations of sucrose or glucose (150 mm), whereas lower levels (10 mm) had no effect on transcript levels\textsuperscript{24}. Sucrose-feeding experiments with detached maize leaves led to an increase in transcript leaves of \textit{ZnSUT1} (Ref. 42) (\textit{DST}). By contrast, no evidence was found for sugar regulation of three monosaccharide-transporter genes (\textit{CST1}–3) (\textit{MSTs}) in suspension-cultured cells of \textit{Chenopodium rubrum}\textsuperscript{43}.

Thus, for sugar transporters, it is now emerging that various levels of control are implemented that allow plant cells to regulate the fluxes of sugars across the plasma membrane during normal growth and development, and also when their natural environment is perturbed.

The future

To comprehend source–sink regulation fully and to be in a position to manipulate the complex interactions for agricultural benefit, it is vital that the underlying membrane transport processes are thoroughly characterized. This includes determining precisely the range of sugar transporters that are involved, their structure–function relationships, and defining their cellular and temporal expression pattern. A particular goal would be the ability to manipulate competition between sinks. For this we need to find out how sugar carriers are regulated in metabolic and storage sinks and to relate this to the information available on the activity of the sucrose metabolizing enzymes, invertase and sucrose synthase. Extracellular invertase is up-regulated in several situations affecting source–sink relations (e.g. following application of phytohormones and elicitors, pathogen attack and wounding)\textsuperscript{44} but further work is required to investigate the coordination of events. In sink cells, it is important to understand why, in some cases, sucrose is cleaved by a cell-wall invertase and therefore hexose carriers are involved, whereas in other cases sucrose is taken up and cleaved inside the cells. In germinating pollen, both monosaccharide and disaccharide transporters are present\textsuperscript{28–30}, although sucrose is the preferred carbon source for \textit{in vitro} germination and hexoses are inhibiting. Clearly, work is needed for a full comprehension of the respective role of each carrier type in such cells.

We need to clarify which mechanisms exist for the efflux of sugars from cells, for example, for efflux from the mesophyll or from apoplastically unloading phloem cells. Under nonenergized conditions, influx carriers might be operating in efflux, allowing sugars to be transported down their concentration gradient; alternatively, different transporters might be involved. In addition, the identification of tonoplast sugar transporters is important for understanding storage and remobilization from the vacuole. We must also consider that entirely different mechanisms might exist for sugar transport, such as those involving ABC transporters.

More evidence is required on the physiological function of sugar transporters to support the information from expression studies. In particular, no antisense studies have been reported for any of the monosaccharide transporters. We eagerly await studies on knockout mutants to dissect the transport processes in greater detail. The phenotype of such plants will provide clues concerning the physiological role and importance of particular transporters. In addition, plants with transporter genes under the control of cell-specific promoters will enable us to learn more about source–sink interactions and pathways of sugar movement.

Sensing functions are essential in allowing plants to adapt to changing environments. One of the major challenges will be to identify sugar-sensing mechanisms and the signal transduction pathways. It will be important to ascertain whether members of the sugar-transporter families are involved in this function.

Acknowledgements

Our work has been supported by a grant from the European Commission DG XII Biotechnology programme (ContractBIO4-CT96-0583). L.E.W. is grateful to the Royal Society for support. R.L.’s work is supported by the CNRS, the French Ministry for Education and Research and by the Région Poitou Charentes. N.S.’s work was supported by the Deutsche Forschungsgemeinschaft. The help of Volker Huss with Figure 3 and the help of Cyril Maingourd with Figure 4 is gratefully acknowledged.

References

5. Boorer, K.J. et al. (1994) \textit{AtSUC1} and \textit{AtSUC2}: two sucrose transporters from \textit{Arabidopsis thaliana} expressed in \textit{Xenopus} oocytes. \textit{J. Biol. Chem.} 269, 20417–20424
20 Lemoine, R. 

7 Stolze, J. et al. (1994) Functional reconstitution of the solubilized Arabidopsis thaliana STP1 monosaccharide−H+ symporter in lipid vesicles and purification of the histidine tagged protein from transgenic Saccharomyces cerevisiae. Plant J. 6, 225−233


14 Stadler, R. et al. (1995) Phloem loading by the PmSUC2 sucrose carrier from Plantago major occurs into companion cells. Plant Cell 7, 1545−1554


16 Riesmeier, J.W. et al. (1994) Evidence for an essential role of the sucrose transporter in phloem loading and assimilate partitioning. EMBO J. 13, 1−7


26 Weschke, W. et al. (2000) Sucrose transport into barley seeds: molecular characterization of two transporters and implications for seed development and starch accumulation. Plant J. 21, 455−467


29 Stadler, R. et al. (1999) The AtSUC1 sucrose carrier may represent the osmotic driving force for autophytic dehiscence and pollen tube growth in Arabidopsis. Plant J. 19, 269−278
