Genetics of Sucrose Transporter in Plants

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ABSTRACT

Sucrose is one of the most common and abundant carbon forms in plants. Most plants synthesize sucrose as a major photosynthetic product and use it for long distance carbon transport. Therefore sucrose transport in plants probably is highly regulated and sucrose transporters have indispensable roles in the regulation. In the Arabidopsis genome, 69 sugar transporter homologues have been found, 9 of which are in the sucrose transporter SUC/SUT family. The SUC/SUT family is further divided into three subfamilies based on homology: SUC2/SUT1, SUC3/SUT2 and SUC4 subfamilies. Gene structures, protein structures, kinetics of sucrose transport and subcellular localizations differ between these three subfamilies. Sucrose transporter genes have been isolated from many different plants and their expressions, regulations and physiological roles have been studied. This review summarizes these studies of sucrose transporters.

CONTENTS

INTRODUCTION

Most plants synthesize sucrose as a major photosynthetic product and use it for long-distance carbon transport. Although some plant species use oligosaccharides or polyols for long-distance carbon transport (Keller and Pharr 1996; Noiraud *et al*. 2001b), such as the raffinose series of oligosaccharides in Cucurbitaceae, sorbitol in Rosaceae and mannitol in Apiaceae, these plants also synthesize sucrose and use it for long-distance carbon transport. Thus sucrose is a universal form of long-distance carbon transport and sucrose transport systems have indispensable roles in plant growth and development. Riesmeier *et al*. (1992) identified sucrose transporter cDNA (*SoSUT1*) in the spinach cDNA library by using a screening system with a yeast mutant. Since then, many sucrose transporter genes have been identified and characterized for various plant species. The importance of sucrose transporters not only in sucrose phloem loading in source leaves, but also in the development of various sink organs and tissues such as seeds and fruits, have been reported. Sucrose transporters in plants may be controlled not only by transcriptional and translational regulations, but also by post-translational regulations, inc-

luding protein phosphorylation and oligomerization of different kinds of sucrose transporters. Recent proteome analyses of vacuolar membrane proteins identified sucrose transporters of vacuolar membrane. Ward *et al*. (1998), Kühn *et al*. (1999), Lalonde *et al*. (1999, 2004), Lemoine (2000), Williams *et al*. (2000) and Kühn (2003) summarized sucrose transporters in plants. Here, sucrose transporter studies in plants are reviewed generally and recent information is added.

SUCROSE TRANSPORTER FAMILY AND SUBFAMILIES

Sugar transporters in different organisms, including human, plants and yeast, belong to a major facilitator superfamily (MFS) (Lalonde *et al*. 2004). At least 69 sugar transporter homologues have been found in Arabidopsis and are classified into eight large families (Shiratake 2007): sucrose transporter (SUC/SUT), hexose transporter (STP/HXT), polyol transporter (PLT), *myo*-inositol transporter (ITR/MIT), plastidic glucose transporter (pGlcT), putative monosaccharide sensing protein (AZT/MSSP), SFP and one uncharacterized monosaccharide transporter family. Nine suc-
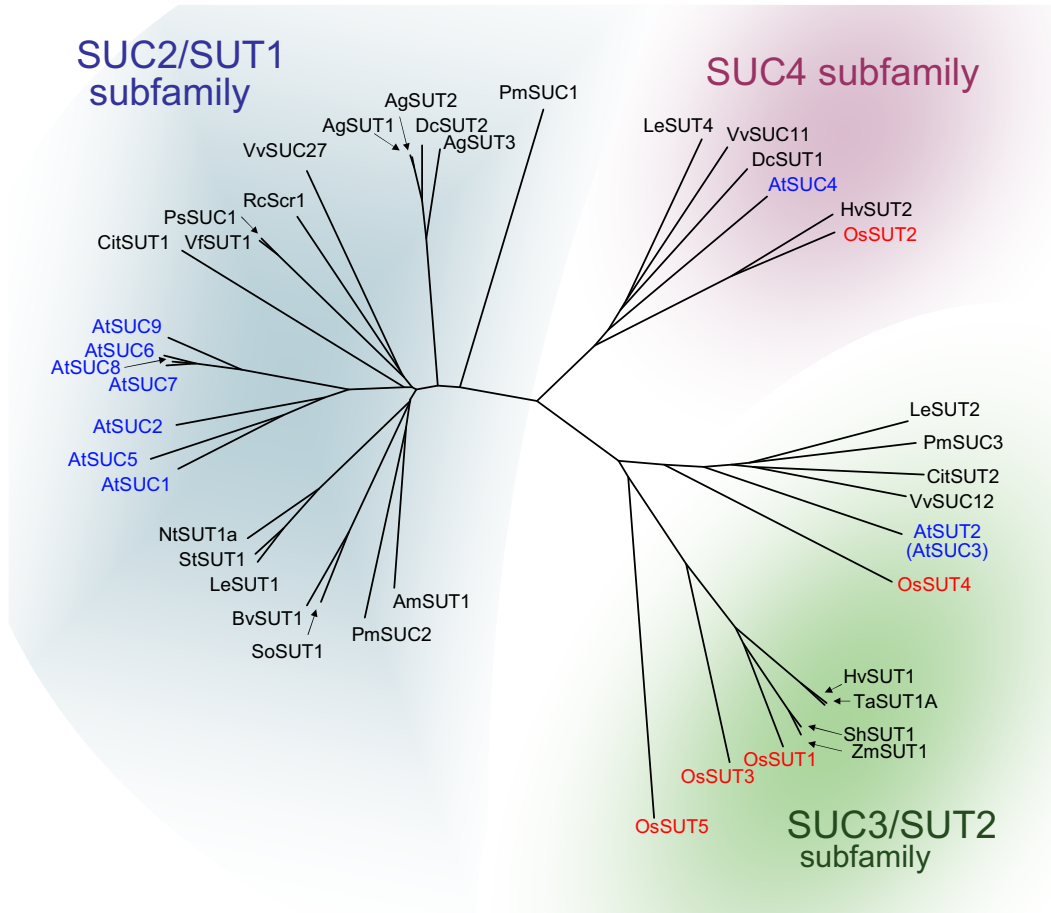
Invited Review

Fig. 1 Phylogenetic tree of the SUC/SUT family. An unrooted N-J tree was constructed for sucrose transporters of various plants in the text by using CLUSTAL W. The SUC/SUT family was further classified into three subfamilies: SUC2/SUT1, SUC4 and SUC3/SUT2 subfamilies. Ag, *Apium graveolens*; Am, *Alonsoa meridionalis*; At, *Arabidopsis thaliana*; Bv, *Beta vulgaris*; Cit, *Citrus sinensis*; Dc, *Daucus carota*; Hv, *Hordeum vulgaris*; Le, *Lycopersicon esculentum*; Nt, *Nicotiana tabacum*; Os, *Oryza sativa*; Pm, *Plantago major*; Ps, *Pisum sativum*; Rc, *Ricinus communis*; Sh, *Saccharm hybrid*; So, *Spinacea oleracea*; St, *Solanum tuberosum*; Ta, *Triticum aestivum*; Vf, *Vicia faba*; Vv, *Vitis vinifera*; Zm, *Zea mays*.
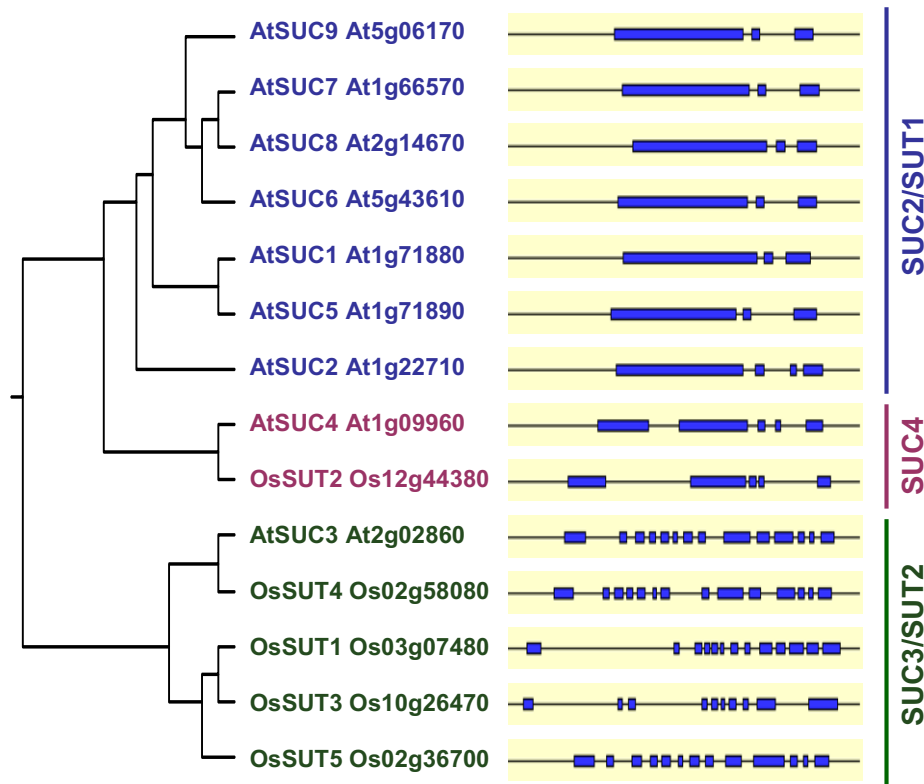

Fig. 2 Gene structures of the SUC/SUT family of Arabidopsis and rice. An N-J tree was constructed by using CLUSTAL W. Gene structures are the predictions in ARAMEMNON (http://aramemnon.botanik.uni-koeln.de/). Exons and introns are shown by a blue box and a black line, respectively.

rose transporter homologues of Arabidopsis belong to the SUC/SUT family, which is, together with the STP/HXT family, the most well-characterized family. Homologues of the SUC/SUT family exist in other higher and lower organisms, including *Escherichia coli*, yeast and human, however, amino acid identity between the homologues and the SUC/SUT family is very low. The homologues are members of the MFS and called oligosaccharide/H^+ symporter (OHS) family (Pao *et al*. 1998). In most organisms, sucrose is a minor sugar and sucrose transport system is not necessary. Therefore, although some members of the OHS family can transport sucrose, they are not for sucrose transport but for other disaccharides or oligosaccharides, such as lactose and raffinose, in organisms other than plants (Pao *et al*. 1998).

Gene structures of sucrose transporters

The SUC/SUT family is further divided into three subfamilies based on homology: SUC2/SUT1, SUC3/SUT2 and SUC4 (**Fig. 1**). Nine and five sucrose transporter genes are in the Arabidopsis and rice genomes, respectively. Their gene structures (compositions of exons and introns) were compared in this study (**Fig. 2**). Interestingly, the gene structures of these sucrose transporters are very similar within each subfamily, but differ between the three subfamilies. Genes in the SUC2/SUT1 subfamily have a large first exon and small second and third exons. One exception in the SUC2/SUT1 subfamily is *AtSUC2* that has a large first exon and three small exons, but its gene structure is still more similar to other members of the SUC2/SUT1 subfamily than to the other two families. Genes of the SUC4 subfamily have large first and second exons and three smaller exons. The first and second exons in the SUC4 subfamily might correspond to the first large exon in the SUC2/SUT1 subfamily. The gene structure of the SUC3/SUT2 subfamily is very different from that of the SUC2/SUT1 and SUC4 subfamilies because it consists of more than ten small exons.

Interestingly, sucrose transporters of dicotyledons are distributed in all three subfamilies, but those of monocotyledons are only in the SUC3/SUT2 and SUC4 subfamilies. This suggests that the SUC3/SUT2 and SUC4 subfamilies existed in primitive plants before the evolutionary divergence of monocotyledons and dicotyledons. The SUC2/SUT1 subfamily might have appeared in dicotyledons after the divergence. Each plant family or species has paralogues close to each other in the SUC2/SUT1 subfamily. For instance, seven paralogues of Arabidopsis and three paralogues of celery in the SUC2/SUT1 subfamily form a cluster in each of the plants (**Fig. 1**). This suggests that paralogues of the SUC2/SUT1 subfamily in each plant species might have differentiated in a later period of evolution. The major sucrose subfamilies of dicotyledons and monocotyledons are the SUC2/SUT1 subfamily and the SUC3/SUT2 subfamily, respectively, and so dicotyledons and monocotyledons each developed their subfamily preferentially during their evolution.

Protein structure and kinetics of sucrose transporters

The SUC/SUT family has typical structures of an MFS, such as 12 transmembrane domains (TMDs) and 11 loops (**Fig. 3**). The N- and C-terminuses are considered to be in the cytosol. The gene (**Fig. 2**) and protein (**Fig. 3**) structures of the SUC3/SUT2 subfamily differ from those of the SUC2/SUT1 and SUC4 subfamilies. The SUC3/SUT2 subfamily, with some exceptions in rice, has extended domains in the central loop (about 50 amino acids longer than the other subfamilies) and the N-terminus is about 30 amino acids longer than for the other subfamilies (Barker *et al*. 2000, **Fig. 3**). Yeast sugar sensor proteins, such as SNF3 and RGT2, have a hexose transporter-like structure with an extended domain (Özcan *et al*. 1996, 1998). Sucrose trans-
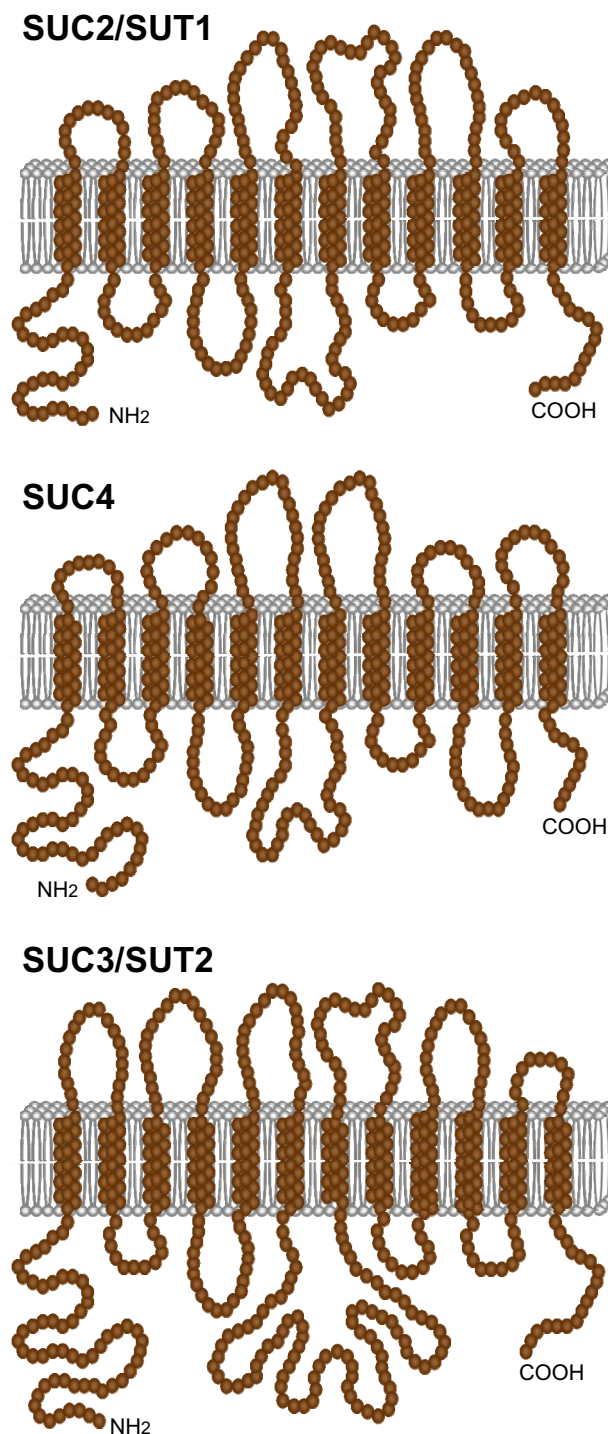

Fig. 3 Protein structure of the SUC2/SUT1 subfamily (AtSUC2/ SUT1), SUC4 subfamily (AtSUC4) and SUC3/SUT2 subfamily (AtSUC3/SUT2). Transmembrane domains were predicted by HMMTOP (http://www.enzim.hu/hmmtop/). Sucrose transporters have 12 transmembrane domains (TMDs) and 11 loops. The SUC3/SUT2 subfamily has extended domains in the central loop and N-terminus.

port activity has not detected for yeast-expressed tomato LeSUT2 (Barker *et al*. 2000), and so LeSUT2 is hypothesized to act as a sucrose sensor. However, the SUC3/SUT2 subfamily, such as common plantain PmSUC3, rice OsSUT1 and barley HvSUT1, have the ability to transport sucrose (Hirose *et al*. 1997; Toyofuku *et al*. 2000; Barth *et al*. 2003; Sivitz *et al*. 2005). The knockout mutant of Arabidopsis *AtSUT2* has no conspicuous phenotype (Barth *et al*. 2003), suggesting that AtSUT2 does not act as a sensor because a more marked phenotype would be expected for such a sensor. Whether members of the SUC3/SUT2 subfamily act as sucrose sensors is still debatable (Eckardt 2003).

The SUC2/SUT1 subfamily was identified first and its sucrose transport activity was characterized well. It includes high-affinity sucrose transporters with Km values for sucrose of 100 µM to 2 mM (Kühn 2003). The SUC4 subfamily with few exceptions, include low-affinity sucrose transporters of Km about 5 mM (Weise *et al*. 2000; Weschke *et al*. 2000). The SUC3/SUT2 subfamily, such as common plantain PmSUC3, rice OsSUT1 and barley HvSUT1, show low-affinity sucrose transport activities (Hirose *et al*. 1997; Toyofuku *et al*. 2000; Barth *et al*. 2003; Sivitz *et al*. 2005). Most members of the SUC3/SUT2 subfamily have extended domains in the central loop and the N-terminus, and the domains are considered to be important for affinity for sucrose or for regulation of transport activity or both. Schulze *et al*. (2000) exchanged the N-terminuses of the SUC3/SUT2 subfamily (AtSUT2, low affinity for sucrose) and the SUC2/SUT1 subfamily (StSUT1, high affinity for sucrose): AtSUT2 with the N-terminus of StSUT1 showed higher affinity and StSUT1 with the N-terminus of AtSUT2 showed lower affinity compared with their native forms. This shows the importance of the N-terminus for affinity of sucrose transport. Conversely, deletion and replacement of the extended central loop domain of the SUC3/SUT2 subfamily does not affect transport activity (Meyer *et al*. 2000; Schulze *et al*. 2000), suggesting that the loop domain is not required for transport. The function of the extended central loop of the SUC3/SUT2 subfamily is still unclear.

Subcellular localization (vacuolar sucrose transporters)

The SUC/SUT family has been shown (Kühn *et al*. 1997; Barker *et al*. 2000; Reinders *et al*. 2002) or are considered to be in the plasma membrane. Therefore, many reports have discussed the roles of the SUC/SUT family for only in plasma membrane (see the next section "PHYSIOLOGICAL ROLES OF SUCROSE TRANSPORTERS"). In plants, the vacuole is the most important organelle for sucrose storage, and some organs and tissues specialized for sucrose storage, such as sugar cane stalk, sugar beet taproot and fruits, accumulate sucrose at almost 1 M. Sucrose transport activities have been reported for isolated vacuoles or vacuolar membrane vesicles from different plant materials, such as beet taproot (Doll *et al*. 1979; Briskin *et al*. 1982; Getz 1991; Getz and Klein 1995; Echeverría and Gonzalez 2000), sugarcane stalk (Thom and Komor 1984; Williams *et al*. 1990; Getz *et al*. 1991; Preisser and Komor 1991), artichoke tuber (Keller 1992; Greutert and Keller 1993; Pontis *et al*. 2002), pineapple leaves (McRae *et al*. 2002) and tomato fruit (Milner *et al*. 1995). Despite the importance of sucrose transport in vacuolar membranes and the detection of its activity, no protein and gene for vacuolar sucrose transporters have been isolated. Getz *et al*. (1993, 1994) and Thom *et al*. (1992) tried to identify sucrose transporters in vacuolar membranes, but they failed.

Recently, proteomic analyses of vacuolar membrane proteins of Arabidopsis have been done and some sugar transporters were identified (Carter *et al*. 2004; Sazuka *et al*. 2004; Shimaoka *et al*. 2004; Szponarski *et al*. 2004). Shimaoka *et al*. (2004) discovered AtSUC1 in their proteomic analysis, but positive subcellular localization of AtSUC1 was not determined. More recently, Endler *et al*. (2006) identified a sucrose transporter homologue (HvSUT2) of the SUT4 subfamily by proteome analysis of vacuolar membrane proteins of barley mesophyll cells. Endler *et al*. (2006) also showed that GFP fusion proteins of HvSUT2 and its homologue of Arabidopsis (AtSUT4) are expressed in the vacuolar membrane of Arabidopsis leaves and onion epidermis. Endler *et al*. (2006) was the first report to clearly show the presence of the SUC/SUT subfamily in the vacuolar membrane and to show that some members of the SUT4 subfamily have roles in the vacuolar membrane. Immunolocalization has shown that LeSUT4 of the SUT4 subfamily in tomato is localized in

the plasma membrane of sieve elements (SE) (Reinders *et al*. 2002). Endler *et al*. (2006) and Reinders *et al*. (2002) suggested that the SUT4 subfamily localizes both in the plasma membrane and in the vacuolar membrane, but whether the same transporter localizes in both membranes or different transporters in different membranes is unclear. The presence of the SUC/SUT subfamily in other organelles has not been reported. Subcellular localization of each sucrose transporter should be checked carefully to determine its physiological functions.

PHYSIOLOGICAL ROLES OF SUCROSE TRANSPORTERS

Sucrose is a major carbon form for long-distance transport in plants, and so sucrose transporters are probably active everywhere in the plant. **Fig. 4** shows a schematic diagram of sucrose transport in plants and the sites of sucrose transporters.

Roles in phloem loading

Generally, sucrose concentration in sieve tubes is higher than in photosynthetic cells, and SE and companion cells (CC) are isolated apoplastically from photosynthetic cells in many sucrose-loading plants (Gamalei 1989). Thus sucrose transporters have to take up sucrose from apoplast to the SE and CC. This mechanism is called apoplastic phloem loading.

Sucrose transporter mRNA and protein are found in the phloem of source leaves, such as potato *StSUT1*, *StSUT2* and *StSUT4* (Riesmeier *et al*. 1993; Kühn *et al*. 1997; Weise *et al*. 2000; Reinders *et al*. 2002), tomato *LeSUT1* and *LeSUT4* (Barker *et al*. 2000; Weise *et al*. 2000; Reinders *et al*. 2002), Arabidopsis *AtSUT2*, *AtSUT3* and *AtSUT4* (Truernit and Sauer 1995; Stadler and Sauer 1996; Schulze *et al*. 2000; Weise *et al*. 2000; Meyer *et al*. 2004; Stadler *et al*. 2005), sugar beet *BvSUT1* (Vaughn *et al*. 2002), wheat *TaSUT1* (Aoki *et al*. 2004), and rice *OsSUT1* (Matsukura *et al*. 2000). Although some of them, such as AtSUC3 (Meyer *et al*. 2000; Schulze *et al*. 2000), are most abundant in the phloem of major veins or petioles and may participate in sucrose retrieval, many of them are localized in minor veins in source leaves and participate in phloem loading.

Knockdown and knockout of sucrose transporter genes expressed in the phloem showed clearly their participation in phloem loading. Antisense-transgenic potato plants of *StSUT1* under the control of the *CaMV35S* promoter or phloem-specific promoters accumulate high amounts of sugars and starch in source leaves and their photosynthetic activity decreases, as shown by Riesmeier *et al*. (1994), Kühn *et al*. (1996, 2003), Lemoine *et al*. (1996) and Schulz *et al*. (1998). Growth of transformants decreases and the plants have a reduced number of smaller tubers. These reports show that sucrose transporters in the phloem have indispensable roles in sucrose phloem loading and long-distance transport of photoassimilates. Antisense-suppression of phloem-specific sucrose transporters has been reported for other plants, such as *NtSUT1* in tobacco (Bürkle *et al*. 1998), *LeSUT1* in tomato (Hackel *et al*. 2006) and *OsSUT1* in rice (Ishimaru *et al*. 2001; Scofield *et al*. 2002). Although antisense-transformation of *OsSUT1* does not affect photosynthetic activity (Ishimaru *et al*. 2001; Scofield *et al*. 2002), other antisense-plants show phenotypes consistent with an essential role of sucrose transporters in phloem loading and long-distance carbon transport. Arabidopsis knockout mutant of phloem-specific *AtSUC2* show a similar phenotype of transgenic plants that suppress their sucrose transporters in the phloem (Gottwald *et al*. 2000). Leggewie *et al*. (2003) produced potato plants that had overexpressed spinach *SoSUT1* under the control of the *CaMV35S* promoter. Sucrose transport activity in plasma membrane vesicles from transformants was higher than for wild-type plants, but the impact of *SoSUT1* overexpression on photosynthesis and on potato tuber yield was little.
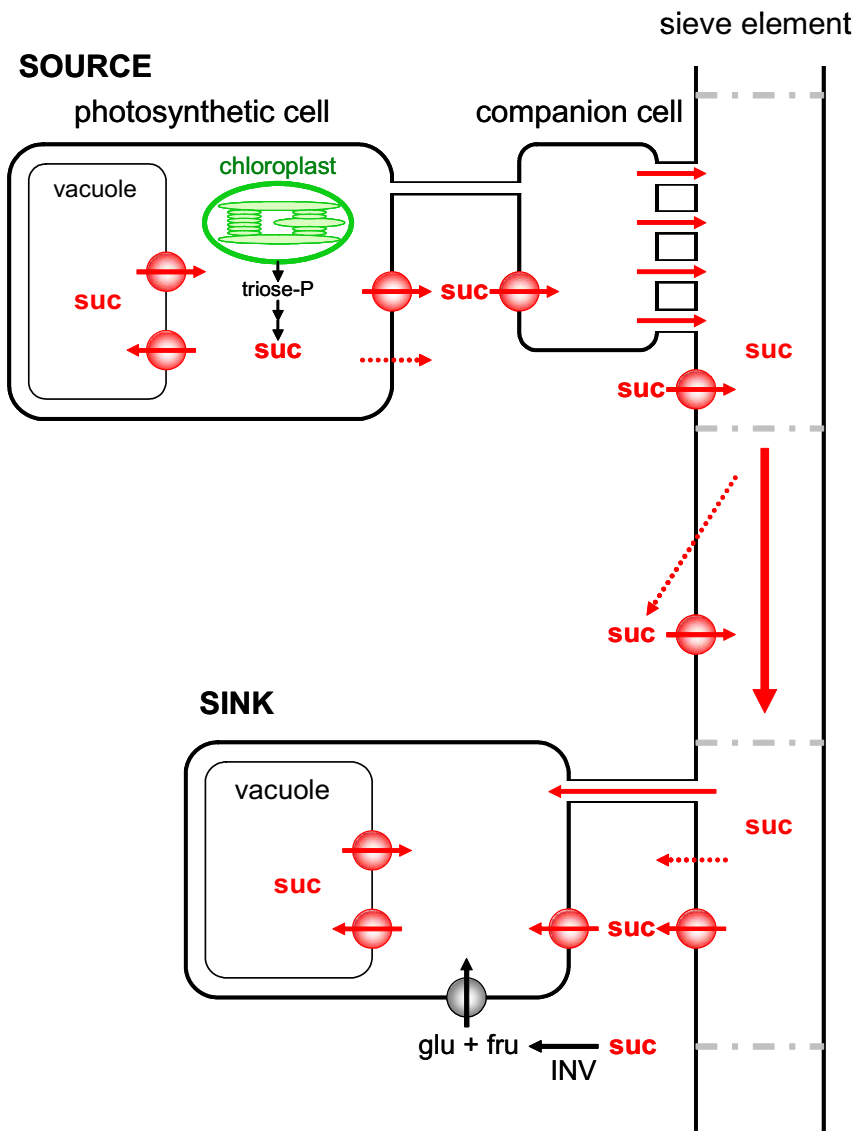
sieve element

SOURCE

photosynthetic cell

companion cell

vacuole

chloroplast

suc

triose-P

suc

suc

suc

suc

suc

suc

suc

suc

SINK

vacuole

suc

suc

suc

suc

glu + fru ← suc

INV

Fig. 4 Sugar transport system in sucrose-loading plants. Sucrose synthesized in the cytosol of photosynthetic cells move to apoplast by putative sucrose transporters or by simple diffusion (dotted line). The sucrose in apoplast is loaded into companion cells (CC) and sieve elements (SE) by sucrose transporters. The sucrose transported into CC move to SE through plasmodesmata. Sucrose loaded into SE of source leaves is considered to move to sinks by mass-flow. Sucrose, which leaks from SE to apoplast, is returned to SE by sucrose transporters. In sinks, sucrose in SE is unloaded symplastically through plasmodesmata or apoplastically. In apoplastic loading, sucrose in apoplast is taken up into sink cells by sucrose transporters, or is converted to fructose and glucose by apoplastic invertase (INV) and then hexose transporters transports them into sink cells. Sucrose is stored in vacuoles in photosynthetic and sink cells by sucrose transporters.

Oligosaccharide-loading plants accumulate photosynthetic products by symplastic phloem loading (Turgeon 2006). That is, sucrose moves from photosynthetic cells to CC through plasmodesmata, oligosaccharides are synthesized from sucrose in CC, and then oligosaccharides move to SE through plasmodesmata. In polyol-loading plants, polyols are considered to accumulate apoplastically by polyol transporters (Noiraud *et al*. 2001c; Watari *et al*. 2004). Sucrose transporters are also expressed in the phloem of oligosaccharide-loading plants, such as *AmSUT1* in *Alonsoa meridionalis* (Knop *et al*. 2001, 2004), and of polyol-loading plants, such as *AgSUT1* in celery (Noiraud *et al*. 2000a) and *PmSUC2* and *PmSUC3* in common plantain (Stadler *et al*. 1995; Barth *et al*. 2003). These results suggest that sucrose transporters partly contribute to phloem loading in oligosaccharide-loading plants (symplastic phloem loaders) and polyol-loading plants.

Roles in sink organs and tissues

Sucrose from source leaves through the phloem is unloaded in sink organs and tissues. Both symplastic and apoplastic mechanisms have been suggested for sucrose unloading (Patrick and Offler 1996). In symplastic unloading, sucrose moves from SE to sink cells thorough plasmodesmata (**Fig. 4**), supported by the existence of relatively high density plasmodesmata between SE and CC to sink cells and by the movement of fluorescent dye from phloem to sink cells (Patrick and Offler 1996). In apoplastic unloading, sucrose moves from the phloem to apoplast first and then it is transported into sink cells by sucrose transporters, or it is converted to fructose and glucose by apoplastic invertase and then hexose transporters transport them into sink cells (**Fig. 4**). Expressions of sucrose transporters in various sink organs and tissues have been reported, and so they very likely participate in sucrose unloading in sink organs and tissues.

Sugar transporters are expressed in various sink organs and tissues, such as *RcScr1* in seedlings of *Ricinus communis* (Weig and Komor 1996; Bick *et al*. 1998), *DcSUT1* in sink tissues of carrot (Shakya and Strum 1998), ShSUT1 protein in veins of sugarcane stem (Rae *et al*. 2005), *NtSUT3* in pollen of tobacco (Lemoine *et al*. 1999), *GhSUT1* in elongating cotton fibers (Ruan *et al*. 2001), *OsSUT1-5* in various sink organs of rice including developing grains (Furbank *et al*. 2001; Aoki *et al*. 2003), common plantain *PmSUC1*, pea *PsSUT1*, fava bean *VfSUT1*, barley *HvSUT1* and *HvSUT2*, and wheat *TaSUT1* in developing seeds (Gahrtz *et al*. 1996; Weber *et al*. 1997; Tegeder *et al*. 1999; Weschke *et al*. 2000; Takeda *et al*. 2001; Aoki *et al*. 2002, 2006). Arabidopsis *AtSUCs* have been detected in sink organs and tissues: *AtSUC3* in, for example, guard cells, trichome, germinating pollen, root tip, carpel cell layer, (Meyer *et al*. 2000, 2004), *AtSUC5* in endosperm (Baud *et al*. 2005), *AtSUC8* and *AtSUC9* in various sink organs including floral tissues (Sauer *et al*. 2004; Sivitz *et al*. 2007). These transporters may have roles in the phloem or post-phloem unloading. Sucrose transporters, which may have a role in sugar accumulation, are also expressed in fruit and include *CitSUT1* and *CitSUT2* in citrus (Li *et al*. 2003), *VvSUC11*, *VvSUC12* and *VvSUC27* in grapevine (Davies *et al*. 1999; Ageorges *et al*. 2000; Manning *et al*.

2001), *LeSUT2* in tomato (Reinders *et al*. 2002).

Tomato *LeSUT2* is expressed predominantly in sink organs, such as immature leaves and fruit (Reinders *et al*. 2002), and its antisense-inhibition markedly decreases in fruit and seed development and pollen germination (Hackel *et al*. 2006). Arabidopsis *AtSUC9* is expressed in sink tissues throughout the shoot to the flowers and knockout mutants of *AtSUC9* are early flowering (Sivitz *et al*. 2007). Seed-specific overexpression of *StSUT1* in pea increases sucrose uptake and the growth rate in developing cotyledons (Rosche *et al*. 2002). These results show the importance of sucrose transporters in plant development, especially in sink strength.

EXPRESSION AND REGULATION OF SUCROSE TRANSPORTERS

Sucrose transport activity is regulated at the gene expression level of sucrose transporters, and gene expressions are regulated by organ or tissue specificity (see the section "PHYSIOLOGICAL ROLES OF SUCROSE TRANSPORTERS"), developmental cues, circadian rhythm, stresses and environmental factors. Expressions of potato *StSUT1* and celery *AgSUT1* expression decreases by salt stress (Noiraud *et al*. 2000a). Sugar beet *BvSUT1* is induced by cutting and ageing (Sakr *et al*. 1997), and Arabidopsis *AtSUC3* is induced by wounding (Meyer *et al*. 2004). Arabidopsis *AtSUC2* gene was induced in a syncytium cell-complex formed by nematode infection, which suggests the *AtSUC2* gene is induced by pathogen infection (Juergensen *et al*. 2003). Walnut *JrSUT1* is expressed in xylem parenchyma cells and the expression is up-regulated by freeze-thaw cycles, suggesting the participation of JrSUT1 in cold tolerance (Decourteix *et al*. 2006). Expression of potato *StSUT1* and Arabidopsis *AtSUC2* is under developmental control and both are induced during sink-to-source transition in leaves (Riesmeier *et al*. 1993; Truernit and Sauer 1995). Maize *ZmSUT1* is expressed in mature leaves and the expression changes diurnally (Aoki *et al*. 1999), suggesting that its expression changes to regulate the sucrose export rate from leaves. Sucrose controls the expression of sucrose transporters: tomato *LeSUT2* is induced (Barker *et al*. 2000), but other *SUT* genes are down-regulated by sucrose (Chiou and Bush 1998; Vaughn *et al*. 2002).

Mysterious occurrence of sucrose transporter mRNA and protein in sieve elements and pollen

In situ hybridization and immunolocalization showed that both *StSUT1* mRNA and StSUT1 protein are localized in SE in potato source leaves (Kühn *et al*. 1997). Both *StSUT1* mRNA and StSUT1 protein have a high turnover rate (Kühn *et al*. 1997). However, SE lacks a nucleus and ribosome, and so SE cannot synthesize *StSUT1* mRNA and StSUT1 protein by itself. How does the StSUT1 protein appear in SE? Although Kühn *et al*. (1997) suggested the possibility of targeting *StSUT1* mRNA or StSUT1 protein or both from CC to SE through plasmodesmata, the mechanism is still unclear.

A large amount of *AtSUC1* mRNA, but no AtSUC1 protein, is in mature pollen of Arabidopsis (Stadler *et al*. 1999), and after pollination the AtSUC1 protein starts to appear inside the pollen. This suggests that *AtSUC1* mRNA in mature pollen might be ready for AtSUC1 protein synthesis after pollination.

Post translational regulation

Many enzymatic activities and transport activities are regulated by protein phosphorylation. Protein phosphatase inhibitors, such as okadaic acid, reduce sucrose transport activity in plasma membrane vesicles of sugar beet (Roblin *et al*. 1998; Ransom-Hodgkins *et al*. 2003), suggesting that protein phosphorylation is included in regulation of suc-

rose transporters. Homo- and hetero-oligomerization of transporters often affect transporter activities, such as Km values and $Vmax$. Oligomerization was reported for tomato sucrose transporters: LeSUT4 colocalizes with LeSUT1 and LeSUT2 in SE (Barker *et al*. 2000), and LeSUT4 interacts with LeSUT1 and LeSUT2 (Reinders *et al*. 2002). The extended domains in the central loop and N terminus of the SUC3/SUT2 subfamily have the potential to regulate sucrose transporters, including oligomerization.

CONCLUSIONS AND FURTHER PERSPECTIVES

Sucrose is a major carbon form for long-distance carbon transport in most plants. Therefore sucrose transporters have indispensable roles in source leaves and in various sink organs and tissues, and sucrose transport activity is likely highly regulated to control carbon partitioning in plants. Since the early 1990s, study of sucrose transporters has advanced dramatically and our understanding has deepened. However, our knowledge is still fragmentary. Information, such as biochemical character, gene and protein expressions and phenotype of transformants or mutants, exists for each sucrose transporter. However, different sucrose transporters always cooperate in sucrose transport in plants. Therefore, we should pay more attention to joint activities by different sucrose transporters.

To understand carbohydrate transport in plants, we also have to pay attention to other sugar transporters, such as the STP/HXT, PLT, ITR/MIT, pGlcT, AZT/MSSP and SFP families. Lalonde *et al*. (2004) and Shiratake (2007) summarize these transporter families. The STP/HXT family is well-characterized and the studies were summarized (Lalonde *et al*. 1999; Büttner and Sauer 2000; Williams *et al*. 2000). Although less information had been reported for other families, the studies about the PLT and ITR/MIT families were summarized by Noiraud *et al*. (2001b). Recently Wormit *et al*. (2006) reported that a member of AZT/MSSP family in Arabidopsis, *At*tMT localizes in vacuolar membrane. Arabidopsis MEX, which localizes in chloroplast envelope, allows growth of *E. coli*, which lacks an endogenous maltose transporter (Niittylä *et al*. 2004), suggesting MEX is a maltose transporter. Interestingly, MEX has no similarity with other sugar transporter families. Further investigations are needed to clarify carbohydrate transport in plants.

ACKNOWLEDGEMENTS

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