SUT sucrose and MST monosaccharide transporter inventory of the *Selaginella* genome

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Most metazoa use hexose transporters to acquire hexoses from their diet and as a transport form for distributing carbon and energy within their bodies; insects use trehalose, and plants use sucrose as their major form for translocation. Plant genomes contain at least three families of mono- and disaccharide transporters: monosaccharide/polyol transporters that are evolutionarily closely related to the yeast and human glucose transporters, sucrose transporters of the SUT family, which similar to the hexose transporters belong to the major facilitator superfamily, but share only minimal amino acid sequence homology with the hexose transporters, and the family of SWEET sugar transporters conserved between animals and plants. Recently, the genome sequence of the spikemoss *Selaginella* has been determined. In order to study the evolution of sugar transport in plants, we carefully annotated of the complement of sugar transporters in *Selaginella*. We review the current knowledge regarding sugar transport in spikemoss and provide phylogenetic analyses of the complement of MST and SUT homologs in *Selaginella* (and Physcomitrella).

Keywords: sucrose, hexose, glucose, carrier, transporter, plasma membrane, vacuole, polyol

INTRODUCTION

A hallmark of vascular plants is the transport of sugars and nitrogen from places of synthesis to sites that depend on external supply (Giaquinta, 1983). Green tissues engage in photosynthesis, produce sugars and assimilate inorganic nitrogen, and export excess to support non-photosynthetic tissues such as roots and reproductive organs. Key features include roots or root-like structures necessary for nutrient acquisition and vascularization of the sporophyte to bring nutrients from the root or root-like structures to the leaves and to transport photosynthates to the root.

While most animals use glucose as the major transport form for carbon skeletons and energy between organs, many higher plants use the disaccharide sucrose for long distance translocation. In addition, plants also contain homologs of the human and yeast hexose transporters, most probably for either transport in and out of the vacuole as well as import of hexoses derived from extracellular metabolism via invertases. Moreover, members of the hexose transporter families in both plants and animals (solute transporter family SLC2) specialize in the transport of polyols. Importantly, as far as it has been tested, both animal and plant sugar transporters can transport a wide spectrum of other compounds such as secondary metabolites as well (for recent reviews, cf. Kühn and Grof, 2010; Ayre, 2011). Interestingly, insects have specific trehalose transporters that are used to transport this disaccharide between cells (Kikawada et al., 2007; Kanamori et al., 2010). Animals also have SUT sucrose transporter homologs (solute transporter family SLC45). The Drosophila homolog SCRT transports sucrose, is potentially located in intracellular melanosomes, and mutation leads to increased lethality. SRCT has been implicated in an essential role in transporting sucrose as an osmolyte as or as a nutrient (Meyer et al., 2011). Mutations in the mammalian SLC45 homologs lead to ocularcutaneous albinism suggesting a critical role in melanosomes (Newton et al., 2001).

Here we will focus on the complement of sugar transporters of the SUT and MST (STP/ERD6) families of sugar transporters in one of the earlier land plants, *Selaginella*, the genome sequence of which has recently been published (Banks et al., 2011). The *Selaginella* genome also contains homologs of the recently identified SWEET transporter family, which will be reviewed independently (Chen et al., 2010, 2012; Sosso et al., in preparation).

*Selaginella* as a member of the lycophytes is part of an ancient lineage of vascular plants that had arisen ~400 million years ago (Banks, 2009). In angiosperms, which have attracted most of the attention for nutrient distribution so far, we have been able to identify many of the key transporters for organic carbon and reduced nitrogen. Sucrose is a dominant transport form for carbon and energy in many angiosperms, and the transporters for loading the phloem and for import of sucrose into the seed have been identified (Riesmeier et al., 1992). Interestingly, plants also have transporters for monosaccharides and sugar alcohols (Lalonde et al., 2004; Büttner, 2010). Their role is not always fully clear, thus an analysis of *Selaginella* as a representative of an ancient vascular plant may help shedding light on the evolution and function of these diverse transporters. Still not all parts of the angiosperms sugar transport engine are identified; major missing components include the efflux transporters required for nectar production, sugar efflux from roots into the rhizosphere, and efflux from the seed coat.

Besides sucrose, nitrogen is quantitatively the most relevant mineral nutrient. We also analyzed the *Selaginella* complement of genes for transporters involved in cellular uptake of ammonium,
ura, and the translocation of amino acids (DeMichele et al., submitted; Wipf et al., submitted).

**SUGAR TRANSPORT IN SELAGINELLA**

Bryophytes and Pteridophytes have been shown to contain glucose, fructose, and sucrose (Allsopp, 1951). Selaginella kraussiana and Selaginella caulescens do not seem to contain significant amounts of sucrose but rather trehalose. Interestingly, the genome of Selaginella moellendorffii contains homologs of both the monosaccharide and sucrose transporter families from Arabidopsis known today.

Physcomitrella growth seems unaffected by the presence of 0.5% glucose (Allsopp, 1951). However, this sugar could not be used by the moss as an alternative carbon source when photosynthesis was blocked by DCMU, nor did they grow in glucose in darkness, while Ceratodon showed some growth on glucose and sucrose (Allsopp, 1951). The ligule of Selaginella kraussiana has been shown to take up 3H-glucose (Sigee, 1976). Trehalose appears to be a dominant sugar in many Selaginella species (cf. ref. in Allsopp, 1951). The desiccation-tolerant Selaginella lepidophylla contains very high trehalose levels and a very high activity trehalose-6-phosphate synthase as compared to other plants, potentially suggesting that trehalose accumulation may be related to the resurrection phenotype (Van Dijck et al., 2002). Trehalose transporters have been identified in insects, where they function as facilitators and belong to the hexose transporter family (MFS; Kikawada et al., 2007). Plant trehalose transporters have not yet been characterized, however since the monosaccharide transporter family has not been analyzed systematically for trehalose transport activity, members of this family are prime candidates for such a function.

**PUTATIVE SELAGINELLA MONOSACCHARIDE/SUGAR ALCOHOL TRANSPORTERS**

Analysis of the ubiquitous monosaccharide or hexose transporters as well as sugar alcohol transporters in Selaginella moellendorffii revealed the presence of at least 26 alleles (Figures 1A–G; Figure S1 in Supplementary Material), while 54 homologs were found in Arabidopsis (Lalonde et al., 2004; Büttner, 2010) and 60 in rice. Moreover, the Selaginella monosaccharide transporter proteins are highly similar to their homologs in Physcomitrella patens (Johnson and Thomas, 2007). To be able to perform a direct comparison, the annotation in Physcomitrella needs to be improved, since in many cases the start codon is not correctly assigned, putative sequencing errors have lead to apparent frameshifts, and intron locations are in several cases probably not correctly assigned. The Selaginella annotation carried out in this project and the resulting improved gene models available for the Selaginella sugar transporters will be useful to improve the Physcomitrella annotation. Close homologs are also found in green algae such as Chlorella and Chlamydomonas, as well as in cyanobacteria, fungi, and in the animal kingdom including the important human GLUT glucose facilitators (HGNC Solute Carrier Family Series SLC2). The putative monosaccharide transporter genes can be divided into seven subclades (Figures 1A–G; Table 1; Figure S1 in Supplementary Material). The MSTs (STP/ERD6-like transporters) typically function as high affinity monosaccharide proton cotransporters in plants, here called MST (monosaccharide transporters) since they transport pentoses and various hexoses (Büttner, 2010). Three groups of transporters have been identified that play roles in vascular transport: (i) vacuolar ERD6-like transporters that function in facilitative transport of monosaccharides across the tonoplast membrane (Yamada et al., 2010); (ii) VGT-like transporters, that in Arabidopsis also localize to vacuolar membranes and function as a hexose transporters (Büttner, 2010); and (iii) TMTs, characterized by extended loops, that also function as vacuolar monosaccharide transporters (Wormit et al., 2006). pGLTs are plastidic glucose transporters (Weber et al., 2000), while INT-like transporters transport inositol (Schneider et al., 2008) and PLTs transport polyols (Reinders et al., 2005).

Consistent with sugar alcohols being involved in resurrection, there are both inositol and polyol transporter homologs in Selaginella. All three types of vacuolar monosaccharide transporters are found as well as plastidic glucose and Mxi1-like maltose transporters (unpublished results). The overall composition is similar in Selaginella as in monocots such as rice, although we find a lower number of MSTs in Selaginella. Arabidopsis is characterized by a larger number of ERD6-like transporters compared to monocots and Selaginella.

**SUCROSE TRANSPORT AND SUT FAMILY MEMBERS**

To our knowledge, sucrose transport has not been studied in detail in mosses. Yet, sucrose can be used in media for axenic culture of mosses. For many higher plants, sucrose is the dominant form for sugar translocation. Sucrose, a disaccharide composed of glucose and fructose [α-d-glucopyranosyl-(1 → 2)-β-d-fructofuranoside] has a low viscosity even at high concentrations (soluble to several molar), has no reducing end, and is thus considered more inert than glucose, the major transport form in animals. Sucrose is produced in the mesophyll cells of plant leaves (as well as other organs) by the combined activity of sucrose phosphate synthase and sucrose phosphate phosphatase or by sucrose synthase. Sucrose is exported into the cell wall space by SWEET sucrose transporters (Chen et al., 2012) (Giaquinta, 1983). Extracellular sucrose is then loaded into the long distance transport system of higher plants, the phloem, with the help of secondary active transporters in the membrane of the sieve element companion cell complex. The first sucrose transporter gene SUT1 was identified by expression cloning from spinach and potato leaf cDNA libraries in an engineered yeast strain (Riesmeier et al., 1992, 1993). Interestingly, the sucrose transporter also mediates transport of the disaccharide maltose and a variety of glucosides (Sivitz et al., 2005). SUT1 has an affinity for sucrose in the low micromolar range (around 1 mM). SUT1 is essential for sucrose export from the leaves of potato and tobacco as shown by antisense repression (Riesmeier et al., 1994; Bürkle et al., 1998). The Arabidopsis homolog was called SUC2 and null mutation in SUC2 is lethal (Gottwald et al., 2000). Two more distantly related sucrose transporter homologs SUT2 and SUT4 were functionally characterized in the yeast expression system and shown to also transport sucrose and maltose (Barker et al., 2010).
Lalonde and Frommer

SUT and MST transporters in Selaginella

FIGURE 1 | Continued
FIGURE 1 | Phylogenetic tree of the monosaccharide transporter family. (A) Clade overview, (B) STP clade, (C) Hxt clade, (D) PLT–VGT clade, (E) SBG–GLT–GLUT1 clade, (F) ERD6-like clade, (G) TMT clade. The tree was obtained by aligning all protein sequences using ClustalW and then building using the software Molecular Evolutionary Genetics Analysis (MEGA v5, Tamura et al., 2011). The bootstrap consensus tree is inferred from 1000 replicates. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test is shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 185 amino acid sequences and a total of 277 positions. At, Arabidopsis thaliana; Ck, Chlorella kessleri; Cr, Chlamydomonas reinhardtii; Hs, Homo sapiens; Os, Oryza sativa; Pp, Physcomitrella patens; Sc, Saccharomyces cerevisiae; Sm, Selaginella moellendorffii.
Table 1 | Number of genes of the different monosaccharide (MST, ERD6, pGLT, VGT, TMT, INT, and PLT) and sucrose transporters (SUT/SUC) found in Arabidopsis, rice, Selaginella, and Physcomitrella.

| Gene functions          | Gene    | Gene used as a query                                      | Arabidopsis thaliana | Oryza sativa | Selaginella moellendorffii | Physcomitrella patens |
|-------------------------|---------|----------------------------------------------------------|-----------------------|--------------|--------------------------|-----------------------|
| Monosaccharide transport| MST     | AtSTP1 (AT1G11260)                                       | 15                    | 27           | 11$^1$                   | 2 (4)                 |
| Monosaccharide transport| VGT     | AtSTP1 (AT1G11260)                                       | 3                     | 1            | 2$^2$                    | None                  |
| Polyl transport         | PLT     | AtSTP1 (AT1G11260)                                       | 6                     | 14           | 3                        | 1$^3$                 |
| Monosaccharide transport| pGLT    | AtGLT1 (AT5G16150)                                      | 4                     | 3            | 4                        | 3 (6)$^5$             |
| Monosaccharide transport| ERD6    | AtSTP1 (AT1G11260)                                       | 19$^4$                | 6            | 1                        | None                  |
| Inositol transport      | INT     | AtSTP1 (AT1G11260)                                       | 4                     | 3            | 2                        | None                  |
| Monosaccharide transport| TMT     | AtTM1 (AT1G20840)                                        | 3                     | 6            | 4                        | 2 (4)                 |
| Sucrose transport       | SUT1    | AtSUC1 (AT1G71880)                                      | 7                     | None         | None                     | None                  |
| Sucrose transport       | SUT2    | AtSUT2 (AT2G02860)                                      | 1                     | 4            | 1                        | 1                    |
| Sucrose transport       | SUT4    | AtSUT4 (AT1G09960)                                      | 1                     | 1            | 4                        | None                  |

$^1$SmMST3 9 and 11 are not in the phylogenetic tree (see Table S1 in Supplementary Material for ID numbers).

$^2$SmVGT2 (ID 133784) is not in phylogenetic tree.

$^3$The alleles of XP 001776003 (pGLT) and XP 00175457 (PLT) were not found.

$^4$AT1G54730 and AT3G05155 are not in the phylogenetic tree.

$^5$SmSUT2L1-1 and SmSUT2L1-2, as well as four genes in the SUT1/SUT4 branch (here named SUT4L1, SUT4L2, SUT4L3, SUT4L4). This classification is supported by similarities in the intron structure and the presence of an extended central loop containing a conserved CCB2 domain in the Selaginella and higher plant SUT2s (the CCB1 box is not conserved between Selaginella and Physcomitrella and all the other candidates containing this longer central loop). Monocots also do not have a SUT1 homolog, which is interesting since this transporter is essential for several dicots. Monocots have two types of SUT2, one with and one without a central loop. While it is conceivable that the mesoses/spikemosses had lost one of the two. However, based on the distance to the higher plant SUT1 and SUT4 clades, it is more likely that this is an ancestral clade and that SUT1 and 4 evolved from this ancestral clade. We therefore name the clade SUT1/SUT4 clade.

Distant SUT homologs have been identified in fungi (Reinders and Ward, 2001). The Schizosaccharomyces pombe homolog was shown to function primarily as a maltose transporter, but also can transport sucrose (Reinders and Ward, 2001). Homologs also exist in the animal kingdom, e.g., medaka and mouse, which are directly or indirectly involved in melanin accumulation (Fukami et al., 2001). Interestingly, no SUT homologs have been found in green algae, while glucose transporters are well conserved in algae (Caspari et al., 1994).

Despite the importance of trehalose for plants and its occurrence in Selaginella, we have not found homologs of the insect-specific trehalose transporter family in Selaginella or Arabidopsis (Kikawada et al., 2007; Kanamori et al., 2010).
FIGURE 2 | Continued
contains homologs of the recently identified SWEET transporter family (Chen et al., 2010, 2012). Unfortunately, at present it is not possible to assess the physiological function of these transporters in Selaginella due to the lack of tools for gene replacement and transformation. However the genome of the moss Physcomitrella appears to contain a similar complement of transporters in the two families, and all necessary tools for analyzing the physiological function of these genes are available. It will however be necessary to carefully annotate the respective gene annotation in Physcomitrella before entering in to such an endeavor. The careful annotation performed here for the Selaginella genes can serve as guidance for improving the Physcomitrella annotation.

MATERIALS AND METHODS

Selaginella moellendorffii genes for monoc saccharide and sucrose transporters were obtained by blasting a set of Arabidopsis transporter homologs (see Table 1) against the Selaginella genome sequence at the JGI website. When necessary (and if possible), gene models were modified according to the available information (i.e., ESTs) and a new gene model was promoted. A list containing protein identifier numbers, sequences, and links to the JGI database of all Selaginella proteins included is presented as Table S1 in Supplementary Material.

Monosaccharide and sucrose transporter families were treated separately. Multiple sequence alignments were generated using MEGA 5.0 software (Tamura et al., 2011). The quality of the alignments was assessed and non-homologous sequences were removed at beginning and end of the sequences. The phylogenetic analysis was done using the maximum likelihood method and the consensus tree was inferred from 1000 bootstrap replicates. The analysis was done using only one Selaginella allele.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at http://www.frontiersin.org/Plant_Traffic_and_Transport/10.3389/fpls.2012.00024/abstract

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FIGURE 2 | Continued

Phylogenetic relationship of the sucrose transporter (SUT) family. (A) Clade overview; (B) SUT1–SUT4 clade; (C) SUT2 clade. The tree was obtained by drawing to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 99 amino acid sequences and a total of 401 positions. Ab, Asarina barclaiana; Ag, Apium graveolens; Am, Alonsoa meridionalis; At, Arabidopsis thaliana; Bn, Brassica napus; Bo, Brassica oleracea; Bv, Beta vulgaris; Ca, Citrus sinensis; Dc, Daucus carota; Dg, Datisca glomerata; Hb, Hevea brasiliensis; Hv, Hordeum vulgare; Jj, Juglans regia; Gm, Glycine max; Le, Lycopersicon esculentum; Lj, Lotus japonicus; Lp, Lolium perenne; Md, Malus x domestica; Me, Manihot esculenta Nt, Nicotiana tabacum; Os, Oryza sativa; Pm, Plantago major; Pp, Physcomitrella patens; Ps, Pismum sativum; Pt, Populus tremula × Populus tremuloides; Pv, Phaseolus vulgaris; Rc, Ricinus communis; Sh, Saccharum hybrid; So, Spinacia oleracea; Sm, Selaginella moellendorffii; St, Solarium tuberosum; Ta, Triticum aestivum; Vl, Vicia fata; Vv, Vitis vinifera; Zm, Zea mays.

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February 2012 | Volume 3 | Article 24 | 7
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