Introduction
Elucidation of the interactome of membrane proteins seems to be a powerful tool to gain insights into signal transduction and regulation of nutrient transport in higher plants. For Arabidopsis, a robotic screening method was established based on the split ubiquitin system in yeast (Stagljar et al., 1998) in order to systematically analyze the membrane-based interactome with potential application in fungi, plants, and metazoans (Lalonde et al., 2010). This review will rather focus on single protein–protein interactions (PPIs) of plant sucrose transporters and summarize recent research in this field published during the past 5 years.

Co-localized sucrose transporters in the phloem can interact with each other
Sucrose transporters from potato and tomato belonging to different phylogenetic clades (Kühn and Grof, 2010) co-localize in phloem sieve elements (SEs; Barker et al., 2000; Weise et al., 2009; Reinders et al., 2002a). Using the split ubiquitin system it was shown that SlSUT1, SlSUT2, and SlSUT4 from tomato (Solanum lycopersicum) are able to form homo- and heterooligomers (Reinders et al., 2002a) and, even when expressed separately from different plasmids, the two halves of SlSUT1 were able to reconstitute a functional transporter (Reinders et al., 2002b).

Controversial localization of Arabidopsis sucrose transporters has been reported. Whereas AtSUC2 is assumed to be localized in phloem companion cells (CCs; Stadler and Sauer, 1996), AtSUC2/SUT2 was finally localized in phloem SEs (Meyer et al., 2004), and AtSUT4 was also detected in mesophyll protoplasts (Endler et al., 2006). Nevertheless, the promoter activity of the genes encoding all three sucrose transporters was mainly detected in phloem CCs (Schulze et al., 2003). This is not unexpected, since SE-specific sucrose transporter (SUT) expression is efficiently inhibited by help of a companion-cell-specific antisense construct (Kühn et al., 1996). Arabidopsis SUTs interact with each other in yeast cells (Schulze et al., 2003). Detection of strong promoter activity of AtSUT4 in phloem minor veins (Weise et al., 2000; Schulze et al., 2003) and the detection of AtSUT4 transcripts in mesophyll cells (Endler et al., 2006) argue for the presence of AtSUT4 in both tissues.

It should be also noted that the subcellular localization of SUT/SUCs does not completely overlap with each other. It is obvious that the subcellular localization of sucrose transporters is crucial for their functionality. Whereas SlSUT1 localization is primarily at the plasma membrane (PM), SlSUT2 is also detectable in intracellular structures (Figure 1). SlSUT2 and SlSUT1 interact completely different populations of proteins (Krügel and Kühn, unpublished results) suggesting different functions. The fact that SlSUT2–YFP fusion mainly localizes to intracellular membranes in
were mainly detected in the endoplasmic reticulum (ER; Krügel et al., 2012). Thus heterodimer formation between SUTs can be experimentally confirmed by biochemical methods such as blue native PAGE, chemical cross-linking, two-dimensional gel electrophoresis, and immunoprecipitation (Co-IP) using specific antibodies or commercially available monoclonal antibodies raised against tagged over-expressed SoSUT1 protein were not successful (Krügel et al., 2012), but large overlap was observed between proteins co-precipitated with SSUT1 and the detergent-resistant membrane (DRM) fraction of potato source leaf plasma membranes. Immunoprecipitation was performed with either PMs from potato wild-type plants using an affinity-purified peptide antibody or alternatively with PMs from potato plants over-expressing a c-myc-tagged version of the sucrose transporter SoSUT1 from spinach (Leggewie et al., 2003) using monoclonal antibody against c-myc tag. Two candidates interact with SSUT1 from potato as well as with the over-expressed SoSUT1 from Spinacia oleracea: a plasma membrane H^+ ATPase (CAA40445) and a temperature-induced lipocalin (TIL, ABB02386). TILs are discussed to be involved in freezing tolerance of plants and/or in membrane stability and abiotic stress responses (Charron et al., 2005; Chi et al., 2009).

**Figure 1** Overlay picture showing subcellular distribution of a SSUT2-YFP construct expressed under control of the constitutive CaMV 35S promoter in the vector pK7WG2.0 (Karimi et al., 2002 in stably transformed tobacco plants (Alconiana tabacum). SSUT2-YFP fluorescence is mainly retained in intracellular structures, a possible argument for its non-functionality at the plasma membrane. Contrast of the overlay picture was enhanced by choosing the RGB mode leading to color modification. YFP fluorescence is therefore shown in green, chlorophyll autofluorescence is shown in red. Color of the transmission image is shown in blue.

**Proteins Involved in Subcellular Protein Targeting**

SSUT1 was shown to undergo endocytosis in response to brefeldin A treatment and to be present in intracellular vesicles recycled at the PM. Motility of these vesicles is efficiently abolished by application of actin polymerization inhibitors such as latrunculin and actinomycin D (Linsche et al., 2010). This strongly suggests that movement of SSUT1-containing vesicles occurs in an actin-dependent manner involving the cellular cytoskeleton. Direct interaction of SSUT1 with actin and actin-related proteins strongly supports this hypothesis. The actin-related protein ARPC1/ARBC1A which was co-precipitated with SSUT1 (Krügel et al., 2012) is a component of the Arp2/3 complex implicated in the control of actin polymerization (Harries et al., 2005).

Also other SSUT1-interacting proteins identified by Co-IP are obviously involved in subcellular protein targeting and endosomal recycling at the PM. The integral membrane protein of the Yip1 family was shown to interact with the spinach SoSUT1 and is assumed to play a role in membrane trafficking. Yip1 family proteins are required for the biogenesis of ER-derived COPII vesicles in yeast and mammalian cells (Heidtman et al., 2005; Lorente-Rodriguez et al., 2009).

Other SSUT1-interacting proteins identified by Co-IP make part of the secretory pathway: Sec34 (NP_177485) is well known to regulate vesicular trafficking from ER to Golgi (Loh and Hong, 2002) and mediates the export of misfolded proteins to the cytoplasm for degradation in various organisms (Pilos et al., 1997; Schmitz et al., 2000). Sec34 (NP_177485) is also known to regulate vesicular trafficking from ER to Golgi (Loh and Hong, 2002) and might be responsible for correct secretion of SSUT1 to the plasma membrane.

**SUT1-Interacting Proteins Involved in Signaling**

Many other SSUT1-interacting proteins that have been identified either by SUS or by Co-IP are metabolic enzymes or involved in signaling or both.
The yeast Gal83 protein (CAB52141) is an important player under glucose limitation conferring specificity of the Snf1 complex to target proteins such as transcription factors (Yang et al., 1994). A correlation between Gal83 expression and assimilate transport in plants was described (Schwachtje et al., 2006).

A similar regulation of SisUT1 via phosphorylation as described for monosaccharide transporters in yeast can therefore be assumed (Carlson, 1998). Experimental data support the hypothesis of regulation of sucrose transporter activity via phosphorylation (Roblin et al., 1998; Schütz et al., 2004; Nüttely et al., 2007). 14-3-3 proteins are described to regulate many cellular processes by binding to phosphorylated proteins. The interaction of Arabidopsis 14-3-3 isoforms in response to changes in the plant nutrient status helped to identify new targets involved in nitrogen and sulfur metabolism (Shin et al., 2011). Among other sugar and mannitol transporters, AtSUC6 from Arabidopsis directly interacts with a 14-3-3-γ protein of Arabidopsis suggesting that AtSUC6 is phosphorylated as well (Shin et al., 2011).

The detailed function of SUT phosphorylation remains to be elucidated. It is still unclear whether or not phosphorylation of the SisUT1 protein affects its subcellular localization or dimerization behavior.

**METABOLISM**

Adenosine diphosphate (ADP)-glucose pyrophosphorylase (AGPase) is the key enzyme in starch biosynthesis and forms an allosteric heterotetramer. The activity of AGPase is regulated by both the level of reactive oxygen species (ROS) is increased in these plants, while the level of ascorbate is reduced (Nahirnak et al., 2012b). Computational prediction suggests that conserved oxidized cysteines in Snakin/GASA proteins can create up to five disulfide bridges that may act catalytically, i.e., playing a role in redox regulation exhibiting antioxidant activity (Wigoda et al., 2016). In Arabidopsis, the GAS4 protein affects the level of H2O2 and NO upon wounding and participates in GA-dependent signaling of flowering induction (Rabinovich and Weiss, 2010).

It is assumed that OsGSR1, a Snakin/GASA protein from rice, plays an important role in the cross-talk of GA and brassinosteroids (BR) signaling pathways (Wang et al., 2009). The expression of OsGSR1 is induced by gibberellins (GAs) and repressed by BR. Thus, members of the Sn1/GASA protein family cover aspects of plant development, beyond their assumed function in response to biotic or abiotic stresses (Nahirnak et al., 2012b).

The physiological role of SnSUT1–SN1 interaction in potato remains to be elucidated. A similar phenotype as in SN1-inhibited potato is observed when the expression of another SUT-interacting protein, the protein disulfide isomerase, is inhibited in transgenic potato plants by RNA interference (RNAi) silencing (E. Eggert and C. Kühn, unpublished results). In view of the fact that SisUT1 forms dimers in a redox-dependent manner (Krügel et al., 2008) it is interesting to note that two out of seven SisUT1-interacting proteins identified by SUS seem to be involved in redox homeostasis.

**INTERACTORS OF SUT4 MEMBERS: MdSUT1 AND AsSUT4 INTERACT WITH PROTEINS OF THE cYb5 FAMILY**

The MdSUT1 protein of Malus domestica, belonging to the SUT4 subfamily, was isolated from the plasma membrane of apple phloem and parenchyma cells. A systematic SUS screen was performed using MdSUT1 and the sorbitol transporter MsdOT6 as bait proteins (Fan et al., 2009). Cytochrome b5 (Cyb5) was identified several times independently as interaction partners of MsdOT1 and of MsdOT6 (Table 1).

Cyb5s are small membrane-anchored proteins with a putative heme/steroid binding domain. They are involved in a number of oxidative reactions. Interaction between MsdOT1 and Cyb5 was confirmed by immunoprecipitation and BiFC. Since MsdUT1 was localized to the PM whereas Cyb5 is expected in the ER, electron microscopic immunolocalization was performed showing accurately that Cyb5 is localized in ER cisternae, which are connected to the PM (Fan et al., 2009).

β-Galactosidase (lacZ) activity tests in yeast have been used to quantify the strength of interaction in the presence or absence of glucose or sucrose in the medium. Increasing sucrose concentrations inhibited MsdOT1 interaction with Cyb5, whereas varying concentrations of glucose (which is not transported by MsdUT1) did not affect the strength of interaction (Fan et al., 2009). Deletion constructs of the SUT-interacting Cyb5 revealed that the C-terminal region containing the membrane spanning domain of Cyb5 is essential for the interaction with sugar transporters,
Table 1 | Protein–protein interaction partners of plant sugar transporters identified by the yeast two hybrid split ubiquitin system.

| Bait protein | Localization | Prey proteins | Confirmation | Reference |
|--------------|--------------|---------------|--------------|-----------|
| StSUT1 (Solanum tuberosum; SUT1 clade) | PM | Protein disulfide isomerase (PDI) | GST pulldown, BFC, DRM protein, FRET acceptor bleaching, also interacts with SUT2 and SUT4 | Krügel et al. (2012) |
| | | Snakin-1 | | |
| | | Inorganic pyrophosphatase (PPi) | DRM protein | |
| | | Tonooplast intrinsic protein (TIP) | DRM protein | |
| | | Enolase | not confirmed | |
| | | Aldehyde de-hydrogenase (ADH) | Several times in independent screens | |
| | | Unknown protein | | |
| | | GST pull-down, BiFC, DRM protein, FRET acceptor bleaching, also interacts with SlSUT2 and StSUT4 | |
| MdSUT1 (Malus domestica; SUT4 clade) | PM | Cytochrome b5 (Cyb5) | BiFC, Co-IP identified in 17 independent colonies | Fan et al. (2009) |
| MdSOT6 (Malus domestica; sorbitol transporter) | PM | Cyb5 | BiFC, Co-IP identified in 20 independent colonies | Fan et al. (2009) |
| AtSUT4 (Arabidopsis thaliana; SUT4 clade) | vacuole | Cyb5-1 | BCF, Co-IP | Li et al. (2012) |
| | | Cyb5-2 | | |
| | | Cyb5-3 | | |
| | | Cyb5-4 | | |
| | | Cyb5-6 | | |

whereas the N-terminus only plays a role in the strength of the interaction. Thus, it is likely that the C-terminal part of Cyb5 interacts with the N-terminal part of MsSUT1 and that interaction takes place within the membrane. Co-expression of the Cyb5 protein with MsSUT1 in yeast increased affinity of MsSUT1 toward the substrate sucrose. Besides inhibiting PPI substitution of leucine73 with proline abolished this increase in affinity. It was suggested that the sugar transporter–Cyb5 complex, which is strengthened under sugar starvation, promotes sugar uptake when sugar availability is limited.

In Arabidopsis, the same authors showed that AtSUT4, but not homologous transporters in the SUT1 or SUT2 subfamily, is able to interact with five different members of the Cyb5 family. Confirmation of interaction was obtained from pull-down assays and via BiFC (Li et al., 2012). Both atsut4 and cyb5-2 mutant plants show decreased sensitivity toward sucrose and glucose with respect to seed germination and it is suggested that the AtSUT4/Cyb5-2 complex might be involved in sensing or signaling not only of sucrose but also of glucose (Li et al., 2012).

SUMMARY AND OUTLOOK

THE POTENTIAL ROLE OF SUBCELLULAR COMPARTMENTATION

Elucidation of the StSUT1 interactome helped to get information about the regulation and subcellular localization of this SUT. Its presence in the DRM fraction was confirmed by liquid chromatography-tandem mass spectrometry (LC-MS/MS; Krügel et al., 2008) and its association to lipid raft-like microdomains was visualized by expression of green fluorescent protein (GFP) fusion constructs in yeast (Krügel et al., 2008). SUT1 is constantly recycled at the SE PM in an actin-dependent manner (Liesche et al., 2010). Identification of actin-related proteins and components of the secretory pathway such as Sec34 and Sec61 among the StSUT1-interacting partners support these findings. A large overlap was observed between SUTS-interacting proteins identified by Co-IP and proteins showing reduced detergent solubility (Krügel et al., 2012).

The question is now whether association of the SSUT1 to membrane microdomains is a prerequisite for endocytosis and recycling. Methyl-β-cyclodextrin (MβCD) causes sterol depletion...
of the plant PM and thereby inhibits raft formation (Roche et al., 2010). The significantly increased activity of the glucose transporter GLUT1 in the presence of MβCD is explained by inhibition of endocytosis thereby increasing the number of transporters at the PM (Barnes et al., 2004; Caliceti et al., 2012). It is indispensable to test the impact of MβCD on the activity of SUT1, whose endocytosis seems to be inhibited by MβCD similarly to GLUT1 in the mammalian system (Liesche et al., 2010).

Raft association of plant membrane proteins may also impact lateral segregation. The potassium channel AtAKT1 was localized to microdomains and a low lateral mobility was observed (Reuff et al., 2010). Cholesterol depletion of the membrane decreases lateral mobility of PM proteins (Krivul and Kühn, 2010). Increased lateral mobility due to raft-like properties of the PM lining plasmodesmata might represent one possible way to facilitate correct targeting of SUTs from CC into enucleate SIs.

A recent paper, however, investigated lateral mobility of minimal membrane proteins by fluorescence recovery after photobleaching (FRAP) and points to the important role of the cell membrane microdomains by fluorescence recovery after photobleaching (FRAP) and points to the important role of the cell membrane microdomains.

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