Delving deeper into the link between sugar transport, sugar signaling and vascular system development

Sylvie Dinant, Rozenn Le Hir

Received: 4 January 2022 | Revised: 31 March 2022 | Accepted: 6 April 2022

DOI: 10.1111/ppl.13684

SPECIAL ISSUE ARTICLE

Physiologia Plantarum

Delving deeper into the link between sugar transport, sugar signaling, and vascular system development

Sylvie Dinant | Rozenn Le Hir

Université Paris-Saclay, INRAE, AgroParisTech, Institut Jean-Pierre Bourgin (IJPB), Versailles, France

Correspondence
Rozenn Le Hir, Université Paris-Saclay, INRAE, AgroParisTech, Institut Jean-Pierre Bourgin (IJPB), 78000, Versailles, France.
Email: rozenn.le-hir@inrae.fr

Edited by Y. Gibon

Abstract

Plant growth and development rely on the transport and use of sugars produced during photosynthesis. Sugars have a dual function as nutrients and signal molecules in the cell. Many factors maintaining sugar homeostasis and signaling are now identified, but our understanding of the mechanisms involved in coordinating intracellular and intercellular sugar translocation is still limited. We also know little about the interplay between sugar transport and signaling and the formation of the vascular system, which controls long-distance sugar translocation. Sugar signaling has been proposed to play a role; however, evidence to support this hypothesis is still limited. Here, we exploited recent transcriptomics datasets produced in aerial organs of Arabidopsis to identify genes coding for sugar transporters or signaling components expressed in the vascular cells. We identified genes belonging to sugar transport and signaling for which no information is available regarding a role in vasculature development. In addition, the transcriptomics datasets obtained from sugar-treated Arabidopsis seedlings were used to assess the sugar-responsiveness of known genes involved in vascular differentiation. Interestingly, several key regulators of vascular development were found to be regulated by either sucrose or glucose. Especially *CLE41*, which controls the procambial cell fate, was oppositely regulated by sucrose or glucose in these datasets. Even if more experimental data are necessary to confirm these findings, this survey supports a link between sugar transport/signaling and vascular system development.

1 | INTRODUCTION

Through photosynthesis, higher plants synthesize carbohydrates from atmospheric carbon dioxide, water, and sunlight. Carbohydrates can then be (1) used as intermediates in the primary and specialized metabolisms, in energetic metabolism, (2) stored as starch in the vacuole or plastids, and finally (3) be sequestered as cell wall polysaccharides. Because the availability of carbohydrates is central to all cellular processes, including cell maintenance, division, expansion, and differentiation, variations of cytosolic sugar content are sensed by cells to modulate a large variety of biochemical and developmental processes (e.g. embryogenesis, germination, seedling development, reproduction, and senescence). Biochemical and genetic evidence has shown that sugar-sensing processes are conditioned by the dual action of SNF1-RELATED PROTEIN KINASE 1/TARGET OF RAPAMYCIN (SnRK1/TOR) kinases together with the glucose-binding sensor HEXOKINASE1 (HXK1), and other signaling pathways recruiting the REGULATOR OF G-PROTEIN SIGNALING1 (RGS1) and TREHALOSE 6-PHOSPHATE SYNTHASE (TPS1) (Li et al., 2021). In addition, sugars are transported cell-to-cell or long-distance via the phloem. This sugar transport between photosynthetic and heterotrophic cells and tissues involves symplasmic (i.e. via plasmodesmata) and apoplasmic (i.e. recruiting sugar transporters) pathways. Because sucrose, glucose, and fructose have different roles in plant cell functioning, a complex set of enzymes (i.e. kinases, glycoside hydrolases, glycoside transferases, phosphatases, synthases) and transporters (i.e. sugar facilitators,

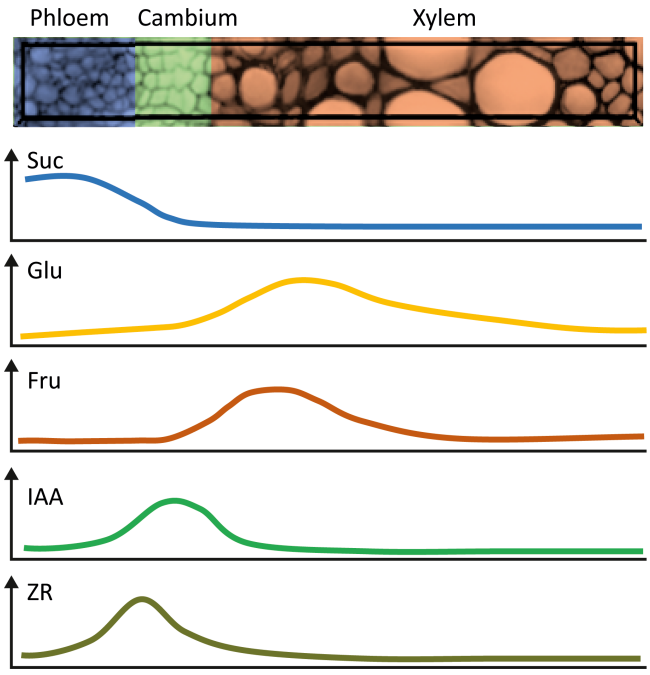

FIGURE 1 Model for shifts in soluble sugars, auxin, and cytokinin across the vascular system in stems. Transverse cross-section of a stem in which the phloem is colored in blue, the cambium in green, and the xylem in orange. The graphs below display the theoretical levels of sucrose (Suc), glucose (Glu), fructose (Fru), IAA (indole 3-acetic acid), and ZR (zeatin riboside) occurring between the different vascular tissues, reconstructed from data obtained from scotpine (*Pinus sylvestris*) wood (Uggla et al., 2001), castor bean hypocotyl (Verscht et al., 2006), and aspen wood (Abreu et al., 2020; Roach et al., 2017)

sucrose and hexoses symporters, inositol transporters, tonoplastic sugar antiporters, and symporters) are responsible for maintaining sugar homeostasis, which will impact plant development and growth, and ultimately plant yield (Patrick et al., 2013). Therefore, sugar transport and signaling coordination represent a cornerstone in plant development.

As the main vehicle for long-distance sugar transport, the vascular system (i.e. phloem and xylem) is also responsible for transporting specialized metabolites, proteins, mRNA, ions, and hormones. In *Arabidopsis thaliana*, the vascular system of roots and hypocotyls originates from embryonic provascular cells, whereas stems developed from the shoot apical meristem (SAM) (De Rybel et al., 2016). Thanks to an intense research investment, our understanding of the molecular network controlling vascular system development at the embryonic and post-embryonic stages has progressed (Fukuda & Ohashi-Ito, 2019). Especially, a network of transcription factors (TFs), under transcriptional control of both environmental (e.g. mechanical stress, drought, temperature, salt) and endogenous cues (e.g. auxin, cytokinins), have been shown to regulate vascular development (Agustí & Blázquez, 2020). However, a remaining open question is whether plants can adjust their vascular development program depending on the sugar availability in the vascular cells' initials.

The hypothesis of a role of sugar signaling, in particular sucrose, in vascular tissues differentiation was first supported by several studies showing, on the callus, the induction of phloem/xylem differentiation by sucrose (for review Krishnamurthy et al., 1999). Moreover, the existence of shifts in sugar concentrations, sugar-related enzymatic activities, and expression of genes related to sugar metabolism across the phloem-cambium-xylem continuum in poplar stem during wood formation (Abreu et al., 2020; Roach et al., 2017) and in the hypocotyl of castor bean during the early development of seedlings (Verscht et al., 2006) further supported a potential role of sugars in vasculature development (Figure 1). Finally, a disruption of the facilitated sugar transport mediated by SUGAR WILL EVENTUALLY BE EXPORTED (SWEET) transporters, is leading to defectuous stem vascular system development and distribution of sucrose between vascular tissues in Arabidopsis hypocotyls (Guendel et al., 2018; Le Hir et al., 2015). However, we still do not know whether there is a direct/indirect link between sugar transport/signaling and vascular system development and which molecular actors could be involved. Although glucose and sucrose have been shown to regulate the expression of many genes at the transcriptional level (Han et al., 2015; Solfanelli et al., 2006), we do not know whether genes coding for TFs, involved in vascular development, are regulated by sugars.

Here, we took advantage of recent transcriptomic databases from different aerial organs in *Arabidopsis thaliana* to address these questions and delve into the possible link between sugar transport/signaling and vasculature development in the shoot. Overall, this exploration allowed us to obtain a more comprehensive view of the genes expressed in the vascular tissues and coding for sugar transport and signaling components. It supports the hypothesis that a tight gene network controls sugar homeostasis in the vascular tissues upstream of the sugar transport in the vasculature, which potentially triggers feedback loops in vascular system development. Identifying such networks might help understand how modifying sugar transport/signaling impacts vascular system development.

2 | DATABASES EXPLOITED TO IDENTIFY SUGAR-RESPONSIVE VASCULAR GENE NETWORKS OR VASCULAR DEVELOPMENT-RELATED GENES

To get new insights into sugar signaling in vascular development, we first addressed whether key factors involved in vascular tissue development are affected by sugar levels. We used a set of 287 genes shown to be part of the PHLOEM INTERCALATED WITH XYLEM (PXY)-mediated transcriptional regulatory network controlling the vascular system development in Arabidopsis (Smit et al., 2020, supplemental dataset 3). This set was identified with a yeast one-hybrid screening using promoters of genes regulating PXY-mediated development as bait and TFs expressed in the stele as prey. *PXY*, one of the central regulator genes for vascular development expressed in the procambium, was one of the prey. We added several additional master genes described in the literature and involved in the development

TABLE 1 Transcriptomic datasets available for the identification of genes expressed in the vascular tissues in the Arabidopsis shoot

Organ	Tissue or cell types	Resolution level	Technique used	References
Embryo	Provascular initials	Single nucleus	Fluorescence-activated nucleus sorting combined with snRNA-seq	Kao et al. (2021)
Shoot apical meristem	Rib meristem, vascular initials	Tissue layers/ domains	Fluorescence-activated nucleus sorting and whole-genome microarray version 5	Yadav et al. (2014)
Shoot apical meristem	Vascular cells	Single cell	Protoplasts generation combined with scRNA-seq	Zhang, Chen, and Wang (2021)
Shoot apical meristem	Shoot apex	Dissected inflorescence apices	Targets of homeodomain protein REPLUMLESS (RPL) by chromatin immunoprecipitation and high-throughput sequencing	Bencivenga et al. (2016)
Inflorescence stem	Phloem cap, vascular bundles, pith	Tissue	Fluorescence-activated nucleus sorting and laser-capture microdissection combined with RNA-seq	Shi et al. (2021)
Leaf	Vascular cells	Single cell	Vascular protoplast generation combined with scRNA-seq	Kim et al. (2021)
Floral stem series				
Inflorescence stem	Beginning, middle, and late stem growth	Organ	Oligonucleotide microarray version 1.0	Ehlting et al. (2005)
Inflorescence stem	Beginning, middle, and late stem growth	Organ	Whole-genome microarray version 3	Vanholme et al. (2012)
Inflorescence stem	Beginning, middle, and late stem growth	Organ	Whole-genome microarray version 5	Hall and Ellis (2013)

of the vascular tissues (Agustí & Blázquez, 2020). Overall, we ended up with a list of 337 vascular factors: transcriptional regulators and factors involved in vascular formation (Table S1). This list of genes was used to query the large Arabidopsis transcriptome datasets focusing on the early responses of seedlings subjected to exogenously-supplied sucrose (Gonzali et al., 2006; Solfanelli et al., 2006) or glucose (Han et al., 2015; Price et al., 2004). For sucrose-responsiveness, Arabidopsis seedlings were grown in a liquid medium for 72 h with 90 mM sucrose (Gonzali et al., 2006; Solfanelli et al., 2006). We selected genes with decreased (D) or increased (I) expression in both biological replicates according to the analysis provided in Table S1 in Solfanelli et al. (2006) or in Table S2 in Gonzali et al. (2006). For glucose responsiveness, we took advantage of the transcription profiling of Arabidopsis seedlings grown either in a solid medium for 6 days in the presence of 5% glucose (Han et al., 2015) or liquid medium for 3 h with 167 mM (about 3%) glucose (Price et al., 2004). We selected TFs with a 2-fold change in gene expression (provided in Table 8 in Han et al. [2015]) and genes responsive to short-term presence of glucose (provided in Table S2 in Price et al. [2004]).

Transcriptomic datasets obtained at the organ, tissue, and cell levels (Table 1) also represent important genomic resources for identifying candidate genes differentially expressed in the vascular tissues. These datasets cover various developmental stages and organs, from the embryo and apical meristems to vascular tissues in inflorescence stem or leaf. In *Arabidopsis thaliana*, four processes lead to vascular system development: specification, establishment (including growth and patterning), maintenance, and differentiation (De Rybel et al., 2016). The specification step, during which the cells acquire their vascular identity from undifferentiated cells, occurs during the early phases of embryo development. At the early globular stage, two cells are considered as vascular initials, while four cells comprise the provascular tissues at the late globular stage. Thanks to fluorescence-activated nuclei sorting combined with single-nucleus (sn)RNA-seq analysis, Kao et al. (2021) identified genes enriched or depleted in the different cell types of the globular-stage embryo, including these four provascular initials (cluster 11 related to vascular initials, named "vas" in Table S3A). At later stages, the formation of the provascular tissues in the meristematic zones at the shoot apex (SAM) or root apex (RAM) depends on the activity of stem cells. Three zones characterize the SAM: (1) the central zone (CZ), where the stem cells are present, (2) the peripheral zone, responsible for the organ initiation, and (3) rib meristem (RM or RZ), which gives rise to the central tissues of the shoot axis (including the vascular system). Again, the power of fluorescence-activated cell sorting allowed Yadav et al. (2014) to generate gene expression profiles of 10 cell populations of these vegetative SAM cell layers and functional domains based on the expression pattern of fluorescent marker lines (Table S1 in Yadav et al., 2014). The features of the provascular cells in the SAM were recently refined with the use of single-cell RNA-seq analysis (Zhang, Chen, & Wang, 2021), which identified genes expressed in the rib zone of the SAM and the subtending provasculature (i.e. phloem and xylem lineages). These genes were gathered in the reconstructed vascular cells populations displayed in Table S4 of Zhang, Wang, et al. (2021). These studies completed the pioneer ChIP-seq study of the genes expressed in the SAM of the inflorescence stem and interacting with the BEL1-like TALE homeodomain (BLH) TF REPLUMLESS (RPL). RPL is expressed in the rib and CZs of the SAM but not in leaf boundaries, nor in floral primordia (Andrés et al., 2015; Smith & Hake, 2003) and controls the rib zone

TABLE 2 List of genes used to query the different transcriptomic datasets

Biological process	Gene names
Sugar transport	Sugar facilitators: *SWEET1*, *SWEET2*, *SWEET3*, *SWEET4*, *SWEET5*, *SWEET6*, *SWEET7*, *SWEET8*, *SWEET9*, *SWEET10*, *SWEET11*, *SWEET12*, *SWEET13*, *SWEET14*, *SWEET15*, *SWEET16*, *SWEET17*
	Sucrose transporters: *SUC1*, *SUC2*, *SUC3*, *SUC4*, *SUC5*, *SUC6*, *SUC7*, *SUC8*, *SUC9*
	Sugar transport proteins: *STP1*, *STP2*, *STP3*, *STP4*, *STP5*, *STP6*, *STP7*, *STP8*, *STP9*, *STP10*, *STP11*, *STP12*, *STP13*, *STP14*
	Polyol/monosaccharide transporters: *PMT1*, *PMT2*, *PMT3*, *PMT4*, *PMT5*, *PMT6*
	Inositol/sugar transporters: *INT1*, *INT2*, *INT3*, *INT4*
	Vacuolar glucose transporters: *VGT1*, *VGT2*, *VGT3*
	Tonoplast monosaccharide transporters: *TST1/TMT1*, *TST2/TMT2*, *TST3/TMT3*
	Monosaccharide facilitators: *ERD6*, *ERDL1/ESL3.08*, *ERDL2/ESL3.05*, *ERDL3/ESL1/ESL3.07*, *ERDL4/ESL1.01*, *ERDL5/ESL3.01*, *ERDL6/ESL1.02*, *ERDL7/ESL2.01*, *ERDL8/ESL2.02*, *ERDL9*, *ERDL10/ESL3.11*, *ERDL11*, *ERDL12/ESL3.10*, *ERDL13/ESL3.04*, *ERDL14/ESL3.02*, *ERDL15/ESL3.03*, *ERDL16/ESL2.03*, *SFP1/ESL3.13*, *SFP2/ESL3.14*
Sugar metabolism	Sucrose synthases: *SUS1*, *SUS2*, *SUS3*, *SUS4*, *SUS5*, *SUS6*
	Fructose 1,6-bisphosphate phosphatase: *FBPase*, *cFBPase*
Sugar signaling	Trehalose phosphate synthase: *TPS1*, *TPS2*, *TPS3*, *TPS4*, *TPS5*, *TPS6*, *TPS7*, *TPS8*, *TPS9*, *TPS10*, *TPS11*
	Trehalose phosphate phosphatase: *TPPA*, *TPPB*, *TPPC*, *TPPD*, *TPPE*, *TPPF*, *TPPG*, *TPPH*, *TPPI*, *TPPJ*
	TOR signaling: *RGS1*, *RHIP1*, *TOR*, *LST8-1*, *LST8-2*, *AtRaptor1*, *AtRaptor2*
	SnRK signaling: *SnRK1,1/KIN10*, *SnRK1,2*, *SnRK2,1*, *SnRK2,2*
	Hexokinases: *HXK1*, *HXK2*

Note: AGI numbers for each gene can be found in Table S2.

development and stem growth (Bencivenga et al., 2016). We used the list of interacting partners of RPL displayed in Table S1 of Bencivenga et al. (2016) to query genes involved in sugar transport and signaling.

In mature organs, transcriptomic data related to the vasculature are sketchier. In Arabidopsis inflorescence stem, primary growth relies on vascular bundles (VBs) development, with phloem and xylem surrounding a fascicular (pro)cambium. The establishment of cambia between primary bundles, also known as interfascicular cambia, characterizes the onset of secondary stem growth (Ragni & Greb, 2018). The recent study of Shi et al. (2021), which used a combination of laser capture microdissection and RNA-seq analysis, identified transcripts present either in the phloem cap, pith, or VB in Arabidopsis inflorescence stem during the secondary growth (data are available in Tables S1 and S13 in Shi et al. [2021]). In addition, despite not being performed at the cell or tissue level, we also took advantage of the three transcriptomics datasets produced in Arabidopsis inflorescence stem (Ehlting et al., 2005; Hall & Ellis, 2013; Vanholme et al., 2012). These transcriptomic resources have been made at different primary and secondary growth stages during the inflorescence stem development. These stages correspond to xylem lignification, and they could also be associated with vascular system development since the vasculature is an important sink for sequestration of carbon skeletons. More precisely, differentially expressed genes ($p < 0.05$) were extracted from Table S1 in Ehlting et al. (2005), Dataset S2 in Vanholme et al. (2012) and Tables S2 – S4 in Hall and Ellis (2013). The three gene lists were used to generate a Venn diagram by an online tool (https://bioinformatics.psb.ugent.be/webtools/Venn/). Finally, a comprehensive transcriptomic resource has been recently produced by Kim et al. (2021), who used a single-cell RNA-seq approach to uncover the genes specifically enriched in each vascular cell type of the Arabidopsis mature rosette leaves (source organs). This included procambium cells, companion cells, S-type cells, phloem and xylem parenchyma, and bundle sheath (data are available in dataset S4 in Kim et al. [2021]).

To identify genes differentially expressed across the vascular system development or specifically enriched in the different vascular cell types, the abovementioned datasets (Table 1) were queried with a selection of 76 genes belonging to the main families of sugar transporters (Table 2; Table S2). This list includes the following transporters families: POLYOL/MONOSACCHARIDE TRANSPORTER (PMT), SUGAR WILL EVENTUALLY BE EXPORTED (SWEET), SUCROSE TRANSPORTER (SUC), SUGAR TRANSPORTER PROTEIN (STP), VACUOLAR GLUCOSE TRANSPORTER (VGT), INOSITOL TRANSPORTER (INT), EARLY RESPONSIVE TO DEHYDRATION 6-LIKE (ERDL/ESL), SUGAR-PORTER (SFP) and TONOPLAST SUGAR TRANSPORTER (TST/TMT). The same approach was applied for known components of three main sugar signaling pathways, including TOR, SnRK, REGULATORY-ASSOCIATED PROTEIN OF TOR (RAPTOR), LETHAL WITH SEC13 PROTEIN 8 (LST8), RGS1, and RGS1-HXK1 INTERACTING PROTEIN 1 (RHIP1), together with enzymes of the sugar metabolism shown or proposed to be important in the sugar signaling pathways, as described in Li et al. (2021), i.e. SUCROSE SYNTHASE (SUS), HEXOKINASE (HXK), TREHALOSE-6-PHOSPHATE SYNTHASE (TPS), TREHALOSE-6-PHOSPHATASE (TPP), and FRUCTOSE-1,6-BIPHOSPHATASE (FBPase) (Table 2; Table S2).

3 | SUGAR-MEDIATED REGULATION OF THE EXPRESSION OF FACTORS INVOLVED IN VASCULAR SYSTEM DEVELOPMENT

An intricate network of TFs, peptides, and transcription regulators are involved in the vascular system development at embryonic and post-embryonic stages (Agustí & Blázquez, 2020; Smit et al., 2020). They control successive processes, including primary vascular tissues

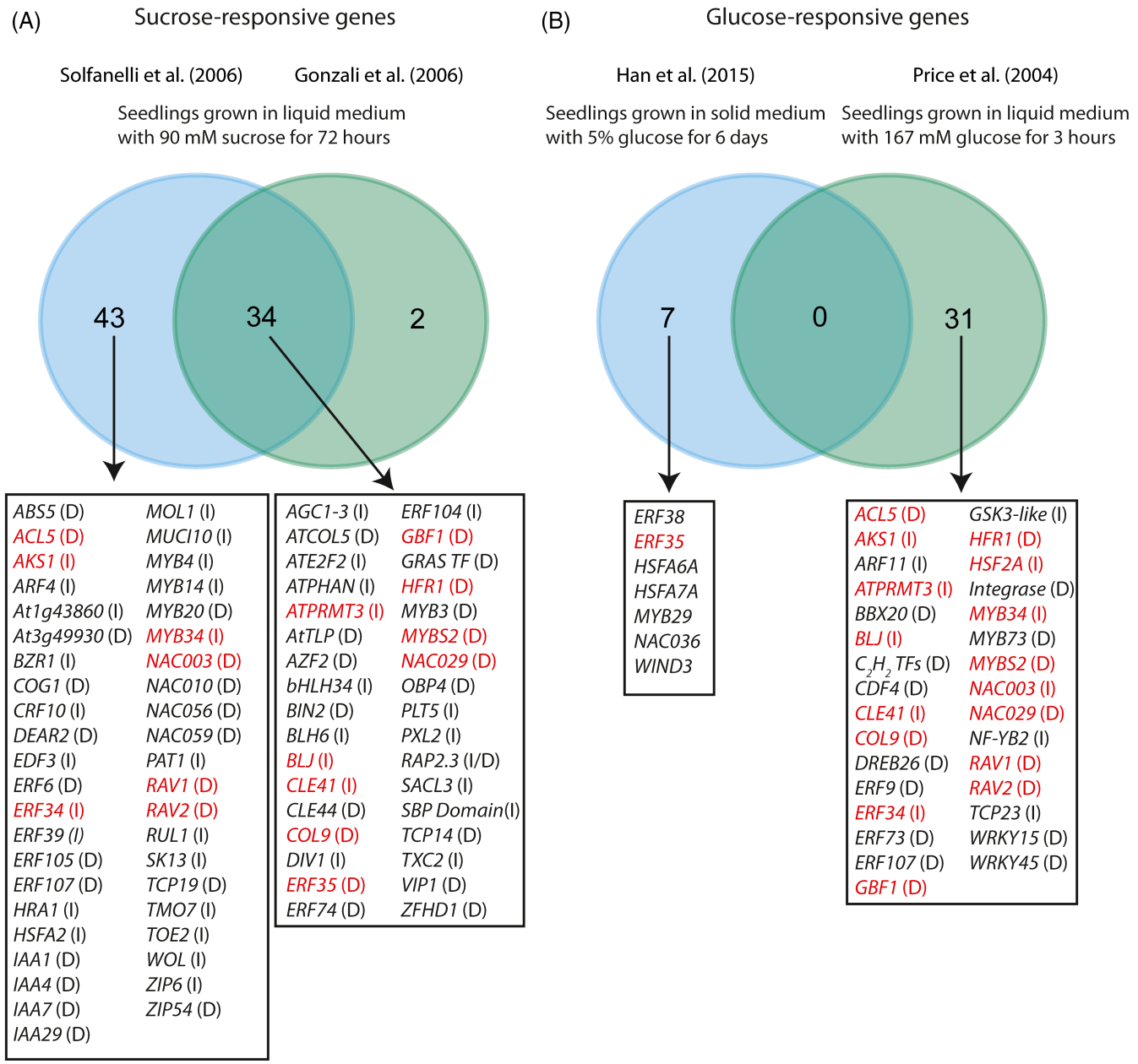

FIGURE 2 Genes associated with vascular development in Arabidopsis and regulated by sugars. Venn diagram comparing the genes for which expression is regulated by sucrose (Gonzali et al., 2006; Solfanelli et al., 2006) (A) or by glucose (Han et al., 2015; Price et al., 2004) (B). When available, the expression in response to sugars, increase (I) or decrease (D), is mentioned in brackets after the gene name. The genes are ranked in alphabetical order. The genes in red are regulated by both sucrose and glucose. The AGI number for each gene can be found in Table S1

formation, vascular patterning, cambial activity, and xylem and phloem specification, during embryo/ root/ hypocotyl/ leaf/stem development. A role of sugars in regulating cambial activity and the development of the vascular tissues has been proposed for a long time. However, the processes involved are not known so far. Several lines of evidence support such a role: (1) concentration gradients of soluble sugars in the vascular tissues (Abreu et al., 2020; Roach et al., 2017; Uggla et al., 2001; Verscht et al., 2006) (Figure 1), (2) modification of sucrose and fructose metabolism alter the development of vascular tissues (Granot et al., 2013), (3) effects of tree girdling on carbon allocation, i.e. alteration of wood formation (Winkler & Oberhuber, 2017), (4) induction of phloem and xylem elements by sucrose in callus during in vitro culture (Wetmore & Rier, 1963; Jeffs & Northcote, 1966, 1967; Wilson et al. Warren et al., 1994), and (5) modification of sugar homeostasis in the vascular tissue alter xylem development (Aubry et al., 2022; Gerber et al., 2014; Mahboubi et al., 2013; Unda et al., 2017). These observations raise the question of how the development of the vascular tissues can adjust to carbon availability and whether sugar signaling pathways are acting upstream of master genes involved in the vascular development. While the phloem contributes to the supply of sugars to distant organs by long-distance transport, a large amount

of sugars is also transported to the adjacent tissues (Gould et al., 2012), in particular for cambial activity and xylem cell development, which are large energy sinks and depend on a continuous supply of soluble sugars (Hansen & Beck, 1994; Muller et al., 2011; Oribe et al., 2003; Spicer, 2014).

From Solfanelli et al. (2006), we found 77 genes differentially expressed in response to sucrose. Among these, 34 were also found in the study of Gonzali et al. (2006), suggesting that these TFs are likely to be sucrose-responsive (Figure 2A). In this list, it is worth mentioning the presence of genes coding for the peptides CLAVATA3/ESR-RELATED41/ CLAVATA3/ESR-RELATED44 (*CLE41/44*) that are expressed in the phloem, promote the (pro)cambial division, and inhibit xylem differentiation (Etchells & Turner, 2010; Hirakawa et al., 2010; Yuan & Wang, 2021). While *CLE41/44* have been shown to additively regulate procambium cells division (Yamaguchi et al., 2017), they display a differential response to exogenous sucrose. Indeed, the expression of *CLE41* is induced in response to sucrose, while *CLE44* is decreased (Figure 2) (Solfanelli et al., 2006). Additionally, induction of *PHLOEM INTERCALATED WITH XYLEM-LIKE 2* (*PXL2*) expression, coding for a receptor-like kinase involved in the regulation of vascular development (Fisher & Turner, 2007), by sucrose is also likely (Figure 2A). Among the other sucrose-responsive TFs identified in these studies (Gonzali et al., 2006; Solfanelli et al., 2006), we found *OBF BINDING PROTEIN2* (*OBP2*) and *PHAVOLUTA* (*PHV*) (Figure 2A). OBP2 belongs to the PHLOEM EARLY DOF (PEAR) group of mobile TFs expressed in the phloem and involved in radial growth (Miyashima et al., 2019). *PHV* belongs to the *HOMEODOMAIN LEUCINE ZIPPER HD-ZIP III* genes encoding the polarity TFs critical for the formation of the vascular tissues (Ilegems et al., 2010; Smetana et al., 2019) and shown to antagonize PEAR TFs (Miyashima et al., 2019) for radial growth. Identifying these genes as potential targets of sugar signaling suggests a potential link between radial growth and sugar signaling. The BR-activated TF BRASSINAZOLE RESISTANT1 (BZR1), which is a transcriptional activator of SHORT ROOT (SHR) (Tian et al., 2022), was also identified as sucrose-responsive (Figure 2A). *BZR1* promotes periclinal cell divisions and is expressed in the same cells as *SHR* in the root stele (Qi et al., 2019). In addition, it has been shown that BRASSINOSTEROID-INSENSITIVE2 (BIN2) acts together with BZR1 and independently from the sugar sensor HXK1 and TOR during seedling growth (Zhang, Sun, et al., 2021). This study, therefore, established a link between sugar and brassinosteroid signaling. Additional transcriptional activators were also identified as sucrose-responsive, including *NAC DOMAIN* (*NAC*) genes (*NAC003*, *NAC010*, *NAC029*, *NAC056*, *NAC059*), *MYB DOMAIN PROTEIN* (*MYB*) TFs (*MYB3*, *MYB4*, *MYB6*, *MYB14*, *MYB20*, *MYB34*, and *MYB91*). Few factors involved in auxin or CK signaling were also identified, such as *AUXIN RESPONSE FACTOR4* (*ARF4*), *INDOLEACETIC ACID-INDUCED PROTEIN* (*IAA1*, *IAA4*, *IAA7*, *IAA29*), and the *CYTOKININ RESPONSE1/WOODEN LEG* (*CRE1/WOL*) cytokinin receptor (Mähönen et al., 2006) (Figure 2A). With these few examples, our study indicates that several master genes expressed in the vascular tissue layers and acting in their formation or on the division or specification of surrounding cells are regulated by sucrose. Whether this suggests a feedback loop by sucrose remains to be tested.

Out of the TFs responding to the long-term presence of glucose (Han et al., 2015), six of them are related either to primary or secondary cell wall synthesis (*ETHYLENE RESPONSE FACTOR038*, *ERF035*, *MYB29*, *HSFA7A*, *HSFA6A*, and *WIND3*) (Nakata et al., 2021; Saelim et al., 2019; Sakamoto et al., 2018; Smit et al., 2020; Taylor-Teeples et al., 2015). It is interesting to note that glucose-responsive factors belong to cellular processes related to the synthesis of the cell wall, which is an important sink for carbon. The TFs *WIND3*, which is involved in vascular reconnection (Iwase et al., 2021), and *NAC036*, which displays a vascular-specific expression (Kato et al., 2010; Figure 2B), were also identified in this list. Interestingly, 31 genes not identified by Han et al. (2015) (Figure 2B) were identified in the report of Price et al. (2004) describing early transcriptional responses to glucose (3% of glucose for 3 h). Among them, half (17 over 31) were regulated both by sucrose and glucose (Figure 2). They include the gene coding for the peptide CLE41 that is involved in vascular system development (Yuan & Wang, 2021), also identified in the surveys of Solfanelli et al. (2006) and Gonzali et al. (2006). In addition, two genes coding for TFs related to light were identified, namely LONG HYPOCOTYL IN FAR-RED (HFR1), a key TF involved in light signaling (Yang et al., 2005), and CONSTANS-like 9 (COL9), responding to changes in light intensities (Kumari et al., 2019), providing a possible link between sugar signaling and the modulation of vascular development by light regimes (Agustí & Blázquez, 2020). Even though these studies have been performed in different conditions and further experiments need to be performed to confirm these findings, these results suggest that sucrose and glucose signaling could be involved in regulating TFs and activators participating in the formation or the differentiation of vascular tissues. Thus, this analysis provides new evidence for a sugar-mediated regulation of vascular tissue development. This issue should be considered to complete our understanding of the endogenous factors modulating vasculature development.

Together with soluble sugars, plant hormones act also as signal molecules and play a role as developmental regulators (Li et al., 2021). Moreover, previous works showed that the concentration maxima of auxin and cytokinin are spatially different from that of soluble sugars (Figure 1) (Abreu et al., 2020; Uggla et al., 2001), suggesting that hormone and sugar signaling pathways might be independent. We queried in the Arabidopsis databases the transcriptional responses of glucose- and sucrose-responsive vascular factors to IAA or Zeatin application. We observed that more than 80% of these sugar-responsive genes are not affected by either cytokinin or auxin (Table S3). Our findings support the hypothesis that the sugar-mediated signaling pathway could be independent of auxin and cytokinin signaling, which are central for regulating vascular tissue differentiation.

4 | IDENTIFICATION OF NEW CANDIDATES INVOLVED IN SUGAR TRANSPORT/HOMEOSTASIS AND POTENTIALLY INVOLVED IN THE VASCULAR SYSTEM DEVELOPMENT AND FUNCTIONING

Phloem functions are intertwined with the long-distance transport of sugars by mass flow, with sucrose being the main form of

translocation in many species. As initially shown in potato for StSUT1 (Riesmeier et al., 1993, 1994), the Arabidopsis sucrose/symporter SUC2 is involved in phloem sucrose loading in minor veins (Sauer & Stolz, 1994; Truernit & Sauer, 1995) in addition to sucrose retrieval into the phloem transport pathway (Gould et al., 2012). Recently, two additional sugar facilitators belonging to the SWEET family, SWEET11/SWEET12, were shown to act together with SUC2 for sugar export from the parenchyma cells into the apoplasm vasculature (Chen, 2014). In addition to these major players in phloem loading, other sugar transporters have been identified and located either in phloem, xylem, (pro)cambium cells, or vascular parenchyma cells. These transporters are involved in intracellular or intercellular transport to fulfill the high carbohydrates demand of vascular cells (Aubry et al., 2019). Some of these sugar transporters have also been proposed to participate in recircularizing sugars from the xylem (van Bel, 2021). This suggests fine-tuned sugar transport between the various vascular cell layers and between the vascular tissues and surrounding tissues. But many actors are still missing on this scheme, and we still do not understand how this is coordinated and which signaling pathways are involved.

In mature leaves, sugar loading occurs in the minor veins, while phloem cells from the main and second-order veins participate in sugar delivery to axial sinks and the retrieval of sugars after leakage from the sieve tubes (Haritatos et al., 2000). In the recent survey of gene networks expressed in Arabidopsis matures leaves and enriched in the various vascular cell types (Kim et al., 2021), the cluster related to the companion cells and associated with *SUC2*, which specifically accumulates in phloem companion cells in Arabidopsis (Stadler & Sauer, 1996), gathered the genes coding the inositol transporter INT4 as well as the sugar transporters SWEET1 and SWEET4. This is consistent with the expression of *INT4* in the phloem companion cells (Schneider et al., 2006), of *SWEET4* in the vascular system of leaves (Liu et al., 2016), and our unpublished data regarding the expression of *SWEET1*, which codes for a glucose transporter (Park et al., 2022), in the phloem cells (Le Hir, unpublished data). A second cluster, enriched in genes expressed in the phloem parenchyma cells and the phloem-cambium-xylem interface, gathered *SWEET11*, *SWEET12* and *SWEET13*. An expression of *SWEET13*, coding for a sugar and gibberellin transporter, has indeed been shown in the leaf vascular system (Han et al., 2017; Kanno et al., 2016). The presence of *SWEET11* and *SWEET12* in this cluster is also consistent with their functional characterization that confirmed a specific expression in vascular parenchyma cells in leaves (Cayla et al., 2019; Chen et al., 2012; Kim et al., 2021). Both proteins are also involved in the export of sugars between the phloem parenchyma cells and companion cells, hinting to a key role in sugar loading of the minor veins (Chen et al., 2012). Interestingly, a third cluster assigned to phloem and xylem parenchyma cells gathered *SWEET11*, *SWEET12*, *SWEET13* and *STP13*. *SWEET11* and *SWEET12* are indeed expressed in the xylem parenchyma cells of the inflorescence stem (Le Hir et al., 2015). The gene coding for the monosaccharide transporter *SFP2/ESL3.14*, whose function is unknown yet (Quirino et al., 2001; Slawinski, Israel, Artault, et al., 2021), was enriched in an additional cluster assigned to xylem parenchyma cells. Finally, Kim et al. (2021) identified two distinct procambium populations (PC) corresponding to the differentiation of phloem cells on one side and xylem cells on the other side. Interestingly, *SUC1*, which codes for a sucrose symporter, was the only gene enriched in procambium cells closely related to developing xylem cells. In procambial cells, SUC1 could uptake sucrose released into the apoplast.

In Arabidopsis, during stem development, the vasculature is an important sink for sequestration of carbon skeletons. Therefore, interrogating transcriptomics datasets produced during inflorescence stem development represents a resource worth exploiting to decipher the relationship between sugars and vascular development. Ehlting et al. (2005) performed a transcript profiling of Arabidopsis primary stems at different stages of the VB and interfascicular fibers differentiation. Over the 76 genes queried, 21 were differentially expressed across the stem development. Four genes code for members of the SWEET transporters family involved in the facilitated transport of sucrose and hexoses (*SWEET2*, *SWEET3*, *SWEET11*, and *SWEET12*), one codes for the sucrose/H^+ symporter SUC2, five for members of the monosaccharides/H^+ symporter family (*STP2*, *STP3*, *STP7*, *STP8*, and *STP11*), *PMT6* codes for a polyol/monosaccharide transporter, *INT3* codes for an inositol transporter and several genes code for tonoplast-localized sugar transporters (*VGT1*, *VGT2*, *ESL3.07*, *ERDL11*, *ESL3.10*, *ESL3.02*, *ESL3.03*, *TST1*, and *TST3*). While a reverse genetic approach confirmed that *SWEET11* and *SWEET12* are involved in the vascular system development of Arabidopsis stem (Le Hir et al., 2015), no such report exists for the other genes identified in these datasets. To provide insight into the lignin biosynthesis, Vanholme et al. (2012) analyzed Arabidopsis wild-type inflorescence stem at four developmental stages to evaluate transcriptomic shifts and identified gene clusters during its development. Especially, the genes coding for vacuolar sugar transporters (*ESL2.02*, *ESL3.04*, *ESL3.02*, and *TST1*) were gathered in a cluster associated with earlier developmental stages and high metabolic rate and enriched in primary metabolism. Despite a recent phylogenetic analysis of the ERDL/ESL transporter family (Slawinski, Israel, Paillot, et al., 2021), no data are available on the localization and functional characterization for most members of the ERDL/ESL vacuolar sugar transporters family. Genes coding for the inositol transporter INT2 (Schneider et al., 2007) and the monosaccharide symporter STP1 (Büttner & Sauer, 2000) were found in a cluster with genes related to defense response, cell death, and lignification process. This is consistent with the role of inositol and monosaccharide as building blocks in cell wall synthesis (Strobl et al., 2018; Verbančič et al., 2018). Most of the genes coding for sugar transporters identified in this dataset, namely *SWEET11*, *SWEET12*, *SUC1*, *STP13*, *STP14*, *PMT5*, *ESL3.08*, and *ESL3.01*, were present in a cluster gathering genes involved in auxin transport, identifying new candidates to explore further the well-known link between sugar and auxin in the vascular system development (Mishra et al., 2021). A similar approach was carried out by Hall and Ellis (2013), with global transcript profiles at four distinct phases of stem growth. We queried this dataset and identified *SWEET3*, *SWEET12*, *SWEET17*, *SUC2*, *SUC4*, *SUC8*, *STP4*, *STP5*, *STP12*, *STP13*, *PMT5*, *INT4*, *VGT1*, *VGT3*, *ESL3.08*, *ESL3.07*, *ESL3.01*, *ERDL9*, *ERDL11*, *ESL3.10*, *ESL3.03* and *ESL3.14* as

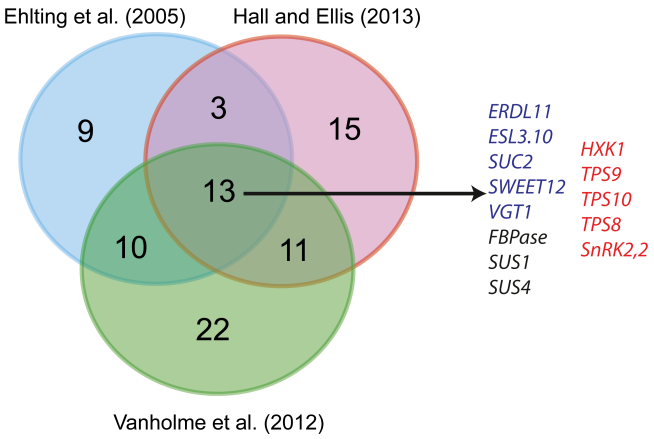

FIGURE 3 Genes involved in sugar transport and signaling are differentially expressed in the inflorescence stem. Venn diagram comparing the genes differentially expressed during stem development in the following databases: (Ehlting et al., 2005; Hall & Ellis, 2013; Vanholme et al., 2012). Genes involved in sugar transport are colored in blue, sugar metabolism in black and sugar signaling in red

differentially expressed across these different developmental phases. Further, the cross-referencing of these three datasets, performed at the organ level, allows us to identify *SUC2*, *VGT1*, *ERDL11*, *ESL3.10*, and *SWEET12* as differentially expressed across Arabidopsis stem development (Figure 3). These findings indicate a developmental regulation of the expression of these genes, which may be related to the higher demand for sugars used as carbon skeletons for the cell wall polysaccharides synthesis. Indeed, an increase in cell wall synthesis is observed during the transition from primary-to-secondary growth in the vascular system of the floral stem. At the tissue level in the inflorescence stem, Shi et al. (2021) identified transcripts present either in the phloem cap, pith, or VB (Figure 4). While no indication of expression of *SWEET8*, *SWEET9*, *SWEET15*, *SUC7*, *SUC8*, *SUC9*, *STP2*, *STP10*, *PMT1*, *PMT2*, *INT3*, and *ESL3.03* was found in this survey, few genes were identified as preferentially expressed in the VBs, including *SWEET1*, *SWEET12*, *SWEET13* and *SWEET14*, *PMT4*, *PMT6*, *INT4*, *TST1*, *ESL3.07*, *ESL2.01*, *ERDL11*, *ESL3.04*, and *ERDL3.13* (Figure 4). Moreover, 10 sugar transporter genes were up-regulated in the pith compared to the VB, i.e. *STP3*, *STP4*, *STP7*, *INT2*, *ESL3.08*, *ESL1.01*, *ESL3.01*, *ERDL11*, *ESL2.03*, and *ESL3.14* (Figure 4), which raises the question of the role of the pith in the stem regarding sugar storage or sequestration. Could this tissue be important in maintaining sugar homeostasis in normal conditions or in response to modifications of the environmental conditions? The study of Shi et al. (2021) also provides data at the cell-specific level by using fluorescence-activated nucleus sorting coupled with next-generation RNA sequencing. The interrogation of this dataset only identified *SWEET11* and *ESL3.11* as significantly enriched in fiber cells ($NST3_{pro}$-positive nuclei) and early xylem vessels ($VND7_{pro}$-positive nuclei), respectively.

The SAM and the embryo are connected to the surrounding tissues by plasmodesmata (Kim et al., 2005; Kitagawa & Jackson, 2017; Stadler et al., 2005). It has been shown that symplasmic transport plays a key role in delivering phloem mobile sugars in the SAM (Gisel et al., 1999, 2002). Nonetheless, regarding the expression of sugar transport-related genes in provascular cells in the SAM or the embryo, few were significantly enriched in the vascular cell population compared to the L2 cell layer (i.e. *STP1*, *SUC2*, *PMT3*, *ESL2.01*, *SWEET11*, *SWEET12*, *SWEET13*, and *SWEET14* (Yadav et al., 2014). Some of them were confirmed by the recent study of SAM cell lineages (Zhang, Chen, & Wang, 2021), in phloem lineages cells, including *SWEET11*, *SWEET12* and *SUC2*, in xylem lineage cells, namely *SWEET17* (belonging to a tracheary element [TE]-specific cluster), *SUC1* and *PMT3*, while *STP1* was shown to be enriched in dividing cells. The presence of these sugar transporters in the SAM should be tempered. In both studies, the SAM samples also include leaf primordia that likely contain provascular cells and protophloem and protoxylem. Nonetheless, several genes coding for sugar transporters (i.e. *ESL3.07*, *ESL2.02*, *ERDL9*, *ESL3.11*, *ERDL11*, *ESL3.10*, *ERDL3.13*, *INT4*, *SUC1*, *SUC4*, *SWEET1*, *SWEET2*, *SWEET14*, and *SWEET17*) were also identified as potential targets of REPLUMLESS TF, which is specifically expressed in the central and rib zones of the SAM (Andrés et al., 2015; Bencivenga et al., 2016). Since SWEET17 codes for a fructose-specific tonoplastic transporter, its expression in meristematic cell populations related to differentiating TE raises the question of the importance of fructose exchanges between cytosol and vacuole during this process. Similarly, the early expression of *SWEET11*, *SWEET12*, and *SUC2* in meristematic cell populations related to differentiating phloem indicates that sugar loading could be operational at very early developmental stages. In Arabidopsis, the expression of *SUC2* in the vascular system of inflorescence apices and floral primordia (Goetz et al., 2021) supports the idea that SUC2 could participate in sucrose retrieval in differentiating protophloem (transport phloem in that case) (Gould et al., 2012). The presence of *SWEET11* and *SWEET12* transcripts, also part of the phloem complex, may also reflect their participation in this process. Interestingly, in the survey of genes expressed in the embryo (Kao et al., 2021), the expression of several genes was enriched in the vascular initials, including *STP1*, *STP12*, *ERDL4/ESL1.01*, *SUC1*, *TMT2*, and *SWEET7*. The presence of genes coding for the plasma membrane monosaccharide transporters STP1, STP12 and SWEET7 (Boorer et al., 1994; Rottmann et al., 2018; Zhang, Wang, et al., 2021) raised the question of the role of hexoses in embryo development. Similarly, the presence of *ESL1.01* and *TMT2* in these datasets, both coding for tonoplast-localized transporters, likely respectively exporting monosaccharides or importing sucrose via an antiport mechanism (Jung et al., 2015; Niño-González et al., 2019; Schulz et al., 2011; Wormit et al., 2006), suggests a tight control of cytosolic sugar signal in the embryo.

Altogether, this analysis indicates that several members of the *ERDL/ESL*, *PMT*, and *STP* transporters families as well as *SUC1*, *SUC4*, *SWEET1*, *SWEET4*, *SWEET11-14* have a preferential expression in the vascular initials or vascular tissues, as shown by different approaches and at various stages of specification or differentiation of vascular cells; however, the function of most of them is unknown.

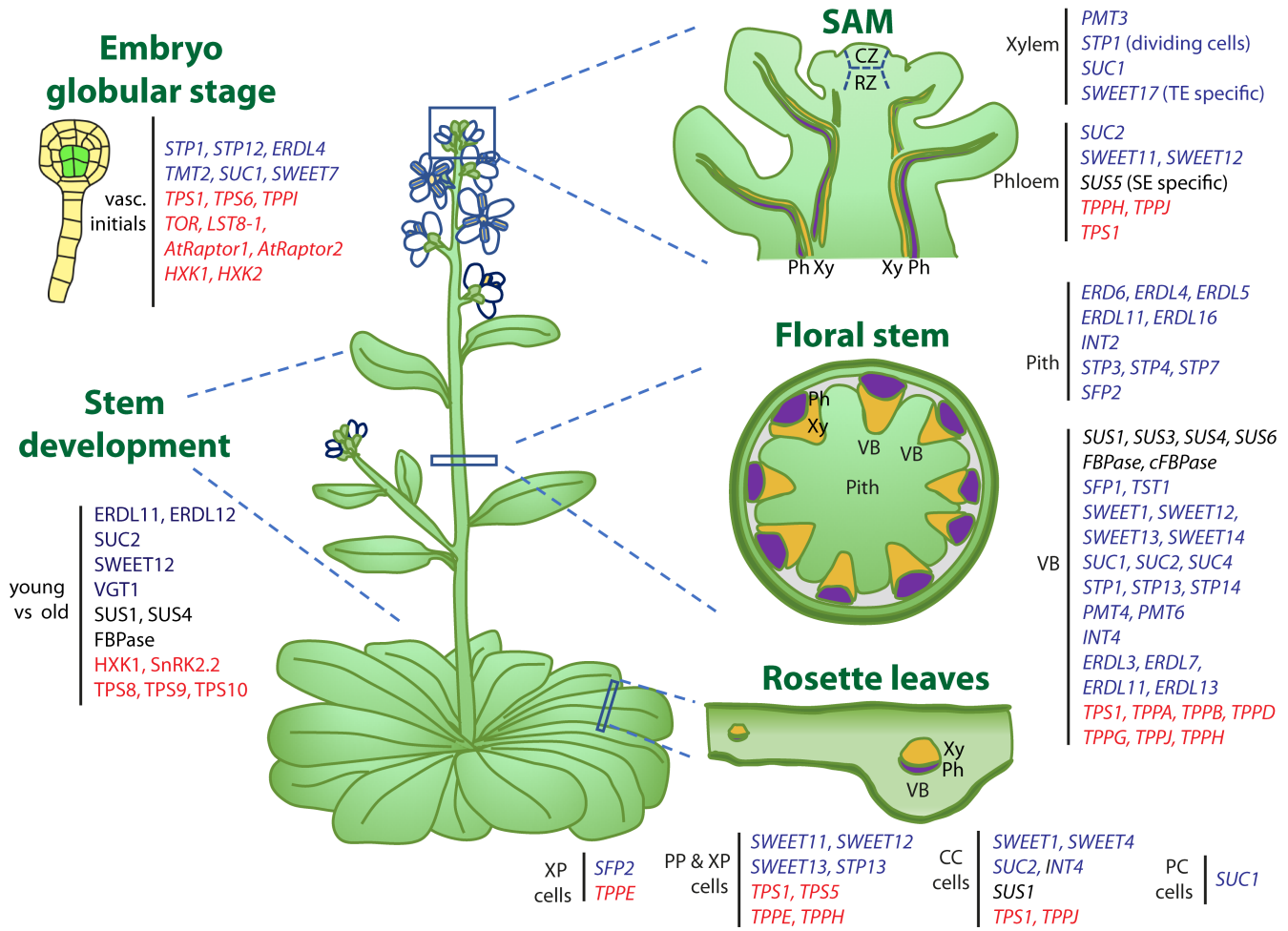

FIGURE 4 Overview of the genes involved in sugar transport and signaling linked to the vascular system development. In the different sketches, the phloem is colored in purple, the xylem in orange and the interfascicular fibers in gray. CC, companion cells; CZ, central zone; PC, procambium; Ph, phloem; PP, phloem parenchyma; RZ, rib zone; SAM, shoot apical meristem; SE, sieve element; TE, tracheary element; VB, vascular bundle; XP, xylem parenchyma; Xy, xylem. Genes involved in sugar transport are colored in blue, sugar metabolism in black and sugar signaling in red

5 | FACTORS ACTING IN SUGAR SIGNALING IDENTIFIED IN THE VASCULATURE AND POTENTIALLY INVOLVED IN ITS DEVELOPMENT/FUNCTIONING

Several sugar-signaling genes were found in the companion cells cluster in mature leaves, including *SUS1*, *TPS1*, *TPPJ*, and *SUC2* (Kim et al., 2021). In phloem parenchyma and phloem-cambium-xylem interface clusters, we also found *TPS1*, *TPPE*, and *TPPH* genes, together with *SWEET11/SWEET12*. In the cluster assigned to phloem and xylem parenchyma cells, we found *TPS1*, *TPS5*, *TPPE*, and *TPPH*. Furthermore, the expression of *TPPE* was enriched in xylem parenchyma cells cluster. The preferential expression in the vascular parenchyma cells of several genes related to the T6P signaling suggests an unsuspected role of the signaling pathway in the xylem parenchyma. Phloem parenchyma transfer cells have recently been proposed to work as a central hub for controlling phloem loading (Wei et al., 2021). However, the function of xylem parenchyma is still poorly understood.

In the transcriptome surveys of Arabidopsis inflorescence stem during its development, we also found *TPS8*, *TPS9*, *TPS10*, *SUS1*, *SUS4*, *SnRK2.2*, and *FBPase* commonly expressed in the three datasets (Ehlting et al., 2005; Hall & Ellis, 2013; Vanholme et al., 2012) (Figure 3). In addition, the study of Vanholme et al. (2012) identified *HXK1* in a cluster enriched in genes related to the primary metabolism and cells with high metabolic rate, while *SUS1*, *TPS10* and *ESL3.10* were identified in a cluster gathering genes related to secondary cell wall development. Some of these genes were confirmed by the recent study of Shi et al. (2021) (Figure 4). Interestingly, several members of the TPP family were found to be preferentially expressed in the VB (including the phloem cap) compared to the pith (i.e. *TPPA*, *TPPB*, *TPPD*, *TPPG*, *TPPJ*, and *TPPH*) (Figure 4). In addition, *TPS5* and *TPPI* were enriched in fiber cells ($NST3_{pro}$-positive nuclei) and the proximal cambium/xylem interface (PXY_{pro}-positive nuclei), respectively (Shi et al., 2021).

In the survey of genes expressed in the embryo (Kao et al., 2021), the expression of nine genes was enriched in the vascular initials, namely *TPS1*, *TPS6*, *TPPI*, *TOR*, *HXK1*, *HXK2*, *LST8-1*, *AtRaptor1* and *AtRaptor2*. On the other hand, in the survey done on the SAM, the expression of *TPS1* and *TPS5* appeared enriched in vascular cell populations compared to the L2 cell layer (Yadav et al., 2014). In SAM cell subpopulations (Zhang, Chen, & Wang, 2021), the expression of *TPS1*, *TPPH*, *TPPJ* was enriched in phloem lineages cells, while the expression of *SUS5* was enriched in a sieve-element (SE) specific cluster. Consistently, the accumulation of SUS5 was recently confirmed in immature and mature phloem SE (Yao et al., 2020). Both works performed by Yadav et al. (2014) and Zhang, Chen, and Wang (2021) highlighted an enrichment of *TPS1*. In agreement with this result, *TPS1* has a confirmed expression in the SAM rib zone and the subtending provasculature and in the leaf and stem vasculature (Fichtner et al., 2021). In addition, modification of T6P levels in the vasculature, especially through the action of *TPS1*, is involved in the regulation of shoot branching (Fichtner et al., 2021). These findings support a key role of *TPS1* (and T6P) in vascular system development (Fichtner et al., 2020). Interestingly, five genes linked to T6P signaling components (i.e. *TPPA*, *TPPE*, *TPPH*, *TPPI*, *TPPJ*), in addition to *TPS1* and *SUS3*, were also identified as targets of RPL during shoot morphogenesis in the SAM rib zone, which potentially overlap with vascular initials (Bencivenga et al., 2016). Together with the data obtained at the cell-specific level in the SAM, these findings confirm that the regulation of sugar signaling via the T6P pathway and the sugar exchanges at both the intracellular and intercellular levels are important at the early stages of the vascular system differentiation. Interestingly, we currently lack functional characterization, including spatio-temporal localization data for most of these genes.

6 | CONCLUSIONS AND PERSPECTIVES

Exploring recent transcriptomics datasets produced at the organ, tissue, and cell level of Arabidopsis shoot and describing expression data in vascular cells now provide a more comprehensive view of the genes involved in sugar transport and signaling (Figure 4). It offers new evidence in *Arabidopsis thaliana* for a role of sugars in vasculature formation or functioning: (1) a spatio-temporal specificity of the expression of genes related to sugar transport in vascular cells during development; (2) a spatio-temporal specificity of the expression of genes related to sugar signaling, in vascular cells during development; (3) a co-regulation of genes involved in sugar transport and signaling with factors associated with the differentiation of vascular cells; (4) a regulation by sucrose, glucose or both of several key factors involved in the vascular formation.

To progress in this area, an important issue that should be addressed in Arabidopsis is the local concentration of sugars on both sides of the (pro)cambium, creating potentially a gradient of sucrose, glucose and fructose in the floral stem but also the leaf and the apical meristems, as described in the hypocotyl of castor bean and the stem of poplar and scot pine (Abreu et al., 2020; Roach et al., 2017; Uggla et al., 2001; Verscht et al., 2006). Nonetheless, the presence of several proteins, which transport sugars along the concentration gradient and are expressed in the vascular system, is consistent with the existence of a gradation in sugar contents either between vascular cells or between subcellular compartments in these cells (apoplasm, vacuole, or cytosol).

In addition, it is worth mentioning that plasmodesmata also contribute to the cell-to-cell transport of sugars and that a complete scheme should integrate both pathways (i.e. apoplasmic and symplasmic). Especially, the symplasmic transport plays a key role in delivering phloem-mobile sugars to root/SAM and developing leaves (Gisel et al., 1999, 2002; Ross-Elliott et al., 2017; Schulz, 2005). It probably also contributes, together with the apoplasmic transport, to the release of sugars from the vasculature to the adjacent tissues in stems and roots (van Bel, 2021). Noticeably, Kim et al. (2021) identified several genes coding for plasmodesmal proteins in leaves (e.g. PLASMODESMATA-LOCATED PROTEIN and MULTIPLE C2 DOMAINS AND TRANSMEMBRANE REGION PROTEIN), whose role in regulating symplasmic sugar transport still need to be elucidated.

Further, our study highlights the need for new approaches to discriminate the metabolic role of sugars from their signaling role in the vascular tissues in which sugars are abundant. It should be emphasized that we did not analyze the role of other sugars, such as fructose, which emerges as an additional signal molecule in the regulation of plant development (Aubry et al., 2022; Stein & Granot, 2018; Valifard et al., 2021).

Strikingly, we found very little evidence for the role of genes related to the TOR/SnRK signaling pathways during vascular development, except in the vascular initials of the embryo, suggesting that transcriptional regulation of these genes does not occur in these tissues. In contrast, many genes related to the T6P signaling, including *TPS* and *TPP*, were enriched in vascular cell initials in the SAM and across the stem development (Figures 3 and 4). Systematic analysis of Arabidopsis mutants defective in the expression of *TPS* and *TPP* genes will provide new clues about their role in vascular system development. In addition, our analysis identified new candidate genes (e.g. *ERDL/ESL*, *STP*, and *SWEET*) coding for sugar transporters that could also be important to study in terms of vasculature development and functioning.

To conclude, these data support the hypothesis of regulation by sucrose or glucose of several TFs involved in vascular development, suggesting that variations of intracellular or intercellular sugars contents could impact fine the vascular system development. However, we do not know whether similar conclusions could be drawn in roots, for which the symplasmic sugar transport likely plays a more significant role than in the inflorescence stem or leaf. Further metadata analysis will have to be performed to explore this issue.

ACKNOWLEDGMENTS

The authors are grateful to both reviewers for their comments that helped to improve the manuscript.

AUTHOR CONTRIBUTIONS

Rozenn Le Hir prepared the primary draft of the manuscript. Sylvie Dinant and Rozenn Le Hir compiled the literature and analyzed the

datasets. Sylvie Dinant and Rozenn Le Hir designed the tables and figures. Both authors equally wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data supporting this study's findings are openly available in the articles mentioned in Table 1.

ORCID

Rozenn Le Hir https://orcid.org/0000-0001-6076-5863

REFERENCES

Abreu, I.N., Johansson, A.I., Sokołowska, K., Niittylä, T., Sundberg, B., Hvidsten, T.R. et al. (2020) A metabolite roadmap of the wood-forming tissue in Populus tremula. *The New Phytologist*, 228, 1559–1572.

Agustí, J. & Blázquez, M.A. (2020) Plant vascular development: mechanisms and environmental regulation. *Cellular and Molecular Life Sciences*, 77, 3177–3728.

Andrés, F., Romera-Branchat, M., Martínez-Gallegos, R., Patel, V., Schneeberger, K., Jang, S. et al. (2015) Floral induction in Arabidopsis by flowering locus t requires direct repression of blade-on-petiole genes by the homeodomain protein pennywise. *Plant Physiology*, 169, 2187–2199.

Aubry, E., Dinant, S., Vilaine, F., Bellini, C. & Le Hir, R. (2019) Lateral transport of organic and inorganic solutes. *Plants*, 8, 1–25.

Aubry, E., Hoffmann, B., Vilaine, F., Gilard, F., Klemens, p.A.W., Guérard, F. et al. (2022) A vacuolar hexose transport is required for xylem development in the inflorescence stem. *Plant Physiology*, 188, 1229–1247.

Bencivenga, S., Serrano-Mislata, A., Bush, M., Fox, S. & Sablowski, R. (2016) Control of oriented tissue growth through repression of organ boundary genes promotes stem morphogenesis. *Developmental Cell*, 39, 198–208.

Boorer, K.J., Loo, D.D.F. & Wright, E.M. (1994) Steady-state and presteady-state kinetics of the H^+/hexose cotransporter (STP1) from *Arabidopsis thaliana* expressed in Xenopus oocytes. *The Journal of Biological Chemistry*, 269, 20417–20424.

Büttner, M. & Sauer, N. (2000) Monosaccharide transporters in plants: structure, fucntion and physiology. *Biochimica et Biophysica Acta*, 1465, 263–274.

Cayla, T., Le Hir, R. & Dinant, S. (2019) Live-cell imaging of fluorescently-tagged phloem proteins with confocal microscopy. In: Liesche, J. (Ed.) *Phloem: methods and procotols*. New York: Springer, pp. 95–108.

Chen, L. (2014) SWEET sugar transporters for phloem transport and pathogen nutrition. *The New Phytologist*, 201, 1150–1155.

Chen, L.-Q., Qu, X.-Q., Hou, B.-H., Sosso, D., Osorio, S., Fernie, A.R. et al. (2012) Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. *Science*, 335, 207–211.

De Rybel, B., Mähönen, A.P., Helariutta, Y. & Weijers, D. (2016) Plant vascular development: from early specification to differentiation. *Nature Reviews. Molecular Cell Biology*, 17, 30–40.

Ehlting, J., Mattheus, N., Aeschliman, D.S., Li, E., Hamberger, B., Cullis, I.F. et al. (2005) Global transcript profiling of primary stems from *Arabidopsis thaliana* identifies candidate genes for missing links in lignin biosynthesis and transcriptional regulators of fiber differentiation. *The Plant Journal*, 42, 618–640.

Etchells, J.P. & Turner, S.R. (2010) The PXY-CLE41 receptor ligand pair defines a multifunctional pathway that controls the rate and orientation of vascularcell division. *Development*, 137, 767–774.

Fichtner, F., Barbier, F.F., Annunziata, M.G., Feil, R., Olas, J.J., Mueller-Roeber, B. et al. (2021) Regulation of shoot branching in arabidopsis by trehalose 6-phosphate. *The New Phytologist*, 229, 2135–2151.

Fichtner, F., Olas, J.J., Feil, R., Watanabe, M., Krause, U., Hoefgen, R. et al. (2020) Functional features of TREHALOSE-6-PHOSPHATE SYNTHASE1, an essential enzyme in Arabidopsis. *Plant Cell*, 32, 1949–1972.

Fisher, K. & Turner, S. (2007) PXY, a receptor-like kinase essential for maintaining polarity during plant vascular-tissue development. *Current Biology*, 17, 1061–1066.

Fukuda, H. & Ohashi-Ito, K. (2019) Vascular tissue development in plants. *Current Topics in Developmental Biology*, 131, 141–160.

Gerber, L., Zhang, B., Roach, M., Rende, U., Gorzsás, A., Kumar, M. et al. (2014) Deficient sucrose synthase activity in developing wood does not specifically affect cellulose biosynthesis, but causes an overall decrease in cell wall polymers. *The New Phytologist*, 203, 1220–1230.

Gisel, A., Barella, S., Hempel, F.D. & Zambryski, p.C. (1999) Temporal and spatial regulation of symplactic trafficking during development in *Arabidopsis thaliana* apices. *Development*, 126, 1879–1889.

Gisel, A., Hempel, F.D., Barella, S. & Zambryski, p.C. (2002) Leaf-to-shoot apex movement of symplastic tracer is restricted coincident with flowering in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 1713–1717.

Goetz, M., Rabinovich, M. & Smith, H.M. (2021) The role of auxin and sugar signaling in dominance inhibition of inflorescence growth by fruit load. *Plant Physiology*, 187, 1189–1201.

Gonzali, S., Loreti, E., Solfanelli, C., Novi, G., Alpi, A. & Perata, P. (2006) Identification of sugar-modulated genes and evidence for in vivo sugar sensing in Arabidopsis. *Journal of Plant Research*, 119, 115–123.

Gould, N., Thorpe, M.R.R., Pritchard, J., Christeller, J.T.T., Williams, L.E.E., Roeb, G. et al. (2012) AtSUC2 has a role for sucrose retrieval along the phloem pathway: evidence from carbon-11 tracer studies. *Plant Science*, 188–189, 97–101.

Granot, D., David-Schwartz, R. & Kelly, G. (2013) Hexose kinases and their role in sugar-sensing and plant development. *Frontiers in Plant Science*, 4, 1–17.

Guendel, A., Rolletschek, H., Wagner, S., Muszynska, A. & Borisjuk, L. (2018) Micro imaging displays the sucrose landscape within and along its allocation pathways. *Plant Physiology*, 178, 1448–1460.

Hall, H. & Ellis, B. (2013) Transcriptional programming during cell wall maturation in the expanding Arabidopsis stem. *BMC Plant Biology*, 13, 14.

Han, L., Li, J.L., Jin, M. & Su, Y.H. (2015) Transcriptome analysis of Arabidopsis seedlings responses to high concentrations of glucose. *Genetics and Molecular Research*, 14, 4784–4801.

Han, L., Zhu, Y., Liu, M., Zhou, Y., Lu, G., Lan, L. et al. (2017) Molecular mechanism of substrate recognition and transport by the AtSWEET13 sugar transporter. *Proceedings of the National Academy of Sciences*, 114, 10094.

Hansen, J. & Beck, E. (1994) Seasonal changes in the utilization and turnover of assimilation products in 8-year-old Scots pine (*Pinus sylvestris* L.) trees. *Trees*, 8, 172–182.

Haritatos, E., Medville, R. & Turgeon, R. (2000) Minor vein structure and sugar transport in *Arabidopsis thaliana*. *Planta*, 211, 105–111.

Hirakawa, Y., Kondo, Y. & Fukuda, H. (2010) TDIF peptide signaling regulates vascular stem cell proliferation via the WOX4 homeobox gene in Arabidopsis. *Plant Cell*, 22, 2618–2629.

Ilegems, M., Douet, V., Meylan-Bettex, M., Uyttewaal, M., Brand, L., Bowman, J.L. et al. (2010) Interplay of auxin, KANADI and Class III HD-ZIP transcription factors in vascular tissue formation. *Development*, 137, 975–984.

Iwase, A., Kondo, Y., Laohavisit, A., Takebayashi, A., Ikeuchi, M., Matsuoka, K. et al. (2021) WIND transcription factors orchestrate wound-induced callus formation, vascular reconnection and defense response in Arabidopsis. *The New Phytologist*, 232, 734–752.

Jeffs, R.A. & Northcote, D.H. (1966) Experimental induction of vascular tissue in an undifferentiated plant callus. *The Biochemical Journal*, 101, 146–152.

Jeffs, R.A. & Northcote, D.H. (1967) The influence of indol-3yl acetic acid and sugar on the pattern of induced differentiation in plant tissue culture. *Journal of Cell Science*, 2, 77–88.

Jung, B., Ludewig, F., Schulz, A., Meißner, G., Wöstefeld, N., Flügge, U.I. et al. (2015) Identification of the transporter responsible for sucrose accumulation in sugar beet taproots. *Nat Plants*, 1, 14001.

Kanno, Y., Oikawa, T., Chiba, Y., Ishimaru, Y., Shimizu, T., Sano, N. et al. (2016) AtSWEET13 and AtSWEET14 regulate gibberellin-mediated physiological processes. *Nature Communications*, 7, 1–11.

Kao, P., Schon, M.A., Mosiolek, M., Enugutti, B. & Nodine, M.D. (2021) Gene expression variation in Arabidopsis embryos at single-nucleus resolution. *Development*, 148, dev199589.

Kato, H., Motomura, T., Komeda, Y., Saito, T. & Kato, A. (2010) Overexpression of the NAC transcription factor family gene ANAC036 results in a dwarf phenotype in *Arabidopsis thaliana*. *Journal of Plant Physiology*, 167, 571–577.

Kim, I., Cho, E., Crawford, K., Hempel, F.D. & Zambryski, p.C. (2005) Cell-to-cell movement of GFP during embryogenesis and early seedling development in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 2227–2231.

Kim, J.-Y., Symeonidi, E., Pang, T.Y., Denyer, T., Weidauer, D., Bezrutczyk, M. et al. (2021) Distinct identities of leaf phloem cells revealed by single cell transcriptomics. *Plant Cell*, 33, 511–530.

Kitagawa, M. & Jackson, D. (2017) Plasmodesmata-mediated cell-to-cell communication in the shoot apical meristem: how stem cells talk. *Plants*, 6, 3–19.

Krishnamurthy KV, Kaliamoorthy S, Rameshkannan K (1999) Xylogenesis in vitro. Plant Tissue Culture and Biotechnology: Emerging Trends, Universiti Ed. pp. 29–36

Kumari, S., Yadav, S., Patra, D., Singh, S., Sarkar, A.K. & Panigrahi, K.C.S. (2019) Uncovering the molecular signature underlying the light intensity-dependent root development in *Arabidopsis thaliana*. *BMC Genomics*, 20, 1–23.

Le Hir, R., Spinner, L., Klemens, p.A.W., Chakraborti, D., De Marco, F., Vilaine, F. et al. (2015) Disruption of the sugar transporters AtSWEET11 and AtSWEET12 affects vascular development and freezing tolerance in Arabidopsis. *Molecular Plant*, 8, 1687–1690.

Li, L., Liu, K. & Sheen, J. (2021) Dynamic nutrient signaling networks in plants. *Annual Review of Cell and Developmental Biology*, 37, 1–27.

Liu, X., Zhang, Y., Yang, C., Tian, Z. & Li, J. (2016) AtSWEET4, a hexose facilitator, mediates sugar transport to axial sinks and affects plant development. *Scientific Reports*, 6, 24563.

Mahboubi, A., Ratke, C., Gorzsás, A., Kumar, M., Mellerowicz, E.J. & Niittylä, T. (2013) Aspen SUCROSE TRANSPORTER3 allocates carbon into wood fibers. *Plant Physiology*, 163, 1729–1740.

Mähönen, A.P., Bishopp, A., Higuchi, M., Nieminen, K.M., Kinoshita, K., Törmäkangas, K. et al. (2006) Cytokinin signaling and its inhibitor AHP6 regulate cell fate during vascular development. *Science*, 311, 94–98.

Mishra, B.S., Sharma, M. & Laxmi, A. (2021) Role of sugar and auxin crosstalk in plant growth and development. *Physiologia Plantarum*, 174(1), e13546.

Miyashima, S., Roszak, P., Sevilem, I., Toyokura, K., Blob, B., Heo, J. et al. (2019) Mobile PEAR transcription factors integrate positional cues to prime cambial growth. *Nature*, 565, 490–494.

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. et al. (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.

Nakata, M.T., Sakamoto, S., Nuoendagula, K.S. & Mitsuda, N. (2021) Fiber cell-specific expression of the VP16-fused ethylene response factor 41 protein increases biomass yield and alters lignin composition. *Frontiers in Plant Science*, 12, 654655.

Niño-González, M., Novo-Uzal, E., Richardson, D.N., Barros, p.M. & Duque, P. (2019) More transporters, more substrates: the Arabidopsis major facilitator superfamily revisited. *Molecular Plant*, 12, 1182–1202.

Oribe, Y., Funada, R. & Kubo, T. (2003) Relationships between cambial activity, cell differentiation and the localization of starch in storage tissues around the cambium in locally heated stems of Abies sachalinensis (Schmidt) masters. *Trees - Structure and Function*, 17, 185–192.

Park, J., Chavez, T.M., Guistwhite, J.A., Gwon, S., Frommer, W.B. & Cheung, L.S. (2022) Development and quantitative analysis of a biosensor based on the Arabidopsis SWEET1 sugar transporter. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2119183119. https://doi.org/10.1073/pnas.2119183119

Patrick, J.W., Botha, F.C. & Birch, R.G. (2013) Metabolic engineering of sugars and simple sugar derivatives in plants. *Plant Biotechnology Journal*, 11, 142–156.

Price, J., Laxmi, A., St. Martin, S.K. & Jang, J.C. (2004) Global transcription profiling reveals multiple sugar signal transduction mechanisms in Arabidopsis W inside box sign. *Plant Cell*, 16, 2128–2150.

Qi, L., Zhang, X., Zhai, H., Liu, J., Wu, F., Li, C. et al. (2019) Elongator is required for root stem cell maintenance by regulating SHORTROOT transcription. *Plant Physiology*, 179, 220–232.

Quirino, B.F., Reiter, W.D. & Amasino, R.D. (2001) One of two tandem Arabidopsis genes homologous to monosaccharide transporters is senescence-associated. *Plant Molecular Biology*, 46, 447–457.

Ragni, L. & Greb, T. (2018) Secondary growth as a determinant of plant shape and form. *Seminars in Cell & Developmental Biology*, 79, 58–67.

Riesmeier, J.W., Hirner, B. & Frommer, W.B. (1993) Potato sucrose transporter expression in minor veins indicates a role in phloem loading. *Plant Cell*, 5, 1591–1598.

Riesmeier, J.W., Willmitzer, L. & Frommer, W.B. (1994) Evidence for an essential role of the sucrose transporter in phloem loading and assimilate partitioning. *The EMBO Journal*, 13, 1–7.

Roach, M., Arrivault, S., Mahboubi, A., Krohn, N., Sulpice, R., Stitt, M. et al. (2017) Spatially resolved metabolic analysis reveals a central role for transcriptional control in carbon allocation to wood. *Journal of Experimental Botany*, 68, 3529–3539.

Ross-Elliott, T.J., Jensen, K.H., Haaning, K.S., Wager, B.M., Knoblauch, J., Howell, A.H. et al. (2017) Phloem unloading in Arabidopsis roots is convective and regulated by the phloem-pole pericycle. *eLife*, 6, 1–31.

Rottmann, T., Klebl, F., Schneider, S., Kischka, D., Rüscher, D., Sauer, N. et al. (2018) Sugar transporter STP7 specificity for L-arabinose and D-xylose contrasts with the typical hexose transporters STP8 and STP12. *Plant Physiology*, 176, 01493.

Saelim, L., Akiyoshi, N., Tan, T.T., Ihara, A., Yamaguchi, M., Hirano, K. et al. (2019) Arabidopsis group IIId ERF proteins positively regulate primary cell wall-type CESA genes. *Journal of Plant Research*, 132, 117–129.

Sakamoto, S., Somssich, M., Nakata, M.T., Unda, F., Atsuzawa, K., Kaneko, Y. et al. (2018) Complete substitution of a secondary cell wall with a primary cell wall in Arabidopsis. *Nature Plants*, 4, 777–783.

Sauer, N. & Stolz, J. (1994) SUC1 and SUC2: two sucrose transporters from *Arabidopsis thaliana*; expression and characterization in baker's yeast and identification of the histidine-tagged protein. *The Plant Journal*, 6, 67–77.

Schneider, S., Schneidereit, A., Konrad, K.R., Hajirezaei, M.R., Gramann, M., Hedrich, R. et al. (2006) Arabidopsis INOSITOL TRANSPORTER4 mediates high-affinity H^+ symport of myoinositol across the plasma membrane. *Plant Physiology*, 141, 567–577.

Schneider, S., Schneidereit, A., Udvardi, P., Hammes, U., Gramann, M., Dietrich, P. et al. (2007) Arabidopsis inositol Transporter2 mediates H^+ symport of different inositol epimers and derivatives across the plasma membrane. *Plant Physiology*, 145, 1395–1407.

Schulz, A. (2005) Role of plasmodesmata in solute loading and unloading. In: Oparka, K.J. (Ed.) *Plasmodesmata*. Oxford: Wiley-Blackwell, pp. 135–161.

Schulz, A., Beyhl, D., Marten, I., Wormit, A., Neuhaus, H.E., Poschet, G. et al. (2011) Proton-driven sucrose symport and antiport are provided by the vacuolar transporters SUC4 and TMT1/2. *The Plant Journal*, 68, 129–136.

Shi, D., Jouannet, V., Agustí, J., Kaul, V., Levitsky, V., Sanchez, P. et al. (2021) Tissue-specific transcriptome profiling of the *Arabidopsis thaliana* inflorescence stem reveals local cellular signatures. *Plant Cell*, 33, 200–223.

Slawinski, L., Israel, A., Artault, C., Thibault, F., Atanassova, R., Laloi, M. et al. (2021) Responsiveness of early response to dehydration six-like transporter genes to water deficit in *Arabidopsis thaliana* leaves. *Frontiers in Plant Science*, 12, 1–21.

Slawinski, L., Israel, A., Paillot, C., Thibault, F., Cordaux, R., Atanassova, R. et al. (2021) Early response to dehydration six-like transporter family: early origin in Streptophytes and evolution in land plants. *Frontiers in Plant Science*, 12, 1–26.

Smetana, O., Mäkilä, R., Lyu, M., Amiryousefi, A., Sánchez Rodríguez, F., Wu, M.F. et al. (2019) High levels of auxin signaling define the stem-cell organizer of the vascular cambium. *Nature*, 565, 485–489.

Smit, M.E., McGregor, S.R., Sun, H., Gough, C., Bågman, A.M., Soyars, C.L. et al. (2020) A PXY-mediated transcriptional network integrates signaling mechanisms to control vascular development in Arabidopsis. *Plant Cell*, 32, 319–335.

Smith, H.M. & Hake, S. (2003) The interaction of two homeobox genes, BREVIPEDICELLUS and PENNYWISE, regulates internode patterning in the Arabidopsis inflorescence. *Plant Cell*, 15, 1717–1727.

Solfanelli, C., Poggi, A., Loreti, E., Alpi, A. & Perata, P. (2006) Sucrose-specific induction of the anthocyanin biosynthetic pathway in Arabidopsis. *Plant Physiology*, 140, 637–646.

Spicer, R. (2014) Symplasmic networks in secondary vascular tissues: parenchyma distribution and activity supporting long-distance transport. *Journal of Experimental Botany*, 65, 1829–1848.

Stadler, R., Lauterbach, C. & Sauer, N. (2005) Cell-to-cell movement of green fluorescent protein reveals post-phloem transport in the outer integument and identifies symplastic domains in Arabidopsis seeds and embryos. *Plant Physiology*, 139, 701–712.

Stadler, R. & Sauer, N. (1996) The *Arabidopsis thaliana* AtSUC2 gene is specifically expressed in companion cells. *Botanica Acta: Journal of the German Botanical Society*, 109, 299–306.

Stein, O. & Granot, D. (2018) Plant fructokinases: evolutionary, developmental, and metabolic aspects in sink tissues. *Frontiers in Plant Science*, 9, 339.

Strobl, S.M., Kischka, D., Heilmann, I., Mouille, G. & Schneider, S. (2018) The tonoplastic inositol transporter INT1 from *Arabidopsis thaliana* impacts cell elongation in a sucrose-dependent way. *Frontiers in Plant Science*, 871, 1–23.

Taylor-Teeples, M., Lin, L., De Lucas, M., Turco, G., Toal, T.W., Gaudinier, A. et al. (2015) An Arabidopsis gene regulatory network for secondary cell wall synthesis. *Nature*, 517, 571–575.

Tian, Y., Zhao, N., Wang, M., Zhou, W., Guo, J., Han, C. et al. (2022) Integrated regulation of periclinal cell division by transcriptional module of BZR1-SHR in Arabidopsis roots. *The New Phytologist*, 233, 795–808.

Truernit, E. & Sauer, N. (1995) The promoter of the *Arabidopsis thaliana* SUC2 sucrose-H^+ symporter gene directs expression of B-glucuronidase to the phloem: evidence for phloem loading and unloading by SUC2. *Planta*, 196, 564–570.

Uggla, C., Magel, E., Moritz, T. & Sundberg, B. (2001) Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in scots pine. *Plant Physiology*, 125, 2029–2039.

Unda, F., Kim, H., Hefer, C., Ralph, J. & Mansfield, S.D. (2017) Altering carbon allocation in hybrid poplar (Populus alba × grandidentata) impacts cell wall growth and development. *Plant Biotechnology Journal*, 15, 865–878.

Valifard, M., Le Hir, R., Müller, J., Scheuring, D., Neuhaus, H.E. & Pommerrenig, B. (2021) Vacuolar fructose transporter SWEET17 is critical for root development and drought tolerance. *Plant Physiology*, 187, 2716–2730.

van Bel, A.J.E. (2021) The plant axis as the command Centre for (re)distribution of sucrose and amino acids. *Journal of Plant Physiology*, 265, 153488.

Vanholme, R., Storme, V., Vanholme, B., Sundin, L., Christensen, J.H., Goeminne, G. et al. (2012) A systems biology view of responses to lignin biosynthesis perturbations in *Arabidopsis*. *Plant Cell*, 24, 3506–3529.

Verbančič, J., Lunn, J.E., Stitt, M. & Persson, S. (2018) Carbon supply and the regulation of cell wall synthesis. *Molecular Plant*, 11, 75–94.

Verscht, J., Tomos, D. & Komor, E. (2006) Sugar concentrations along and across the *Ricinus communis* L. hypocotyl measured by single cell sampling analysis. *Planta*, 224, 1303–1314.

Warren, W., Roberts, L.W., PMW, W. & Gresshoff, p.M. (1994) Stimulatory and inhibitory effects of sucrose concentration on xylogenesis in lettuce pith explants; possible mediation by ethylene biosynthesis. *Annals of Botany*, 73, 65–73.

Wei, X.Y., Collings, D.A. & McCurdy, D.W. (2021) Review: more than sweet: new insights into the biology of phloem parenchyma transfer cells in Arabidopsis. *Plant Science*, 310, 110990.

Wetmore, R.H. & Rier, J.P. (1963) Experimental induction of vascular tissues in callus of angiosperms. *American Journal of Botany*, 50, 418–430.

Winkler, A. & Oberhuber, W. (2017) Cambial response of Norway spruce to modified carbon availability by phloem girdling. *Tree Physiology*, 37, 1527–1535.

Wormit, A., Trentmann, O., Feifer, I., Lohr, C., Tjaden, J., Meyer, S. et al. (2006) Molecular identification and physiological characterization of a novel monosaccharide transporter from Arabidopsis involved in vacuolar sugar transport. *Plant Cell*, 18, 3476–3490.

Yadav, R.K., Tavakkoli, M., Xie, M., Girke, T. & Reddy, G.V. (2014) A high-resolution gene expression map of the Arabidopsis shoot meristem stem cell niche. *Development*, 141, 2735–2744.

Yamaguchi, Y.L., Ishida, T., Yoshimura, M., Imamura, Y., Shimaoka, C. & Sawa, S. (2017) A collection of mutants for CLE-peptide-encoding genes in Arabidopsis generated by CRISPR/Cas9-mediated gene targeting. *Plant & Cell Physiology*, 58, 1848–1856.

Yang, J., Lin, R., Sullivan, J., Hoecker, U., Liu, B., Xu, L. et al. (2005) Light regulates COP1-mediated degradation of HFR1, a transcription factor essential for light signaling in Arabidopsis. *Plant Cell*, 17, 804–821.

Yao, D., Gonzales-Vigil, E. & Mansfield, S.D. (2020) Arabidopsis sucrose synthase localization indicates a primary role in sucrose translocation in phloem. *Journal of Experimental Botany*, 71, 1858–1869.

Yuan, B. & Wang, H. (2021) Peptide signaling pathways regulate plant vascular development. *Frontiers in Plant Science*, 12, 1–7.

Zhang, L., Wang, L., Zhang, J., Song, C., Li, Y., Li, J. et al. (2021) Expression and localization of SWEETs in Populus and the effect of SWEET7 overexpression in secondary growth. *Tree Physiology*, 41, 882–899.

Zhang, T.-Q., Chen, Y. & Wang, J.-W. (2021) A single-cell analysis of the Arabidopsis vegetative shoot apex. *Developmental Cell*, 56, 1056–1074.e8.

Zhang, Z., Sun, Y., Jiang, X., Wang, W. & Wang, Z.Y. (2021) Sugar inhibits brassinosteroid signaling by enhancing BIN2 phosphorylation of BZR1. *PLoS Genetics*, 17, 1–14.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Dinant, S. & Le Hir, R. (2022) Delving deeper into the link between sugar transport, sugar signaling, and vascular system development. *Physiologia Plantarum*, 174(2), e13684. Available from: https://doi.org/10.1111/ppl.13684