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MOLECULAR GENETIC MECHANISMS OF SUGAR TRANSPORT IN PLANTS IN THE ABSENCE AND DURING ARBUSCULAR MYCORYZA DEVELOPMENT

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❀ The review is aimed to analyze molecular mechanisms of carbohydrate transport during the formation of arbuscular mycorrhiza (AM), a widespread symbiosis of plants with *Glomeromycotina* subdivision fungi. Due to AM-symbiosis, plants receive microelements, mainly phosphorus, and fungi are supplied by products of carbon assimilation. The study of sugar transport mechanisms in plants as well as between plants and symbiont is methodologically difficult because of the obligatory status of AM fungi. The mechanisms of carbohydrate transport in leaf and root cells are concerned, particular interest is paid to transporters, specific to AM structures. Several resumptive schemes are designed. SWEET family of transporters (Sugars Will Eventually be Exported Transporters), including AM-specific uniporters are reviewed. We summarize results on expression of genes encoding transporter in cells of plants without AM, in AM-plant cells with arbuscules and AM-plant cells without arbuscules. The data on genes of MST proteins family (Monosaccharide Transporters) participating in direct transport of sugars from the soil to the foliar mycelium of AM fungi are considered.

❀ **Keywords:** arbuscular mycorrhiza; sugar transport; sucrose; glucose; sugar transporter genes; SWEET; SUT; MST; symplast; apoplast.

МОЛЕКУЛЯРНО-ГЕНЕТИЧЕСКИЕ МЕХАНИЗМЫ ТРАНСПОРТА САХАРОВ У РАСТЕНИЙ В ОТСУТСТВИЕ И ПРИ РАЗВИТИИ АРБУСКУЛЯРНОЙ МИКОРИЗЫ

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❀ Обзор посвящен анализу молекулярных механизмов транспорта углеводов при формировании арбускулярной микоризы (АМ) — широко распространенного симбиоза наземных растений с грибами подотдела *Glomeromycotina*. В результате образования АМ-симбиоза растение получает от микосимбионта микроэлементы, главным образом фосфор, а гриб — продукты ассимиляции углерода. В связи с облигатным статусом АМ-грибов по отношению к растениям изучение механизмов транспорта сахаров в растения и между растением и симбионтом является методически сложной задачей. В обзоре перечислены механизмы транспорта углеводов в клетках листа, а также перемещения сахаров в клетках корня. Особое внимание уделено изменению спектра транспортеров при формировании арбускул, а также выявлению специфичных для АМ переносчиков. Предложены оригинальные обобщающие схемы. Рассматривается значение открытого в 2010 г. семейства двунаправленных энергонезависимых транспортеров — SWEET (Sugars Will Eventually be Exported Transporters), включающего специфичные для АМ унипортеры. Обобщены результаты активных исследований экспрессии генов, кодирующих транспортеры растений в клетках растений без АМ / с АМ с арбускулами / с АМ без арбускул. Приводятся данные о генах, кодирующих у грибов белки семейства моносахаридных транс-

портеров MST (Monosaccharide Transporters), некоторые из которых принимают участие в прямом транспорте сахаров из почвы во внекорневой мицелий АМ-грибов.

❀ **Ключевые слова:** арбускулярная микориза; транспорт сахаров; сахароза; глюкоза; гены транспортеров сахаров; SWEET; SUT; MST; симпласт; апопласт.

INTRODUCTION

Symbiosis biology is curretly focuses on revealing the mechanisms behind efficient symbiosis between plants and fungi in the form of arbuscular mycorrhiza (AM). AM is the most common rhizosphere symbiosis formed between plants (>92% of families) and fungi of the *Glomeromycotina* subdivision of the *Mucoromycota* subphylum [1]. AM is distributed from alpine meadows to tundra and deserts, achieving the most diverse communities in the taiga zone [2, 3]. AM has also been used actively to create artificial agrosystems. However, the successful development of biological farming is impossible without understanding the mechanisms of formation and development of effective plant–microbe interactions within agroecosystems.

AM fungus may have enabled plants' occupation of land ecosystems almost 0.5 billion years ago, which played a key role in forming the contemporary biosphere [4]. Under the conditions of symbiosis, the fungus receives carbohydrates and fatty acids from the plant. These fatty acids constitute up to 70% of the total volume of metabolites received [5, 6], whereas the host plant receives phosphorus, water, and a number of macro- and microelements from the AM fungus [3]. Thus, the effectiveness of AM symbiosis probably depends largely on transport processes' intensity. The transport of metabolites from plants to mycosymbionts, which are not able to feed themselves autotrophically since they have limited ability to synthesize the necessary organic substances, is very important. This is why they are considered plant symbionts [3]. In the case of carbohydrate metabolism violations and/or transport of its products to mycosymbiont, the plant–microbial interaction can change; specifically, it can shift from a mutualistic relationship to a parasitic one [3, 7, 8]. Revealing the genes encoding the enzymes involved in regulating carbohydrate metabolic intensity, as well as the transporters of host plant metabolites to AM, should contribute to a deeper understanding of the formation and development of effective AM symbiosis. This review presents the latest data on carbohydrate exchange and the transport of metabolites within plants without AM fungi and upon their inoculation.

TRANSPORT OF SUGARS FROM ABOVEGROUND PARTS OF PLANTS

In the 1980s and 1990s, research on carbohydrate transport within living organisms provided information about a wide range of proteins involved in this process: β-galactoside transporter, namely, LacY lactose permease, discovered in *Escherichia coli* [9]; uniporter of glucose human GLUT1 (Glucose Transporter 1) [10], sodium glucose human symporter SGLT1 (Sodium Glucose Linked Transporter 1) [11], and glucose transporter SNF3 (Sucrose Non-Fermenting 3) detected in *Saccharomyces cerevisiae* (identified in a mutant, not fermenting sucrose) [12]; chlorella hexose uptake protein HUP1 (Hexose uptake 1; supposed glucose/H^+ chlorella symporter) [13]; plant sugar symporter STP (Sugar Transport Protein) revealed in *Arabidopsis thaliana* [14]; yeast hexose uniporter Hxt (Hexose Transporter), discovered in *S. cerevisiae* [15]; and plant sucrose/H^+-symporter SUT (Sucrose Transporter) [16]. These plant studies have helped describe, in detail, the mechanisms of sugar transport both within cells and between different organs [17-20]. Subsequently, in 2006, tonoplastic protein antiporters of tonoplast membrane hexose transporter (TMT) family (Tonoplast Monosaccharide Transporters) monosaccharides were identified [21]. Later, in 2010, bidirectional sugar uniporters of the SWEET family (Sugars Will Eventually be Exported Transporters) were detected [22]. Moreover, in 2015, it was shown that the BvTST2.1 protein of the red beet (*Beta vulgaris* Tonoplast-localized Sucrose Transporter 2.1) is characterized by high similarity of amino acid sequences, with members of the transporter monosaccharide tonoplast family identified in *A. thaliana*. The authors renamed this group of proteins the Tonoplast Sugar Transporters (TST) [23]. The overall data accumulated, to date, provide an overview of sugar synthesis and transport within plant leaves (Fig. 1).

Fig. 1 presents the conducting tissues array (xylem and phloem complex, leaf mesophyll cells) in which carbohydrate synthesis and transformation takes place, as well as the mechanisms of apoplastic and symplastic sugar transport. In the light phase of photosynthesis on thylakoid membranes, chlorophyll light energy is transformed into chemical bound energy. The energy is carried by the molecules of adenosine triphosphate acid (ATP) and nicotinamide adenine dinucleotide phosphate (① Fig. 1). This process is linked to the water photolysis system. In the dark phase of photosynthesis, the ribulose bisphosphate carboxylase/oxygenase Rubisco activities in the chloroplasts' stroma are involved in fixating carbon dioxide gas in the Cal-

vin cycle (in the case of C_3 plants; ② Fig. 1) and the synthesis of a number of organic compounds, including triosephosphate (TP). The TP then either leaves the chloroplasts' stroma and enters the mesophyll cells' cytosol, via Triose Phosphate/Phosphate Translocator [24, 25] (③ Fig. 1), or, at the violation of outflow triose, is stocked up in the form of starch ("Sta" in Fig. 1). Splitting starch into glucose in the plastids enables its export to the cytosol via the plastidic Glucose Transporter/Suppressor of the G Protein Beta 1 (pGlct/SGB1) [26, 27] (④ Fig. 1). The chloroplast maltose transporter 1, namely, MEX1 (Chloroplast Maltose Exporter 1; ⑤ Fig. 1) [28], transports maltose from plastids to the cytoplasm. Sucrose's output, probably by sucrose transporter type 4 (SUT4) (⑥ in Fig. 1), on the plastid membrane has also been demonstrated [17].

Triose phosphate's transformation into glucose-6-phosphate and then into uridine diphosphate glucose (⑦ Fig. 1) [17], as well as glucose phosphorylation by the hexokinase-1 enzyme (⑧ Fig. 1),

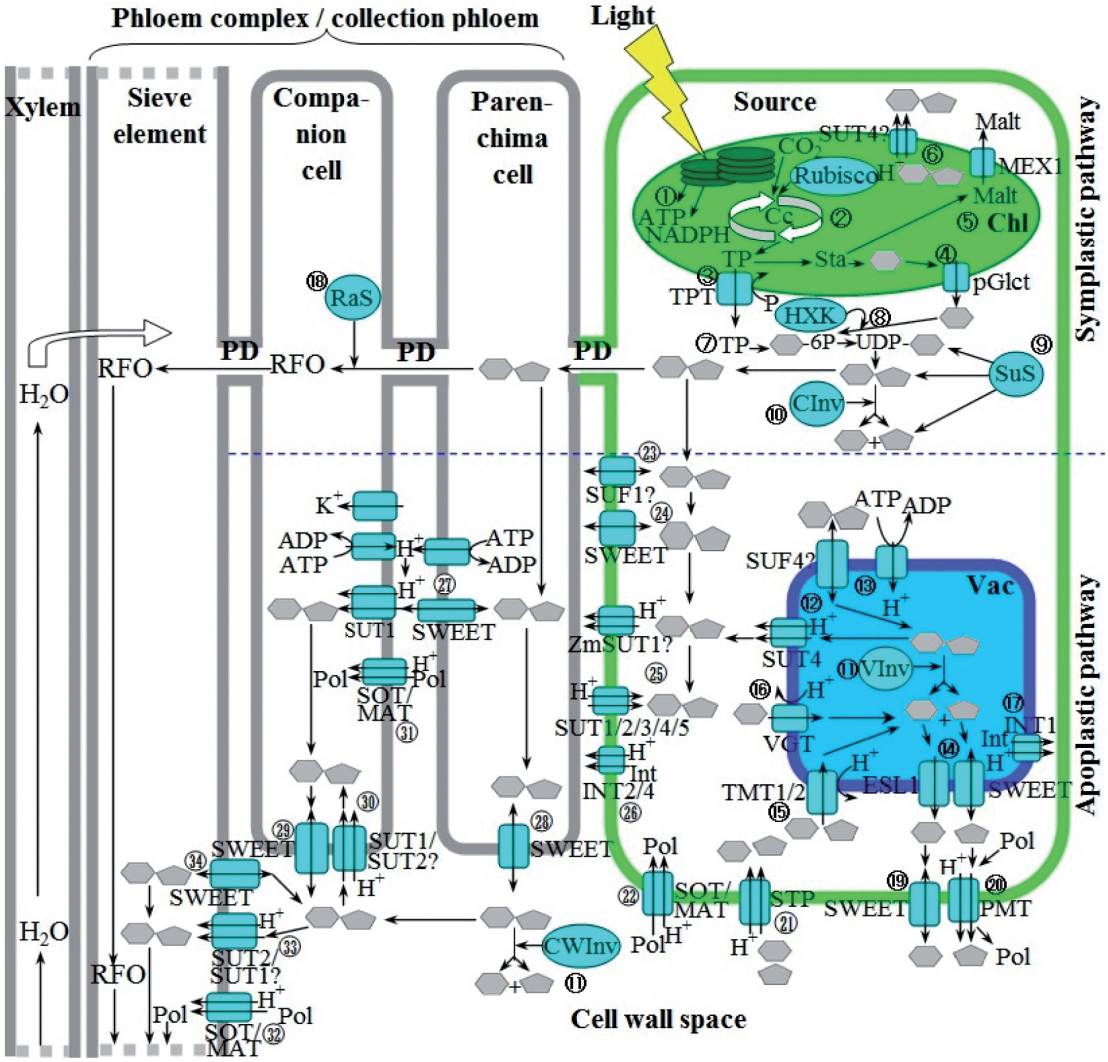

Fig. 1. General scheme of transport of sugars from the aerial parts of the plants (based on materials presented by [17-20] with changes and additions). Source – leaf mesophyll donor cell (Source mesophyll cell), PD – Plasmodesma, Malt – Maltose, Sta – Starch, Chl – Chloroplast, Rubisco – Ribulose-1,5-bisphosphate carboxylase/oxygenase, Vac – Vacuole, ATP – Adenosine triphosphate, ADP – Adenosine diphosphate, NADPH – reduced form of NADP+ – Nicotinamide Adenine Dinucleotide Phosphate, Cc – Calvin cycle, P – inorganic orthophosphate , TP – Triose-Phosphate, UDP-⬣ – Uridine diphosphate Glucose, ⬣-6P – glucose 6-phosphate, HXK – hexokinase, ⬣⬟ – sucrose, hexoses: ⬣ – glucose, ⬟– fructose, RFO – Raffinose Family Oligosaccharides, CInv – Cytosolic Invertase, VInv – Vacuolic Invertase, CWInv – Cell Wall Invertase, Pol – Polyols, Int – Inositol. Description of scheme is presented in the text. To simplify the comparison of the text and data presented in the figures, the continuous numbering for transporters and ferments was carried out, which is represented by numbers in circles; a similar approach was used by [19–20]

takes place in mesophyll cytoplasm [29]. The HXK1 enzyme (Hexokinase 1), which is now considered responsible for the perception and transmission of metabolic signals, mediates the glucose-induced repression of genes associated with photosynthesis, such as the gene encoding the small Rubisco subunit [30, 31]. *HXK1* gene overexpression in *Arabidopsis*, tomato, and rice leads to decreased growth and chlorophyll content, inhibited photosynthesis, and decreased *rbcS* expression [31]. Sucrose Synthase (SuS) catalyzes the reversible reaction, which explains its involvement in both the synthesis of sucrose from uridine diphosphate glucose, and fructose, and in its catabolism (⑨ Fig. 1) [17]. SUS-glycosyltransferase is believed to play a major role in providing the activated form of glucose (Uridine diphosphate glucose) during cellulose synthesis. In *Medicago truncatula*, five *SUS* genes were identified [32]. These encode a number ofof SUS specific for different plant tissues. The plant sucrose synthase gene family is usually represented by six forms, grouped into several subfamilies [33–35]. The leaf development stage shift causes expressions of various *SUS* forms. SUS synthesis intensifies under stress conditions [36].

Cytosolic Invertase (CInv) [17] splits sucrose up to glucose and fructose in donor cells' cytoplasm (⑩ see Fig. 1), whereas vacuolar invertase (VInv) [17, 18] splits sucrose in the vacuole of the donor cell (see Fig. 1), Cell Wall Invertase (CWInv) [17, 18] does the same in the cell wall space (⑪ see Fig. 1). Regarding transport from the vacuole to mesophyll cytoplasm, sucrose arrives through the sucrose symporter SUT4 (⑫ see Fig. 1), which is localized in the mesophyll vacuoles' tonoplasts [37–39]. It should be noted that not all SUT4 transporters are localized in the vacuole membrane [38]. In contrast, regarding transport from cytoplasm to vacuole, sucrose probably moves via bidirectional energy-independent SUF4 (facilitator), as detected in *Pisum sativum* and *Phaseolus vulgaris*, (⑬ see Fig. 1) [17, 40]. A representative member of the Early responsive to dehydration protein 6 monosaccharide transporters (ERD6-like transporters) localized in tonoplasts, namely, Early responsive to dehydration Six Like 1 (ESL1) (see Fig. 1) [17, 27]. ESL1 provide glucose export from vacuoles. In contrast, fructose withdrawal occurs via SWEET family proteins localized in the mesophyll cells' tonoplasts (Sugars Will Eventually be Exported Transporters; ⑭ Fig. 1) [19, 22, 41]. Absorption of glucose and fructose into vacuole (⑮ see Fig. 1) [17, 21], and that of glucose alone is mediated by the Vacuolar Glucose Transporter (VGT) (⑯ see Fig. 1) [42]. Moreover, inositol's transport from vacuoles is mediated by inositol transporter 1 (INT1) (⑰ see Fig. 1) [17].

The symplastic pathway of sucrose transport from mesophyll cells to parenchyma cells passes through the plasmodesma. Thus, the transport of sugars from donor cells to the cells of phloem conducting elements can be completely symplastic [20]. This transport is followed by the formation of Raffinose Family Oligosaccharides (RFO) from sucrose via Raffinose Synthase (RaS) (⑱ see Fig. 1) in the phloem's companion cells [18, 43], which increases transport intensity. It is assumed that RFOs are carried through plasmodesma to the conducting elements, symplastically arriving at the cells that consume sugar in an as-yet-unidentified way [18].

The apoplastic pathway includes the transport of sugars through the cell wall, by which glucose arrives from the cytoplasm as a result of the SWEET transporter operation (⑲ Fig. 1) [19, 22, 41], whereas fructose and polyols do so via Polyol/Monosaccharide Transporter (PMT) (⑳ Fig. 1) [17]. Glucose's and fructose's retrograde transport from the cell wall space to mesophyll cell cytoplasm is carried based on STP activity, related to a group of monosaccharide transporters (MST) (Sugar Transport Protein and Monosaccharide Transporter; ㉑ see Fig. 1) [17]. Polyol transport involves sorbitol transporters (SOT) and mannitol transporters (MAT), namely, sorbitol and mannitol symporters, respectively (㉒ in Fig. 1) [44]. A total of 17 SOT transporters have been identified (㉒ in Fig. 1) [20]. The transport of sucrose from the cell wall space to the cytoplasm is mediated by a number of transporters: probably sucrose transporter of 1st type – Sucrose Facilitator 1 (SUF1), dicovered in pea and bean (㉓ see Fig. 1) [17, 40], specific SWEET sugar transporters (㉔ Fig. 1) [19, 22, 41], and also sucrose/H^+ symporter of 1st type (SUT1) (and less often SUT2/3/4/5, which have been less studied than SUT1; ㉕ Fig. 1) [17]. In turn, from the cytoplasm, inositol exported into at the cell wall space via Inositol Transporters 2 and 4 (INT2 and INT4) (㉖ see Fig. 1) [17].

Bidirectional transport of sucrose by specific SWEET sugar transporters takes place in the phloem parenchyma cells (㉗ and ㉘ see Fig. 1) and in companion cells (㉙ see Fig. 1) [19, 22, 41]. Sucrose arrives, through the apoplast, to the companion cells (㉗ see Fig. 1) via sucrose symporter of type 2, namely, SUT1 (SUC2, Sucrose transporters of type 2) [18]. The energy required for sucrose symport is provided by H^+-transport ATPase, which determines the proton gradient and transmembrane potential, adjusted by the AKT2/3 type (Arabidopsis K^+ transporter 2/3)'s potassium channels (K^+ channels in the inward direction) [18]. H^+-trans-

port ATPase can be localized, not only on the companion cells' plasmalemma, but also on the parenchymal cells' plasmalemma [19]. Sucrose transport from the cell wall to companion cells is carried out by SUT1 and, possibly, SUT2 symporters (SUC2 and SUC3, respectively; ㉚ Fig. 1) [18]. The import of polyols to companion cells and conducting phloem elements is mediated by sorbitol and mannitol symporters, namely, SOT and MAT, respectively (㉛ ㉜ Fig. 1) [44]. However, we currently know little about the further distribution of polyols in the sugar-consuming cells.

At the final stage of the apoplastic pathway, sucrose is transported from the cell wall to the conducting elements of phloem via SUT2, and possibly SUT1, symporters (SUC3 and SUC2; ㉝ Fig. 1) [18, 45]; bidirectional transport of sucrose to the conducting elements of phloem and back to the cell wall can occur via a SWEET uniporter (㉞ Fig. 1) [19, 41]. After transport into the conducting elements of phloem, sugars (sucrose, glucose, and fructose) are supplied to different consuming organs (Sink in Fig. 2) by those same transporters, i.e., sucrose by SUT1 and hexoses by MST [17, 18]. From the consuming bodies of donor cells of sugars (source), water and mineral substances are supplied through conducting xylem tissues (Fig. 1 and 2).

It can be concluded that sugars, the primary products of photosynthesis, are the form of transported carbon (sucrose and hexoses) and energy used as substrates for carbohydrate, protein, and lipid metabolism. Additionally, sugars are considered regulatory gene expression messengers in plant ontogenesis [17, 18, 46, 47]. It has also been shown that, during AM formation, plants' carbohydrate metabolism can change markedly [48]. Up to 20% photoassimilated by plant metabolites can be supplied to AM fungus [48]. Nevertheless, many mechanisms of this process remain unknown. Perhaps this is because there are no specific pathways for assimilate transformation and transport during AM formation, but the activity of the genes encoding transporters, and of the protein enzymes that are involved in sugar metabolism, may be regulated [17, 49, 50]. Nevertheless, this field still remains understudied. For example, the expression dynamics of the genes encoding proteins, such as Rubisco, has not been investigated in depth. In the near future, our understanding of these concepts may expand significantly as a result of research conducted at the transcriptional and proteomic levels.

SUGAR TRANSPORT TO PLANT ROOTS

Having considered the transport mechanisms of sugars from the photoassimilating leaf cells to the cells consuming these metabolites through phloem, we focus here on the unloading mechanisms in the root cells. Unloading at phloem elements occurs through symplasts or predominantly the symplast pathway, with an intermediate apoplastic post-phloem stage [51]. Unfortunately, there has been only fragmented study of the phloem unloading mechanisms, partly based on indirect results or modeling [51]. However, based on the latest data, a summary scheme can be drawn, as shown in Fig. 2.

The symplast pathway of sucrose transport in roots includes its supply through plasmodesmata from source cells (donor cells) to sink cells (sugar-consuming cells) through conducting phloem elements and further through companion cells and phloem parenchyma (㉟ Fig. 2). The sucrose synthase (SuS) enzyme, catalyzing the reversible reaction of sucrose synthesis/decay in sink cells of root cortex consuming sugars (㊱ Fig. 2), plays an important role in this [17, 52]. Cytoplasmic invertase (CInv) [17] is involved in splitting of sucrose into glucose and fructose in the root cortex cells cytoplasm (㊲ Fig. 2), while vacuolar invertase (VInv) [17, 18] does this in vacuoles (㊳ Fig. 2), and cell wall invertase (CWInv) [17, 18] does this in the cell wall space (㊴ Fig. 2).

After the splitting of sucrose by invertase in the cytoplasm (㊲ Fig. 2), the obtained glucose can be used to synthesize glucose-6-phosphate via hexokinase (HXK), involving transformation into glucose-1-phosphate as a result of phosphoglucomutase (PGM) activity, and then into adenosine diphosphate glucose via adenosine diphosphate glucopyrophosphorylase. This can be further transported into amyloplasts via BT1 protein, which is encoded by the *BT1* gene (*Brittle1*) in *Zea mays* (㊵ Fig. 2) [55, 56]. Adenosine diphosphate glucose can also be obtained in the glucose-1-phosphateamyloplasts via adenosine diphosphate glucose pyrophosphorylase (㊶ Fig. 2) [47, 56]. Adenosine diphosphate glucose is involved in synthesizing starch via a number of enzymes, such as Starch Synthase (SS), Starch Branching Enzyme, and Starch Debranching Enzyme (SDE) [47]. If necessary, in amyloplast, starch is split up by amylase (AMY) into hexoses, which are, in turn, subjected to phosphorylation by hexokinase (HXK) with glucose-6-phosphate synthesis. The splitting of starch can involve a number of enzymes, such as alpha and beta amylase, limit dextrinase, and maltase [56]. Glucose-6-phosphate can be reversibly turned into glucose-1-phosphate via phosphoglucomutase (PGM) [47].

It is still unclear how glucose-6-phosphate arrives at the cytoplasm of the cells, consuming sugars (㊷ Fig. 2) [18]. Sugars may be exported from amylo-

plasts to the cytoplasm in the form of glucose-6-phosphate via a transporter (㊸ Fig. 2) [47], which supplies glucose-6-phosphate from the cytoplasm to amyloplasts (㊷ Fig. 2) [47, 54]. Glucose-Phosphate Transporter [encoded, e.g., in the *Vitis vinifera* genome (*VvGPT1*)] [54] of the MST family is a phosphate-dependent antiporter [53, 56]. Unfortunately, the earlier identified transporter, carrying glucose-1-phosphate from the cytosol to amyloplasts and back (㊷ Fig. 2) [47], has not been described in other studies [56]. Both chloroplasts and amyloplasts may contain the glucose and maltose transport proteins pGlcT and MEX, respectively [56], but no evidence for this has yet been presented. In cytoplasm, glucose-6-phosphate exposed to phosphoglucose isomerase can be reversibly turned into uridine diphosphate glucose which, alongside fructose-6-phosphate, is involved in sucrose synthesis when exposed to the effect of sucrose phosphate synthase enzyme, followed by the detachment of phosphate by means of Sucrose Phosphate Phosphatase (SPP) [47].

Sucrose is supplied from the vacuoles to cytoplasm by SUT4 (㊹ Fig. 2) [37–39]. Tonoplast H^+, transporting ATPase, generates the necessary proton gradient [19]. From vacuoles, glucose is exported by the tonoplast monosaccharide transporter ESL1 (㊺ Fig. 2) [17, 27], and fructose is exported by a SWEET protein localized in tonoplasts (㊺ Fig. 2) [19, 22]. The transport of glucose and fructose to vacuoles is mediated by the

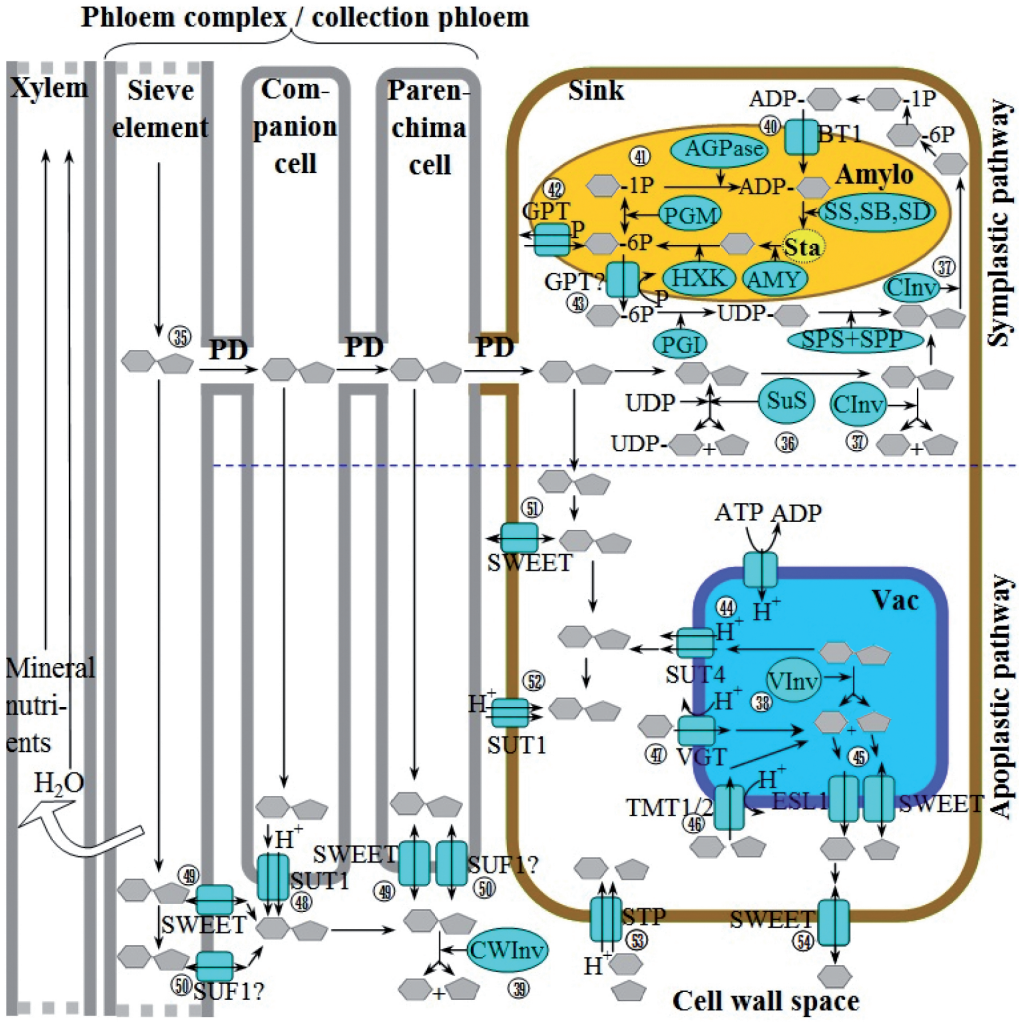

Fig. 2. Scheme of the transport of sugars in the cells of the roots of a plant without AMsymbiosis (based on materials presented by [17-18, 20, 47, 50, 52-54] with changes and additions). In Fig. 2: for abbreviations see explanations to Fig. 1; Sink – a root cortex cell consuming sugar (Sink cortex cell), Amylo – Amyloplast, ⬣-1P – glucose-1-phosphate, ADP-⬣ – adenosine diphosphate Glucose, AGPase – ADP-glucopyrophosphorylase, PGM – phosphoglucomutase, SS – Starch Synthase, SB – Starch Branching enzyme, SD – amylopectin cleaving enzyme (Starch Debranching enzyme), AMY – amylase, PGI – phosphoglucose isomerase, SPS – Sucrose-Phosphate Synthase, SPP – Sucrose-phosphate phosphatase. Description of scheme see the text

tonoplastic membrane transporter of hexoses TMT1 or TMT2 (㊻ in Fig. 2) [17, 21], and that of glucose alone is also mediated by vacuolar monosaccharide VGT transporter (㊼ Fig. 2) [42].

Sucrose's apoplastic transport involves the sucrose symporter of the 2nd type (SUT1) (㊽ Fig. 2; localized on the membrane of phloem cells, namely, companion cells) [18, 57]. Bidirectional transport of sucrose from the conducting elements of phloem, from phloem parenchyma, and back to apoplast, is enabled by the specific transporters of SWEET sugars (㊾ Fig. 2) [19, 41], as well as, probably, by the sucrose facilitator SUF1 (energy-independent bidirectional transporter) (㊿ Fig. 2) [19, 40]. However, these proteins were only accurately localized in seeds [40]. From the cell wall, sucrose is supplied to the root cortex cells consuming sugars by SWEET facilitators (51 Fig. 2) [19, 22, 41], and also as a result of the action of the H^+-dependent symporter SUT1 (52 Fig. 2) [17, 18]. Hexoses are supplied to root cortex cells by STP transporters [53 Fig. 2; e.g., by *Vitis vinifera* Hexose Transporter 1 (VvHT1)] [19, 58], and also by SWEET hexose transporters (54 Fig. 2) [19, 41].

TRANSPORT OF SUGARS IN SYMBIOTIC CELL STRUCTURES OF PLANT ROOTS WITH ARBUSCULAR MYCORRHIZAL FUNGUS

Plants' interaction with AM fungus leads to redistribution of nutritious substances in the roots, the formation of new symbiotic bodies, such as arbuscules (involving the in-growth of plant plasma membrane into the plant cell at the site of AM fungus hyphal penetration; the plasma membrane in arbuscules is called the periarbuscular membrane: PAM), and subsequent multiple branching of the arbuscule trunk with formation of the new AM symbiosis partners interactions interface – periarbuscular space (PAP) formed on the cell wall of the host plant between PAM and the arbuscular membrane (ArM) with arbuscule cell wall (Fig. 3). AM symbiosis is followed by the transport of nutritious substances from plants to AM fungus, particularly organic acids, lipids, and sugars. The plants' photosynthetic products are supplied to the symbiotic partner by sugar transporters of a number of families; the main ones are SWEET, SUT, and MST. Currently, all transporters' functions and localizations are unclear and, from the data of transcriptional profiles, not all transporters have been detected [50].

The specificity of transport processes in AM has been analyzed in cells with and without arbuscules [60]. It has been shown that, in *Solanum tuberosum*, sugars are transported from host plants to the AM fungus *Rhizophagus irregularis,* mainly by sucrose and glucose facilitators, StSWEET12 and StSWEET7a, respectively (Fig. 3) [55 50, 61], acting on PAP and transporting sugars from cytoplasm to PAP and back. Through ArM to PAP, glucose is transported in arbuscules via the fungal R. *irregularis* Monosaccharide Transporter 2 (RiMST2) (56 see Fig. 3) [50, 61–63] or as a result of *Geosiphon pyriformis* Monosaccharide Transporter 1 (GpMST1) activity [64]. Through ApM, sucrose can be transported by the *Rirregularis* Sucrose transporter 1 (RiSUC1) (information about the transcript is available at https://www.ncbi.nlm.nih.gov/nuccore/HQ848966; 56 Fig. 3); however, there is little information about *RiSUC1* since only one group is conducting research [62]. Then, sugar is transported through the intraradical mycelium, in the form of glycogen, to the extraradical mycelium of AM fungus (Fig. 3) [50, 52]. The content of sugars in root cortical cell cytoplasm is regulated by their transfer from vacuoles to tonoplastic transporters, which is related to sucrose symporter SUT4 and glucose StSWEET2c facilitator (57 Fig. 3) [50]. The host plant regulates the outflow of unnecessary sugars from periarbuscular spaces by sucrose symporter SlSUT2 *(Solanum lycopersicum* Sucrose Transporter 2; 58 Fig. 3) [49, 50, 63, 65] and hexose STP Symporter (58 Fig. 3) [18, 50].

There is another significant pathway involved in supplying carbon-containing metabolites from host plants to AM fungal tissues. This includes forming a number of fatty acids (with 16 carbon atoms) from hexoses, which are synthesized through the synthase Fatty Acid System (FAS) and released from FAS using thioesterase [52]. Palmitic acid (C16:0) is converted into 2-monoacylglycerol (2MAG) by RAM2 (the *RAM2* gene encodes glycerol-3-phosphate acyltransferase) [52]. Lipids are exported to the periarbuscular space by 2-MAG transfer through PAM, using STR1 and STR2 proteins (stunted arbuscule transporters) [52, 66], from the heterodimer ABC-transporter (ATP Binding Cassette) family [66] localized on the periarbuscular membrane (59 Fig. 3) [52]. Further, the lipids are transported by unknown fungal transporters on ArM (60 Fig. 3) [52]. In the intraradical 2-MAG mycelium, they can be transformed into triacylglycerol (TAG), which, in turn, is transported to extraradical mycelium (Fig. 3).

Apoplastically, the sugars are transported to cells, both with and without AM fungus, by SWEET hexose transporters (61 Fig. 3) [19, 41]. However, we suppose there are facilitators of this family specific to AM symbiosis. Candidates for the specific transport of sucrose and glucose in *S. tuberosum* through the plasma membrane of root cortical cells containing AM are StSWEET12 and StSWEET7a,

respectively (⑫ in Fig. 3) [50, 61]. In this context, the effectors secreted by AM fungi either directly or indirectly activate *SWEET* gene expression through the activation of transcription factors [67]. Sucrose can be transported to cells with arbuscules in two ways: in *Z. mays*, by means of the non-specific symporter ZmSUT1 (⑬ Fig. 3) [17, 57]; and in *Lotus japonicus*, in a manner involving the specific facilitator LjSWEET3 (⑭ Fig. 3) [50]. Hexoses are transported to cells with arbuscules by the STP symporter (⑮ Fig. 3) [18, 50].

Although this review is aimed at providing an overview of data on carbohydrate transport between the host plant and AM fungus, we will touch upon one more issue: Can sugars be supplied to the extraradical mycelium of AM fungus directly from the soil, where they are excreted by plants? In the over century-long history of physiological research on AM fungi, scientists have been unable to provide a reliable answer to this question. AM fungi are believed to be obligate plant symbionts since they cannot feed saprotrophically and absorb organic substances important for their development from soil, particularly sugars [3]. However, in the late 1990s, it was suggested that, by uptake carbon-containing compounds from the soil, fungi control carbohydrate transport in plant–microbial systems [68]. However, this hypothesis was disproved in further research. Currently, it is considered that the host plant controls the supply of sugars to AM fungus by adjusting the action of sucrose symporter SlSUT2 [49, 50, 63, 65] and hexose STP symporter [18, 50]. Nuclear

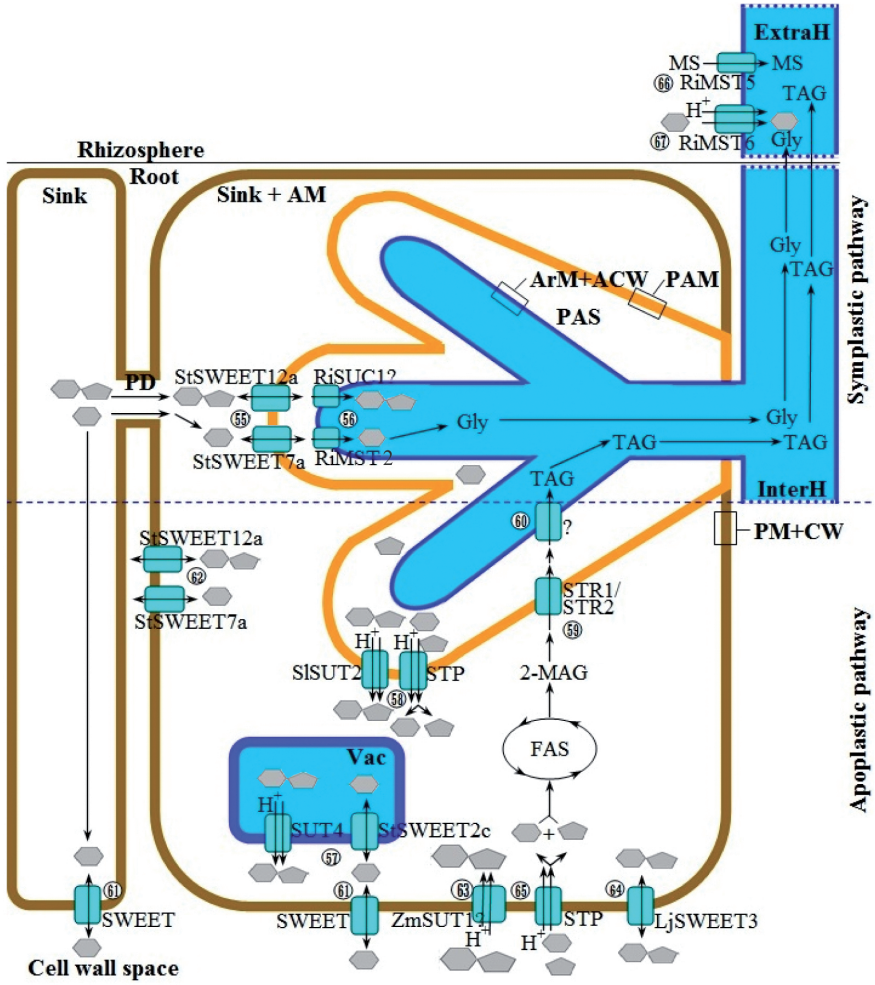

Fig. 3. Scheme of sugar transport to the roots of AM plants with arbuscules (based on materials presented by [18, 50, 52, 59] with changes and additions). In Fig. 3: for abbreviations see explanations to Fig. 1; Sink – a root-sugar cell that consumes sugar (Sink cortex cell); "Sink + AM" – a root cortex cell with AM that consumes sugar (Sink cortex cell with Arbuscular Mycorrhiza), "PM + CW" – Plasmatic Membrane and Cell Wall, PAM – Peri-Arbuscular Membrane, PAS – Peri-Arbuscular Space, "ArM + ACW" – Arbuscule Membrane and Arbuscule Cell Wall, InterH – Intercellular intraradical Hypha, ExtraH – Extraradical Hypha, FAS – Fatty Acid Synthase system, 2-MAG – 2-Monoacylglycerol, TAG – Triacyl-glycerol, Gly – Glycogen, MS – Monosaccharides. Description of transporters, see the text

magnetic resonance spectroscopy showed that sugars are supplied to AM fungus through intraradical mycelium in the form of hexoses, mostly in the form of glucose but, to a lesser degree, in the form of fructose. However, it was not revealed whether AM fungus can receive sucrose [69]. This is consistent with the hypothesis of mandatory biotrophy, obligate status of AM fungi in relation to the host plant as well as also by the necessity to transport sugar from the plant through intraradical mycelium to the extraradical hyphae of the AM fungus. It is assumed that arbuscules and intercellular hyphae are sites where AM fungi receive carbon [3, 70, 71], whereas conjugate phosphate transport is localized mainly in periarbuscular space [72]. Supposedly, intercellular hyphae can also be important sites for carbohydrate exchange [62].

The first fungus glucose symporter, *Geosiphon pyriformis* Monosaccharide Transporter 1 (GpMST1), was discovered in 2006 [64]. In 2011, RiMST2, RiMST3, and RiMST4 transporters were discovered in *R. irregularis* and studied [62]. It turned out that extraradical AM fungus mycelium can actively uptake not only glucose, but also xylose. Consequently, the monosaccharides obtained by extraradical hyphae can also be a source of carbon for AM fungi. The supposed monosaccharide transporter *Glomus intraradices* GiMST2 (RiMST2, based on the data on DAOM strain No. 181,602 *G. intraradices* = *Rhizophagus irregularis* according to https://www.uniprot.org/taxonomy/747089) is characterized by intense and specific expression in the cells with arbuscules, whereas RiMST4 is characterized by expression in extraradical mycelium [62]; however, further experiments did not confirm preferential RiMST4 expression in extraradical mycelium [59]. The 2016 analysis of RiMST2, RiMST3, RiMST4, RiMST5, and RiMST6 transporters on plants, such as *Medicago truncatula*, *Sorgum bicolor*, and *Populus trichocarpa,* deserves special attention in this context [59]. For the first time, researchers discovered RiMST5 and RiMST6 transporters, which are involved in transporting sugars from soil to extraradical AM fungus mycelium. RiMST5 is a high-affinity monosaccharide transporter (⑯ Fig. 3) [50, 59], whereas RiMST6 is a high-affinity symporter specific for glucose. Both transporters allow the import of sugars to AM fungi from soil directly by extraradical mycelium (⑰ Fig. 3) [50, 59]. The discovery of this group of transporters should allow revised approaches to maintaining axenic culture of AM fungi, enabling their growth without the host plant. We need to search for new working hypotheses to explain the obligate status of AM fungi in relation to plants.

PLANT SUGAR TRANSPORTERS DURING THE DEVELOPMENT OF AM SYMBIOSIS

Many transporters of model plants, such as *A. thaliana,* have been studied in detail. However, these studies have not included the group of plants forming AM symbiosis under natural conditions (only under some artificially created conditions) [73]; therefore, the study of carbohydrate metabolism upon AM symbiosis on the given plant is not entirely correct. In this context, we analyze transporters of those plant species that form AM, considering their homology with *A. thaliana* transporters. Organisms that form mycorrhiza include common model plants, such as *Medicago truncatula*; the authors can also select the highly mycotrophic black medick (*Medicago lupulina*) as a new focus for AM research [74]. Analysis of the literature prompted the conclusion that many plant sugar transporters are not specific for AM except for the recently discovered bidirectional SWEET uniporters [22, 61]. The transporters that are promising for further study in plant species forming AM are presented in the Table.

Plant transporters of sugars are divided into three key families: SUT (SUC), MST (including the subfamilies STP, TMT, PMT, VGT, pGlct/SGB1, ESL, INT) and SWEET, and others, for example, SUF and MEX (see Table and Fig. 1–3).

M. truncatula was revealed to have six *SUT* genes [49] forming three *SUT* clades (clades I, II, and IV) [49]; *A. thaliana* has nine genes (*AtSUT1* – *AtSUC2*, *AtSUC1*, *AtSUC5*, *AtSUC6*, *AtSUC7*, *AtSUC8*, *AtSUC9*; *AtSUT2* = *AtSUC3*; *AtSUT4* = *AtSUC4*), which also form three *SUT* clades [49, 77]. Other plant species have *SUT* genes of the third clade that are not homologous to these genes, for example, *OsSUT3* in *Oryza sativa* and *ZmSUT3* in *Z. mays*. At the same time, some species can have many more *SUT* genes; for example, *O. sativa* has the *OsSUT5* gene, while *Z. mays* has the *ZmSUT5* and *ZmSUT6* genes [49]. *M. truncatula* has the *MtSUT4-1* gene, which has generated great interest since it encodes the sugar transporter protein SUT4, intensively accumulating in cells with arbuscules and in cells of leaves localized in tonoplasts. It is also involved in transporting sucrose from vacuoles to cytoplasm [79]. On the other hand, *MtSUT1-3*, *MtSUT2*, *MtSUT4-1*, and *MtSUT4-2* are expressed at similar levels in leaves and roots. *MtSUT1-1* is characterized by a 20-fold increase of transcript accumulation in leaves compared to roots [49]. This indicates *MtSUT1-1's* significant role in transporting sucrose in

the aboveground parts of lucerne. At the same time, *MtSUT4-1* works mainly in the roots. Based on the analysis of expression levels, the most important genes in AM development with regard to sugar transport are the following:

1) Gene of tonoplast sucrose symporter *MtSUT4-1* in the AM roots of *M. truncatula* [49];

2) Gene of sucrose symporter *MtSUT1-1* in the leaves of *M. truncatula*; the protein acts on the plasma membrane of mesophyll cells [49];

3) Gene of sucrose symporter *SlSUT2* in *S. lycopersicum* (㊺ Fig. 3) [49, 50, 63, 65], which regulates the outflow of unnecessary sugars from PAP;

4) Gene of sucrose symporter *ZmSUT1* in *Z. mays* (㊸ Fig. 3) [17, 57]; the protein acts on PM.

Proton-dependent symporters include SUT, STP (from MST), PMT (from MST), and INT (from MST); meanwhile, proton-dependent antiporters include TMT (from MST) and VGT (from MST). Uniporters are MEX, pGlct/SGB1 (from MST), ESL (from MST), and bidirectional uniporters (facilitators), namely, SUF and SWEET (which do not belong to the MST family). *SUF* genes (facilitators) include *SUT* genes' homologs (symporters), but it is evident that they are functionally markedly different from the *SUT* genes. At the same time, SUF proteins are analogs of SWEET proteins: they are functionally similar, but have different origins. *PsSUF1*, *PsSUF4*, *PvSUF1*, and *PvSUF4* genes have been detected in two species: *P. sativum* and *P. vulgaris* [17, 40]. A further search for genes of the given groups in other plant species is required to identify their significance in plants' carbohydrate metabolism.

M. truncatula has 62 *MST* genes, including 23 *STP*, 5 *TMT*, 11 *PMT*, 2 *VGT*, 3 *pGlct/SGB1*, 8 *ESL*, and 10 *INT* [17]. Apparently, the most common are STP proteins, which function as H^+/hexose symporters localized on the plasma membrane, many of which have low specificity in the substrate with the greatest affinity to glucose [80–82]. The homology of *MST* genes from *M. truncatula* with *A. thaliana* genes is presented in the Table. The number of *MST* genes in different plant species also varies (e. g., 53 *MST* gene in *A. thaliana*, 59 in *Vitis vinifera*, and 68 in *O. sativa*) [17]. Incorporating these genes into the *MST* family is conditional since, functionally, the family includes symporters and antiporters along with uniporters. Analysis of the literature showed that all of the well-known *SUT*, *MST*, and *MEX* genes are not specific for AM symbiosis. From the perspective of sugar transport and the high level of expression of MST transporter genes, the hexose *STP* symporter gene regulating the outflow of unnecessary sugars from PAP should be highlighted in AM development. The protein acts on PAM (㊽ Fig. 3) [50] and PM (㊺ Fig. 3) [50].

Table 1

Some sugar transporter genes in plants forming arbuscular mycorrhiza

Gene of interest	Homologues of gene	Family*	Plant	Link
MtSUT1-1	*AtSUT1* (including *AtSUC2*)	SUT family of sucrose symporters	*Medicago truncatula*	[49]
MtSUT1-2				
MtSUT1-3				
GmSUT1			*Glycine max*	[75]
PsSUT1			*Pisum sativum*	[40]
ViSUT1			*Vicia faba*	[76]
MtSUT2			*M. truncatula*	[49]
OsSUT3	*ZmSUT3*, no homology with *A. thaliana*		*Oryza sativa*	[38, 49, 77]
MtSUT4-1	*AtSUT4* (=*AtSUC4*)		*M. truncatula*	[49]
MtSUT4-2			*M. truncatula*	[49]
ZmSUT5	*OsSUT5*, no homology with *A. thaliana*		*Zea mays*	[38, 49, 77]
PsSUF1	*AtSUT1*	SUF family of bi-directional sucrose uniporters (facilitators)	*Pisum sativum*	[40, 49]
PsSUF4	*AtSUT4*		*Pisum sativum*	[40, 49]
MEX-genes have not yet been studied in AM species	*AtMEX1*	MEX family of maltose uniporters	*Arabidopsis thaliana*	[19, 28]

Table 1 (continued)

Gene of interest	Homologues of gene	Family*	Plant	Link
MtSWEET1a = Medtr1g029380	*AtSWEET1*	SWEET family of bi-di-rectional sugar uniporters	*M. truncatula*	[78]
MtSWEET1b = Medtr3g089125				
MtSWEET2a = Medtr8g042490	*AtSWEET2*			
MtSWEET2b = Medtr2g073190				
MtSWEET2c = Medtr6g034600				
MtSWEET3a = Medtr3g090940	*AtSWEET3*			
MtSWEET3b = Medtr3g090950				
MtSWEET3c = Medtr1g028460				
MtSWEET4 = Medtr4g106990	*AtSWEET4*			
MtSWEET5a = Medtr6g007610	*AtSWEET5*			
MtSWEET5b = Medtr6g007637				
MtSWEET5c = Medtr6g007623				
MtSWEET5d = Medtr6g007633				
MtSWEET6 = Medtr3g080990	*AtSWEET6*			
MtSWEET7 = Medtr8g099730	*AtSWEET7*			
MtSWEET9a = Medtr5g092600	*AtSWEET9*			
MtSWEET9b = Medtr7g007490				
MtSWEET11 = Medtr3g098930	*AtSWEET10*			
MtSWEET12 = Medtr8g096320				
MtSWEET13 = Medtr3g098910	*AtSWEET13*			
MtSWEET14 = Medtr8g096310	*AtSWEET14*			
MtSWEET15a = Medtr2g007890	*AtSWEET15*			
MtSWEET15b = Medtr5g067530				
MtSWEET15c = Medtr7g405730				
MtSWEET15d = Medtr7g405710				
MtSWEET16 = Medtr2g436310	*AtSWEET16*			

Table 1 (continued)

Gene of interest	Homologues of gene	Family*	Plant	Link
Mtst1	*AtSTP1*	STP subfamily of MST family of monosaccharide symporters	*M. truncatula*	[17]
Medtr4g091370				
Medtr4g090600				
Medtr3g008160	*AtSTP3*			
Medtr3g008170				
Medtr1g038630	*AtSTP4*			
Medtr5g082540				
Medtr3g093010				
Medtr3g007910				
Medtr3g023480				
Medtr5g041550				
Medtr3g093060				
CAD31121	*AtSTP5*			
Medtr5g094760	*AtSTP7*			
Medtr4g116770				
Medtr4g116800				
Medtr5g006070	*AtSTP13*			
MtHext1				
Medtr1g104750				
Medtr1g104770				
Medtr8g103010	*AtSTP14*			
Medtr6g087040				
Medtr8g102860				
Medtr3g118530	*TMT2* y *A. thaliana*	TMT subfamily of MST family of monosaccharide antiporters	*M. truncatula*	[17]
Medtr3g116060				
Medtr5g024740	*TMT3* y *A. thaliana*			
Medtr5g044910				
Medtr8g073100				
Medtr2g013310	*AtPMT4*	PMT subfamily of MST family of monosaccharide and polyol symporters	*M. truncatula*	[17]
Medtr6g007340				
Medtr4g071950	*AtPMT5*			
Medtr4g072030				
Medtr3g116240				
MtC00740				
Medtr6g088450	*AtPMT3*			
Medtr8g103500				
Medtr8g077890	*AtPMT6*			
Medtr5g075300				
Medtr5g019870				
Medtr4g077770	*VGT2* y *A. thaliana*	VGT subfamily of MST family of monosaccharide antiporters	*M. truncatula*	[17]
Medtr4g064820	*VGT1* y *A. thaliana*			

Table 1 (continued)

Gene of interest	Homologues of gene	Family*	Plant	Link
Medtr1g116830	*INT1* y *A. thaliana*	INT subfamily of MST family of inositol symporters	*M. truncatula*	[17]
Medtr1g116660				
Medtr1g116650				
Medtr3g084110				
Medtr7g005910				
Medtr2g048720	*INT2* y *A. thaliana*			
Medtr5g077580				
Medtr2g049020				
Medtr2g026140	*INT3* y *A. thaliana*			
Medtr2g026160				
Medtr7g082270	*pGlcT* y *A. thaliana*	pGlct/SGB1 subfamily of MST family of glucose uniporters	*M. truncatula*	[17, 27]
Medtr6g087910	*At1g67300*			
Medtr3g080240	*At1g05030*			
Medtr8g077310	*At1g19450*	ESL subfamily of MST family of glucose uniporters	*M. truncatula*	[17]
Medtr5g020270				
Medtr8g077300				
MtC20248				
Medtr7g113960	*At1g54730*			
Medtr7g113970				
Medtr4g118610	*At5g18840*			
Medtr2g020710				

Note: "Family*" – the following reductions of families and subfamilies of conveyors are specified:

- family of active sucrose/H+ Sucrose Transporters – SUT (synonym – SUC, Sucrose transporters);
- family of bi-directional non-volatile sucrose unipores – SUF (SUcrose Facilitators, type 1 and 4 facilitators) discovered in plants forming AM – *Pisum sativum* and *Phaseolus vulgaris*;
- family of chloroplast maltose exporters – MEX;
- family of monosaccharide transporters – MST [27], including 7 subfamilies:
  - H^+-symporter monosaccharides subfamily – STP (Sugar Transport Proteins),
  - tonoplast H^+-antiporter monosaccharides subfamily – TMT (Tonoplast Membrane Transporters),
  - subfamily of vacuolar H^+-symporters of monosaccharides and polyols – PMT (Polyol / Monosaccharide Transporters),
  - vacuolar H^+-antiporter monosaccharides subfamily – VGT (Vacuolar Glucose Transporters),
  - subfamily of H^+-inositol importers – INT (Inositol Transporter),
  - subfamily of nonvolatile glucose uniporters – pGlct/SGB1 (plastidic Glucose transporter / Suppressor of G protein Beta 1, [27]),
  - tonoplast glucose uniporter subfamily – ESL (Early-responsive to dehydration Six-Like);
- family of bi-directional nonvolatile uniporters – SWEET (Sugars Will Eventually be Exported Transporters).

The only known family of transporters in which, according to the current understanding, the genes specific for AM symbiosis development can be identified is the SWEET family, which was first discovered by Chen et al. [22]. Localization of the proteins encoded by *SWEET* genes in cells with AM is presented in Fig. 3. The high variability of SWEET protein functions should be highlighted: some of them act as bilateral, energy-dependent uniporters for monosaccharides, while others do this for sucrose (see Fig. 1–3). SWEET transporters functionality depends on the domain structure of the genes encoding them [83]. Phylogenetically, SWEET transporters can be divided into four clades: proteins of clades I and II predominantly transport hexoses, while proteins of clades III and IV predominantly transport sucrose and fructose, respectively [22, 83, 84]. SWEET proteins play an important role in a number of processes: in AM development, pollen maturation, and the aging of plants [22, 61], and also in responses to biotic and abiotic stresses [22, 83, 85].

Based on the level of expression during AM development, the most important SWEET transporter genes, from a sugar transport perspective, are the following:

1) sucrose and glucose facilitator genes in *S. tuberosum*, namely, *StSWEET12a* and *StSWEET7a*, respectively [50, 61]; the proteins act on PAM (⑤⑤ Fig. 3) and PM (⑥② Fig. 3);

2) the vacuolar glucose facilitator gene *StSWEET2c* in *S. tuberosum* (⑤⑦ Fig. 3) [50, 61]; the protein acts in tonoplasts;

3) *LjSWEET3* facilitator gene in *L. japonicus* (⑥① Fig. 3) [50]; the protein acts on PM.

The SWEET family includes 17 genes in *A. thaliana* [86]. Single-celled and green seaweed have only 1–3 copies of *SWEET* genes, while monocotyledons have 18–23 such genes and dicotyledons have 15–68 [83]. Plants have more *SWEET* genes than animals and prokaryotes [87]. All of the genes discovered in other plant species are *A. thaliana* gene homologs (numeration of the gene titles is the same). However, different plant species have a large number of SWEET protein isoforms. The number of discovered *SWEET* genes increases yearly. For example, in 2005, *M. truncatula* was identified as having 18 [88] or 24 [67] *SWEET* genes, but this number increased to 26 [78] and, later, 35 [61]. Different plant species have different numbers of *SWEET* genes: *Glycine max* has 52 genes [88], *Solanum tuberosum* has 35, and *S. lycopersicum* has 29 [61].

In this context, there is good reason to believe that not all *SWEET* genes have been discovered. This bolsters our belief that a number of new *SWEET* genes will be found in the coming years, which should broaden our knowledge of the functions of the transporters that they encode.

CONCLUSION

This review summarizes findings on the diversity of sugar transport pathways in plants, both inside cells and between different organs. There should be special consideration of the mechanisms by which sugars are supplied to fungal symbionts during the development of AM. Contemporary methodological approaches have allowed identification of not only transporter proteins localized on the membranes of symbiotic structures, but also the genes encoding them.

Critical analysis of the literature showed that the genes specifically involved in sugar transport to the AM probably belong to SWEET transporters. The other genes associated with sugar transport are apparently not specific with respect to AM. Nevertheless, the genes important for AM symbiosis development are as follows:

1) gene of the tonoplast sucrose symporter *MtSUT4-1* in AM roots and *MtSUT1-1* in leaves; the proteins are localized on the plasma membrane of mesophyll cells;

2) gene of the sucrose symporter *SlSUT2*; the protein is localized on the periarbuscular membrane;

3) gene of the sucrose symporter *ZmSUT1*; the protein is probably localized on the plasmalemma of root cortex cells;

4) gene of the hexose symporter *STP*; the protein is localized on periarbuscular membrane and plasmalemma of root cortex cells;

5) AM-specific genes of sucrose and glucose facilitators, *StSWEET12a* and *StSWEET7a*; the proteins are localized on the periarbuscular membrane and plasmalemma of root cortex cells;

6) AM-specific gene of the vacuolar glucose facilitator *StSWEET2c*; the protein is localized in root cortex tonoplast cells with AM;

7) facilitator gene *LjSWEET3*; the protein is localized on plasmalemma.

Fungal candidate genes involved in carbohydrate exchange during AM symbiosis development are the following:

1) fungus transporter genes of *RiMST2* and *GpMST1* monosaccharides; the proteins are localized on the ArM;

2) gene of fungus sucrose transporter *RiSUC1*; the protein is probably localized on the ArM;

3) genes of fungus transporters *RiMST2*, *RiMST3*, and *RiMST4* (data on function and localization of proteins are still fragmentary and contradictory);

4) gene of fungus high-affinity uniporter of *RiMST5* monosaccharides and fungus glucose symporter *RiMST6*; the proteins are likely to be localized on the plasmalemma of extraradical AM fungus mycelium.

Data on the functions and localizations of different transporters are still rather debatable in a wide range of cases. Thus, the work of Doidy et al. refers to TMT1 and TMT2 transporters as sucrose antiporters, but they actually transport hexoses, namely, fructose and glucose [17]. The functions of TMT [21] and TST [23] transporters are still unclear. Localization of transporters on the amyloplast membrane for the import and export of glucose-1-phosphate has been confirmed by only one study [47].

Analyses of *StSWEET2b*, *StSWEET10a*, and *StSWEET10b* gene expression levels may be inaccurate due to mismatching between the data on the phylogenetic tree created based on *SWEET* genes and data on the expression in histograms, although this does not reduce the value of the research on *SWEET* genes in *Solanum tuberosum* [61].

Apparently, classifying SUT and SUC transporters in different plant species cannot be considered definitive. Thus, *A. thaliana* and *M. truncatula* for the SUT transporters are divided into three clades, while *O. sativa* and *Z. mays* are represented by more clades [49].

The localization of PsSUF1, PsSUF4, PvSUF1, and PvSUF4 sucrose facilitators (energy-independent bidirectional transporters), which were found on the membrane of phloem cells [19], or in plasmalemma and tonoplasts [17], remains unclear. Transmission electron microscopy of plant seeds made it possible to conclude that PvSUF1 and PvSUT1 are localized in the cells of conducting elements and parenchyma, whereas PsSUT1, PsSUF1, and PsSUF4 are localized in all of the tissues (parenchyma, cambium, etc.), except palisade tissues and hypodermis [40]. Thus, we need to continue studies in this field to draw definitive conclusions. In a number of studies, the researchers themselves stated that conclusions about the mechanisms of sugar transport in plants are mostly based on indirect data or on modeling results [51], so the findings are still only based on assumptions.

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The authors declare that there are no conflicts of interest.

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