

REVIEW

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Influence of sugar metabolism on the dialogue between arbuscular mycorrhizal fungi and plants

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Abstract

Arbuscular mycorrhizal (AM) symbioses in plants are broadly significant because of their capacity to facilitate water and nutrient acquisition and thus, to promote vigorous growth and development among host plants. Many horticultural plants, especially citrus plants, are highly dependent on AM fungi. In return, AM fungi receive sugars and lipids from their host plants. The sugars (mainly sucrose) are transported from the aerial parts of host plants to the roots and thus, form a mycorrhizal carbon pool. In roots, sucrose is converted to hexoses, which are then taken up by AM fungal intraradical hyphae and converted to trehalose and glycogen for growth and storage in extraradical hyphae and potentially participate in the soil carbon cycle through as the glomalin-related soil proteins. Therefore, the root mycorrhizal carbon pool influences the sugar (mainly sucrose) metabolism of plants, providing a guarantee for mycorrhizal plants to maintain better plant growth, stress resistance, fruit quality, lateral root development, and soil carbon sequestration. Thus, sugar metabolism is a player in the dialog between AM fungi and plants. This review briefly summarizes the processes of sucrose synthesis, transport, and metabolism, and highlights the relationship between AM fungi and plant sugars with an emphasis on AM-carbon pools, osmotic adjustment, fruit quality, and sugar-associated gene expression. Future research prospects are discussed.

Keywords Glucose, Mycorrhiza, Sucrose, Symbiosis, SWEET (sugars will eventually be exported transporters)

Introduction

Sugars are the most important form of chemical energy for living organisms. In glycobiology, free carbohydrates are metabolized, including simple sugars, sucrose-derived oligosaccharides, starch, and its decomposition products (Ende et al. 2014). In plants, sugar production occurs during photosynthesis, and plays a crucial role in most cellular processes, such as carbon (C) metabolism, energy storage, and the provision of carbon skeletons for the biosynthesis of organic compounds (Baslam et al. 2021). For example, soluble sugars, such as glucose, fructose,

and sucrose, serve as osmoregulatory substances that maintain cell pressure, protect cell structure, influence stomatal aperture, and regulate cell potential and redox poise (Saddhe et al. 2021). Sugars also influence signal transduction during stress responses (Lucho et al. 2022). In addition to serving as a major transport form of sugar, sucrose also induces plant defense responses (Ciereszko 2018). There are two mechanisms for hexose perception in plants: the hexose kinase (HXK)-dependent pathway and the HXK-independent pathway (Lucho et al. 2022). Thus, the perception of a hexose may induce a signal transduction cascade involving mitogen-activated protein kinases, protein phosphatases, Ca²⁺ and calmodulin (Barker 2000). Drought stress leads to the accumulation of polyols, oligosaccharides, proline, and betaine in potato (Legay et al. 2011). Inositol is an essential component associated with seed phosphate storage, pollen

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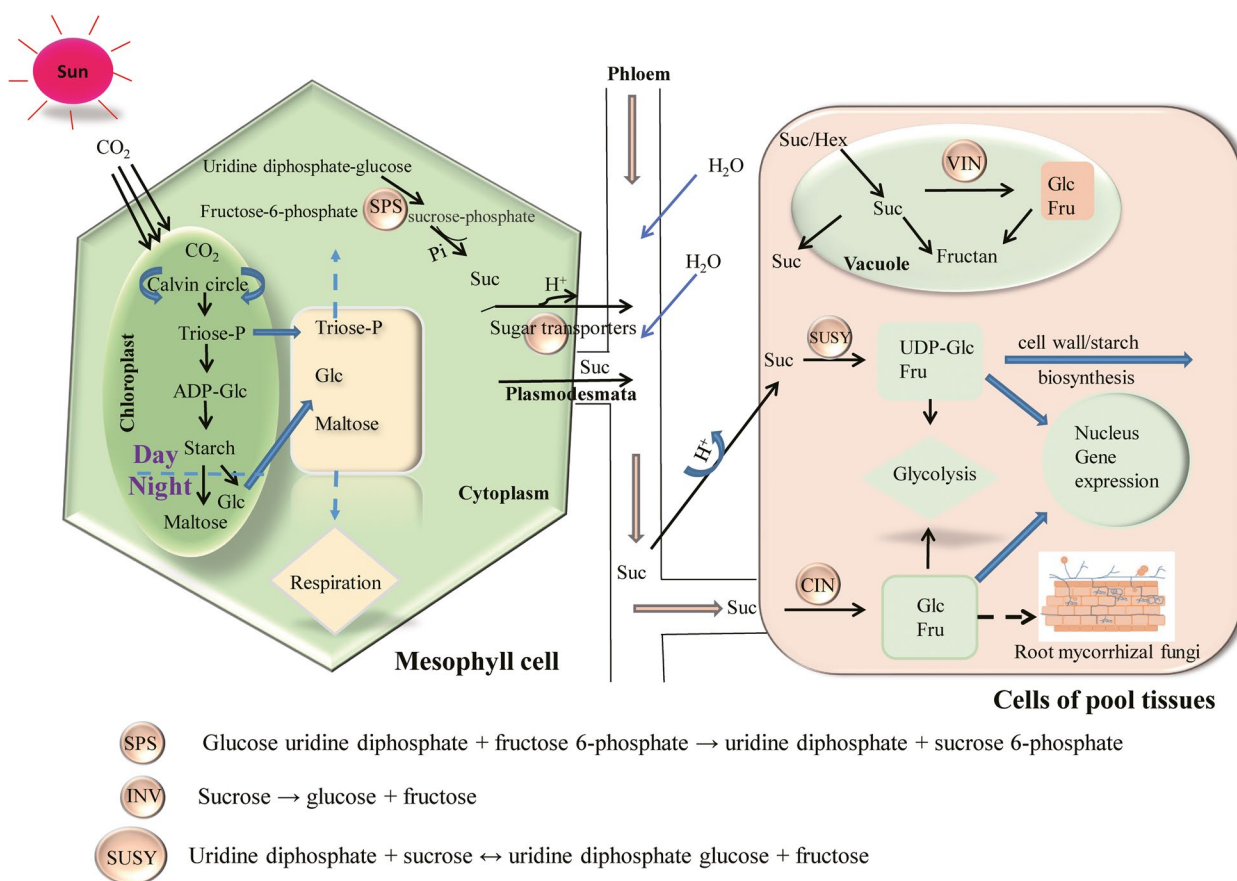


Fig. 1 Sucrose synthesis, transport, and metabolism in plants. Adapted from Feng et al. (2021) and Ruan (2014) with minor modifications. ADP-Glc, adenosine diphosphate-glucose; CIN, cytoplasmic invertase; Fru, fructose; Fru-6-P, Fructose-6-phosphate; Glc, glucose; Hex, hexose; INV, invertase; SPS, sucrose phosphate synthase; Suc, sucrose; SUSY, sucrose synthase; Triose-P, triose-phosphate; UPD-Glc, uridine diphosphate-glucose; VIN, vacuolar invertase

cell wall polysaccharides, and signaling molecules (Valuru and Ende 2011). Alginate is not only a carbohydrate storage molecule but also helps plants to tolerate abiotic stress by helping to protect membranes and proteins (Magazù et al. 2012; Redillas et al. 2012).

Arbuscular mycorrhizae are a symbiosis established between soil arbuscular mycorrhizal (AM) fungi and 80% of terrestrial plants (Das et al. 2022). An important role of mycorrhizae is to obtain sugars, mainly hexoses, from the sucrose that is cleaved by host plants. Lipids are also important sources of organic carbon provided to the AM fungi by host plants that promote mycorrhizal fungal colonization (Jiang et al. 2017; Luginbuehl et al. 2017). In return, AM fungi are directly involved in water uptake and transport by plants, improve mineral nutrition, enhance osmoregulation and antioxidant systems, improve soil structure, and influence stress-related gene expression (Wang et al. 2023). Former research found that inoculations with *Rhizoglossum intraradices* distinctly elevated the glucose, fructose and sucrose content of leaves in

trifoliate orange and white clover and simultaneously reduced the glucose, fructose and sucrose content of roots in trifoliate orange (Xiang et al. 2016). When the soil moisture content was only 30%, *Claroideoglossum etunicatum* increased root activity and soluble sugar levels in ryegrass (Li et al. 2019). Therefore, AM fungi are intricately connected with sucrose metabolism.

Overview of sucrose metabolism in plants

Sucrose, an important carbohydrate in plants, is the main end product of photosynthesis that is transported over long distances (Fig. 1) and one of the main forms of sugar that accumulates in fruits (Patrick et al. 2013). After arriving in sink organs, sucrose is degraded by enzymes to yield hexose or its derivatives for use in the various metabolic processes that occur in seeds, fruits, roots and tubers (Barratt et al. 2009; Ruan et al. 2009), such as energy production and the biosynthesis of cellulose, starch, fructans, proteins and antioxidants (O’Hara et al. 2013; Ruan et al. 2012). In contrast to

glucose, sucrose is a nonreducing sugar that is not easily degraded in plants even during long-distance transport. Sucrose is highly soluble and can reach concentrations of 200–1600 mmol/L in the phloem. The low viscosity of sucrose ensures high flow rates during transport which can reach 0.5–3 m/h (Kühn et al. 1999). Sucrose generates an extremely high osmotic potential on a per carbon atom basis (Bel 1996). These characteristics of sucrose provide unique advantages for long-distance transport in plants.

The key enzymes of sucrose metabolism include invertase (INV, EC 3.2.1.26), sucrose phosphate synthase (SPS, EC 2.4.1.14), and sucrose synthase (SUSY, EC 2.4.1.13) (Barratt et al. 2009; Hashida et al. 2016). Among them, SUSY is involved in several biochemical processes, such as cell construction, regulation of starch biosynthesis, cellulose biosynthesis, and influencing fruit sink strength (Yuan et al. 2019). SUSY catalyzes both sucrose synthesis and decomposition (Fig. 1): Uridine diphosphate + sucrose \leftrightarrow uridine diphosphate glucose + fructose. The optimum pH for sucrose biosynthesis is 7.5–9.5 and for sucrose catabolism is 5.5–7.5. However, SUSY is thought to play a major role in sucrose catabolism in plants (Schmölzer et al. 2016). It is detected that the expression of six *Sucrose synthase* (*CitSus1–6*) genes in mature leaves, fruit sacs, petals, and juice sacs of citrus subjected to mild drought stress (Islam 2015). *CitSus1*, 2, 5 and 6 were expressed mainly in fruit juice sacs. *CitSus2* was expressed at significantly different levels in fruit sac petals and juice sacs, which provides evidence that *CitSus2* contributes to sucrose unloading and the distribution of sucrose in fruit. *CitSus2–4* was expressed in immature leaves. In contrast, *CitSus1*, 5 and 6 were expressed in mature leaves. Only the expression levels of *CitSus2* were induced nearly 2.5-fold in citrus subjected to mild drought stress (Islam 2015). These results indicate that the different SUSY homologs of citrus have tissue-specific expression patterns.

SPS is a soluble, low-abundance dimer or tetramer composed of 119–138 kDa subunits that accumulate primarily in the cytoplasm of photosynthetic and non-photosynthetic tissues, with a pH optimum of approximately 7.0 (Klein et al. 1993). SPS is the principal enzyme for sucrose biosynthesis in higher plants. The activity of SPS is regulated by allosteric regulation and phosphorylation (Zhou et al. 2006). SPS catalyzes the following reaction: glucose uridine diphosphate + fructose 6-phosphate \rightarrow uridine diphosphate + sucrose 6-phosphate (Fig. 1). Sucrose-phosphate phosphatase (SPP) catalyzes the irreversible hydrolysis of sucrose 6-phosphate to yield sucrose (Huber and Huber 1996). Indeed, sucrose accumulates in sugarcane, sugar beet, citrus, tomato and other crops when SPS activity

increases and INV activity decreases (Lunn and Macrae 2003). SPS activity is negatively correlated with the accumulation of starch and positively correlated with sucrose formation (Zhou et al. 2006). During periods of drought stress, increases in SPS activity led to changes in the allocation of carbon that promoted sucrose biosynthesis, substantial accumulations of sucrose and thus stress tolerance (Nemati et al. 2018).

INVs can regulate sugar accumulation because they irreversibly catalyze the hydrolysis of sucrose to yield the corresponding nucleoside diphosphate glucose, glucose, or fructose (Yuan et al. 2021). INV activity is regulated by several signals, including sugar signals, plant hormones, environmental stress, and INV inhibitors (Shen et al. 2022). INVs can be classified into three categories based on subcellular localization, solubility and pH optimum: soluble acid invertase (SAI), cell wall-bound invertase (CWIN), and neutral (NI) or alkaline invertase (Fugate et al. 2019; Xie et al. 2009). SAI has a low isoelectric point and mainly accumulates in a glycosylated form in vacuoles, which regulates sugar accumulation in plant tissues and sucrose utilization in vacuoles by catalyzing the hydrolysis of sucrose to yield hexose (Fugate et al. 2019). For example, SAI promoted increases in sugar content in grapes when root growth was restricted (Xie et al. 2009). NI accumulates in the cytoplasm in a nonglycosylated form and has a neutral or weakly alkaline pH optimum. NI degrades sucrose in plant tissues to provide glucose and fructose for metabolism, with generally low activity (Wu et al. 2017). When the phloem is unloaded into the apoplast, CWIN irreversibly catalyzes the hydrolysis of sucrose to yield glucose and fructose, which helps to maintain sucrose concentration gradients between sources and sinks (Wei et al. 2020).

Starch is a major end product of photosynthesis that accumulates transiently in the chloroplast. At night, the major end products of starch catabolism are transported to the cytosol where complexes formed by SPS and SPP use these hexoses to synthesize sucrose. Sugars can be stored, consumed by respiration or transported to "sink organs" and used for growth, biosynthesis, and storage. Three steps are indispensable for the long-distance transport of carbohydrates from "source" to "sink" tissues: (1) phloem loading at a source tissue, (2) transport through the vascular bundle and (3) phloem unloading. These steps are key for the synthesis and utilization of organic matter in plants (Fig. 1) (Zhang et al. 2015). The sugar transporter (SUT), sugar carrier (SUC), monosaccharide transporter (MST), and sugars that will eventually be exported transporters (SWEET) play key roles in the transport of sucrose across membranes (Feng et al. 2021; Jeena et al. 2019; Ruan 2014; Zhang et al. 2015).

Sugars as carbon sources for AM fungi

AM fungi need the host plant to provide both sugars and lipids as carbon sources to sustain their growth and their capacity for colonization (Luginbuehl et al. 2017). The sugars produced by host plants through photosynthesis are used as carbon sources for the growth of AM fungi, and AM fungi store sugars to support their growth. Experiments that utilized isotope labeling and nuclear magnetic resonance spectroscopy demonstrated that AM fungi cannot take up and utilize sucrose as a carbon source (Solaiman and Saito 1997). The sucrose in mycorrhizae must be hydrolyzed into glucose and fructose by sucrose cleavage enzymes before the intracellular hyphae produced by mycorrhizal fungi take up and utilize these carbon sources (Schubert et al. 2004). INV, SUSY and SPS probably contribute to this process. In intracellular hyphae, glucose and fructose are transformed into trehalose and glycogen or are metabolized by the pentose phosphate pathway (Pfeffer et al. 1999). Meanwhile, enzymes associated with glycolysis and the tricarboxylic acid cycle, such as hexokinase, were also detected in root mycelia (Saito 1995). After the conversion of hexose into glycogen, it can also be transported to the extraradical hypha of arbuscular mycorrhizas for fungal growth and stored in the mycorrhizal carbon pool of roots (Bago et al. 2000). In addition, a carbon source can promote both spore germination and mycelial growth (Becard and Piche 1989). However, AM fungi cannot perform photosynthesis and thus, must rely on the products of photosynthesis provided by host plants to form symbioses with host plants (Feng et al. 2010). AM fungi can directly absorb carbohydrates formed by photosynthesis of host plants and then store these carbohydrates in vesicles in the form of triacylglycerols in liposomes, anhydride sugars or organic acids (Gaspar et al. 1997; Liu et al. 2011). Although these substances are difficult for host plants to absorb and utilize, they can promote the formation of carbohydrate concentration gradients between AM fungi and their plant partners that facilitate the continuous transport of carbohydrates from host plants to AM fungi, accelerate the metabolism of AM fungi, and lead to synchronous development of AM fungi and host plants (Li et al. 2002). In citrus, sucrose cleavage is influenced by the citrus genotype and the type and activity of sucrose lyase that provide high levels of glucose in the roots as a carbon source for fungal partners (Wu et al. 2013).

Plants allocate 10–20% of the carbon fixed by photosynthesis to their fungal partners in exchange for nutrients and water provided by AM fungi, which means that mycorrhizal plants store carbon in the rhizosphere (Adyari et al. 2022). The carbon absorbed by AM fungi is used for direct storage (Ullah et al. 2019; Subramanian et al. 2019), redistribution (Diao et al. 2021, 2022; Grman

et al. 2012; Williams et al. 2017; Zhang et al. 2016), and the soil carbon cycle (Wang et al. 2022). Soluble organic carbon, microbial biomass carbon and readily oxidized carbon in the rhizosphere were increased after maize plants were inoculated with *Rhizoglyphus intraradices* (*R. intraradices*) (Xu et al. 2019). In another experiment, maize inoculated with AM fungi improved the active carbon pool (Subramanian et al. 2019). A weak link between AM fungi and low phosphorus levels triggering the slow growth of ancient forests indicates that the stimulation of AM fungi may have a critical role in the growth of ancient forests (Ullah et al. 2019). In addition, the common mycorrhizal network established between adjacent plants in the same ecosystem can transfer excess carbon between plants to maintain the carbon balance and cycle, but not from native to exotic and then to native plants (Chen et al. 2021).

Early transcriptome analyses revealed that AM fungi promoted plant growth by regulating carbohydrate and energy metabolism, including downregulating differentially expressed genes (DEGs) associated with photosynthesis (Diao et al. 2021). In general, AM fungal inoculation accelerated the accumulation of glucose in leaves and roots but reduced the accumulation of sucrose in these tissues (Wu et al. 2015). The mycorrhization induced change in sucrose and glucose was associated with the activities of SAI, NI and SUSY and dependent on plant tissues (Wu et al. 2015). In a saline environment, AM fungi increased the accumulation of C, N and P in *Suaeda salsa*, increased C/N and C/P ratios, and were associated with the regulation of photosynthetic biological carbon sequestration pathways enriched in the KEGG database (Diao et al. 2022). Mycorrhizal plants also modify their allocations of carbon resources according to their needs (Grman et al. 2012). For example, as the intensity of soil flooding increased, plants preferentially retained carbon and reduced carbon allocation to the root-AM symbiosis, which provides evidence that a carbon allocation strategy for plants is part of a stress response that diminishes C-P exchange (Bao et al. 2019). As a result, when plants can obtain more P directly from their roots, their carbon allocation to AM fungi is reduced (Williams et al. 2017). AM fungi also release a large amount of carbon into the soil and thus, induce the growth and activity of phosphorus solubilizing bacteria that enhance the mineralization of organophosphorus, and increase P availability only when soil P levels are adequate (Zhang et al. 2016). In forests, the respiration rate of mycorrhizal mycelia was 1.4 t ha/yr and thus, accounted for 14±6% of the total soil respiration and 26±12% of root respiration (Nottingham et al. 2010). Therefore, it is possible for respiration of particular carbon sources in mycorrhizal mycelia to influence the natural carbon cycle and for

respiration in mycorrhizal mycelia to return carbon to the atmosphere.

In addition, AM fungi can release a glycoprotein containing various metals, known as glomalin-related soil protein (GRSP), into the soil (Liu et al. 2022). Although when the soil was subjected to drought, an AM fungal inoculation significantly promoted the carbon content of both easily extractable and difficult to extract GRSP,

mycorrhizal extraradical hyphae only increased the amount of carbon from the difficulty to extract GRSP (Table 1) (Wang et al. 2022). The difficulty of extracting GRSP was suggested to explain soil carbon sequestration. GRSP has a turnover time of 6 to 42 years (Rillig et al. 2001) and therefore, may be useful for reducing soil carbon emissions and mitigating the greenhouse effect.

Table 1 Changes in soluble sugar levels in plants in response to AM fungal inoculation and stress

Stresses	Host plants	AM fungi	Effects	References
Drought	<i>Poncirus trifoliata</i> (<i>P. trifoliata</i>)	<i>Funnelformis mosseae</i> and <i>Paraglomus occultum</i>	Fructose↑; glucose↑; sucrose↑; SS↓; SPS↑; leaf relative water content↑	Wu et al. 2017
Drought	<i>P. trifoliata</i>	<i>Rhizophagus intraradices</i>	Soil organic carbon↑; carbon in glomalin-related soil protein↑; carbon in difficultly extractable glomalin-related soil protein and soil organic carbon↑; leaf water potential↑	Wang et al. 2022
Drought	<i>Hevea brasiliensis</i>	Mixed AM fungi (<i>Funnelformis</i> sp., <i>Acaulospora</i> sp., <i>Gigaspora</i> sp., and <i>Scutellospora</i> sp.)	Osmotic potential↑; proline↑; soluble sugar↑	Tisarum et al. 2022
Drought	<i>Cucumis melo</i>	Mixed AM fungi (<i>Glomus</i> sp., <i>Sclerocystis</i> sp., and <i>Acaulospora</i> sp.)	Soluble sugar↑	Meddich et al. 2021
Drought	<i>Fragaria × ananassa</i> var. Paros	<i>Rhizophagus clarus</i> (<i>R. clarus</i>)	Soluble sugar↑; Osmotic potential↑	Moradtalab et al. 2019
Drought	<i>Glycine max</i>	<i>Septoglomus constrictum</i> , <i>Glomus</i> sp., and <i>Glomus aggregatum</i>	Soluble sugar↑	Grümberg et al. 2015
Drought	<i>Cyclobalanopsis glauca</i>	<i>Glomus mosseae</i> (<i>G. mosseae</i>) and <i>Glomus intraradices</i> (<i>G. intraradices</i>)	Soluble sugar↑; proline↓	Zhang et al. 2014
Salt	<i>Camellia sinensis</i>	<i>G. mosseae</i>	Soluble sugar↑; proline↓	Guo et al. 2022
Salt	<i>Lycopersicon esculentum</i>	Mixed AM fungi (<i>G. clarum</i> and <i>G. intraradices</i>)	Soluble sugar↑	Kong et al. 2020
Salt	GF677 (peach × almond)	<i>Rhizophagus intraradices</i> (<i>R. intraradices</i>) and <i>Funnelformis mosseae</i> (<i>F. mosseae</i>)	Soluble sugar↑	Shahvali et al. 2020
Salt	<i>Phoenix dactylifera</i>	<i>Glomus</i> sp., <i>Sclerocystis</i> sp., <i>Acaulospora</i> sp.	Soluble sugar↑	Ait-El-Mokhtar et al. 2020
Salt	<i>Sorghum bicolor</i>	<i>Acaulospora mellea</i>	Soluble sugar↑	Wang et al. 2019
Low temperature	<i>Perennial ryegrass</i> and <i>Lolium perenne</i>	<i>G. intraradices</i>	Soluble sugar↑	Yan et al. 2021
Cd	<i>Thymus vulgaris</i>	<i>F. etunicatum</i> and <i>F. mosseae</i>	Soluble sugar↑; membrane stability index↑	Hosseini et al. 2021
P	<i>Echinacea purpurea</i>	<i>Rhizophagus irregularis</i> (<i>R. irregularis</i>)	Soluble sugar↑; proline↑	Attarzadeh et al. 2019
Infection of <i>Phytophthora sojae</i>	<i>Glycine max</i>	<i>G. intraradices</i>	Soluble sugar↑	Li et al. 2013
Infection of <i>Nacobbus aberrans</i>	<i>Capsicum annuum</i>	<i>R. intraradices</i> B1, <i>R. intraradices</i> A2 and <i>F. mosseae</i>	Soluble sugar↓	Bernardo et al. 2021

AM, Arbuscular mycorrhizal; P, phosphorus; Cd, cadmium

↑ and ↓ indicate increases and decreases after mycorrhizal fungal inoculation

AM fungi-induced accumulation of sugars for improved osmotic adjustment

Plants are able to retain water during periods of abiotic stress by accumulating solutes (e.g. proline, betaine, sucrose, mannitol, and inorganic ions) (Chen et al. 2022). Sugars play a key role in sensing and signal transduction in adverse conditions and are associated with a number of physiological activities, such as osmotic adjustment and the scavenging of reactive oxygen species (Sadhe et al. 2021). After AM fungi form a symbiotic relationship with the host, AM fungi improve the biomass, photosynthesis, antioxidant defense systems, osmoregulatory capacity and therefore increase the stress tolerance of the host (Cheng et al. 2021; Wang et al. 2023). In trifoliolate orange, AM fungal inoculation dramatically increased leaf sucrose and root glucose concentrations but decreased leaf glucose and root sucrose concentrations during drought stress, which significantly improved osmotic adjustment (Zou et al. 2015). The root mycorrhizal carbon pool and AM fungi may have led to the maintenance of higher glucose and lower sucrose content in the root and thus, facilitated root growth (Cheng et al. 2021).

In mycorrhizal plants, sugar content changes in stressful environments and enhances osmotic potential (Table 1). After inoculating *Cucumis melo* plants with a mixture of AM fungi, the inoculated plants maintained higher leaf relative water content, water potential, and stomatal conductance when subjected to drought conditions (Meddich et al. 2021). This elevated drought tolerance was accompanied by a significant increase in total soluble sugar content. Moreover, the combination of AM fungi and the endophytic fungus *Serendipita indica* synergistically induced total soluble sugar content in strawberry and thus enhanced osmotic potential (Moradtab et al. 2019). Hence, AM fungi appear to improve host water status by regulating the accumulation of total soluble sugar. The application of AM fungi and low doses of exogenous trehalose induce the expression of stress-associated genes (Schluepmann et al. 2004), which provides evidence that AM fungi and trehalose use the same mechanism to enhance stress tolerance and that mycorrhizae may induce stress tolerance by influencing trehalose signaling, but more evidence needs to be provided to establish this link.

Of course, the influence of AM fungi on total soluble sugars in host plants varies among AM fungi and host species. Inoculation of two AM fungi on GF677 (peach × almond) rootstock revealed that the AM fungi-treated plants had greater salt tolerance than non-AM plants. However, the total soluble sugar content was greater in plants inoculated with *R. intraradices* than in plants inoculated with *Funneliformis mosseae* (*F.*

mosseae) (Shahvali et al. 2020). In addition, the increase in soluble sugar content induced by AM fungi was more prominent in salt-sensitive varieties than in salt-tolerant varieties (Wang et al. 2019).

AM fungi also help plants tolerate biotic stress (Table 1). For example, AM fungi help soybean tolerate *Phytophthora sojae* infections (Li et al. 2013) and pepper tolerate *Nacobbus aberrans* infestations (Bernardo et al. 2021). Nevertheless, in response to biotic stress, the soluble sugar content increased in soybean and decreased in pepper. Thus, the influence of AM fungi on soluble sugar content during biotic stress appears complex.

AM fungi-induced increases in sugar content improve fruit quality

In addition to improving stress resistance, in recent years, AM fungi were reported to improve fruit quality by inducing increases in sugar content. In Ponkan mandarin, AM fungal inoculation in the field improved the soluble solid content of fruit, along with higher root AM fungal colonization and root vitality (Cao et al. 2021). Similar results were reported for *Citrus iyo* (*C. iyo*) and *Citrus sinensis* (*C. sinensis*) (Sui et al. 2007; Yao et al. 1999). Moreover, there was a significant and positive correlation between root AM fungal colonization and the soluble solid content of fruits (Cheng et al. 2022), which indicates that the introduction of AM fungi could improve citrus fruit quality. In Newhall navel orange, only *Diversispora versiformis* inoculation induced increases in the soluble solid, glucose, fructose, and sucrose contents of fruits (Cheng et al. 2022). These data provide evidence that AM fungi improve fruit quality by triggering sugar translocation to fruits. However, in another citrus variety, Lane Late navel orange, fruit sugar content was dependent on AM fungal species. For example, fructose, glucose, and trehalose contents were increased in fruit after colonization with *Diversispora spurca* (*D. spurca*) and *Acaulospora scrobiculata* (*A. scrobiculata*) and D-arabinose, L-fucose, inositol, and xylitol contents were elevated only after colonization with *A. scrobiculata* (Li et al. 2023). AM fungi induced changes in fruit sugar content were associated with AM fungi-induced changes in the expression of sugar-associated genes. *A. scrobiculata* and *D. spurca* colonization upregulated the expression of *vacuole acid invertase 1* (*CsVINV1*), *CsSPS1*, *cell neutral invertase 4* (*CsA/NINV4*), and *CsSWEET* in the fruit from Lane Late navel oranges (Li et al. 2023). Thus, AM fungi have important roles in sucrose transport, biosynthesis, and cleavage in fruits.

In *Polygonum cuspidatum*, a medicinal plant, *F. mosseae* induced increases in the levels of maltose, sucrose, trehalose, inositol, fucose, and xylitol and induced decreases in the levels of fructose, glucose, and lactose in

roots (Sun et al 2022). Thus, although AM fungi can elevate sugar accumulation in fruits and roots, the specific effects vary among different AM fungi and host plant species.

Regulation of sugar-associated gene expression by AM fungi

The mechanisms used by AM fungi to affect changes in hosts influence gene expression. For example, the growth of mycorrhizal plants is promoted by regulating the expression of host genes and involves in the auxiliary regulation of genes that encode sugar transport proteins, such as *SWEET*, *MST*, *SUT* and thus, intercellular nutrient exchange and the redistribution of carbon (An et al. 2019; Boldt et al. 2011; Chong et al. 2014; Doidy et al. 2012; Mandal et al. 2015; Zhao et al. 2019). After inoculation of *R. intraradices* on *Stevia rebaudiana* plants, a transcriptome analysis revealed that the AM symbiosis upregulated the expression of 11 genes associated with steviol glycoside biosynthesis because the AM fungus increased photosynthesis in the plant and allowed for nutrient improvement and ultimately induced an increase in the sugar content of the plant (Mandal et al. 2015). Moreover, the expression of the β -glucuronidase (*GUS*) reporter gene driven by the *GmSWEET6* promoter was highly expressed in the cortical cells that contained arbuscules in roots, which was correlated with an increase in the fructose, glucose, and sucrose contents in soybean (Zhao et al. 2019).

SUT, *MST* and *SWEET* genes with expression that is responsive to AM fungi are involved in the translocation of sugar and lead to carbon accumulation in plants (An et al. 2019; Zhao et al. 2019). The expression patterns of particular isoforms of *SUT* and *SWEET* transporters were influenced by plant carbon allocations, as indicated by a positive correlation between the expression of *MtSUT2* and *MtSUT4-1* and the carbon allocation of symbiotic partners in *Medicago truncatula* (Kafle et al. 2019). In addition, sugar transporters are influenced by plant N levels, as indicated by the upregulated expression of the *MtSWEET* genes in alfalfa roots after N was provided to AM fungi and the expression of the *MtSWEET* genes was downregulated in alfalfa plants that did not suffer from N starvation (Kafle et al. 2019). Inoculation of *Solanum lycopersicon* with *Glomus mosseae* (*G. mosseae*) upregulated the expression of *SISUT1*, *SISUT2* and *SISUT4* in leaves and roots and thus, enhanced the ability to translocate sucrose to roots (Boldt et al. 2011). In alfalfa, the relative expression of *MtSUT1-1* (H^+ /sucrose transporter) was 20 times higher in leaves than in roots when plants were grown in *G. intraradices* colonization conditions, which is consistent with an important role for *MtSUT1-1* in the flux of sucrose from the photosynthetic source

leaves to the phloem (Doidy et al. 2012). In addition, the expression of *SWEET1b* was significantly upregulated in the *R. intraradices*-colonized cells of *M. truncatula* and that the *SWEET1b* protein accumulated in the periarbuscular membrane (Fig. 2) (An et al. 2019). Consistent with these data, the overexpression of *SWEET1b* promoted root mycorrhizal hyphal growth. Although the colonization of *Solanum tuberosum* roots with *Rhizophagus irregularis* (*R. irregularis*) can rewire the expression of 22 among the 35 *SWEET* gene family members, the effect was not specific to particular species of mycorrhizae (Manck-Götzenberger and Requena 2016). Twelve of the mycorrhiza-inducible *SWEET* proteins were mainly associated with hexose and sucrose transport and could be repositioned in root cells containing arbuscules. In conclusion, AM fungi have a major influence on the transport and utilization of sucrose by regulating the expression of sugar transporter genes in hosts. When roots are colonized by AM fungi, the symbiotic sucrose in the root cortex cells can be cleaved in the cytoplasm by sucrose synthase or cytoplasmic invertase to provide glucose for AM fungi. Sucrose can also be directly exported from the cytosol and then converted into glucose and fructose by cell wall bound invertase (Manck-Götzenberger and Requena 2016).

Although AM fungi upregulate the expression of sugar-associated genes in host plants, other studies have reported the opposite result. In plants subjected to salt stress, AM fungal inoculation induced decreases in the expression of the *UDP-glycosyltransferase 73C6* gene in the leaves produced by GF677 rootstock (Shahvali et al. 2020), which is consistent with AM fungi affecting stress responses by controlling the glucosylation of brassinosteroids (Husar et al. 2011). The regulation of transporter gene expression by AM fungi is a rather complex process, as seen in tomato with the downregulation of *LeSUT1* and *hexose transporter 2* (*LeHT2*) and the upregulation of *sugar transporter 3* (*LeST3*) after inoculation with either *G. caledonium* or *G. intraradices* (Ge et al. 2008).

In addition, AM fungi (e.g. *R. irregularis*) also upregulate the expression of sugar transporter genes (e.g. *fruT* and *gluT*) in plant growth promoting bacteria (e.g. *Rahnella aquatilis*). These effects increase the expression of genes that contribute to the secretion of acid phosphatase in plant growth promoting bacteria, which accelerates the hydrolysis of organophosphates and provides a mechanism for the host to obtain more P (Zhang et al. 2018).

Two high affinity monosaccharide transporters, *RiMST5* and *RiMST6*, were identified from *R. intraradices* (Lahmidi et al. 2016). Their expression levels and the localization of the *RiMST5* and *RiMST6* proteins vary among different host plants. The expression of *RiMST*

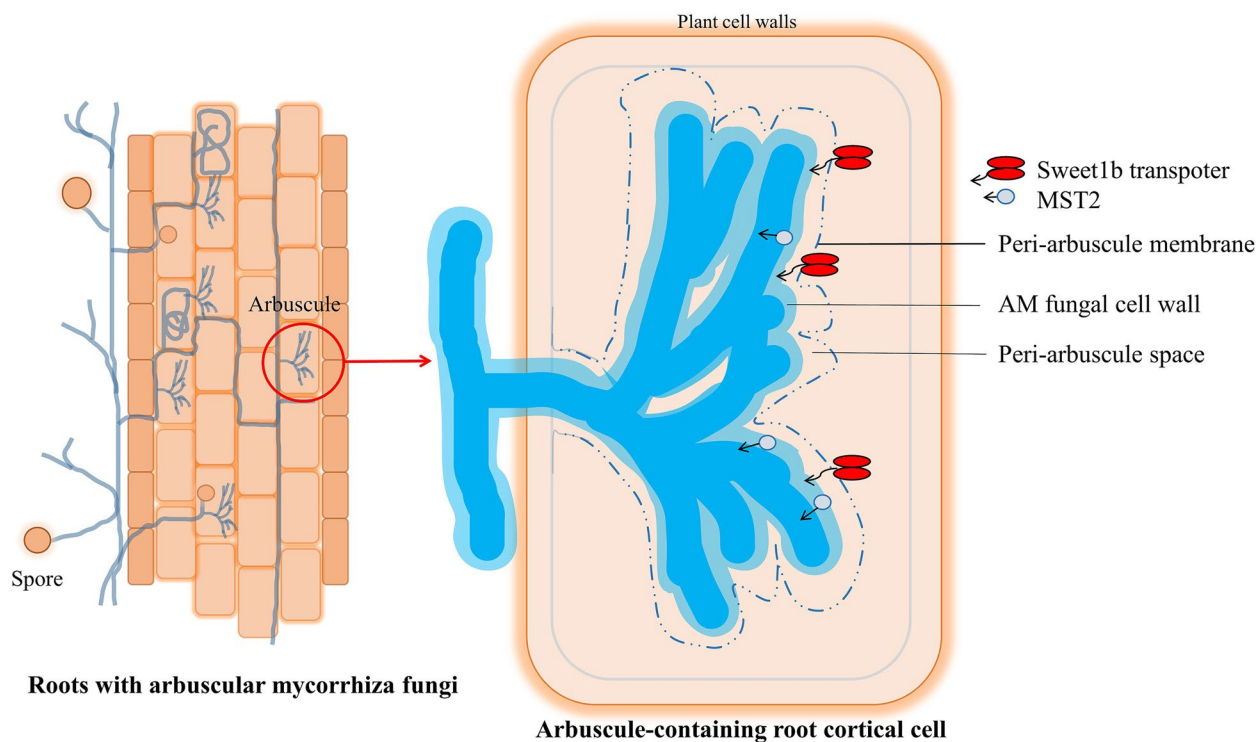


Fig. 2 Model for SWEET1b function in the root arbuscule-containing cortical cells of *Medicago truncatula* plants. Adapted from An et al. (2019) with major modifications. AM, Arbuscular mycorrhizal; MST, monosaccharide transporter; SWEET1b, sugars that will eventually be exported transporters

genes is responsive to light intensity (e.g. shading and dark treatments), which provides evidence that the MSTs of AM fungi help to enhance fungal sugar content during carbon-limiting conditions (Lahmidi et al. 2016). In addition, *RiMST2* was expressed at higher levels in mycorrhizal roots than in extraradical hyphae, which indicates that *RiMST2* is a major component of the hexose uptake machinery in *R. intraradices* (Lahmidi et al. 2016).

Identification of sugar-associated genes expressed during mycorrhization

RNA-seq technology helps researchers to identify genes that are differentially expressed during mycorrhization—including genes that encode sugar transporters. Prolonged or intense exposure to heat or chemical stress led to increases in trehalose in the hyphae of *G. intraradices* and was associated with transiently induced expression of *trehalose-6-P phosphatase 2 (GiTPS2)*, which encodes trehalose-6-P phosphatase (Ocon et al. 2007). The application of a 1 mg/mL chitosan solution to mycorrhizal tomatoes significantly reduced the transcription level of *Chi3* (a defense-related gene for AM fungal growth) in roots but had no significant effect on *Chi9* (El Amerany et al. 2020). The RNA-seq technology was used to analyze sunflower roots on 4 and 16 d of mycorrhization and detected the expression of 7 genes

that encode glycotransporters, 4 genes that encode glycogen-related genes and 4 genes that encode trehalose synthase on 16 d, which are related to glycolipid transport and metabolism (Vangelisti et al. 2020). However, the expression of these genes was not detected 4 d after inoculation with *R. irregularis*. These data indicate that sugar-associated gene expression is induced during mycorrhization.

The RNA-seq technique also revealed that the AM regulation of sugar metabolism is important for the enhancement of physiological activities, such as the enhancement of growth, stress tolerance and lateral root formation. After infection with *Botrytis cinerea* (*B. cinerea*) in *R. irregularis*-colonized tomato plants, increased expression levels of the gene encoding β -amylase 1 (responsible for starch hydrolysis) led to an increase in the rate of starch degradation, which initiates callose biosynthesis and thus, facilitates resistance to *B. cinerea* (Sanmartín et al. 2020). It was identified that 32 DEGs associated with glucose metabolism in the lateral roots of trifoliolate orange and the upregulated expression of 24 genes during mycorrhization (Chen et al. 2017). The upregulated genes mainly encoded polygalacturonase and chitinase, which is consistent with mycorrhiza-regulated sugar metabolism influencing lateral root formation. In fact, the allocation of glucose and sucrose to roots in AM

plants is associated with root morphological parameters and depends on the AM fungal species (Wu et al. 2011).

Interestingly, some DEGs associated with sugar metabolism and translocation, such as *GmSWEET6*, *GmSWEET15*, and *Glyma.17G227900*, were upregulated only when plants were inoculated with *R. irregulare* and *Glomus aggregatum* (*G. aggregatum*) and were synchronized with the positive growth response induced by AM fungi (Zhao et al. 2018). Among these genes, only the *GUS* reporter gene expressed by the *GmSWEET6* promoter was highly expressed in the arbuscule-containing cortex cells of roots (Zhao et al. 2018). These data are consistent with the mycorrhiza-specific induced expression of *GmSWEET6*, which remains to be explored. In conclusion, after forming a symbiotic relationship with plant roots, AM fungi affect the transport and utilization of sugar by regulating the expression of sugar-associated genes in the host and thus, participate in various functions. However, the functions of particular AM fungus-induced genes that were identified in transcriptome sequencing experiments remain to be clarified.

Conclusions

Sugars are an essential source of chemical energy in plants. In plants experiencing adversity, sugars also contribute to osmoregulation and signal transduction. Sucrose is the principal sugar transported from source to sink organs to meet growth requirements. Mycorrhizal plants transport approximately 20% of their photosynthetic products into the AM fungi. To facilitate the transfer of sugars between AM fungi and plants, during AM fungal colonization, the expression of genes that encode sugar transporters is upregulated. AM fungi enhance osmoregulation by accumulating sugars. In addition, AM fungi can promote their own accumulation of sugars to induce growth of mycelia by up-regulating the expression of genes that encode sugar transporters. We know most about the effects of AM on sugars at the physiological level. We know less about genes associated with sugar metabolism from applied research and plants experiencing adversity. Although our knowledge of sugar content, such as sucrose content, in AM plants is increasing, a deeper understanding of the influence of small sugars, such as inositol and alginose, is needed. More research on the specialized functions of sugars is also needed. Future research on the relationship between AM fungi and plant sugars should focus on the following:

1. Transition from physiological observations to molecular mechanisms used by sugars to influence interactions between AM fungi and plants.
2. Determine whether the AM fungi-regulated expression of genes encoding sugar-associated enzymes is involved in the response to adversity and whether manipulation of these genes can enhance stress tolerance.
3. Although the effects of AM on sucrose and glucose are well studied, other sugars, such as inositol and trehalose require more attention.
4. Isotopic labeling of carbon will reveal how carbon is transported from the host leaves to the root cortex cells containing arbuscules, how mycorrhizal carbon is distributed and transported in the mycorrhiza, and how mycorrhizal carbon is released into the soil as glomalin, affecting the sequestration of soil organic carbon (SOC).
5. Additional monosaccharide transporters need to be identified from the known genomes of AM fungi and analyzed for potential functions in sugar transport.

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Authors' contributions

QSW conceived of the idea, YJW collected and analyzed the literature, YJW drew the figures, YJW wrote the first draft of the manuscript, and QSW reviewed and prepared the final draft of the manuscript. Both author(s) read and approved the final manuscript.

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