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Plant carbon nourishment of arbuscular mycorrhizal fungi

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Reciprocal nutrient exchange between the majority of land plants and arbucular mycorrhizal (AM) fungi is the cornerstone of a stable symbiosis. To date, a dogma in the comprehension of AM fungal nourishment has been delivery of host organic carbon in the form of sugars. More recently a role for lipids as alternative carbon source or as a signalling molecule during AM symbiosis was proposed. Here we review the symbiotic requirement for carbohydrates and lipids across developmental stages of the AM symbiosis. We present a role for carbohydrate metabolism and signalling to maintain intraradical fungal growth, as opposed to lipid uptake at the arbuscule as an indispensible requirement for completion of the AM fungal life cycle.

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Introduction

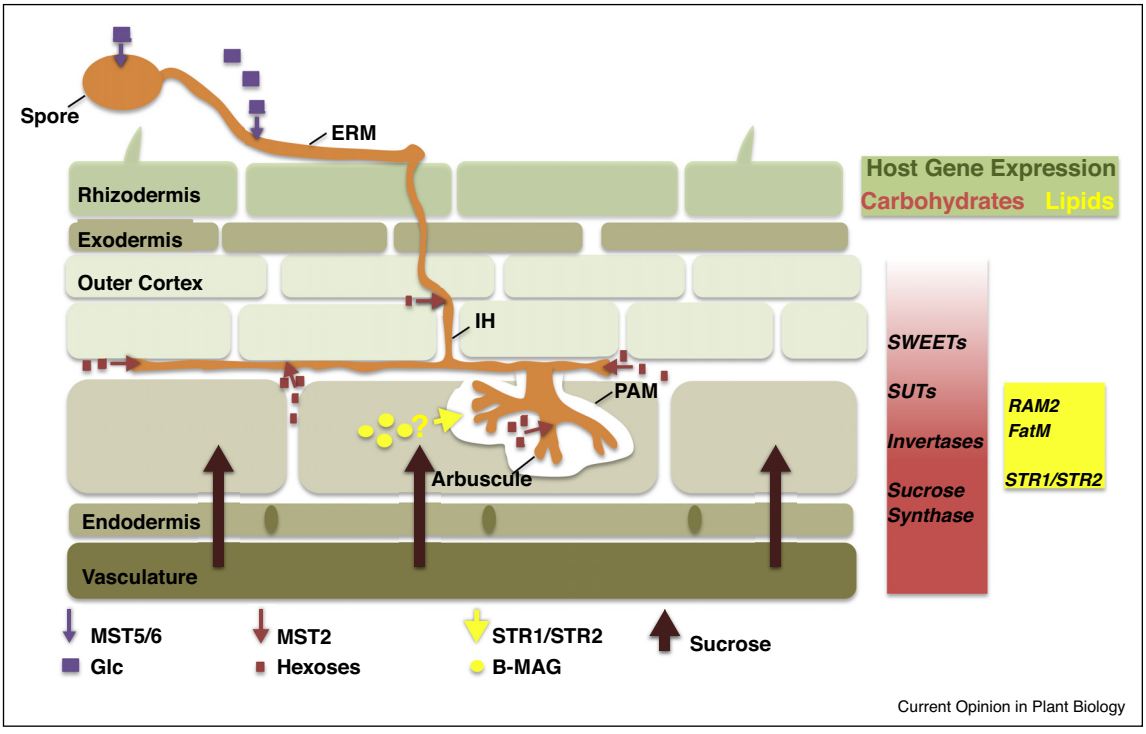
The symbiotic success in arbuscular mycorrhizal (AM) symbioses for over 400 million years has involved host–fungal transactions, underpinned by a tightly regulated reciprocal nutrient exchange based on mutual rewards. For AM fungi, forming a successful symbiosis with plants is an obligate requirement to complete their life-cycle, manifested by the production of daughter spores [1]. During the association, extensive hyphal growth occurs in the intercellular space of root epidermis and cortex tissue (intraradical mycelia, IRM), accompanied by the development of highly branched haustoria, the arbuscules, inside cortex cells. Arbuscules form by dichotomous hyphal branching while invaginating the cortex cell membrane. On a micrometer scale, an enormous symbiotic interface is created for the exchange of signals and nutrients. Concomitantly, fungal growth also extends into the soil where large extraradical mycelia (ERM) develop that are involved in the uptake of minerals and the generation of spores.

In the absence of a host, AM fungal spores contain sufficient resources to support modest hyphal growth, whereas plant derived organic carbon (C) is thought to fuel intense fungal proliferation and spore formation [2]. Sugars as the key symbiotic C currency transferred from plant to fungus was suggested over 40 years ago [3]. Indeed, intraradical hyphal (IH) uptake of C in the form of hexoses, particularly glucose, was later confirmed by *in vivo* NMR spectroscopy, radiorespirometry and stable isotope labelling [4–6]. Once acquired by IRM, hexoses can be converted into glycogen and lipids for long distance transport and storage in vesicles and spores inside and outside mycorrhizal roots, respectively. An emerging body of evidence more recently proposes fatty acids (FA) as an additional form of plant-delivered C [7••,8,38••]. Here, we review knowledge on fungal carbon requirements across the developmental stages of the symbiosis and propose that uptake of FA at the arbuscules is required for the completion of the fungal life-cycle.

A role for carbohydrates in sustaining fungal growth during AM symbiosis

AM fungi acquire sugar in the form of hexoses, predominantly glucose [6,9,10]. The first sugar transporter reported from a glomeromycotan fungus was the monosaccharide transporter from *Geosiphon pyriformis*, GpMST1, which engages in symbiosis with the cyanobacterium *Nostoc punctiforme* [11]. The genome of *Rhizophagus irregularis* (formerly *Glomus intraradices*) contains related *Monosaccharide Transporters* (*RiMSTs*) with different spatial expression patterns and substrate specificity. While *RiMST2* is highly expressed *in planta*, *RiMST5* and *RiMST6* transcripts accumulated preferentially in germinated spores (Figure 1, Table 1A, [12•,13]). RiMST5 and RiMST6 are proton co-transporters with high specificity for glucose, indicating the possibility of glucose acquisition during spore germination [13]. In contrast, RiMST2 has promiscuous substrate specificity for hexoses with preference for xylose and is present in extraradical mycelium (ERM), around IH and arbuscules during the interaction with potato and *M. truncatula* [12•], indicating that sugar uptake in AM fungi might involve IH in addition to arbuscules, which is supported by earlier radiotracer-based observations (Figure 1, [6]). Furthermore, addition of xylose induced *RiMST2* expression in

Figure 1



Summary of fungal carbon nourishment during AM symbiosis.
AM fungal colonization results in increased expression of source-to-sink metabolizing genes *Sucrose Transporters* (*SUTs*) and *Sugars Will Eventually Be Exported Transporters* (*SWEETs*) as well as genes encoding sucrose metabolizing enzymes *Sucrose Synthase* and *Invertases*. Fungal uptake of apoplastic hexoses are likely mediated by *Monosaccharide Transporter2* (*MST2*) that is induced around intra-radical hyphae (IH) and arbuscules. Upregulation of *MST5/6* in spores and extra-radical mycelia (ERM) suggest that AM fungi may also be able to take up glucose (Glc) from their surrounding. AM-conserved genes, *RAM2 and FatM* are induced in arbuscule-containing cells and are required for synthesis of the C16:0 fatty acid, β-monoacylglycerol (β-MAG). ABC transporters *STR1/STR2* that localize to the peri-arbuscular membrane (PAM) might play a role in the transport of β-MAG into the symbiotic interface from where it is taken up by the fungus and utilized for arbuscule formation.

ERM, and may therefore also represent the trigger for *RiMST2* expression *in planta* [12•]. Consistently, fungal xylose reductase genes, required for xylose catabolism, were induced during AM colonization. Functional analysis of *RiMST2* by knocking down *RiMST2* using host-induced gene silencing (HIGS) led to severely compromised fungal colonisation and abnormal arbuscule morphology [12•]. This confirmed the importance of plant carbohydrates for the maintenance of IH and arbuscule growth and moreover suggested cell wall monosaccharides as a source of organic C for AM fungi.

During fungal colonisation of roots, an increased source-to-sink flux occurs through redirection of sucrose from leaves to roots. Sucrose in- and efflux, monosaccharide uptake, or also sucrose cleaving Sucrose Synthase (SucS) and cell wall Invertases (cwInv) all regulate aspects of sugar partitioning. It is well established that distinct

Table 1A

Fungal carbohydrate transporters induced during AM symbiosis

Fungal carbohydrate transporters induced during AM symbiosis	Gene expression	Mutant description	AM symbiosis phenotype: quantitative	Mutant phenotype: arbuscule
RiMST2	IH and arbucules [12•]	HIGS KD [1]	Reduced colonization compared to WT	Senescent
RiMST5/6	Spores and ERM [13]	n.d.	n.d.	n.d.