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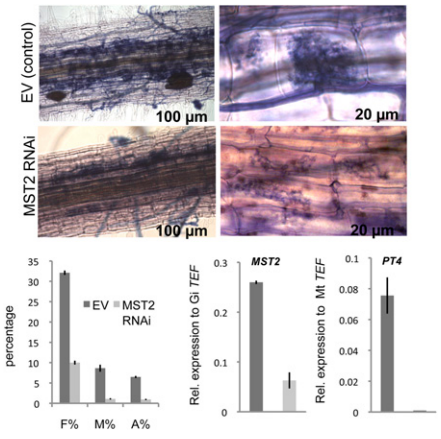
IN BRIEF

A Symbiotic Sugar Transporter in the Arbuscular Mycorrhizal Fungus *Glomus* sp

Arbuscular mycorrhizal (AM) fungi live in mutualistic symbioses with plant roots, in which the fungus provides the plant with enhanced mineral uptake from the soil, principally phosphate, in exchange for carbon to support fungal growth (reviewed in Bonfante and Genre, 2010). Phosphate status is a critical parameter controlling the development of the symbiosis, as both high phosphate levels in the soil and inactivation of symbiotic plant phosphate transporters lead to reduced fungal growth within the root. Because of its role in plant nutrition and key role in the symbiosis, symbiotic phosphate transport has been well characterized. By contrast, carbon transport to the fungus is less well understood, and fungal transporters involved have not been identified to date. Now, **Helber et al. (pages 3812–3823)** present a detailed characterization of a high-affinity monosaccharide transporter in the AM fungus *Glomus* sp DAOM 197198, which plays a major role in sugar uptake and growth and development of the fungal partner.



MST2 is essential for mycorrhizal colonization. Top panels: Mycorrhizal colonization of control and *MST2* RNA interference roots 25 d after inoculation with *Glomus intraradices* shown by ink staining. Bottom left: Estimations of mycorrhization in MST2 RNA interference hairy roots in comparison to control roots (EV); parameters are frequency (F%) and intensity (M%) of mycorrhiza and arbuscule abundance (A%). Transcript accumulation of *MST2* (bottom middle) and Mt-*PT4* (bottom right) in MST2 RNA interference and control roots measured by quantitative real-time PCR. (*Figure reprinted from Figure 6 of Helber et al. [2011].*)

A search of the first draft of the genome of *Glomus* sp DAOM 197198 (Martin et al., 2008) yielded three sequences with similarity to genes encoding monosaccharide transporters and one with similarity to a Suc transporter. One of these, named *MST2*, showed high expression during the in planta symbiotic phase of the fungal life cycle that was highly correlated with that of the the mycorrhiza-specific plant phosphate transporter gene *PT4*, which is used as an indicator of a functional AM association. In situ hybridization showed expression in arbuscules and in intercellular hyphae of the fungus colonizing the roots of *Medicago truncatula*.

The authors investigated the biochemistry and substrate specifity of MST2 by heterologous expression in a monosaccharide transport-deficient strain of *Saccharomyces cerevisiae*. The protein was found to be a membrane-localized high-affinity transporter of Glc with a pH optimum at a likely apoplastic pH at the plant-fungal interface (pH 5). It was also capable of transporting Xyl, Man, and Fru, with affinity decreasing in that order, but was unable to transport the disaccharides Suc and maltose.

Intriguingly, Xyl, but none of the other monosaccharides anaylzed, was found to induce *MST2* expression of the extraradical mycelium (ERM), suggesting that xylose could be the trigger for *MST2* expression in planta.

Experiments with radiolabeled Xyl and Glc fed to ERM cultivated in carrot root culture showed that the ERM is capable of taking up both sugars. Uptake was blocked by the presence of a protonophore, suggesting it occurs by an active proton pumping mechanism. In addition, no radioactivity was found in plant root tissue in these assays, suggesting that sugar imported by the ERM is retained for fungal use. A tight connection between *MST2* and AM symbiosis was confirmed by experiments showing that (1) a high concentration of phosphate in the medium led to rapid downregulation of *MST2* in parallel with the decline in expression of the symbiotic phosphate transporter *PT4*, and (2) knockdown of *MST2* using RNA interference led to decreased mycorrhization in *M. truncatula* hairy root culture, as measured by a decreased number of arbuscules, abnormal arbuscule morphology, and several other parameters (see figure).

This work demonstrates that the fungal sugar transporter MST2 is required for functional AM symbiosis and is likely the major transporter supplying the fungus with carbon from its plant host.

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