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Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi

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Arbuscular mycorrhizal (AM) fungi facilitate plant uptake of mineral nutrients and draw organic nutrients from the plant. Organic nutrients are thought to be supplied primarily in the form of sugars. Here we show that the AM fungus *Rhizophagus irregularis* is a fatty acid auxotroph and that fatty acids synthesized in the host plants are transferred to the fungus to sustain mycorrhizal colonization. The transfer is dependent on RAM2 (REQUIRED FOR ARBUSCULAR MYCORRHIZATION 2) and the ATP binding cassette transporter–mediated plant lipid export pathway. We further show that plant fatty acids can be transferred to the pathogenic fungus *Golovinomyces cichoracerum* and are required for colonization by pathogens. We suggest that the mutualistic mycorrhizal and pathogenic fungi similarly recruit the fatty acid biosynthesis program to facilitate host invasion.

About 80 to 90% of plant species are colonized by arbuscular mycorrhizal (AM) fungi, which facilitate the uptake of mineral nutrients such as phosphate and nitrogen from the soil (*1*–*3*). Evidence suggests that the fungus receives carbon from the plant in the form of sugars (hexoses) in return (*4*–*7*); however, plants could transfer alternative carbon sources. The AM fungal genome of *Rhizophagus irregularis* lacks genes encoding type I multidomain fatty acid synthases (FASs), which synthesize palmitic acid (C16:0) in fungi (*8*–*10*). Although the mitochondrial type II FAS genes are present in *R. irregularis*, the genes support production of octanoic acid (C8:0) rather than palmitic acid (*10*–*12*).

To investigate whether AM fungi can synthesize fatty acids de novo, we performed isotope labeling experiments. Isotope ratios can be used as tracers to understand complex substrate metabolism (fig. S1A) (*13*). We used the *R. irregularis*–carrot (*Daucus carota*) root monoxenic culture system in divided petri plates, which prevents diffusion of nonvolatile solutes between compartments (fig. S1, A to C) (*4*, *5*, *7*). When isotopically labeled (1,3-^{13}C)glycerol was added to the fungal extraradical mycelium (ERM) (fig. S1B), we found that 10.52 ± 2.02% and 3.47 ± 0.53% of glycerol moieties in the ERM and the intraradical mycelium/root compartment (IRM/R), respectively, were labeled at the fragment containing C1 or C3 atoms (Fig. 1A), indicating that glycerol absorbed by the ERM can be transferred between it and the IRM/R. Also, 6.54 ± 0.73% and 1.01 ± 0.21% of glucose moieties in the ERM and IRM/R, respectively, were labeled at the fragment containing C2 and C3 atoms (Fig. 1A), indicating that fungi can synthesize glucose from glycerol. We did not detect an enrichment of labeling in fatty acid moieties (Fig. 1A). Similar results were observed when (2-^{13}C)glycerol was supplied in the ERM (fig. S1D). Thus, the AM fungus *R. irregularis* cannot synthesize fatty acids de novo from glucose and glycerol.

To follow carbon transfer during AM symbiosis, we added (1,3-^{13}C)glycerol to the IRM/R in the *R. irregularis*–carrot root culture system (fig. S1C). If sugars are the sole form of carbon transferred from the plant to the AM fungus, we would expect higher or equal labeling ratios of sugars in the IRM/R relative to the ERM when labeled glycerol is supplied in the IRM/R. We observed 7.62 ± 0.35% of glucose moieties in the IRM/R labeled at the fragment containing C2 and C3 atoms, one-fourth that in the ERM, where 28.31 ± 0.71% of glucose moieties were labeled at the fragment containing C2 and C3 atoms (Fig. 1B). (2-^{13}C)glycerol supplied in the IRM/R (fig. S1E) had similar effects. The greater enrichment of ^{13}C that we detected in glucose in the ERM compared with that in the IRM/R (Fig. 1B) suggests that glycerol is not directly metabolized to glucose within plant roots for transfer to the fungus. Instead, these data suggest that glycerol might be incorporated into the backbone of glycerolipids that are transferred to the ERM, then converted to glucose by gluconeogenesis in the fungus.

Several fatty acid biosynthesis genes, including those encoding pyruvate kinase (*MtPK*), ketoacyl-ACP synthase II (*MtKAS II*), ketoacyl–acyl carrier protein (ACP) reductase (*MtKAR*), enoyl-ACP reductase I (*MtENR I*), and acyl-ACP thioesterase B (*MtFatM*, also known as *FatB* in *Arabidopsis*), were induced by mycorrhizal fungal infection in *Medi-*