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Evolution of lipid transfer from plants to fungi allowed plants to colonize land

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FL-OH product, 4C7SFL-OH, even at a 25% state of charge. The authors also studied the comproportionation reaction by combining 4C7SFL and 4C7SFL-OH, and they detected a small amount of the $[4C7SFL]^-$ radical by electron paramagnetic resonance spectroscopy. The FL^- generated from the comproportionation can be used for electrochemical discharge. These studies suggest that an equilibrium exists between FL^- , FL, and FL-OH, and also favors the disproportionation.

The formation and cleavage of the benzylic C-H bond of FL in the disproportionation and comproportionation reactions are likely regulated by subtle proton-coupled electron transfer processes that are subject to further study. The singly protonated species, $FL-O^-$, may be the final charged state and involves the chemical reactions under the strong alkaline condition. In addition, the reduction of ketones to alcohols typically involves a catalyst (12), so the reversible, uncatalyzed hydrogenation of FL represents an unusual two-electron storage mechanism for flow battery applications and is mechanistically different from the direct electrochemical two-electron reduction of viologen and anthraquinone anolytes (2).

The work by Feng *et al.* expands the selection of stable organic anolytes and serves as a good example of rational molecular engineering to develop durable electrolyte materials. However, a large excess of the $K_4Fe(CN)_6/K_3Fe(CN)_6$ catholyte was needed in the flow battery tests because of the long-term instability of ferro- and ferricyanide in alkaline solutions (13). Thus, developing catholyte molecules with durabilities and capacities comparable to those of fluorenone, viologen, and anthraquinone anolyte molecules is urgently needed to fully unleash the energy storage potential of aqueous organic redox flow batteries. ■

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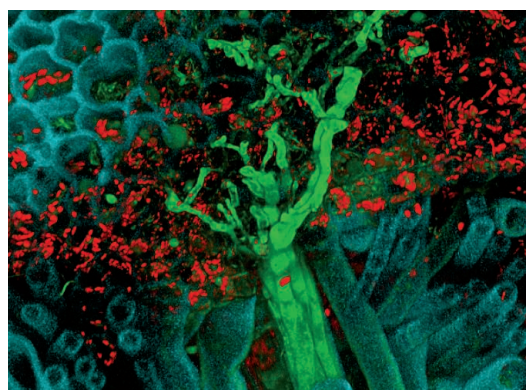
SYMBIOSIS

Plant lipids enticed fungi to mutualism

Evolution of lipid transfer from plants to fungi allowed plants to colonize land

By Harro J. Bouwmeester

The migration of plants from water to newly emerged land some 450 million years ago required plants to acquire a number of crucial new traits. Fossil records provide compelling evidence that one of these traits is the symbiosis (or mutualism) between these early land plants and arbuscular mycorrhizal (AM) fungi. On page 864 of this issue, Rich *et al.* (1) show that the primitive land plant *Marchantia paleacea* produces lipids that are transferred to the fungus and that this process is essential for a functional symbiosis (see the image). This localized lipid biosynthesis also occurs in higher plants that engage in symbiosis with AM fungi (2, 3), but not in algae, suggesting



The confocal microscopy image shows a symbiotic fungus (*Rhizophagus irregularis*) colonizing the liverwort *Marchantia paleacea* (plant cell walls, cyan; chloroplasts, red; fungus, green).

that this process evolved 450 million years ago, allowing plants to colonize land, and is conserved across the plant kingdom.

The symbiosis of plants with AM fungi is so crucial for plant growth on land that about 80% of land plants engage in it (4). The plant allows AM fungi to enter its roots and form nutrient exchange structures called arbuscules in its cells (see the figure). Outside the root, the fungal hyphae grow into the soil, up to 30 cm from the plant root, where they

can take up water, phosphorus, nitrogen, and other elements that the plant cannot reach (4). For a long time, it was assumed that plants, in return for the resources supplied by the fungus, provided carbohydrates from photosynthesis to the fungus. Only recently, it was discovered that in addition to carbohydrates, plants also supply lipids to the fungus (2, 3). To investigate how old this mechanism is, Rich *et al.* used an elegant approach: a comparison of RNA sequencing gene expression data on the AM fungal interaction in the primitive *M. paleacea* with data of AM fungal interactions in higher plants. With this comparison, the authors show that orthologs of many of the known higher-plant symbiotic genes are also expressed in *M. paleacea* upon AM fungal colonization, confirming conservation across 450 million years of plant diversification [also see (5)]. Rich *et al.* report that this includes genes that have been shown in higher plants to be responsible for lipid exchange from the plant to the fungus, such as the lipid biosynthesis-related *REQUIRED FOR ARBUSCULAR MYCORRHIZATION 2 (RAM2)* and the lipid transporter *STUNTED ARBUSCULE 1* and *2 (STR1* and *STR2)* (see the figure). With a number of experiments, they subsequently show that *M. paleacea* is indeed producing lipids and that they are essential for the symbiosis with AM fungi.

Lipid biosynthesis and transfer are not the only evolutionarily conserved processes that occur in *M. paleacea* upon colonization by AM fungi. Rich *et al.* also report orthogroups of genes involved in strigolactone biosynthesis that show a conserved response across the plant kingdom, including in *M. paleacea*. Strigolactones are rhizosphere signaling molecules that have been shown to play a key role in the colonization of roots by AM fungi (6) and are regularly claimed to have been instrumental for terrestrialization (7) (see the figure). Rich *et al.* do not go into detail on these genes, but it can be safely assumed that they refer to *CAROTENOID CLEAVAGE DIOXYGENASE 8a* and *8b (CCD8a* and *CCD8b)*. The enzyme

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CCD8 catalyzes the second dedicated step in strigolactone biosynthesis (8). Of the two homologs, only *CCD8a* expression is notably up-regulated upon AMF colonization. In higher plants, this pattern is less clear; *CCD8* expression is up-regulated in rice, petunia, and *Medicago truncatula* but not in sunflower and poplar. Rich *et al.* list other carotenoid biosynthesis-related and cytochrome P450 genes that are potentially involved in strigolactone biosynthesis. Some of these are also up-regulated under AM fungi colonization in *M. paleacea*, but a consistent pattern in both *M. paleacea* and the higher plants is lacking. Recent evidence suggests that strigolactone biosynthesis is up-regulated upon AM fungal colonization (9), whereas other studies show that AM fungal colonization results in reduced exudation of strigolactones (10).

Intriguingly, Rich *et al.* also describe an ABC transporter (Marpal_utg000130g0170881), which has orthologs in all the higher plants included in this study, with up-regulated expression under AM fungal colonization across the plant kingdom. The only unambiguously identified strigolactone transporter so far is the petunia ABC transporter *PLEIOTROPIC DRUG RESISTANCE 1 (PDR1)*, with expression that is up-regulated under AM fungal colonization and was shown to be required for AM fungal symbiosis (11). It would be very exciting if this *M. paleacea* ABC transporter turns out to be a strigolactone transporter as well.

Rich *et al.* then focus on the processes that maintain the symbiotic relationship after it has been established, in particular, the transcriptional regulation of lipid biosynthesis. They identify two transcription factors that seem to be highly conserved across the plant kingdom and coincide with terrestrialization: *WRINKLED* (*WRI*) and *REQUIRED FOR ARBUSCULE DEVELOPMENT 1 (RADI)*. Overexpression of *WRI* in *M. paleacea* resulted in increased expression of fatty acid biosynthesis-related genes, whereas inactivation of *WRI* resulted in severely compromised AM fungi colonization.

Higher plants contain multiple paralogs of *WRI*, of which several function, apparently

redundantly, in symbiosis (12). *M. paleacea* contains only one copy of *WRI*, and extensive orthology searches led Rich *et al.* to conclude that *WRI* (and *RADI*) are absent from the nonsymbiotic algae. The likelihood that recruitment of *WRI* and *RADI* occurred specifically for this purpose is further strengthened by the observation that fatty acid and lipid biosynthesis also occur in algae (13) but are not used for symbiosis. In all, the findings of Rich *et al.* show that these transcription factors specifically evolved to facilitate symbiosis, which was required for terrestrialization.

The presence of a single copy of *WRI* in *M. paleacea* suggests that the multiple paralogs of *WRI* in higher plants (12) have evolved from a single ancestor. One of these orthologs, *WRINKLED1*, is involved in the

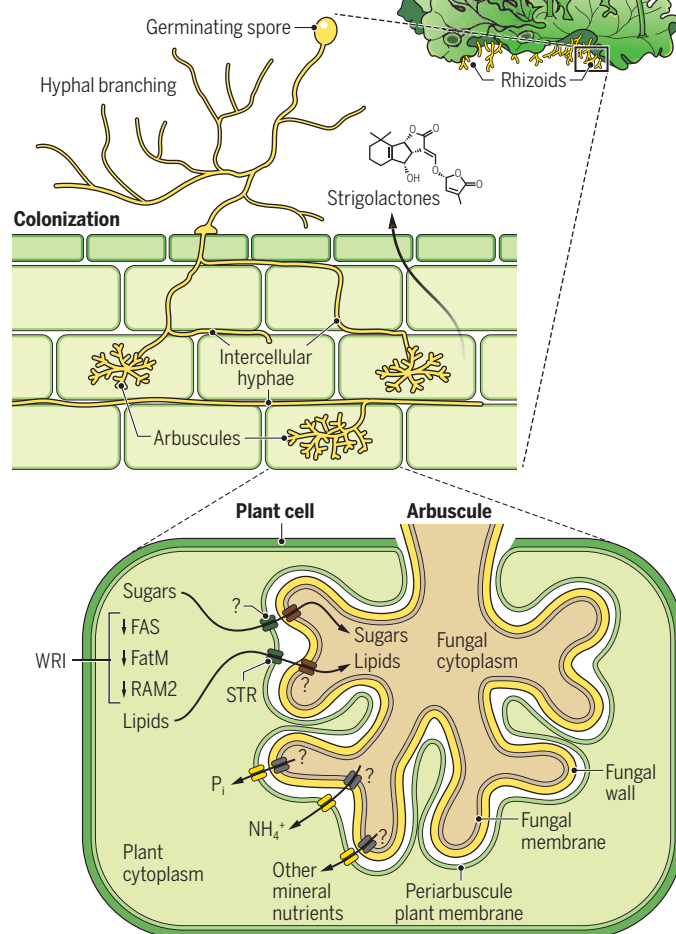
regulation of lipid biosynthesis in seeds (14). Evidently, duplication and neofunctionalization of the ancestral *WRI* in higher plants not only resulted in the apparent specialization of its function in symbiosis but also resulted in the loss of its symbiotic function to allow for the large accumulation of lipids in the seeds of seed plants.

With their study, Rich *et al.* highlight the importance of the mutual exchange of resources between plants and AM fungi as a driver of the symbiosis. They show that plants have evolved transcriptional regulators, such as *WRI*, to allow for the production of lipids for the AM fungi in the cells where the AM symbiotic organ, the arbuscule, has formed. The further radiation of *WRI* during the evolution of higher plants confirms the importance of this process for symbiosis with AM fungi.

It will be of interest to see why multiplication of *WRI* arose in higher plants and what the specific roles and fitness benefits of these paralogs might be. The datasets generated by Rich *et al.* could also provide information about other symbiotic genes that may have evolved to allow terrestrialization. This could, for example, further illuminate the presumptive role of strigolactones in the terrestrialization process. ■

Evolution of lipid transfer from plants to fungi

Plants colonized newly emerged land about 450 million years ago. Rich *et al.* show that lipids are traded with symbiotic fungi for phosphorus and nitrogen by the liverwort *Marchantia paleacea*. This process was essential for successful colonization of land.



FAS, type I fatty acid synthase; FatM, acyl-ACP (acyl carrier protein) thioesterase required for arbuscular mycorrhizal symbiosis; P_i, inorganic phosphorus; RAM2, REQUIRED FOR ARBUSCULE MYCORRHIZATION 2; STR, STUNTED ARBUSCULE; WRI, WRINKLED.

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