Special relationship between fungi and plants may have spurred changes to ancient climate

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Look at a plant, and you're probably also looking at a fungus. More than 80% of land plants partner with fungi to help those plants extract nutrients—nitrogen and phosphorus—from the ground (1, 2). The plants return the favor with carbon from their photosynthesis. Biologists suspect that this partnership was a major factor in allowing plants to move from water to land about 470 million years ago. But exactly how the partnership arose remains a mystery.

Only recently have experiments shown that modern analogs of those plants and fungi indeed trade carbon for nutrients. Researchers are also finding that fungal partners are more diverse than expected. Partners differ in how much soil nutrients they offer up in return for carbon. And while some partnerships thrive in the modern atmosphere, others do best at the higher carbon dioxide levels. These findings could therefore help shape our picture of the ancient atmosphere and possibly the future climate.

Carbon for Phosphorus

For decades, researchers assumed that early land plants partnered with the same fungi they see most often in

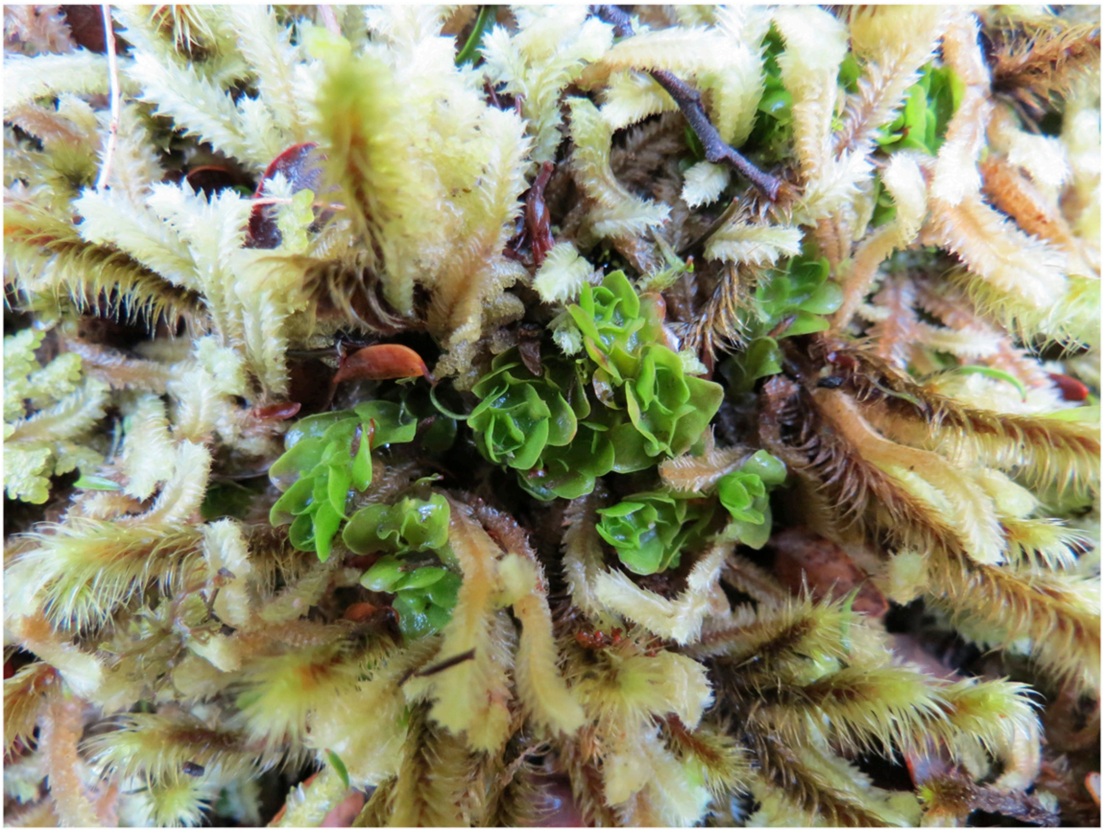

Fig. 1. Dating back 480 million years, the liverwort plant *Treubia pygmaea* contains mucoromycote endophytes. Here it is growing in situ over other liverworts, at Rahu Saddle, South Island, New Zealand. Image courtesy of Jeff Duckett and Silvia Pressel (Natural History Museum, London, UK).

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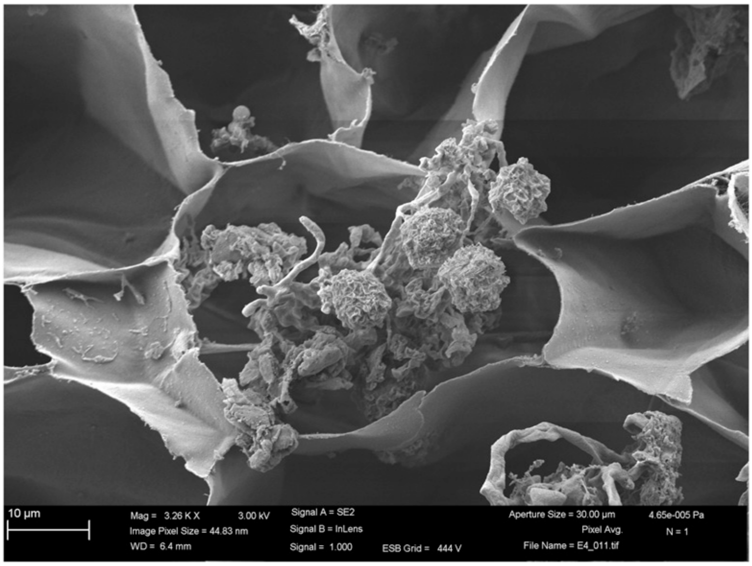

Fig. 2. **The liverwort plant *Treubia lacunosa* has fungal lumps (shown here in scanning electron micrograph) that are unique to the mucoromycote fungus. They are found on the earliest liverwort lineage, the Haplomitriopsida. Image courtesy of Jeff Duckett and Silvia Pressel (Natural History Museum, London, UK).**

modern plants, now known as Glomeromycotina. "We call them 'gloms,'" explains Katie Field, a plant physiologist at the University of Leeds in the U.K.

The fungus forms branched, tree-like structures within plant cells and sends out fibers that break up soils and suck out nutrients. This ability likely allowed early plants, which lacked their own roots, to colonize the land (3). Fossils of some of the earliest land plants have similar-looking fungi in close association, and to this day, gloms continue to associate with plants.

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>
> —Christine Strullu-Derrien

To investigate this theory of an early partnership, Field is exploring how fungi and plants interacted in the Paleozoic era when plants made the leap to land—before they proliferated, altering ecosystems and possibly helping to boost atmospheric oxygen concentrations. She and her colleagues grow liverworts, the closest modern counterpart to the first terrestrial plants, in wardrobe-sized chambers. The researchers alter carbon dioxide levels to mimic ancient climates. To identify phosphorus that comes into the plant via the fungus, the researchers put radioactive phosphorus in a "fungus-only zone"—soil-filled cylinders with mesh-covered holes that the fine threads of the fungus can reach, but plant parts can't. To identify carbon the plant shares with the glom, the team uses radioactive carbon dioxide.

Field and her team showed that liverworts and gloms do indeed trade phosphorus for carbon. According to their experiments, the process takes place both at carbon dioxide concentrations of 440 parts per million (roughly equivalent to today's) and at the 1,500 ppm that prevailed on Earth 470 million years ago. But at 1,500 ppm, the exchange is much more efficient for the plant; it gains 10–100 times as much phosphorus per unit of carbon as it does at 440 ppm (4).

The work, published in 2012, provided relatively direct evidence of a mutualistic association between ancient plants and fungi, says Christine Strullu-Derrien, a paleomycologist at the Natural History Museum in London, who was not involved in the study. Of course, experiments with modern plants can't prove that those plants' ancestors engaged in the same kind of tit-for-tat symbiosis. "It's the best we can do, at the moment," says Field, "unless we find a time machine."

A New Partner

Other researchers have shown that the fungus–plant story was more complicated than once believed. In 2011, just as Field was writing up her findings, botanist Jeff Duckett and colleagues at the Natural History Museum reported they had found a liverwort with a funny-looking fungal associate. Instead of tree-like structures, the fungus formed spheres and coils within the plant. The researchers assumed they had discovered an unusual sort of glom, and for identification they sent samples to Martin Bidartondo, a molecular ecologist at Imperial College London and the Royal Botanic Gardens in Kew, U.K. However, all Bidartondo's efforts to find glom genes came up empty. He decided to widen his scope and found genetic sequences from another sort of fungus, the Mucoromycotina ("mucs" for short) (5).

The finding was a surprise for the field, says Duckett: "It means we're looking at a whole new type of fungal symbiosis in land plants." Bidartondo has since found mucs, and sometimes mucs and gloms together, in other modern plants (5–7), while Strullu-Derrien et al. (8) reported a muc-like fossil fungus associated with a land plant in a 407-million-year-old fossil formation from Scotland. "It puts mucs in the right time frame to be important for land plant colonization," says Field.

Before Bidartondo's findings of mucs in modern liverworts, mucs were known mainly as decomposers of dead material, not partners of living plants. Did they, like the gloms, enter into a nutrients-for-carbon agreement? Field headed to New Zealand to collect some of the muc–liverwort partners. Her chamber experiments showed they did indeed make the exchange (9).

"From the plant point of view, it's a kind of winning strategy to be able to associate with one fungal partner or the other, or two of them," says Strullu-Derrien. Sprouts rely on the fungi to find them in soil, so being open to multiple partners could have given them a better chance of achieving beneficial symbiosis.

Field discovered something unexpected, though, when she compared the muc–liverwort partners under modern and ancient carbon dioxide levels. For reasons still unclear, the plants got the worse deal at ancient concentrations, taking up less nitrogen and phosphorus than they did at low, modern carbon dioxide levels—in contrast to Field's results with gloms (4, 9).

So why would ancient plants partner with mucs that were less efficient in that atmosphere, especially if gloms were an option? Field notes that even if mucs didn't provide much in the way of nutrients to the early plants, compared with gloms, mucs could have offered other benefits, such as helping collect water or aerate soil.

When mucs and gloms colonized the same liverworts, it cost the plants even more carbon but also provided them with more nutrients. Depending on the species, the trade was three or more times as efficient for the plants at modern-day carbon dioxide levels as at Paleozoic ones (10). Field isn't entirely sure what that might have meant for early land plants, but she suggests that it gives the plant flexibility in responding to a changing climate. The plants could be open to one kind of symbiosis for high carbon dioxide concentrations, another for lower ones.

Climate Control

Not only did plants have to adapt to the lowering of atmospheric carbon dioxide, it's likely they helped create that climate. Between 450 and 300 million years ago, the Earth's oxygen levels rose to about 21%, comparable to levels today—an occurrence known as the mid-Paleozoic oxygenation event. A leading hypothesis to explain the change is that as plants expanded across the land, they sucked up atmospheric carbon. Some of that carbon was stored below ground in dead plant material that ultimately turned into fossil fuels and other carbon-bearing rocks. At the same time, the plants expelled oxygen.

Benjamin Mills, a geochemical modeler at the University of Leeds and collaborator of Field's, has simulated the ancient atmosphere based on data about modern-day plant productivity. But there's a hole in those models, he says. They don't take into account the plant–fungus dynamic and what kind of access to phosphorus the early plants might have had. A good supply of phosphorus, provided by fungi such as mucs or gloms, would boost their growth and their ability to exchange atmospheric carbon for oxygen.

Based on Field's experiments, Mills tweaked his model to include phosphorus uptake. It made a huge difference. If the phosphorus mining rate by early biosphere organisms was high, as in Field's experiments with gloms, the model shows oxygen levels rising earlier and higher than if phosphorus was extracted at a lower, muc-based rate.

Researchers don't know which fungal symbiont dominated in the Paleozoic, leaving Mills unsure exactly how early land plants altered the atmosphere. But the work shows the fungus–plant exchange rate is relevant. "We need to start building these considerations into climate models," says Field.

Understanding how living organisms extract and use phosphorus could also make a difference in future climate models, says Mills. However, phosphorus cycles slowly, so these data are most relevant to long-term models over, say, the next 1,000 years.

Field is now investigating how plant–fungus associations could change as carbon dioxide levels rise in the near future. Bumping up the carbon dioxide concentration in her chambers to levels that might occur in a half-century or so, she's looking for effects on wheat growth. "We're seeing huge repercussions in carbon-nutrient exchange," says Field. Such insights, she adds, could eventually provide clues as to how to best feed the world's growing population in the decades ahead.

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