The threads that bind: symbiotic fungi in the garden

▲ Fruiting body of the ectomycorrhizal fungus *Thelephora terrestris*. *Robert L. Anderson, USDA Forest Service (www.forestryimages.org)*

Most people think of fungi and plants in terms of disease, but as **Alastair Fitter** explains, certain fungi are essential to plant growth. They form mycorrhizas – mutually beneficial associations with plant roots. Without this symbiosis our gardens would not be so green.

Everyone knows that a plant has leaves and flowers, and below ground its roots branch and explore the soil. Yet that picture misses an essential component as virtually all plants live with a fungus in a symbiosis called a mycorrhiza (from the Greek, meaning 'fungus root') that is essential to both partners. The plants get phosphate and some other nutrients from the fungus, and the fungus gets all its sugars from the plant. Plants gain other benefits too from the symbiosis and sustainable farming, forestry and gardening will all increasingly rely on understanding how it behaves.

Meet the ancestors

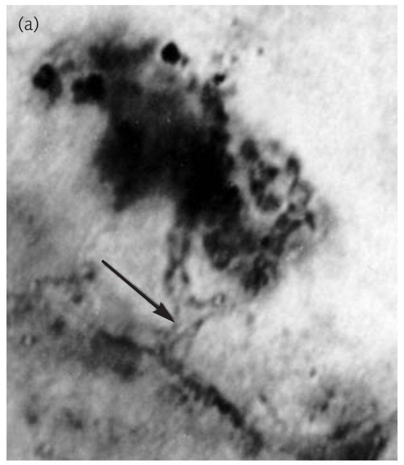
To explain why they are mycorrhizal, we need to go back to when plants first colonized the land more than 400 million years ago, in the Ordovician and Devonian periods. The first land plants had no roots; their coarse, branching rhizomes lay on or near the surface of the ground. The obvious problem for these plants was getting water, but in practice they probably grew in wet places where water may not have been the challenge. A greater difficulty was getting phosphate. The aquatic ancestors absorbed it from the water, where it was present, although very dilute. On land, a new problem emerged: phosphate ions form extremely insoluble compounds with elements such as iron, aluminium and calcium (think of bone), all of which are abundant in rocks and soil; hence phosphate ions diffuse extremely slowly into soils, taking days to move a few millimetres. Phosphate would not therefore move to the plants, and with no roots, the plants could not forage for phosphate in the soil. Instead they formed a symbiosis with fungi, whose growing network of threads (the mycelium) allowed them to explore the soil and forage for phosphate. In return the plant provided the fungus with organic compounds.

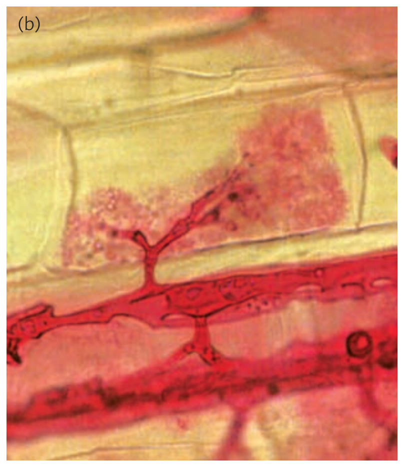
Three lines of evidence support this story: first, molecular evidence shows that this group of fungi originated at or before that distant time; second, we find plants that form this type of mycorrhiza in all branches of the evolutionary tree of land plants, showing that they must all have shared a common mycorrhizal ancestor; and most convincingly, there are fossils from Devonian rocks nearly 400 million years old that contain the fungal structures (Fig. 1a) and older Ordovician spores that are unequivocally from the group. This ancestral type is known as an arbuscular mycorrhiza, after the tiny structures called arbuscules that develop inside the cells of the root and branch like trees (Fig. 1b). The arbuscule is where the plant obtains phosphate from the fungus. Surprisingly, we still do not know where the fungus gets sugars from the plant, but it may be in the intercellular spaces where the fungal hyphae proliferate inside the root. The plant is the only source of organic carbon for the fungus, which apparently cannot grow solo; no-one has yet cultured these fungi without a plant.

Thoroughly modern mycorrhizas

The reasons for the origin of this symbiosis do not, however, explain why about two-thirds of modern plant species form arbuscular mycorrhizas. Most modern plants have well developed root systems and can obtain phosphate themselves: they can grow in pots of sterilized soil. However, the root

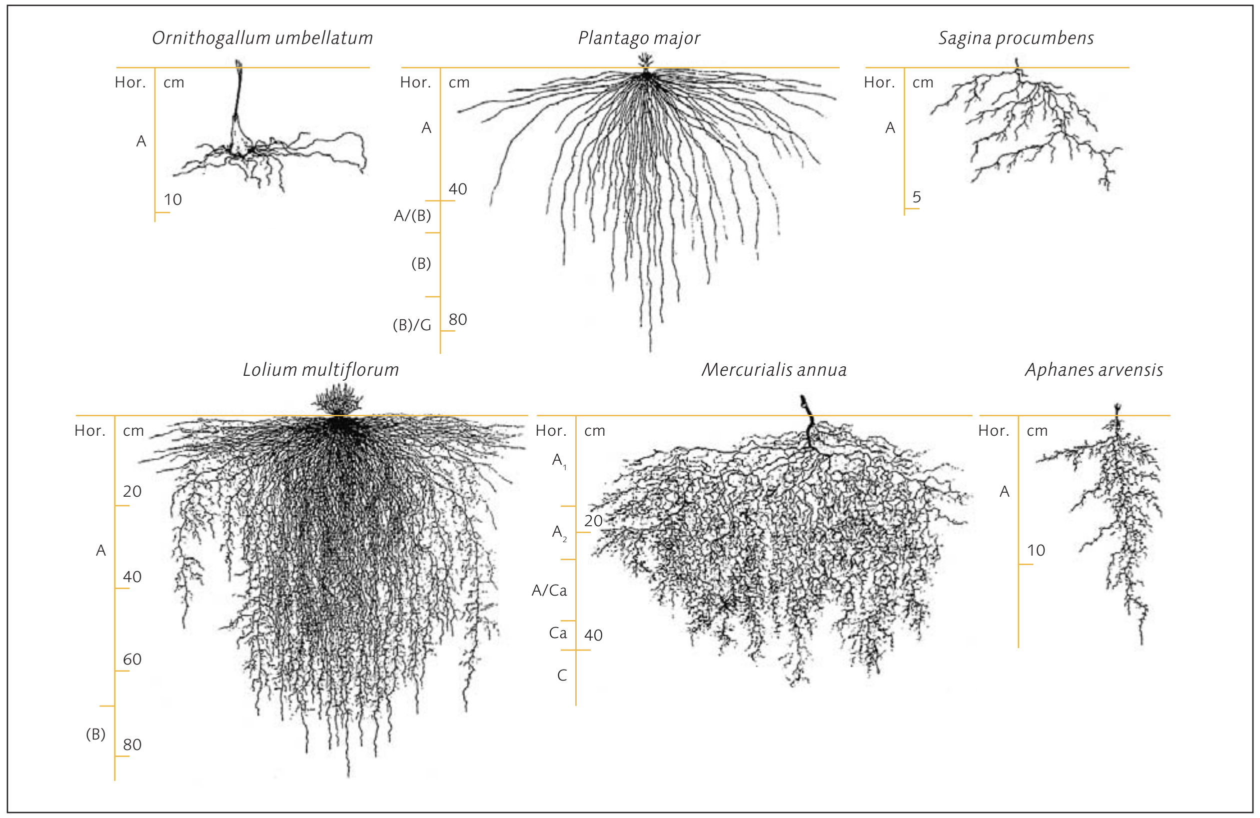
▲ Hyphae (white) of a fungus (phylum Basidiomycetes) growing on the roots (brown) of the strawberry tree (*Arbutus unedo*). *Dr Jeremy Burgess / Science Photo Library*

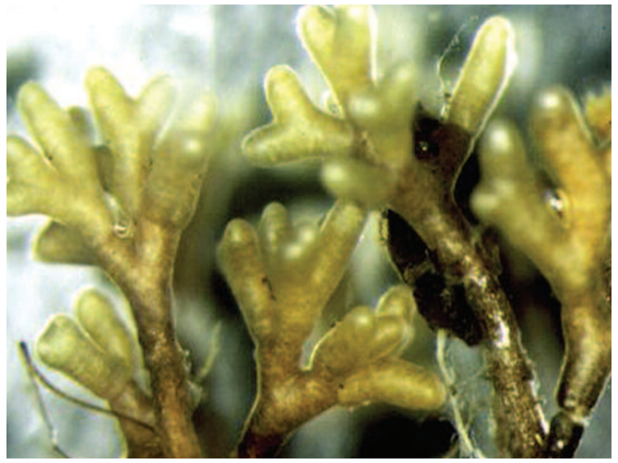




◀ Fig. 1a. Arbuscule in a fossil rhizome of *Aglaophyton major*. The arrow points to the dichotomously branching hypha that gives rise to the arbuscule, as also seen in the modern root. *Reprinted with permission from Taylor et al. (1995) Mycologia* ***87***, *567*

◀ Fig. 1b. Arbuscules of an arbuscular mycorrhizal fungus (Glomeromycota) in a modern root of *Hyacinthoides non-scripta*. *J. Merryweather*





◄ Fig. 2. Variation of root system architecture displayed by root tracings of a range of species. *Reproduced with permission from L. Kutschera (1960) Wurzelatlas mitteleuropäischer Ackerunkräuter und Kulturpflanzen (Frankfurt: DLG)*

▲ Fig. 3. An ectomycorrhizal root of pine, colonized by *Lactarius* sp. The roots are stunted and branch dichotomously; the sheath of fungal hyphae surrounding the root is clearly visible. *F. Martin*

► Fig. 4. The achlorophyllous orchid *Epipogium aphyllum* growing at one of its last British sites in 1966; it is now apparently extinct in Britain. The plant has no leaves and virtually no roots either, and is wholly reliant on a mycorrhizal fungal partner for all its nutritional requirements. *A. Fitter*

systems of plants display enormous variation in form: grasses have densely branched root systems with very fine roots (Fig. 2, bottom row), whereas plants with bulbs and corms (snowdrops, crocuses, onions) have coarse, unbranched root systems (Fig. 2, top row). Plants with dense, fine roots rely on the fungus for phosphate only in very infertile soils, whereas the bulbs and other thick-rooted species may be wholly dependent on the symbiosis except in the most heavily fertilized soils. In modern agriculture, biological solutions to problems that could be solved technologically have been unfashionable, and little attention has been paid to the potential benefits of this symbiosis. However, phosphate fertilizers are all mined unsustainably, and farmers and gardeners may therefore need to rely more on their fungal partners in future.

Modern plants with fine root systems still form mycorrhizas, even though they can often acquire phosphate themselves, because the fungi do more than forage for phosphate: they can acquire other nutrients from soil, especially the less soluble and hence less mobile ones such as zinc; they can protect roots from other fungi that may be parasitic or pathogenic; and they can bind roots to soil so improving their drought resistance. There are other functions, too, for which the experimental evidence is less strong, but even this list shows that mycorrhizal fungi are powerful partners. Consequently, they have profound impacts on plant communities, and can determine the competitive hierarchies amongst plant species.

Amazing fungi

The fungi themselves are remarkable. Their separate phylum, Glomeromycota, has only about 150 described species. However, since the taxonomy is entirely based on spore features, this paucity almost certainly hides greater diversity: again, molecular evidence points to that. They are apparently asexual, but their unique spores contain thousands of nuclei that appear to be genetically diverse, so that a single fungal mycelium may be the genetic equivalent of a population of individuals (or even possibly a community of species!). We are only just beginning to understand the basic biology of these organisms, even though they are among the most abundant creatures on earth.

Ectomycorrhizas

There is no way to tell whether a plant is symbiotic with an arbuscular mycorrhizal fungus just by looking at it. You need to stain the roots to reveal the fungal structures, though under a microscope you can also see hyphae around the root. However, this is not the only form of mycorrhiza. Later in evolution, a new mycorrhizal symbiosis emerged: this one is visible to the naked eye, because the fungus changes the way the roots develop, and the resulting stubby, often branched root tips, coated with fungal hyphae, are very distinctive, hence the name ectomycorrhiza (Fig. 3). The ectomycorrhizal symbiosis seems to have evolved at least twice, in each case with woody plants – first with pines and their relatives, and later with woody flowering plants, such as oaks, beeches and birches (Fagales). The same fungi are involved in each case, and they are very different from those that form arbuscular mycorrhizas. Ectomycorrhizal fungi are almost all Basidiomycota or Ascomycota, often forming well known and distinctive fruiting bodies: fly agaric (*Amanita muscaria*) is an ectomycorrhizal associate of birch and pine.

Ectomycorrhizas function similarly to arbuscular mycorrhizas: the fungus explores soil and obtains nutrients that it exchanges for sugars with the plant. However, ectomycorrhizal fungi can be grown in pure culture, without a plant, because they can decompose and obtain nutrients – especially nitrogen – directly from organic materials. Without this direct access to nutrients, plants rely on other fungi and bacteria to break down the materials and release them, for which they must compete with other microbes. The ectomycorrhizal symbiosis seems to have evolved as an adaptation to growing in ecosystems where plant litter accumulates because decomposition (and hence the nitrogen cycle) is slow, leading to nitrogen deficiency. As far as we know, arbuscular mycorrhizal fungi cannot directly breakdown organic matter, and are not heavily involved in increasing the uptake of nitrogen, of which the ionic forms, nitrate and ammonium, are generally quite soluble in soils. Nowadays, ectomycorrhizal plants dominate forests in the temperate and boreal zones, whereas trees with an arbuscular mycorrhizal symbiosis are found in most tropical forests, where decomposition and nitrogen cycling are rapid and litter does not accumulate.

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Other symbioses

These two types of mycorrhiza are the commonest and most important, whether in natural communities or in managed systems, such as farms, forestry and gardens. However, there are many other root–fungus symbioses, generally confined to particular groups of plants, which suggests that they have evolved recently. One is with heathers and their allies (Ericales). This symbiosis is with a group of fungi that are especially effective at breaking down organic materials for nitrogen. Heathers grow typically in soils where peat forms, which shows that decomposition has almost ceased and that the nitrogen cycle has also ground to a halt. Again, the symbiosis works as an exchange: the heather gets nitrogen and the fungus gets sugars.

Orchids too form their own mycorrhiza, but a very odd one: the orchid is parasitic on the fungus, shown most clearly in orchids that form no chlorophyll (Fig. 4). Once described as saprophytes, suggesting that they live off dead organic matter, these plants obtain all their nutrition (mineral and organic) from their fungal partner. Nobody has yet found anything that the fungus gets from the orchid. How orchids trick their fungal partners (some of which are parasites on other plants) into entering this one-sided relationship is a mystery.

In conclusion

Mycorrhizas are ubiquitous: most plants exist in symbiosis. There are several distinct types with unique ecological properties. In natural ecosystems mycorrhizal fungi appear to control the diversity of the plant community and the speed of the carbon cycle; in managed systems, except in some types of forestry, their potential has yet to be exploited and will not be until we understand better the biology and ecology of the organisms involved.

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Further reading

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