Mycorrhizal symbiosis - a way of succeeding together

A Fungus Among Us

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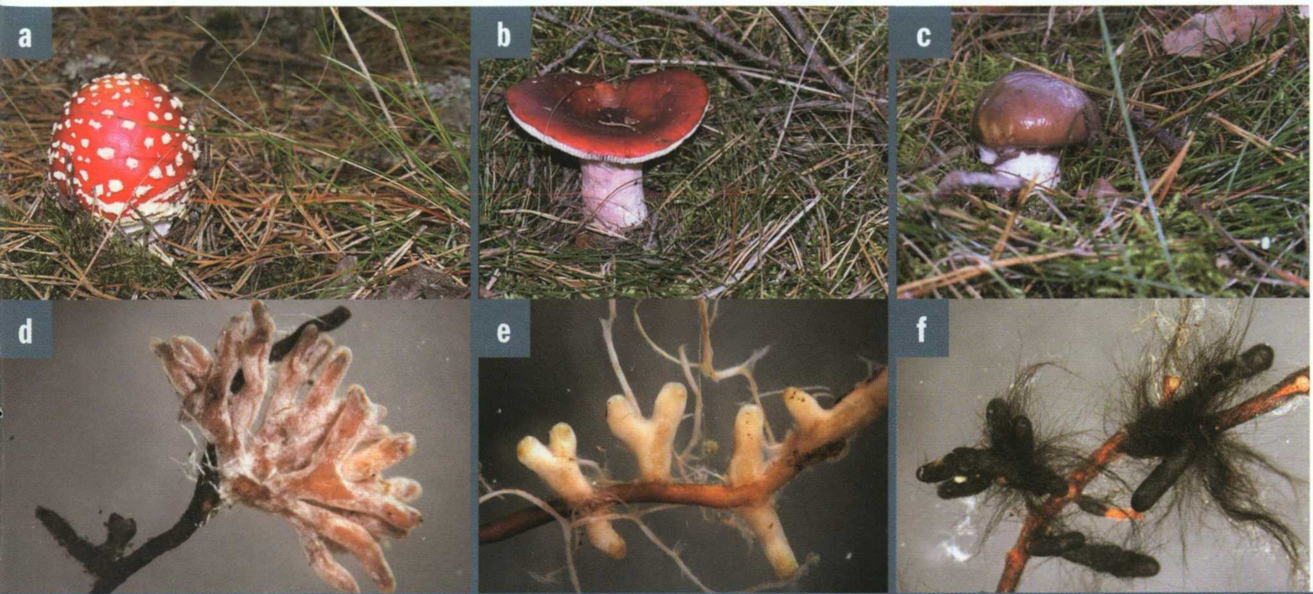
It is quite common in nature for two different species to form a special relationship. In such symbiosis, they both thrive without harming one other, and even frequently benefit one another. One prominent type is known as mycorrhiza, in which plant roots and fungal hyphae work together for mutual gain

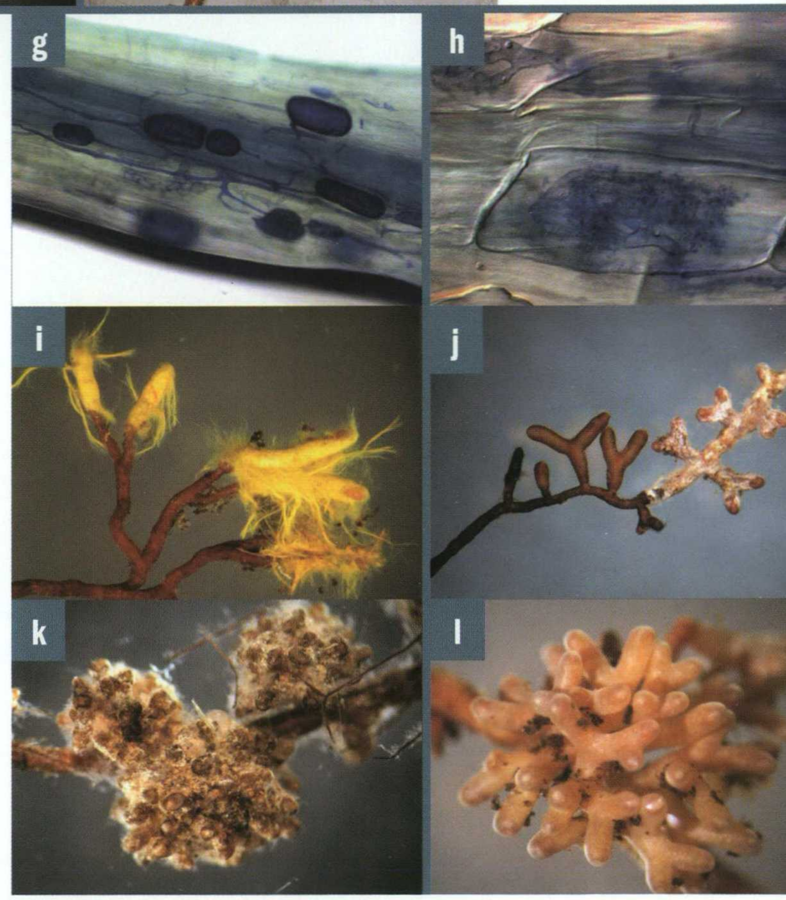
The term 'mycorrhiza' combines the Greek 'mykos' (fungus) and 'rhiza' (root). It describes a very close symbiotic, mutualistic relationship between specialized soil fungi (mycorrhizal fungi) and plant roots. Mycorrhiza is one of the most widespread symbiotic relationships on our planet; it occurs commonly in all significant plant species in all ecosystems. Plants that do not participate in mycorrhiza are exceptions (for instance including *Chenopodiaceae, Brassicaceae, Caryophyllaceae* and *Juncaceae*).

It is widely believed that one of the most important evolutionary steps in the plant kingdom, when photosynthesizing plants first moved from aquatic environments to colonize land, would have been impossible without symbiotic fungi. During the transition process, plants encountered significant problems with absorbing water and key mineral nutrients, in particular phosphorus. They managed to overcome these obstacles by forming mutualistic associations with fungi, in which both partners developed complementary adaptations to life on land. Fungal hyphae are extremely well adapted to penetrating soil in many directions to absorb water and mineral salts; additionally, some symbiotic fungus species are able to digest bedrock to release insoluble nutrients. In turn, plants are very well adapted to the photosynthesis process, and some of the resulting photoassimilates are passed on to the fungal partner.

Scientists currently recognize seven types of mycorrhiza: arbuscular mycorrhiza, ectomycorrhiza, ectendomycorrhiza, ericoid mycorrhiza, arbutoid mycorrhiza, monotropoid mycorrhiza, and orchid mycorrhiza (the first two of which we will examine in the remainder of this article). Each type is closely tied to a specific climate, ecosystem, and soil environment. In different environmental conditions, natural selection has favored the development of distinct sets of traits defining the scope of function of various types of mycorrhiza. They manifest as structural and functional aspects, depending on the type and ecosystem.

The most widespread form, present in around 80-90% of plants, is arbuscular mycorrhiza. It is formed by primitive fungi with multi-nucleate hyphae. The diversity of arbuscular fungi is relatively low, numbering around 220 species from the *Glomeromycota* phylum. All arbuscular mycorrhizal fungi are obligate biotrophs; this means they are fully dependent on living plant roots as a carbon source. Arbuscular mycorrhizal fungi are symbiotic with all types of plant vegetation - a total of over 250,000 species of land-based vascular plants in all climate zones. Arbuscular mycorrhiza occurs in angiosperms and gymnosperms, as well as sporophytes of ferns and lycopods, and even





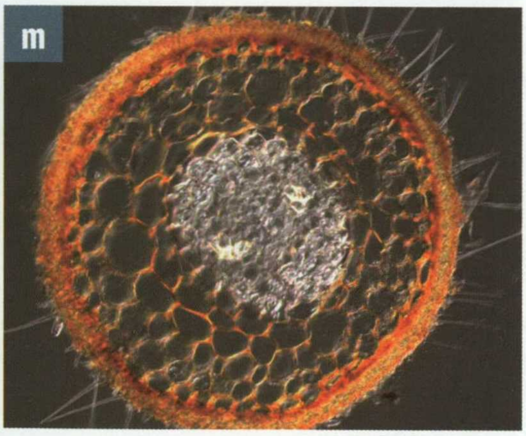
Characteristic structures of arbuscular mycorrhiza (g, h) and ectomycorrhiza (a-f, i-m)

gametophytes of some *Marchantiophyta* and *Pteridophytes*. The symbiosis tends to be obligate, which means the organisms depend on each other for development and survival. Arbuscular mycorrhiza is found in the majority of green plants, including many important crop species such as wheat, maize, rice, soya, grapevines and fruit trees. It is believed to be the oldest form of mycorrhiza, likely to have been accompanying plants for over 450 million years.

The second most widespread and significant form of such symbiosis is ectomycorrhiza. It is a far more recent phenomenon than arbuscular mycorrhiza; the first ectomycorrhizal fungi likely arose during the Jurassic, when the first *Pinaceae* plants appeared around 200 million years ago. The earliest fossilized remains of ectomycorrhiza were found in sedimentary rock deposits near the town of Princeton in British Columbia, Canada; the discovery includes well preserved fragments of dichotomous pine mycorrhiza, dating back around 50 million years. Due to the extremely delicate structure of the mycelium, fossilized remains of ectomycorrhizal fungi are very rare. Even so, they can be used to date the *Agaricomycetes* and *Pezizales* orders to around 200 and 150 million years, which approximately reflects the development of ectomycorrhiza in plants.

Phylogenetic analysis of plants shows that ectomycorrhiza evolved independently many times in various species. A more in-depth analysis conducted on data from over 3600 species (263 families) of embryophytes reveals that the ability to enter into ectomycorrhiza may have evolved at least 30, perhaps even 60 times. The history of evolution of plants and fungi provides some explanation as to how ectomycorrhizal symbiosis arose on a number of separate occasions. Plants which enter into these relationships are likely to occur in environments with a poor supply of minerals. From a phylogenetic perspective, they represent lines originating from some of the main clades of plants which once existed in richer environments. In turn, species of fungi involved in ectomycorrhizal symbiosis evolved many times from saprotrophic ancestors, and as a result they form numerous independent clades. In *Ascomycetes*, the ability to enter into ectomycorrhizal symbiosis evolved independently at least four times, and in *Basidiomycetes* at least six times.

The evolution of ectomycorrhizal symbiosis may be understood as an adaptation of the main plant and fungal clades to climatic and environmental changes, and/or an adaptation to environments with a low availability of nutrients; it is also a bilateral response from both the plant and the fungus to the accumulation of organic matter. Ectomycorrhiza made it possible for the symbionts to colonize regions that were previously inaccessible due to poor climate and soil. The formation of new ecological niches resulted in a rapid parallel radiation of plants and their fungal symbionts. Evolutionary plasticity (a repeated convergent ability to form ectomycorrhizal symbiosis) reflects the opportunistic character of these relationships as a joint response from plants and fungi to changing environmental challenges. In contrast with arbuscular mycorrhiza, which is the oldest and most important evolutionary innovation solving the problem of water and mineral shortages, ectomycorrhiza is a relatively recent, short-term, less evolutionarily-stable strategy. The polyphyletic origins of ectomycorrhizal fungi indicate their potential functional diversity. It seems that repeated convergent evolution from saprotrophic ancestors is responsible for the vast diversity of physiological traits that enable ectomycorrhizal fungi to break down different fractions of organic matter. The diversity of a range of other traits essential for ectomycorrhizal symbiosis (such as population dynamics, survival strategies, and resistance to stress) may also result from the polyphyletic origins of ectomycorrhizal relationships.



The majority of fungi forming ectomycorrhizal relationships are *Basidiomycota*, some *Ascomycota*, and Endogone, a genus in the class *Zygomycota*. Scientists believe that in many tree and shrub species, Basidiomycota and Ascomycota have largely replaced primitive arbuscular relationships, helping the fungi colonize regions where organic matter tended to accumulate (temperate and boreal zones in the northern hemisphere). This is due to the saprobiotic properties of the fungi that allow them to use organic nitrogen and phosphorus compounds and pass them on to their plant partners. Ectomycorrhizal fungi are estimated to number from 6,000 to 25,000 species, although only a small proportion have been studied. Each tree species can enter into ectomycorrhizal symbiosis with as many as hundreds of different species of fungi. Certain species of fungi, known as generalists, form ectomycorrhiza with all types of trees, while others specialize in symbiotic relationships with trees from specific genera or even specific species. Today, ectomycorrhizal symbiosis is an important element of forest ecosystems in boreal, temperate, and Mediterranean zones. In these regions, ectomycorrhizal fungi form obligate relationships with trees from the *Pinaceae*, *Abietaceae*, *Fagaceae*, *Tiliaceae*, *Betulaceae*, and *Myrtaceae* families. Trees from the *Salicaceae* family, and certain *Rosaceae* species, form arbuscular mycorrhiza and ectomycorrhiza, as does the genus *Alnus* (*Betulaceae*). Additionally, ectomycorrhizal fungi can be found in Africa, where some families – such as *Dipterocarpaceae* – are exclusively ectomycorrhizal. Ectomycorrhizal symbiosis is also found in parts of South America, rainforests in India and Indonesia, and forest habitats in Australia.

The fungi kingdom is one of the most diverse groups of living organisms on our planet, and mycorrhizal fungi are an extremely important part of this kingdom (even though they do not account for an exceptionally large share of all fungal species overall). Their close relationships with plants have made them very successful in evolutionary terms, and they can be found in almost all land habitats around the globe, supporting the optimal growth and development of their symbiont plants. ■