The Hidden Life of Forest Fungi

Although mycology has historically been taught as a botanical discipline, the resemblance of fungi to plants is clearly superficial and an artifact of human biases. Fungi have several “plant-like” qualities such as a high surface area to volume ratio, reproduction by spores, and possess cell walls. However, unlike plants, the cell walls are composed of chitin rather than cellulose. Where plant cells have a nucleus with two sets of chromosomes, fungi possess cells of two separate nuclei each with a single set of chromosomes. Fungal cells of this construction are referred to as a dikaryon. In addition, biologists use the term “spore” loosely to describe a self-contained cellular dispersal unit. Spores have arisen multiple times in evolutionary history and are found in virtually all groups of organisms.

Fungi are now recognized as sharing a more recent common ancestor with animals than with plants. Multiple forms of data support this idea. Chitin is found in cell walls of fungi and the exoskeletons of arthropods (insects, spiders, crustaceans). It is a polymer of acetylglucosamine which is a nitrogenous derivative of glucose and not chemically related to cellulose. Animals and fungi utilize a unique biosynthetic pathway to produce glycogen as a storage carbohydrate rather than starch as is produced in plants. Even the heterotrophic life of fungi and animals supports their evolutionary relationship. Both groups are able to export enzymes from cells to digest biological molecules and then to absorb the subunits for nutrition.

Modern genetic techniques have allowed taxonomists to investigate the relationships among large taxonomic groups. Gene sequences from nuclear and mitochondrial genomes supports the monophyletic lineage of animals, fungi, and four groups of protists known as Opisthokonts. This phylogenetic group evolved between 1 and 1.5 billion years ago. The name is derived from the observation that motile cells within these are propelled by a single, posterior flagellum. The morphology of Opisthokonts is very diverse, but they do share a number of unique features that includes flattened mitochondrial cristae. Flagella in other protists and plants are anterior and occur in pairs.

The three major terrestrial groups of fungi that are important in eastern deciduous forests are the cup fungi (Ascomycota), the club fungi (Basidiomycota), and the Glomeromycota (arbuscular mycorrhizal fungi). The Glomeromycota are ancient terrestrial fungi that evolved shortly after the split with animal lineage. Depending on the methods and assumptions used, the origin of Ascomycetes and Basidiomycetes is between 0.5 and 0.9 billion years. Thus, the major groups of fungi were well defined before the formation of land plants.

The earlier rise of fungi relative to land plants is significant. Nearly all land plants have symbiotic relationships with fungi. Fungi are ubiquitous and spread by spores through air and by thin filaments in the soil. Terrestrial plants can’t avoid contacting soil fungi! Terrestrial vascular plants and some soil fungi are married in one of the most important symbiotic relationship called mycorrhizae (myco, fungus; rhizae, root).

Mycorrhizal fungi are soil miners. The high surface area of fungi allows them to aggregate soil particles, strip important mineral nutrition from the soil, and absorb large quantities of water. It has been estimated that 80% of the water absorption surface area of pine seedlings is through fungi. Mycorrhizal fungi interact directly with plant roots and deliver nutrients and water to the plant. In return, green plants allocate carbohydrates and other biomolecules to fungi that are used for growth. Some mycologists have creatively referred to these interactions as the original “internet.” Hundreds of mycorrhizal fungi are at work within the forest and even within individual trees.
The fungal network interconnects and shifts minerals, water, and carbohydrates through a forest. These interconnections can shift carbohydrates from one tree species to another. Simard (1997) et al used carbon isotopes to track the movement of carbohydrates within a paper birch and Douglas fir plantation. They discovered that carbohydrates shuttled between these two species via mycorrhizal fungi. Shade grown plants were the biggest beneficiary of this carbohydrate highway. Mycorrhizal interactions are now recognized for their importance in the horticulture trade. Mycorrhizal inoculates are now provided to nursery grown trees to facilitate their growth and survivorship. In the true sense of “mutualism”, both fungi and terrestrial vascular plant benefit from the relationship and their growth and survivorship is enhanced by partaking in this marriage.

There are two predominate forms of mycorrhizal relationships. In arbuscular mycorrhizae, the fungal hyphae infect and grow into plant root cells. The fungi that form arbuscular relationships are members of the Glomeromycota, a common terrestrial group that infects herbaceous plants and tropical trees. You will never see members of the Glomeromycota in the forest unless you take a microscope and collect, section, and stain root tips. Arbuscules or branches form an intricate network in the vicinity of plant roots. These branches increase the surface area and contact between the fungus and the cells in the roots. Sexual spores are unknown as are above ground fruiting bodies of this group. Their reproductive cycle of Glomeromycota is entirely by asexual spores. Glomeromycota fossil spores suggest that these fungi have been successful on land for 600 million years predating the plant land invasion by 150 million years. In fact, one might be correct in arguing that these fungi were a driving force behind the terrestrial invasion of plants from the oceans.

Ectomycorrhizal (outside, fungus, root) relationships form between members of the Ascomycota and Basidiomycota with vascular plants. In these groups, the filaments of the fungus grow over the surface of root tips rather than invade root cells. Rootlets of infected plants are usually short with bifurcated root tips. The Basidiomycota or club fungi are the most diverse group with more than 1/3 of all fungi. Club fungi have three discrete evolutionary groups with the plant pathogenic rusts, and smuts as well as the more recognizable mushrooms or toadstools. It is within the mushrooms that many of the more important ectomycorrhizal fungi are found. Two key characteristics unite the club fungi. First, the hyphal filaments possess cells with two haploid nuclei. In sexual club fungi, sexual spores are produced by club-like structures called basidia. Each basidum typically produces four haploid spores on top of short wicks called sterigma. Mature basidiospores are forcibly ejected from the fruiting body at a high velocity that will allow the spore to be captured by wind currents. The cup fungi or Ascomycetes form the second group of ectomycorrhizal fungi (Figure Common Ascomycetes in Forests). The cup fungi include some well-known delicacies such as truffles and morels. In addition to mycorrhizae, many Ascomycetes are saprobic but some are pathogens of plant and humans. Cryphonectria parasitica is best known as the chestnut blight which quickly and efficiently killed off the magnificent American chestnut forests in eastern North America. Ascomycetes also include the fungi responsible for thrush and diaper rash. Despite these detrimental qualities, cup fungi are best known for the antibiotic penicillin. In the forest, cup fungi are the
most common fungus in lichens which are “super organisms” composed of a fungus and green alga or blue-green bacterium (see below).

A brief examination of a field guide to fungi demonstrates just how common these mycorrhizal relationships are. Genera of fungi such as Amanita, Boletus, Russula, are all widespread groups and commonly recognized club fungi that are mycorrhizal with forest trees. Many, if not most, woodland herbs develop mycorrhizal associations shortly after germination. This association appears to be very important in nutrient uptake for the herb. In fact, it now appears that much of the water redistribution in hydraulic lift is due to hyphal connections between roots in the soil.

Other members of the Basidiomycota are parasites and saprobic. The forest floor is laden with fungi that specialize on wood and leaf litter. The fact that fungi can dismantle plant material illustrates an important aspect of their genetics. They possess genes to manufacture enzymes that digest cellulose, pectins, and lignin. These are biological molecules that are only digested by fungi or bacteria. Saprobic fungi are important recyclers in the forest ecosystem. Nitrogen and phosphorus that is locked in plant biomass is released and returned to the

environment. In temperate and boreal forests, the recycling process of fungi is slowed by cool temperature; short growing seasons, and secondary chemicals produced by plants as fungicides. This explains the abundance of wood and leaf litter in temperate and boreal systems and the absence of soil organic matter in tropical forests.

Saprobic fruiting bodies are abundant on the deciduous forest, but locating them takes more effort. The saprobic lifestyle of some fungi does not provide the same riches as a mycorrhizal lifestyle. Obtaining energy from plant litter, as compared with the pipeline of sugars, requires more labor and energy to digest plant material. The return on the energy investment for acquiring resources is lower for saprobic fungi. As such, many common saprobic fungi, Marasmius, Mycena, Entoloma, Gymnopus have smaller fruiting bodies than fruiting bodies of mycorrhizal fungi (Figure Saprobic Fungi).
Bracket or shelf fungi frequently parasitize forest trees but then continue to decompose the woody material long after the tree has died. Hemlock is parasitized by the lacquer fungus, birch by the elephant’s hoof, and white pine by the butt rot. The presence of these fruiting bodies on the host tree is a signal of a slow death from the inside. A wise camper might take note of the fungi on surrounding forest trees and not park the tent too close to a tree riddled with parasitic fungi. The popular “humongous fungus”, Armillaria solidipes (formerly A. ostoyae), is a parasite of fir and hemlock in Washington and Oregon. Researchers noted that fir and hemlock forests of considerable size in the western temperate forests where dying. DNA fingerprinting confirmed that two clones or A. solidipes, also known as the honey mushroom, were responsible for the die off. One clone measured 1500 acres and the second at 2200 acres. These humongous honey mushrooms illustrate the ability of fungi to live long lives (2000 years) and ability of fungi to grow over considerable distances.

The Indian pipe (Monotropa uniflora) and pinesap (Monotropa hypopithys) like all members of the Monotropaceae are heterotrophic flowering plants (Figure Indian Pipes). Instead of possessing green stems and leaves these plant bear white or yellow stems and achlorophylous small leaves that are observed for a few weeks of August and September in New York State. Members of the Monotropaceae have evolved as food sleuths in the botanical underworld.

Indian pipe and pinesap coerce some mycorrhizal fungi through molecular trickery to cohabit. Unlike other mycorrhizal relationships, this partnership is distinctly one-sided. $^{14}C$ labeling has shown that organic compounds produced in the tree may pass through the fungus and ultimately into the Indian pipe or pinesap. At present, neither Indian pipe nor pinesap offer anything of value to the relationship and in essence are hidden parasites of the tree.

Recent studies have shown that fungal inoculation of Indian pipe and pinesap seeds quickly initiate a mycorhizal partnership and that seedling growth quickly arrests in sterile conditions. Indian pipe has established specific relationships with Russula and Lactarius while Pinesap has adapted to Tricholoma. Species specific interactions exist between other members of the Monotropaceae and the mycorrhizal Basidiomycota. One can examine these relationships by observing small plots of Indian pipe flowering in the forest and then by periodically returning to identify associated fungi. Single observation points are unlikely to identify the most likely fungal cohabitant, but several plots will allow one to narrow the field of potential associates.

Orchids and Mycorrhizae. The orchid family remains one of the more mystical groups of terrestrial flowering plants. Eastern North America is blessed with more than 150 orchid species that occupy wetlands and forests. The remarkable reproductive and pollination biology of this group will be described elsewhere, but the unique interaction between orchids and fungi is
warranted here. Orchid fruits produce thousands of brownish-white dust-like seeds that resemble human dandruff more than a flowering plant seed. The seed body contains a miniscule embryo and practically no food reserves for a developing seed or seed germination. Instead orchids rely on a mycorhizal relationship.

Most orchid seeds die or wither away before the successful fungal invasion. For the few seeds that escape predation by fungi, but instead develop a life-long relationship with a mycorhizal species, germination may begin after infection. The fungus shuffles carbohydrate, water, and minerals to the seed and allow for the embryo to develop, mature, and germinate. Recent studies have suggested that orchids maintain this partnership throughout its life and that seed germinate best in close proximity to pre-established plants.

Coral root orchid (Corallorhiza sp.) is a non-photosynthetic plant lacking chlorophyll similar to those woodland herbs in the Monotropaceae. Like pinesap and Indian pie, coral root receives all carbon nutrition via mycorrhizal fungus that forms ectomycorrhizae with tree roots. Thus, coral root is acting as a secondary parasite on the tree (Whigham, 2004). Lady slipper orchids become dormant and hide as a below ground root for several years before magically reappearing. It is believed that lady slipper orchids derive their carbon from mycorrhizal fungi during their cryptic years (Figure Mycorrhizal Orchids).

Fungi as Food. Fungi provide a rich resource of amino acids and carbohydrates for communities of woodland animals. During the late summer/early autumnal flush of fungal fruiting bodies, squirrels and deer utilize this seasonal resource until nuts and fruits ripen on deciduous trees. In return, the feet and fur of these mammals become important in spore dispersal. Fungal hyphae and spores form the base of many soil ecosystems. Springtails, mites, and nematodes are consumers of fungi in the soil. Fungus gnats and some flies lay their eggs in the fruiting bodies of some fungi. As many students have learned, a collection of rotting fungi left on a laboratory table for a few days rapidly becomes a smelly attraction for flies. Slugs are important invertebrate predators of fungi in the autumn. Slugs show distinct preferences for different genera of forest mushrooms. A quick observation for slime trails, radula marks, and even the presence of slugs will suggest their preferences. One can follow-up an inventory of predated fungi, with a laboratory smorgasbord of fungi presented to slugs. Several of my students have concluded that slugs follow chemical trails that lead them to the fungi of preference in the field.

Lichens—kidnapped greenhouse workers. Earlier in the chapter, several paragraphs were devoted to convincing you that fungi aren’t plants. Fungi, however, are involved in an interesting symbiotic relationship where they act like plants. Lichens represent a partnership between a fungus and an alga. The alga may represent one of several genera of unique green alga or an ancient group of photosynthetic bacteria, blue-green bacteria. More than 85% of the lichens have green alga with the minority possessing blue-green bacteria. Lichens with both photobionts are rare, but can be found. There are rare examples of either a crustose brown alga or a golden alga married with a fungus. Although the fungus remains heterotrophic and derives its organic nutrition from the alga, the fungus does provide a greenhouse to cultivate and care for the photosynthetic alga. Despite the importance of the alga to the survival of the lichen, the alga typically accounts for less than 10% of the lichen biomass. The fungus initiates the relationship
with the alga and recognizes suitable photobionts through the interaction of proteins on the cell wall.

The fungus must facilitate photosynthesis in the alga by providing ample sunlight, carbon dioxide, and water. In foliose or leaf-like lichens, the fungus has adapted a form that is resembles modern plant leaves. The fungus provides the upper and lower surface scaffolding to support a middle layer rich in photosynthetic cells. The high surface area and porosity of the fungal mycelium allow gases to diffuse quickly and efficiently as well as allow water to wick inward toward the photosynthetic algae. Occasionally, pores may exist on the lower surface to improve gas exchange. Proteins secreted by the fungus improve the exchange of raw materials and organic compounds with the alga.

Lichens have received too little attention from evolutionary biologists and geneticists. Lichen fungi are usually Ascomycetes and rarely Basidiomycetes. Similarly, there are relatively few green algae and blue-green bacteria able to participate in the relationship. The fungus must have an arsenal of tactics for encouraging and maintaining a happy culture of algae. What are the molecular signals involved in the initial attraction? How does the fungus keep the culture or algae pure? How are molecules and materials trafficked between these different organisms? What genes are present in algae and fungi that allow the interaction to occur? Why don’t other algae and fungi participate in this relationship? And while we ask these evolutionary questions about lichens, it is important to note that lichens have no evolutionary tree. Lichen species are very different from other groups of organisms that have evolutionary histories. In fact, some lichen fungi are able to form the same species of lichen with a different species of photobiont.

Do lichens represent a mutualism or parasitism? In a classic case of mutualism, both partners should benefit from the relationship. It is unfair to determine who benefits the most provided the standard of living increases for both. However, some algal partners seem to be better off when they live outside of the lichen. In this case, it appears that the algae are working hostages of the fungus. Some fungi actively destroy the algae, albeit slowly, to gain access to the carbohydrate rich nutrition of the alga. As long as the algae reproduce at a faster rate than they are destroyed by the fungus, the lichen can persist.

Other organisms have capitalized on the photosynthetic capacity of algae. Dinoflagellates are known to steal chloroplasts from some algae and hold them as working hostages. Even in higher plants substantial biochemical, morphological, and molecular evidence has been gathered which supports the endosymbiotic hypothesis for chloroplasts origin. This hypothesis argues that chloroplasts originated as photosynthetic cells that were captured and packaged into a large set of membranes. Why can’t there be an exosymbiotic hypothesis to explain the origin of lichens? The fungus has chosen to work with the photobiont on the outside rather than the inside.

Lichens are an important biological indicator for environmental assessment and air quality. The high surface area to volume ratio allows lichens to traps and collect rainwater and fog. Pollutants dissolved in atmospheric moisture are readily trapped and accumulate in lichens. Lichen species vary in their degree of sensitivity to heavy metals, fluorine, nitrous oxides, sulfur oxides, polychlorinated biphenyls, polycyclic aromatic hydrocarbons and photochemical smog. Lichen sensitivity to air pollution may be manifested through irregular or stunted growth, bleaching of photosynthetic pigments, or die-back from the center of the lichen colony. Thus, the type and severity of pollution can be ascertained by examining species composition and growth traits. The United States Forest Service monitors air quality using lichens and they maintain a web page with a database and technical reports. Because lichens accumulate
environmental pollutants, they can be collected in the field and analyzed for each contaminant. In 198X, Canadian environmental scientists developed the Index of Atmospheric Purity based on lichen sensitivity. The index examined the number of lichen species, their relative abundance, and pollution sensitivity of each lichen species in a geographic region. Using lichens as biological indicators have allowed scientists to map the plume of contamination around industrial cities and mining operations.

Lichens are also known accumulators or radioisotopes such as strontium-90. Radioactive fallout from nuclear testing or the Chernobyl reactor accident deposits strontium-90 on the landscape. In contaminated regions of Europe following Chernobyl, strontium-90 accumulated in reindeer moss. During winter months, this moss provides caribou with 90% of their diet. Strontium-90 is passed from lichen to caribou where it mimics calcium and is deposited in the bones. Humans in northern Europe hunt and eat caribou and thus inherit the strontium that was initially collected by the reindeer lichen. The food web passage of radioactive strontium has lead to increased rates of bones cancer with some indigenous Europeans near the Chernobyl disaster.

Lichens fill an important role in primary succession on bare rock. Lichens colonize and grab onto bare rock by root-like fungal threads called rhizines. As rain, wind, and freeze-thaw cycles break rock into small fragments, lichens hold and stabilize the coarse soil particles. Acids secreted by the lichen further assist the genesis of soil. Lichens also reflect excess light in the summer and warm the rock in the winter by their diverse pigments that absorb and then reflect infra-red light. The thin biomass of lichens on bare rock is sufficient to improved the water retention on bare rock and allow other organisms to become established. Carbon dioxide from the lichen community dissolves in water to produce a weak acid. In addition, organic acids produced from the mycobiont liberate mineral ions that become important in the weathering process of rock to create soil.

In areas where blue-green bacteria are the dominant photobiont of the lichen community a significant nitrogen input can occur. Blue-green bacteria hold a trick up their little membranes called nitrogen fixation. They have the cellular machinery to grab inert nitrogen from the atmosphere and convert it into biologically active ammonia and nitrate. These molecules are fertilizers in the plant world and allow plants to build chlorophyll, amino acids, proteins, DNA, and energy transfer molecules. Lichens are abundant in the temperate rainforest of Washington state and British Columbia. Here the plant life flourishes from the nitrogen input of lichens with blue green algae.

References:


