classified, they are less well described in comparison to members of other fungal taxa. Most imperfect fungi live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.

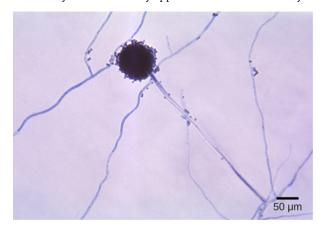


Figure 24.18 Aspergillus. Aspergillus niger is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is an asexual conidiophore. Molecular studies have placed Aspergillus with the ascomycetes and sexual cycles have been identified in some species. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

The fungi in this group have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi had killed the bacterial growth surrounding it. Other fungi in this group cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

Glomeromycota

The **Glomeromycota** is a newly established phylum that comprises about 230 species, all of which are involved in close associations with the roots of trees. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that nearly all members of this family form **arbuscular mycorrhizae**: the hyphae interact with the root cells forming a mutually beneficial association in which the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant. The exception is *Geosiphon pyriformis*, which hosts the cyanobacterium *Nostoc* as an endosymbiont.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

24.3 Ecology of Fungi

By the end of this section, you will be able to do the following:

- Describe the role of fungi in various ecosystems
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms
- Describe the beneficial relationship between some fungi and insects

Fungi play a crucial role in the constantly changing "balance" of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Within their communities, fungi are not as obvious as are large animals or tall treas. Like bacteria, they act behind the scene as major decomposers. With their versatile metabolism, fungi break down organic matter, which would otherwise not be recycled.

Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled,

thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter (Figure 24.19). Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



Figure 24.19 Bracket fungi. Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk. (credit: Cory Zanker)

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways (Figure 24.20).



Figure 24.20 Shelf fungi. Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. (credit: Cory Zanker)

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. This definition does not describe the type or quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

Fungus/Plant Mutualism

One of the most remarkable associations between fungi and plants is the establishment of *mycorrhizae*. **Mycorrhiza**, which is derived from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the fungal partner of a mutualistic association between vascular plant roots and their symbiotic fungi. Nearly 90 percent of all vascular plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are several basic types of mycorrhizae. **Ectomycorrhizae** ("outside" mycorrhizae) depend on fungi enveloping the roots in a sheath (called a mantle). Hyphae grow from the mantle into the root and envelope the outer layers of the root cells in a network of hyphae called a *Hartig net* (Figure 24.21). The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. **Endomycorrhizae** ("inside" mycorrhizae), also called *arbuscular mycorrhizae*, are produced when the fungi grow inside the root in a branched structure called an *arbuscule* (from the Latin for "little trees"). The fungal partners of endomycorrhizal associates all belong to the Glomeromycota. The fungal arbuscules penetrate root cells between the cell wall and the plasma membrane and are the site of the metabolic exchanges between the fungus and the host plant (Figure 24.21b and Figure 24.22b). Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that typically produce very small airborne seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their life cycle.

WISUAL CONNECTION

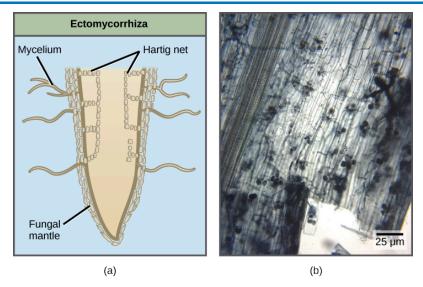


Figure 24.21 Two types of mycorrhizae. (a) Ectomycorrhizae and (b) arbuscular or endomycorrhizae have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

If symbiotic fungi were absent from the soil, what impact do you think this would have on plant growth?

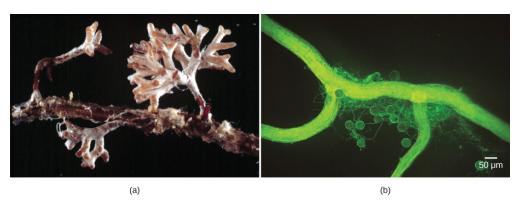


Figure 24.22 Mycorrhizae. The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The *Amanita* hyphae cover these small roots with a white mantle. (b) Spores (the round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza by a fungus on the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

Other examples of fungus—plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.



EVOLUTION CONNECTION

Coevolution of Land Plants and Mycorrhizae

As we have seen, mycorrhizae are the fungal partners of a mutually beneficial symbiotic association that coevolved between roots of vascular plants and fungi. A well-supported theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most ancestral plants and the first to survive and adapt on land, have simple underground rhizoids, rather than a true root

system, and therefore cannot survive in dry areas. However, some bryophytes have arbuscular mycorrhizae and some do not.

True roots first appeared in the ancestral vascular plants: Vascular plants that developed a system of thin extensions from their roots would have had a selective advantage over nonvascular plants because they had a greater surface area of contact with the fungal partners than did the rhizoids of mosses and liverworts. The first true roots would have allowed vascular plants to obtain more water and nutrients in the ground.

Fossil records indicate that fungi actually preceded the invasion of ancestral freshwater plants onto dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae: About 90 percent of today's vascular plants have associations with fungi in their rhizosphere.

The fungi involved in mycorrhizae display many characteristics of ancestral fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats and allowed the increased uptake of nutrients, which gave them an enormous selective advantage over plants that did not establish symbiotic relationships.

Lichens

Lichens display a range of colors and textures (Figure 24.23) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.

LINK TO LEARNING

Explore the world of lichens using this site (http://openstax.org/l/lichenland) from Oregon State University.

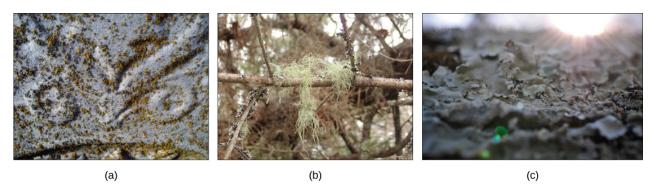


Figure 24.23 Lichens. Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker)

It is important to note that lichens are *not* a single organism, but rather another wonderful example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota) lives in a physical and physiological relationship with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium) (Figure 24.24). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria additionally fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the lichen to its substrate.

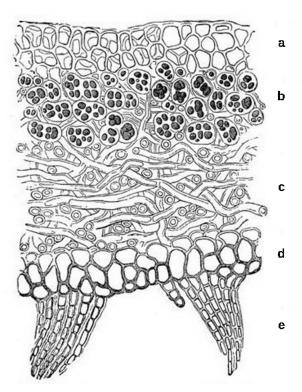


Figure 24.24 Structure of a lichen. This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) *rhizines* to anchor the thallus to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units, called soredia—clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogenous and sulfurous compounds. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes. The pigments used in litmus paper are also extracted from lichens.

LINK TO LEARNING

Lichens are used to monitor the quality of air. Read more on this <u>site (http://openstax.org/l/lichen_monitrng)</u> from the United States Forest Service.

Fungus/Animal Mutualism

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: joint-legged invertebrates with a chitinous exoskeleton. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus.

In a second example, leaf-cutter ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in subterranean gardens (Figure 24.25). Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from this mutualistic association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.



Figure 24.25 Leaf-cutter ant. A leaf-cutter ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

Fungivores

Animal dispersal is important for some fungi because an animal may carry fungal spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some "dung fungi" actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground ascomycete. Almost all truffles are ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles (female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.)

24.4 Fungal Parasites and Pathogens

By the end of this section, you will be able to do the following:

- Describe some fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is hampered by the similarity between fungal and animal cells

Parasitism describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, pathogens cause disease, damage to host tissues or physiology, whereas parasites usually do not, but can cause serious damage and death by competition for nutrients or other resources. **Commensalism** occurs when one member benefits without affecting the other.

Plant Parasites and Pathogens

The production of sufficient high-quality crops is essential to human existence. Unfortunately, plant diseases have ruined many crops throughout human agricultural history, sometimes creating widespread famine. Many plant pathogens are fungi that cause tissue decay and the eventual death of the host (Figure 24.26). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins that can further damage and kill the host plant. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as *ergotism*. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is *lysergic acid*, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.