

Mutualism between cellulose-digesting microorganisms and arthropods is quite common and is often a major factor in detritus food chains. The termite-intestinal flagellate partnership is a classic case, first worked out by Cleveland (1924, 1926). Without the specialized flagellates, many species of termites cannot digest the wood they ingest, as demonstrated by the fact that they starve to death when the flagellates are experimentally removed. The symbionts are so well coordinated with their host that they respond to the termite's molting hormones by encysting, thus ensuring transmission and reinfection when the termite molts its gut lining and then ingests it.

In termites, the symbionts live inside the body of the host. However, even more intimate interdependence may develop with the microorganism partners living outside the body of the animal host, and such associations may actually represent a more advanced stage in the evolution of mutualism (less chance that the relationship might revert to parasitism). One example are the tropical attine ants, which cultivate fungal gardens on the leaves they harvest and store in their nests. The ants fertilize, tend, and harvest the fungal crop in much the same manner as an efficient human farmer would. The ant-fungal system accelerates the natural decomposition of leaves. A succession of microorganisms is normally required to decompose leaf litter, with basidiomycete fungi normally appearing during the late stages of decomposition. However, when leaves are "fertilized" by ant excreta in the fungal gardens, these fungi can thrive on fresh leaves as a rapidly growing monoculture that provides food for the ants. Much ant energy is, of course, required to maintain this monoculture, just as much energy is required in intensive crop culture by humans.

By cultivating a cellulose-degrading organism as a food crop, the ants gain access to the vast cellulose reserves of the rain forest for indirect use as a nutrient. What termites accomplish by their *endosymbiotic* association with cellulose-degrading microorganisms, the attine ants have achieved through their more complex *ectosymbiotic* association with a cellulose-degrading fungus. In biochemical terms, the contribution of the fungus to the ant is the enzymatic apparatus for degrading cellulose. In turn, the fecal material of the ant contains proteolytic enzymes that the fungus lacks, so that the ants contribute their enzymatic apparatus to degrade protein. The symbiosis can be viewed as a *metabolic alliance* in which the carbon and nitrogen metabolisms of the two organisms have been integrated.

Coprophagy, or the reingestion of feces, which appears to be characteristic of detritivores, can probably be viewed as a much less elaborate but much more widespread case of mutualism that couples the carbon and nitrogen metabolism of microorganisms and animals—an "external rumen." Rabbits, for example, reingest their feces, illustrating the role of coprophagy in natural communities.

Ants and *Acacia* trees are involved in another striking tropical mutualistic symbiosis, as first described by Janzen (1966, 1967). The trees house and feed the ants, which nest in special cavities in the branches. In turn, the ants protect the tree from would-be herbivorous insects. When the ants are removed experimentally (as by poisoning with an insecticide), the tree is quickly attacked and often killed by defoliating insects.

Mineral cycling as well as food production are enhanced by mutualistic relationships between microorganisms and plants. Prime examples are *mycorrhizae* ("fungus-root"), mycelia of fungi that live in mutualistic association with the living roots of plants (not to be confused with parasitic fungi, which kill roots). As with nitrogen-fixing bacteria and legumes, the fungi interact with root tissue to form composite "organs" that enhance the ability of the plant to extract minerals from the soil.

In return, of course, the fungi are supplied with some of the plant's photosynthate. So important is the energy flow pathway through mycorrhizae that this route can be listed as a major food chain.

There are two main types of mycorrhizae. In the **ectomycorrhizae**, the fungus forms a *sheath* or network around actively growing roots, from which hyphae grow out into the soil, often for long distances. These mycorrhizae associate mostly with trees, especially pines and other conifers and tropical trees. The **vesicular-arbuscular** or **VA mycorrhizae** (formerly called *endomycorrhizae*) penetrate into root tissue, where they form characteristic vesicle-like structures (hence the name). Hyphae extend out into the soil, as in the ectomycorrhizae. These mycorrhizae colonize all but a few genera of plants, including herbs, shrubs, and trees in all climatic regions.

Mycorrhizae are not generally host-specific, which means that they can often colonize whatever plant root comes into contact with their spores. Some ectomycorrhizae produce large aboveground sporocarps or mushrooms that facilitate dispersal. The VA types produce spores underground, where they may be dispersed by soil-dwelling animals. Mycorrhizae are found in virtually every terrestrial ecosystem, including the rain forests of the Tropics, the prairies of the North Temperate Zone, and the Arctic Tundra. The mycorrhizal relationship between fungi and plants is both ubiquitous and ancient. About 90 percent of plant species, including most crops, form some kind of beneficial association with these fungi (Picone 2002). These benefits include:

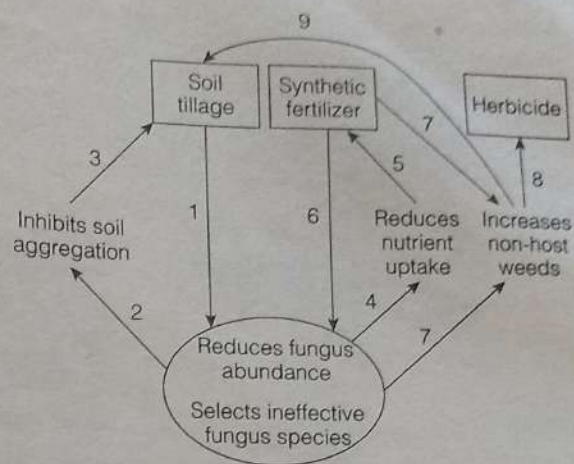
- Mycorrhizal fungi increase nutrient uptake, especially of nitrogen and phosphorus. The hyphae extend from the colonized root into the soil. Because of their high rate of surface area to volume, hyphae are highly proficient at absorbing soil nutrients and transporting them to the root. The fungi receive carbohydrates, especially sugars, from the plant in this mutualistic relationship.
- Mycorrhizal fungi help suppress certain weeds. Colonized roots are better able to resist soil pathogens, including nematodes and pathogenic fungi.
- Mycorrhizae play an important role in improving soil texture, and are considered the most important biological agent for aggregating most soil types. This aggregation, termed **tilth**, is what makes for a healthy soil structure. Such soil is loose, permits roots to penetrate, lets water percolate easily, and allows biota, such as earthworms, to burrow unimpeded.

Unfortunately, conventional agricultural practices tend to disturb this beneficial relationship between mycorrhizal fungi and plant colonization—the result being that soil properties and ecosystem processes such as nutrient cycling are impeded (Coleman and Crossley 1996).

Figure 7-11 depicts how conventional agricultural practices affect the soil containing the mycorrhizal community (Picone 2002). Step 1 depicts how tillage crushes soil aggregates, destroys webs of mycorrhizal fungus, and reduces fungus abundance. This disturbance inhibits soil aggregation and tilth formation (Step 2). Thus, the soil becomes compacted and poorly aerated, frequently requiring further tillage (Step 3).

Tillage also promotes dependence on fertilizers due to the disruption of fungal mechanisms of nutrient recycling (Step 4); modern agricultural practices therefore compensate by applying synthetic, commercial fertilizers (Step 5). Synthetic fertilizer, unlike organic fertilizers, reduces the abundance of mycorrhizal fungi and selects for fungi that are ineffective at nutrient uptake (Step 6). Soil with an impoverished mycorrhizal community creates an optimal environment for non-host weeds

Figure 7-11. A model depicting the effects of conventional agricultural tillage practices on the mycorrhizal soil community (see text for details; with permission of The Land Institute, Salina, Kansas).



(Step 7). Hence, biological mechanisms for weed control (Step 8) and even more tillage (Step 9) are required. Thus, agricultural tillage helps create an industrial cycle rather than the ecological (biotic) cycle that has evolved in natural systems. Farm productivity frequently plummets as a result of this farming practice, until the network of mycorrhizal fungi becomes reestablished and mechanisms of nutrient recycling based on soil health are restored.

Many trees will not grow without mycorrhizae. Forest trees transplanted to prairie soil in a different region often fail to grow unless inoculated with the fungal symbionts. Pine trees with healthy mycorrhizal associates grow vigorously in soil so poor by conventional agricultural standards that corn or wheat could not survive. The fungi can metabolize "unavailable" phosphorus and other minerals by chelation or by other means. When labeled minerals (such as radioactive tracer phosphorus) are added to the soil, as much as 90 percent may be quickly taken up by the mycorrhizal mass, then slowly released to the plant. It is fortunate that the pine tree mycorrhizal system does so well on the millions of acres in the southern United States where topsoil was devastated by the row-crop monoculture and absentee-owner system that persisted for so long; otherwise, many of these eroded acres would be deserts today.

Figure 7-12A depicts mycorrhizal clusters around the roots of a spruce (*Picea pungens*). The role of mycorrhizae in direct mineral recycling, their importance in the Tropics, and the need for crops with such built-in recycling systems were emphasized in Chapter 4. For additional information on mycorrhizal mutualisms, see Mosse et al. (1981) and E. I. Newman (1988).

Ahmadjian (1995) noted that lichens are probably the most misunderstood and poorly appreciated organisms in the biological world. Lichens are an important part of the biological web that links all of us together. They are a unique combination of traits, being primarily fungal, but also cyanobacterial. Approximately 8 percent of the terrestrial surface of Earth has lichens as its most dominant life-form. For example, in the boreal forests of North America, Europe, and Russia, vast areas of the ground are covered with reindeer lichen (frequently termed "reindeer moss"), especially species of the genus *Cladonia*. It is likely that lichens play a role in regulating the gaseous composition of the atmosphere of Earth, possibly by functioning as a CO₂ sink (Ahmadjian 1995).

Lichens are an association of specific fungi and algae, so intimate in terms of

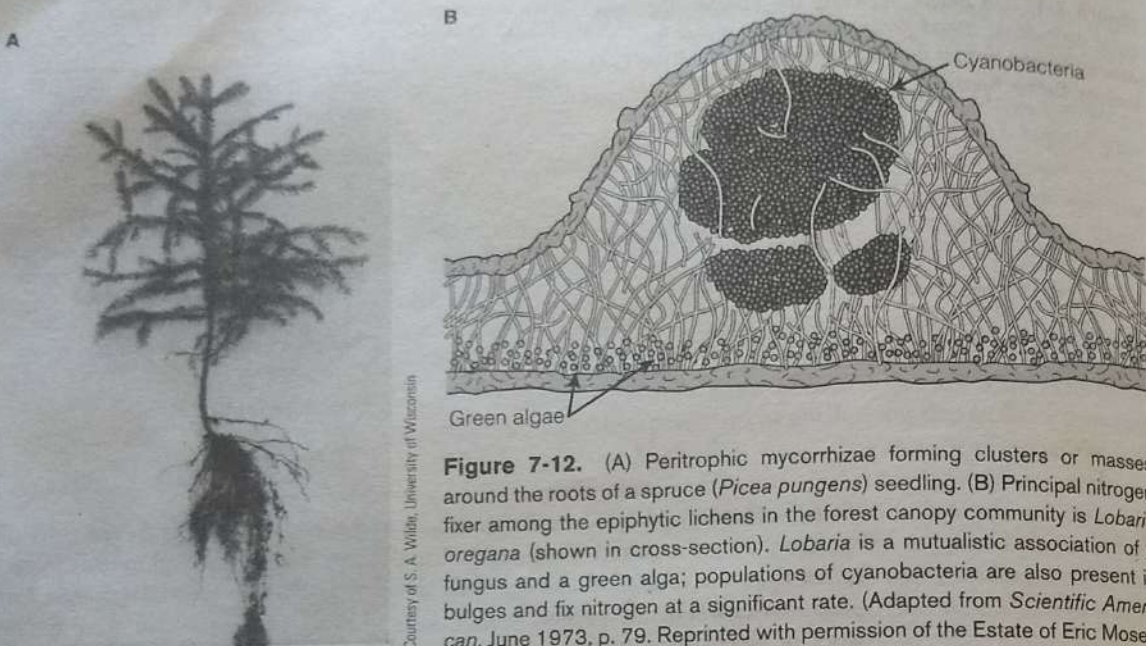


Figure 7-12. (A) Peritrophic mycorrhizae forming clusters or masses around the roots of a spruce (*Picea pungens*) seedling. (B) Principal nitrogen fixer among the epiphytic lichens in the forest canopy community is *Lobaria oregana* (shown in cross-section). *Lobaria* is a mutualistic association of a fungus and a green alga; populations of cyanobacteria are also present in bulges and fix nitrogen at a significant rate. (Adapted from *Scientific American*, June 1973, p. 79. Reprinted with permission of the Estate of Eric Mose.)

functional interdependence and so integrated morphologically that a third kind of organism, resembling neither of its components, is formed. Lichens are usually classified as single species, even though they are composed of two or more unrelated species. In lichens, one sees evidence of an evolution from parasitism to mutualism. In some of the more primitive lichens, for example, the fungi actually penetrate the algal cells and are thus essentially parasites of the algae. In the more advanced species, the fungal mycelia or hyphae do not break into the algal cells, but the two live in close harmony. Figure 7-12B depicts a principal nitrogen fixer among the epiphytic lichens (*Lobaria oregana*) in the forest-canopy community. *Lobaria* is a mutualistic association of a fungus and a green alga, but also contains populations of cyanobacteria that fix nitrogen at a significant rate.

The mutualistic lichen lifestyle has had at least five independent origins in different branches of the fungus family tree; at least 20 percent of all fungal species are lichens (Gargas et al. 1995). Such multiple origins demonstrate that mutualism may be just as important as competition in evolution, as Kropotkin (1902) suggested more than a century ago.

It is evident that mutualism has special survival value when resources become tied up in the biomass, as in a mature forest, or when soil or water is nutrient poor, as in some coral reefs or rain forests. Like corals and other highly organized heterotroph-autotroph mutualistic complexes, lichens are well adapted to natural scarcities and stress, but they are very vulnerable to pollution stress, especially air pollution. With regard to the restoration of landscape in Sudbury, Ontario, which was devastated by air pollution (as mentioned in Chapter 3), the return of lichens is a welcome sign that restoration is working.

For general reviews of symbiotic associations, see Boucher et al. (1982) and Keddy (1990). We also recommend the supplement to *The American Naturalist*, 2003, Vol-