Underground Connections in the Forest

When walking through the forest with a broad tree canopy high overhead and a profuse understory of shrubs, ferns, and herbs, one rarely considers the ecological interactions taking place beneath the forest floor. Most people are aware that plants are generally rooted in the soil, from which they acquire nutrients and water. Combining these soil resources with radiant energy from the sun, carbon dioxide from the air, and the genetic information programmed into their DNA, plants grow and develop through photosynthesis (the process by which sunlight is used to synthesize foods from carbon dioxide and water). However, there is much more going on below the soil surface. Of special interest are the underground connections created by natural root grafts, mychorrhizal networks, and symbiotic nitrogen fixation. These connections are examples of *protocooperation* (root grafts) and *mutualism* (mychorrhiza and nitrogen fixation). Protocooperation is an interaction which stimulates both partners, but is not obligatory; that is, both participants can survive and develop in the absence of the other. Mutualism, however, is an obligate interaction; the absence of the interaction depresses both partners.

As the roots of individual trees infiltrate the soil they may come in contact with each other and unite in a natural graft. This is quite a common event, with more than 150 tree species known to form such grafts. Many of these grafts can occur between different species, and some can even form between different genera; for example, birch with elm or birch with maple. Little is known regarding the ecological significance of natural root grafting, but many researchers agree that it might confer evolutionary advantages to forests stands. For example, joined root systems can give trees better wind stability, preventing weaker trees from blowing down. Interconnected trees can also share resources like water, photosynthates (i.e., sugars), or nutrients, which could enhance survival of suppressed trees through support by their connected neighbors. If both partners are equally successful in the exchange of nutrients and photosynthates, then the relationship created by the root graft is considered to be protocooperation. However, root grafting also enhances survival of roots, snags, and stumps of dead or cut trees, which could in this case constitute a drain on resources for the living trees. The relationship might then be seen as a form of parasitism if assimilates acquired through root grafts prolong survival of suppressed trees at the expense of dominant trees.

Mycorrhiza, literally “fungus root,” is a close physical association between a fungus and the roots of a plant. Mychorriza are believed to represent a mutually beneficial symbiotic relationship with plants which probably evolved from an original host/parasite affiliation. Mycorrhizal networks have been shown to function by transferring carbon or nutrients from one plant to another. In most natural environments, which are characterized by mineral nutrient deficiency and various abiotic stress conditions, mycorrhizal plants are thought to have a selective advantage over non-mycorrhizal individuals of the same species. The long, filamentous threads of the fungus (i.e., hyphae) extend out into the soil forming a mycelial mat that greatly increases the ability of the associated plant to absorb nutrients.

There are two main types of mychorriza: endomychorrhiza and ectomychorriza. The fungal hyphae of endomychorrhiza actually penetrate the cells of the root cortex, whereas the hyphae of ectomychorriza do not penetrate the cells but instead cover the root with a mantle and grow between the root cells. The most prominent member of the endomychorriza group is *arbuscular mycorrhiza*, whose hyphae penetrate the cortical cells of vascular plant roots forming arbuscules (branched finger-like hyphae that serve as sites for the exchange of water, phosphorus, carbon, and other nutrients). Arbuscular mycorrhizal (AM) fungi comprise the most common mycorrhizal association and form mutualistic relationships with over 80% of all vascular plants. AM fungi are obligate mutualists and have a ubiquitous distribution around the world.

In temperate and boreal forest communities, most trees associate with ectomycorrhizal (EcM) fungi. EcM fungi are also widespread in their distribution but associate with only 3% of vascular plant families. Ectomycorrhizas occur in certain woody gymnosperms (e.g., Pine family) and angiosperms (e.g., Birch family). The fungal partners in EcM associations account for an estimated 30 percent of the microbial biomass in forest soils. Under natural conditions the presence of the fungal partner is vital for the establishment and growth of a variety of tree species, such as pines. Likewise, it has been shown that association with trees is necessary for the development and reproduction of the fungus.

Finally, nitrogen fixation by bacteria in mutualistic relationships with higher plants can enrich the soil environment and increase plant productivity. A familiar example is the association of *Rhizobium* bacteria with the root nodules of legumes (members of the Pea family), but other symbioses may have an equal or greater ecological importance. For example, the presence of nitrogen-fixing trees in forests substantially alters soil fertility, tree production, and nutrient cycles. Alder is particularly noted for its important symbiotic relationship with *Frankia alni*, an actinomycete, filamentous, nitrogen-fixing bacteria. This bacteria is found in root nodules and absorbs nitrogen from the air, making it available to the tree. Alder, in turn, provides the bacteria with sugars, which it produces through photosynthesis. As a result of this mutually beneficial relationship, alder improves the fertility of the soil where it grows and, as a pioneer species, it helps provide additional nitrogen for the successional species which follow. Red alder stands have been found to supply between 130 to 320 kg of nitrogen per hectare annually to the soil. The long-term impacts of nitrogen-fixing red alder were found to remain very strong after seven decades in mixed conifer stands in Washington, greatly increasing ecosystem productivity on a nitrogen-poor site.

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