The Role of Mycorrhizal Symbioses in the Health of Giant Redwoods and Other Forest Ecosystems[1]

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Abstract: The roots of nearly all land plants form mycorrhizal symbioses with specialized soil fungi. The mycorrhizal fungi serve as extensions of plant roots, taking up nutrients and water and transferring them to the roots. In return, the mycorrhizal fungi receive their primary energy source in the form of simple sugars from plant photosynthates translocated to the roots. *Sequoiadendron giganteum* forms a type of mycorrhizae referred to as vesicular-arbuscular mycorrhizae; seedlings inoculated with mycorrhizal fungi in nurseries can be two to three times larger than noninoculated control seedlings. Mycorrhizal fungi also function in soil nutrient cycling, and their hyphae and reproductive structures (spores, mushrooms, and truffles) are vital components in the complex forest food web. Management strategies that protect the biological component of the soil will ultimately protect the health and functioning of the entire forest ecosystem.

Ecological management of natural resources requires a broad understanding of how ecosystems function. Likewise, conserving biodiversity requires knowledge not only of the population biology of individual organisms but also the interactions and interdependencies of organisms. Such management perspectives provide a means to include the myriad of "less visible" organisms along with the "charismatic" megafauna and flora in our management schemes.

This integrated approach is essential for managing the great diversity of species and functions of soil microorganisms in forest ecosystems. Total species richness is greatest in the soil: the functions of soil microbes power the complex biochemistry of nutrient cycling that yields soil fertility and ultimately, plant and animal productivity.

This paper focuses on the role of fungi in forest ecosystems, particularly mutualistic mycorrhizal fungi of giant redwoods and other forest plants, and provides examples of biotic connections between forest organisms via belowground microbial linkages.

Intrinsic Value of Fungi in the Forest

Fungi must first be viewed for their intrinsic values. Many fungi produce beautiful and elegant reproductive structures known as mushrooms. These fruiting bodies or sporocarps are collected regularly by thousands of amateur and professional mycologists who marvel at their complex forms, learn their identification, study their ecology, or simply savor the edible species for their unique and delectable tastes. Regional mushroom clubs and societies are scattered across North America and other continents. They organize collection trips and meetings to discuss their findings and share in their mycological experiences. Just as we recognize the enthusiasm of bird watcher, native plant, and other "nature loving" societies, so too must we recognize society's longtime interest in and fondness for fungi as part of our recreational pastimes.

Perhaps the most obvious social value of fungi comes from their use in medicine. Many "molds" are famous for their production of antibiotics, such as penicillin. Ancient pharmacopoeia list numerous medicinal uses of fungi. Yet, we have barely explored the medicinal potential of fungi. Any conservation discussion that emphasizes efforts to preserve plant species for as yet unknown medicinal value must also include the fungi.

Several species of wild, edible, forest mushrooms are harvested commercially in Alaska, Oregon, Washington, and California, and a multimillion dollar wild mushroom industry has developed (Molina and others 1993). This new industry has created conflicts between traditional recreational users of forest mushrooms and commercial mushroom harvesters and prompted resource managers to develop new permit systems to protect and regulate this resource. The monetary value of this new, special forest crop and the regional conflict over its proper use has brought attention to this previously unheralded group of forest organisms. Such social and economic values underscore the need to understand the biodiversity of fungi in relation to the forest community.

Ecosystem Functions of Fungi

Fungi are key organisms in the functioning of ecosystems, and while we may marvel at their great numbers, understanding their "functional diversity" is critical to comprehending their importance in ecosystem health. Fungi are most known for their role in the decomposition cycle, particularly for the breakdown and mobilization of recalcitrant organic compounds in dead wood. Fungi not only cycle nutrients through the decomposition process, they also retain nutrients within their enormous living biomass in the soil, thereby reducing nutrient loss through leaching. This great fungal biomass is a primary food source for many grazing soil insects. Indeed, most soil microarthropods feed strictly on fungal hyphae, and in so doing return these stored nutrients to the soil and make them available to plants.

Another important role of fungi is as pathogens, directly killing or weakening forest plants. Such a role is typically viewed as having negative impacts on forest health and productivity. But fungal diseases also have positive influences on ecosystem productivity and biodiversity (Trappe and

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Luoma 1992). For example, disease-killed trees leave openings in the forest where light-requiring-plants can establish. Such habitats are frequented by wildlife. Standing dead trees also provide habitat for cavity-nesting birds and mammals. Thus, although it is important that we not exacerbate diseases with our management practices, it is important to realize that pathogens are a natural component of the forest ecosystem and contribute to landscape diversity.

Another large group of forest fungi are the mutualists who live in beneficial symbioses with forest plants. Understanding the closeness of these co-evolved plant-fungus relationships helps us to visualize how organisms are ecologically linked, and from that understanding we can build a basis for ecological management.

Mycorrhizal Fungi of Forest Plants

Mycorrhiza literally translates as "fungus-root" and defines the common association of specialized soil fungi with the fine roots of nearly all forest plants. Mycorrhizal associations represent one of the more widespread forms of mutualistic symbioses in terrestrial ecosystems. Indeed, these plant-fungus associations have co-evolved over the millennia such that each partner depends upon the other for survival.

The mycorrhizal fungus basically serves as an extension of the plant root system, exploring soil far beyond the roots' reach and transporting water and nutrients to the roots. The uptake of phosphorus and nitrogen are especially critical functions of mycorrhizal fungi, which can release bound forms of these nutrients otherwise unavailable to the roots. In return, the plant is the primary energy source for the fungus, providing simple sugars and vitamins produced in photosynthesis and transported to the roots and then the fungus. It is important to realize that mycorrhizal fungi have limited saprophytic ability, that is, they possess few of the enzymes needed to break down efficiently complex organic matter in the soil. Therefore, their survival in natural ecosystems depends on the supply of sugar (photosynthate) from their associated host plants. Likewise, many plants strongly depend on their mycorrhizal fungi for nutrient and water uptake. This co-evolution in dependency reinforces the need to view organisms through their relationships within the forest.

There are several classes of mycorrhizae, but only the three most common will be discussed: ectomycorrhiza, vesicular- arbuscular mycorrhiza, and ericoid mycorrhiza (Harley and Smith 1983, for a comprehensive review of mycorrhizae; and Castellano and Molina 1990, for color photos of mycorrhiza morphology and anatomy). *Ectomycorrhiza* is the most common type appearing on forest trees in the Western United States and Canada. Ectomycorrhizal hosts include all species in the Pinaceae *(Abies, Larix, Picea, Pinus, Pseudotsuga,* and *Tsuga),* Fagaceae *(Castinopsis, Lithocarpus, Quercus),* Salicaceae *(Salix, Populus),* and Betulaceae *(Alnus, Betula, Corylus).* Additionally, scattered genera such as *Arbutus, Arctostaphylos, Cercocarpus,* and *Eucalyptus* form ectomycorrhizae. The dominant nature of these species in western forest ecosystems, especially Pinaceae, contributes to the pervasiveness of ectomycorrhizae in western forests.

Ectomycorrhizae develop on the short, feeder roots. The fungus forms a sheath or *mantle* of fungal tissue around the feeder root. The mantle serves as a storage tissue for nutrients received from mycelium in the soil and physically protects the fine roots from some pathogens and desiccation. The fungus also penetrates between the root's cortical cells to form a network of fungus tissue called the *Hartig net.* Nutrient exchange occurs within this extensive, intimate contact zone: sugars and vitamins move into the fungus, and water and nutrients move into the plant. Many ectomycorrhizal fungi produce plant hormones that cause extensive branching of colonized feeder roots. This branching greatly increases the root surface area and provides an extensive contact zone between the fungus and root.

The fungus grows from the colonized roots into the surrounding soil. Mycelial colonization of the soil varies among ectomycorrhizal fungi; some may only grow a few centimeters into the soil and others can grow several meters from the ectomycorrhiza. Some fungi produce dense, hyphal mats that strongly bind the soil and organic matter. If the mycelium is white or brightly colored, these extensive mats may be readily visible when a bit of the upper organic layer is removed. Other fungi produce colorless or dark mycelia that are more difficult to see with the unaided eye, but their growth into the soil is likewise extensive.

Thousands of ectomycorrhizal fungus species occur in the forests of Western North America; Douglas-fir *(Pseudotsuga menziesii)* alone associates with nearly 2000 species (Trappe 1977). Most ectomycorrhizal fungi are basidiomycetes and ascomycetes and many produce mushroom fruiting bodies that abound in western forests during the moist times of the year. Many ectomycorrhizal mushroom-forming fungi are especially prized for their edibility. Well-known edible species occur in the genera *Cantharellus* (chanterelles), *Boletus* (boletes), *Lactarius* (milky caps), *Tricholoma* (matsutake), *Hydnum* (tooth fungi), and *Ramaria* (coral fungi) (Molina and others 1993 provide a complete listing of ectomycorrhizal fungus genera). Another large and diverse group of less well known ectomycorrhizal fungi are the truffles, which produce fruiting bodies beneath the duff or soil surface. Few truffle species are harvested commercially, but, as will be discussed later, truffle fungi are a central part of the forest food web.

The habitat requirements of ectomycorrhizal fungi and their interactions with particular plant species are poorly understood. Some fungi are more abundant in certain age classes of forests. As plant-species composition changes during forest succession, the fungus communities similarly undergo change. This fungus succession is in response to changes in tree composition, tree age, and soil qualities such as accumulation of organic matter. The ecological requirements of mycorrhizal fungi, particularly their relation to forest community succession and disturbance events, represent large knowledge gaps needing research attention.

The second important class of mycorrhizae in our forests is called *vesicular-arbuscular (VA) mycorrhiza.* Unlike ectomycorrhizae, VA mycorrhizae do not cause obvious morphological changes in colonized roots; the roots must be stained to reveal the internal fungus colonization. The fungus mycelium ramifies through the cortex of the fine roots, and produces the characteristic arbuscules and vesicles. *Arbuscules* (literally meaning 'little tree') are finely branched hyphal structures that proliferate within a single cortical cell and function as the exchange site between fungus and host. *Vesicles* are balloon shaped and function as storage organs VA mycorrhizae also proliferate in the soil but their mycelium is typically colorless and thus not visible to the unaided eye.

Unlike ectomycorrhizal fungi, VA mycorrhizal fungi do not produce large, fleshy fruiting bodies. They typically produce large spores (50 to 1,000 µm in diameter) either singly or in clusters in the soil (Gerdeman and Trappe 1974). The spores can be sieved from the soil for identification, study, and inoculum production. The VA mycorrhizal fungi number only in the hundreds worldwide, so their species diversity is less than ectomycorrhizal fungi. But, because the vast majority of plants form VA mycorrhizae, the fungi are widespread throughout most terrestrial ecosystems. Western forests are no exceptions, because most understory plants and early successional herbs are VA mycorrhizal.

Giant redwood *(Sequoiadendron giganteum)* forms VA mycorrhizae as does the coastal redwood *(Sequoia sempervirens)* (Mejstrik and Kelly 1979). Other dominant VA mycorrhizal tree species in western forests include members of the Cupressaceae *(Calocedrus, Chamaecyparis, Juniperus,* and *Thuja).* Pacific yew *(Taxus brevifolia,* Taxaceae) also forms VA mycorrhizae. Common VA mycorrhizal broadleaf trees include species in the genera *Acer* (maples), *Aesculus* (buckeyes), *Cornus* (dogwoods), *Fraxinus* (ashes), *Platanus* (sycamores), *Prunus* (cherries), *Sambucus* (elderberries), and *Ulmus* (elms).

The third prevalent mycorrhiza type in western forests is called *ericoid mycorrhiza.* As the name implies, this type is restricted to the species in the Ericaceae. Because ericaceous plants (for example *Gaultheria, Rhododendron,* and *Vaccinium* spp.) are abundant and often dominant components of the understory, ericoid mycorrhizal fungi are likewise widespread. The fungal symbionts are mostly ascomycetes. Ericoid mycorrhizae are characterized by the intracellular colonization of the epidermal cell layer of the fine hair-like roots. Ericoid mycorrhizal fungi differ enzymatically from ectomycorrhizal and VA mycorrhizal fungi because they are able to breakdown and mobilize nitrogen from organic sources. Thus, ericoid mycorrhizae play an important role in nitrogen cycling in forest ecosystems.

Mycorrhizae of Giant Redwood

The physiology and ecology of giant redwood mycorrhizae are poorly known. In general, however, woody plants depend upon mycorrhizae for survival in natural ecosystems (Trappe 1977) and giant redwoods are no exception. Kough and others (1985) inoculated seedlings of giant redwood, coastal redwood, incense cedar *(Calocedrus decurrens),* and western red cedar *(Thuja plicata)* with VA mycorrhizal fungi and compared them to noninoculated seedlings; superimposed on this design was high and low phosphorus fertilization. All species responded dramatically to VA mycorrhizal inoculation . At both high and low phosphorus fertilization, inoculated giant redwood seedlings were two to three times larger than noninoculated control seedlings. Adams and others (1990) report similar growth responses of redwood and cedar seedlings grown in bareroot nurseries. They developed a nursery management scheme to ensure mycorrhizal inoculation with selected beneficial VA mycorrhizal fungi that dramatically improves seedling productivity and health.

Because of the difficulty in separating mycorrhizal effects from other biological and environmental effects on mature plants in natural ecosystems, most work in mycorrhiza research has been done on seedlings under controlled conditions. Recent field studies in Oregon, however, show the strong dependence of forest recovery and productivity on maintenance of mycorrhizal fungus populations following disturbance (Molina and Amaranthus 1991, Perry and others 1987). Reports from Europe on forest decline also point to the positive relationship between abundant, active mycorrhizal activity with healthy forest stands (Jensen and others 1988). With this view in mind, it is important to manage our forests to maintain the health of beneficial soil microorganisms. For example, mycorrhizal fungi are strongly aerobic and need ample oxygen for efficient physiological functioning. Minimizing compaction disturbance that reduces soil aeration is critical to the functioning of these soil microorganisms. This management consideration is especially important in giant redwood groves that have frequent visitors and foot traffic.

Amaranthus and others (1989) and Molina and Amaranthus (1991) reviewed the ecology of soil microorganisms in forest ecosystems and discussed several management strategies to ensure their health and integrate their functions into an ecological management scheme. They stress that although soil microorganisms are adapted to disturbance, those adaptations fall within the limits of natural phenomena and intensity. They recommend management strategies that minimize disturbance to soil structure, maintain organic matter and woody debris, and promote rapid recovery of vegetation.

Trees, Truffles, and Beasts

Organisms do not live in isolation from other organisms. The ecological literature is rich with examples of interdependencies within plants, animals, or between plants and animals. Mycorrhizal interactions within forest ecosystems illustrate how "invisible" soil organisms that perform important ecosystem processes also serve as biological linkages between diverse groups of forest organisms. For example, research on the reproductive biology of mycorrhizal fungi shows its connection to ecology of the northern spotted owl (Strix occidentalis). A primary prey of the northern spotted owl is the northern flying squirrel *(Glaucomys sabrinus)*. During certain times of the year, the northern flying squirrel feeds on a wide variety of mycorrhizal truffle fungi (Maser and others 1985). As truffles mature, the interior tissue fills with spores and emits a distinctive odor. Small mammals such as the northern flying squirrel forage for these truffles by smell, excavate, and devour them. The spores pass through the mammals unharmed and are dispersed during defecation. The spores then re-enter the soil where they germinate and form new mycorrhizae with tree roots.

Hundreds of truffle fungi occur in western forests and most forest mammals consume them. Thus, in this example of tree-fungus-prey-predator connections, resource managers can view the northern spotted owl within the context of its ecosystem linkages rather than through a simple dependency on old-growth forests. Such holistic perspectives enable development of ecosystem management tools and avoid the often devisive nature of single species conservation approaches.

Conclusions

As we develop holistic approaches to understanding forest ecosystems and integrated, ecologically based management tools, we must factor in the inseparable connections to soil organisms. Forest fungi are one of the more numerous groups of forest organisms and play a critical role in nutrient cycling, soil fertility, and thus ecosystem productivity. They are also cornerstones in the complex forest food web. Forest plants have co-evolved mutualistic relationships with symbiotic root fungi such that their survival and fitness depends upon the healthy functioning of these fungi and vice versa. Just as forests invest tremendous capital in the form of photosynthates to fuel beneficial soil organisms, so too must we protect the unseen and overlooked belowground ecosystem.

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