Mycorrhizae and Soil Structure
Ted St. John, Ph.D.

Mycorrhizae can produce better plant growth and otherwise be of benefit to individual plants, but perhaps the most important reasons to inoculate may have to do with effects on the plant community and the soil.

Structure is one of the most important qualities of a soil, and is perhaps the crucial difference between soil and "dirt". The tiniest soil particles attach themselves to each other, and those clumps cling to each other, on up through a size hierarchy of soil aggregates. The aggregates define pore space that is vital for movement of water, air, soil animals, and for the growth of roots.

Soil aggregates are held together by different forces at different size scales. In the smallest sizes ionic forces dominate, then bacterial polysaccharides take over in somewhat larger aggregates. In the size range that is readily visible in soil, mycorrhizal fungi play the central role. They produce a glycoprotein called "glomalin", named after the group of fungi that form endomycorrhizae. You can find a great deal of information on the internet by performing a search for the word "glomalin".

Mycorrhizae and Weeds
Ted St. John, Ph.D.

The best ecological term for a weed is "ruderal". A ruderal is a plant adapted for life on disturbed soil. Ruderals grow fast, a property that depends heavily on readily available forms of plant nutrients. For example, nitrogen tied up in organic form is not of much use to ruderals; they need soluble nitrate to realize their fast growth rates. Other components of the ruderal strategy are high reproductive rates and independence of symbiotic fungi. In other words most ruderals, at least in arid climates, do not need to become mycorrhizal.

These traits make ruderals very well suited for life on disturbed sites and newly graded soil, exactly the places where restoration projects are planted. Slower-growing native plants on the other hand do not benefit from these characteristics and must find mycorrhizal symbionts in the soil if they are to survive. Nitrate and other readily available forms of plant nutrients are of no particular advantage to natives, which get along on very slowly released forms of nutrients in their native habitats.

The differences in optimum soil conditions are only some of the factors that select for either late successional natives or ruderals. The network of mycorrhizal fungi exerts an effect of its own on many ruderal plant species. In the case of Russian thistle, the mycorrhizal fungi behave almost as pathogens, causing death of the ruderal plant's roots. Other ruderal species do not react in quite such a dramatic way, but most cannot grow rapidly in the presence of a well-developed mycorrhizal network. The

mechanisms are not understood, but a number of experiments have demonstrated the effect. See the restoration project section of this web site for examples from practical projects.

Mycorrhizae and Plant Diversity
Ted St. John, Ph.D.

Most kinds of plants need to be mycorrhizal in order to survive in the wild, but every flora includes a few species that are independent of the symbiosis. Among these non-hosts and independent species are most ruderals (weeds).

If the fungi are missing from the soil, plants that depend upon the symbiosis, known as "mycotrophs", will be unable to survive. In between the extreme forms are facultative mycotrophs, which can survive on their own if the soil is rich in plant nutrients, but need to be mycorrhizal in nutrient poor soils.

Even if your seed mix includes a diversity of species, the diversity that you see on the project will depend on the presence of mycorrhizal fungi in the soil. Non-mycotrophic species will do fine if the soil has some fertility, and many such plants are in common use for roadside plantings, mine reclamation, and casual attempts at restoration. The wheat grasses, widely used in the Great Basin, are representative of such plants. Facultative mycotrophs can survive in soil with some fertility, but must be mycorrhizal in most conditions. The obligate and facultative mycotrophs are the plants that appear on an inoculated job but do not appear, or perform poorly, on an uninoculated project.

The Kinds of Mycorrhiza
Ted St. John, Ph.D.

Seven kinds of mycorrhiza are recognized in the scientific literature. The most common is arbuscular (named for internal structures called arbuscules) or vesicular-arbuscular (arbuscules and another structure called vesicles), abbreviated as AM. This is an endomycorrhiza, which means the fungus enters the cells of the root. There are other kinds of endomycorrhiza, but this one is so much more common that many people are now just calling AM endo, and referring to the others by other names. AM are found on grasses, most crop plants, many trees, shrubs, flowers, and in fact about 80% or so of the world's plant species. The fungi are nondescript soil fungi that are not evident without a microscope.

The next most common kind is ectomycorrhiza (ECM), which means that the fungus enters the root but not the root cells. There is only one kind of ECM, so this name is unambiguous. The host plants are pines, firs, spruce, oaks, and several other kinds of plants, mostly forest trees. The fungi often form mushrooms or truffles. A related category is ectendomycorrhiza, in which the fungus enters the root cells.

Manzanita, madrone, and a few other plants form arbutoid mycorrhizas. These look like ECM and have similar fungi, but are technically endomycorrhizas. A separate but apparently related category is monotropoid, found on certain plants without chlorophyll. While these traditionally have been called "saprophytic," it turns out that they share a mycorrhizal fungus with a nearby tree, and they are in effect parasites of the tree by way of the mycorrhizal fungus.

Blueberries and related plants have ericoid mycorrhizas. The fungi are obscure and there is apparently no commercial inoculum.

Orchid mycorrhizas are unique in that they are required for seed germination. Some kinds of orchids never photosynthesize, but instead parasitize the mycorrhizal fungi.

Mycorrhizae and the Plant Community
Ted St. John, Ph.D.

Endomycorrhizal fungi, and to a lesser extent ectomycorrhizal fungi, are quite non-specific for host plants. In other words, you do not need a "right" mycorrhizal fungus for each plant species, except that an endomycorrhizal plant needs and endomycorrhizal fungus. One consequence of this non-specificity is that the same mycorrhizal fungus can interconnect a number of unrelated plant species.

The interconnected plants are, to some extent, suggestive of the old ecological idea (largely discredited among ecologists) that the plant community is a sort of "super organism." The interconnected plants share a nutrient uptake system, and jointly contribute to its energetic support.

In a natural ecosystem, the network interconnects a number of plant species, and also consists of between one and two dozen fungal species, each with its own network, either patchy in distribution or interwoven through other networks.

The Benefits of Mycorrhizal Inoculation
Ted St. John, Ph.D.

The main benefit is improved uptake of soil phosphorus. Because of better phosphorus nutrition, mycorrhizal plants can grow much more quickly than non-mycorrhizal plants. The experiments that show this growth response are done in controlled conditions, and it is unusual for a user in the field to see responses of the kind that are often shown in scientific (or advertising) photos. The user may see a gain of a few percent up to double or triple, depending on plant species, soil factors, fertilization, and whether they already may have native mycorrhizal fungi.

Mycorrhizas appear to have only a minimal effect on uptake of nitrogen, although ECM and ericoids may have some effect. Mycorrhizas do not fix nitrogen, but some people may confuse this symbiosis with the N-fixing symbiosis between legumes and bacteria of the genus Rhizobium. There are sometimes big effects of mycorrhizas on certain micronutrients, especially zinc and copper.

Mycorrhizal plants are often more drought tolerant. This is a tricky point, since big mycorrhizal plants in pots use water much more quickly than little non-mycorrhizal plants in pots. However, it appears that it can be a very real effect in the ground. This is probably an indirect effect of phosphorus nutrition; plants fertilized with phosphorus show the same improvement. However, in natural conditions, mycorrhizal plants are certainly better suited to face dry conditions than non-mycorrhizal plants.

Mycorrhizal plants are more resistant to many root diseases. The scientific results do not all agree, and tests with certain pathogens have shown the reverse. However, in nature it appears that a range of beneficial organisms really do fight disease, and those good guys are more abundant if the plants are mycorrhizal. This explains most of the inconsistent findings, and we can now say with some confidence that mycorrhizal inoculation is an important part of a holistic disease-fighting program.

In restoration, reclamation, and erosion control, a very important ingredient is the network of mycorrhizal fungi in the soil. The network builds soil structure, which helps hold the soil together. It also allows survival of many kinds of seedlings that would otherwise never get big enough to be evident on the job site. Because some species in the seed mix show up only when inoculated, inoculation in effect increases plant diversity.

The soil network, in combination with healthy mycorrhizal host plants, is very important in resisting weed invasion. There have now been a good number of field projects that have successfully fought off weeds, where other methods that did not involve inoculation have consistently led to nightmare weed infestations. Inoculation is often not enough in itself, but must work with rapidly growing native plants and in many cases, some means to temporarily immobilize nitrate, such as a layer of straw or wood chips.

The Plants That Become Mycorrhizal
Ted St. John, Ph.D.

See the myco-bit on types of mycorrhizas for part of the story here. This part is intended to quickly figure out what kind of inoculum your plants may need.

In the majority of cases the right kind is arbuscular mycorrhiza (AM), often just called endomycorrhiza. In this group are all grasses, palms, almost all bulb plants, anything

related to roses, apples, peaches, pears, strawberries etc. (the rose family), most tropical plants apart from orchids, and the great majority of horticultural species. Almost all crop plants, apart from the mustard and spinach families, have this kind. The majority of wild plants, including shrubs, wildflowers, and broad leaf trees, have this kind. A few conifers do, especially the ones related to redwoods, cedars, and junipers. It is easier to list the non-host species (no mycorrhizae) than the ones that have AM.

The forest timber trees (apart from redwoods and cedars) are ectomycorrhizal (ECM). This includes all pines, firs, Douglas firs, spruce, larch, oaks, birch, beech, and some willows and cottonwoods, which have both ECM and AM. A few nut crops have EM, including chestnut, hazel, and sometimes walnut and pecan. There are recent reports that very old grape vines might be EM, although grape is normally a good AM host.

Manzanita and madrone have the arbutoid type, and there seems to be no commercial inoculum for those. Blueberry, huckleberry, heather, and related plants have ericoid mycorrhizas, and there is also no inoculum for those.

Orchids have their own kind and there is no need to inoculate them. Commercial orchid production is done with special chemical media that bypass the need for mycorrhizas. Grown orchids usually have rejected the fungus and are non-mycorrhizal.

Some plants do not become mycorrhizal at all- the "non-hosts". These include the mustard family (cabbage, radish) and the spinach family. Some related wild plants and many kinds of weeds also lack mycorrhizas. Inoculation is often part of a program to fight weeds, since non-host weeds have more trouble competing with mycorrhizal plants.

In your list of plants, look for the ones that may be ECM, arbutoid, ericoid, and non-hosts. Since the mycorrhizal status is known with certainty for only a fraction of the world's plant species, many recommendations will have to be guesses. The best guess is usually AM.

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