The Importance of Mycorrhizal Fungi and Other Beneficial Microorganisms in Biodiversity Projects[1]

Ted St. John[2]

Abstract.-- Ecosystem processes are the combined activities of a variety of microorganisms. The most important functional groups include mycorrhizae, nitrogen fixers, decomposers, plant growth promoting rhizobacteria, pathogen-suppressive organisms, builders of soil structure and of protective surface crusts. These organisms do not reliably disperse to the nursery or to a planting site. They require a focused inoculation program from stockpiled top soil or from pre-inoculated plants. Current technology allows introduction of mycorrhizae, nitrogen fixers, and pathogen suppressive organisms. Other functional groups may soon become available commercially.

BENEFICIAL MICROORGANISMS

In the great majority of natural communities, the primary producers depend heavily on microorganisms. Some of the microbes are symbionts, as in the case of mycorrhizae and nitrogen fixers. Others are free-living, but nevertheless linked tightly to the well-being of the primary producers. These include the organisms that decompose and mineralize organic detritus, others that promote plant growth and suppress plant pathogens, and some that build soil structure. There is considerable overlap between some of these groups.

Plant species that are highly dependent upon mycorrhizae or other microbes have been difficult to work with during and after the nursery stage, because the symbionts are lacking on site or suppressed by horticultural practices. Intentional introduction of the beneficial microorganisms sometimes makes the difficult plant species easier to grow. It is the intention of this paper to suggest the most important kinds of organisms, and to provide a few ideas on how one might experiment with some of them. In most cases, the use of these organisms is not yet a turnkey operation.

The importance of the beneficial microorganisms is in ecosystem functionality. These organisms help the roots take up nutrients, bring nutrient elements into the ecosystem from atmospheric or mineral reserves, break down detritus, release mineral elements in soluble form, and protect the roots from pathogens. They also hold soil aggregates together, creating channels through which roots grow, soil animals move, and water percolates.

This assumes great importance when we wish to produce a functional ecosystem on a previously disturbed site. A functional ecosystem, with its defining properties of sustainability, resistance to invasion, productivity, nutrient retention, and biotic interactions (Ewel 1987), is a product of photosynthesis and all the microbial processes. To establish these processes, all organisms must be present and conditions must be compatible with their needs.

Few of the organisms, and none of the functions, are present at severely disturbed planting sites. Unlike pathogens and opportunistic fungi, the important organisms do a poor job of dispersing. If we do not assure their presence and functionality, there will be no ecosystem.

The kinds of organisms we will consider are mycorrhizae, nitrogen fixers, decomposers, plant growth promoting rhizobacteria, pathogensuppressive microorganisms, soil structure-building organisms, and cryptogamic crust organisms.

MYCORRHIZAE

The term "mycorrhizae" includes several distinct

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[1] Paper presented at the Western Forest Nursery Associations meeting at Fallen Leaf Lake, September 14-18, 1992.

[2] Ted St. John is Plant Ecologist, Tree of Life Nursery, San Juan Capistrano, CA 92693.

kinds of associations between fungi and roots (Harley and Smith 1983). All mycorrhizae have in common a fungal connection between the soil and the root. Some host species may have more than one kind of mycorrhiza, but. most form only one. The most widespread types of mycorrhiza are vesicular-arbuscular mycorrhiza (VAM) and ectomycorrhiza (ECM).

Vesicular-arbuscular mycorrhizae involve aseptate fungi, and are named for characteristic structures found in the root cortex. VAM are the mycorrhizae of most agricultural crops and most native plant species. VAM fungi are present in almost all natural soils, but are consistently lacking in graded or eroded soil, and on sites that have supported only weeds. Nursery plants grown in sterilized or soiless media lack VAM, at least during the first months. Verifying the presence of VAM usually requires special laboratory preparation.

Ectomycorrhizae involve mushroom and other higher fungi. Oaks, some conifers, and some other woody species are ectomycorrhizal. As we grow a wider range of native species for revegetation, we will discover more expected VAM hosts that turn out to be ectomycorrhizal. Recently we have found some members of the rose family to be ectomycorrhizal. Unlike VAM, ECM are often evident without special staining of the roots.

The Ericaceae and related families have several distinct kinds of mycorrhizae, more closely related to ECM than VAM (Harley and Smith 1983). These are "arbutoid" (Arbutus, Arctostaphylos, Pyrola), "ericoid" (Vaccinium, *Rhododendron),* and "monotropoid"(Monotropa). Other distinct kinds of mycorrhizae occur in the orchids and in some minor tropical families.

The main benefit of mycorrhizae is improved uptake of nutrients, especially phosphorus. Phosphorus nutrition brings with it drought resistance and other benefits. ECM in some cases directly aid in water uptake (Boyd et al. 1986, Brownlee et al. 1982), and there is some evidence that VAM may do so as well (Hardie 1986). Some kinds of ECM fungi offer significant protection from certain pathogens (Harley and Smith 1983). It is likely that all kinds of mycorrhizae figure importantly in soil structure.

We think of microorganisms as ubiquitous and quick to disperse. That is true of the opportunistic species that cause food spoilage, but it is not true of most mycorrhizal fungi or other beneficial organisms. The desirable species may disperse by very slow methods, such as growing from root to root, or moving with small invertebrate vectors. VAM fungi and many others make little progress without suitable host plants, and may fail to cross bare ground or weedy fields. In nursery conditions, they often are unable to become established because of fertilization or fungicide use.

It is almost certainly necessary to introduce mycorrhizae and other beneficial organisms after severe disturbance or a long fallow. All or most of the beneficial organisms can be introduced with carefully salvaged and stored top soil. It is very important that this be the upper layer (the soil volume that held most fine roots) of a native soil very similar to the soil of the planting site.

Sometimes the need to restore becomes evident only after the top soil has been lost. If top soil is to be collected off-site, it is important that the donor site have the right kind of vegetation. Soil from a pine forest, for instance, may provide little benefit to a grassland or deciduous forest. Weed patches are the worst possible donor sites; most weeds do not need mycorrhizae, and there is little assurance that such soil will provide inoculum. The weed load in such soil often makes it worse than no top soil at all.

Any top soil donor areas will suffer in proportion to the amount of soil removed, since the disturbance of collecting kills roots and opens up the site for invasion by weeds. To conserve other natural areas and assure compatibility of the organisms, the best option is collection and stockpiling of top soil from the planting site before disturbance. Collection should take place when soil organisms are dormant, as during a dry or cold season, because the resting stages are generally more resistant to disturbance than the actively growing stages. Stockpiling should be for the shortest possible time. Covering the pile to keep it cool and dry may improve survival of most organisms.

When top soil is not available, or is of doubtful quality, mycorrhizae and many other beneficial organisms can be introduced with the container plants. Forest Service and commercial nurseries are now routinely producing ectomycorrhizal conifers, and standard procedures are available (Castellano and Molina 1990). Both VAM and ECM inoculum have been commercially available, but due to the limited market commercial sources remain unpredictable.

Inoculating nursery stock with mycorrhizal fungi is not enough. Nursery procedures must be consistent with the needs of the symbiosis. Heavy fertilization and incompatible fungicides commonly prevent mycorrhizal establishment. It takes a large-scale commitment to switch away from chemicals and toward beneficial organisms, but most of the problems now solved by chemicals are amenable to other solutions. Readily available phosphorus can be quite inhibitory, but such insoluble forms as rock phosphate are not. Graham and Timmer (1984) reported the additional benefit of better retention of rock phosphorus in a soiless mix.

A further example is control of the damping-off and root rot fungus Rhizoctonia solani. Benlate and PCNB are effective for control of R. solani, but are also very toxic to VAM fungi (Trappe et al. 1984). However, *Trichoderma* viride, a pathogen suppressive microorganism known to effectively control R. solani, does not harm VAM fungi (Calvet et al. 1990, Kohl and Schlosser 1989, Linderman et al. 1991). By incorporating two beneficial organisms rather than one, it is possible to dispense with some fungicide applications. It is important to note that Trichoderma spp. may detrimentally effect ECM fungi (Summerbell 1987).

In some cases it will be possible to postpone mycorrhizal inoculation until outplanting. This frees the nursery from fundamentally changing its procedures, but ultimately requires more labor and larger amounts of inoculum than would be required at the nursery stage. Inoculation in a hydroseed mix is not promising, since VAM inoculum is ineffective if spread on the surface of the soil (Hayman et al. 1981). Hayman et al. (1981) were able to inject inoculum into the soil with a fluid drilling system. Some kinds of inoculum can be positioned in the root zone with agricultural equipment (Menge and Timmer 1982), but doing so requires level, largely stone-free ground.

As with nursery inoculation, it is important that cultural procedures be compatible with the beneficial microorganisms. Heavy fertilization and pesticide use are the most likely problems. Other potential problems include insufficiently composted organic matter, which often harbors inhibitory microorganisms, or sludge or other amendments containing excessive amounts of copper, zinc, or cadmium.

NITROGEN FIXING MICROORGANISMS

Plants with nitrogen-fixing associations are important in some native vegetation types. Among our native nitrogen-fixing plants are alders; Ceanothus species, and various legumes. Some of the microorganisms are available commercially and some are probably available only from native soil. Some may be difficult to establish, others just require introduction of the microorganism, and others appear to take care of themselves.

Where commercial inoculum is available, the supplier may provide procedures. Where laboratory cultures of the nitrogen-fixing symbionts are not available, inoculation may be a matter of trial and error. There will be cases in which it is preferable to leave the nitrogen-fixers out of the mix rather than risk the host-specific pathogens and other dangers of native soil in the nursery. Carefully preserved top soil, applied at the job site, will meet most of the needs of the plants.

DECOMPOSER ORGANISMS

The degradation of plant remains is a critical step in nutrient cycling. Decomposition is carried out by a sequence of functional groups. The first on the scene are the opportunistic "sugar fungi" and fast-growing bacteria. They quickly metabolize readily available cell contents and leachable materials, and may complete their life cycles within a few days of the death of the plant material. A second wave of organisms also arrives quickly, and makes use of slightly more resistant plant compounds such as hemicellulose and cellulose (Alexander 1971).

The most resistant compounds are vulnerable only to specialized organisms, many of which disperse and grow slowly. Lignin and other phenolics are quite resistant to biochemical breakdown, and form complexes with cellulose and proteins that are even more resistant. Their degradation may require an infusion of "starter glucose," which in nature often comes through fungal tissue from other regions of the soil. Soil-dwelling invertebrates provide comminution of plant materials (Witkamp 1971). They are important in local dispersal of the primary decomposers.

The animal components of the detrital food web are the most important agents of mineralization. The primary decomposers tend to absorb plant nutrients into their own tissues and reproductive structures. Only when they are consumed by the next trophic level are the nutrients released in forms available to higher plants (Coleman et al. 1977).

The opportunistic organisms usually take care of themselves, since they are ubiquitous and quick to disperse (Alexander 1971). The process of decomposition might be hastened by adding invertebrates and specialized microorganisms in top soil.

PLANT GROWTH PROMOTING RHIZOBACTERIA

Plant growth-promoting rhizobacteria (PGPR) include a range of organisms that live in close association with roots. PGPR are of great potential importance, and their culture and modes of action are the subject of active research (Burr and Caesar 1984, Linderman and Paulitz 1990, Okon and Hadar 1987). The possible mechanisms by which PGPR aid plant growth include suppression of root pathogens through chelation of iron or production of antibiotics (Burr and Caesar 1984, Kloepper et al. 1991, Welter 1985), fixation of nitrogen (Chanway and Holl 1991), and production of plant hormones (Holl et al. 1988). PGPR are synergistic with mycorrhizae in stimulating plant growth (Chanway and Holl 1991, Meyer and Linderman 1986), and PGPR may stimulate root colonization by mycorrhizal fungi (Meyer and Linderman 1986). There has been some success with PGPR in agriculture, and commercial preparations are likely to become available (Burr and Caesar 1984, Linderman and Paulitz 1990, McIntyre and Press 1991, Okon and Hadar 1987).

No practical recommendations are offered in this paper, except to note that PGPR will be among the beneficial organisms present in quality top soil.

PATHOGEN-SUPPRESSIVE MICROORGANISMS

Natural soil contains organisms that inhibit pathogens (Papavizas 1970). In the nursery or on a newly disturbed planting site, the complex balance of microbes has often been severely altered. There may be a nearly sterile environment, where the first organisms to arrive on the scene have a competitive advantage. All too often, the first ones to arrive are seed-borne plant pathogens (Leach and Garber 1970).

Fungi of the genus Trichoderma have repeatedly been implicated as suppressive factors in soils (Baker and Martinsen 1970, Leach and Garber 1970). Other pathogen-suppressive fungi have been reported from the genera Gliocladium (Sreenivasaprasad and Manibhushanrao 1990, Wu and Lu 1984) and Penicillium (Wu and Lu 1984). Certain fluorescent Pseudomonad bacteria are able to suppress various root diseases (Weller 1985).

Disease suppression may be associated with a mixture of fungi rather than a single species (Kuter et al. 1983). Kwok et al. (1987) reported that combinations of bacterial antagonists with Trichoderma hamatum were more effective than the fungal isolate alone.

Hyphae o1' fungal antagonists may coil around hyphae of the pathogen. Antagonistic bacteria lysed the cell wall and plasmolysed conidia of the pathogen (Papavizas 1970, Wu and Lu 1984). T. viride produces antibiotics that can protect seedlings from damping off (Leach and Garber 1970).

Top soil, as always, is a good source of organisms for field planting. In the nursery, a commercial preparation of Trichoderma or pathogensuppressive bacteria would be safer than introduction of field soil. Certain ectomycorrhizal fungi are among the organisms that suppress pathogens (Zhao and Guo 1989) and could theoretically be dual-purpose symbionts.

Even soil invertebrates may be of value in disease control. Certain Collembola, soil insects that eat fungi, may be able to help control pathogens (Curl and Gudauskas 1985). Other Collembola eat VAM fungi (Moore et al. 1985, Warnock et al. 1982), casting doubt on whether the good effects outweigh the damage.

SOIL STRUCTURE-BUILDING ORGANISMS

Soil particles bind together to form aggregates, which help define the movement of air and water through the soil. Relatively large spaces between aggregates (macropores), allow rapid movement of water and air and permit. ready penetration by 'roots. Graded or otherwise severely disturbed soil has no structure. The particles function as individuals, and there are no distinct pore spaces (Kramer 1969). Since roots must grow into pores near their own diameter (Taylor 1974), it is very likely that many plant species cannot become established in non-aggregated soil.

Binding forces that hold soil particles into aggregates include chemical reactions and biological processes. Soil bacteria produce adhesive mucilages that cement small aggregates. The hyphae of soil fungi, particular mycorrhizal fungi,
confer stability to mid-size aggregates (Miller and Jastrow 1990, Tisdall and Oades 1979). Macropores are short-lived unless the aggregates are waterstable (Kemper and Rosenau 1986).

CRYPTOGAMIC CRUST ORGANISMS

The surface layer of many natural soils is stabilized by a thin biological layer sometimes called a "cryptogamic crust." Cryptogams are plants such as mosses, lichens, algae and fungi that produce spores (Rushforth and Brotherson 1982). There has been considerable interest in them in the inter-mountain west, where certain cyanobacteria (blue-green algae) form conspicuous layers on the soil surface (Skujins 1984).

Cryptogamic soil crusts not only stabilize the soil surface, but fix significant amounts of nitrogen: three to eight or more Kg per hectare per year (DuBois and Kapustka 1983, Isichei 1980). The nitrogen is fixed by cyanobacteria (blue-green algae), which are often the dominant components of cryptogamic crusts.

'The trampling associated with heavy grazing may destroy the cryptogamic crust along with the native shrubs (Anderson et al. 1982). The loss has significant effects on soil chemistry and structure in the top ten centimeters (Graetz and Tongway 1986). Recovery from grazing damage occurs naturally within 14-18 years (Anderson et al. 1982), and recovery from fire in about five years (Johansen et al. 1984).

St. Clair et al. (1986) showed that a simple re-inoculation can greatly hasten the return of cyanobacteria after fire. However, a commercial cyanobacteria inoculant was apparently ineffective in a range of forest soils (Tiedemann et al. 1980). Quality native top soil often contains propagules of the important cryptogamic crust organisms.

SUMMARY

Primary producers are the conspicuous members of natural ecosystems, but microorganisms and associated microfauna carry out most ecosystem functions, apart from photosynthesis. Beneficial microorganisms provide a wide range of vital services in natural ecosystems. These services include nutrient uptake, nitrogen fixation, decomposition of organic residues, promotion of plant growth, protection of plants from pathogens, and formation of soil structure.

The survival and performance of many native plant species depends heavily upon beneficial microorganisms, especially after planting and cessation of artificial inputs. Nursery production of a diversity of plant species will depend upon effective use and management of beneficial microorganisms.

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