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Richard C. Schultz
Iowa State University

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Mycorrhizal Manipulation for Improved Reforestation of Adverse Sites

Tree growth on adverse sites is mainly limited by low fertility and excess or deficient soil moisture. When sites are managed under shorter rotations using genetically improved stock, the loss of nutrients from the site with frequent harvesting may reduce site productivity. The use of specific mycorrhizal inoculum may be promising since individual species of mycorrhizal fungi can be selected that tolerate the stress conditions, clearcut sites, spoil banks, etc. and, thus enhance seedling growth.

by Richard C. Schultz

Reforestation of cutover lands and disturbed sites such as mine spoils promises to be one of the major challenges facing the professional forester in the 1980's. Forest management practices will continue to become more intensive as the demand for timber products increases while the base of forest land decreases. Forest rotations will become shorter, more material on the site will be utilized at harvest time and more genetically improved stock will be used to reforest the harvested sites. These practices have the two-fold impact of potentially decreasing the natural fertility of the site while at the same time demanding more from the site by the use of high quality planting stock. Any management scheme will, therefore, be faced with the problem of increasing yields on sites that are becoming more adverse to high yield forestry.

Conifers and intolerant pioneer hardwood species will continue to be the major species of high yield forestry in the 1980's. Clearcutting is the most efficient regeneration technique for many of these species. But clearcutting on any site generally produces adverse microclimatic conditions which add to the challenge of reforestation. Removal of the vegetation and surface organic matter during harvesting and site preparation raises soil temperatures providing more energy for increased evaporation of surface soil moisture. The increased temperature also tends to increase soil organic matter decomposition by accelerating microorganism activity. Under these conditions of extreme heat, severe surface soil moisture deficits and accelerated losses of readily available nutrients, even the most productive site is adverse to the newly planted seedling.

Aside from the radiant energy from the sun and the carbon dioxide from the atmosphere, the soil provides most of the raw materials and the

anchorage needed by the newly planted seedling. Soil can be considered as unconsolidated mineral material serving as a natural medium for plant growth and covering most of the non-water surface of the earth. This conceptual model, however, frequently results in the misunderstanding and mismanagement of the soil complex. The soil is a dynamic body with a multitude of floral and faunal organisms that are involved in a complex of organic and inorganic transformations. The flux of energy, water, and organic matter in the soil profile is constantly changing in response to the seasons, the growth and development of the plant and animal community, and the manipulation of that community by man.

The regeneration phase of forest management provides the greatest opportunities for man's positive or negative impacts on the soil complex. The high heat energy at the soil surface can be reduced by minimizing the disturbance of the forest floor during the harvest operation. This reduced disturbance will also minimize evaporational loss of surface soil moisture and the accelerated decomposition of soil organic matter. On sites where surface disturbance is widespread, decreasing surface soil moisture and available nutrients will result in an adverse site which limits seedling growth. Fertilization may provide a method for increasing the quantity of readily available nutrients, but the increasing cost of and competition for available fertilizer is making this alternative less feasible. We must, therefore, find ways to increase the efficiency of tree nutrient uptake.

The forest community efficiently and conservatively cycles nutrients through the ecosystem. However, the increased use of shorter rotations and more efficient harvest of all the plant parts reduces the conservative nature of the forest nutrient cycle and demands more efficient nutrient

uptake or more artificial fertilization. The forest community is efficient at nutrient uptake because of the dynamic interactions between the root system, the mineral soil and the soil microorganisms. Microorganisms are present in great numbers, especially in the rhizosphere, and are involved in numerous ways in the physiological processes of the plant. Probably the most universal of the plant-microorganism associations is the symbiosis of mycorrhizal fungi with the feeder roots of trees. With few exceptions all plants in nature develop mycorrhizae (fungus roots) to varying degrees. Under the optimum moisture and high nutrient conditions of many agricultural crops, the inoculation rate of roots by mycorrhizal fungi may be low or nonexistent, however, few forest trees grow under such conditions.

The significance of the mycorrhizal relationship in forest trees has been recognized for some time. The potential for manipulation of that relationship for reforestation practices has recently become a possible management alternative. It is likely that manipulation of the mycorrhizal fungi in the field is not feasible, nor warranted, but the introduction of seedlings on adverse sites that have a mycorrhizal root system tailored to the stress conditions of the site should provide more rapid and more complete reestablishment of the forest cover. A brief review of the major types of mycorrhizal fungi and their function in the growth of the host should be enough to indicate their role in forest tree growth and their management potential.

Ectomycorrhizae

There are three kinds of mycorrhizae. The ectomycorrhizae develop on all members of the gymnosperm family Pinaceae as well as *Salix* (willow), *Populus* (aspen), *Carya* (hickory), *Quercus* (oak), *Fagus* (beech), and others. Several of these species can be either

ectomycorrhizal or endomycorrhizal depending on soil conditions. Ectomycorrhizal infection of the feeder roots is initiated from spores or hyphae (collectively called 'propagules') of fungi belonging to the higher Basidiomycetes (mushrooms and puffballs) and Ascomycetes (cup fungi and truffles). These propagules are stimulated by root exudates; they grow vegetatively over the feeder root surface forming a dense fungal mantle. Following mantle development hyphae develop intercellularly in the root cortex, forming the Hartig-net which may completely replace the middle lamellae between cortical cells. This Hartig-net is the major distinguishing feature of ectomycorrhizae. Ectomycorrhizae may appear as simple unforked roots, multi-forked roots or nodule-like roots that are readily visible to the naked eye. These visible structures are referred to as "short roots", each individual one, regardless of branching pattern, being an ectomycorrhiza. Individual hypha, numerous hyphae or rhizomorphs may radiate from the fungus mantles on short roots into the soil and eventually unite with the base of fruiting bodies of the fungus.

Over 2100 species of ectomycorrhizal fungi have been estimated to exist on trees in North America. The fruiting bodies of these fungi are produced above ground and yield millions of spores that are readily and widely disseminated by wind and water. Ectomycorrhizal fungal spores are therefore present in large numbers in most forest soils. Nurseries proucing bare-root stock often have sufficient natural inoculum in the soil to produce mycorrhizal development even if the nursery beds are fumigated to control pathogens because of the rapid recolonization of the soil by the wind borne spores. However, the fungal species that naturally recolonize the highly fertile and moist nursery soils are not necessarily those that function well on adverse sites. Artificial inoculation of nursery beds with fungal species that are competitive on adverse sites provides a means of increasing survival and growth of seedlings in the field. Methods are presently being developed that will make artificial inoculation with specific ectomycorrhizal fungi a viable nursery practice.

VA Endomycorrhizae

The second major type of mycorrhizae are caused by the en-

domycorrhizal fungi, commonly referred to as the "vesicular-arbuscular" (VA) type. They are the most widespread and important of the root symbionts. They are not restricted to specific groups of plants, but occur in practically all families of angiosperms, gymnosperms, and many pteridophytes and bryophytes. Most of the economically important forest trees, such as *Liquidambar* (sweetgum), *Platanus* (sycamore), *Ulmus* (elm), *Juglans* (walnut), *Fraxinus* (ash), and *Liriodendron* (tulip-poplar) normally form endomycorrhizae. Endomycorrhizal fungi form large, conspicuous, thick-walled spores on the root surfaces, in the rhizosphere, and sometimes in feeder root tissues. Endomycorrhizal fungal hyphae penetrate the cell walls of the epidermis and then grow into the cortical cells of the root. The infective hyphae may develop specialized absorbing or nutrient-exchanging structures called "arbuscules" in the cortical cells. Arbuscules consist of dense clusters of very fine, dichotomously-branched filaments which may occupy the entire lumen of the cell. Vesicles are developed later, generally in the middle and outer cortex and appear as terminal swellings either within or between cells. Vesicles are currently thought to function as temporary storage organs. No external morphological changes occur in roots infected with endomycorrhizal fungi, although with some hosts a yellow or brown pigmentation has been reported. Endomycorrhizae have been largely ignored by plant scientists because of the difficulty in identifying them.

The fungi which form endomycorrhizae are mainly Phycomycetes. They do not produce large, above-ground fruiting bodies or wind-disseminated spores as do most ectomycorrhizal fungi. Spread of these fungi in soil is by root contact, moving water, insects or mammals. In the absence of a host, the spores of these fungi are able to survive for many years in the soil. As with ectomycorrhizal fungus spores, these spores are apparently stimulated to germinate by root exudates in the rhizosphere.

Endomycorrhizal fungi have not been grown in pure culture as have the ectomycorrhizal fungi. This makes it more difficult to produce specific inoculum for artificial inoculation of nursery beds. Inoculated roots on infected soils can be used as inoculum. The

inoculum can be added in small quantities to containerized seedlings or to nursery beds where a host crop plant such as sorghum can be grown to increase the inoculum density. Techniques are presently being developed to increase the efficiency of inoculum introduction into various growth media.

The third group of mycorrhizal fungi are the ectendomycorrhizae. This type of mycorrhizae has the features of both ecto- and endomycorrhizae. Ectendomycorrhizae have a limited occurrence and, with regard to forest trees, are found primarily on roots of normally ectomycorrhizal trees. Very little is known about the species of fungi involved or their importance to growth of trees because little research has been done on them.

Mycorrhizae Host Interactions

It has been well established that mycorrhizal fungi can increase the growth of trees. This growth increase is generally considered to be the result of increased nutrient and water absorption, as well as increased disease resistance of the host, increased growth regulator production by the root system and the fungi, and increased tolerance to high soil temperatures, soil toxins, and extremes in pH. Probably the most important of these is the role of the mycorrhizae in nutrient uptake, especially of immobile soil ions such as phosphate, zinc, copper, molybdenum and even ammonium.

Mycorrhizal plants absorb and accumulate more of these ions than nonmycorrhizal plants, especially when grown in soils low in concentration. The rate of uptake is limited by the movement of the immobile ions to the roots. Some tree species produce few fine feeder roots hairs and are unable to exploit large soil volumes. These species, especially, benefit from the presence of mycorrhizae whose radiating hyphae greatly expand the absorbing volume of the soil. It has been shown that the normal phosphorus depletion zone of 1-2 mm around nonmycorrhizal roots can be increased to at least 7 cm with an endomycorrhizal root symbiont. An endomycorrhizal root system can therefore absorb larger quantities of phosphorus than a nonmycorrhizal root system, especially in species with fewer fine roots.

Results from studies on increased uptake of the other more mobile elements by mycorrhizal plants have

been variable. Sometimes the elements N, K, Ca, Fe, Mn, Na, Si, Al and B are present in greater concentrations in mycorrhizal plants than in nonmycorrhizal plants. In other cases, the concentrations of these same elements are higher in nonmycorrhizal plants, and sometimes no significant difference in concentration between the two groups of plants is observed. This differential uptake may reflect the relative concentrations of elements in soil. If an element is deficient and limiting plant growth, it will likely appear in higher concentrations in the mycorrhizal plants. Characteristically, if mycorrhizal infection causes striking growth increases, the total amounts of all elements will be greater in the mycorrhizal plants, but the elements whose concentrations are affected most by mycorrhizal infection are very likely to be those limiting growth in the soil.

Soil temperature has been shown to influence the infection of specific mycorrhizal fungi. It has been suggested that soil temperature affects inoculation by influencing the rate of elongation and maturation of root cells. It has been shown that different species of fungus have different soil temperature requirements and, therefore, can be selectively used to stimulate the growth of seedlings on sites with known temperature regimes.

Specific species of mycorrhizal fungi have also been shown to increase seedling survival and growth under highly acid soil conditions. In several tests on acid (pH > 4.0) coal spoils, pine seedlings inoculated in the nursery with *Pisolithus tinctorius* outgrew seedlings inoculated with *thelephora terrestris*. Both of these fungi form ectomycorrhizae but *Thelephora* is the species most commonly found in forest nurseries and appears to be more suited to the high moisture and fertility regimes found in them.

Mycorrhizal root systems are generally larger and physiologically more active than root systems with only a few or no mycorrhizae. This increased size and activity has already been shown to play a role in the increased uptake of immobile nutrients. It is also involved in the increased absorption of soil water. Mycorrhizal seedlings have been shown to grow better on drier soils. The increased growth may again be related to the large exploitation of soil by a mycorrhizal root system, especially in those plants with few

roots hairs and feeder roots. This response suggests that plants could be tailored to compete better on droughty sites through mycorrhizal manipulation.

One final area where mycorrhizae may be involved in increasing tree growth is in plant hormone stimulation. Although little work has been done in this area, accumulated data on growth hormones produced by ectomycorrhizal fungi suggest that benefits to the host provided by the symbiotic fungus are not limited to supplying inorganic and organic nutrients from the soil. The fungal symbiont also provides the host plant with growth hormones, including auxins, cytokinins, gibberellins, and growth-regulating vitamins. These hormones are homologous to those formed endogenously by the host plant, but the fungus may be increasing the supply. These increased hormonal levels could significantly influence growth and development of the ectomycorrhizal host plant.

The manipulation of forest stands modifies site conditions including those which affect the mycorrhizal fungi population in the soil. Because of the widespread occurrence and the ubiquitous nature of most of these fungi, it is unlikely that mycorrhizal fungi populations can be manipulated in the field. This is not the case for all natural soils of the world, however. In many areas of the world, ectomycorrhizal trees and their symbiotic fungi do not occur naturally. In such areas the introduction of exotic ectomycorrhizal trees should be closely associated with the introduction of ectomycorrhizal fungi. On some severely disturbed sites such as mining spoils or borrow pits, similar deficiencies of either ecto or endomycorrhizal fungi exist. Introduction of mycorrhizal seedlings on such sites is imperative for good seedling growth if high levels of fertilizer are not used.

Under most other situations natural mycorrhizal fungi rapidly infect the root systems of introduced trees. However, since initial infection by the fungi means contact with a host root system, introduced tree seedlings must have vigorously growing root systems. It is at this point that the potential for mycorrhizal manipulation becomes evident. As has been shown in the preceding discussion, species of fungi respond differently to varying soil conditions. Thus, seedling mycorrhizal root systems can be "tailored" to adapt seedlings to

adverse site conditions such as temporarily develop after clear-cutting. The ability to plant seedlings that will survive and grow on almost any site will increase the efficiency and productivity of the forest industry.

Summary

Tree growth on adverse sites is mainly limited by low fertility and excess or deficient soil moisture. In natural stands that have reached an equilibrium in the nutrient cycle, changes in growth are seldom seen because the trees are producing the maximum growth allowed by the fertility and soil moisture of the site. This is not to say that growth could not be increased by the addition of fertilizer or through drainage or site irrigation. When sites are managed under shorter rotations using genetically improved stock, the loss of nutrients from the site with frequent harvesting may reduce site productivity. Heavy fertilization, soil drainage modification, proper selection of genotypes and modified harvesting practices can be used to maintain this productivity. However, present economics suggest that not all of these alternatives will be viable in the coming years.

Under intensive management, the most critical phase as far as tree growth and survival is concerned comes at the time of stand establishment. As a result of clearcutting, soil temperatures increase and surface soil moisture and organic matter content decrease. Such conditions are adverse to seedlings that have generally been grown under nursery conditions with high rates of fertilizer and moisture. The use of specific mycorrhizal inoculum in this phase of the forestry operation may be promising since individual species of mycorrhizal fungi can be selected that tolerate the stress conditions of clearcut sites, spoil banks, etc. and, thus, enhance seedling growth. These introduced fungi may not persist on the seedling root system in the field, but their presence during the first few years while the native fungi are infecting the root system can sufficiently increase survival and growth to make the method a feasible one. As the demand for wood increases and the land base to grow wood decreases, the forester will have to use every tool at his disposal to produce the fiber needed in the shortest time while maintaining long-term site productivity. ■