ECTOMYCORRHIZAE: A VIABLE ALTERNATIVE FOR SUCCESSFUL MINED LAND RECLAMATION[1]

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Abstract.--The term mycorrhizae is given to structures that are formed by the association of plant roots with fungi. The existence of ectomycorrhizae is distinguishable by a sheath of fungal tissue around the short lateral and sometimes longer roots of trees. Many forest trees which form ectomycorrhizae are often dependent on the mycorrhizal association for normal growth under natural conditions. This is a point of considerable practical significance in reforestation programs. It has been observed that the introduction of trees into areas devoid of mycorrhizal fungi is often unsuccessful unless concurrent introduction of essential mycorrhizal fungi is made. The relationship which exists between roots and these fungi is symbiotic since both partners benefit from the association. In general, the benefits to the host include the increased uptake of nutrients, increased tolerance to varying soil temperatures, increased resistance to drought and pH extremes. In return, carbonaceous compounds that originate from photosynthesis of the host are transported to the ectomycorrhizal fungi. Many of the factors that make the establishment of seedlings difficult on sites disturbed by mining, i.e. low nutrient availability, low soil moisture, high substrate temperature, toxic substances, low microflora population, etc., dictate a good potential for the use of ectomycorrhizal seedlings.

INTRODUCTION

Mining and the resulting surface materials do not physically, environmentally, chemically or biologically resemble any type of natural landscape in the world. The conditions that mining imposes on returning a site to a normal ecological condition are very severe and result in many revegetation problems (Nicholas and Hutnik 1971). Physically, the effects of mining that limit proper revegetation practices are; soil texture, stoniness, erosion, steep topography and frost heaving. Environmentally, lethal surface temperatures, moisture stress and high evaporation demand are important. Chemically, pH, nutrient deficiencies and salinity are characteristics that must be considered. Biologically, disturbance by mining of the litter-soil system, with their complement of microflora and organisms, reduces or removes soil biological activities which are normally present. With an environment under such a variety of stress factors, intensive reforestation practices must be applied to obtain the best results possible. The use of seedlings inoculated with ectomycorrhizal fungi along with other mine reclamation practices should increase the chance that revegetation of a disturbed site will be successful.

MORPHOGENIC STRUCTURE AND REQUIREMENTS FOR THE OCCURRENCE OF ECTOMYCORRHIZAE

Ectomycorrhizal fungi are characteristically found on the principal forest tree species in both temperate and cool climates (i.e. Pinaceae Betulaceae, Fagaceae, Juglandaceae, Ulmaceae, Cupressaceae) as well as on tropical and subtropical species (Harley and Smith 1983). It is believed there are over 2100 species of ectomycorrhizal fungi which exist on trees in North America (Kormanik et al. 1977). With the vast array of fungal species and the large number of tree species that are influenced by the association, the importance of this symbiotic relationship must be considered significant.

The appearance of ectomycorrhizae is distinguished by a sheath of fungal tissue around the short lateral and sometimes longer lateral roots of trees (Bowen 1965, Harley 1969).

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The fuugal sheath is usually connected with the soil by hyphae which radiate out into the soil complex and serve to increase the absorbing area of the root system (Went and Stark 1968). Hyphae also develop intercellularly into the root cortex, extending between the epidermal cells and the first few layers of the cortex (Bowen 1965, Harley 1969). These intercellular hyphae are commonly referred to as the "Hartig net" and together with the fungal mantle are the major distinguishing characteristics of ectomycorrhizae (Harley and Smith 1983).

Most ectomycorrhizal fungi are able to enter into a symbiotic relationship with more than one tree species. The ectomycorrhiza _Cenococcum geophilum_ Fr. has been found on over two hundred tree species in both the northern and southern hemispheres (Trappe 1964), while _Pisolithus tinctorius_ (Pers.) Coker and Couch has been confirmed in thirty-three countries of the world and on at least eight tree species (Marx 1977).

Review publications on mycorrhizal research have led to the general finding that the rate of ectomycorrhizal development is directly related to macronutrient levels, the intensity of sunlight, pH, soil moisture content, temperature, O_2 availability, and competition by other microorganisms (Harley 1969, Slankis 1974). Ectomycorrhizal development is also influenced by vitamins (i.e. thiamine), simple amino acids, simple carbohydrates, and other unknown substances which are derived from the roots (Melin 1954, Harley 1969). Whether or not a symbiotic relationship is formed between the tree species and ectomycorrhizal fungus depends upon the environment and the ability of the fungus to induce and maintain a specific physiological and metabolic state in the root which is conducive to the mycorrhizal fungi.

ECTOMYCORRHIZAL ENHANCEMENT OF TREE GROWTH

Nutrient Uptake

Nutrients are an essential part of the plant's ability to survive in any type of environment let alone that of a disturbed site. Ectomycorrhizae result in an increased rate of absorption of essential nutrients needed for plant growth. Hatch (1936) found that _Pinus_ seedlings infected with ectomycorrhizal fungi had an increased biomass weight and greater nutrient content than uninfected seedlings. Similar findings were reported in _Pinus_ seedlings by McComb (1938) and Finn (1942).

Results as shown above gave rise to the "Mineral Salt" theory which stated that all nutrients are absorbed through the fungus, and ectomycorrhizal infection tends to improve the absorption of whatever major nutrient is most deficient (Harley and Smith 1983). Increased nutrient absorption was partly explained by Hatch (1937) as being due to the physical increase of the effective surface area for absorption caused by ectomycorrhizal infection. Current research has shown that nutrient absorption by ectomycorrhizae does not differ in essentials from that of other absorbing organs in relation to metabolic processes (Harley and Smith 1983).

Greater nitrogen absorption by ectomycorrhizal seedlings has been shown in pine using N^{15} (Melin and Nilsson 1952, 1953) and with beech using ammonium and nitrate (Carrodus 1966). Carrodus (1966) found that NH_4^+ absorption was dependent on the supply of carbohydrates in the roots and the mycorrhizal metabolic rates. Recent work by Rygiewicz et al. (1984) showed _Hebeloma crustuliniforme_ (Bull. ex St. Amans) can significantly improve ammonium acquisition in three Pacific northwest coniferous species.

Phosphorus is absorbed by ectomycorrhizae and passed into the roots in higher quantities than that which occurs in noninfected plants. Melin and Nilsson (1950, 1954) demonstrated the movement of phosphorus from the mycorrhizal mycelium to the host pine seedling. Henderson and Stone (1967) and Skinner and Bowen (1974) found that mycorrhizal roots were able to exploit more soil volume with the net result being a greater phosphorus uptake. Mejestrik (1970, 1975) and Morrison (1954, 1962a) examined phosphorus uptake using ^{32}P on different ectomycorrhizae of pine and found that the mycorrhizae absorbed phosphorus more rapidly than nonmycorrhizal roots.

Studies have also shown that mycorrhizal fungi increase the uptake of elements other than nitrogen and phosphorus, which are also essential to the plant for it to function properly.

Melin and Nilsson (1955) studied the uptake of radioactive calcium in mycorrhizal seedlings. They found that considerable amounts of calcium ions were transferred from a distant source to the mycorrhizal roots and that the calcium was distributed throughout the seedlings.

Rosendahl (1942) and Harley and Wilson (1959) found that seedlings of both conifers and angiosperms had an increase in the amount of potassium absorbed in mycorrhizal seedlings in comparison to noninfected seedlings. Bowen, Skinner, and Bevege (1974) found that zinc uptake and absorption by the plants occurred in greater quantities in mycorrhizal plants than in uninfected plants.

Morrison (1962b) determined that mycorrhizae are of no significance in sulfur accumulation by radiata pine even after a period of sulfur starvation. He concluded that unlike other needed elements, sulfur has a free pathway through the mycelium of mycorrhizal fungi.

McComb (1938) using Virginia pine and White (1941) using red pine determined that seedlings infected with mycorrhizae exhibited height growth that was significantly greater than nonmycorrhizal plants. Studies conducted by numerous researchers (Henderson and Stone 1967, McComb and Griffith 1946, Marx 1975, Marx, Bryan and Cordell 1976, Miller 1938, Mitchell, Finn and Rosendahl 1937, Rosendahl 1942, Trappe and Strand 1969, Vozzo and Hacskaylo 1971) described mycorrhizae as being essential for vigorous growth of conifer seedlings. Their results indicated that certain nutrients were made more available to mycorrhizal seedlings than nomycorrhizal seedlings.

Temperature

Temperature stress is an important factor to be considered when establishing seedlings on a disturbed site. Schramm (1966) recorded growing season soil temperatures as high as 75°C in mining wastes at a depth of 6 cm, while Grossnickle and Reid (1983) recorded growing season soil temperatures (10 cm) as low as 5°C on a high-elevation mine site. These extreme temperatures not only restrict growth of tree seedlings, but also limit the ability of mycorrhizal fungi to function.

It has been found that mycorrhizae exhibit their greatest frequency of formation in the spring and early summer (Hacskaylo 1957). This abundance of mycorrhizae is thought to be correlated with higher temperatures and increased soil moisture. Low temperatures during mid-winter limit the development of mycorrhizae, suppressing root and fungus growth. Throughout the spring as the shoots are starting to break dormancy, roots may grow extensively and become invaded by mycorrhizal fungi (Hacskaylo 1957).

Theodorou and Bowen (1971) found that five different fungal species grown in pure culture declined rapidly in growth between 20°C and 16°C. This same effect also occurred in the colonization of the rhizosphere of radiata pine seedlings with three fungal species. They found mycorrhizal production in the soil to be optimal at 25°C and declined markedly between 20°C and 15°C. Their findings showed that large differences occurred between strains within a fungal species in length of root colonized and in the intensity of growth on the root at 16°C. They suggested that the decrease in mycorrhizal infection as temperature decreased was first, the probability of root exudates changing in amount and/or composition, and second, the decrease in lateral root production which serves as potential sites for mycorrhizal formation.

Marx, Bryan and Davey (1970) reported that root substrate temperature significantly influenced the survival and growth of loblolly pine seedlings. Nonmycorrhizal plants died at temperatures greater than 24°C, while mycorrhizal plants with the fungal symbiont Thelephora terrestris (Ehrh.) Fr. survived and exhibited good growth at 29°C. However, no ectomycorrhizae formation took place at 34°C. Seedlings infected with P. tinctorius survived and grew well at 29°C and 34°C with greater ectomycorrhizal formation occurring at 34°C. It is interesting to note that even though mycorrhizal formation increased above 29°C, igor of the seedlings at 34°C declined.

The findings of the preceding studies show that fungi exhibit a species specific tolerance to high and low temperatures. Wide extremes of optimum temperature for mycorrhizal fungi growth is illustrated by Leucopaxillus ceralis var. piceina (Lasch) Sing., which has optima ranging between 10°C to 20°C, and P. tinctorius which has an optimum range of 30°C to 35°C. However, most mycorrhizal fungi grow best between 18°C and 27°C (Marx 1969). Marx and Bryan (1971) point out that the ability of specific ectomycorrhizal seedlings and the inability of nonmycorrhizal seedlings to survive in soils at high temperature suggest new techniques in the reforestation of areas exposed to regimes of high temperature. Grossnickle and Reid (1983) also point out that low soil temperatures may result in the reduction of specific ectomycorrhizal isolates on seedling root systems. Theodorou and Bowen (1971) state that due to extremely poor colonization on some fungi at low temperatures, it is necessary to select fungi on the basis of root colonization at soil temperatures appropriate to the area and season as well as on ability to stimulate plant growth.

Soil Moisture

Soil moisture is very important for the formation of mycorrhizae (Slankis 1974). The abundance of mycorrhizae may be correlated with higher soil moisture levels (Hacskaylo 1957, Reid 1979), but excessive soil moisture has also been shown to severely limit the formation of mycorrhizae (Filer 1975). In natural habitats some mycorrhizal associations can endure prolonged exposure to excessive moisture, but in soils with excess water, oxygen deficiencies limit the development of both the fungus and the root system (Slankis 1974, Theodorou 1978. Thus the tolerance of mycorrhizae to excess moisture depends on the physiological state of the roots and their ability to supply oxygen to the fungus (Slankis 1974).

Mycorrhizal fungi differ in their tolerance to soil moisture. Studies by Meyer (1964), and Worley and Hacskaylo (1959) indicated that soil moisture deficits decreased the abundance of mycorrhizae formed by all symbionts tested except C. geophilum. Mexal and Reid (1973) found that C. geophilum was very tolerant of low water potentials and exhibited maximum growth at a solute water potential of -1.5 MPa in pure culture. Hacskaylo (1967) found that C. geophilum is more vigorous under drought conditions due to the reduced vigor of other competing fungi. Bowen and Theodorou (1967) attributed enhanced survival of radiata pine seedlings during a summer drought to the vigorous growth associated with mycorrhizal infection. Palmer (as cited by Nicholas and Hutnik 1971) stated that drought conditions increase the degradation of mycorrhizal roots, while moisture promotes the regeneration of new roots.

Early field studies have shown seedlings with ectomycorrhizae seem to be more resistant to dessication than uninfected seedlings (Cromer 1935, Harley 1940). Possible explanations for this phenomenon are: 1) the addition of hyphae and mycelial strands of ectomycorrhizae increases the absorbing area of the root system, 2) fungal hyphae may penetrate smaller soil pores than root hairs, and 3) hyphal strands from the fungus-root association are connected to the soil particles which prevents the shrinkage of soil away from the fungus-root surface and thus improves root-soil contact (Reid 1979). Work by Dixon et al. (1983) showed ectomycorrhizal seedlings to have less plant/soil resistance to water flow, i.e. greater available seedling moisture, in comparison to nonmycorrhizal seedlings. However, Sands and Theodorou (1978) found mycorrhizal seedlings to have a slightly greater plant/soil resistance to water flow, i.e. less available seedling moisture, than nonmycorrhizal seedlings. Further work by Sands et al. (1982) found the movement of water through roots of seedlings similar in mycorrhizal and nonmycorrhizal pine roots. Parke et al. (1983) showed Douglas-fir seedlings inoculated with *Rhizopogon vinicolor* Smith were least affected by drought in comparison to seedlings inoculated with other mycorrhizal symbionts or nonmycorrhizal seedlings. The above finds are inconclusive and further experimental work on the water relations of mycorrhizal plants appears to be needed.

pH Reaction

The pH level plays an important role in the regeneration of disturbed sites. Depending upon the region of the country and the type of overburden that is exposed, the pH level can range from 2.6 on mine spoils of Pennsylvania (Horn as cited by Nichols and Hutnik 1971), to a pH level of 12.0 on retorted spent shale in the western region of Colorado (Culbertson et al. 1970). It is generally assumed that most ectomycorrhizal fungi are acidophilic, although there are some notable exceptions (Slankis 1974). Hacskaylo (1957) stated that mycorrhizae of trees develop most extensively in acidic soils. It has been similarly reported that mycorrhizae of *Pinus* species did not develop profusely on trees growing in neutral or alkaline soils (Richards 1961). Harley (1969) has reported that highly aerated, acidic media was not only favorable to the development of, but was also favorable to the functioning of mycorrhizal roots.

Theodorou and Bowen (1969) found that the pH level for optimum performance of most forest tree seedlings as well as mycorrhizal fungi was in the soil pH range 5 to 6.5. Similarly, Tesic (as cited by Nicholas and Hutnik 1971) found that mycorrhizal fungi grew best in acid soils with pH levels of 4 to 5, and found that some would form fruiting bodies only in acid media. Schramm (1966) found sporophores of *P. tinctorius* and other ectomycorrhizal fungi in moderately acidic (pH 4.6 to 5.2) spoils in Pennsylvania. Lampky and Peterson (1963) discovered fruiting bodies of *P. tinctorius* associated with jack pine and eastern redcedar on an abandoned stripmine in Missouri which had pH levels of 3.1 to 3.4. Rice et al. (1982) found that on surface mined land in Kentucky strains of *P. tinctorius* resulted in increased seedling growth and fruiting body development on more acidic spoils and had little beneficial effects on spoils with a neutral pH.

As the soil pH approaches neutrality, different mycorrhizal types develop (Goss 1960). Goss (1960) found that in a soil of pH 7.8 mycorrhizae were produced on ponderosa pine seedlings. Dale et al. (1955) found that on high lime soils (pH 7.8 to 8.2) inoculation with mycorrhizal fungi permitted normal, although not maximum growth, but the lack of mycorrhizae resulted in pine seedlings with lime-induced chlorosis. Bowen (1965) found that in an inoculation study where the soil pH was 8.0, most of the existing mycorrhizal roots were formed by *C. geophilum*. Theodorou and Bowen (1969) found that at pH 8.0, mycorrhizae formation was lower by 60 percent than at pH 6.2, and ectomycorrhizae were completely replaced by ectendomycorrhizae. Grossnickle and Reid (1983) on a high-elevation mine site (pH 8.0) and Riffle and Tinus (1982) on a grassland site (pH 8.4) found that *P. tinctorius* ectomycorrhizae cultured on seedling root systems in the greenhouse disappeared after field planting and were replaced by ectomycorrhizae more suited for the sites edaphic conditions.

Marx and Zak (1965) reported that soil pH not only influences the formation of different mycorrhizal associations, but also the distribution of different tree root-fungal associations. When they examined seedlings grown with *C. geophilum*, they noted that the fungus contributed to increased seedling growth at pH 4.0 and 4.6. While the number of rootlets infected remained the same at a higher pH (5.6 to 6.6), the effectiveness of this fungal symbiont to induce beneficial plant fungus reactions was reduced.

USE OF ECTOMYCORRHIZAL FUNGI ON RECLAMATION AND REFORESTATION SITES

Numerous field studies have been conducted on the effects of mycorrhizal infection on growth and nutrient uptake of various gymnosperms and angiosperms, but limited research has been undertaken to examine the effects of mycorrhizal-plant associations on mined land reclamation sites. Only recently has research on the use of ectomycorrhizal fungi in revegetation practices been published.

Investigations of Schramm (1966) have shown that early ectomycorrhizal development was essential for the establishment of seedlings of various tree species on anthracite mining wastes in Pennsylvania. He found that the only successful plant colonizers on the predominantly nitrogen deficient wastes were either nitrogen fixing plants or certain tree species that were infected with ectomycorrhizal fungi.

Marx (1975) found on coal waste sites in several southern and eastern states that *P. tinctorius* was the predominant if not the only, ectomycorrhizal fungi on the roots of several species of *Pinus* and *Betula*. On kaolin wastes in Georgia, *P. tinctorius* was also found on some *Pinus* species. *P. tinctorius* also has been reported on coal wastes associated with *Populus*, Salix, and Betula in West Germany (Meyer as cited by Marx 1975), on jack pine in Missouri (Lampky and Peterson 1963) and Pinus spp. in Indiana and Tennessee (Hile and Hennen 1969).

Data from field studies which have involved seedlings inoculated with ectomycorrhizae indicate the importance of the fungi in establishing vegetation on disturbed sites. On eroded soils, Pina (1977) found that Pinus species showed a large increase in growth when infected with the mycorrhizal fungi P. tinctorius and Laccaria laccata (Scop. ex Fr.) Bk. & Br. compared to noninoculated seedlings. Harris and Jurgensen (1977) found that cuttings of willow and hybrid poplar grew poorly on copper tailings in comparison to better growth on iron tailings. Better seedling growth and development on iron tailings in comparison to copper tailings was due to increased ectomycorrhizal development, better soil fertility and/or fewer toxic chemicals. Brisco (1959) observed that slash pine seedlings inoculated with mycorrhizal fungi had an 85 percent survival compared to only 36 percent survival for non-inoculated seedlings two years after outplanting on a reforestation project.

In a review by Marx (1980), findings confirmed that ectomycorrhizae formed by P. tinctorius in nurseries lead to subsequent increased growth and survival of outplanted pine seedlings on lands disturbed by mining. Other research studies with this isolate confirm this observation. Numerous studies on acid coal spoils in Appalachia determined that seedlings inoculated with P. tinctorius in most instances grew better than seedlings that were inoculated with T. terrestris (Berry and Marx 1977, 1978, Marx and Artman 1979, Berry 1982, Rice et al. 1982). Containerized and bare-root seedlings inoculated with P. tinctorius have also shown good growth performance on borrow pits (Ruehle 1980, Goodwin 1982), prairie soils (Baer and Otta 1981), disturbed road sites (Anderson et al. 1983) and routine reforestation sites in southern United States (Marx et al. 1977, Mexal 1980, Dixon et al. 1981, Kais et al. 1981, Ruehle et al. 1981).

Nicholas and Hutnik (1971) described P. tinctorius to be a valuable fungal symbiont in increasing seedling growth, compared to C. geophilum, on less toxic but moderately acidic spoils, but they questioned whether P. tinctorius can increase growth on highly toxic acidic spoils. The findings of Medve et al. (1977) showed increased growth response for seedlings inoculated with P. tinctorius or C. geophilum in comparison to control seedlings on bituminous stripmine spoils.

Though the isolate P. tinctorius has been found to be effective in enhancing growth and survival on disturbed sites, caution must be observed in using an isolate in all ecological settings. Marx et al. (1977) and Berry and Marx (1980) showed seedlings inoculated with T. terrestris ectomycorrhizae survived and grew as well as seedlings inoculated with P. tinctorius on poor soils amended with fertilizer or sewage sludge. Ruehle et al. (1981) found mycorrhizal treatments P. tinctorius and T. terrestris provided no consistent advantage in containerized pine seedlings, while Dixon et al. (1981) found no advantage for these isolates on bare-root oak seedlings outplanted on reforestation sites. Beckjord and McIntosh (1984) found no growth differences between northern red oak seedlings inoculated with P. tinctorius, C. geophilum and Scleroderma auranteum Pers. planted on a strip mine even though the isolates were still present on the root systems two years after planting. Also, no effect of P. tinctorius ectomycorrhizae was observed with pine on grasslands (Riffle and Tinus 1982) or with pine on fertile abandoned fields (Powers and Rowan 1983).

Use of mycorrhizal infected seedlings in revegetation practices on disturbed sites with cooler climatic conditions (i.e. high elevation, northern latitudes) has thus far been of limited scope. Gobl (1965) found Pinus species on high altitude sites with good regeneration irrespective of soil type tended to have abundant mycorrhizae which tolerated adverse environmental conditions. But on sites with little or no natural regeneration, the types of mycorrhizae were not ecologically compatible, and plants and seed for reforestation would require inoculation. Moser (1958) determined that mycorrhizal formation appears to be fairly retarded above timberline but mycorrhizal formation may be accelerated considerably by introducing suitable mycorrhizal inoculum. Research by Grossnickle and Reid (1982, 1983) on a high-elevation mine site found seedlings inoculated with Suillus granulatus (L. ex Fr.) Kuntze had the greatest growth and a continual presence of the isolate on the seedling root system after 5 years in the field. Seedlings inoculated with P. tinctorius and C. geophilum showed less growth and no presence of the isolate on the root systems after 5 years. Suillus granulatus was isolated from fruiting bodies collected in the Colorado Front Range, while P. tinctorius and C. geophilum were isolates obtained from the southeastern United States. In contrast, work by Navratil et al. (1981) found that P. tinctorius resulted in greater height growth in jack pine seedlings and was able to overwinter successfully on boreal reforestation sites in northern Canada. Benecke (1978) has noted growth differences between mycorrhizal isolates on mountainous sites in New Zealand, which were attributed to their ability to colonize roots at low soil temperatures.

CONCLUSIONS

The concurrent introduction of ectomycorrhizae with seedlings on sites disturbed by mining is critical if successful establishment is going to occur. Findings reported in this paper for the most part show that ectomycorrhizae formed by any fungus on the roots of seedlings is better than no ectomycorrhizae at all. Also, ectomycorrhizae formed by certain fungal species are more beneficial to seedlings on certain sites than ectomycorrhizae formed by other fungi. Parkinson (1979) warns that research and field application should not be directed at just one fungal symbiont, but the direction should be on the potential values of a wider range of ectomycorrhizal fungi. This will enable reclamation and reforestation specialists to match the tree species with an ectomycorrhizal symbiont which would be most ecologically adapted to the conditions of the disturbed site. Further research is required to identify the proper species-fungus combinations for a wider range of ecological conditions. Amending mine spoils is a major way reclamation specialists manipulate the site's soil conditions to enhance the reclamation success. Further work needs to be conducted which will examine the influence of soil amendments on the activity of ectomycorrhizal symbionts on the seedling root systems.

Harley (1969) emphasizes that mycorrhizal development should not be viewed as a cure all since this symbiosis is not the only factor that determines successful plant growth. The use of seedlings inoculated with ectomycorrhizal fungi must be a part of a comprehensive rehabilitation program. Ectomycorrhizal inoculated seedlings cannot be considered an end in themselves, but must be considered as part of the means to an end, which is the successful reestablishment of vegetation on a disturbed area.

Most of the links to DOIs are on the last page

LITERATURE CITED

Anderson, L.M., A.L. Clark and D.H. Marx. 1983. Growth of oak seedlings with specific ectomycorrhizae in urban stress environments. J. of Arboriculture 9:156-159.

Baer, N.W., and J.D. Otta. 1981. Outplanting survival and growth of ponderosa pine seedlings inoculated with Pisolithus tinctorius in South Dakota. For. Sci. 27:277-280.

Beckjord, P.R., and M.S. McIntosh. 1984. Growth and fungal persistence by Quercus rubra inoculated with ectomycorrhizal fungi planted on a clear-cutting and strip mine. Can. J. Bot. 62:1571-1574.

http://dx.doi.org/10.1139/b84-210

Benecke, U. 1978. Tree symbiosis in mountainland reforestation. p. 161-173. In Revegetation in the rehabilitation of mountain lands. Ed. J. Orwin. New Zealand Forest Service, Forest Research Institute Symposium No. 16.

Berry, C.R. 1982. Survival and growth of pine hybrid seedlings with Pisolithus ectomycorrhizae on coal spoils in Alabama and Tennessee. J. Environ. Qual. 11:709-715.

Berry, C.R., and D.H. Marx. 1977. Growth of loblolly pine seedlings in stripmined kaolin spoil as influenced by sewage sludge. J. Environ. Qual. 6:379-381.

Berry, C.R., and D.H. Marx. 1978. Effects of Pisolithus tinctorius ectomycorrhizae on growth of loblolly and Virginia pines in Tennessee Copper Basin. USDA For. Ser. Res. Note SE-264, 6 p.

Berry, C.R., and D.H. Marx. 1980. Significance of various soil amendments to borrow pit reclamation with loblolly pine and fescue. Reclam. Rev. 3:87-94.

Bowen, G.D. 1965. Mycorrhizae inoculation in forestry practice. Aust. For. 29:231-237.

Bowen, G.D. 1965. The roles of mycorrhizae and root nodules in tree nutrition. p. 1-35. Commonwealth Scientific and Industrial Research Organization, Univ. of New England, Armidale, NSW.

Bowen, G.D., and C. Theodorou. 1967. Studies on phosphate uptake by mycorrhizae. IUFRO Proc. 14th Congress, 5:116-138.

Brisco, C.B. 1959. Early results of mycorrhizal inoculation of pine in Puerto Rico. Carib. For. 20:73.

Carrodus, B.B. 1966. Absorption of nitrogen by mycorrhizal roots of beech. I. Factors affecting the assimilation of nitrogen. New Phytol. 65:358-371.

Cromer, D.A.N. 1935. The significance of the mycorrhiza of Pinus radiata. Aust. Commonwealth For. Bul. 16:1-19.

Culbertson, W.J., Jr., T.D. Nevens, and R.D. Hollingshead. 1970. Disposal of oil shale ash. Colorado School of Mines Quarterly 65: 89-132.

Dale, J., A.L. McComb, and W.E. Loomis. 1955. Chlorosis, mycorrhizae and the growth of pines on a high-lime soil. Forest Sci. 1:148-157.

Dixon, R.K., H.E. Garrett, G.S. Cox, P.S. Johnson, and I.L. Sanders. 1981. Container- and nursery-grown black oak seedlings inoculated with Pisolithus tinctorius: Growth and ectomycorrhizal development following outplanting in an Ozark clear-cut. Can. J. For. Res. 11:492-496.

Dixon, R.K., S.G. Pallardy, H.E. Garrett, G.S. Cox, and I.L. Sander. 1983. Comparative water relations of container-grown and bare-root ectomycorrhizal and nonmycorrhizal Quercus velutina seedlings. Can. J. Bot. 61:1559-1565.

Filer, T.H. 1975. Mycorrhizae and soil microflora in a greentree reservoir. For. Sci. 21:36-39.

Finn, R.F. 1942. Mycorrhizal inoculation of soil of low fertility. Black Rock Forest apers 1:116-117.

Gobl, F. 1965. Mycorrhiza studies in a sub-alpine spruce forest. Mitt. Forstl. Vers Anst., Mariabrunn, 66:173-195.

Goodwin, O.C. 1982. Four year results of loblolly and Virginia pine containerized seedlings colonized with Pisolithus tinctorius ectomycorrhizae. N.C. For. Serv., Div. of For. Res., For. Note 57, 3 p. Raleigh, NC

Goss, R.W. 1960. Mycorrhizae of ponderosa pine in the Nebraska grassland soils. p. 1-47. Nebr. Agric. Exp. Sta. Res. Bull. 142.

Grossnickle, S.C., and C.P.P. Reid. 1982. The use of ectomycorrhizal conifer seedlings in the revegetation of a high-elevation mine site. Can. J. For. Res. 12:354-361.

Grossnickle, S.C. and C.P.P. Reid. 1983. Ectomycorrhiza formation and root development patterns of conifer seedlings on a high-elevation mine site. Can. J. For. Res. 13:1145-1158.

Hacskaylo, E. 1957. Mycorrhizae of trees with special emphasis on physiology of ectotrophic types. Ohio J. Sci. 57:350-357.

Hacskaylo, E. 1967. Mycorrhizae: indispensible invasions by fungi. Agric. Sci. Rev. 5:13-20.

Harley, J.L. 1940. A study of the root system of the beech in woodland soils with especial reference to mycorrhizal infection. J. Ecol. 28:107-117.

Harley, J.L. 1969. The biology of mycorrhiza. Second edition. 334 p. Leonard Hill, London.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. 483 p. Academic Press, New York.

Harley, J.L., and J.M. Wilson. 1959. The absorption of potassium by beech mycorrhizas. New Phytol. 58:281-298.

Harris, M.M., and M.F. Jurgensen. 1977. Development of Salix and Populus mycorrhizae in metallic mine tailings. Plant and Soil 47:509-517.

Hatch, A.B. 1936. The role of mycorrhizae in afforestation. J. For. 34:22-29.

Hatch, A.B. 1937. The physical basis of mycotrophy in the genus Pinus. Black Rock Forest Bull. 6:1-168.

Henderson, G.S., and E.L. Stone. 1967. Interactions of phosphorus availability, mycorrhizae and soil fumigation of conifer seedlings. Agron. Abstracts, p. 134.

Hile, N. and J.F. Hennen. 1969. In vitro culture of Pisolithus tinctorius mycelium. Mycologia 61:195-198.

Kais, A.G., G.A. Snow, and D.H. Marx. 1981. The effect of benomyl and Pisolithus tinctorius ectomycorrhizae on survival and growth of longleaf pine seedlings. South. J. Appl. For. 5:189-195.

Kormanik, P.P., W.C. Bryan, and R.C. Schultz. 1977. The role of mycorrhizae in plant growth and development. p. 1-10. In Physiology of root-microorganisms associations. Ed. H.M. Vines. Proc. of a Symposium of the South. Sect. Am. Soc. Plant Physiol., Atlanta, Georgia.

Lampky, J.R. and J.E. Peterson. 1963. Pisolithus tinctorius associated with pines in Missouri. Mycologia 55:675-678.

Marx, D.H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathol. 5:153-163.

Marx, D.H. 1975. Mycorrhizae and establishment of trees on strip-mined land. The Ohio J. Sci. 75:288.

Marx, D.H. 1977. Tree host range and world distribution of the ectomycorrhizal fungus Pisolithus tinctorius. Can. J. Microbiol. 23:217-223.

Marx, D.H. 1980. Role of mycorrhizae in forestation of surface mines. p. 109-116. In Trees for reclamation. USDA For. Serv. Gen. Tech. Rep. NE-61. Northeast For. Exp. Sta., Broomall, Pennsylvania.

Marx, D.H., and J.D. Artman. 1979. Pisolithus tinctorius ectomycorrhizae improve survival and growth of pine seedlings on acid coal spoils in Kentucky and Virginia. Reclam. Rev. 2:23-31.

Marx, D.H., W.C. Bryan, and C.E. Cordell. 1976. Growth and ectomycorrhizal development of pine seedlings in nursery soils infested with the fungal symbiont Pisolithus tinctorius. For. Sci. 22:91-100.

Marx, D.H., W.C. Bryan, and C.E. Cordell. 1977. Survival and growth of pine seedlings with Pisolithus ectomycorrhizae after two years on reforestation sites in North Carolina and Florida. For. Sci. 23:363-373.

Marx, D.H., W.C. Bryan, and C.B. Davey. 1970. Influence of temperature on aseptic synthesis of ectomycorrhizae by Thelephora terrestris and Pisolithus tinctorius on loblolly pine. For. Sci. 16:424-431.

Marx, D.H., and B. Zak. 1965. Effect of pH on mycorrhizal formation of slash pine in aseptic culture. For. Sci. 11:66-75.

McComb, A.L. 1938. The relation between mycorrhizae and the development and nutrient absorption of pine seedlings in a prairie nursery. J. For. 36:1148-1154.

McComb, A.L., and J.E. Griffith. 1946. Growth stimulation and phosphorus absorption of mycorrhizal and nonmycorrhizal northern white pine and Douglas-fir seedlings in relation to fertilizer treatment. Plant Physiol. 21:11-17.

Medve, R.J., F.M. Hoffman, and T.W. Gaither. 1977. The effects of mycorrhizal-forming amendments on the revegetation of bituminous stripmine spoils. Bull. Torrey Bot. Club, 104, 3:218-225.

Mejstrik, V.K. 1970. The uptake of ^{32}P by different kinds of ectotrophic mycorrhiza of Pinus. New Phytol. 69:295-298.

Mejstrik, V.K. 1975. The effects of mycorrhizal infection of Pinus sylvestris and Picea abies by two Boletus species on the accumulation of phosphorus. New Phytol. 74:455-459.

Melin, E. 1954. Growth factor requirements of mycorrhizal fungi of forest trees. Svensk Bot. Tidskr. 48:86-94.

Melin, E., and H. Nilsson. 1950. Transfer of radioactive phosphorus to pine seedlings by means of mycorrhizal hyphae. Physiol. Plant. 3:88-91.

Melin, E., and H. Nilsson. 1952. Transfer of labelled nitrogen from glutamic acid to pine seedlings through the mycellium of Boletus variegatus. (Sw. ex. Fr) Nature 171:134.

Melin, E., and H. Nilsson. 1954. Transport of labelled phosphorus to pine seedlings through the mycelium of Cortinarius glaucopus (Schaeff. ex Fr.). Fr. Svensk Bot. Tidskr. 48:555-558.

Melin, E., and H. Nilsson. 1955. Ca^{45} used as an indicator of transport of cations to pine seedlings by means of mycorrhizal mycelium. Svensk Bot. Tidskr. 49:119-122.

Mexal, J.G. 1980. Aspects of mycorrhizal inoculation in relation to reforestation. N.Z. J. For. Sci. 10:208-217.

Mexal, J.G., and C.P.P. Reid. 1973. The growth of selected mycorrhizal fungi in response to induced water stress. Can. J. Bot. 51:1579-1588.

Meyer, F.H. 1964. The role of the fungus Cenococcum graniforme. p. 23-31. In Soil micromorphology. Ed. A. Jongerius.

Miller, F.J. 1938. The influence of mycorrhizae on the growth of shortleaf pine seedlings. J. For. 36:526-527.

Mitchell, H.L., R.F. Finn, and R.O. Rosendahl. 1937. The relation between mycorrhizae and the growth and nutrient absorption of coniferous seedlings in nursery beds. Black Rock Forest Papers No. 10.

Morrison, T.M. 1962a. Absorption of phosphorus from soils by mycorrhizal plants. New Phytol. 61:10-20.

Morrison, T.M. 1962b. Uptake of sulfur by mycorrhizal plants. New Phytol. 61:21-27.

Moser, M. 1958. Der enifluss tiefer temperatureu auf das wachstum und die lebenstatiglaeit hoherer pilze mit spezieller berucksichtigung von mykorrhizapilzen. Sydowis, Annales Mycologici Ser. II, Horn 12(1/6), p. 386-99.

Nicholas, A.K., and R.J. Hutnik. 1971. Ectomycorrhizal establishment and seedling response on variously treated deep-mine coal refuse. 121 p. Dep. Environ. Resour. of the Commonwealth of Pennsylvania Special Rep. No. SR-89.

Navratil, S., N.J. Phillips, and A. Wynia. 1981. Jack pine seedling performance improved by *Pisolithus tinctorius*. For. Chron. 57:212-217.

Parke, J.L., R.G. Linderman, and C.H. Black. 1983. The role of ectomycorrhizae in drought tolerance of Douglas-fir seedlings. New Phytol. 95:83-95.

Parkinson, D. 1979. Microbes, mycorrhizae and mine spoil. p. 634-642. *In* Ecology and coal resources development. *Ed.* M.K. Wali. Pergamon Press, New York.

Pina, F., R. Grada, R. Ferrera, and M. Vales. 1977. Mycorrhizal inoculation and growth of pine seedlings on eroded soil. p. 29. Third North Am. Conf. on Mycorrhizae, Athens, Georgia.

Powers, H.R., Jr., and S.J. Rowen. 1983. Influence of fertilization and ectomycorrhizae on loblolly pine growth and susceptibility to fusiform rust. South. J. Appl. For. 7: 101-103.

Reid, C.P.P. 1979. Mycorrhizae and water stress. p. 392-408. *In* Root physiology and symbiosis. Vol. 6. *Eds.* A. Riedacker and J. Gagnaire-Michard. CNFR, Nancy, France.

Rice, C.W., R.I. Barnhisel, and J.L. Powell. 1982. The establishment of loblolly pine (*Pinus taeda* L.) seedlings on mined land with *Pisolithus tinctorius* ectomycorrhizae. p. 527-534. *In* Proc. 1982 Symposium on Surface Mining, Hydrology, Sedimentology and Reclamation. *Ed.* D.H. Graves. University of Kentucky, Lexington, Kentucky.

Richards, B.N. 1961. Soil pH and mycorrhizae development in *Pinus*. Nature 190:105-106.

Riffle, J.W. and R.W. Tinus. 1982. Ectomycorrhizal characteristics, growth and survival of artificially inoculated ponderosa and Scots pine in a greenhouse and plantation. For. Sci. 28:646-660.

Rosendahl, R.O. 1942. The effect of mycorrhizal and nonmycorrhizal fungi on the availability of difficultly soluble potassium and phosphorus. Soil Sci. Soc. Am. Proc. 7: 477-479.

Ruehle, J.L. 1980. Growth of containerized loblolly pine with specific ectomycorrhizae after 2 years on an amended borrow pit. Reclam. Rev. 3:95-101.

Ruehle, J.L., D.H. Marx, J.P. Barnett, and W.H. Pawule. 1981. Survival and growth of container-grown and bare-root shortleaf pine seedlings with *Pisolithus* and *Thelephora* ectomycorrhizae. South. J. Appl. For. 5:20-24.

Rygiewicz, P.T., C.S. Bledsoe, and R.J. Zasoski. 1984. Effects of ectomycorrhizae and solution pH on ^{15}N ammonium uptake by coniferous seedlings. Can. J. For. Res. 14:885-892.

Sands, R., E.L. Fiscus, and C.P. Reid. 1982. Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. Aust. J. Plant Physiol. 9:559-569.

Sands, R., and C. Theodorou. 1978. Water uptake of mycorrhizal roots of radiata pine seedlings. Aust. J. Plant Physiol. 5:301-309.

Schramm, J.R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Trans. Am. Phil. Soc. 56:1-94.

Skinner, M.F., and G.D. Bowen. 1974. The uptake and translocation of phosphate by mycelial strands of pine mycorrhizas. Soil Biol. Biochem. 6:53-56.

Slankis, V. 1974. Soil factors influencing formation of mycorrhizae. Ann. Rev. Phytopathol. 12:437-457.

Theodorou, C. 1978. Soil moisture and the mycorrhizal association of *Pinus radiata* D. Don. Soil Biol. Biochem. 10:33-37.

Theodorou, C., and G.D. Bowen. 1969. The influence of pH and nitrate on mycorrhizal associations of *Pinus radiata* D. Don. Aust. J. Bot. 17:59-67.

Theodorou, C., and G.D. Bowen. 1971. Influence of temperature on the mycorrhizal association of *Pinus radiata* D. Don. Aust. J. Bot. 19:13-20.

Trappe, J.M. 1964. Mycorrhiza host and distribution of *Cenococcum graniforme*. Lloydia 27: 100-106.

Trappe, J.M., and R.F. Strand. 1969. Mycorrhizal deficiency in a Douglas-fir region nursery. For. Sci. 15:381-389.

Vozzo, J.A., and E. Hacskaylo. 1971. Inoculation of *Pinus caribaea* with ectomycorrhizal fungi in Puerto Rico. For. Sci. 17:239.

Went, F.W., and N. Stark. 1968. Mycorrhiza. Biosci. 18:1035-1039.

White, D.P. 1941. Prairie soil as a medium for tree growth. Ecol. 22:398-407.

Worley, J.F., and E. Hacskaylo. 1959. The effect of available soil moisture on the mycorrhizal association of Virginia pine. For. Sci. 5:267-268.

Beckjord,	http://dx.doi.org/10.1139/b84-210
Berry	http://dx.doi.org/10.2134/jeq1977.00472425000600040009x
Bowen,	http://dx.doi.org/10.1080/00049158.1965.10675964
Carrodus	http://dx.doi.org/10.1111/j.1469-8137.1966.tb06372.x
Dixon, R.K., H.E. Garrett	http://dx.doi.org/10.1139/x81-067
Dixon, R.K., S.G. Pallardy	http://dx.doi.org/10.1139/b83-168
Grossnickle, S.C., and C.P.P. Reid. 1982	http://dx.doi.org/10.1139/x82-051
Grossnickle, S.C. and C.P.P. Reid. 1983	http://dx.doi.org/10.1139/x83-153
Harley, J·.L., ·and J.M. Wilson.	http://dx.doi.org/10.1111/j.1469-8137.1959.tb05360.x
Harris,	http://dx.doi.org/10.1007/BF00011507
Hile	http://dx.doi.org/10.2307/3757362
Lampky	http://dx.doi.org/10.2307/3756442
Marx	http://dx.doi.org/10.1139/m77-033
McComb	http://dx.doi.org/10.1104/pp.21.1.11
Mejstrik	http://dx.doi.org/10.1111/j.1469-8137.1970.tb02428.x
Mejstri	http://dx.doi.org/10.1111/j.1469-8137.1975.tb01357.x
Melin	http://dx.doi.org/10.1111/j.1399-3054.1950.tb07495.x
Mexal	http://dx.doi.org/10.1139/b73-201
Morrison,	http://dx.doi.org/10.1111/j.1469-8137.1962.tb06266.x
Parke	http://dx.doi.org/10.1111/j.1469-8137.1983.tb03471.x
Richards	http://dx.doi.org/10.1038/190105a0
Rosendahl	http://dx.doi.org/10.2136/sssaj1943.036159950007000C0080x
Rygiewicz,	http://dx.doi.org/10.1139/x84-158
Sands	http://dx.doi.org/10.1071/PP9820559
Skinner,	http://dx.doi.org/10.1016/0038-0717(74)90011-X
Theodorou,	http://dx.doi.org/10.1016/0038-0717(78)90007-X
White,	http://dx.doi.org/10.2307/1930714