Mycorrhizae, mycorrhizospheres, and reforestation: current knowledge and research needs

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Although not a panacea, management of mycorrhizae and associated organisms is an important reforestation aid. Its three major components are protection of the indigenous soil community and evaluation of inoculation needs, integration of inoculation programs into existing reforestation technology, and research. Clear-cutting frequently results in reduced mycorrhizae formation, particularly when reforestation is delayed and no other host plants are present to maintain fungal populations. Implications of such reductions for reforestation vary with environmental factors and tree species. Adequate mycorrhiza formation is especially critical for ectomycorrhizal trees growing on poor soils or in environments where seedlings must establish quickly to survive. It may also be important where early successional, noncrop plants do not support the same mycobiont as the crop. In such circumstances, a self-reinforcing trend may develop, with poor mycorrhiza formation reducing seedling survival and poor tree stocking leading to further loss of mycorrhizal inocula. Inoculating nursery seedlings with mycobionts holds promise for improving outplanting performance only if site-adapted fungi are used. A practical alternative is to improve nursery practices to enhance natural populations of mycorrhizal fungi. Seedlings leaving the nursery with diverse mycorrhizae may perform better than those leaving with only one or a few nursery-adapted types. Research is needed in three broad areas: on adaptations of mycorrhizal fungi to particular environmental factors; on interactions between tree seedlings and processes occurring within the sphere of influence of roots (the rhizosphere) or of mycorrhizal roots (the mycorrhizosphere); and on the role of mycorrhizae and associated organisms in ecosystem structure and processes, particularly nutrient cycling, plant-plant interaction, and soil structure.

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Bien qu'il ne s'agisse pas d'une panacée, l'aménagement des mycorhizes et des organismes associés constituent une aide précieuse à la reforestation. Les trois constituants majeurs sont la communauté indigène du sol et l'évaluation du besoin en inoculum, l'intégration des programmes d'inoculation aux technologies usuelles de reforestation et la recherche. La coupe à blanc entraîne fréquemment une réduction de la formation des mycorhizes en particulier lorsqu'il y a un délai dans la reforestation et qu'il n'y a aucune autre plante hôte susceptible de maintenir la population de champignons mycorhiziens. Les implications pour la reforestation d'une telle réduction varient en fonction des facteurs environnementaux et des espèces d'arbre impliqués. La formation adéquate de mycorhizes est particulièrement critique pour les arbres mycotrophes venant sur des sols pauvres ou sur des milieux où les jeunes plants doivent s'établir rapidement pour survivre. Ceci pourrait aussi être imporant là où les plantes constituant la végétation de transition ne supportent pas les mêmes espèces de mycobiontes que les espèces d'arbre utiles venant par après. Dans de telles circonstances, il peut s'établir un cercle vicieux où la faible formation des mycorhizes réduit la survie des plants conduisant à une pénurie d'arbres avec une nouvelle diminution de l'inoculum mycorhizien. L'inoculation des plants en pépinière avec des mycobiontes ne sera utile pour augmenter le succès des plantations, que dans la mesure où des champignons adaptés aux sites pourront être utilisés. Une alternative pratique pourrait consister à améliorer les pratiques de pépinière de façon à augmenter la population naturelle de champignons mycorhiziens. Les plants quittant la pépinière avec divers types de mycorhizes pourraient mieux réussir que ceux avec seulement un ou quelques types de mycorhizes adaptés en pépinières. Des recherches sont nécessaires dans trois vastes domaines: sur l'adaptations des champignons mycorhizes aux facteurs d'un environnement spécifique; sur l'interaction entre les jeunes plants et les processus prenant place dans la sphère d'influence des racines (rhizosphère) ou des racines mycorhiziennes (mycorhizosphère); et sur le rôle des mycorhizes et organismes associés dans la structure et le processus de l'écosystème, particulièrement en ce qui concerne le cycle des bioéléments, l'interaction de plante à plante et la structure du sol.

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Introduction

Successful reforestation depends on the capacity of tree seedlings to capture resources early. Early growth assures space, hence a continuing resource supply and the vigor necessary to resist pests and pathogens and to survive climatic stress. Clear-cuts, shelterwoods, and forest gaps are quickly recolonized in mesic environments, and competition for even abundant soil resources may be keen. On droughty, nutrientpoor, or otherwise stressful sites, there may be only a brief period favorable for growth, and the seedling that does not become well established within that window is unlikely to survive (e.g., Amaranthus and Perry 1987*a*).

Mycorrhizae improve seedling survival and growth by enhancing uptake of nutrients (particularly phosphorus) and

water, lengthening root life, and protecting against pathogens (Harley and Smith 1983). Trees forming ectomycorrhizae (EM), including most of the important commercial species in the temperate and boreal zones and 70% of the species planted in the tropics (Evans 1982), virtually always have mycorrhizae. The same is probably true of vesicular-arbuscular (VA) mycorrhizae-forming dominants in the canopy of tropical forests (Janos 1980). Ectomycorrhizae are generally thought to be crucial, if not for survival, at least for acceptable growth. Pines and oaks planted on sites that have not previously supported ectomycorrhizae die or do not grow well unless inoculated (Mikola 1970, 1973; Marx 1980). For the trees forming VA mycorrhizae, including those of most tropical and many temperate deciduous families, the symbiosis often is critical. Janos (1980) hypothesizes that late successional trees of moist tropical forests are usually obligately mycorrhizal, while trees of earlier successional stages and those on relatively fertile soils are facultative. Ectomycorrhizal (EM) trees often predominate on highly infertile tropical soils (Janos 1980).

The three major sections of this paper parallel the steps required for integrating the management of mycorrhizae and associated soil organisms into reforestation programs: evaluation and management of indigenous soil biota, development of inoculation programs, and research. First, we review the influence of harvest and site preparation on mycorrhiza formation, and the influence, in turn, of mycorrhiza formation on reforestation. Second, we review inoculation technology. Finally, we discuss important areas for research: the interactions between mycorrhizal fungal species and environmental factors; processing occurring within the sphere of influence of roots (the rhizosphere), mycorrhizae (the mycorrhizosphere), and mycorrhizal hyphae (the mycosphere); and the role of mycorrhizae and associated organisms in ecosystem processes such as nutrient cycling, soil structure, and plant-plant interactions. We have, of necessity, cited only some of the many relevant papers that have appeared in the past few decades. Our intent is to provide a framework for thinking about managing the belowground ecosystem in reforestation programs.

Indigenous mycorrhizal fungi and reforestation

Management of indigenous soil organisms must begin at the harvest and site-preparation stage. Although abundant formation of epigeous ectomycorrhizae and even of VA mycorrhizae has been found on highly disturbed sites such as coal spoils (e.g., Schramm 1966; Daft and Hacskaylo 1977), most studies find fewer mycorrhizae formed on highly disturbed than on undisturbed sites (Reeves et al. 1979; Allen and Allen 1980; Loree and Williams 1984). Ectomycorrhiza formation is sometimes reduced in the soils of clear-cuts, particularly where logging slash has been burned (Wright and Tarrant 1958; Harvey et al. 1980, 1983; Perry et al. 1982; Parke et al. 1984; Perry and Rose 1983). Reductions sometimes persist for years. In the most extensive study to date, in which Douglas-fir and ponderosa pine seedlings were grown in soils from 10- to 20-year-old poorly reforested clear-cuts in California and Oregon, fewer mycorrhizae formed on seedlings grown in soil from clear-cuts than in forest soils, and reductions were greatest in soils from slash-burned areas (Parke et al. 1984).

Ectomycorrhiza formation is not always reduced by clearcutting. It may be enhanced and impacts vary among tree species. One study in the Oregon Cascade Mountains showed that the number of mycorrhizae on Douglas-fir seedlings in 1-year-old burned and unburned clear-cuts and adjacent forest soils did not differ (Pilz and Perry 1984); another study showed that Douglas-fir trees formed significantly more mycorrhizae in soil from an unburned clear-cut than in forest soil, although clear-cutting and burning reduced mycorrhizae on western hemlock growing in the same soil (Schoenberger and Perry 1982).

Two important questions that emerge from the studies we have cited will be considered here. First, why is mycorrhiza formation affected in some cases and not in others? Second, how do reduced numbers of mycorrhizae affect seedling performance?

Factors influencing mycorrhiza formation on disturbed sites

Mycorrhiza formation depends on environmental factors, host physiology, and soil microorganisms, as well as on inocula (e.g., Bowen 1972; Slankis 1974; Bowen and Theodorou 1979; Parke *et al.* 1983*b*; Chakraborty *et al.* 1985). Alteration of any of these may influence the number of mycorrhizae that can be formed in a particular soil (the mycorrhizae inoculation potential, MIP). Three factors influence MIP following disturbances such as clear-cutting and slash burning: the balance between mortality and input of propagules; the recovery of host plants, which provide the energy for populations of mycorrhizal fungi to stabilize and grow; and the diversity of fungal species, which buffers the mycorrhizal community against environmental changes accompanying disturbance.

Balance of mortality and input of propagules

How long soils remain infective in the absence of hosts depends on the balance between mortality and input of infective propagules. Past work strongly suggests that the MIP of unreforested clear-cuts in the Pacific Northwest declines with time (Perry and Rose 1983; Parke *et al.* 1984), and most evidence indicates that input of spores and survival of propagules in disturbed soils are generally insufficient to maintain MIP at levels found in undisturbed soils.

Persistence of EM-fungus spores and hyphal fragments probably varies with climate and soil. Metabolically active, presumably infective, hyphae have persisted as long as 2 years in the field in Scandinavia, although the numbers of active fragments dropped sharply (Persson 1982; Ferrier and Alexander 1985). To the extent that survival of a fragment is related to its respiration rate, the period would be shorter in warmer climates. Hyphal fragments of some species of VA mycorrhizal fungi remain viable for at least 6 months at the matric water potential -50 MPa (Tommerup and Abbot 1981), which suggests that they may persist longer in soil when dessicated. Presumably, resting spores survive for long periods; however, they may germinate prematurely in response to chemical secretions from nonhosts (Harley and Smith 1983) or they may be lost through erosion or leaching. In rangelands, the greatest impacts on mycorrhiza formation occur when topsoil is lost through erosion (Powell 1980) or mechanical disruption (Doerr et al. 1984). It is likely that erosion from deforested areas also reduces inocula.

Spores of EM fungi that are epigeous (fruiting aboveground), hence disseminated by wind, may enter sites at high rates. However, many EM and nearly all VA mycorrhizal fungi are hypogeous (fruiting belowground). Although spores of these fungi may be dispersed with wind-blown topsoil, mammals, insects, and birds are the primary vectors (Maser *et al.* 1978; McMahon and Warner 1984; Malajczuk *et al.* 1987); therefore, it may be that conditions affecting animal movements from forests to clear-cuts, such as cover in the form of logs and vegetation, also affect spore input.



FIG. 1. Hypothesized relationships between MIP and seedling survival following soil disturbance.

Host plants

Rapid establishment of hosts preserves fungal populations on disturbed sites and assists them to rebuild to predisturbance levels. Although MIP is reduced on older unreforested clearcuts, particularly when slash has been burned, abundant inocula exist on older burned clear-cuts that are reforested (Schoenberger and Perry 1982; Amaranthus and Perry 1987*a*).

Where pioneering noncrop plants host the same species of mycorrhizal fungi as the crop, they act as reservoirs of fungal inoculum during crop establishment. VA mycorrhizal plants are widespread and most are capable of sharing the same fungi; EM plants share fungi with fewer, though important, noncrop hosts. In the dry-summer forests of southern Oregon and northern California, *Arbutus menziesii* (madrone), *Lithocarpus densiflorus* (tanoak), and members of the Ericaceae, particularly *Arctostaphylos* sp., host some of the same fungi as do conifers (Largent *et al.* 1980; Molina and Trappe 1982*b*). Conifer seedlings are often found in association with these plants, apparently benefitting from high levels of mycorrhizal inocula (Amaranthus and Perry 1987*b*).

Diversity of fungal species

Thousands of fungal species form ectomycorrhizae, and host-symbiont specificity is generally low. In ecosystems with diverse EM-forming fungal species, the proportions of EM types forming on seedlings shifts after disturbance (Schoenberger and Perry 1982; Perry and Rose 1983; Pilz and Perry 1984), probably because types differ in response to environmental factors. Diversity likely provides a buffering capacity not found on a site with only one or few species, such as the montane lodgepole pine forest studied by Perry *et al.* (1982). Unlike EM fungi, the VA mycorrhizal guild contains only a few hundred known fungus species, and little is known about their response to abrupt changes in environment.

Mycorrhiza formation and seedling growth and survival

We might expect one of three general patterns to occur after harvest and site preparation (Fig. 1): MIP is not reduced and reforestation success or failure is therefore not related to it; MIP is reduced, but reforestation succeeds and populations of mycorrhizal fungi are stabilized and rebuilt by established seedlings; MIP is reduced, reforestation fails, and the lack of host plants further reduces MIP, making reforestation increasingly difficult with time. The last situation is most likely to occur in rigorous physical environments where seedling survival depends on rapid exploitation of soil resources, or in environments where competing plants require no mycorrhizae or do not have the same mycobionts as the crop species. In such cases, a self-reinforcing trend may develop in which reduced MIP leads to poor seedling survival, further reducing MIP. Successional trends resulting from the links between vegetation and soils on such sites can be drastically altered if the links are broken (e.g., Amaranthus and Perry 1987*a*).

Seedling survival has been enhanced by mycorrhizal inoculation or, particularly, by whole-soil inoculation in mountainous areas of the western United States (Amaranthus and Perry 1987*a*), Mexico (Valdés 1986), and India (Sharma 1983; G. D. Sharma personal communication). Janos (1980) has hypothesized that conversion of moist tropical forest to scrub or grasses when cultivation is too frequent (e.g., Arimitsu 1983) is hastened by the loss of VA mycorrhizal fungi, which puts obligately mycotrophic trees at a competitive disadvantage. We do not really know how rapidly deforested sites lose the capacity to support mycotrophic trees; in some cases the loss is apparently quite rapid. In the dry Miombo woodlands of Africa, natural regeneration fails following as little as 2 years without indigenous ectomycorrhizal trees (J. Maghembe, personal communication).

For two reasons, simply counting numbers of mycorrhizae may not indicate seedling performance. First, the rate of mycorrhiza formation on outplanted seedlings is likely to be at least as important as the numbers. Douglas-fir seedlings of the same size outplanted with different numbers of mycorrhizae onto a droughty site in southwest Oregon had the same numbers of mycorrhizae by the end of the first growing season, but seedlings that initially had more grew best (Amaranthus *et al.* 1987).

Second, seedling performance is probably related to mycorrhizal diversity. Ectomycorrhiza-forming tree species are likely to host several types of mycorrhiza at a given time, and each type may have a different cost and return. The contribution of a given type is likely to vary with the physical and biotic environment over both space and time. Some idea of the complexity of relationships can be seen in the cost benefit of different EM-fungus species (Fig. 2) synthesized on Douglas-fir and ponderosa pine growing in differing proportions in pots (D. A. Perry, M. Margolis, C. Choquette, R. Molina, and J. Trappe, unpublished). The cost benefit is estimated as the difference between average weights of inoculated and uninoculated seedlings growing in the same tree-species mix. EM types were synthesized on seedlings before their transfer into common pots containing pasteurized soils from a mixed stand of Douglas-fir and ponderosa pine. (Formation of some Thelephora terrestris mycorrhizae on uninoculated seedlings late in the experiment probably did not affect seedling growth). When the Douglas-fir seedlings were grown in monoculture, the net energy cost of Laccaria laccata was zero, while that of Hebeloma crustiliniforme and Rhizopogon vinicolor was negative, i.e., the fungi drew more energy from the host than they returned. However, L. laccata strongly benefitted Douglas-fir mixed with ponderosa pine, and R. vinicolor paid its own way. None of the fungus species yielded a net benefit to ponderosa pine. Hebeloma crustuliniforme was a net cost to both tree species in all mixes.

Results such as these are highly specific to the experimental conditions. *Rhizopogon*, for example, is a strong rhizomorph former and therefore benefits water relations (Parke *et al.* 1983*a*). Growing seedlings under water stress might yield quite different results. *Hebeloma crustuliniforme* mycorrhizae respire at a greater rate than those of *L. laccata* (Marshall and Perry 1987), which partially explains their higher energy cost. However, such a respiration rate may yield benefits in some situations.

Although the specific responses cannot be extended beyond



FIG. 2. Influence of mycorrhizal species on growth of Douglas-fir and ponderosa pine seedlings in pure stands and in mixture. Seedling size is that relative to size of seedlings without added mycorrhizae (but with some contamination by *Thelephora terrestris*).

the experimental conditions, a useful generalization is represented by Fig. 2: fungi do different jobs for different hosts in different environments, and the diversity of mycorrhizal types is likely to contribute to seedling success. Determining the best mix of fungi in a given situation, however, may be difficult. Although some mycorrhizal fungi benefit hosts in clearly identifiable ways (such as nutrient or water gathering), others may confer an advantage only in some environmental contexts, at specific periods of plant development, or only indirectly through influences on ecosystem processes such as soil aggregation (e.g., Forster 1979). Native populations should be maintained to assure the diversity of seedling responses necessary for success in often unpredictably varying environments. Where native populations are reduced or nonexistent, inoculation with more than one fungal species is a good strategy only if the fungal mix is appropriate; random choices are unlikely to pay dividends even when inoculation is by means of soil transfers, which may or may not produce positive results (e.g., Amaranthus and Perry 1987a).

Integrating inoculation technology into nursery and forest management

Inoculating nursery seedlings to improve stem caliper or to obtain even growth with fewer culls requires a strategy different from that for enhancing seedling survival in harsh habitats, which in turn requires a strategy different from that for improving tree yield over a forest rotation. Research programs must separate these different purposes in order not to oversimplify a complex biological problem. Techniques of inoculation with mycorrhizal fungi in nurseries (Trappe 1977; Marx 1980; Molina and Trappe 1982*a*, 1984) do not need to be repeated here. Instead, we will discuss the technology as one of several nursery and forest-management tools.

The Pisolithus tinctorious mycorrhiza program developed by

Marx and colleagues illustrates the difficulties and successes of an inoculation program (Marx 1980, 1985, Cordell 1985). They have developed a technology for readily inoculating nursery seedlings with pure cultures of a selected fungus species and have clearly demonstrated that seedlings perform best with fungi adapted to the planting site. On heavily disturbed sites, especially mine spoils, where *P. tinctorius* is a prevalent pioneering fungus on establishing Pinaceae, seedlings inoculated with *P. tinctorius* performed better than uninoculated nursery stock (Marx 1980). On highly eroded sites in Mexico, inoculation with *P. tinctorius* significantly increased survival of pine seedlings, whereas inoculation with *L. laccata* had no effect (Valdés 1986).

Nationwide testing of a commercial preparation of P. tinctorius in bare-root and container-seedling nurseries (Marx et al. 1982, 1984a) showed the feasibility of the technology and generated momentum for other programs. However, even after routinely successful laboratory preparation, P. tinctorius failed or had poor results in bare-root nurseries in areas such as the Pacific Northwest, one of the largest timber-producing regions and potential inoculum markets in the United States. The poor performance was likely related to extreme differences between the physical and biotic environment and nursery practices of the southern and southeastern United States, where the isolate and technology were developed, and those of distant experimental locations where the inoculum was tested. Regionalized research programs should have more success.

Mycorrhizae in nursery management

Because of the limited availability of inocula, and because of inconsistent success, inoculation of bare-root nursery trees with individually selected fungal species, either as pure, vegetative cultures or as spores, should be considered only one way to apply mycorrhiza technology (Molina and Trappe 1984). Maintaining or fostering native mycorrhizal fungus populations may provide similar benefits. In management workshops (e.g., Molina 1981; Molina and Trappe 1984), nursery personnel can be shown how mycorrhizae benefit the host plant and fungus, and, especially, how nursery practices affect the population levels and functions of mycorrhizal fungi. Managers can learn to monitor seedling roots and record mycorrhiza development for first-hand feedback on the effects of nursery practices.

Mycorrhizae are often deficient in modern bare-root nurseries, especially in those located far from large forest tracts that provide natural fungal inocula. Routine fumigation with gases, such as the commonly used methyl bromide mixes, may be responsible. Nursery managers who recognize that fumigation destroys mycorrhizal fungi as well as pathogens and weed seed will be more likely to select biocides that eliminate specific pests (Trappe *et al.* 1984) or to fumigate specific problem sites rather than entire areas.

After fumigation, aggressive symbionts such as *Thelephora* species may quickly dominate root systems, reducing diversity within the 1- to 3-year production cycle. However, organic amendments, fertilizers, crop rotation, and routine nursery practices can be used to foster mycorrhiza development and diversity as well as healthy nursery stock (Molina and Trappe 1984). Seedlings leaving a nursery with many species of mycorrhizal fungi on their roots may have greater survival potential than those with one or a few dominant, aggressive fungi adapted to the nursery or field planting site.

Inocula and inoculation tests

Inoculation with pure cultures of selected fungi allows

introduction of specific fungi, prevents contamination by potential pathogens, and permits commercial production in large quantities. Abbott Laboratories produced large batches of a viable P. tinctorius inoculum, MycoRhiz®, and showed that it worked well within a specific region; however, production has been stopped because of insufficient demand. Sylvan Spawn Laboratory of Butler County Mushroom Farms produces effective inoculum in small bags (7 to 12 L) by techniques flexible enough to provide small or large quantities of a diverse array of fungi. Of their EM fungi for inoculating containergrown seedlings, L. laccata and H. crustuliniforme have generally performed well, even at low levels of inoculation and after a 2- to 4-month storage (Hung and Molina 1986a, 1986b). Commercial production is therefore feasible, but industry and researchers must make a long-term commitment to make and keep commercially produced inoculum available.

With a reliable source, spore inoculation remains a viable alternative to vegetative inoculum. Pisolithus tinctorius spores have been successfully used to inoculate pines and a commercial preparation for custom-coating seeds is available (Marx et al. 1984b). Rhizopogon spores have also been successfully used to inoculate pines in Australia and elsewhere; in the Pacific Northwest, spore inoculation of Douglas-fir in both container and bare-root nurseries has been effective (Castellano et al. 1985). Rhizopogon species are of particular interest in the Pacific Northwest because at least one species, R. vinicolor, is common on young Douglas-fir seedlings in clear-cut forests, and seedlings inoculated with this fungus have better drought tolerance (Parke et al. 1983a). Vegetative inoculum of Rhizopogon spp. has not been successful (Molina 1980), but spores are an effective alternative. M. A. Castellano (unpublished data) has recently begun studies of inoculation of large areas of container nurseries by means of spores in automatic mistirrigation systems. Preliminary results show high success in the nursery and significantly improved stem caliper.

The oldest form of mycorrhizal inoculation is by means of forest duff or soil. Soil (or humus) adds a diversity of organisms, including not only mycorrhizal fungi but bacteria, actinomycetes, and perhaps pathogenic fungi Marx (1980). Such a complex of organisms, presumably adapted to field conditions, may or may not be more beneficial to seedlings than inoculation with pure cultures of mycorrhizal fungi. The few studies comparing the two approaches have yielded contradictory results (e.g., Momoh and Gbadegesin 1980; Sharma 1983; G. D. Sharma, personal communication). The source of soil inocula appears to be critical. Inocula from young plantations has significantly increased seedling growth and ectomycorrhizal formation, while inocula from mature forests has not (Amaranthus and Perry 1987*a*).

Concepts of ectomycorrhiza use can also be applied to crops harboring VA mycorrhizae. For such crops (e.g., sweetgums, maples, redwoods, cedars), crop rotation, cover cropping, and soil fumigation are increasingly important in nursery management. However, fumigation destroys VA mycorrhizal fungi, and because spores are not wind dispersed and natural recolonization is slow and spotty, reinoculation is necessary. The expense and effort required to inoculate with VA mycorrhizal fungi make fostering populations an economic advantage.

Fungus selection

Reliance on one isolate, as has been shown, is not always biologically sound. Seedlings inoculated with a Georgia isolate of *P. tinctorius* (produced by Abbott Laboratories) performed much less well on southwest Oregon outplanting sites than seedlings inoculated with spores from a local source (M. A. Castellano and J. M. Trappe, unpublished data). Trappe (1977) emphasized early the importance of selecting fungal species, or strains within species, by their capacity to enhance adaptation of inoculated seedlings to the destined planting site. They might, for example, impart drought resistance, tolerance to temperature extremes, or adaptation to trees on particular soil types. Trappe envisioned a system whereby strains of mycorrhizal fungi already proven effective in diverse reforestation habitats would be available for nursery operators. Just as growing seedlings from seed collected from the reforestation zone is biologically sound, so, too, is inoculating seedlings with fungi originating from the outplanting site or its environmental equivalent.

However, we are not yet close to realizing Trappe's scheme for inoculum. A major problem has been the ineffective performance of desirable candidate fungi. For example, while L. laccata has performed well, often completely colonizing entire root systems, several Suillus and Rhizopogon species have performed poorly or failed completely in an early test of vegetative inoculum (Molina 1980). Several strains of Laccaria have produced abundant mycorrhizae on many Pinaceae species grown in containers (Molina 1982), even with the high fertility levels known to inhibit mycorrhiza formation of other fungus species (Molina and Chamard 1983). Hung and Molina (1986a, 1986b), working cooperatively with Sylvan Spawn Laboratory, have found that commercial preparations of Laccaria and Hebeloma effectively form mycorrhizae on container-grown Douglas-fir seedlings under standard nursery conditions. The Sylvan Spawn product, shipped from Pennsylvania to Oregon, has a long shelf life and has performed well at low ratios of inoculum to potting substrate (Hung and Molina 1986a, 1986b), desirable characteristics for a commercial inoculum preparation. Unfortunately, outplanting performance of the seedlings has improved little (M. A. Castellano and R. Molina, unpublished data).

Have we gained from our research programs? The gains appear to outweigh the poor results. A technology has been developed and shown to be feasible. However, poor outplanting results return us to the original objective: to be able to select fungi for particular traits that will lend an advantage to outplanted seedlings. Coupled with the selection process must be active laboratory research designed both to improve inoculum performance of desirable but recalcitrant fungi such as *Rhizopogon* spp. and to explore the native inoculum potential of disturbed planting sites.

Research needs

It is clear that we need to better understand the interactions among mycorrhizal fungus species, host species, and environment. Important biotic interactions, however, are not confined to those between fungus and host, and organisms are not passive prisoners of the abiotic environment but rather are participants in the creation and maintenance of favorable growing conditions. Future research must therefore enlarge its scope to include the mycorrhizosphere and the ecosystem as a whole. We see three interrelated areas as having highest priority.

(1) Benefits of mycorrhizae, in particular of mycorrhizal diversity, must be studied in field environments, which are characterized by variability in biotic and abiotic factors and in space and time.

(2) Reciprocal interactions between trees and soil must be better understood. Research is needed on the links between the structures and processes within soils and the energy input from trees; on the influence on tree growth of belowground processes that are fueled directly by tree photosynthate; on the stability of the soil ecosystem in the absence of trees; and on the influence of changes in the soil ecosystem on reforestation.

(3) We must better understand how soil organisms mediate interactions among plant species, and how this mediation influences reforestation. Research will therefore be needed on material transfers through mycorrhizal linkages, on the patterns imposed by plant species on soil and how these help or hinder tree growth, and on mycorrhizal detoxification of allelochemics.

In this last section, we will briefly discuss those structures and processes within the soil ecosystem that may significantly influence reforestation.

The rhizosphere: extended symbioses

The belowground microbial community is not distributed homogeneously within the soil volume but rather in islands of intense activity centered on energy sources: roots, mycorrhizae, and mycorrhizal hyphae. Photosynthates flowing into the soil through roots and mycorrhizae support a diverse community of soil organisms, many of which influence plant growth (reviews include Rambelli 1973; Newman 1978, 1985; Bowen 1980*a*; Coleman 1985; Linderman 1985; Foster 1986; Whipps and Lynch 1986).

Labeling experiments indicate that 12 to 40% of the total net carbon fixed by cereals is exuded from roots in nonsterile soils (Whipps and Lynch 1986). Few such experiments have been made with trees, but Reid and Mexal (1977) found that as much as 80% of the carbon allocated to roots by drought-stressed lodgepole pine seedlings was exuded into the rhizosphere. From what we know of carbon allocation to roots, it is likely that this was at least 50% of the total amount fixed.

What proportion of the energy flowing into and beyond the rhizosphere is lost to the tree, and therefore represents carbohydrate that could be diverted to aboveground biomass? What proportion fuels processes that directly or indirectly enhance tree growth and vigor? The answer to these questions may be important not only to reforestation but to long-term forest productivity.

Processes occurring in the rhizosphere (for brevity, the term "rhizosphere" will here include mycorrhizospheres and mycospheres) undoubtedly influence rooting characteristics, mycorrhiza formation, and probably many other factors bearing directly or indirectly on tree-seedling vigor (Rambelli 1973; Bowen and Theodorou 1979). In the healthy rhizosphere, a dynamic balance exists between plant, mycorrhizal fungi, and other organisms. Their interactions are, within limits, stable against external perturbation. However, disrupting the balance can change the community of rhizosphere organisms from one that is mutualistic with trees to one that is pathogenic. For example, when their numbers are low, Collembola stimulate growth of VA mycorrhizal plants, but they inhibit it when their numbers are high (Warnock et al. 1982; Finlay 1985). The question relevant to reforestation is "Do management practices disrupt or reinforce the mutualistic nature of the rhizosphere?"

Clear-cutting, particularly when slash is burned, increases pathogenic organisms in the soil and, in some cases, dampingoff diseases on seedlings (Julaluddin 1968; Laine 1968; Ahlgren 1974; Widden and Parkinson 1975). However, we must not overgeneralize the effects of practices such as burning, which may have complex, highly site-specific effects on microbial communities, as shown by the root-tip production by Douglas-fir



FIG. 3. The effect of soil pasteurization on root-tip formation by Douglas-fir seedlings grown in disturbed and undisturbed soils of four different sites (Perry and Rose 1983). UF, undisturbed forest soil; W, clear-cut with logging slash windrowed; BB, clear-cut with logging slash broadcast burned; UB, clear-cut with neither windrowing nor broadcast burning.

seedlings grown in pasteurized and unpasteurized soils from four different sites (Fig. 3 from Perry and Rose 1983). On two sites, clear-cutting and windrowing or broadcast burning apparently converted the soil microbial community from one that enhanced root-tip production to one that inhibited root-tip production (Fig. 3A and 3C). Unpasteurized soils from both a forest and a burned clear-cut of a third site inhibited root-tip production (Fig. 3B), but burning apparently shifted the microbial community of a fourth site so that root-tip production was enhanced (Fig. 3D).

To understand the mechanisms behind such diverse responses, we must understand the processes occurring in the rhizosphere community (Fig. 4). The first trophic level for most plants is composed of mycorrhizae or the hyphae and rhizomorphs extending from them into the soil. Organic exudations and root sluffing support a second level dominated by bacteria. A complex community of protozoa and invertebrates graze the microorganisms, and vertebrates consume fungal fruiting bodies. Foster (1986) defines three zones: the rhizoplane, within $10 \,\mu m$ of the root (or mycorrhizal) surface; the inner rhizosphere, 10 to 400 μ m from the root surface; and the outer rhizosphere, 400 to 3000 µm from the root surface. Both absolute numbers and species diversity are highest in the rhizoplane; however, microbial numbers are affected as much as 1000 µm from the surface (the probable limit of diffusion of soluble organics), and nematodes can detect roots 3000 µm away (Foster 1986). The character of exudates, and consequently of the rhizosphere community, differs between mycorrhizal and nonmycorrhizal plants, the former releasing more complex organics and supporting fewer pathogens (Katznelson et al. 1962; Krupa and Fries 1971; Rambelli 1973; Foster 1986; Meyer and Linderman 1986).

The rhizosphere community influences plant growth by ways other than drawing energy: by releasing a complex of hormones, allelochemicals, and chelators that probably affect plants both



FIG. 4. Schematic diagram of biotic processes within the mycorrhizosphere. Most energy exuded by mycorrhizae probably passes directly to bacteria; however, arrow widths do not necessarily reflect relative quantities of energy flow.

positively and negatively; by fixing nitrogen; by competing for nutrients but enhancing mineralization rates; by decomposing minerals; and by welding mineral elements together into organically sustained soil aggregates. We will look at four biologically mediated processes that are particularly relevant to the health of individual trees: nitrogen fixation, nutrient cycling, chelate production, and ethylene production.

With some exceptions (e.g., areas of heavy acid rain), nitrogen is the nutrient most limiting for forest growth. Harvest and site preparation (particularly burning) often result in nitrogen loss that greatly exceeds known input to an ecosystem over the length of most rotations (Perry and Rose 1987). If long-term forest growth is to be maintained, nitrogen must be replaced, and biological nitrogen fixation is often the most sensible means (Domingo 1983; Gordon and Avery 1985). Various genera of bacteria fix nitrogen under the low oxygen tensions that occur in rhizospheres (Florence and Cook 1984; Giller and Day 1985), and fixation may sometimes be enhanced by, or totally dependent on, mycorrhizae (Li and Hung 1987). Research on the conditions under which fixation occurs, its significance to the nitrogen economy of forest ecosystems, and the possibility of enhancement has high priority.

Much recent work has been devoted to the role of microbial grazers in cycling nutrients (e.g., Elliot et al. 1980; Coleman et al. 1984; Anderson et al. 1985; Clarholm 1985a, 1985b; Curry et al. 1985; Ingham et al. 1985; Verhoeff and De Goede 1985; Visser 1985). The work consistently shows that nematodes, protozoa, amoebae, and microarthropods grazing fungi and bacteria accelerate the release of nitrogen in a form available to plants. Nutrient fluxes resulting from grazing can be significant. For example, Persson (1983, cited in Verhoeff and De Goede 1985) estimated that 10 to 50% of total nitrogen mineralization in a Swedish pine forest was mediated by soil invertebrates. In three oak woodlands in Great Britain, more than 10 times the ammonium was released from litter in plots with millipedes (Glomeris marginata) than in plots without them (Anderson et al. 1985). Louisier and Parkinson (1984) estimated that testate amoebae alone consumed more than 13 000 kg \cdot ha⁻¹ of bacteria annually in an aspen woodland soil, and 85% of that consumption was respired or excreted. This would release from 25 to 50 kg $N \cdot ha^{-1} \cdot year^{-1}$ from bacterial biomass, an amount roughly equivalent to that taken up annually by the trees. Within rhizospheres, N fixation fueled by plant photosynthate and subsequent N release through grazing could be important mechanisms providing N to seedlings.

Among many compounds released by roots, mycorrhizae, and rhizosphere organisms are various metal chelators that directly or indirectly alter nutrient availability, weather primary minerals, and inhibit root pathogens (e.g., Cromack *et al.* 1979; Olsen *et al.* 1981; Schroth and Hancock 1982; Leong 1986). Among the most powerful and important of these, particularly in pathogenesis, are the siderophores produced by various bacteria and fungi, including mycorrhizal fungi. Siderophores occur in lower concentrations in soils of clear-cuts (particularly those broadcast burned) than in forest soils (Perry *et al.* 1984). Research is needed to identify why siderophores are reduced, how quickly they recover, and how seedlings are affected.

Ethylene, a plant hormone also produced by microorganisms, may inhibit or stimulate root growth, depending on concentration, and may also play a role in pathogenesis (Smith 1977; Graham and Linderman 1981). Ethylene-producing organisms are facultative anaerobes that are likely to be active within soil aggregates (Smith 1977) and under the low oxygen tensions resulting from high levels of respiration in the rhizosphere (Linderman 1985; Meyer and Linderman 1986). Although ethylene may reach relatively high levels in soils, its effect on seedlings under natural conditions is unknown. In agricultural soils, plowing invariably reduces the number of anaerobic microsites and therefore reduces ethylene production (Smith 1977). In this area, research is needed to determine whether ethylene production is influenced by harvest and site preparation, and if so, whether this affects seedling performance.

Ecosystem processes

The health of tree seedlings ultimately depends on the health of the ecosystem within which they exist. Two aspects of ecosystem structure that result at least in part from processes originating within the rhizosphere, and that in turn directly influence tree seedlings, are plant-plant interactions and soil structure.

Mycorrhizal fungi directly mediate interactions between plants in at least three ways. First, they allow trees to compete successfully with grasses and herbs for resources (Bowen 1980b) and may detoxify allelochemicals produced by these plants as well (Perry and Choquette 1987). Second, pot tests show that mycorrhizae may decrease competitive interactions between plants (e.g., Fig. 2, from D. A. Perry, H. Margolis, C. Choquette, R. Molina, and J. Trappe, unpublished) and increase the productivity of species mixtures, particularly in soils where phosphorus is limiting (C. Puga and D. P. Janos, unpublished). Third, mycorrhizal hyphae link plants of the same and different species and act as routes of material transfer among plants (Brownlee et al. 1983; Read et al. 1985). To date, studies have been under controlled conditions rather than in the field. However, direct relevance to reforestation seems probable. For example, allelochemicals are known to have caused reforestation failures in both Europe and North America (Fisher 1980, 1987; Horsley 1987), and the capacity of some species of mycorrhizal fungi to detoxify allelochemicals could be important in reforesting vegetation-rich environments. On the other hand, some plants that appear to be aboveground competitors of tree seedlings may emerge as allies belowground. In the droughty environments of southern Oregon and northern California, conifer seedlings often associate in disproportionate numbers with nonconiferous EM plants, where their survival is probably enhanced because of the rich concentration of mycorrhizal inocula (Amaranthus and Perry, 1987b).

Mycorrhizae and other microbes affect soil formation and structural characteristics by producing humic compounds (e.g., Tan et al. 1978), accelerating decomposition of primary minerals (Cromack et al. 1979), and producing organic "glues" that bind soil particles into water-stable aggregates (Sutton and Sheppard 1976; Forster 1979; Tisdall and Oades 1979, 1982). The importance of the first two processes to soil fertility and plant nutrition is well known. The latter has received less attention in forest soils and may be important to reforestation. Plants and microbes produce extracellular polysaccharides (ECPs) that link mineral grains and homogeneous clay domains (tactoids) into stable aggregates (see reviews by Lynch and Bragg 1985; Emerson et al. 1986). Aggregation in turn influences soil properties, providing the diversity of pores necessary to permit both water drainage, therefore aeration, and water retention. Since pores are defined by aggregate structure, stable pores are possible only where aggregates are also stable. Fungi produce particularly stable soil aggregates (Emerson et al. 1986). However, ECPs are degraded by microbial activity and stable soil aggregation depends on a relatively continuous flow of energy (in the form of ECPs) into the soil. It follows that, without plants, soil structure is altered. In some instances this may happen quickly: the number of large soil aggregates declined 80% within 1 year of cultivation of a grassland (Low 1955). Reestablishment of grasses resulted in reaggregation, but the process was much slower than the disaggregation (Graecen 1958; Low 1972).

Other than on compaction, little work has been done on the structure of disturbed forest soils. Borchers and Perry (1987) found that the proportion of large aggregates declined by about 14% in two southern Oregon clear-cuts that were unreforested for 15 years or more (Fig. 5). The two sites differed greatly in soil texture (Cedar Camp soils were 80% sand, Holcombe Peak only 20% sand), reflecting the importance of organic matter in stabilizing large aggregates. Although total soil organic matter



FIG. 5. Change in the distribution of soil aggregate sizes between forest and adjacent clear-cuts of two sites in southwest Oregon (Borchers and Perry 1987). Negative values indicate reduced proportion in clear-cut soils. Cedar Camp soils have greater than 80% sand, Holcombe Peak soils less than 20%.

was lower in soils of clear-cuts than in forest soils at Holcombe Peak, this was not true at Cedar Camp, which suggests that chemical structure rather than amount of organic matter is more important in determining aggregate stability.

The internal structure of aggregates may also be altered in unreforested clear-cuts. Scanning electron micrographs of large aggregates from the Cedar Camp site clearly show differences between the clear-cut and the adjacent forest (Fig. 6). Note the relatively large pores ($>50 \ \mu m$) and fungal hyphae within the forest soil aggregate (Fig. 6A) and the absence of fungal hyphae within the aggregate from the clear-cut (Fig. 6B). Figure 7 shows fine detail of the forest soil aggregate, including the smaller pores ($<15 \mu m$) that hold water against gravitational drainage. Degradation of soil structure in clear-cuts is likely to make reforestation difficult on sites that tend toward droughtiness, especially on those with sandy soils, and it was probably a factor in the reforestation failures at Cedar Camp. As with reduced MIP, loss of biologically mediated soil aggregation could start a feedback loop, reduced aggregation reducing seedling survival, further reducing aggregation. Research is needed to learn how quickly aggregation declines after harvest, how quickly aggregation is reestablished by pioneering vegetation, how different plants affect soil aggregation characteristics, and how the interactions vary with environment and soil characteristics (e.g., sands vs. clays).



FIG. 6. Scanning electron micrographs of soil from (A) a forest and (B) an adjacent unreforested clearcut of the Cedar Camp site, southwest Oregon.



FIG. 7. Scanning electron micrograph of fine-pore structure and hyphae in the forest soil of Fig. 6. (Hyphae collapsed during sample preparation.)

Coda

Foresters are faced with an unprecedented challenge. Forests are the major terrestrial links in global carbon and water cycles, and the earth's climate is almost certainly tied to its forests. In this context, the importance of rapid, successful reforestation goes far beyond the need to produce a new crop in a timely fashion and understanding the processes that confer stability and resilience on forests takes on new urgency. It is increasingly clear that the rhizosphere, the soil community as a whole, and the entire ecosystem, including the trees that are our main object of interest, form a coherent, dynamic unit, and that stability and resilience must ultimately be understood in terms of patterns emerging from interrelationships within this unit. The real challenges for the future lie in the largely untilled ground of holism.

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