PART F

ROOT GROWTH STUDIES

ASPECTS OF MYCORRHIZAL INOCULATION IN RELATION TO REFORESTATION

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ABSTRACT

The use and manipulation of the mycorrhizal symbiosis has enormous potential benefits in tree nurseries and in artificial regeneration programmes. This paper discusses the role of a mycorrhizal inoculation programme in reforestation. Included in this discussion are type of inoculation and response of the host to inoculation. The direct impact of a mycorrhizal inoculation programme will depend upon the symbionts selected and, of course, site characteristics. Inoculation generally improves survival and growth following outplanting. However, this advantage may be a function of the larger seedling size resulting from inoculation rather than from transplanting fungal inoculum to the forested site. This paper also points out current problems and future directions of any inoculation programme.

INTRODUCTION

The mycorrhizal association of forest trees has long been recognised as an obligatory symbiosis (Harley, 1969; Marks and Kozlowski, 1973). The mycorrhizal structure is involved in nutrient uptake, water absorption (Reid, 1979) and protection against certain root pathogens (Marx, 1973). The biological functions of mycorrhizal roots have been studied in over 3000 publications (Hacskaylo and Tompkins, 1973), with much of this research published in the last 20 years.

There are two basic types of mycorrhiza, endomycorrhiza and ectomycorrhiza. The symbiosis of greater importance to forest regeneration is the ectomycorrhizal association. Only 5% of all vascular plants are ectomycorrhizal, with many of the major forest tree species included in this category. These forest species include not only many coniferous species (all species of the family *Pinaceae*) but also many angiosperms (e.g., members of the families, Fagaceae, Betulaceae, Juglandaceae, Myrtaceae; Meyer, 1973).

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Fungi associated with these higher symbionts belong to the classes Basidiomycetes and Ascomycetes. It is estimated that over 2000 fungal species are potential ectomycorrhizal symbionts (Trappe, 1977).

Endomycorrhiza are by far the most prevalent type of mycorrhiza, occurring on about 90% of all herbaceous and woody plants. However, only a few genera of forest trees of economic importance form endomycorrhiza (e.g.,*Acer, Ulmus, Liquidamber, Fraxinus*). Fungi which form endomycorrhizal associations are mainly Phycomycetes in the Family Endogonaceae.

The obligatory nature of host plants on the ectomycorrhizal symbiosis is well accepted (Hatch, 1937; Harley, 1969). Nonmycorrhizal plants can be maintained only in highly fertile soils and species establishment trials inevitably fail in the absence of suitable inoculum (Vozzo, 1971). However, the role of an inoculation scheme in artificial regeneration of previously forested lands which contain abundant mycorrhiza inoculum is less clearly understood. The presence of mycorrhizas on pine seedlings outplanted on previously forested lands can influence their performance (Shoulders and Jorgensen, 1969). Therefore, the opportunity to improve seedling quality and, thereby, performance through inoculation becomes apparent. An inoculation programme must consider not only the amount of infection, but also the timing of infection, and the sources of infection.

The objectives of this paper are to discuss the practical aspects of mycorrhizal inoculation as they relate to reforestation and plantation development. The physiology of mycorrhizas was reviewed previously (Marks and Kozlowski, 1973; Sanders *et al.*, 1975) and except as it may relate to reforestation will not be discussed. Similarly, the importance of suitable sources of mycorrhizal inoculum for afforestation and reclamation is beyond the scope of this paper.

METHODS OF INOCULATION

In many nurseries, soil fumigation to eliminate noxious weeds and pathogens frequently precedes sowing. Soil fumigation usually destroys most of the microbial population in the upper 20 cm of soil layer. Along with undesirable organisms, many desirable organisms, including mycorrhizal fungi, may also be eliminated from the upper soil layer by fumigation. Typically, nurseries rely on the slow and somewhat erratic process of recolonisation from inoculum surviving fumigation or via air-borne spores for ectomycorrhizal development. This practice of natural recolonisation may be satisfactory for many nurseries. However, inoculation of fumigated nursery soil may be desirable if the source of natural inoculum is limiting, or if the natural reinfection process is too slow. It may also be used to establish specific mycorrhizal relationships.

There are four types of inocula which have been used for mycorrhizal inoculation of nurseries: (A) soil or litter from forests and old nurseries, (B) mycorrhizal "mother" seedlings, (C) basidiospores, and (D) pure cultures of fungal mycelium. Although the first two techniques have been successfully practiced in the tropics and subtropics (Mikola, 1970), they may be impractical in many large nurseries because forest litter may reintroduce pests such as weeds or pathogens, and mother trees do not lend themselves to production systems. Therefore, further discussion will centre around vegetative and basidiospore inoculation.

Basidiospore Inoculum

The use of basidiospores of mycorrhizal fungi is perhaps the most practical infection technique. Basidiospores are easily stored, shipped, and introduced into nursery soil because of their size and weight (Marx *et al.,* 1979; Theodorou and Skinner, 1976). Nursery soil inoculation can be accomplished successfully by several methods: (A) incorporating either crushed sporocarps or (B) basidiospores into the soil prior to sowing, (C) encapsulating the seed, or (D) inoculating the soil following sowing. Successful infection is dependent upon spore germination and colonisation of the cortical tissues of primary roots. This is not always achieved with soil incorporation of basidiospores. Soil inoculation generally results in variable growth response compared to mycelial inoculation (Marx, 1976). In spite of variable host response to soil inoculation following fumigation, a large scale trial using basidiospores of *Pisolithus tinctorius* (Mich. ex Fr.) Coker & Couch resulted in improved yield in a *Pinus taeda* L. nursery in Oklahoma (Marx *et al.,* 1979). The most effective inoculation technique was applying basidiospores in an aqueous suspension (550 mg basidiospores/m^2) immediately after sowing. Inoculation in this manner resulted in a 15% increase in plantable seedlings (seedlings larger than 15 cm in height) compared to noninoculated seedlings. Other inoculation techniques were tested, but were less effective, and apparently basidiospore inoculation was ineffective if delayed beyond the sowing date. Others have also reported poor infection levels and growth response if inoculation is delayed until 6 to 12 weeks after sowing (Marx and Bryan, 1975; Lamb and Richards, 1974). However, incorporation of basidiospores into the soil up to four months prior to sowing has been effective with *P. radiata* D.Don (Theodorou and Bowen, 1973).

The large-scale adoption of basidiospore inoculation has been hindered by lack of available sources of inoculum. Mycorrhizal fungi, as yet, cannot be cultured artificially to produce copious quantities of basidiocarps from which spores can be harvested, and only a few species grow in sufficient quantities to make field collections practical. The most notable species is *Pisolithus tinctorius.* In 1975, over 7 kg of basidiospores were collected from kaolin clay spoils and processed in about 20man-hours. Sufficient basidiospores were collected to inoculate 1.4 ha of nursery soil. Using reported results (Marx *et al.,* 1979), yield could be increased from about 2.7 million to approximately 3.2 million trees from this one spore collection. Unfortunately, very few other fungal species offer this potential in basidiospore yield. Certain *Rhizopogon* or *Suillus* species may afford some potential as suitable sources of basidiospore inoculum (Theodorou and Bowen, 1970).

Mycelial Inoculum

Mycelial inoculum has advantages over other forms of inocula or no inoculation in that the inoculum is generally free of contaminants, and it appears to be more virulent. Inoculation with mycelia results in mycorrhizas forming sooner and in greater numbers than with basidiospores (Marx *et al.,* 1976). Artificial inoculation of fumigated nursery soil with select mycorrhizal fungi has been successful in many nurseries (Bowen *et al.,* 1971; Göbl, 1975; Marx *et al.,* 1978). Recently, progress has been made in the large-scale commercial production of mycelial inoculum. Potentially, this may allow the forester to select a desired fungal symbiont for his specific regeneration needs. However, in the developmental stages, work has centred on one species, *Pisolithus* *tinctorius,* and results to date have been mixed. Currently, the inoculum includes vermiculite as an inert carrier. Consequently, large quantities of inoculum must be shipped and applied to the nursery beds (approximately 100 m^3/10 ha) to achieve acceptable results. The material must also be incorporated into the soil before it dries out, which presents logistical problems.

SEEDLING RESPONSE IN THE NURSERY

Inoculation regardless of method is designed to provide a suitable source of infection for seedlings and thereby promote seedling development. Fungal species can vary markedly in their efficiency in promoting seedling growth (Theodorou and Bowen, 1970). It is not uncommon that in short term trials, inoculation with certain species actually depresses seedling growth (Bowen, 1980). Trappe (1977) reported the results of inoculating three coniferous species with several mycorrhizal fungi. The growth of *Pinus ponderosa* Laws. after six months was depressed following inoculation with all mycorrhizal species tested. Conversely, the growth of *Tsuga heterophylla* (Raf.) Sarg. was improved as a result of mycorrhizal inoculation. *Pisolithus tinctorius* was the best symbiont for *T. heterophylla* .Inoculation failed to improve the growth of *Pseudotsuga menziesii* (Mirb.) Franco. However, the ratio between tops and roots was changed by inoculation with either *Pisolithus tinctorius* or *Thelephora terrestris* Ehrh. ex Fr. This reallocation of biomass could have important implications in seedling establishment and warrants further investigation.

Other studies have demonstrated more pronounced growth responses following inoculation. Marx *et al.* (1978) indicated that *Pisolithus tinctorius* and *Thelephora terrestris* were equally effective in promoting the growth of *Pinus taeda* in fumigated soil. However, in some nurseries, *P. tinctorius* may be more effective than *T. terrestris* in improving total fresh weights of seedlings (Marx and Artman, 1978).

Lamb and Richards (1974) inoculated *P. radiata* and *P. elliotii* Engelm. growing in unfumigated soils with basidiospores of several species. *Pinus radiata* exhibited the greatest response with spores of *Suillus granulatus* (L. ex Fr.) O. Kuntze, while *P. elliotii* responded greatest to *Rhizopogon roseolus* (Cda.) Th. Fr. In another trial, *P. radiata* responded equally to inoculation with either species (Lamb and Richards, 1978). There appeared to be no interaction between growth response to inoculation and soil fumigation.

The above studies indicate that there are significant host × symbiont interactions in the mycorrhizal symbiosis, and there are some indications that significant within-species variation may also exist. Marx and Bryan (1971) have shown that a significant host genotype × fungus interaction exists in *Pinus elliotii* var. *elliottii,* and others have indicated a host × fungus genotype interaction may also exist for *Betula verrucosa* Ehrh. (Mason, 1975), and *Pinus radiata* (Theodorou and Bowen, 1970).

Most inoculation programmes have considered host growth response as the sole criterion in evaluating fungal symbionts. Perhaps this system of selection should be re-evaluated for particular situations. For example, *Cenococcum geophilum* Fr. is a drought tolerant fungus (Mexal and Reid, 1973), and may be a valuable symbiont for the reforestation of arid zones. However, this fungus is generally inefficient in promoting seedling growth in the nursery. It is conceivable that growth promotion should be secondary to drought tolerance in fungal species selection for these sites. A greater understanding of the physiological interaction between host and fungus is mandatory before a rational selection programme can be designed for a particular forest region. Bowen (1973) stated "An integration of mycorrhizal selection into plant introduction, plant selection, and plant breeding programmes must eventually come about, since it is obvious that assessment of the species or provenance suitability for a particular area could be markedly affected by the associated mycorrhizal fungus".

SEEDLING RESPONSE IN THE PLANTATION

Survival

The goal of any regeneration programme is the successful establishment of a vigorous plantation. Nursery cultural practices (including mycorrhizal inoculation) should be designed with this goal in mind. Several studies have demonstrated the importance of mycorrhizas in seedling survival (Marx *et al.,* 1977; Theodorou and Bowen, 1970). However, all these studies are confounded by the effects of initial seedling size on survival. Generally, the best survivors were also the largest at time of outplanting. Seedling size alone can have an enormous impact on survival (Wakeley, 1954). The question which remains to be answered is whether field survival differences caused by a nursery mycorrhizal inoculation are due to: (A) the amount of infection carried to the planting site; or (B) the improved seedling morphology and physiology resulting from inoculation. No study has been made of seedlings of similar size and vigour with varying levels of mycorrhizal infection or, conversely, of dissimilar sized seedlings with comparable levels of infection.

Even the selection of specific fungal symbionts has been confounded by the size covariate. No consistent survival differences can be attributed to a specific fungal inoculum without consideration of size differences (Marx *et al.,* 1977; Theodorou and Bowen, 1970). The survival of *Pinus taeda* in out-planting trials in Arkansas and Oklahoma was not affected by fungal symbiont. Seedlings were outplanted on eight sites. After three years, large seedlings with a high infection of *Pisolithus tinctorius* survived better (77% survival) than slightly smaller seedlings with a high infection of *Thelephora terrestris* (73%), but smaller seedlings with intermediate levels of infection of both species survived least well (68%) (Marx, Mexal, Morris, unpubl.). All three treatments had similar levels of total infection, and performance differences presumably were due to subtle differences in seedling morphology. In a similar trial, Grand and Krugner (unpubl.), reported no difference in survival following inoculation with either *P. tinctorius* or *T. terrestris.* There were also no differences in initial seedling heights at time of outplanting. Inoculation may increase seedling survival. However, the mechanisms involved in improving survival are not understood, and are confounded by other factors, including seedling size.

Growth and Yield

There is little known about the long-term advantages of planting inoculated nursery stock on previously forested lands. It is fairly well accepted that the introduced species will, with time, be overcome by the indigenous fungal population (Mikola, 1969), and the future growth of the stand will be dependent upon the relative efficiencies of the indigenous mycorrhizal fungi in promoting growth (Theodorou and Bowen, 1970).

In the outplanting trial on eight reforestation sites in Arkansas and Oklahoma, five seedling stock types were outplanted (Table 1). The seedling stock types were grown in the same nursery as part of a mycorrhizal inoculation trial (Marx *et al.,* 1978) and a fertiliser trial (Morris, unpubl.). Seedling morphologies were similar, but apparently subtle physiological differences existed which were manifested following outplanting. The average ranking of the treatments across all eight sites has remained unchanged through three field seasons (Table 1).

TABLE 1—Fourth-year performance from seed of **Pinus taeda** in response to nursery cultural practices

Ranking	[1]Treatment	Height (m)	Ground Level Diameter (mm)	Survival (%)
1	**Pisolithus** [2]High	1.19	25.4	77
2	Ammonium sulphate [3]1000 kg/ha	1.10	24.5	77
3	**Thelephora**	1.10	23.6	73
4	Ammonium sulphate [3]120 kg/ha	1.02	22.4	72
5	**Pisolithus** [2]low	1.10	23.3	68

[1] Mycorrhizal treatments applied as vegetative inoculum prior to sowing in nursery. Fertiliser treatments applied over growing season of noninoculated seedlings in nursery.

[2] High and low refer to the percentage of mycorrhizas formed by **P. tinctorius** relative to natural inoculum.

[3] Amount of ammonium sulphate applied over the course of the growing season.

On six of the eight sites, height at four years from seed was correlated with height two years from seed (Fig. 1). That is, differential establishment success the first year following outplanting is responsible for growth differences present through time. Beyond these differences in height growth the first year, there is no indication that trees with mycorrhizas of one species are performing at a rate different from another.

Marx *et al.* (1977) reported similar findings on various reforestation sites in North Carolina and Florida (Table 2). Larger seedlings tended to maintain and expand on their height advantage. This early height advantage may have been due in part to the timing of mycorrhizal infection. The best field treatment involved seedlings which formed mycorrhizas within 9 weeks of seedling emergence in the nursery. The poorest treatment was seedlings which formed mycorrhizas from wind-disseminated spores which resulted in infection rates much slower than artificial inoculation (Marx and Bryan, 1975).

The above studies illustrate that small differences in the nursery may translate into substantial height differences in the plantation, and in fact, may represent conservative estimates of future growth differences. Bowen (1973) reported the absolute growth rate (AGR) of *Pinus radiata* seedlings inoculated with *Suillus granulatus* has continued over five years to diverge from uninoculated seedlings (Fig. 2). However, this enormous difference in height at year 5 may simply be a manifestation of the establishment success of the inoculated seedlings. The relative growth rate (RGR) (Sweet and Wareing, 1966) of the seedlings illustrates this establishment success (Fig. 3). The inoculated seedlings

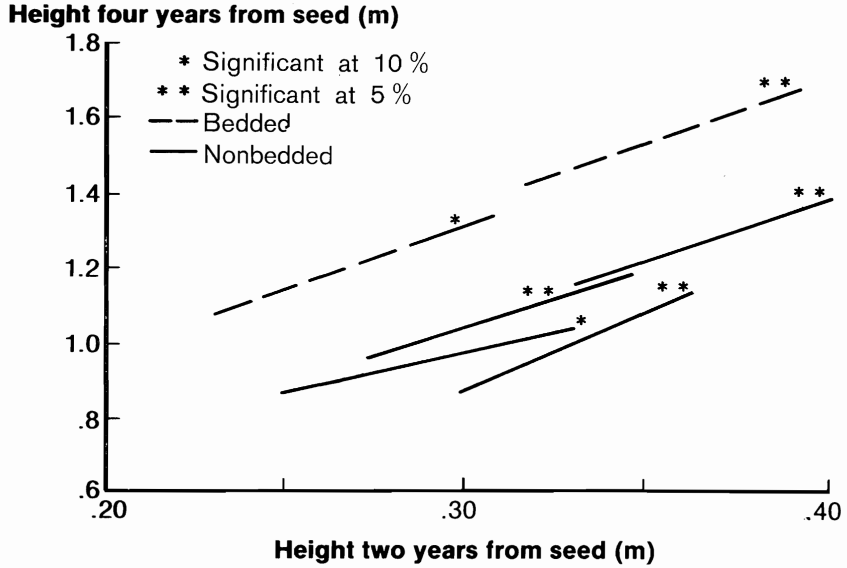

FIG. 1—Relationship between height two years from seed and height four years from seed for **Pinus taeda** on six reforestation sites in Arkansas and Oklahoma.

TABLE 2—Effect of source of mycorrhizal inoculum on height growth in plantations of two conifer species (Marx **et al.,** 1976, 1977)

Species	Inoculum source	Initial Height (cm)	Second-year Height (cm)
P. taeda	Mycelium	21a[1]	87a
	Spores	18b	80ab
	Natural	15c	74b
P. strobus	Mycelium	9a	86a
	Natural	7b	75b

[1] Means followed by the different letters are significantly different according to Duncan's Multiple Range Test ($\alpha = .05$).

maintained a higher RGR in sterilised potting medium and through the establishment year in the field. Thereafter, the uninoculated seedlings had a RGR greater than or equal to the inoculated. This establishment success in the first two years which is attributed to inoculation has resulted in a 1.5 m height advantage at 5 years in spite of a lower RGR the subsequent three years. This conclusion that small differences at time of outplanting may translate into enormous differences later in the life of the stand is similar to the conclusion drawn by Sweet and Wareing (1966) concerning seedling size in general. The RGR of two stock types may be identical but due to

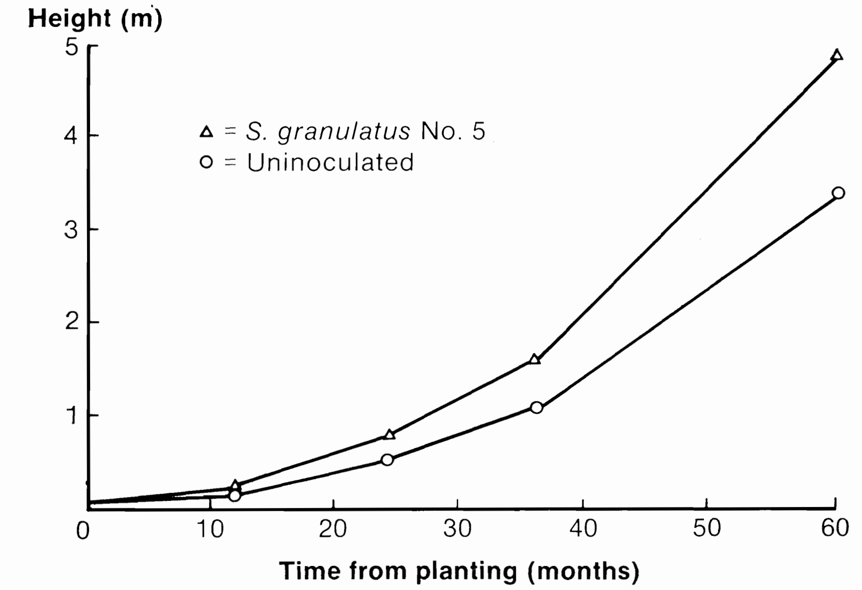

FIG. 2—Absolute growth rates of inoculated and uninoculated **Pinus radiata** seedlings (redrawn from Theodorou and Bowen, 1970).

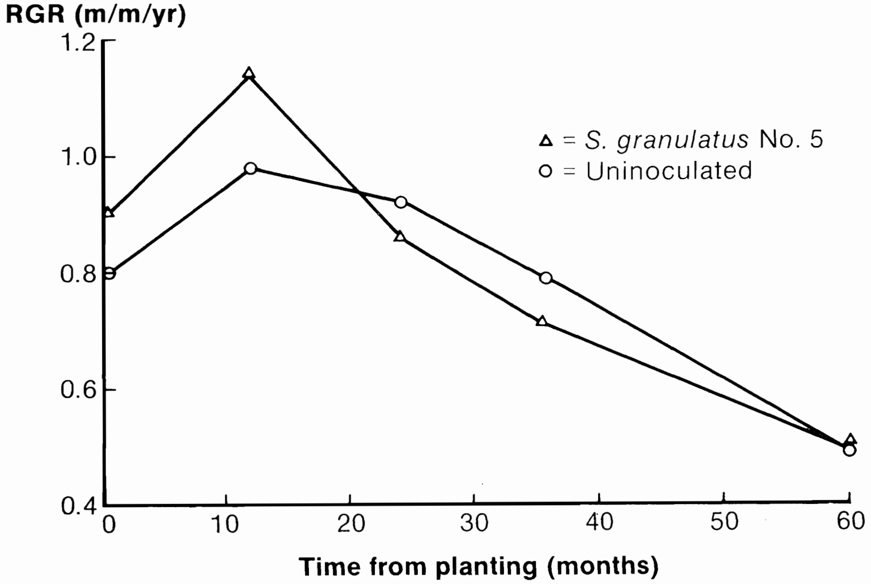

FIG. 3—Relative growth rates of inoculated and uninoculated **Pinus radiata** seedlings (Theodorou and Bowen, 1970).

initial size differences, the AGR will vary considerably. Probably the greatest advantage an inoculated seedling has over an uninoculated seedling is expressed during establishment following transplanting, that is, the inoculated seedling maintains a high RGR the first year or two in the field.

FUTURE DIRECTIONS IN MYCOTROPHY

Artificial inoculation of forest nursery crops affords potential to improve the uniformity and yield of regenerated forests. However, in order to reach this point, several questions remain to be answered. The first question concerns symbiont selection. *Pisolithus tinctorius* appears to be an excellent symbiont for Southern pines, but this symbiont is not a panacea for all inoculation programmes. Symbionts compatible with other major timber species will have to be identified and selected. This has been done to some extent for several species (Theodorou and Bowen, 1970; Trappe, 1970). However, future selection programmes should be more intensive. Attention to genotype × genotype interactions and genotype × environment interactions is a prerequisite to achieving the growth potential offered by an inoculation programme.

Another major area of incomplete knowledge concerns the management of inoculum. Any inoculation programme must be integrated with other nursery management practices. For example, how should fertilisation schedules be altered, or how do root pruning regimes affect an inoculaton programme? *Pinus taeda* seedlings appear to exhibit increased mycorrhizal development following frequent undercutting (Mexal, unpublished data). This could affect the success of an inoculation programme, and possibly, even supplant the need for inoculation. This is especially important, if simply the presence of inoculum is required and not a particular species. Finally, an appreciation of the importance of mycorrhizas in alleviating transplanting shock is required before true economic and biological gains can be estimated.

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