WILLIAM WOLFF: I have tried varying hormone strengths with a number of *Acer* species. The conclusion we came to was that high IBA concentrations act as growth inhibitors.

## ADJUSTING NURSERY PRACTICES FOR PRODUCTION OF MYCORRHIZAL SEEDLINGS DURING PROPAGATION

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During the past few years, there has been a growing interest in mycorrhizal research. There are many reports citing the possible benefits mycorrhizal fungi may afford nursery crops, such as increased nutrient uptake, growth, disease resistance, cold hardiness, drought tolerance, rooting of cuttings, and fertilizer conservation. Information pertaining to these benefits has been thoroughly discussed in previous Proceedings (8,19,20) as well as for other horticultural and forestry crops (25,47).

A major requirement in developing uses for mycorrhizal fungi in the nursery industry will be to determine cost-efficient methods of producing plants infected with specific mycorrhizal fungi and no others. We feel that one of the most efficient methods of producing mycorrhizal plants will be through the inoculation of seedlings at time of propagation. During propagation, the amount of mycorrhizal inoculum required is minimal, and regulation of environmental conditions and/or cultural practices can be closely monitored and controlled.

The primary objective of this paper is to place in perspective some of the current information pertaining to mycorrhizal formation so that the propagator has a better understanding of how to develop techniques for the production of specifically infected mycorrhizal seedlings. This objective will be accomplished in three steps: first, through a review of mycorrhizal occurrences and chief characteristics; second, through a brief discussion of plant-fungus interactions and mycorrhizal formation; and third, through a discussion of how production practices may have to be adjusted and/or new ones developed to inoculate and grow mycorrhizal seedlings economically.

**Mycorrhizal occurrence and characteristics.** Mycorrhizal associations are so prevalent that the nonmycorrhizal plant is more the exception than the rule (9). Consequently, it is easier to name the plant groups in which the associations do not occur or have yet to be reported: the order Centrospermae and the families Cruciferae, Cyperaceae, Fumariaceae, Commelinaceae, Urticaceae, and Polygonaceae (9). However, Gerdemann (10) has cited exceptions where endomycorrhizae have been found for several members of the order Centrosperme, family Chenopodiaceae (17,40,48) and several speices in the Cyperaceae (35) and Cruciferae (17,40). Hirrel et al. (15) and Ocampo et al. (36) found several species of Chenopodiaceae and Cruciferae to become infected to a limited extent if grown in the presence of a mycorrhizal plant, but not if grown alone.

Mycorrhizae can be divided into three anatomic classes; ecto-, endo- and ectendomycorrhizae. Of these, ecto- and endomycorrhizae are the two major classes of mycorrhizae. The three types of mycorrhizal relationships are typified by the fungal intrusion being limited to the cortical region of unsuberized roots. The association involving only unsuberized roots may in part be the result of root expansion and subsequent loss of the primary cortex in mature roots. Attempts to penetrate further into the inner layers of the root by the fungus may be overcome by defense mechanisms of the host (33).

Ectomycorrhizae are most common among forest and ornamental tree species in the families Pinaceae, Salicaceae, Betulaceae and Fagaceae as well as in some members of the Rosaceae, Leguminosae, Ericaceae and Juglandaceae (32,46). The fungal partner in an ectomycorrhiza most frequently belongs to the Basidiomycetes, primarily in Amanitaceae, Boletaceae, Cortinariaceae, Russulaceae, Tricholomataceae, Rhizopoganaceae and Sclerodermataceae (27). Some orders of Ascomycetes, Eurotiales, Tuberales, Pezizales and Helotiales contain species that form ectomycorrhizae. Basidiomycetes include those fungi which produce mushrooms and puffballs while the major Ascomycetes which form ectomycorrhizae are the truffles, some of which are gourmet delights in many European countries.

Structurally, ectomycorrhizae can be distinguished by the presence of hyphal strands coalescing to form a thick weft or sheath around the feeder roots known as a mantle. The mantle can range from thin to profuse and the texture can vary from smooth to cottony or granular (49). The mantle replaces the root hairs with fungal strands, greatly enhancing root surface absorptive area. These hyphal strands are capable of permeating outward from the root surface several meters or more and exploring regions not accessible by root hairs Hyphae also penetrate through the epidermis into the intercellular spaces of the cortical cells apparently replacing the middle lamella and forming an interconnecting network known as the 'Hartig Net'. Ectomycorrhizal roots are generally recognizable by their short, swollen appearance and distinctive colors of either white, black, orange, yellow and olive green which are contingent on interactions between the plant species and its fungal associate. Ectomycorrhizae are also characterized by specific branching patterns ranging from monopodial to multiforked (ramiform) or coralloid.

Ectomycorrhizal fungi can exist in the soil as spores, sclerotia and rhizomorphs. A rhizomorph is a coalesced group of hyphal strands which may extend from the ectomycorrhiza to or near the surface of the soil forming fruiting bodies containing spores that can be disseminated by wind, surface water, or animals.

Most endomycorrhizal fungi belong to the order Phycomycetes, genera *Glomus, Sclerocystis, Endogone, Gigaspora* and *Acaulospora* (12). These form what is known as vesicular-arbuscular (VA) mycorrhizae with plants. Endomycorrhizae are the most widely distributed of any of the mycorrhizae, being found in many herbaceous, shrub and tree species including most agronomic and horticultural crops (10). A few endomycorrhizae are formed by an association with Basidiomycetes which differ somewhat in cellular morphological structure from endomycorrhizae in having septate hyphae. Those endomycorrhizae occur primarily in the Orchidaceae, *Gentianaceae and Ericaceae.*

Endomycorrhizae differ from ectomycorrhizae in that there are essentially no discernible morphological changes in the external root structure of the host. A fungal mantle is not present, but a loose network of hyphase which radiate outward several cm or more from the root may be seen on feeder roots (38). Hyphae of endomycorrhizal fungi generally penetrate through the epidermis or root hair into the cortical cells, hence the prefix 'endo' is used. The penetrating hyphae often form specialized structures called vesicles and arbuscules. The longevity of arbuscules is short, 5 to 15 days (3), as they continually disintegrate (16), leading to the hypothesis that this process may be a valuable source of mineral nutrients to the host (9). Round or oval bodies known as vesicles are also formed in the cortex and in some instances outside the root. Little is known about vesicles; however, it has been suggested that they may function in some storage capacity (11).

Spores of endomycorrhizae are borne in small sporocaps or occur individually in the soil or in the root. The sporocarps are often not easily observed as in the Basidiomycetes and must be extracted from the soil using wet sieving techniques (11)

Some plants are capable of forming both ecto- and endomycorrhizal associations Those include the families Salicaceae, Juglandaceae, Tiliaceae, Myrtaceae as well as some species of *Juniperus* and *Chamaecyparis* (10).

**Plant-fungal interactions and mycorrhizal formation.** The interactions between the fungus and host are complex and appear to be influenced by a myriad of interrelated biochemical, physiological and environmental processes. Furthermore, there also appears to be some reciprocal relationships between the fungus and the plant host, but it is difficult to interpret the exact contribution either organism lends to the association (33). We do know that the fungal symbiont must enter and maintain a parasitic relationship with its host for procurement of organic compounds required for its growth and reproduction. It is during mycorrhizal formation that we can begin to understand how the biochemical interactions between the partners develop and how these interactions may influence plant growth and development of nursery crops Most of the work on mycorrhizal formation has centered around ectomycorrhizae, where the morphological changes brought about by various biochemical influences are more easily discernible.

Plant and fungal hormones are suspected of being involved in mycorrhizal development. Auxins, cytokinins, gibberellins and vitamins have been shown to be produced by mycorrhizal fungi in pure culture (7,37,41), and the effects of these compounds on rooting of cuttings and on plant growth and development are well documented (45). Although no one has yet shown that any mycorrhizal fungus produces a growth hormone while in association with the root, Linderman and Call (18) have obtained enhanced rooting of cuttings with some mycorrhizal fungi.

The involvement of plant growth hormones such as auxin in mycorrhizal formation is further complicated by the need for simple carbohydrates (sugars) for fungal growth. Auxin has been shown to influence translocation of sugar from starch reservoirs of the plant (44) as well as the hydrolysis of starch into sugar (1,2,6). The quantity of soluble sugar in the roots may also have a direct relationship to the degree of ectomycorrhizal development (13). Bjorkman (4,5) suggested that since mycorrhizal fungi generally assimilate soluble carbohydrates, the absence or presence in small quantities of soluble carbohydrates could influence mycorrhizal formation.

The available soluble carbohydrates and the presence of plant growth hormones or other substances found in the root are not considered solely responsible for mycorrhizal formation and maintenance of the symbiosis. Some environmental factors affecting mycorrhizal development as well as plant growth and development include light, soil conditions (moisture, mineral nutrients, pollutants) and interaction with other soil organisms

The importance of photoperiod and light intensity for mycorrhizal formation is unclear. Although light is essential for carbohydrate production and plant carbohydrate levels are known to influence mycorrhizal formation, conflicting evidence exists regarding the light intensity needed for mycorrhizal formation. Mycorrhizal formation has been found to increase at both low and high light intensities (5,14). These variations may be related to host-fungal specificity and/or to a photoperiodic response. However, additional work is needed in this area to determine the relationship between fungal-plant carbohydrate relationships and subsequent mycorrhizal formation.

Mycorrhizal formation can also be influenced by temperature. Most mycorrhizal fungi have an optimum temperature for establishment of the symbiotic relationship and the survival of the mycorrhizal condition There is, however, considerable variation in the temperature-range tolerance of individual fungi. Marx *et al.* (29) found that the fungus *Thelephora terrestris* Ehrh. ex Fr. had a considerably lower tolerance to a wide temperature range than *Pisolithus tinctorius* (Pers.) Coker & Couch. *T. terrestris* formed ectomycorrhizae on 45% of the feeder roots of loblolly pine (*Pinus taeda*) at 14, 19 and 24°C, but the percentage dropped to 30% at 29°C and none at all at 34°C. *P. tinctorius* formed mycorrhizae in increasing numbers up to a maximum of over 80% at 34°C. *P. tinctorius* has been shown even to have a good survival rate at 40°C (30). Schenck and Schroder (42) also found a temperature response by an endomycorrhizal fungus, with arbuscular development being favored at 30°C, mycelial development greatest at 28-34°C, and spore and vesicle production being greatest at 35°C.

**Production of Mycorrhizal Seedlings.** We recommend that production of specifically infected mycorrhizal seedlings begin at the time of plant propagation Our recommendations are based on economic considerations and understanding the ecology of these fungi. From the economic standpoint, during propagation, the least amount of inoculum would be required per volume of growing medium, and per unit area of the root system with which the inoculum can come in contact. Furthermore, mycorrhizal development occurs in the nonlignified portion of a root system, primarily the root tip, just behind the apical meristem. The newly developing root system of a cutting or seedling should be receptive to mycorrhizal infection since it is initially nonlignified. Also, mycorrhizal fungi have been shown to increase the rooting of cuttings and/or increase root development during propagation (18). Finally, it may be more cost efficient to develop a mechanized inoculating system during the propagation stage than at any other stage of plant production.

Although mycorrhizal fungi occur naturally, they are often eliminated from the propagating medium through the use of soilless media, fumigation or sterilization, and pesticides. Mature mycorrhizal fungi are in competition with other soilborne organisms. However, many mycorrhizal fungi are slow growing and do not compete well with other fungi. The absence of soilborne organisms in a propagation medium leads one to hypothesize that simply adding mycorrhizal inoculum back to a "sterile" medium is all the propagator will have to do to reap the benefits of mycorrhizal fungi. Unfortunately, this may not often work. Through the years, mycorrhizal fungi have become adapted to specific environments. Successful use of mycorrhizal fungi will require identification and isolation of superior fungi, production of pathogen-free inoculum to prevent losses during propagation, development of inoculation techniques, and adjustment of current cultural practices to facilitate plant infection and maintenance of the plant-fungal association. Linderman and Call (18) were successful in increasing the rooting of some cuttings with mycorrhizal fungi. However, not all fungi used stimulated rooting.

We feel that adjusting fertilization practices will be an important factor in developing mycorrhizal technology. Most mycorrhizal fungi are adapted to low fertility levels. Current production practices often employ very heavy fertilization practices which often inhibit mycorrhizal development (9,31). The rate of fertilizer release may be a critical factor in controlling mycorrhizal formation. We have been able to produce mycorrhizal plants at an adequate or accelerated growth rate, depending on the plant and fungal species, by using slow release fertilizer (21,22,23,24,26). These results showed that recommended rates of a slow release fertilizer (4.5 $Kg/m^3$) were not inhibitory to formation of ectomycorrhizae by *Pisolithus tinctorius* or endomycorrhizae by *Glomus fasciculatus* on a variety of woody species. Apparently, mycorrhizal development may not always be indicative of nutritionally poor soils, but may also be dependent on a balance of nutrients.

Mycorrhizal fungi can also exhibit ecological selectivity. The ectomycorrhizal fungus *Pisolithus tinctorius* is one of a few ectomycorrhizal fungi with which a considerable amount of research work has been done *Pisolithus tinctorius* has a broad host plant range and generally is found colonizing plants on disturbed landscape sites (28). We have been able to synthesize *P. tinctorius* mycorrhizae on a number conifer seedlings by inoculating the container medium just before direct seeding in containers (20). In growing shortleaf pine seedlings for 9 months in the greenhouse, the mycorrhizal seedlings were significantly smaller than nonmycorrhizal plants (Table 1) However, when these seedlings were planted on a surface mine site, the mycorrhizal plants outperformed the nonmycorrhizal plants.

We have also found that endomycorrhizal fungi may have deleterious side effects on plant growth, but these side effects only become manifested under certain cultural conditions. The endomycorrhizal fungi *Glomus fasciculatus* and *G. clarus* were used to inoculate container-grown sweetgum seedlings fertilized at various rates, 1.1, 2.2, 4.5 (manufacturer's recommended rate), 9.0 $kg/m^3$, with the slow release fertilizer 18N-2.6P-10K Osmocote (Sierra Chemical Company, Milipitas, California). The *G. clarus* isolate was isolated from a superior volunteer plant growing on an abandoned surface coal mine site. At one-fourth the recommended fertilizer rate, inoculating sweet gum seedlings with either mycorrhizal fungus significantly increased plant growth when compared to noninoculated control plants (Figure 1). However, at higher fertility rates, the *G. clarus*-inoculated seedlings had a significant inhibitory effect on plant growth, 4.5 $kg/m^3$ whereas, height of *G. fasciculatus* inoculated plants was similar to control plants. These results suggest that mycorrhizal fungi adapted to low fertility sites may be deleterious to plant growth at high fertility rates. Understanding the ecology of mycorrhizal fungi will be essential to developing applications for their use in production of nursery crops.

Although research is intensifying on the ecology of mycorrhizal fungi, we presently have little information on the species present in nursery cropping systems. For the immediate future most research with mycorrhizal fungi will deal with fungi that are easily cultured, e.g. the ectomycorrhizal fungi *Pisolithus tinctorius* and *Laccaria laccata* and the endomycorrhizal fungi *Glomus fasciculatus* and *G. mosseae*. Initially, these fungi will serve as models facilitating the developing of techniques for inoculation of plant material and for determining the effects specific cultural practices may have on mycorrhizal fungi. However, in order for the nursery industry to maximize the uses of mycorrhizal fungi, we will have to determine which mycorrhizal fungi are in our cropping systems and under what parameters these mycorrhizal fungi may benefit nursery crops. What influence such factors as monocropping, crop rotation systems, winter cover crops, green manure crops, fertilization practices, and the effects of soil fumigants, herbicides, and fungicides have on mycorrhizal fungi must be determined. It is with this knowledge that we will be able to determine the role mycorrhizal fungi will play in production of nursery crops.

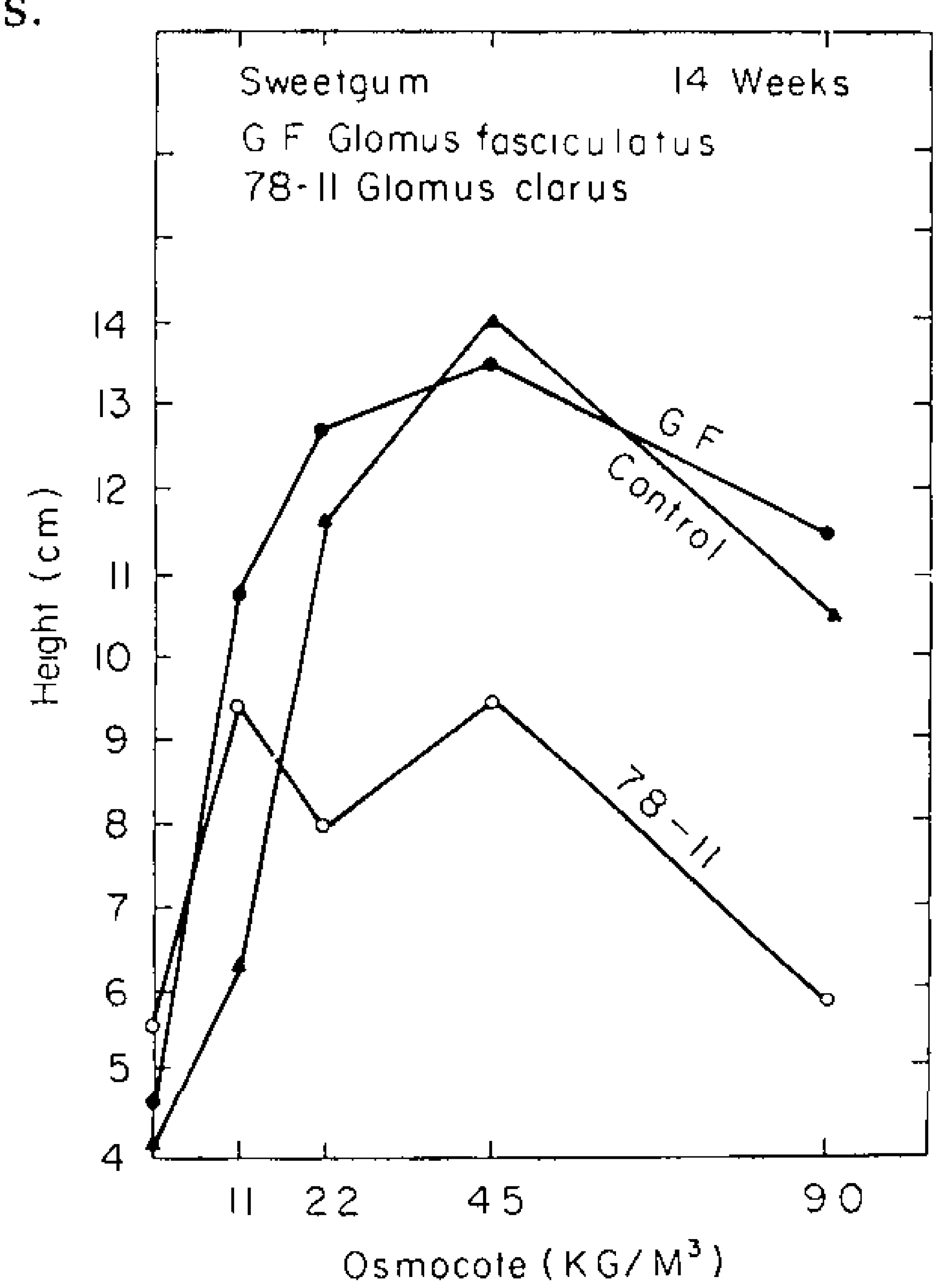


**Figure 1.** The effect of selected rates of 18N-2 6P-10K Osmocote and the endomycorrhizal fungi *Glomus fasciculatus* and *G. clarus* on growth of container grown sweetgum seedlings (*Liquidambar styraciflua* after 14 weeks)

**Table 1.** The effect of ectomycorrhizal fungus *Pisolithus tinctorius* on growth of shortleaf pine (*Pinus echinata*) seedlings after 9 months [z]

| | Height | Caliper | Percent Mycorrhizae |
|---|---|---|---|
| Noninoculated control | 39 6 cm | 9 1 mm | 0 |
| Inoculated | 32 0* | 7 3** | 78** |

[z] All plant were fertilized with 4 5 Kg/M³ of 18N-2 6P-10K Osmocote (8 to 9 month release rate) at time of planting Means of 80 trees. Means significantly different statistically at P = 0 05 (*) or P = 0 01 (**)

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DON SHADOW: I had a problem growing b&b *Fagus sylvatica* from the West Coast. I went to our local stands of *F. grandiflora* and dug soil from under them and put it under the *F. sylvatica*. It seemed to solve the problem. Do you have any comments?

DALE MARONEK. That has been a standard practice for a lot of people *Fagus* is an ectomycorrhizal plant and it has a requirement under certain propagation systems for a mycorrhizal association

JACK DOMIN: Would you care to comment on the cost involved in inoculating on a nursery scale?

DALE MARONEK: It is feasible In fact, there are a number of nurseries in the U.S. that are inoculating their beds. There is a commercial source of mycorrhizal inoculum for sale. It sells for $16 per liter but you have to purchase 50 liters. They estimate that 50 liters will inoculate 50,000 conifer seedlings in seed beds. There are several commercial inoculators that are being utilized in commercial forest tree seedling production.

PETER VERMEULEN: Dale, could you discuss the interactions of soil sterilants with mycorrhizal fungi?

DALE MARONEK They all take their toll on mycorrhizal fungi. In some cases you can get resistance to a degree. May not destroy but can really knock it down.