

Mycorrhizal responsiveness of *Thuja*, *Calocedrus*, *Sequoia*, and *Sequoiadendron* species of western North America¹

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Four western conifers inoculated or not inoculated with three species of vesicular–arbuscular mycorrhizal fungi were grown in pasteurized soil and maintained at 11 or 43 ppm phosphorus. Compared with controls, vesicular–arbuscular mycorrhizal colonization increased biomass more of younger than older seedlings. In young seedlings, species with large seeds responded less to phosphate addition or vesicular–arbuscular mycorrhizal colonization than smaller seeded species. Vesicular–arbuscular mycorrhizal seedlings with low phosphorus were always larger than noninoculated low phosphorus controls and comparable in size or larger than nonmycorrhizal controls at moderate phosphorus. Vesicular–arbuscular mycorrhizal plants produced from 100 to 2000% more biomass than noninoculated plants at low phosphorus, and from equality to 500% at moderate phosphorus. Vesicular–arbuscular mycorrhizal fungal species did not differ in plant growth enhancement or root colonization at any seedling age or phosphorus fertility examined. Tree species' responsiveness ranged as follows: *Thuja plicata* > *Sequoia sempervirens* > *Calocedrus decurrens* > *Sequoiadendron giganteum*. Vesicular–arbuscular mycorrhizal fungi enhanced seedling uniformity and size in all the tree species.

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Quatre espèces de conifères de l'ouest américain ont été inoculées ou non avec trois espèces de champignons mycorrhiziens à vésicules–arbuscules. Les semis ont été cultivés sur sol pasteurisé et fertilisé avec la solution nutritive de Long Ashton pauvre en phosphore (11 ppm) ou adéquate en phosphore (43 ppm). Par comparaison avec les témoins, la colonisation mycorrhizienne à vésicules–arbuscules a augmenté la biomasse des jeunes plants plus que celle des plants plus âgés. Chez les jeunes semis, les espèces à grosse semence ont moins bien répondu à l'addition de phosphate ou à la colonisation mycorrhizienne à vésicules–arbuscules que les espèces à petite semence. Sur milieu pauvre en phosphore, les semis mycorrhizés ont toujours été de plus forte taille que les semis non mycorrhizés; sur milieu adéquat en phosphore, ils étaient de dimensions comparables ou de plus forte taille que les semis non mycorrhizés. Selon l'espèce de champignon mycorrhizateur à vésicules–arbuscules, on n'a pas observé de différence dans l'amélioration de la croissance des plants ou de différences dans la colonisation des racines, quel que soit l'âge des semis ou le niveau de fertilité en phosphore. Le degré de réponse des espèces d'arbres était dans l'ordre suivant: *Thuja plicata* > *Sequoia sempervirens* > *Calocedrus decurrens* > *Sequoiadendron giganteum*. Les champignons mycorrhiziens à vésicules–arbuscules ont favorisé l'uniformité et la taille des semis chez les quatre espèces d'arbres.

[Traduit par le journal]

Introduction

Commercial production of tree seedlings routinely includes a biocidal treatment of the planting media for pest control. Such treatments also eliminate beneficial organisms such as mycorrhizal fungi which may be highly sensitive to biocides (Menge 1982; Trappe *et al.* 1984).

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Growth of plant species that benefit from mycorrhizal symbiosis for nutrient absorption may be reduced or uneven in biocide-treated soil, even if soil analysis reveals apparently adequate fertility. Uptake of immobile nutrients such as phosphorus, copper, and zinc may be contingent upon mycorrhizae, especially in woody plants with thick, magnolioid-type roots lacking root hairs (Baylis 1975; St. John 1979; Silberbush and Barber 1983). The relative dependence of woody species on mycorrhizae in nature for nutrient uptake and completion of life cycle is hypothetical, as nonmycorrhizal specimens of symbiotic species are rare. However, seedling growth responses to vesicular–arbuscular mycorrhizal (VAM) colonization under controlled conditions are easily quantified. Therefore, we prefer the term “responsiveness” rather than “dependency” to describe the effects of VAM colonization compared with noncolonized tree seedlings in this study. Tree species, used

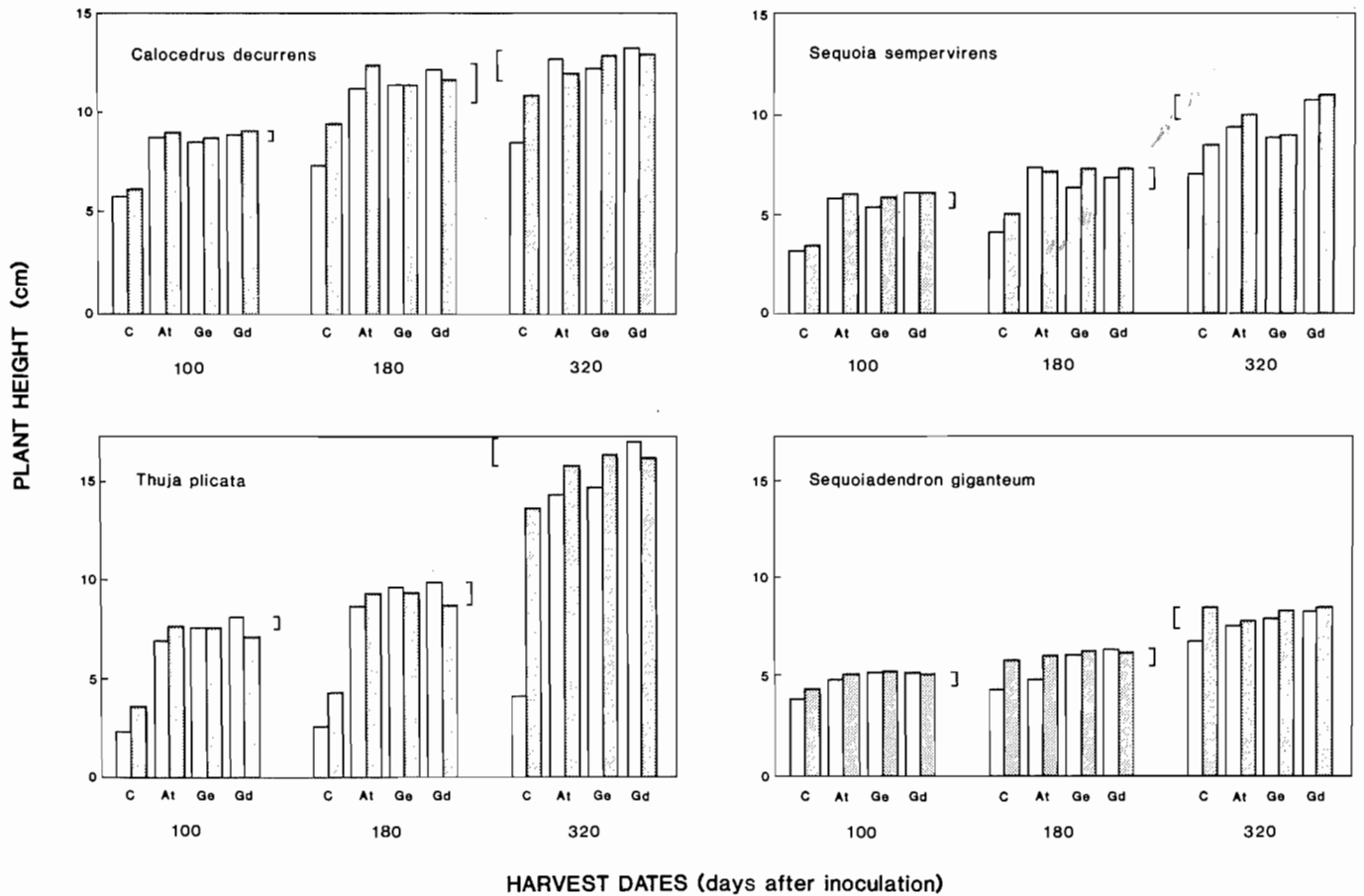


FIG. 1. Effect of mycorrhizal colonization on top height of *Calocedrus decurrens*, *Sequoia sempervirens*, *Thuja plicata*, and *Sequoiadendron giganteum* at three dates after inoculation. C, control; At, *Acaulospora trapei*; Ge, *Glomus epigaeum*; Gd, *Glomus deserticum*; □, one-quarter strength P LANS; ▨, full-strength LANS. Brackets represent Tukey's honestly significant difference, $p > 0.05$.

largely for timber production and landscape plantings, are propagated in nurseries throughout the world. Some tree species appear nutrient deficient when grown in fumigated soil and respond with improved growth when inoculated with appropriate mycorrhizal fungi.

While VAM fungi have been noted by numerous researchers in many western coniferous species (Gerdemann and Trappe 1974; Meistrick and Kelley 1979), only Bärtschi *et al.* (1981), Parke (1982), and Parke *et al.* (1983) demonstrated growth response of any of these trees to VAM inoculation. Neither, however, examined the variation of VAM plant growth response over time or inoculation response with known cultures of VAM fungi.

Our studies were designed to determine relative mycorrhizal responsiveness of four tree species grown in western nurseries: *Sequoia sempervirens* (D. Don) Endl. (coast redwood), *Thuja plicata* J. Donn ex D. Don (western red cedar), *Calocedrus decurrens* (Torr.) Florin (incense cedar), and *Sequoiadendron giganteum* (Lindl.) Buchh. (grant sequoia). The growth response was monitored over time at two phosphorus fertility levels after inoculation with three VAM fungi: *Glomus deserticum* Trappe and Bloss, *Glomus epigaeum* Daniels and Trappe (*Glomus versiforme* (Karst) Berch), and *Acaulospora trapei* Ames and Linderman.

Materials and methods

Tree species

Seeds of the four tree species were stratified separately in plastic

bags with moist paper towels at 5°C for 3 weeks and then sown on a flat of peat-sand-soil (1:1:1) pasteurized at 60°C for 30 min. After 2 weeks growth, seedlings with fully expanded cotyledons were transplanted into plastic growth tubes (Leach "Super-cells," Ray Leach Cone-Tainer Nursery, Canby, OR) with approximately 160 cm³ of soil mix.

Soil mix

The soil mix was a 1:1 mixture of pasteurized (60°C for 30 min) river sand and silt loam with the following characteristics: pH, 6.8; sodium bicarbonate extractable phosphorus, 11 ppm; potassium, 80 ppm; calcium, 8.4 mequiv./100 g; magnesium, 4.3 mequiv./100 g; sodium, 0.38 mequiv./100 g; total nitrogen, 0.06%; soluble salts, 0.30 mequiv./100 g.

VAM inoculum

Colonized roots, spores, and river sand from *Asparagus officinalis* L. plant cultures of *G. deserticum*, *G. epigaeum*, and *A. trapei* were chopped and diluted 1:1 (v/v) with pasteurized river sand. Twenty millilitres of each mixture, containing sand, spores, and root pieces, was used as inoculum for each fungus and was layered approximately 5 cm below the soil surface in the VAM treatments. Noninoculated control treatments received 20 mL of pasteurized river sand, similarly placed, inoculated with a 1-mL aliquot of a solution of microorganisms from a combination of three VAM fungal inocula. This solution had passed through a 10- μ m filter to exclude VAM propagules. Three 20-mL aliquots of each VAM fungus inoculum were examined for spore number by sieving and decanting (Gerdemann and Nicolson 1963) and percent root length colonized (Biermann and Linderman 1981) after clearing and staining roots with trypan blue (Phillips and Hayman 1970). Twenty millilitres of inocu-

lum were characterized as follows: *G. deserticum*, 560 spores, root pieces 68% colonized; *G. epigaeum*, 417 spores, root pieces 31% colonized; *A. trappei*, 772 spores, root pieces 49% colonized.

Growth conditions

Plants were maintained in the glasshouse at 22:15°C (day:night) average temperature with supplemental lighting for a 16 h light:8 h dark photoperiod from high-pressure sodium vapor lights at an average irradiance (lights plus daylight) of 200 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. After 1 month, during which seedlings were only watered, plants were fertilized with 10 mL of Long Ashton's nutrient solution (LANS) (Hewitt 1966) with either the full concentration of phosphorus (43 ppm) or one-quarter strength (11 ppm). Plants were fertilized biweekly at first and then weekly as growth increased. On all other days, plants were only watered.

Harvest procedures

Emergence of true foliage was noted 60 and 75 days after transplanting and top height was measured at 100 days. At 180 and 320 days after transplanting, seedlings were removed from growth tubes, measured for top height and stem diameter, and fresh weight of tops and washed roots was determined. Fine roots of 10 root systems per tree species - fungus - phosphorus fertility regime were sampled at each harvest to determine the percent root length with VAM colonization. Roots were cleared with two changes of 10% (w/v) KOH for 48 h at 70°C, bleached for 4 h with 3% H₂O₂, stained with trypan blue (Phillips and Hayman 1970; Kormanik *et al.* 1980), and the percent root length with VAM colonization was determined (Biermann and Linderman 1981). The remaining root tissue and shoots were dried to a constant weight at 70°C. At each harvest, dried shoot and root tissue for each tree species - fungus - phosphorus fertility regime were separately combined for chemical analysis. Tissue was analyzed by the Plant Analysis Laboratory, Soil Science Department, Oregon State University, Corvallis, OR, U.S.A. 97331.

Data analysis

The experiment was a complete factorial design of four tree species \times four inoculation treatments \times two phosphorus fertility regimes in a completely randomized design. Data for each harvest are based on 30 single-plant replications for each treatment in the *S. sempervirens*, *S. giganteum*, and *T. plicata* experiments and 18 single-plant replications for *C. decurrens*. Data were processed by an analysis of variance with mean separation determined by Tukey's test (Steel and Torrie 1960).

Results

Sixty days after transplanting, all VAM-inoculated seedlings had a higher percentage of individuals with true foliage than noninoculated seedlings. The percent of seedlings with true foliage ranged from 89 to 91% for VAM seedlings at the lower phosphate (11 ppm) LANS compared with 21 to 47% for non-inoculated seedlings (range of treatment means). At full-strength phosphate (43 ppm) LANS, the percentages of VAM seedlings with true foliage ranged from 83 to 91% compared with 38 to 66% for noninoculated seedlings. Two weeks later this developmental difference was less distinct at full-strength phosphate LANS (98-100% for VAM seedlings compared with 78-97% for noninoculated seedlings), but persisted at the lower phosphate LANS, especially in *S. sempervirens* and *T. plicata*.

At 100 days after transplanting, all VAM-inoculated seedlings were significantly larger than noninoculated seedlings, irrespective of the phosphate fertility regime (Fig. 1). Non-inoculated seedlings of *S. giganteum* and *T. plicata* were significantly taller with the full-strength phosphate regime than the lower phosphate, indicating phosphorus deficiency at the lower regime (11 ppm). In addition, seedlings of *T. plicata* inoculated with *G. deserticum* and *A. trappei* had signifi-

TABLE 1. Biomass and VAM colonization of *Thuja plicata*, *Sequoia sempervirens*, *Calocedrus decurrens*, and *Sequoiadendron giganteum* seedlings 180 and 320 days after inoculation

VAM species, fertility treatment*	<i>Thuja plicata</i>						<i>Sequoia sempervirens</i>						<i>Calocedrus decurrens</i>						<i>Sequoiadendron giganteum</i>					
	180 days		320 days		180 days		320 days		180 days		320 days		180 days		320 days		180 days		320 days		180 days		320 days	
	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM	Dry weight (g)	% root length VAM
NC,1/4P	0.05b	0	0.18a	0	0.26d	0	0.74a	0	0.54b	0	2.03a	0	0.41d	0	1.78b	0	0.41d	0	1.78b	0	0.41d	0	1.78b	0
NC,1P	0.14b	0	2.33b	0	0.67c	0	3.18b	0	0.70b	0	2.79ab	0	1.02c	0	4.38a	0	1.02c	0	4.38a	0	1.02c	0	4.38a	0
GD,1/4P	0.86a	30a	3.84c	28a	1.35a	28a	4.09cd	31a	1.57a	18a	4.18cd	31a	1.35ab	32a	4.04a	23bc	1.35ab	32a	4.04a	23bc	1.35ab	32a	4.04a	23bc
GD,1P	0.88a	30a	3.78c	25a	1.28ab	26ab	4.14d	30a	1.47a	28a	4.76d	35a	1.27ab	36a	4.45a	21c	1.27ab	36a	4.45a	21c	1.27ab	36a	4.45a	21c
GE,1/4P	0.94a	38a	3.84c	31a	1.18a	24ab	3.31b	29a	1.35a	23a	3.80bcd	34a	1.30ab	34a	4.09a	28ab	1.30ab	34a	4.09a	28ab	1.30ab	34a	4.09a	28ab
GE,1P	0.80a	32a	4.00c	26a	1.04b	17ab	3.38bc	28a	1.57a	27a	4.04cd	31a	1.14bc	30a	4.50a	25abc	1.14bc	30a	4.50a	25abc	1.14bc	30a	4.50a	25abc
AT,1/4P	0.72a	39a	3.74c	35a	1.28ab	16b	3.53bcd	33a	1.49a	17a	3.65bc	36a	1.42a	25a	4.01a	27ab	1.42a	25a	4.01a	27ab	1.42a	25a	4.01a	27ab
AT,1P	0.81a	40a	4.05c	34a	1.30ab	25ab	3.82bcd	32a	1.33a	22a	4.32cd	35a	1.41a	25a	4.55a	30a	1.41a	25a	4.55a	30a	1.41a	25a	4.55a	30a

NOTE: Means within columns not followed by the same letter are significantly different at $\alpha = 0.05$ by Tukey's honestly significant difference test. *VAM fungus treatments: NC, noninoculated control; GD, *Glomus deserticum*; GE, *Glomus epigaeum*; AT, *Acaulospora trappei*. Fertilizer treatments: 1P, full-strength phosphate LANS; 1/4P, one-quarter strength phosphate LANS.

TABLE 2. Mycorrhizal responsiveness* of four western North America conifers inoculated with three different VAM fungi and maintained at two levels of phosphorus fertility

VAM species, fertility treatment†	<i>Thuja plicata</i>		<i>Sequoia sempervirens</i>		<i>Calocedrus decurrens</i>		<i>Sequoiadendron giganteum</i>	
	180 days	320 days	180 days	320 days	180 days	320 days	180 days	320 days
GD,1/4P	17.2	21.3	5.2	2.9	2.9	2.1	3.3	2.3
GD,1P	6.3	1.6	1.9	1.3	2.1	1.7	1.2	1.0
GE,1/4P	18.8	21.4	4.5	2.3	2.5	1.9	3.2	2.3
GE,1P	5.7	1.7	1.6	1.1	2.2	1.4	1.1	1.0
AT,1/4P	14.4	20.8	4.9	2.6	2.8	1.8	3.5	2.3
AT,1P	5.9	1.7	1.9	1.2	1.9	1.5	1.4	1.0

*Responsiveness values are the means of the total dry weight for each fungus-fertility treatment divided by the mean of the total dry weight of the corresponding noninoculated control at the same level of phosphate fertility.

†VAM fungus treatments: NC, noninoculated control; GD, *Glomus deserticum*; GE, *Glomus epigaeum*; AT, *Acaulospora trapei*. Fertilizer treatments: 1P, full-strength phosphate LANS; 1/4P, one-quarter strength phosphate LANS.

cantly greater top height when grown at full-strength phosphate LANS than when grown at lower phosphate LANS.

At 180 days after transplanting, noninoculated seedlings of all four tree species showed increased height, stem diameter, and fresh and dry weights in response to increased concentrations of phosphate (Table 1). Growth increases in all noninoculated seedlings with added phosphate indicated that all tree species had become phosphate limited at the lower phosphate (11 ppm) LANS regime. Root cortical cells of the VAM-inoculated plants were colonized by VAM fungi. Percentage root colonization by different symbionts did not differ significantly in relation to phosphorus fertility within tree species.

All VAM seedlings at 180 days were consistently larger than noninoculated seedlings regardless of phosphorus fertility (Table 1). Even VAM seedlings with one-quarter strength phosphate LANS were larger than noninoculated seedlings at full-strength LANS. However, regardless of the species of mycorrhizal fungus or tree, VAM seedlings rarely differed in biomass owing to fertility regime. In general within a tree species, all VAM seedlings were of similar size.

At 320 days after transplanting, differences in biomass between noninoculated seedlings and VAM seedlings at full-strength phosphate (43 ppm) LANS were reduced. This was particularly true for *S. giganteum*, where the production of plant biomass by full-strength phosphate LANS noninoculated seedlings equalled that of VAM seedlings (Table 1). For other tree species, growth enhancement from VAM remained significant, although decreased in magnitude, compared with values obtained at 180 days. With *T. plicata*, the biomass of VAM-colonized seedlings was increased in magnitude compared with noninoculated seedlings, which continued to grow very slowly.

Mycorrhizal responsiveness values (Table 2), derived by dividing total dry matter produced by a VAM seedling at a given fertility level by dry matter produced by a noninoculated seedling at the same fertility, reflected these variable responses to VAM. Response of seedlings to VAM decreased with time except for one-quarter strength phosphate LANS *T. plicata* seedlings. Magnitude of response was always lowered at the full-strength phosphate regime, reaching equality between noninoculated and VAM-colonized seedlings of *S. giganteum* at

320 days. In general, *T. plicata* and *S. sempervirens* had greater VAM-induced growth enhancement than *C. decurrens* and *S. giganteum* under phosphate-limited conditions. *Calocedrus decurrens* was less responsive to VAM colonization than the other species at the first harvest.

Besides being larger than nonmycorrhizal seedlings, VAM seedlings were more uniform. This was indicated by lower coefficients of variability for top height and stem diameter (Table 3). Regardless of their mycorrhizal status, *S. sempervirens* seedlings were more variable in these dimensions than the other species.

Fungal colonization of root tissue was erratic: large portions of cortical tissue were not colonized while other portions were heavily colonized. Vesicles were evident in roots of all VAM-inoculated seedlings, especially those harvested at 320 days. Coiled hyphae, the most frequently observed evidence of fungal colonization, were scattered in outer cortical cells just beneath the epidermal layer and occasionally in adjacent cells. Arbuscules were rarely observed. Root hairs were rare on either inoculated or noninoculated seedlings. VAM root colonization values did not differ significantly between tree species or phosphate fertility (Table 1).

Discussion

In this study, growth response to VAM inoculation was modified by phosphorus fertility, by tree species inoculated, and, to a lesser extent, by species of VAM fungus. VAM seedlings of all tree species were always significantly larger than noninoculated controls when both were maintained with one-quarter strength phosphate LANS. These VAM seedlings were equal to or larger than noninoculated seedlings maintained at full-strength phosphate LANS. Growth enhancement from VAM colonization generally decreased as seedlings aged.

Reduction in the magnitude of growth enhancement over time and with high-phosphate LANS occurred only in mycorrhizal *S. giganteum* and could be explained by an inherently more efficient phosphate uptake mechanism in the roots of this species. Weekly fertilization should have provided enough phosphate to saturate most of the phosphate-binding sites in the soil so that added phosphate should have been readily available to roots (Marconi and Nelson 1984). Even so, the higher level of phosphate was apparently inadequate for sufficient P uptake by all species except *S. giganteum* when nonmycorrhizal.

Conversely, container-restricted root growth in VAM *S. giganteum* seedlings may have slowed their further development and allowed noninoculated seedlings to catch up to the VAM seedlings' growth by 320 days. This possibility is suggested by the lack of significantly different root masses at 320 days of *S. giganteum* VAM and non-VAM seedlings at the full-strength phosphate fertility regime. Finally, differences in root physiology between these conifer species may exist and could reflect an ecological adaptation: *S. giganteum* characteristically occurs on drier sites than either *T. plicata* or *S. sempervirens*. However, it does coexist with *C. decurrens* suggesting that rooting habit or phosphate utilization may differ between these two species.

Young seedlings clearly produced more biomass per unit time when colonized by VAM fungi than older seedlings with VAM. From the time of emergence of true foliage to 320 days after transplanting, VAM seedlings developed faster than non-VAM seedlings regardless of phosphorus fertility. At the seedling stage of plant growth, phosphorus uptake presumably is limited by the relatively small volume of soil occupied by

TABLE 3. Effect of mycorrhizal colonization of 320-day-old seedlings on dimensions used for selection of stock suitable for outplanting

VAM species, fertility treatment*	<i>Thuja plicata</i>		<i>Sequoia sempervirens</i>		<i>Calocedrus decurrens</i>		<i>Sequoiadendron giganteum</i>	
	Top height (cm)	Stem diameter (cm)	Top height (cm)	Stem diameter (cm)	Top height (cm)	Stem diameter (cm)	Top height (cm)	Stem diameter (cm)
NC, 1/4P	4.0a(17.8)	1.1c(15.4)	6.9a(21.6)	2.8a(23.6)	8.6a(18.0)	2.8a(25.7)	6.8a(20.3)	2.8a(10.4)
NC, 1P	13.6b(20.7)	3.1b(15.5)	8.4b(18.1)	4.0b(24.9)	10.9b(17.9)	3.4b(25.7)	8.4b(17.9)	3.8b(11.0)
GD, 1/4P	17.0d(11.4)	3.8a(9.0)	10.7d(11.3)	4.7c(11.1)	13.3c(10.8)	3.9c(9.7)	8.2b(14.9)	4.0bc(7.0)
GD, 1P	16.1d(12.7)	3.7a(7.3)	10.9d(13.8)	4.5bc(11.3)	13.0bc(9.4)	3.9c(9.2)	8.4b(11.3)	4.3d(8.6)
GE, 1/4P	14.6bc(10.8)	3.9a(10.8)	8.8bc(16.1)	4.5bc(14.4)	12.3bc(11.4)	3.8bc(6.3)	7.8ab(11.4)	4.2cd(10.5)
GE, 1P	16.2d(11.6)	3.7a(8.7)	8.8bc(22.5)	4.4bc(16.4)	12.9bc(7.4)	4.0c(9.0)	8.3b(12.5)	4.5d(9.8)
AT, 1/4P	14.3b(8.4)	3.8a(6.0)	9.3bc(14.8)	4.5bc(12.2)	12.8bc(8.1)	3.9c(7.4)	7.6ab(17.8)	4.0bc(9.0)
AT, 1P	15.8cd(9.4)	3.8a(6.0)	10.0cd(18.0)	4.6c(11.5)	12.1b(12.8)	3.8bc(5.3)	7.8ab(11.0)	4.2c(10.0)

NOTE: Means within a column not significantly different at $\alpha = 0.05$ by Tukey's test are followed by the same letter. Values in parentheses represent the coefficient of variability for each treatment derived from the treatment standard deviation divided by the treatment mean expressed as a percentage.

*VAM fungus treatments: NC, noninoculated control; GD, *Glomus deserticum*; GE, *Glomus epigaeum*; AT, *Acaulospora trapeei*. Fertilizer treatments: 1P, full-strength phosphate LANS; 1/4P, one-quarter strength phosphate LANS.

root systems. Uptake of phosphorus by VAM hyphae occupying a greater soil volume could significantly aid seedling nutrition. Seedlings, especially those with magnolioid-type roots, are therefore more responsive to mycorrhizal colonization than older plants (Baylis 1962; Harley 1978). This does not imply that older plants do not require or benefit from VAM, but that growth response to VAM differs with age. Critical work exploring the role of VAM in mature perennials and trees compared with noncolonized individuals has yet to be done owing at least in part to the lack of mature nonmycorrhizal specimens.

While phosphorus is generally very mobile in plant tissue, the only phosphorus reserve in young seedlings comes from the seed itself. Species with large seed reserves might be expected to lag in VAM-induced growth enhancement compared with plant species with smaller seeds. *Calocedrus decurrens*, which has the largest seeds of the species examined in this study, responded least to VAM under phosphorus-limiting conditions in the early growth stage. Kormanik *et al.* (1982) found that large-seeded hardwood tree species, such as *Juglans nigra*, were less responsive to VAM inoculation than small-seeded species, and surmised this could be due to the large seed P reserves.

Glomus epigaeum and *G. deserticum* have both been shown to be effective VAM fungi in studies on other tree hosts (Graham *et al.* 1982; Pope *et al.* 1982; Furlan *et al.* 1983). In the present study, these two species significantly increased growth compared with noninoculated controls. *Glomus deserticum* tended to give better overall growth enhancement than the other fungi on the host plants examined here. Occasionally, seedling response to colonization by *G. deserticum* was significantly greater than from either *G. epigaeum* or *A. trapeei*. *Glomus deserticum* colonized seedlings did not produce significantly greater plant biomass with higher phosphate addition, whereas both *A. trapeei* and *G. epigaeum* colonized seedlings did in numerous instances. Reasons for the differential response of VAM isolates to phosphorus are unclear.

Plant growth responses to colonization by these fungi differed despite their similar level of colonization of root cortical tissue and irrespective of phosphorus fertility, seedling age, and tree species. Given the similar level of root colonization, differences in plant response may indicate variations among the fungi, possibly relating to differences in growth regulator induction or differences in the amount of extramatrical hyphae

produced by the different VAM fungal isolates (Graham *et al.* 1982).

All four tree species produced significantly more biomass in response to VAM colonization than noninoculated controls, especially with *T. plicata* and *S. sempervirens*. However, all these species also showed a significant growth response to increased phosphate fertility when not colonized with VAM fungi. This response to increased phosphorus when noncolonized indicates the trees are responsive to mycorrhizae but not dependent. These results also emphasize that mycorrhizal responsiveness is a function of the host plant species and age, the fungus endophyte, as well as physical and probably biological features of the soil.

VAM colonization generally increased seedling uniformity as well as size compared with the noninoculated controls. This uniformity effect of VAM inoculation has been reported on other hosts (Cooper 1981; Janos 1981; Biermann and Linderman 1983) and indicates an additional economic factor in favor of VAM fungus inoculation of fumigated soil. Greater seedling size and uniformity with VAM inoculation means more seedlings acceptable for outplanting and less loss as a result of culling.

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