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Effects of Three Vesicular-Arbuscular Mycorrhizal Fungi on Sweetgum Seedlings from Nine Mother Trees

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ABSTRACT. Soil in microplots was infested with three vesicular-arbuscular (VA) symbionts then sown with seed of half-sib progeny from nine sweetgum mother trees. The VA treatments were *Glomus fasciculatus*, *Glomus* spp. (a mixture containing both *Glomus mosseae* and *Glomus etunicatus*), or a VA mixture of several fungi from the genera *Glomus* and *Gigaspora*. Before the seed was sown, all plots had calcium standardized and received an application of commercial fertilizer. During the growing season, NH_4NO_3 was applied to all plots in equal portions. Mycorrhizal seedlings with *G. fasciculatus* were slightly but not significantly larger in both height and root-collar diameter than were seedlings with the *Glomus* spp. or the VA mixture. Seedlings from all VA treatments were approximately 32 cm tall with root-collar diameters of approximately 0.70 cm. Nonmycorrhizal seedlings averaged 4.5 cm in height and 0.19 cm in root-collar diameter. Progeny from four of the mother trees were consistently larger than those from the other five, but progeny from three of these five were consistently smaller regardless of the VA mycorrhizal treatment. From a given mother tree, no significant difference in progeny ranking was observed among treatments. Significant differences in percentage of roots infected and in intensity of infection within root segments were found among the three treatments, but these differences were not correlated with seedling growth. There were some differences in mineral analyses of tissue from seedlings among the different mycorrhizal treatments and the control but no consistent trends were observed in any of the parameters in the tests. FOREST SCI. 27:327–335.

ADDITIONAL KEY WORDS. *Liquidambar styraciflua*, endomycorrhizae, forest nurseries.

RECENT RESEARCH indicates that vesicular-arbuscular (VA) mycorrhizal fungi play a significant role in quality seedling production of sweetgum (*Liquidambar styraciflua* L.) in nursery beds (Bryan and Kormanik 1977, Kormanik and others 1977b, South 1977). From eight mother trees Kormanik and others (1977a) reported large differences in growth among half-sib progeny which were either mycorrhizal or nonmycorrhizal with a VA mixture of *Glomus mosseae* (Nicol. and Gerd.) Gerdemann and Trappe and *Glomus etunicatus* Becker and Gerdemann. In the latter study, Kormanik and others (1977a) detected no significant fertilizer responses among any of the half-sib progeny at fertilizer levels of 140, 280, 560, and 1,120 kg/ha of a commercial 10-10-10 fertilizer. Their data suggested

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that ecotypic differences among the half-sib progeny, as represented by mother-tree location, may influence the responses of seedlings to VA mycorrhizae. Thus, while all the half-sib progeny responded favorably to the VA symbionts used, those seedlings from mother trees on the less favorable upland sites, as a group, grew larger than those from the more fertile bottomland selections.

While little has been published on the site specificity of VA mycorrhizal fungi, these fungi appear to have rather broad host ranges (Gerdemann 1968, Nicolson 1967, Smith 1974). Thus, while sweetgum may respond favorably to any VA symbiont, the physiological response of specific half-sib progenies to specific symbionts may vary considerably. Clarification of this response to different VA symbionts is important to improve nursery practices that will assure quality seedling production in forest tree nurseries throughout the United States.

The purpose of this study was to determine how half-sib progeny would respond to different VA symbionts and how family ranking in terms of growth and nutrient concentrations would be affected.

Materials and Methods

Nine mother trees from the dominant canopy and which phenotypically represented the best trees on the site were selected for seed collection. Seed were collected from six trees growing on the Scull Shoals Experimental Forest in northeast Georgia. Three of the trees (74-7b, 75-6b, 75-8b) were from fertile bottomland sites which normally flood at least once each spring, and three (74-9u, 75-4u, 75-2u) were from dry upland sites. Seed was also collected from three trees (SC-2, SC-3, SC-4) growing along the edge of Little Wambaw Swamp on the Francis Marion National Forest on the lower Coastal Plain of South Carolina. The seed were stratified in water at 2°–4°C for 24 days before sowing.

The study was installed in 20 microplots at the Whitehall Experimental Forest maintained in cooperation with the University of Georgia, Athens. The microplots were redwood frames, 1 × 1 × 0.6 m, with marine-grade plywood, 2 cm thick, placed on the bottom of each frame to prevent contamination. A series of 2.5-cm holes at the juncture of the frame and the bottom plate provided drainage. The empty microplots were placed on recently tilled soil and fumigated under plastic with Dowfume MC-2 (Dow Chemical Co., Midland, Mich.) for 48 h. The microplots were filled with a 2:1:1 mixture of sandy loam forest soil, sand, and finely ground pine bark fumigated with Dowfume MC-2 at 1 kg/18 m^2 of soil surface (25 cm deep) under clear plastic. Analysis of this mixture revealed that the extractable ions in kg/ha were: NO_3-N, 39; P, 26; K, 77; and Ca, 366. Hydrated lime ($Ca(OH)_2$) was added to the soil mixture in each microplot to bring elemental calcium up to the equivalent of 1,120 kg/ha.

Microplots were inoculated with coarsely chopped sorghum roots and soil from pot cultures of sorghum containing a *Glomus* spp. mixture (*G. mosseae* and *G. etunicatus*), *Glomus fasciculatus* (Thaxter) Gerd. and Trappe, or a mixture of VA symbionts from both the genera *Glomus* and *Gigaspora*. The pot cultures were approximately 9 months old and mycorrhizal evaluation indicated that the sorghum root systems were heavily mycorrhizal but the spore counts varied considerably among the specific VA symbionts. Microplots were randomly assigned mycorrhizal treatments and 2 liters of inoculum were uniformly spread on the soil surface and thoroughly worked into the top 15 to 20 cm of soil with potato rakes. The number of spores added to the microplots along with the chopped root fragments were 850 *Glomus* spp., 6,600 *G. fasciculatus* and 2,650 VA spp. Root washings were obtained from the three different pot cultures and passed through a 44 μm mesh sieve, then filtered through Whatman No. 1 paper. Each mycorrhizal treatment received filtered washings from the two other symbionts while

the control treatment received filtered washings from all three symbionts to standardize the rhizosphere microflora at the time of sowing.

All plots received 280 kg/ha of a commercial 10-10-10 fertilizer which was incorporated into the top 7 to 10 cm of soil before the seed were sown. In addition, all microplots received a total of 1,680 kg/ha of NH_4NO_3 applied in 10 equal amounts about every 2 weeks during the growing season.

Seed were sown in the microplots during the last week of May; the experimental design was a randomized block design with four mycorrhizal treatments replicated four times. There were 45 planting locations in each microplot and each of the nine families were randomly assigned to five of these locations. Six to eight seed were planted at each spot and the soil was lightly covered with fumigated pine needle mulch. After germination, seedlings were thinned to one per planting spot.

The seedlings were harvested in early November. Height and root-collar diameter were measured and root and top weight were obtained after drying to a constant weight at 70°C.

Root samples were collected from each of the 720 seedlings at three to seven different positions on the root system depending on its development. The presence or absence of infection by VA mycorrhizal fungi was determined by the Phillips and Hayman (1970) procedure. From each sampling position, 3- to 6-cm segments of second- and third-order laterals, with their attached feeder roots, were included in the sample. After processing, the percentage of roots infected and the intensity of infection within roots were evaluated with a dissecting microscope. The percentage of roots infected, based on the total root sample, was divided into four classes: 0–24, 25–49, 50–74, and 75–100. The intensity of infection within individual roots of the entire sample was classified as: (1) Low—small infection sites widely scattered along the root segments, (2) Medium—larger infection sites more uniformly distributed through the root segments but rarely showing infection sites coalescing, and (3) Heavy—feeder roots almost solidly infected with a few easily identified isolated patches of infection. Finally, with a binocular microscope at 150×, the infection was evaluated as the percentage of total infection made up of hyphae, arbuscules, and vesicles.

Levels of Kjeldahl nitrogen, phosphorus, potassium, calcium, and magnesium concentrations were determined for the leaves, stem, and roots of each seedling. Kjeldahl nitrogen was determined by digestion with a sulfuric-selenious acid mixture and detected on a Technicon Autoanalyzer II (Industrial Method No. 334-74A, Technicon Instruments Corp., Tarrytown, N.Y.). Samples were digested with a nitric, perchloric, sulfuric acid mixture for phosphorus and cation analysis. Phosphorus was detected with the Technicon Autoanalyzer (Industrial Method No. 144-71A). The cations were detected on a Perkin-Elmer Model 560 Atomic Absorption Spectrophotometer (Agricultural Analytical Method AY-5, Perkin Elmer Corp., Norwalk, Conn.).

Results and Discussion

Mycorrhizal Infestation.—Although the same amount of stock inoculum was added to each microplot for the different VA mycorrhizal treatments, spore counts revealed a significant range in spore density. The qualities of spores added, along with the infected root segments, however, were sufficient to result in early root infection and subsequent favorable seedling development. This variance in inocula spore density may preclude some direct comparison among the symbionts but would not affect comparisons of progeny within symbionts.

Initial spore density was not correlated with percentages or intensity of root infection within pooled root data, after one growing season (Table 1). When the tree data were pooled, the *Glomus* spp. which had the lowest initial spore count

TABLE 1. Mean infection responses of nine families of sweetgum seedlings grown in microplots filled with a soil-sand-bark mixture infested with Glomus fasciculatus, Glomus *spp., or a VA fungal mixture.*

Mycorrhizae	Infection	Intensity	Hyphae	Arbuscules	Vesicles
			Percent		
G. fasciculatus	32.3 b[1]	2.1 b	63.1 b	33.5 b	3.4 a
Glomus spp.	49.3 a	2.3 a	53.5 c	44.8 a	1.7 b
VA fungi mixture	28.2 b	1.4 c	78.9 a	20.6 b	0.5 c

[1] Values followed by the same letter are not significantly different at the 0.05 level by Duncan's Multiple Range Test.

not only had the greatest percentage of roots infected but also resulted in the greatest intensity of infection. Despite almost a threefold difference in initial spore density, *G. fasciculatus* and the VA fungi mixture had the same percentage of root infection at the end of the study. However, the intensity of infection within the host between these three VA sources differed significantly at the end of the growing season.

During the growing season VA mycorrhizae sequentially develop first hyphae, then arbuscules, and finally vesicles—the fungal food-storage organ. At the end of the growing season in a natural forest environment, one might expect to observe increases in percentages of vesicles at the expense of the other two morphological structures, but we observed few in our root samples. Among the fungi, the percentage of infection represented by hyphae, arbuscules, and vesicles differed significantly.

These differences in fungal morphology can be attributed to symbiont characteristics and growing conditions in the nursery. The formation of vesicles occurs as the host plants senesce or, in the case of perennial plants, go into winter dormancy. Seedlings in the nursery, under optimum conditions, continue active growth late into October and early November. The seedlings in this study were harvested before dormancy and this can account for the low vesicle percentages we observed. *Glomus fasciculatus,* however, has a reputation for developing large numbers of vesicles in host plants far in excess of what other species in this genus tend to develop (Gerdemann and Trappe 1974). *G. fasciculatus* was not found in our *Glomus* spp. mixture; the VA fungal mixture contained species from the genus *Gigaspora* as well as from the genus *Glomus*. Species in the former genus produce external vesicles that would have been lost during root excavation and processing and one would expect fewer vesicles to be observed in this treatment.

We have observed in other work (unpublished data) that the relative percentages of hyphae and arbuscules on infected sweetgum seedlings vary considerably during the growing season. Seedling development does not appear to be related to fungal morphology under growing conditions maintained in our nursery. We do not know whether the morphology of a specific VA fungus on sweetgum is affected by fertility or if differences in fungal morphology are related to the symbionts' growth characteristics on sweetgum. Additional tests using single symbiont treatments with varying fertility regimes are underway to attempt to clarify the biological significance of fungal morphology to sweetgum seedling development.

Mycorrhizal Effects—Pooled Growth Data.—VA mycorrhizal fungi are usually not host specific. A single fungal species will often form mycorrhizae with plants

TABLE 2. Pooled growth responses of nine families of sweetgum seedlings grown in a soil-sand-bark mixture containing Glomus fasciculatus, Glomus *spp., a VA fungi mixture, or no VA mycorrhizal inoculum.*

Mycorrhizae	Diameter	Height	Leaf weight	Stem weight	Root weight
	cm		*g*		
G. fasciculatus	.77 a[1]	34.6 a	4.2 a	3.4 a	5.4 a
Glomus spp.	.68 b	29.9 b	4.1 a	3.1 a	4.8 ab
VA fungi mixture	.67 b	31.6 b	4.3 a	3.2 a	4.7 b
Control	.19 c	4.5 c	0.1 b	0.1 b	0.2 c

[1] Values followed by the same letter are not significantly different at the 0.05 level by Duncan's Multiple Range Test.

from diverse plant taxonomic groups. Although a direct comparison of symbionts may not be technically accurate because of the differences in initial spore densities, a comparison among the symbionts with pooled data suggests that seedling growth was not correlated with percentage of root infection determined at the end of the growing season (Table 2). Thus, *G. fasciculatus,* which produced less total infected roots than did the *Glomus* spp. and the same as the VA fungal mixture, produced the largest seedlings. We have observed both in this study and in other work (unpublished) conducted at the Institute for Mycorrhizal Research and Development that seedlings grown in soils infested with *G. fasciculatus* begin height growth several weeks earlier than seedlings growing in soils infested with other VA symbionts. Usually this early growth advantage of *G. fasciculatus* infected seedlings is lost by the end of the growing season. The 1976 growing season was abnormally hot for extended periods during the latter half of June and throughout July and August. These conditions may have been more beneficial to *G. fasciculatus* or affected all VA symbionts adversely and the early-season advantage of seedlings infected with *G. fasciculatus* was simply maintained. We believe that high temperatures may have had an adverse effect on all symbionts because the percentages of infected roots were about 30 percent less than we normally expect at these fertility regimes with sweetgum.

It is difficult to interpret the data in Tables 1 and 2 due to the limited amount of data available from which to draw comparisons among VA symbionts on trees. The hosts for VA symbionts in most published reports are annual plants that have far different growth patterns and nutritional regimes (especially N and P) than we standardized in this test with sweetgum. One would expect that infection data from annual plants that mature in midsummer might differ from nursery-grown sweetgum seedlings that reach peak growth in this climatic region during September and early October. It can, however, be interpreted from this data (Table 1) as well as other unpublished work at this location that all of a plant's feeder roots are not necessarily mycorrhizal at the same time. This suggests that caution must be exercised when biochemical and physiological data are presented and interpreted on the basis of a presumed number of infected root segments.

In this and other work, we have obtained no significant correlations between percentage of roots infected and seedling size with any of the VA symbionts we have tested. With the nutritional regimes and low P used in this research, the nonmycorrhizal seedlings failed to grow; however, it may be the length of time that the root system per se is mycorrhizal that ultimately determines the hosts' growing season response (Table 2).

These results suggest that some mycorrhizal fungi on sweetgum in nurseries

TABLE 3. Growth responses of nine families of sweetgum seedlings grown in a soil-sand-bark mixture containing Glomus fasciculatus, Glomus *spp., or VA fungi mixture.*

Family	*Glomus fasciculatus*			*Glomus* spp.			VA fungi mixture		
	Diam-eter	Height	Total weight	Diam-eter	Height	Total weight	Diam-eter	Height	Total weight
	cm	*cm*	*g*	*cm*	*cm*	*g*	*cm*	*cm*	*g*
SC-2		38.3 bc	15.9 ab	0.69 abc	30.1 b	11.5 abcd	0.76 ab	37.4 a	14.6 ab
SC-3	0.79 abc[1]	40.8 ab	15.5 ab	0.62 bc	29.8 b	11.2 abcd	0.60 bc	34.2 ab	13.4 abc
SC-4	0.88 ab	44.7 a	17.2 a	0.79 ab	39.2 a	15.6 a	0.81 a	41.8 a	16.3 a
74-7b	0.90 a	35.6 bcd	12.4 bcd	0.71 abc	29.3 b	13.6 abc	0.84 a	35.4 ab	16.8 a
74-9u	0.75 bcd	31.9 def	14.0 abc	0.82 a	30.8 b	14.7 ab	0.70 ab	26.2 c	11.2 abc
75-2u	0.84 ab	33.3 cde	9.6 de	0.59 c	25.2 b	7.5 d	0.51 c	26.1 c	6.8 c
75-4u	0.67 cd	26.6 f	6.9 e	0.60 bc	26.7 b	8.8 cd	0.58 bc	28.6 bc	7.8 bc
75-6b	0.79 abc	29.3 ef	13.4 abcd	0.62 bc	29.1 b	10.0 bcd	0.62 bc	29.0 bc	11.7 abc
75-8b	0.69 cd	29.0 ef	10.3 cde	0.71 abc	28.0 b	15.0 ab	0.59 bc	25.7 c	9.6 bc

[1] Values followed by the same letter are not sigificantly different at the 0.05 level by Duncan's Multiple Range Test.

may be more effective symbionts than others. However, although the data are not presented here, we found no significant differences in seedling size within families across symbiont treatments. Thus, at the present level of VA mycorrhizal technology in forestry, any species of mycorrhizal fungi would be preferable to none for consistently producing plantable size sweetgum seedlings.

Progeny from four families, SC-2, SC-4, 74-7, and 74-9, consistently produced the largest seedlings regardless of symbiont. Progeny from families 75-2, 75-4, 75-6, and 75-8 consistently had coefficients of variation larger than the means for all families for a given symbiont treatment for the growth parameters (Table 3). Families 75-2, 75-4, and 75-6 had coefficients of variation of up to 52 percent, and their progeny were usually significantly smaller than those from the four best families. Some seedlings from the poorer families were only three times larger than the controls, but these larger seedlings were as large as the largest seedlings produced from any of the families. There were no significant correlations between either percentage of root infection or intensity of VA infection within root segments and seedling size in any of the families' progeny.

Some mother trees produced a higher percentage of quality seedlings than others. This response may reflect the mother tree genotype × symbiont interactions that could be of significance for screening sweetgum trees in tree improvement programs now underway in the southeastern United States.

Progeny from the three Little Wambaw Swamp mother trees were consistent and grew well. These seedlings started height growth several weeks earlier than those from the other six mother trees regardless of symbiont, and maintained this advantage throughout the growing season. A similar growth response in nurseries was observed with a south Coastal Plain ecotype of yellow-poplar (*Liriodendron tulipifera* L.) by Kellison (1970). Swamp ecotypes may be under strong genetic control and their early rapid growth may be related to complex morphological adaptations and physiological interactions and unrelated to VA mycorrhizae (Hook and others 1970, 1971). However, swamp ecotypes of yellow-poplar do not maintain this rapid growth for more than 3 or 4 years when planted on drier upland sites (Kellison 1970).

TABLE 4. Combined data of nutrient concentrations in the leaves, stems, and roots of nine sweetgum families grown in a mixture of soil-sand-bark containing Glomus fasciculatus, Glomus *spp., a VA fungi mixture, or no VA mycorrhizal inoculum.*

Plant part and mycorrhizal fungus	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Iron	Manganese	Zinc
Leaves	*mg/g*							
G. fasciculatus	2.16 a[1]	1.01 a	7.54 a	5.51 a	1.25 a	0.98 a	3.34 a	0.06 a
Glomus spp.	2.24 a	1.14 b	7.24 a	5.35 a	1.06 b	0.60 b	3.29 a	0.04 a
VA fungi mixture	2.19 a	1.16 b	7.19 a	5.39 a	1.21 a	0.82 a	2.63 b	0.04 a
Control	1.25 b	—	—	—	—	—	—	—
Stems								
G. fasciculatus	0.56 a	0.57 a	4.37 a	6.53 a	1.24 a	0.32 a	1.26 a	0.04 a
Glomus spp.	0.59 a	0.68 b	4.32 a	6.71 a	1.28 ab	0.17 b	1.30 a	0.04 a
VA fungi mixture	0.59 a	0.74 c	4.68 b	6.53 a	1.34 b	0.25 ab	0.97 b	0.04 a
Control	1.15 b	—	—	—	—	—	—	—
Roots								
G. fasciculatus	0.61 a	0.65 a	4.97 a	3.70 a	1.26 a	2.88 a	0.53 a	0.02 a
Glomus spp.	0.60 a	0.76 b	4.82 a	3.69 a	1.41 b	2.62 b	0.54 a	0.02 a
VA fungi mixture	0.70 b	0.80 b	4.37 b	3.19 b	1.13 c	3.41 c	0.40 b	0.02 a
Control	1.10 c	0.45 c	3.51 c	3.85 a	1.38 b	3.05 a	0.72 c	0.06 b

[1] Values within a component followed by the same letter are not significantly different at the 0.05 level by Duncan's Multiple Range Test.

Symbiont-Nutrient Responses.—Variability in concentrations of specific elements in tissue of both mycorrhizal and nonmycorrhizal plants is common (Schultz and others 1979, Gerdemann 1964, Baylis 1959, Mosse 1957) in spite of growth stimulation by the VA symbionts. Normally, however, VA plants will have higher P concentrations in tissue regardless of tissue concentrations of other elements. Soil P is commonly standardized in VA experiments because of the strong influence VA mycorrhizae have on P uptake. The variability of the other elements that have been reported may be a reflection of their relative concentration in the test soils.

Schultz and others (1979) found that sweetgum seedlings colonized with one symbiont contained higher total quantities of some elements because of their greater biomass; but generally with the single VA symbiont they contain no more of all elements on a per unit dry weight basis. In our experiment, the same trends were found in nutrient concentrations with the three VA symbiont treatments (Table 4). Biomass production of the nonmycorrhizal controls was only sufficient to obtain nitrogen data for the leaves and stem tissue, but root biomass was adequate to allow for a more complete nutrient analysis (Table 4).

The apparent increase in total nitrogen of stems and roots of nonmycorrhizal seedlings (Table 4) may be due to sampling procedure and probably does not reflect the nutritional status of the seedlings. There is considerably less N found in xylem tissue than in phloem and cortical tissue. The greater proportion of xylem tissue in the larger inoculated seedlings may have had a greater dilution effect on the nitrogen-rich phloem and cortical cells, thus resulting in lower N values for these seedlings compared to the smaller noninoculated seedlings. A second possibility is that N in the nonmycorrhizal seedlings, which had terminal buds set early in the growing season, was tied up in other compounds in the roots

and stem and was not translocated to the foliage. Foliage of nonmycorrhizal seedlings consisted primarily of 2 to 5 small (0.50 to 1.5 cm) purple leaves and the crowns exhibited no appreciable growth throughout the study.

Considerable data have been accumulated at the Institute for Mycorrhizal Research and Development at Athens which suggest that nutrient concentrations per gram of dry tissue of VA mycorrhizal sweetgum seedlings are not significantly greater than for nonmycorrhizal seedlings. If the differences (Table 4) in nutrient concentrations of some elements among symbionts are biologically important, the relationships are not readily apparent and require further biochemical clarification. In spite of this lack of biochemical information, the importance of the VA mycorrhizae to sweetgum seedling development is substantial. Within the phosphorus levels tested, nonmycorrhizal sweetgum seedlings remained quiescent during the growing season and the shoot apicies did not become centers of intense mobilization requiring high levels of inorganic nutrients, carbohydrates, and organic acids for synthesis of new cellular components.

To an exaggerated degree, the nonmycorrhizal seedlings exhibit those gross morphological features associated with severe phosphorus deficiencies in plants (Noggle and Fritz 1976). High soil P is known to reduce the growth differential between mycorrhizal and nonmycorrhizal plants, and at some soil P levels no growth differences are apparent. This soil P level varies considerably among different hosts but is far in excess of what is normally found in natural soils. In our continuing work, we have been testing available P up to approximately 50 ppm, or in the range of 6 to 10 times higher than normally found in southeastern forest soils, and have observed little growth of any of the nonmycorrhizal sweetgum seedlings. However, even with available soil P at 8 to 10 ppm, mycorrhizal sweetgum seedlings have grown very well. These results suggest that in its evolution sweetgum has developed a high degree of dependency on mycorrhizal fungi and its wide site adaptability to a great extent may be attributed to this VA symbiotic association. Thus far we have tested only a few of the numerous VA symbionts found in natural soils, but the degree of dependency on these fungi may partially explain why we have found so little difference in growth responses of sweetgum with our different VA symbionts and fertility regimes.

Most plant species used in VA mycorrhizal research have had a great deal of selection pressure exerted upon them to suit specific cultivation properties important to man. Such selection pressures have not been directed toward sweetgum in forestry, and this species may be an ideal host for study of the basic physiological interactions of VA mycorrhizae and plant development.

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