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Richard C. Schultz, *University of Georgia*

Paul P. Kormanik

W. Craig Bryan

G. H. Brister, *University of Georgia*



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## Vesicular-arbuscular mycorrhiza influence growth but not mineral concentrations in seedlings of eight sweetgum families

R. C. SCHULTZ<sup>1</sup>

*School of Forest Resources, University of Georgia, Athens, GA, U.S.A.*

P. P. KORMANIK AND W. C. BRYAN

*Institute for Mycorrhizal Research and Development, Southeastern Forest Experiment Station, Forest Service, United States Department of Agriculture, Athens, GA, U.S.A.*

AND

G. H. BRISTER

*School of Forest Resources, University of Georgia, Athens, GA, U.S.A.*

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Seedlings of eight half-sib sweetgum (*Liquidambar styraciflua* L.) families were grown for 6 months in a fumigated soil mixture, with or without inoculum from a mixture of *Glomus mosseae* and *Glomus etunicatus* fungi, at levels of 140, 280, 560, and 1120 kg/ha of 10-10-10 fertilizer. All seedlings received three additions of 187 kg/ha of N during the growing season. Inoculated seedlings had significantly greater biomass, height, and stem diameters at each fertilizer level than nonmycorrhizal control seedlings. Significant differences in growth occurred between families in mycorrhizal plants. However, fertilizer did not significantly affect growth or nutrient uptake of the seedlings. Inoculation with VA mycorrhizal fungi did not increase N, P, K, or Mg concentrations in the leaves, stems, or roots. Leaves of VA mycorrhizal seedlings had higher concentrations of calcium but stems and roots had lower concentrations of this element than the nonmycorrhizal seedlings. Seedlings with endomycorrhizae contained higher absolute quantities of each nutrient simply because of their greater biomass. The results suggest that the role of VA mycorrhizal fungi in the initial growth of sweetgum seedlings may be the result of physiological stimuli other than increased nutrient uptake.

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Les plantules de huit familles de demi-frères du *Liquidambar styraciflua* L. ont été cultivées pendant 6 mois dans un mélange de sol fumigé, avec ou sans inoculum fongique, constitué à la fois du *Glomus mosseae* et du *Glomus etunicatus*, avec l'addition de 140, 280, 560 et 1120 kg/ha de fertilisant 10-10-10. Toutes les plantes ont reçu en plus 187 kg/ha de N pendant la saison de croissance. Les plants inoculés ont montré des biomasses, des hauteurs et des diamètres de tiges plus élevés que les plants témoins non-inoculés, quelles que soient les quantités de fertilisants ajoutées. Des différences significatives se sont manifestées dans la croissance des différentes familles. Cependant, les fertilisants n'ont pas influencé significativement la croissance ou l'absorption des éléments nutritifs avec les champignons mycorrhizateurs à VA n'a pas augmenté les concentrations en N, P, K et Mg dans les feuilles, les tiges et les racines. Les plants porteurs de mycorrhizes à VA avaient des teneurs plus élevées en calcium dans leurs feuilles, mais plus faibles dans les tiges et les racines que les plants non-mycorrhizés. C'est simplement à cause de leur plus forte biomasse que les plants porteurs d'endomycorrhizes contenaient, en valeurs absolues, de plus fortes quantités de chacun des éléments. Les résultats suggèrent que le rôle des champignons mycorrhizateurs à VA au cours des premières phases de la croissance du *L. styraciflua* pourrait être le résultat de stimuli physiologiques autres qu'une absorption accrue des éléments minéraux.

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### Introduction

Sweetgum (*Liquidambar styraciflua* L.) is a com-

mercially important hardwood species in the southeastern United States but is difficult to regenerate artificially due to inconsistent seedling size. Seedling size is hard to control in the forest nursery despite high levels of soil fertility (Webb 1969). Outplanted

<sup>1</sup>Present address: Department of Forestry, Iowa State University, Ames, IA, U.S.A. 50011.

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seedlings frequently grow very slowly during the first few years and are overtopped by weeds.

Sweetgum seedling growth can be improved by inoculation of soil with VA mycorrhizal fungi (Gray and Gerdemann 1967; Mosse *et al.* 1969; Mosse 1973; Bryan and Ruehle 1976; Bryan and Kormanik 1977; Kormanik *et al.* 1977). The erratic occurrence of VA mycorrhizae on sweetgum seedlings in fumigated soils accounts for uneven seedling growth in the nursery (Bryan and Kormanik 1977).

Many plants which grow well with VA mycorrhizae and average soil fertility levels can also be grown under conditions of high soil fertility in the absence of VA mycorrhizae (Gerdemann 1968; Smith 1974). This suggests that VA mycorrhizae increase mineral absorption, especially under conditions of low fertility (Nicholson 1967). It is well known that VA mycorrhizae increase the uptake and accumulation of phosphorus (Gray and Gerdemann 1967; Sanders and Tinker 1971; Hayman and Mosse 1972; Mosse 1972; Mosse *et al.* 1973; Rhodes and Gerdemann 1975). Smith (1974) concludes that increased uptake of phosphorus may be a result of (1) "efficient pumping" by mycorrhizal roots; (2) increased use of soluble soil phosphorus by external hyphae; and (3) possible solubilization of insoluble phosphorus by the fungus.

Although there is strong evidence for increased phosphorus uptake by VA mycorrhizae, evidence for such a role with other nutrients is not consistent. Mosse (1957) found significantly higher concentrations of K, Ca, Fe, and Cu and lower Mn in mycorrhizal apple seedlings than in nonmycorrhizal seedlings growing in sterilized soil. Baylis (1959) found mycorrhizal seedlings of *Griselinia littoralis* had a higher concentration of P and K but a lower content of N than nonmycorrhizal seedlings grown in sterilized soil low in P and other nutrients. Powell (1975), using *Griselinia littoralis*, also found higher P and K concentrations in mycorrhizal seedlings than in nonmycorrhizal seedlings. On the other hand, Gerdemann (1964) found higher concentrations of P but lower concentrations of K, Mg, Bo, and Mn in mycorrhizal maize seedlings than in nonmycorrhizal seedlings. Ross and Harper (1970) and Ross (1971) found mycorrhizal soybean plants accumulated greater amounts of N, P, Ca, Cu, and Mn than nonmycorrhizal plants. Concentrations of K, Mg, and Fe were not increased in the mycorrhizal seedlings. Gilmore (1971), La Rue *et al.* (1975), and Benson and Covey (1976) have shown that VA mycorrhizae increased Zn uptake of peach and apple seedlings over nonmycorrhizal seedlings.

In the above studies, seedling growth was reportedly stimulated by inoculation with VA mycorrhizal fungi despite differences in nutrient uptake. Thus seedling growth was increased by inoculation even though specific nutrient concentrations in the seedling tissues may not have been increased. The discrepancy in the varying rates of uptake by VA mycorrhizae has been related to soil fertility. It is generally assumed that the nutrient which is limiting plant growth under conditions of low fertility will have the greatest increase in uptake after the seedlings are inoculated with VA mycorrhizal fungi (Gerdemann 1968). Jackson *et al.* (1973) have also shown that VA mycorrhizae can markedly increase the uptake of cations in soils of normal fertility. Thus, the question is whether growth increases associated with mycorrhizal fungi are due to, or merely accompanied by, increased nutrient uptake.

The present study was undertaken to clarify the effect of the soil fertility - VA mycorrhizal interaction on sweetgum seedling development. The specific purpose of the study is to determine whether inoculation with a VA mycorrhizal fungal mixture of *Glomus mosseae* and *Glomus etunicatus* at different soil fertility levels could enhance the growth and nutrient uptake of seedlings from eight sweetgum families.

### Materials and Methods

The study was designed as a factorial experiment with eight families, four fertilizer treatments, and two VA mycorrhizal conditions. Sweetgum seedlings were grown in a nursery in 32 redwood boxes  $1 \times 1 \times 0.3$  m. The empty boxes were fumigated in place, under plastic with methyl bromide (Dowfume MC-2, Dow Chemical Co.) for 48 h at a rate of 450 g/12 m<sup>2</sup> soil surface. The boxes were then filled with equal volumes of mixture containing a sandy loam forest soil, sand, and finely ground pine bark, previously fumigated with methyl bromide at the rate of 450 g/12 m<sup>2</sup> soil surface, 25 cm deep. Analysis of this mixture before fertilizer treatments were added revealed the following amounts of extractable ions in kilograms per hectare: NO<sub>3</sub>-N, 39.2; P, 25.8; K, 77.3; and Ca, 366.2.

All boxes were inoculated with 270 g of coarsely chopped sorghum roots taken either from pot cultures of sorghum containing *G. mosseae* plus *G. etunicatus* or nonmycorrhizal control sorghum pots. What was thought to be a pure culture of *G. mosseae* was found, after the study was completed, to be composed of a mixture of *G. mosseae* and a species recently described and named *G. etunicatus* by Becker and Gerdemann (1977). Throughout the rest of the paper this mixture will be referred to as *Glomus* spp. The top 7-10 cm of soil were removed from each box and the inoculum was uniformly spread before replacing the soil. Root-washings from the pot cultures were passed through a 45- $\mu$ m mesh sieve (openings smaller than the spore diameter of the *Glomus* spp.) and filtered through Whatman No. 1 paper. To help standardize the rhizosphere microflora, soil with

TABLE 1. Total weight and major nutrient contents per seedling in VA mycorrhizal and nonmycorrhizal sweetgum seedlings of eight families grown for 6 months in a soil-sand-bark mixture containing 140, 280, 560, and 1120 kg/ha of commercial 10-10-10 fertilizer

Fertilizer level, kg/ha	Mycorrhizal treatment	Total weight, g	Nutrient content, mg/seedling				
			N	P	K	Ca	Mg
140	Mycorrhizal	14.69	213.0	36.5	229.4	333.3	44.7
	Nonmycorrhizal	0.27	11.8	1.5	5.8	9.8	1.2
280	Mycorrhizal	13.83	221.3	32.3	242.5	297.1	44.5
	Nonmycorrhizal	0.26	12.6	0.8	4.4	8.1	0.9
560	Mycorrhizal	17.03	268.1	36.5	329.1	380.5	49.8
	Nonmycorrhizal	0.40	18.2	1.7	9.3	12.4	1.5
1120	Mycorrhizal	16.30	259.2	38.5	282.0	319.2	43.1
	Nonmycorrhizal	0.32	15.3	1.6	7.8	9.2	3.8

*Glomus* spp. received washings from nonmycorrhizal sorghum pot cultures and the control soil received washings from the pot cultures of *Glomus* spp.

Four treatment levels of 10-10-10 fertilizer consisting of 11.7, 23.5, 47.0, and 93.8 g/box (equivalent to 140, 280, 560, and 1120 kg/ha) were randomly assigned to the boxes. The fertilizer was incorporated into the top 7-10 cm of soil when the soil was removed for placement of inoculum. Hydrated lime (CaO) at the rate of 147 g/box was added to bring the elemental calcium to 1120 kg/ha.

Seeds from eight half-sib sweetgum families were sown in the boxes during the 3rd week of April. The seed had been collected from trees on the Scull Shoals Experimental Forest in northeastern Georgia. Five of the trees were on fertile bottomland sites (families 4, 5, 6, 7, and 51) and three were from dry upland sites (families 2, 8, and 9). The seeds were stratified in water at 2-4°C for 24 days before sowing. Each box had 40 planting locations and each family was randomly assigned to 5 of those locations. Four to six seeds were planted at each location and the soil was lightly covered with fumigated pine needle mulch. After germination, seedlings were thinned to one per planting location. All seedlings received 46 g/box or 560 kg/ha of  $\text{NH}_4\text{NO}_3$  three times during the growing season.

The seedlings were harvested in mid-October. The presence of infection by *Glomus* spp. was determined from root samples from two seedlings per family per box using the chloral hydrate acid-fuchsin clearing and staining procedure of Phillips and Hayman (1970). Heights and root collar diameters were measured and root, stem, and leaf weights were obtained after drying to constant weight at 70°C.

Total Kjeldahl nitrogen, phosphorus, potassium, calcium, and magnesium concentrations were determined for the leaves, stems, and roots of each seedling. Replicates were combined where one seedling did not provide enough sample for analysis. The methods of analysis were those used by the University of Georgia Soil Testing and Plant Analysis Laboratory, Athens, Georgia (Anonymous 1974). Cation analysis was done by wet digestion using 2 g of material in a nitric-perchloric-sulfuric acid mixture and detection by atomic absorption spectroscopy. Total phosphorus was determined from the same digestion mix and was detected in a Technicon Auto-Analyzer II system. Total Kjeldahl nitrogen was determined by digestion of 250 mg of sample in a mixture of sulfuric and selenious acid and hydrogen peroxide. The

digestion was accomplished in a Technicon Block Digester model BD-40. The digestion solution was analyzed for ammonia in a Technicon Auto-Analyzer II system. Nutrient content of a given seedling component was calculated as the product of the nutrient concentration and the dry weight of the component.

## Results

Inoculation with *Glomus* spp. had profound effects on the growth of sweetgum seedlings but the different levels of soil fertility had little effect. VA mycorrhizal seedlings outgrew the control seedlings in biomass at each fertilizer level (Table 1). Height and root collar diameter showed the same response to VA mycorrhizae. High mortality in the nonmycorrhizal seedlings precluded any specific family comparisons between nonmycorrhizal and VA mycorrhizal seedlings. Examination of the cleared and stained root samples showed that all seedlings grown in the soil inoculated with *Glomus* sp. had VA mycorrhizae after 6 months and that control seedlings were nonmycorrhizal.

Significant differences in growth of VA mycorrhizal seedlings were found among families (Table 2). In most cases seedlings from families 6, 8, and 9 outgrew seedlings from at least one other family.

## Nutrient Contents

High mortality and small seedling size in the nonmycorrhizal treatment precluded any comparisons of the nutrient data among families and any statistical comparisons between VA mycorrhizal and nonmycorrhizal seedling parts grown at different fertilizer levels. Values for the nonmycorrhizal seedlings are based on one pooled sample of all seedlings from all families grown at each fertilizer level. Values for VA mycorrhizal seedlings are based on 32 samples.

Nonmycorrhizal seedlings generally had higher

TABLE 2. Growth responses of VA mycorrhizal sweetgum seedlings of eight families grown for 6 months in a soil-sand-bark mixture

Family	Weight, g			
	Total	Leaf	Stem	Root
2	12.2 bcd*	4.0 bc	3.4 b	4.8 bd
4	10.8 d	3.6 c	3.1 b	4.1 d
5	13.1 bcd	4.2 bc	3.8 b	5.1 bcd
6	19.5 ab	6.3 ab	6.1 a	7.2 ab
7	11.1 cd	3.6 c	3.2 b	4.3 d
8	18.3 abc	6.0 ab	5.2 ab	7.1 abc
9	23.9 a	7.5 a	7.1 a	9.3 a
51	14.9 bcd	4.5 bc	4.5 ab	5.9 bcd

\*Values with the same letter within columns are not significantly different at the 95% confidence level.

concentrations of N, P, K, Ca, and Mg in the leaves, stems, and roots than did VA mycorrhizal seedlings at all fertilizer levels (Table 3). For both types of seedlings nitrogen, phosphorus, and potassium were highest in the leaves. Calcium was highest in the stems and magnesium concentrations did not vary between components.

Higher absolute nutrient contents were found in VA mycorrhizal rather than in nonmycorrhizal seedlings (Table 1).

Significant variations in the total nutrient content of the leaves, stems, and roots occurred among VA mycorrhizal families.<sup>3</sup> Leaves and roots generally had higher contents than stems. In most cases seedlings from families 6, 8, and 9 had higher contents than seedlings from at least one other family.

### Discussion

The fertility regimes in this experiment approximate the range found in most southeastern forest nurseries (unpublished data). It was assumed that the highest levels could produce large seedlings despite the absence of VA mycorrhizal fungi (Kormanik *et al.* 1977). Literature on agronomic crops has shown that under high fertility, especially high phosphorus, seedling growth is unaffected by the presence or absence of VA mycorrhizae (Gerdemann 1968). The results of this experiment suggest that if the same response occurs in sweetgum seedlings then 1120 kg/ha of 10-10-10 fertilizer with an additional 1680 kg/ha of  $\text{NH}_4\text{NO}_3$  is not enough to produce large nonmycorrhizal seedlings. At this level of fertilization only the VA mycorrhizal seedlings grew large enough for outplanting. Fertility

<sup>3</sup>These data are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

level had no significant effect on the biomass, height, or diameter growth of the VA mycorrhizal seedlings. It is suggested that VA mycorrhizal sweetgum seedlings could be grown under similar conditions in forest nurseries at the 280 kg/ha per year level without jeopardizing seedling quality.

Nonmycorrhizal seedlings grew so poorly that sufficient numbers were not available for a replicated nutrient analysis. It is unlikely that a fumigated nursery soil would remain as free of VA mycorrhizal fungi as the soil used in this experiment. However, the value of early inoculation with the appropriate fungi is obvious. The later the development of VA mycorrhizae, the smaller the seedlings will be at the end of the growing season. Under natural conditions slow growth of the seedlings throughout a nursery bed would be expected because endomycorrhizal fungal spores are not wind disseminated and reinfection must come from the residual inoculum below the effective zone of fumigation or must be carried in on infested equipment, rodents, birds, etc.

The family response to the VA mycorrhizal stimulus suggests that experiments such as this one could be used to select genotypes which respond best to specific VA mycorrhizal fungi. At least three families tested in this experiment could be identified as producing superior seedlings with *Glomus* spp. VA mycorrhizae. Family 6, a bottomland family, and families 8 and 9, both upland families, should be further tested in outplantings to determine whether their excellent 1st-year nursery growth would continue in the field.

Of major interest in this study are the nutrient responses. It is frequently stated that mycorrhizal roots are more efficient in absorbing ions from the soil (Nicholson 1967; Gerdemann 1968; Smith 1974). There is strong evidence for increased phosphorus uptake, especially, in agronomic crops. There are few studies that describe the nutrient uptake of VA mycorrhizal trees.

In general nutrient concentrations were higher in the nonmycorrhizal seedlings for all the elements tested. Phosphorus and nitrogen concentrations showed the greatest increases in tissues of nonmycorrhizal seedlings compared with tissues in VA mycorrhizal seedlings. Potassium and magnesium concentrations were slightly higher in the nonmycorrhizal seedlings while calcium was higher in only the stems and roots of the nonmycorrhizal seedlings. Calcium concentration in the leaves of VA mycorrhizal seedlings was either higher or equal to those in the leaves of nonmycorrhizal seedlings.

These findings are inconsistent with those gener-

TABLE 3. Nutrient concentration (parts per million) of the leaves, stems, and roots of VA mycorrhizal and nonmycorrhizal sweetgum seedlings of eight families grown for 6 months in a soil-sand-bark mixture containing 140, 280, 560, and 1120 kg/ha of commercial 10-10-10 fertilizer\*

Ferti- lizer level, kg/ha	Com- ponent	N		P		K		Ca		Mg	
		Mycor- rhizal	Nonmycor- rhizal								
140	Leaves	10 200	12 500	1166	2000	6693	8272	8983	7 584	1097	1206
	Stems	2 080	16 300	543	1563	3585	6958	9363	21 532	1086	2100
	Roots	2 180	14 800	773	1962	5336	6270	4343	8 628	859	1494
280	Leaves	11 520	17 200	1065	1700	7602	3611	6893	3 207	945	601
	Stems	2 160	—†	524	1275	4454	6521	9113	18 325	1016	1626
	Roots	2 300	14 200	746	1612	5479	6659	5415	7 746	1257	1333
560	Leaves	11 240	17 200	984	1980	8146	9975	7696	7 994	983	1173
	Stems	2 060	17 200	580	1225	6144	6696	9110	16 446	998	1452
	Roots	2 440	11 000	653	1075	5034	6659	5189	6 717	946	1285
1120	Leaves	10 580	—	1081	1900	8022	9885	7548	7 584	989	—
	Stems	2 660	—	528	1337	3990	7220	7882	14 455	892	1253
	Roots	2 720	15 400	752	1662	5290	7126	4154	7 452	762	1333

\* High mortality and small seedling size of the nonmycorrhizal seedlings precluded any statistical comparisons between VA mycorrhizal and nonmycorrhizal seedlings. Values for the nonmycorrhizal seedlings are based on one pooled sample of all seedlings grown at each fertilizer level.

† Not enough tissue available for analysis.

ally reported in the literature. Most studies suggest that phosphorus uptake is enhanced by VA mycorrhizae (Gray and Gerdemann, 1967; Sanders and Tinker 1971; Hayman and Mosse 1972; Mosse 1972; Mosse *et al.* 1973; and Rhodes and Gerdemann 1975). Mosse (1957), Baylis (1959), Ross and Harper (1970), and Ross (1971) generally found higher concentrations of nitrogen, potassium, calcium, and magnesium in VA mycorrhizal plants than in nonmycorrhizal plants. Baylis (1959) found higher nitrogen concentrations in nonmycorrhizal *Griselinia littoralis* whereas Gerdemann (1964) found higher concentrations of potassium and magnesium in nonmycorrhizal maize plants. Ross and Harper (1970) and Ross (1971) found little difference in potassium concentrations between VA mycorrhizal and nonmycorrhizal plants.

All of the elements in this experiment were present in the soil in quantities generally considered sufficient for seedling growth. Soil nutrient analysis at the end of the study showed no significant differences between concentrations of the inoculated and non-inoculated soil. It can be assumed that soil fertility was adequate for growth as the quantities of nutrients removed by the VA mycorrhizal seedlings did not measurably reduce the quantity of nutrients available in the soil (Gerdemann 1964). Therefore, rates of activity or the interactions between the fungus and the seedling must be different in sweetgum than in the plant species normally used by the other authors. Forest trees can grow better under

lower soil nutrient conditions than most agronomic crops because trees have had little selection pressure for fertilizer responses.

In contrast with the higher nutrient concentrations in the nonmycorrhizal seedlings, total nutrient content per seedling was always higher for the VA mycorrhizal seedlings and was correlated with seedling size.

The role of the VA mycorrhizal fungi in the nutrition of the sweetgum seedling remains unclear. VA mycorrhizae do not cause greater nutrient concentrations in the tissue but rather, greater tissue production. The mass of soil exploited by the VA mycorrhizal root system results in the absorption of greater quantities of nutrients than are absorbed by smaller nonmycorrhizal root systems. However, the stimulus for the initial increase in growth after inoculation is not clear. It may be that hormonal activities stimulated by the inoculation are more important than the initial efficiency of nutrient uptake. It is also possible that enhanced water uptake by VA mycorrhizae stimulates growth (Safir *et al.* 1971, 1972). We observed that cessation of diurnal leaf wilting is an indicator of mycorrhizal formation. For 2 or 3 weeks after germination, the leaves of seedlings wilt during the day. Soon after the seedlings cease wilting, height growth normally begins and leaves expand rapidly. Nonmycorrhizal seedlings continue to exhibit diurnal wilting and leaves eventually turn red or purple.

Phenotypic variation among the progeny of the

eight mother trees was obvious in total nutrient accumulations but not in nutrient concentrations. Differences in total accumulations were associated with variations in seedling size. No significant differences in root to shoot ratios of endomycorrhizal seedlings were found across the fertilizer levels or between families, suggesting that nutrition was adequate for growth. A final attempt to identify nutritional influences on VA mycorrhizal seedlings was made by comparing the distribution of total nutrients in the tissues of pooled seedlings across fertilizer levels. Significant differences between tissues were measured, as expected, but no obvious trends between fertilizer levels within tissues could be defined.

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