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Vesicular-Arbuscular Mycorrhiza and Soil Fertility Influence Mineral Concentrations in Seedlings of Eight Hardwood Species

Abstract
Eight hardwood species were grown under two sets of fertilizer and vesicular–arbuscular mycorrhizae (VAM) treatments. In the first study three treatments of 140, 560, and 1120 kg/ha of 10– 10– 10 (% N, P_2O_5, and K_2O, respectively) fertilizer were added to fumigated soil with or without a mixture of *Glomusmosseae* Nicol. and Gerd. and *Glomusetunicatus* Becker and Gerd. (GM). In the second study, seedlings were grown with VAM treatments of (*i*) the same *Glomus*(GM) mixture as in study 1, (*ii*) *Glomusfasiculatus* (Thaxter) Gerd. and Trappe (GF), or (*iii*) mixed cultures of several *Glomus* and *Gigaspora* species (GG). A fertilizer treatment of 280 kg/ha of 10– 10– 10 was added to all seedlings. All treatments, in both studies, also received 10 equal applications of NH_4NO_3, totaling 1680 kg/ha, during the growing season. No single nutrient was consistently higher in nonmycorrhizal or VAM seedlings in either study and no symbiont produced consistently high concentrations of all nutrients in all species. Uninoculated seedlings frequently had higher N, K, Ca, and Mg concentrations than VAM seedlings. Inoculated seedlings generally had higher total P concentrations than uninoculated seedlings. For uninoculated seedlings of five of the species, P concentrations increased with higher fertility levels. Seedlings inoculated with GM and GG had higher P concentrations than those inoculated with GF. In numerous instances, uninoculated seedlings had higher mineral concentrations than VAM seedlings even though the uninoculated seedlings were always the smallest. This suggests that VAM provide stimulation other than or in addition to the enhanced nutrient uptake

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This article is from *Canadian Journal of Forest Research* 12 (1982): 829, doi:10.1139/x82-124.

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Vesicular–arbuscular mycorrhiza and soil fertility influence mineral concentrations in seedlings of eight hardwood species

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Received December 31, 1981[1]

Accepted June 25, 1982

SCHULTZ, R. C., and P. P. KORMANIK. 1982. Vesicular–arbuscular mycorrhiza and soil fertility influence mineral concentrations in seedlings of eight hardwood species. Can. J. For. Res. **12**: 829–834.

Eight hardwood species were grown under two sets of fertilizer and vesicular–arbuscular mycorrhizae (VAM) treatments. In the first study three treatments of 140, 560, and 1120 kg/ha of 10–10–10 (% N, P_2O_5, and K_2O, respectively) fertilizer were added to fumigated soil with or without a mixture of *Glomus mosseae* Nicol. and Gerd. and *Glomus etunicatus* Becker and Gerd. (GM). In the second study, seedlings were grown with VAM treatments of (*i*) the same *Glomus* (GM) mixture as in study 1, (*ii*) *Glomus fasiculatus* (Thaxter) Gerd. and Trappe (GF), or (*iii*) mixed cultures of several *Glomus* and *Gigaspora* species (GG). A fertilizer treatment of 280 kg/ha of 10–10–10 was added to all seedlings. All treatments, in both studies, also received 10 equal applications of NH_4NO_3, totaling 1680 kg/ha, during the growing season. No single nutrient was consistently higher in nonmycorrhizal or VAM seedlings in either study and no symbiont produced consistently high concentrations of all nutrients in all species. Uninoculated seedlings frequently had higher N, K, Ca, and Mg concentrations than VAM seedlings. Inoculated seedlings generally had higher total P concentrations than uninoculated seedlings. For uninoculated seedlings of five of the species, P concentrations increased with higher fertility levels. Seedlings inoculated with GM and GG had higher P concentrations than those inoculated with GF. In numerous instances, uninoculated seedlings had higher mineral concentrations than VAM seedlings even though the uninoculated seedlings were always the smallest. This suggests that VAM provide stimulation other than or in addition to the enhanced nutrient uptake.

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Les auteurs ont cultivé huit espèces de feuillus en présence de deux traitements de fertilisants et de champignons endomycorhiziens à vésicules et arbuscules (VAM). Dans une première étude, ils ont appliqué trois traitements de fertilisants aux taux de 140, 560, 1120 kg/ha de 10–10–10 (% N, P_2O_5 et K_2O respectivement), dans un sol fumigé ayant reçu ou non un mélange de *Glomus mosseae* Nicol. and Gerd. et *Glomus etunicatus* Becker and Gerd. (GM). Dans une deuxième étude, ils ont cultivé les plantules avec les traitements VAM suivants: (*i*) le même mélange de *Glomus* (GM) utilisé dans la première étude; (*ii*) le *Glomus fasciculatus* (Thaxter) Gerd. and Trappe (GF); ou (*iii*) un mélange de plusieurs espèces de *Glomus* et de *Gigaspora* (GG). Une fertilisation au taux de 280 kg/ha de 10–10–10 a été appliquée à toutes les plantules. Dans les deux études tous les traitements ont également reçu 10 applications égales de NH_4NO_3 pour un total de 1680 kg/ha, au cours de la saison de croissance. Aucun des éléments n'était régulièrement plus élevé chez les plantules inoculées ou non dans l'une ou l'autre des études et aucun des symbiontes n'a entraîné régulièrement de fortes concentrations de tous les éléments chez toutes ces espèces. Il est arrivé souvent que les plants non inoculés avaient une plus forte teneur en N, K, Ca et Mg que les plants mycorhizés. Les plants inoculés avaient généralement des teneurs plus élevées en phosphore que les plants non inoculés. Dans le cas de cinq espèces d'arbre, les teneurs en phosphore ont augmenté avec les niveaux de fertilité. Les plants inoculés avec GM et GG avaient des teneurs en P plus élevées que ceux inoculés avec GF. Dans plusieurs cas les plants non inoculés avaient des teneurs en minéraux plus élevées que les plants mycorhiziens, même si les plants non inoculés étaient toujours les plus petits. Ceci suggère que les VAM sont responsables d'une stimulation autre ou supplémentaire à l'augmentation de l'absorption des éléments.

[Traduit par le journal]

Consistent production of plantable-size seedlings of many species of hardwoods in tree nurseries is difficult, particularly after soil fumigation to control weeds and pests (Bryan and Kormanik 1977). Populations of vesicular–arbuscular (VAM) fungi are reduced or eliminated by fumigation, and natural recolonization of the soil may take more than a growing season to reach prefumigation levels (Riffle 1980). Early growth of important timber species of hardwoods such as sweetgum (*Liquidambar styraciflua* L.) and yellow-poplar (*Lirodendron tulipfera* L.) can be stimulated by inoculation with VAM fungi (Gray and Gerdemann 1967;

[1]Revised manuscript received June 14, 1982.

0045-5067/82/040829-05$01.00/0

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Kormanik *et al.* 1977; Schultz *et al.* 1979).

Many plants which grow well in average soil fertility can also be grown under conditions of high soil fertility in the absence of mycorrhizal development. Although there is strong evidence for increased phosphorus uptake by VA mycorrhizae, evidence for such a role with other nutrients is not consistent (Mosse 1973; Smith 1974). Differences in uptake of elements other than phosphorus may be a reflection of their relative concentrations in soils used to study plant responses to VAM fungi and (or) specific hosts' differential requirements of specific elements.

Schultz *et al.* (1979) and Kormanik *et al.* (1977) found that fertilizer additions of 140 to 1120 kg/ha of 10−10−10 (% N, P_2O_5, K_2O, respectively) had no effect on the growth of sweetgum seedlings inoculated with a mixture of *Glomus* spp. nor on noninoculated seedlings that were 15 times smaller than the inoculated seedlings. Uninoculated seedlings generally had higher concentrations of N, P, K, Ca, and Mg although inoculated seedlings contained higher absolute amounts of these minerals. Soil-fertility levels had no influence on nutrient concentrations. Two studies were undertaken to determine if seven other hardwood species respond to soil fertility and infection by the mixture of *Glomus* spp. in the same way as sweetgum.

Methods

Seven species, plus sweetgum, were planted intermixed, in plots to determine general growth and nutrient responses. It was recognized that competition between the species might develop but establishment of absolute growth potentials was not the objective. The species were selected for their potential as high fiber producers under intensive management. All of the species except sugar maple (*Acer saccharum* Marsh.) are native to the southeastern coastal states. Growth responses and VAM infection rates are reported elsewhere (Schultz *et al.* 1981; Kormanik *et al.* 1982).

The species used in the two studies were *Acer negundo* L. (box elder), *Acer rubrum* L. (red maple), *Acer saccharum* Marsh. (sugar maple), *Fraxinus pennsylvanica* Marsh. (green ash), *Juglans nigra* L. (black walnut), *Liquidambar styraciflua* L. (sweetgum), *Platanus occidentalis* L. (sycamore), and *Prunus serotina* Ehrh. (black cherry). With the exception of sugar maple, black cherry, and black walnut, all the seeds were collected in northeast Georgia. The sugar maple came from Vermont, the black walnut from North Carolina, and the black cherry from Tennessee. The sweetgum seeds were soaked in water at 2−4°C for 24 days prior to sowing and the other species were stratified according to procedures recommended in the Agriculture Handbook No. 450 (Anonymous 1974).

Seedlings were grown in twenty-four 1 × 1 × 0.6 m redwood boxes at the Whitehall Experimental Forest of the School of Forest Resources, University of Georgia, Athens. The bottoms of the boxes were constructed from 2-cm marine-grade plywood to prevent contamination from below. Drainage was enhanced by 15 cm of gravel and a series of 2.54-cm holes at the base of the redwood sides. The empty boxes were covered with polyethylene plastic and fumigated with methyl bromide (one can Dowfume MC-2, Dow Chemical Co. per two boxes) for 48 h. The boxes were then filled with a 2 : 1 : 1 mixture of a sandy loam forest soil, sànd, and finely ground pine bark fumigated as above. Analysis of this mixture before fertilizer treatments were added revealed the following amounts of double acid extractable (Issac and Jones 1971) ions in kilograms per hectare: NO_3-N, 39; P, 26; K, 77; and Ca, 366. Elemental calcium levels were adjusted to a value of 1120 kg/ha by the addition of hydrated lime ($Ca(OH)_2$).

The first study consisted of four replications of three fertilizer levels and two levels of mycorrhizal inoculum. The second study contained four mycorrhizal treatments and five replications. Four treatment levels of 10−10−10 fertilizer consisting of 11.7, 47.0, and 93.8 g/box (equivalent to 140, 560, and 1120 kg/ha) for study 1 and 28.1 g/box (280 kg/ha) for study 2 were assigned to each of the mycorrhizal treatments. The fertilizer was incorporated into the top 7−10 cm of soil before the seeds were sown. In addition, all microplots received a total of 1120 kg/ha of NH_4NO_3 applied in 10 increments at 2-week intervals during the growing season.

All treated plots received 2 L of coarsely chopped roots from pot cultures of sorghum (*Sorghum vulgare* var. *roxburghi* (Stepf.) Haines). The treatments in study 2 consisted of a mixed culture of *Glomus mosseae* and *G. etunicatus* (GM); *G. fasiculatus* (Thaxter) Gerd. and Trappe (GF); or mixed cultures of several *Glomus* and *Gigaspora* species (GG). Study 1 received only the GM treatment. Although all pot cultures were approximately 9 months old, the spore counts varied considerably among different VAM symbionts. Average number of spores added per microplot were: GM, 854; GF, 6600; and GG, 2644. The inoculum was thoroughly worked into the top 15−20 cm of soil. The root washings from all inoculum sources were passed through a 25-mesh sieve and then filtered through Whatman No. 1 paper. To standardize the rhizosphere microflora at sowing time, each mycorrhizal treatment received leachate from the two other inoculum sources while the control treatment received leachates from all three.

Seeds from the eight species were sown in the boxes during the last week of May. Each box had 40 planting locations and each of the eight species were randomly assigned 5 of those locations. Several seeds were planted at each location to ensure at least one plant would survive. Seedlings were thinned to one per planting spot. After planting, the boxes were lightly covered with fumigated pine needle mulch.

Seedlings were harvested in early November. Total weights were computed from root, stem, and leaf weights obtained after drying to a constant weight at 70°C. Some seedlings had lost their leaves and no total weights were computed for them. Infection by VAM fungi was determined by collecting feeder roots from at least five locations on each seedling. Root samples were processed by Phillips and Hayman procedure (1970) except that lactophenol was used in place of a chloral hydrate.

After clearing and staining the roots, VAM infection was evaluated with the aid of a dissecting microscope. The whole

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TABLE 1. Nutrient concentrations for eight hardwood species grown in a mixture of soil–sand–bark containing three levels of 10–10–10 fertilizer and a VA mycorrhizal mixture of *Glomus* spp. (GM) or no mycorrhizal inoculum (CN)

	N, mg/g		P, mg/g		K, mg/g		Ca, mg/g		Mg, mg/g		Total weight, gm		Infection	
	GM	CN	GM	CN	GM	CN	GM	CN	GM	CN	GM	CN	%	Intensity
Black cherry														
140	18.0a*	26.0a	1.2a	—†	6.2a	—	8.2a	—	1.8a	—	14.4a	0.3b	47.9a	2.7a
560	17.7a	22.8a	1.3a	—	5.6a	—	9.0a	—	1.4a	—	17.1a	0.5ab	64.3a	2.9a
1120	18.6a	22.2a	1.4a	—	6.1a	—	7.6a	—	1.7a	—	6.6a	0.8a	62.5a	2.8a
Box elder														
140	14.0a	16.0a	1.3a	0.9c	11.3a	7.3a	6.7a	4.3a	2.1a	2.1a	20.2b	—	70.0a	2.5a
560	14.8a	19.2a	1.3a	1.1a	11.4a	7.5a	7.1a	3.4b	2.3a	1.6b	27.0ab	—	74.6a	2.4a
1120	15.4a	16.8a	1.3a	1.0b	10.9a	6.5a	7.1a	3.0b	2.0a	1.4b	36.9a	—	80.0a	2.6a
Green ash														
140	11.7a	14.5a	1.1a	0.6c	7.9a	5.7b	7.1a	1.7b	1.5a	1.5a	21.6ab	—	78.3a	3.0a
560	11.0a	5.5c	1.1a	0.7b	7.4a	7.8a	7.1a	4.6a	1.4a	1.1b	28.8a	—	82.5a	2.9a
1120	13.0a	9.2b	1.0a	0.9a	7.1a	6.0b	5.5a	3.8a	1.3a	1.0b	18.9b	—	80.1a	3.0a
Red maple														
140	11.2a	16.0a	1.3b	—	6.2a	—	7.7a	—	1.3a	—	9.7b	0.2a	68.4a	2.4a
560	12.6a	6.7c	1.4a	0.8b	5.8ab	5.5a	8.3a	7.7a	1.3a	0.9a	9.6b	1.1a	68.8a	2.5a
1120	11.6a	9.8b	1.3b	0.9a	5.2b	5.1a	7.4a	7.9a	1.2a	1.0a	17.9a	3.7a	67.8a	2.5a
Sugar maple														
140	15.9a	11.1c	1.7a	0.6c	4.8b	5.7c	8.7a	5.9a	1.2a	1.1b	1.5b	—	41.3a	2.1ab
560	16.8a	21.0a	1.8a	0.7b	4.7b	7.0a	7.6a	2.6b	1.1ab	1.3a	1.7b	—	46.7a	1.7a
1120	16.7a	14.1b	1.8a	1.0a	5.0a	6.1b	7.5a	5.5a	1.0b	1.0b	2.4a	—	68.8b	2.4a
Sweetgum														
140	9.2b	15.2b	1.0a	0.5b	7.2a	4.1c	7.1a	7.0a	1.5a	0.8c	12.6a	0.4a	40.1a	2.3a
560	13.6a	10.2b	1.1a	0.7a	6.9a	4.8b	6.4a	6.3a	1.3b	0.9b	10.8a	0.7a	56.3b	2.5ab
1120	14.1a	24.2a	1.0a	0.7a	7.0a	5.4a	6.9a	7.1a	1.3b	1.1a	14.5a	2.3a	72.5c	2.8b
Sycamore														
140	11.7a	9.8a	1.1b	0.8a	5.3a	7.6a	5.9a	5.2a	1.2a	1.4a	46.9a	2.3b	77.0a	2.8a
560	12.2a	11.1a	1.1b	0.7ab	5.6a	7.4a	6.4a	5.6a	1.1a	1.5a	64.8a	5.5b	86.2a	3.0a
1120	11.6a	11.1a	1.2a	0.6b	6.1a	6.8a	6.1a	5.1a	1.1a	1.3a	88.5a	10.3a	85.0a	2.9a
Walnut														
140	12.8a	13.3a	0.9a	0.5a	4.7a	5.1a	6.1a	6.8a	1.2a	1.3a	—	—	68.1a	2.9a
560	11.2a	12.8a	0.9a	0.5a	5.2a	5.4a	7.0a	6.1a	1.2a	1.3a	—	—	66.1a	2.5ab
1120	12.2a	11.9a	0.9a	0.5a	5.3a	5.4a	6.7a	5.4a	1.2a	1.2a	—	—	64.0a	2.4b

*Values within columns, within species labeled with the same letter are not different at the 0.05 level of probability by Duncan's multiple range test.
†Insufficient material for analysis.

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petri dish of roots was classified as being 0–24, 25–49, 50–74, and 75–100% infected. Three classes of infection intensity were used to classify the degree of infection within individual roots: low (small infection sites widely scattered along entire root), medium (larger infection sites more uniformly distributed throughout infected roots but rarely coalescing), and heavy (feeder roots almost entirely infected).

Total Kjeldahl nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (MG) concentrations were determined for leaves, stems, and roots of each seedling. 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 (Perkin-Elmer Agricultural Analytical Method AY-5, Perkin-Elmer Corp., Norwalk, CT). Phosphorus was detected from the same digest on a Technicon Autoanalyzer II (Industrial Method No. 95-70W, Technicon Instruments Corp., Tarrytown, NY). Total Kjeldahl nitrogen was detected on a Technicon Autoanalyzer II (Industrial Method No. 334-74A). Data were analyzed by analysis of variance and significance among treatment means determined by Duncan's multiple range test.

Results and discussion

No single nutrient was consistently higher in concentration in the nonmycorrhizal or VAM seedlings in either of the two studies and no symbiont produced consistently high concentrations of all nutrients in all species of seedlings.

Neither VAM seedlings nor nonmycorrhizal seedlings had consistently higher concentration of N (Tables 1 and 2). Fertility level had an effect on N concentrations only in the VAM seedlings of sweetgum (Table 1). Higher fertility levels produced higher tissue N concentrations. For uninoculated green ash and red maple seedlings, N concentrations were higher at the lowest fertilizer level of 140 kg/ha of 10–10–10, while for sugar maple and sweetgum, N concentrations were higher at the two other fertilizer levels. In sycamore and walnut there was no difference in N concentrations between the VAM and uninoculated seedlings.

At the 280-kg/ha level of 10–10–10, sweetgum and walnut demonstrated no significant differences in N concentrations among any of the VAM or the control seedlings (Table 2). The uninoculated seedlings of black cherry and red maple had the highest N contents, whereas the uninoculated seedlings of sycamore had the lowest. Black cherry and box elder generally had the highest N concentrations with each of the symbionts.

The large differences in spore densities among treatments did not influence uptake of N. Except for box elder, root infection percentages between the VAM seedlings were not different for the various symbionts. Although uninoculated seedlings of red maple and black cherry had N concentrations that were higher than those of VAM seedlings, total dry weight production of asymbiotic seedlings was, in all instances, significantly less. Differences in nitrogen concentrations in other species of plants have also been inconsistent (Baylis 1959; Gerdemann 1964; Ross and Harper 1970). For the fertilizer levels and symbiont treatments used in these studies no consistent nitrogen differences were found. However, a study by Brown *et al.* (1981) using the same media and *Glomus etunicatus* found significant differences in growth of VAM sweetgum seedlings fertilized with different rates and sources of N. They applied ammonium sulfate, ammonium nitrate, and potassium nitrate at rates ranging from 0 to 2240 kg N/ha and found that the 560-kg N/ha rate produced the largest and most infected VAM seedlings. They concluded that since VAM root systems are able to adequately supply seedling P needs even at low soil P concentrations, N availability is probably more critical than P availability in achieving optimum growth of VAM sweetgum.

As found in other studies, P levels were more consistent than those of N. Most studies suggest that P uptake is enhanced by VAM (Rhodes and Gerdemann 1975; Menge *et al.* 1978). For all of the species tested here, VAM seedlings generally had higher total P concentrations than uninoculated seedlings. However, P concentrations of uninoculated black cherry and green ash seedlings were no different than those of seedlings inoculated with one or two of the VAM treatments, respectively (Table 2). For seedlings inoculated with the GM only, red maple and sycamore revealed differences in P among fertilizer levels (Table 1). For uninoculated seedlings of box elder, green ash, red maple, sugar maple, and sweetgum, P concentrations increased with higher fertility levels (560 and 1120 kg/ha). The reverse was true for sycamore, and no fertilizer effects occurred for uninoculated walnut seedlings. The increased P concentrations, in uninoculated seedlings at the higher fertility levels, is the typical response described in the literature. These increased concentrations are generally accompanied by increased plant growth, and mycorrhiza-free seedlings grown with sufficient P are generally the same size as VAM seedlings growing at lower P levels. Clearly, the level of soil P produced by addition of 1120 kg/ha of 10–10–10 was insufficient to produce large nonmycorrhizal seedlings in this study (Table 1). Seedlings inoculated with GM and GG consistently had higher P concentrations than those seedlings inoculated with GF. The multiple species mixtures were more effective at increasing P uptake than the single species even though GF had a greater initial spore density at the time of infection. There were no differences in infection percentages between the symbionts even with the large variance in initial spore densities. Possibly the lowest spore density was higher than the threshold needed for

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TABLE 2. Nutrient concentrations for eight hardwood species grown in a mixture of soil–sand–bark containing *Glomus fasiculatus* (GF), a mixture of *Glomus* spp. (GM), a mixture of VA endomycorrhizae (GG), or a nonmycorrhizal control (CN) and 280 kg/ha 10–10–10 fertilizer

	N, mg/g	P, mg/g	K, mg/g	Ca, mg/g	Mg, mg/g	Total weight, gm	Infection %	Intensity
Black cherry								
GF	15.03*b**	0.93*b*	3.91*b*	7.83*a*	1.17*a*	29.3*a*	78.1*a*	2.9*a*
GM	13.69*b*	1.12*ab*	4.31*b*	6.78*a*	1.21*a*	6.5*b*	54.7*a*	2.2*a*
GG	17.94*ab*	1.31*a*	4.21*b*	6.83*a*	1.22*a*	26.4*a*	73.2*a*	2.6*a*
CN	22.94*a*	0.71*b*	7.64*a*	2.75*a*	1.63*a*	0.4*b*	—	—
Box elder								
GF	13.60*a*	1.00*c*	8.89*b*	6.51*ab*	1.78*a*	23.7*a*	71.5*b*	2.0*b*
GM	14.42*a*	1.20*a*	9.37*a*	7.04*a*	1.79*a*	20.4*a*	83.1*a*	2.6*a*
GG	13.54*a*	1.09*b*	7.63*c*	6.25*ab*	1.85*a*	23.8*a*	76.6*ab*	2.1*b*
CN	13.42*a*	0.90*d*	7.38*c*	4.42*b*	1.86*a*	0.9*b*	—	—
Green ash								
GF	10.68*a*	0.71*b*	5.97*b*	6.25*a*	1.09*b*	23.1*ab*	81.5*a*	3.0*a*
GM	10.43*a*	1.07*a*	7.33*a*	6.13*a*	1.14*b*	15.9*b*	84.1*a*	3.0*a*
GG	11.44*a*	1.05*a*	6.94*a*	6.44*a*	1.40*a*	25.0*a*	83.3*a*	2.9*a*
CN	9.57*a*	0.61*b*	7.30*a*	2.17*b*	0.89*b*	0.5*c*	—	—
Red maple								
GF	11.11*b*	0.91*c*	5.07*a*	7.66*a*	0.99*a*	10.4*a*	68.5*a*	2.2*a*
GM	11.93*b*	1.35*a*	5.54*a*	8.29*a*	1.06*a*	13.5*a*	71.3*a*	2.3*a*
GG	11.41*b*	1.22*b*	3.74*b*	7.59*a*	1.05*a*	10.4*a*	66.7*a*	1.9*a*
CN	14.01*a*	0.75*d*	5.76*a*	3.77*b*	1.17*a*	0.4*b*	—	—
Sugar maple								
GF	12.84*a*	1.19*c*	4.67*b*	7.28*a*	0.77*b*	3.1*a*	74.5*a*	2.2*a*
GM	11.19*b*	1.37*b*	4.67*b*	5.29*b*	0.83*b*	1.5*b*	67.3*a*	1.8*b*
GG	13.48*a*	1.60*a*	4.67*b*	6.95*a*	1.19*a*	3.8*a*	72.9*a*	1.9*ab*
CN	13.34*a*	0.63*d*	6.14*a*	4.91*b*	0.91*b*	0.6*b*	—	—
Sweetgum								
GF	9.41*a*	0.80*b*	5.30*a*	6.85*a*	1.18*ab*	12.2*a*	67.5*a*	3.0*a*
GM	10.57*a*	0.97*a*	5.43*a*	6.25*ab*	1.13*b*	12.7*a*	68.3*a*	2.5*b*
GG	10.96*a*	0.99*a*	4.90*a*	5.96*b*	1.32*a*	15.5*a*	80.5*a*	2.7*b*
CN	10.59*a*	0.50*c*	2.90*b*	3.84*c*	0.49*c*	0.3*b*	—	—
Sycamore								
GF	11.02*ab*	0.83*c*	4.58*b*	5.97*a*	1.03*ab*	71.3*a*	86.5*a*	3.0*a*
GM	12.14*a*	1.10*a*	5.16*ab*	5.93*a*	0.90*b*	60.9*a*	84.5*a*	2.9*a*
GG	11.90*a*	1.02*b*	4.61*b*	6.14*a*	1.13*ab*	53.6*a*	82.2*a*	2.8*a*
CN	9.66*b*	0.56*d*	6.07*a*	6.84*a*	1.15*a*	3.7*b*	—	—
Walnut								
GF	11.19*a*	0.69*b*	4.92*a*	8.88*a*	1.16*a*	85.4*ab*	84.6*a*	3.0*a*
GM	13.16*a*	0.76*ab*	5.31*a*	8.61*a*	1.36*a*	41.4*b*	72.5*a*	2.7*a*
GG	11.84*a*	0.84*a*	4.52*a*	6.13*a*	1.11*a*	101.3*a*	71.3*a*	2.7*a*
CN	11.20*a*	0.54*c*	4.37*a*	7.48*a*	1.46*a*	—	—	—

*Values within columns, within species labeled with the same letter are not different at the 0.05 level of probability by Duncan's multiple range test.

an adequate infection or that spore density may not have been important at all in light of the infected sorghum roots and hyphae present in the inoculum.

Potassium, Ca, and Mg responses were similar to those of N. For seedlings inoculated with GM few fertilizer effects on concentration of these minerals were observed (Table 1). For K, only red maple and sugar maple showed any concentration differences. There were no fertilizer effects on Ca concentrations for any of the VAM seedlings. For Mg, only sugar maple and sweetgum responded to soil fertility, and Mg tissue concentrations decreased as fertility increased. Fertility levels had no effect on concentrations of K, Ca, or Mg in the uninoculated seedlings of red maple, walnut, or sycamore. In addition, K concentrations in uninoculated box elder seedlings were not affected by adding 10–10–10 fertilizer. The other uninoculated seedlings responded to fertility level but no consistent trends

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could be identified (Table 1).

At the fertilizer levels of this experiment, no one symbiont treatment was most efficient at stimulating nutrient uptake (Table 2). This response could be expected since these tree species generally are found on a variety of sites with different microfloral and faunal populations. In numerous instances, uninoculated seedlings had higher mineral concentrations than inoculated seedlings. The uninoculated seedlings were again the smallest seedlings grown indicating that the VAM must provide some stimulation other than or in addition to the enhanced nutrient uptake.

The range of nutrients tested in this study generally covers that considered sufficient to grow hardwood seedlings. The results of the study show, however, that even at the highest level of nutrient addition (1120 kg/ha) nonmycorrhizal seedlings of all species were significantly smaller than VAM seedlings. Many plant species that grow well with VAM under average soil fertility levels can also be grown asymbiotically under conditions of high soil fertility (Gerdemann 1964; Smith 1974). The results suggest that higher levels of fertilizer than were obtained in this study are needed to produce large nonmycorrhizal seedlings of the eight hardwood species tested. Even with the addition of 1120 kg/ha of 10−10−10 nonmycorrhizal seedling dry weights were not increasing sufficiently to indicate that the threshold of P for nonmycorrhizal seedling production had been reached. Larger quantities of added nutrients, particularly P, would be needed to produce large seedlings. The field performance of such nonmycorrhizal seedlings has not been fully tested although failures or poor early performance of large commercial outplantings may be the result. VAM seedlings produced at lower soil P levels would be likely to perform more adequately under field conditions. Since fertilizer level did not affect the size of the inoculated seedlings it is recommended that 1-year-old seedlings of these eight hardwood species be produced using VAM inoculum and 560 kg/ha of 10−10−10 and 1680 kg/ha of NH_4NO_3.

Acknowledgements

This study was supported in part by McIntire-Stennis and Georgia Forest Research Council funds.

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