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Abstract
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Keywords
Glomus etunicatus, Liquidambar styraciflua, VA endomycorrhizae

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ABSTRACT. Sweetgum seedlings were grown outdoors in pots filled with fumigated soil, were inoculated with the endomycorrhizal fungus *Glomus etunicatus*, and were treated with fertilizers to determine growth response to different sources and levels of nitrogen. Ammonium sulfate, ammonium nitrate, and potassium nitrate were applied eight times during the growing season, at seasonal rates equivalent to 0, 140, 280, 560, 1,120, or 2,240 kg N/hectare. Application of 560 kg N/ha as ammonium sulfate or ammonium nitrate produced seedlings with greatest mean heights, diameters, and top weights. The 280 and 560 kg N/ha treatments of each N source produced the greatest percentages of mycorrhizal roots and highest intensities of infection per infected root segment. Mycorrhizal development was maximum in treatments that produced maximum growth. Ammonium nitrate was considered superior to ammonium sulfate because of a lesser tendency of the former to acidify the soil. FOREST SCI. 27:413–420.

ADDITIONAL KEY WORDS. *Liquidambar styraciflua, Glomus etunicatus,* VA endomycorrhizae.

SWEETGUM (*Liquidambar styraciflua* L.) is one of the most promising species for hardwood plantation management in the South because of its ability to grow well on a wide range of sites. Methods have been developed for producing high quality sweetgum planting stock in nurseries by inoculating seedlings with vesicular-arbuscular (VA) endomycorrhizal fungi (Kormanik and others 1976, 1977a, 1977b, 1977c; Schultz and others 1979). Recent work by Kormanik, Schultz, and Bryan with sweetgum has shown that all VA symbionts tested (*Glomus fasiculatus, Glomus etunicatus, Glomus mosseae,* and a natural mixture of *Glomus* and *Gigaspora* spp.) were equally effective in producing high quality seedlings (unpubl. data). Nonmycorrhizal seedlings seldom exceed 7 cm in height at soil P levels (weak acid extractable, Isaac and Jones 1971) less than ca. 45 ppm (Kormanik and others 1977a).

Higher plants require greater amounts of nitrogen (N) than any other soil nutrient, thus nitrogen often becomes a limiting factor during seedling development. The amount of ammonium-N and nitrate-N required by plants for satisfactory

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growth varies among species (Bowen 1973, Kirkby and Hughes 1970, McKee 1962, Scarsbrook 1965, Warncke and Barber 1973). The preference of most fungi for ammonium-N is well known (Burnett 1968), and this form is apparently a major source of N for ectomycorrhizal fungi (Carrodus 1966 and 1967, Lundeberg 1970). Transfer of absorbed N from the fungal symbiont to the host was shown in Melin and Nilsson's (1952, 1953) ^{15}N tracer experiments with pine ectomycorrhizae. Ho and Trappe (1975) reported that two species of VA endomycorrhizal fungi were capable of utilizing nitrate-N. The purpose of this study was to determine optimum nitrogen sources and fertilization levels for growth of sweetgum seedlings inoculated with a specific VA symbiont.

Methods

An outdoor pot study at the Whitehall Experimental Forest near Athens, Ga., consisted of three nitrogen fertilizers applied at five levels each and a control with no added nitrogen. There were 12 replications of each of the 16 treatments in 20.3 cm diameter pots.

The potting soil consisted of equal volumes of a sandy loam forest soil, sand, and coarsely ground pine bark. Soil was fumigated with methyl bromide-chloropicrin (Dowfume MC-2, Dow Chemical Co.) for 48 hours to kill indigenous mycorrhizal fungi and most other organisms. Analysis of the soil mixture revealed the following amounts of extractable ions in kg/ha: NO_3-N, 19.9; P, 28.2; K, 145.2; Ca, 270.1; and Mg, 56.3. Hydrated lime ($Ca(OH)_2$) was added to bring the level of Ca to 1,120 kg/ha, which raised soil pH from 5.5 to 6.8. Thirty-two liters of soil inoculum of *Glomus etunicatus* (Becker and Gerdemann 1977) from pot cultures of *Sorghum vulgare* Pers. were mixed thoroughly with the limed soil, resulting in a spore count of approximately 1,200 per pot.

Sweetgum seeds from one upland mother tree from the Scull Shoals Experimental Forest in northeast Georgia were planted May 10, 1978. Seedlings were thinned to one per pot 3 weeks after germination. Nitrogen was added to the pots as ammonium sulfate ($(NH_4)_2SO_4$), ammonium nitrate (NH_4NO_3), or potassium nitrate (KNO_3) at levels equivalent to 140, 280, 560, 1,120, or 2,240 kg N/ha. Fertilizer, in aqueous solution, was added to the top of each pot with a graduated cylinder. The total amount of fertilizer applied to each pot was divided into eight equal applications, the first being made just prior to planting, the second 4 weeks after germination, and the remainder at 2-week intervals during the balance of the growing season.

Root collar diameter and total height were measured monthly from July through October. At harvest in mid-October, root samples were collected from each seedling for mycorrhizal assay. Samples were cleared and stained by a modification of the method of Phillips and Hayman (1970) in which lactophenol was substituted for chloral hydrate. Roots were then evaluated with a dissecting microscope. Percentage of roots colonized by the endomycorrhizal fungus and intensity of infection within roots were evaluated according to a classification scheme devised by Kormanik and others (1980). In that scheme, five classes of percentage root infection are used: class 1, 0–5 percent; class 2, 6–25; class 3, 26–50; class 4, 51–75; class 5, 76–100. The three categories of infection intensity are: 1, small infection sites widely scattered along the roots; 2, infection sites more uniformly distributed through the infested roots but rarely coalescing; 3, feeder roots almost solidly infected with no easily identified, isolated patches of infection. In this study, the percentages of hyphae, arbuscules, and vesicles comprising the infection were estimated as well.

Stem and leaf weights were obtained after drying to constant weight at 70°C. Plant N, P, K, Ca, and Mg levels were obtained for leaf and root samples by wet

TABLE 1. Effect of three sources of N on height growth of mycorrhizal sweetgum seedlings.[a]

N source-level (kg/ha)		July 6	August 2	September 1	October 2
		cm			
$(NH_4)_2SO_4$	140	2.8 de	5.5 gh	7.9 f	11.4 e
	280	3.6 bcd	9.3 abc	16.0 abc	27.6 ab
	560	3.7 bc	10.1 ab	19.1 a	31.3 a
	1,120	3.5 bcd	7.7 cdef	13.3 bcd	19.0 cd
	2,240	4.5 a	9.2 abcd	11.7 de	14.1 de
NH_4NO_3	140	3.1 cde	6.1 efgh	8.6 ef	10.4 e
	280	3.4 bcde	7.6 cdef	12.1 de	19.8 c
	560	3.9 ab	10.6 a	19.3 a	31.4 a
	1,120	3.1 cde	8.2 bcde	16.8 ab	26.1 b
	2,240	3.1 cde	7.2 defg	13.0 cd	17.2 cd
KNO_3	140	2.9 de	5.0 hi	7.1 fg	9.1 e
	280	3.1 cde	5.7 fgh	9.8 def	14.0 de
	560	3.4 bcd	7.5 cdefg	12.6 cd	17.2 cd
	1,120	3.4 bcde	7.9 cde	12.1 de	16.9 cd
	2,240	2.8 de	4.4 hi	3.1 g	([b])
Control		2.6 e	3.1 i	3.8 g	4.1 f

[a] Figures within a column with the same letter are not significantly different at the 5 percent level of probability by Duncan's multiple range test.
[b] Data not available because of seedling mortality.

digestion followed by detection of K, Ca, and Mg on a Perkin-Elmer 560 atomic absorption spectrophotometer (Agricultural Analytical Method AY-5; Perkin-Elmer Corp., Norwalk, Conn.) and detection of N (total Kjeldahl) and P on a Technicon Auto Analyzer II (Industrial Method Nos. 334-74A and 144-71A respectively; Technicon Instruments Corp., Tarrytown, N. Y.). Soil samples were collected one month prior to seedling harvest for determination of pH; NH_4-N (steam distillation, Bremner and Keeney 1966); NO_3-N (hot water-extractable) and total Kjeldahl N (Technicon Ind. Meth. Nos. 100-70W and 325-74W, respectively); P (weak acid-extractable and total, Isaac and Jones 1971); K, Ca, and Mg (weak acid-extractable, Perkin-Elmer Agric. Anal. Meth. AY-2).

Data were analyzed using the Statistical Analysis Systems (SAS) procedures of Barr and others (1976). Differences among treatments, as revealed by analysis of variance, were considered significant when $P < 0.01$.

Results and Discussion

Nitrogen source, level of N application, and their interaction had highly significant effects on seedling height (Table 1), stem diameter, stem weight, leaf weight, and total top weight. All growth parameters were greatest on seedlings treated with ammonium sulfate or ammonium nitrate at 560 kg/ha. The least effective fertilizer treatments were those at the lowest application level (140 kg N/ha). Poorest seedling growth occurred in the control treatment, in which no nitrogen was applied. Potassium nitrate at 2,240 kg N/ha killed all seedlings. Some seedling mortality also occurred among those seedlings exposed to 1,120 kg N/ha of potassium nitrate.

Mean growth values at each measurement date were, in general, significantly lower when potassium nitrate was the N source. At the N application level op-

TABLE 2. Chemical analysis of soil from treatment receiving three sources of N.[a]

N source-level (kg/ha)		NH_4-N	NO_3-N	Total mineral N (NH_4 + NO_3)	Extractable P[b]	K	Ca	Mg
		ppm						
$(NH_4)_2SO_4$	140	2.8	4.0	6.8	8.6	18.4	283.6	19.6
	560	4.1	9.0	13.1	7.3	11.2	183.6	8.8
	2,240	11.0	12.0	23.0	9.9	8.0	56.0	5.2
NH_4NO_3	140	2.5	9.0	11.5	7.3	18.8	341.2	23.2
	560	2.8	8.0	10.8	6.6	14.4	249.6	14.8
	2,240	6.6	33.0	39.6	7.9	8.4	86.0	6.8
KNO_3	140	2.7	7.0	9.7	7.6	57.6	327.6	22.0
	560	2.8	18.0	20.8	6.1	198.0	286.8	15.6
	2,240	3.0	15.0	18.0	6.4	345.6	228.4	11.6
Control		3.5	2.0	5.5	9.1	22.4	382.0	28.8

[a] Each figure represents the value of a composite sample consisting of four individual samples selected at random within a given treatment.
[b] Weak acid-extractable phosphorous.

timum for growth (560 kg N/ha), the level of soil mineral nitrogen (NH_4-N + NO_3-N) in pots fertilized with potassium nitrate was comparable to that in pots fertilized with ammonium nitrate or ammonium sulfate (Table 2). This indicates that the poor growth of seedlings fertilized with potassium nitrate was not due to excessive leaching of nitrates. Preferential uptake of NH_4^+ over NO_3^- by seedling roots, hyphae of the VA symbiont, or both may be responsible in part for the superior growth obtained with NH_4-N. Although NH_4-N is known to be a major source of N for some mycorrhizal fungi, it is not known whether *Glomus etunicatus* or sweetgum seedlings exhibit nitrogen form preferences. The mycorrhizal control seedlings (no supplemental nitrogen) attained mean height and mean root-collar diameter values of only 4.1 cm and 1.3 mm, respectively. This lack of growth response is similar to that exhibited by nonmycorrhizal sweetgum seedlings grown at soil P levels of less than 45 ppm by Bryan and Kormanik (1977), Kormanik and others (1977a) and Schultz and others (1979). These authors showed that mycorrhizal sweetgum seedlings grown in soils with extractable-P levels of 8-45 ppm all grew equally well, but within this P range nonmycorrhizal seedlings seldom exceeded 5 cm in height. Extractable soil phosphorus levels of 7–11 ppm in the present study were high enough to produce large mycorrhizal seedlings, but satisfactory growth occurred only when adequate nitrogen was available. This agrees with data reported by Koucheki and Read (1976) in which a growth response in *Festuca ovina* L. to increasing soil phosphorus levels was obtained only when nitrogen was present in sufficient amounts. Since mycorrhizal root systems are able to adequately supply seedling phosphorus needs even at low soil P concentrations, nitrogen availability is probably a more critical factor than phosphorus availability in achieving optimum growth of mycorrhizal sweetgum in forest nurseries.

Nitrogen source, level of N application, and their interaction had highly significant effects on mycorrhizal development and arbuscule formation (Table 3). Treatments with the largest growth response were among those with greatest mycorrhizal development. Lowest infection percentages were recorded for seedlings receiving the highest levels of N and for those receiving no supplemental

TABLE 3. Effect of N from three sources of mycorrhizal infection in sweetgum.

N source-level (kg/ha)		Infection	Intensity rating[a]	Arbuscules
		percent		*percent*
$(NH_4)_2SO_4$	140	79.2 a[b]	2.17 cd	38.17 cd
	280	86.6 a	2.75 ab	41.83 bcd
	560	79.2 a	3.00 a	25.25 ef
	1,120	48.4 b	2.33 bc	20.58 fg
	2,240	27.1 c	1.73 de	4.00 h
NH_4NO_3	140	80.6 a	2.42 bc	34.92 cde
	280	77.8 a	2.33 bc	51.67 ab
	560	82.2 a	2.75 ab	40.58 bcd
	1,120	74.8 a	2.75 ab	62.83 a
	2,240	52.8 b	2.67 abc	10.92 gh
KNO_3	140	74.8 a	2.17 cd	33.17 de
	280	85.0 a	2.67 abc	52.58 ab
	560	88.0 a	2.58 abc	45.92 bc
	1,120	86.2 a	2.50 abc	58.80 a
	2,240	—	—	—
Control		45.4 b	1.50 e	59.83 a

[a] 1.0 = low intensity; 2.0 = medium intensity; 3.0 = high intensity.

[b] Figures within a column with the same letter are not significantly different at the 5 percent level of probability by Duncan's multiple range test.

nitrogen. Highest infection intensities were found in root samples from seedlings grown at N application levels optimum for growth. Arbuscule formation was poorest in seedlings grown at the highest N level. Very few vesicles were observed in any treatment.

Level of N application strongly influenced N content of leaf and root samples (Table 4). Assay of leaves or roots for N content may have value for predicting N fertilizer needs of sweetgum seedlings. Since best growth was obtained with nitrogen additions of 560 kg/ha, the data indicate that seedlings with leaf N levels less than 20 mg/g or root N levels less than 10 mg/g may benefit from additional nitrogen.

Comparison of N sources showed that when a given large amount of N was applied, ammonium sulfate gave greater root and leaf N contents than did ammonium nitrate or potassium nitrate (Table 4). This may indicate that mycorrhizal sweetgum seedlings preferentially take up NH_4-N over NO_3-N. Soil nitrogen data (Table 2) suggested that conversion of NH_4-N to NO_3-N by microbial nitrofication processes was limited in soil receiving high levels of ammonium sulfate. Almost half of soil N was in the ammonium form 2 weeks after addition of the highest level of ammonium sulfate. Limited nitrification was probably a result of low soil pH. In mid-September, the mean soil pH for pots receiving the three highest levels of ammonium sulfate was 4.6–4.8. Mean soil pH in pots fertilized with ammonium nitrate or potassium nitrate at the three highest levels was 4.8–5.6 and 6.9–7.0, respectively.

Concentrations of P, K, Ca, and Mg in leaf and root samples (Table 4) were, in general, inversely correlated with N content of leaves and roots and with level of N applied to the soil. A notable exception was the positive correlation observed between root and leaf K and N levels of seedlings fertilized with potassium nitrate, which would be expected given the chemical composition of that fertilizer. Cationic and anionic competition would seem to explain much of the decrease of

TABLE 4. Chemical analysis of seedling tissues from treatments receiving three sources of N.

N source-level (kg/ha)		Nitrogen		Phosphorus		Potassium		Calcium		Magnesium	
		Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Root
		mg/g									
$(NH_4)_2SO_4$	140	15.9 h[a]	5.6 g	1.8 a	1.9 a	8.7 cd	8.2 c	6.9 ab	6.2 abc	0.9 b	1.4 a
	280	17.8 fg	9.5 ef	1.3 b	1.4 bcd	7.6 cd	7.3 cd	5.5 b	6.3 ab	0.9 b	1.4 a
	560	20.6 de	13.6 c	1.2 bc	1.3 cde	6.4 d	6.2 de	4.4 c	5.1 bc	0.6 de	1.1 bcd
	1,120	24.0 b	17.8 b	1.0 cd	1.0 f	6.4 d	4.7 f	3.9 cd	3.2 e	0.5 ef	0.7 f
	2,240	28.4 a	21.7 a	0.9 d	0.8 g	5.3 d	2.4 g	3.4 d	1.9 f	0.6 de	0.4 g
NH_4NO_3	140	15.8 h	5.4 g	1.5 ab	1.9 a	8.6 cd	7.8 cd	7.7 a	7.0 ab	1.2 a	1.3 ab
	280	17.7 fg	8.8 f	1.3 b	1.5 abc	8.5 cd	7.7 cd	6.1 b	7.1 a	1.1 a	1.3 ab
	560	17.7 fg	10.6 e	1.1 bc	1.2 de	7.0 d	5.9 de	5.6 b	5.7 bc	0.8 c	1.2 bc
	1,120	19.4 ef	12.1 d	1.1 bc	1.2 de	8.1 cd	5.7 e	4.4 c	4.9 bc	0.6 de	1.0 cd
	2,240	23.1 bc	14.8 c	0.9 d	0.9 fg	8.8 c	3.9 f	3.6 d	3.4 de	0.5 ef	0.6 f
KNO_3	140	16.1 gh	5.7 g	([b])	—	—	—	—	—	—	—
	280	19.0 ef	9.1 f	1.6 a	1.7 ab	16.1 b	10.4 b	5.6 b	5.4 bc	1.0 ab	1.0 cd
	560	21.4 cd	10.9 de	1.3 b	1.4 bcd	15.1 b	11.1 b	4.1 cd	4.5 c	0.7 cd	0.9 e
	1,120	22.2 bcd	10.8 de	1.3 b	1.5 abc	18.8 a	13.9 a	3.4 d	1.9 f	0.4 f	0.7 f
	2,240	—	—	—	—	—	—	—	—	—	—
Control		11.3 i	5.2 g	—	—	—	—	—	—	—	—

[a] Figures within a column with the same letter are not significantly different at the 5 percent level of probability by Duncan's multiple range test.
[b] Data not available because of insufficient plant material for nutrient analyses.

plant and soil P, K, Ca, and Mg brought about by large applications of N (Hiatt and Leggett 1974). Ionic competition would not only involve antagonism between NH_4^+ and K^+, Ca^{++}, and Mg^{++} ions, and between NO_3^- and HPO_4^{--} ions for absorption by plant roots, but would also extend to soil exchange sites, especially in the case of cations. Soil chemical data (Table 2) show a greater loss of cations, especially Ca^{++}, from soil in treatments receiving N solely in the cation (NH_4^+) form. With potassium nitrate, large inputs of K^+ ion may be responsible for decreasing soil calcium levels. Geraldson (1967) reported diminishing Ca availability with increasing levels of K or NH_4-N in soils.

Phytotoxicity in seedlings exposed to 1,120 or 2,240 kg N/ha as potassium nitrate is believed to have been the result of nutritional imbalances brought about by excessive additions of K to the soil (Geraldson 1957). Symptoms preceding mortality were a gradual blackening of leaves beginning at the leaf margin and progressing inward, and the appearance, in most cases, of interveinal black spots. Symptoms appeared earliest in the season in seedlings receiving the highest level of potassium nitrate.

Seedlings given ammonium sulfate at the 2,240 kg N/ha level had the greatest mean height of any treatment when first measured on July 6, but within 3 weeks most had ceased height growth completely. Foliage of seedlings in this treatment became very dark green and flaccid, indicating ammoniacal-N toxicity (Bennett 1974). By the third week in September, the foliage of all seedlings receiving 2,240 kg N/ha as ammonium sulfate was extremely dark (7.5 GY 4/6 to 2.5 G 3/4, compared to 7.5 GY 5/6 for normal seedlings, Munsell Plant Color Charts). Foliage of seedlings receiving 2,240 kg N/ha as ammonium nitrate was also appreciably darker than normal, though not as dark as seedlings fertilized with the same level of N as ammonium sulfate. Seedlings fertilized with ammonium nitrate at 2,240 kg N/ha also ceased height growth prematurely, though not until mid-August.

Conclusions

Since this study was conducted with a heavily irrigated, loamy sand typical of many southeastern forest nurseries, these findings may be applicable to those nurseries that produce sweetgum seedlings. Although both ammonium sulfate and ammonium nitrate at 560 kg N/ha gave maximum growth responses, the latter had less tendency to acidify soil. This level of application included division of the total amount into eight equal applications made at regular intervals throughout the growing season. Since maximum mycorrhizal development was achieved in those treatments with the largest growth response, application of nitrogen at optimum levels for growth should result in production of sweetgum planting stock of maximum size with well-developed mycorrhizal root systems.

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