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The Influence of Vesicular-Arbuscular Mycorrhizae on the Growth and Development of Eight Hardwood Tree Species

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Abstract
Eight hardwood forest species were grown in fumigated soil without vesicular-arbuscular mycorrhizal (VAM) fungi or in soil infested with either Glomus fasciculatus (GF), a mixture of Glomus mosseae and G. etunicatus (GM), or a mixture of several fungal species in the genera Glomus and Gigaspora (GG). With the exception of sugar maple, VAM development increased stem weight of seedlings by 2- to 80-fold over nonmycorrhizal controls. Root weight of all seedlings was increased by 4- to 70-fold by VAM. Generally, GF stimulated more seedling growth than other fungi. Laboratory assays of the root samples indicated that feeder root infection by the fungi varied from 55 to 85 percent, but generally there were no significant differences among the VAM treatments within tree species. Differences among hosts were observed in the amount of hyphae, arbuscules, and vesicles produced by the fungi, which could be attributed to growth and development characteristics among hosts and VAM fungi. The data suggest that high-quality seedling stock of these hardwood tree species can be obtained in nurseries where cultural practices in the nursery encourage VAM development.

Keywords
Nursery practices, black cherry, black walnut, boxelde, green ash, red maple, seedling production, sugar maple, sweetgum, sycamore

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ABSTRACT. Eight hardwood forest species were grown in fumigated soil without vesicular-arbuscular mycorrhizal (VAM) fungi or in soil infested with either *Glomus fasciculatus* (GF), a mixture of *Glomus mosseae* and *G. etunicatus* (GM), or a mixture of several fungal species in the genera *Glomus* and *Gigaspora* (GG). With the exception of sugar maple, VAM development increased stem weight of seedlings by 2- to 80-fold over nonmycorrhizal controls. Root weight of all seedlings was increased by 4- to 70-fold by VAM. Generally, GF stimulated more seedling growth than other fungi. Laboratory assays of the root samples indicated that feeder root infection by the fungi varied from 55 to 85 percent, but generally there were no significant differences among the VAM treatments within tree species. Differences among hosts were observed in the amount of hyphae, arbuscules, and vesicles produced by the fungi, which could be attributed to growth and development characteristics among hosts and VAM fungi. The data suggest that high-quality seedling stock of these hardwood tree species can be obtained in nurseries where cultural practices in the nursery encourage VAM development. FOREST SCI. 28:531–539.

ADDITIONAL KEY WORDS. Nursery practices, seedling production, sugar maple, red maple, sweetgum, black walnut, green ash, boxelder, sycamore, black cherry.

MANY COMMERCIALLY IMPORTANT HARDWOOD FOREST TREES are hosts for fungi that form vesicular-arbuscular mycorrhizae (VAM). Little work has been directed toward determining whether these fungi can be manipulated to improve seedling quality in forest tree nurseries. Recent work, however, indicates that these fungi can be a significant factor in quality seedling production of sweetgum in nurseries (Bryan and Kormanik 1977, Kormanik and others 1977b, South 1977). Kormanik and others (1977a) reported large differences in growth among half-sib progeny from eight mother trees which were either nonmycorrhizal or mycorrhizal with a mixture of the fungi *Glomus mosseae* (Nicol. & Gerd.) Gerdemann & Trappe and *Glomus etunicatus* Becker & Gerdemann. Nonmycorrhizal sweetgum seedlings grown in soil containing less than ca 40 ppm of extractable soil phosphorus (Bray II) were severely stunted, a response similar to that of nonmycorrhizal citrus seedlings (Kleinschmidt and Gerdemann 1972).

Seedling development of hardwood species that normally form VAM has not been satisfactory in forest tree nurseries and, consequently, seedling quality re-

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mains a major problem in artificial establishment of hardwood plantations. This problem could be due to lack of adequate VAM as has been found with sweetgum.

The purpose of this study was to determine whether a significant VAM fungi × hardwood host interaction exists among some important forest species, and to explore correlations in mycorrhizal morphological features with seedlings exhibiting diverse seasonal growth patterns.

Materials and Methods

Seed were collected from eight hardwood species: boxelder (*Acer negundo* L.), red maple (*A. rubrum* L.), sugar maple (*A. saccharum* Marsh.), green ash (*Fraxinus pennsylvanica* Marsh.), black walnut (*Juglans nigra* L.), sweetgum (*Liquidambar styraciflua* L.), sycamore (*Plantanus occidentalis* L.), and black cherry (*Prunus serotina* Ehrh.). All seed, except that from sugar maple, black cherry, and black walnut, were collected in northeast Georgia. Seed of sugar maple, black walnut, and black cherry came from Vermont, North Carolina, and Tennessee, respectively. The sweetgum seed were stratified in water at 2° to 4°C for 24 days prior to sowing and seed of the other seven species were stratified according to recommended procedures (USDA FS 1974).

The meter square microplots described earlier (Kormanik and others 1981) were filled with equal volumes of a soil mixture fumigated with Dowfume MC-2 (Dow Chemical Co., Midland, Mich.) at recommended rates. The soil mixture consisted of a sandy loam forest soil, sand, and finely ground pinebark. Analysis of this mixture before fertilizer treatments were added revealed the following amounts of extractable ions in kg/ha: NO_3-N, 39; P, 26; K, 77; and Ca, 366. Hydrated lime ($Ca(OH)_2$) was added to the soil in each microplot to bring elemental calcium up to the equivalent of 1,120 kg/ha. All plots also received 280 kg/ha of a commercial 10-10-10 fertilizer. All plots 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.

All mycorrhizal infested microplots were inoculated with two liters of coarsely chopped sorghum roots, *Sorghum bicolor* (L.) Monench (Shallu.), from pot cultures containing (1) mixed cultures of *Glomus mosseae* and *G. etunicatus* (GM), (2) *G. fasciculatus* (Thaxter) Gerd. and Trappe (GF), or (3) mixed cultures of several *Glomus* and *Gigaspora* species (GG). Although all pot cultures were approximately 9 months old, the spore counts varied considerably among the fungal treatments. The total spores added per microplot were as follows: GM 850, GF 6600, and GG 2650. The assay of pot cultures and incorporation into the microplots are fully described elsewhere (Kormanik and others 1981). Briefly, the inoculum was uniformly spread on the soil surface and thoroughly worked into the top 15 to 20 cm of soil. Root washings were obtained from the pot cultures of the three different inoculum sources to standardize the rhizosphere microflora at the time of sowing. The root washings were passed through a 35 mesh sieve and then filtered through Whatman No. 1 paper. Each mycorrhizal treatment received leachate from the two other symbiont treatments while the control microplots received leachate from all three symbionts. Seed were sown during the last week of May 1977.

The experimental design was a randomized block design with four mycorrhizal treatments. Each treatment had five microplots, each containing five seedlings of the eight hardwood species. There were 40 planting locations in each microplot and each of the eight species were randomly assigned to five of these locations. Only two seed of walnut were planted at each designated spot, but six to eight seed of the other seven species were planted at each spot. Seed were covered with 0.5 cm of 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 diameters were measured and root samples were collected from each seedling for VAM assay. Root and top weights were obtained after drying to a constant weight at 70°C. Root samples for VAM assay were collected from 3 to 7 different positions on the root system depending on its development. 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. The presence or absence of VAM was determined by using a new procedure (Kormanik and others 1980) that eliminates the toxic phenols from the root staining and clearing solution. 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 upon 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 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.

Results and Discussion

Several points need to be clarified before specific results are discussed. First, the experimental design precluded maintenance of optimal growing conditions for each hardwood species; some may have been affected by interspecies competition or by the high temperatures characteristic of central Georgia. Randomization of species location within the plots was helpful in reducing interspecies competition, but abnormally high temperature effects were especially pronounced with black cherry and sugar maple. Second, absolute size of the seedlings among the eight species cannot be directly compared since each species has some finite potential for growth in nurseries even under optimum conditions. Third, although the same volume of inoculum from each symbiont source was added to the plots, the spore density varied among the VAM symbiont treatments. Adequate inocula were added with all VAM treatments to result in acceptable root infection with all symbionts.

Seedling Growth Responses to Different Symbionts.—Only 40 percent of the black cherry seedlings survived regardless of VAM treatment. Early seedling establishment was good, but sporadic mortality occurred in June and July when daily temperatures always exceeded 34°C. None of the nonmycorrhizal seedlings grew as fast as those with VAM (Table 1). Growth of VAM seedlings, however, was quite variable. The black cherry seed collection was a composite from eight different mother trees that represented a rather broad geographical range as well as a broad elevational distribution. This genetic and geographical variability may account for the growth responses observed here. None of the nonmycorrhizal black cherry seedlings developed much beyond the primary leaf stage, but some of the individual GM seedlings did not grow much more. The significant difference in seedling growth (Table 1) among the three VAM treatments may represent a host preference for a given symbiont, but may also indicate symbiont adaptability to local environmental conditions.

Survival of sugar maple seedlings was between 96 and 100 percent regardless of treatment, but none of the seedlings attained plantable size. The first-year growth of these seedlings, however, was similar to first-year growth obtained in many forest tree nurseries (USDA FS 1974). Sugar maple seedlings are extremely

sensitive to high temperatures and even in its natural range must be provided with shade during the early part of the growing season until they become established. The most important data with this species is the relatively large differences in root biomass between the VAM and the nonmycorrhizal seedlings (Table 1). Further research is needed under optimum nursery conditions within this species' natural range to more accurately assess the influence of VAM on seedling production.

There was a significant difference (0.05 level) in survival between the nonmycorrhizal and VAM black walnut seedlings. Only 30 percent of the nonmycorrhizal black walnut seedlings survived compared to 65 percent survival of those with VAM. There was no significant difference in survival among the three VAM treatments. Both VAM and nonmycorrhizal seedlings grew equally well during the first half of the growing season, presumably due to the large carbohydrate reserves in the nuts. However, the foliage of the nonmycorrhizal seedlings became chlorotic by mid-August and the leaves abscised several weeks later, thus the absence of foliar data (Table 1). The VAM seedlings did not become chlorotic and retained their foliage until they were harvested. Root data (Table 1) suggested that photosynthates of the VAM seedlings were utilized in root biomass rather than in aboveground biomass production. This increase in root size associated with VAM could improve the outplanting performance of seedlings. Top desiccation and stem dieback from lack of water is a severe problem in hardwood seedlings immediately following outplanting. Enhanced root moisture relationship has been correlated with VAM infection (Safir and others 1972).

The development of the other five hardwood species, regardless of symbiont treatment, was quite satisfactory for outplanting stock (Table 1). None of the nonmycorrhizal seedlings from any of these species were large enough for outplanting. Seedlings with VAM formed by the GM symbionts were consistently smaller than those with other VAM symbionts. Seedlings with VAM formed by GF were rather consistently the largest but the differences were not always statistically significant (Table 1). The GF isolate has been used for 6 years at this location. Characteristically, seedlings grown in plots infested with it exhibit an early season height advantage over most other VA mycorrhizal fungi used for comparative purposes. These early season differences are normally not maintained and other VAM fungi are usually equally effective in affecting seedling size under our test conditions. This year (1977) with such a long sustained period when temperatures were constantly in the mid-30°C range, we did not observe the leveling out of height growth we expect in August and September when temperatures were still above normal. Thus, we feel that the GF infected seedlings just maintained their early height advantage attained before the high temperature regimes started.

We feel that the consistently poorer performance of the GM treatment was probably a temperature mediated response. It was readily apparent to us when spore counts from the GM inoculum were made that there were more *G. etunicatus* spores in the sample than *G. mosseae* spores. No attempt was made to estimate the percentage of spores for either fungus because we had no experience or data at that time that suggested one species would be more effective than the other. Subsequent work at this nursery location, however, indicates that this specific *G. etunicatus* isolate, originally obtained from Illinois, produces erratic results in tests in this location. Its effectiveness seems to be adversely affected by elevated soil phosphorus levels as well as abnormally high temperatures during the growing season. Unfortunately, spore populations were not obtained at the end of the growing season, but based on later experiences, most of the effectiveness of this fungus mixture might be attributed to the *G. mosseae* portion of the

TABLE 1. Growth responses for eight hardwood species grown in a mixture of soil-sand-bark containing Glomus fasciculatus *(GF),* Glomus *spp. (GM), a mixture of VAM fungi (GG), or no VAM fungi (CN).*

Species	Height	Diameter	Root weight	Stem weight	Leaf weight
	cm	*cm*	*g*	*g*	*g*
Black cherry					
GF	70.0a[1]	0.69a	14.7a	8.4a	6.2a
GM	18.3c	0.28b	2.8a	1.6b	1.8b
GG	44.9b	0.60a	10.7a	6.6a	6.4a
CN	12.8c	0.15c	0.2a	0.1b	0.1b
Boxelder					
GF	45.1a	1.01a	12.5a	7.8a	3.4a
GM	36.2b	0.86b	10.5a	6.2a	3.7a
GG	45.3a	0.98ab	12.0a	7.9a	3.9a
CN	12.8c	0.32c	0.3b	0.3b	0.1b
Green ash					
GF	37.4a	0.86a	13.1a	5.9a	4.0ab
GM	27.9b	0.70b	8.8b	3.9b	3.2b
GG	34.9a	0.86a	13.4a	6.4a	5.2a
CN	6.7c	0.20c	0.2c	0.1c	0.1c
Red maple					
GF	35.8a	0.66a	4.9a	2.2a	3.3a
GM	34.8a	0.63a	5.7a	3.2a	4.6a
GG	33.3a	0.59a	4.0a	2.7a	3.6a
CN	8.3b	0.24b	0.2b	0.1b	0.1b
Sugar maple					
GF	9.3a	0.33a	1.8a	0.3b	0.9a
GM	6.8b	0.26b	0.9b	0.2c	0.4b
GG	11.1a	0.33a	2.2a	0.5a	1.1a
CN	7.1b	0.25b	0.4c	0.4a	—
Sweetgum					
GF	29.6ab	0.70ab	6.1a	3.0a	3.0b
GM	25.8a	0.60b	5.5a	3.1a	3.5ab
GG	32.9a	0.72a	6.5a	4.3a	4.7a
CN	4.4c	0.20c	0.2b	0.1b	0.1c
Sycamore					
GF	66.6a	1.29a	35.4a	21.0a	14.9a
GM	57.2b	1.19ab	29.7ab	18.8a	12.4a
GG	53.9b	1.09b	24.9b	15.9a	12.8a
CN	19.9c	0.42c	1.8c	1.0b	0.8b
Black walnut					
GF	24.8a	0.79a	75.4b	5.9a	4.3a
GM	20.9b	0.62b	35.0c	3.3a	2.8a
GG	25.7a	0.79a	80.0a	7.0a	4.8a
CN	21.0ab	0.57b	14.9d	2.1a	—

[1] Values followed by the same letter within species are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

TABLE 2. Type and degree of vesicular-arbuscular mycorrhizal infection of eight species of hardwoods by Glomus fasciculatus *(GF), a mixture of* Glomus *spp. (GM), and a* Glomus *and* Gigaspora *spp. mixture (GG).*

Mycorrhizae	Infection	Intensity	Hyphae	Arbuscules	Vesicles
			Percent		
GF	76a[1]	2.6a	62c	29a	8.7a
GM	74a	2.5b	70b	26ab	3.2b
GG	76a	2.4b	74a	24b	0.9c

[1] Values in the same column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

inoculum. Late-season VAM development appeared adequate within the GM treatment but it may have taken longer to become established than the other two VAM treatments resulting in less growth stimulation in this test.

It was observed that those species that developed fibrous root systems instead of stronger taproots had less pronounced growth differences among the VAM treatments. If spore density was a significant factor in the GM response, the seedlings growing in this treatment could be expected to have become infected at a slower rate than seedlings from the other VAM treatments. There is no doubt, however, that significant improvement in seedling grade could be achieved with boxelder, green ash, red maple, sweetgum, and sycamore in nurseries if nursery practices were altered to include provision for adequate VAM inoculum in the soil.

VAM Fungal Infection and Morphology Interactions with Hosts.—VAM infection characteristically follows a sequential development from hyphae to arbuscules to vesicles. This development may be related to seasonal development from seed germination through maturity or dormancy. In annual plants this development may be more rigidly fixed than with perennial woody plants that have a permanent root system. In this test, the plants were harvested before leaf abscission and onset of winter dormancy. This could have affected the fungal characteristics in roots. Other work (Kormanik, unpublished data) indicates that while the percentage of roots with VAM infection may remain constant during the growing season, the fungal morphology may vary. During the peak of seedling growth when nutrient demands are at a maximum, arbuscule percentages are high, but these are significantly reduced throughout the dormant season.

Table 2 contains the infection and fungal morphological data for the three symbionts with all tree data pooled. There are no significant differences in the percentage of roots with VA mycorrhizal infection among fungal symbiont treatments and only small differences in intensity of infection within the roots. These data would tend to substantiate nonspecificity of VAM symbionts but may not have any bearing on the relative effectiveness of the different fungi. The differences in fungal morphology, expressed as the percentage of total infection made up of hyphae, arbuscules, and vesicles, may be controlled more by the fungi than host but our data indicate that the host affect can be quite substantial.

Gigaspora species develop vesicles external to the root in the soil (Gerdemann and Trappe 1974) and these may have been lost during the root excavation and processing. Thus, the significant differences in morphological data for the GG symbiont might not reflect real biological differences but rather limitations in sample procedures. Furthermore, one would not expect all *Glomus* species to develop the number of vesicles which are characteristically produced by *G. fas-*

TABLE 3. Inoculation response of eight hardwood species grown in a mixture of soil-sand-bark containing Glomus fasciculatus *(GF),* Glomus *spp. (GM), or a mixture of VAM fungi (GG).*

Species	Infection	Intensity	Hyphae	Arbuscules	Vesicles
			Percent		
Black cherry					
GF	78.1a[1]	2.88a	50.1a	43.4a	6.5a
GM	54.7a	2.19a	60.0ab	36.8a	3.2a
GG	73.2a	2.57a	76.9b	22.5a	0.6a
Boxelder					
GF	71.5b	2.00b	65.8a	29.1a	5.1a
GM	83.1a	2.63a	65.9a	32.9a	1.1b
GG	76.6ab	2.13b	72.3a	26.9a	0.8b
Green ash					
GF	81.5a	3.0a	60.5a	31.5a	8.0a
GM	84.1a	3.0a	80.7b	18.8b	0.5b
GG	83.3a	2.9a	75.6b	23.9ab	0.5b
Red maple					
GF	68.5a	2.16a	65.0a	31.8a	3.2a
GM	71.3a	2.25a	66.2a	33.5a	0.3b
GG	66.7a	1.92a	79.3b	20.3b	0.4b
Sugar maple					
GF	74.5a	2.2a	79.2a	13.8b	7.0a
GM	67.3a	1.8b	90.4a	6.6c	3.0b
GG	72.9a	1.9ab	77.6a	21.0a	1.4b
Sweetgum					
GF	67.5a	3.0a	75.2a	20.7a	4.1a
GM	68.3a	2.5b	67.5ab	30.2b	2.3ab
GG	80.5a	2.7b	62.1b	37.4b	0.5b
Sycamore					
GF	86.5a	3.0a	42.6a	45.8a	11.6a
GM	84.5a	2.9a	64.6b	34.5b	0.9b
GG	82.2a	2.8a	79.0b	20.7c	0.3b
Black walnut					
GF	84.6a	3.0a	42.9a	27.9a	29.2a
GM	72.5a	2.7a	58.3b	21.2a	20.5a
GG	71.3a	2.7a	78.0c	18.7a	3.3b

[1] Values within species followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

ciculatus (Gerdemann and Trappe 1974), thus the differences between the GM and GF symbionts may be simply a reflection of basic fungal differences.

Table 3 presents more comprehensive data on fungal morphology, with information for each species and symbiont treatment. There are few significant differences in percentages of infected roots and intensity of infection within roots among the symbionts and specific tree species. It is difficult to predict how important these infection parameters are when sampling was completed so late in the fall. The period during which the root system per se is infected by VAM fungi is probably of greater significance than the infection percentages at the end of the

growing season. Seedlings which become infected late in the growing season may have high infection percentages, but the mycorrhizal value to these seedlings would be less evident in terms of growth than to those infected early in the growing season.

Our data indicate that growth characteristics of tree species affect fungus morphology. For example, sycamore has indeterminate terminal growth and under optimum growing conditions, as in a nursery environment, stem elongation continues until the apical region is aborted by frost. This species would make continued demand for high levels of inorganic nutrients throughout the growing season and a larger percentage of arbuscules might be expected to occur in roots into the fall as a result of this nutrient demand. This was observed to occur here. The apices of sugar maple were essentially quiescent for most of the growing season and, therefore, the demand for high levels of inorganic nutrients was minimal. In this species there were few arbuscules observed.

The host effect on the VAM and the reverse relationship with black walnut were especially noteworthy and may indicate, as with sycamore and sugar maple, that while the physiological processes of a host plant may affect VAM fungi morphological development, the fungi are also affecting host development. In a typical nursery where walnut seedlings are grown, yearly fumigation is a normal procedure because of walnut's susceptibility to numerous soil-borne root pathogens. The effectiveness of soil fumigation determines the survival of VAM mycorrhizal fungi in a given nursery soil and this effectiveness can vary considerably depending on environmental and soil properties. In nurseries, walnut seedlings characteristically set their buds after 10 to 12 weeks and stem elongation is essentially completed in a single flush of short duration. In some cases, leaf chlorosis is apparent soon after stem elongation ceases and leaf abscission is completed by late August or early September. This pattern was observed in the nonmycorrhizal seedlings in this study. In other instances, leaves do not become chlorotic and remain functional until later in the fall and this latter leaf retention pattern occurred uniformly with our VAM seedlings. While there has been no satisfactory physiological explanation for differences in leaf retention in this species under nursery conditions, it is noteworthy that in this and two other trials at this location, walnuts with VAM have characteristically retained their foliage longer than did the nonmycorrhizal seedlings.

Since seasonal changes in fungal morphology may be controlled or influenced by the growth habit of the tree host, physiological or biochemical investigations must take into consideration the complete symbiotic association and not simply the tree host or the fungal symbiont. At any given time, the predominance of hyphae, arbuscules, or vesicles in roots could significantly affect inorganic chemical or other analytical analyses of plant tissue since these fungal structures have specific functions in mobilization and storage of various elements. Further research to clarify the basic physiology of this symbiotic relationship in trees is desirable to realize the full potential of VAM in forestry. The results from this study indicate, however, that the potential benefits from VAM in nursery seedling production are of such magnitude that cultural practice changes to favor VAM fungi appear justifiable.

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Imbibition, Desiccation, and Reimbibition Effects on Light Requirements for Germinating Southern Pine Seeds

T. E. Campbell

ABSTRACT. Slash (*Pinus elliottii* Engelm. var. *elliottii*) and loblolly (*P. taeda* L.) pine seeds were stratified, exposed to light, then placed in total darkness and air-dried to 30, 25, 20, 15, and 10 percent moisture. They were then reimbibed and half were germinated in continued darkness, the other half under light.

When total germination, days to reach 90 percent of total, and germination values were assessed, only germination values for loblolly pine in the dark were affected by desiccation and reimbibition. Light during germination increased all three measurement parameters of both species. FOREST SCI. 28:539–543.

ADDITIONAL KEY WORDS. Slash pine, loblolly pine, direct seeding, seed covering.

CONIFER SEEDS sown directly on a forest site or in a nursery for seedling production are often covered with shifting debris, mulch, or soil, all of which limit or prevent exposure to light during germination. After seeds are sown, complete germination is important for seed conservation, but prompt germination is essential to reduce the time of exposure to predators and adverse weather. Moreover, the greater the interval of exposure, the less likely they are to germinate at all.

Experience has shown that stratification of slash, loblolly, and shortleaf pine (*P. echinata* Mill.) seed usually increases rate and amount of germination. Exposure to light after imbibition and stratification is necessary for more rapid germination, and this light requirement is normally satisfied in routine handling procedures. Reduced germination will take place in total darkness if a high moisture content is maintained, but is increased by

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