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Growth of Longleaf and Loblolly Pine Planted on South Carolina Sandhill Sites

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ABSTRACT

Performance of longleaf (*Pinus palustris* Mill.) and loblolly pine (*P. taeda* L.) were compared 15–19 years after outplanting on 10 different sites in the sandhills of South Carolina. The study was established from 1988 to 1992 with bareroot seedlings artificially inoculated with *Pisolithus tinctorius* (Pt) or naturally inoculated with mycorrhizae in the nursery. A containerized longleaf pine treatment with and without Pt inoculation was added to two sites in 1992. Effects of the Pt nursery treatment were mixed, with a decrease in survival of bareroot longleaf pine on two sites and an increase in survival on another site. The containerized longleaf pine treatment substantially increased survival, which led to greater volume compared with bareroot longleaf pine. Loblolly pine yielded more volume than longleaf pine on all sites but one, where survival was negatively affected by fire. Depth of sandy surface horizon affected mean annual height growth of both loblolly and longleaf pine. Height growth per year decreased with an increase in sand depth for both species. Multiple regression analysis of volume growth (ft^3/ac per year) for both species indicated a strong relationship to depth of sandy soil and survival. After 15–19 years, loblolly pine has been more productive than longleaf pine, although longleaf pine productivity may be equal to or greater than that of loblolly pine on the soils with the deepest sandy surface layers over longer rotations.

Keywords: *Pinus palustris, Pinus taeda, Pisolithus tinctorius*, mycorrhizae, volume, containerized seedlings

Longleaf pine (*Pinus palustris* Mill.) was once the dominant pine species on dry upland soils of the southeastern United States, where a greater tolerance of fire and drought allowed longleaf pine to out-compete other, more aggressive species (Wahlenberg 1946, Outcalt 2000). Loblolly pine (*Pinus taeda* L.) has replaced longleaf pine as the dominant forest species in the South during the 20th century in part because of fire control and its rapid growth on a wide variety of sites (Schultz 1997). Although the commercial value of longleaf pine was high, foresters found the species difficult to regenerate both naturally and artificially (Wahlenberg 1946). The slow early growth and lower survival rate of longleaf pine led land managers to choose loblolly or slash pine for reforestation (Brockway et al. 2005); however, methods in longleaf pine seedling production and planting techniques have improved considerably in the past 40 years (Kush et al. 2004). These improvements were necessary before a large program to restore longleaf pine to the South was possible. Restoration of longleaf pine began on federal and state lands, which later expanded under incentive programs and state cost-share programs for private landowners (Brockway et al. 2005).

The Savannah River Site (SRS) is a National Environmental Research Park located near Aiken, South Carolina. The physiographic provinces of the SRS are predominately upper coastal plain and sandhills. Historically, most of the site was once a fire-maintained longleaf pine savannah that was cut over and farmed until the 1950s when the U.S. Atomic Energy Commission acquired the land (Kilgo and Blake 2005). The site was reforested with seed and seedlings that were available at that time, and much of the site was planted with loblolly pine and, to a lesser degree, slash pine (*Pinus elliottii* Engelm.). Reforestation of SRS with longleaf pine was limited because of low availability of seed, poor seedling quality, and low survival. It was not until the 1980s that techniques in longleaf pine production and establishment had improved enough to convert off-site slash pine to longleaf pine on excessively drained soils (Kilgo and Blake 2005).

One cultural technique tested during the 1980s was the addition of *Pisolithus tinctorius* (Pers.) Coker and Couch (Pt) ectomycorrhizae to seedlings for reforestation. These studies suggested that inoculating seedlings with Pt in the nursery provided positive responses in survival and growth for both longleaf pine (Hatchell and Marx 1987) and loblolly pine (Marx et al. 1988). An expanded study was installed from 1988 to 1992 on the SRS to assess the survival and growth of both longleaf and loblolly pine seedlings artificially inoculated with Pt on 10 different sites. An additional containerized longleaf pine treatment was added to the last two sites, established in 1992. The 4-year (5-year for site 5) results of this study were reported earlier (Cram et al. 1999); they showed that seedlings with naturally occurring mycorrhizae performed as well or better than seedlings inoculated with Pt. A comparison of growth between the tree species was not performed on the previously reported data because of physiological differences in early growth. Loblolly pine is recognized to have faster early growth, but with longer rotations,

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Table 1. Planting dates, soil series, and site preparation for loblolly and longleaf pine planting sites in South Carolina sandhills.

Site	Planting date	Soil series: depth of sandy soil[a]	Site preparation
1	January 1988	Blanton sand: 3.9 ft of sand	Chopped, burned, and hexazinone (1.5 lb/ac)
2	January 1988	Troup sand: 4.4 ft of sand	Chopped, burned, and hexazinone (2.5 lb/ac)
3	January 1989	Lakeland sand: 6.6 of sand	Chopped, burned, and hexazinone (2.5 lb/ac)
4	January 1989	**Wagram sand: 1.8 ft of sand** Blanton sand: 3.9 ft of sand	Chopped and burned
5	January 1990	Blanton sand: 3.9 ft of sand	Sheared and raked
6	January 1990	Blanton sand: 3.9 ft of sand	Chopped, burned, and hexazinone (2.5 lb/ac)
7	January 1991	Lakeland sand: 6.6 ft of sand	Chopped, burned, and hexazinone (2 lb/ac)
8	January 1991	**Fuquay sand: 1.8 ft of sand** Dothan sand: 0.6 ft of sand	Sheared, raked, and hexazinone (2.5 lb/ac)
9	January 1992	Blanton sand: 3.9 ft of sand **Lakeland sand: 6.6 ft of sand**	Burned and partially raked
10	January 1992	Troup sand: 4.4 ft of sand	Raked

[a] In sites with two soil series, boldface indicates the predominant soil type (Rogers 1990)

longleaf pine may be equally productive on some sites (Schultz 1997). Outcalt (1993) has found that longleaf pine can produce more wood than loblolly pine after 28 years on deep sandy soil. The objective of remeasuring the SRS sites was to determine relative productivity of loblolly and longleaf pine on a range of sandy soil types. The 10 sites were remeasured in 2007 at ages 15–19 for comparisons of growth, survival, and yield.

Methods

All seedlings were produced from 1987 to 1991 by the State of South Carolina at Taylor Nursery in Trenton and the State Creech Seed and Orchard-Container facility in Wedgefield. The longleaf pine seed sources were from South Carolina and Georgia. The improved loblolly pine seed sources were from the coast of South Carolina. The Pt bareroot seedlings were produced by applying vegetative inoculum at 3.52 oz (volume)/linear foot of seedbed (4 ft^2) just prior to sowing. The Pt containerized longleaf pines were produced using spores applied at 0.017 oz (mass)/1,000 seedlings just after seedling emergence. Only seedbeds and containerized seedlings with a Pt index of 50 or greater (Marx et al. 1984) were used for the Pt treatment in this study. The nursery methods used to produce the bareroot and container seedlings for the study were described in the data previously published by Cram et al. (1999).

Two sites each year from 1988 to 1992 were selected from stands that were clearcut the previous year. The criteria for selection were excessively drained sandy soils, little slope, with minimal compaction (Table 1). Each site was prepared for planting on the basis of its condition (Table 1). The treatments for all 10 sites consisted of planting loblolly and longleaf pine artificially inoculated with *P. tinctorius* (Pt) or naturally inoculated (Ni) with mycorrhizae in the nursery. Sites 9 and 10 included a longleaf pine container treatment with Pt or Ni. Trees on all sites were machine planted in a randomized complete block design with eight replications of plots. Each plot consisted of three rows of 50 trees each with rows 10 ft apart and a 6-ft tree spacing within rows.

Data on survival and growth were collected in the summer of 2007 from the middle rows (50 trees each) of the treatment plots. None of the 10 sites had been thinned. Diameters (in.) were measured at breast height (4.5 ft) for all live trees, and heights (ft) were taken on every fifth live tree without a broken top. The few trees encountered with broken tops were skipped, and the next live tree with an unbroken top was measured. Survival data reflect only trees that died from "natural causes," such as fire, lightning, or drought. The few trees removed by mechanical methods for access road projects were deleted from the data set. Tree volumes inside bark were based on equations by Bailey and Clutter (1970) for loblolly and Farrar (1981) for longleaf pine, which use diameter and height. Plot volumes were calculated by summing volumes for trees with height data and then multiplying by the ratio of total live trees to trees with height measurements.

The experimental design for the analysis of each site was a randomized complete block with a two-way treatment structure consisting of species (longleaf and loblolly pine) and mycorrhizae (Pt and Ni). On sites 9 and 10, where containerized longleaf pine was also planted, the species treatment included container longleaf pine as a third species treatment (the container could not be used as a third study treatment because it was not applied to loblolly pine). The statistical analysis of the data was performed using a linear mixed model approach for the individual tree variables (diameter, height, and survival) and per-acre variables (basal area and volume). Blocks were defined as random effects and mycorrhizal treatments, and the tree species were defined as fixed effects. Each site was analyzed separately because of the effects of differing site preparation, soil series, and year of planting. Significant differences were determined using a critical value of $\alpha = 0.05$. Linear regression was used to analyze the relationship between average tree diameter and depth of sandy soil for both tree species. Average tree height to depth of sandy soil was also analyzed by linear regression for both species. A multiple regression model was developed to investigate the relationship between volume production of bareroot seedlings (ft^3/ac per year) and survival, depth of sandy soil, and their interaction. Site 3 was excluded from the multiple regression analyses to avoid the confounding effects of an unplanned fire on survival that occurred in the 5th year after planting.

Results

The Pt treatment had no significant effect on diameter or height growth of longleaf or loblolly pine after 15–19 years. The only positive effect from Pt inoculation was on site 2 ($P = 0.016$), where survival was 89% with Pt compared with 79% with the Ni treatment. Pt had a significant negative impact on survival of bareroot longleaf pine on sites 9 and 10 (Table 2). Differences in survival between Pt and Ni trees for the other sites ranged from 1 to 7% and were nonsignificant.

Mean diameters of loblolly pine were greater than those of longleaf pine on all 10 sites, whereas mean heights of loblolly pine were greater on 6 of the sites (Tables 3 and 4). The relationship between height growth and the depth of sandy soil to a finer textured horizon

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Table 2. Percentage survival of 15-year-old longleaf and loblolly pines by seedling type and treatment with *P. tinctorius* or natural mycorrhizae planted on South Carolina sandhills.

Site	Species	Seedling type	Nursery treatment[a]	Survival (%)[b]
9	Longleaf pine	Container	Ni	86.9[a]
			Pt	83.0[a]
	Longleaf pine	Bareroot	Ni	63.1[b]
			Pt	43.3[c]
	Loblolly pine	Bareroot	Ni	66.8[b]
			Pt	72.6[ab]
10	Longleaf pine	Container	Ni	75.1[a]
			Pt	73.7[a]
	Longleaf pine	Bareroot	Ni	50.6[b]
			Pt	34.9[c]
	Loblolly pine	Bareroot	Ni	78.6[a]
			Pt	78.9[a]

[a] Nursery treatments: Pt, *P. tinctorius*; Ni, natural inoculated.
[b] Treatments within a site followed by the same letter are not significantly different at the Bonferroni adjusted 0.05 level (each pairwise comparison tested at the 0.05/15 = 0.0033 level); $n = 8$ blocks.

Table 3. Diameter, height, survival, and yield of bareroot longleaf and loblolly pine on South Carolina sandhills.[a]

Site	Species	Age	Diameter (in.)	Height (ft)	Survival (%)	Total basal area (ft^2/ac)	Total volume (ft^3/ac)[b]
1	Longleaf pine	19	5.2[b]	46.0	85.6[b]	159[b]	3,150
	Loblolly pine	19	5.8[a]	48.0	91.6[a]	220[a]	3,859
2	Longleaf pine	19	5.2[b]	43.5	82.0	154[b]	2,712[b]
	Loblolly pine	19	5.9[a]	44.4	85.6	204[a]	3,272[a]
3	Longleaf pine	18	4.8[b]	39.7[b]	80.3[a]	131	2,316
	Loblolly pine	18	6.1[a]	43.2[a]	46.6[b]	122	1,960
4	Longleaf pine	18	5.6[b]	47.3[b]	78.9	174[b]	3,427[b]
	Loblolly pine	18	6.9[a]	52.2[a]	83.5	275[a]	5,087[a]
5	Longleaf pine	17	5.0[b]	41.1[b]	71.9	124[b]	2,123[b]
	Loblolly pine	17	6.1[a]	44.9[a]	75.5	194[a]	3,224[a]
6	Longleaf pine	17	5.2[b]	42.1	68.1[b]	129[b]	2,325[b]
	Loblolly pine	17	5.8[a]	43.8	81.6[a]	198[a]	3,211[a]
7	Longleaf pine	16	4.5[b]	35.7	65.6[b]	94[b]	1,429[b]
	Loblolly pine	16	5.1[a]	35.3	84.4[a]	153[a]	2,053[a]
8	Longleaf pine	16	5.2[b]	38.4[b]	45.3[b]	84[b]	1,381[b]
	Loblolly pine	16	6.1[a]	45.3[a]	62.9[a]	163[a]	2,776[a]

[a] Treatments within a site and variable followed by different letters are significantly different at the 0.05 level. Least square means computed on a species basis are shown because the two-way factorial analysis did not result in a significant species by inoculum interaction; $n = 16$ (8 blocks × 2 plots).
[b] Volume of bole to 2 in. top inside bark is based on equations by Bailey and Clutter (1970) for loblolly pine and Farrar (1981) for longleaf pine.

was significant for both longleaf ($P = 0.0083$) and loblolly ($P = 0.0176$) pine. Height growth per year decreased with an increase in sand depth for both species (Figure 1). Depth of sandy soil did not significantly affect diameter growth.

Survival of loblolly pine was greater than that of bareroot longleaf pine on six sites (Tables 2 and 3). However, the survival of containerized longleaf pine was greater than that of bareroot loblolly pine on sites 9 and 10 (Table 2). Site 3 was the only planting where bareroot longleaf pine survival was substantially greater than loblolly pine because of mortality caused by a fire that occurred during the 5th year. This reduction in survival of loblolly pine from fire damage also resulted in the only numerically lower total volume compared with longleaf pine. The total volume of longleaf pine was significantly less than that of loblolly pine on all other sites except site 1. On sites 9 and 10, the containerized longleaf pine was significantly greater in basal area than bareroot longleaf pine, but it was not different in diameter or height (Table 4).

Multiple regression analysis of volume production (ft^3/ac per year) for both bareroot longleaf pine and loblolly pine show that

Table 4. Diameter, height, and yield of 15-year-old loblolly and longleaf pine by seedling type from two sites on South Carolina sandhills.[a]

Site	Species	Seedling type	Diameter (in.)	Height (ft)	Total basal area (ft^2/ac)	Total[b] Volume (ft^3/ac)
9	Longleaf	Container	4.6[b]	35.2[b]	121[b]	1829[b]
	Longleaf	Bareroot	4.7[b]	35.1[b]	80[c]	1208[b]
	Loblolly	Bareroot	5.6[a]	38.9[a]	160[a]	2488[a]
10	Longleaf	Container	4.8[b]	35.9[b]	121[b]	1837[b]
	Longleaf	Bareroot	5.0[b]	36.9[b]	76[c]	1259[c]
	Loblolly	Bareroot	5.8[a]	40.9[a]	183[a]	2743[a]

[a] Treatments within a site and variable followed by the same letter are not significantly different at the Bonferroni adjusted 0.05 level (each pairwise comparison tested at the 0.05/3 = 0.0167 level). Least square means computed on a species basis are shown because the two-way factorial analysis did not result in a significant species by inoculum interaction; $n = 16$ (8 blocks × 2 plots).
[b] Volume of bole to 2 in. top inside bark is based on equations by Bailey and Clutter (1970) for loblolly pine and Farrar (1981) for longleaf pine.

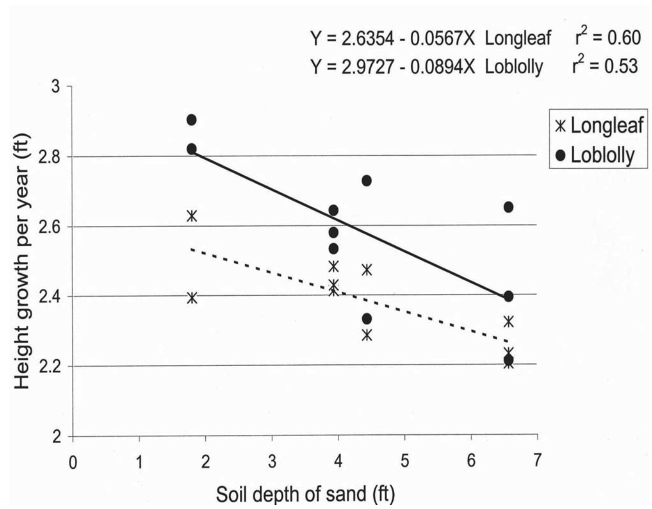

Figure 1. Average height growth per year (bareroot) as related to the depth of sandy soil for longleaf and loblolly pine on 10 sites in the South Carolina sandhills.

survival and depth of sandy soil affected stem volume (Table 5). The interaction of survival with depth of sand on volume accumulation was also significant. The volume of both species appears to be affected more by survival when trees are on shallow, sandy soils (1.8 ft deep).

Discussion

Methods for establishment of longleaf pine in the southeast have vastly improved since Wahlenberg (1946, p. 136) noted that it was "almost impossible to obtain early height growth or satisfactory survival in plantations" in the southeastern longleaf belt. The majority of longleaf pine seedlings in this study initiated height growth by the second year after outplanting (unpublished data), and current stocking levels are adequate to meet the goals of reforestation (Kilgo and Blake 2005). Survival rates of the bareroot longleaf pine from sites 1–4 clearly show that it is possible to obtain high survival rates using bareroot seedlings. The 47% or greater mortality in bareroot longleaf pine on sites 9 and 10 could be from differences in sites or weather following outplanting but likely resulted from less intensive site preparation, as well as a greater mortality of Pt seedlings (Cram et al. 1999). More intensive site preparation is recommended when using bareroot longleaf seedlings to reduce competition and increase

Table 5. Parameter estimates, R^2, standard error, and *P* values for bareroot longleaf and loblolly pine volume growth (ft³/ac per year) multiple regression model consisting of depth of sandy soil and survival.[a]

Species	R^2	Variable	Parameter estimate	Standard error	*t* value	*P* value
Longleaf	0.98	Intercept	−92.74	29.79	−3.11	0.0265
		Soil depth	23.24	7.56	3.07	0.0277
		Survival	406.85	47.45	8.57	0.0004
		Soil depth × survival	−55.13	12.29	−4.49	0.0065
Loblolly	0.95	Intercept	−309.19	87.96	−3.51	0.0170
		Soil depth	110.03	22.46	4.90	0.0045
		Survival	759.24	116.55	6.51	0.0031
		Soil depth × survival	−169.57	29.49	−5.75	0.0022

[a] Site 3 was excluded to avoid the confounding effects of an unplanned fire; $n = 9$ sites.

survival (Brockway et al. 2006). Survival of containerized seedlings was significantly greater than that of bareroot longleaf pine, and this was the primary cause of greater volume. Increased survival of containerized longleaf pine is a typical outcome in many studies, but it is one that may be affected by seedling size (South et al. 2005). Because data were not taken on the initial seedling size for sites 9 and 10, we are unable to determine whether it had an effect on survival; however, initial diameters recorded for sites 1–8 showed no interaction with survival (Cram et al. 1999). Given the high survival rates of bareroot longleaf pine in earlier plantings, the increase in container survival for sites 9 and 10 may simply indicate that containerized seedlings had an advantage under poor field conditions for regeneration (Boyer 1988, Barnett 2002).

A previous publication of results from this study found that reforestation of the South Carolina sandhills is generally not enhanced by inoculation of seedlings with Pt ectomycorrhizae (Cram et al. 1999). One of the unexpected results previously reported was a significant decrease in survival of bareroot longleaf pine inoculated with Pt on sites 6–10. Although this negative response was still present for sites 9 and 10, decreases in survival with Pt-inoculated longleaf pine could no longer be detected at a significant level in the other three sites. In containerized seedlings, the increased height growth at 4 years with Pt inoculation was also lost after 15 years. Pt inoculation of some pine species for mine reclamation is still considered beneficial (Marx and Artman 1979, Berry 1982, Walker et al. 1989) but has not been found necessary for general reforestation (Leach and Greshan 1983, Castellano and Trappe 1991, Cram et al. 1999). Artificial inoculation of pine seedlings with Pt ectomycorrhizae is not recommended for reforestation of the South Carolina sandhills.

The impact of fire damage on loblolly pine survival for site 3 demonstrates why longleaf pine was once a predominant species in the South and why it may be better suited to fire-maintained landscapes. In the absence of fire, loblolly pine had equal or greater survival and has an advantage in early growth (Outcalt 2000). The grass stage of longleaf pine is one of the primary reasons early growth is less than that of other southern pines. Other factors are the greater root growth and hydraulic conductivity of loblolly pine when soil moisture is not limited (Sword Sayer et al. 2005). The root growth of longleaf pine can surpass that of loblolly pine under severe drought conditions; thus, longleaf pine is better adapted to drought-prone sites (Sword Sayer et al. 2005). Our results suggest an interaction of tree growth with depth of sandy surface layer. Although both species had better height growth on more shallow, sandy soils, the difference between loblolly and longleaf pine appeared greater on the Wagram, Fuquay, and Dothan soils, where a finer textured horizon was more quickly reached by the root system.

Delay of longleaf pine volume growth by the grass stage may still be a factor in volume differences between longleaf and loblolly pine at 15–19 years old. The comparison of longleaf pine growth to other pines may be more equitable at 25–30 years because of early growth differences with other pines (Schmidtling 1987, Boyer 1997). This is illustrated by a study located on sandhills in Georgia and South Carolina, where longleaf equaled loblolly pine in diameter and height at age 15 (Hebb 1982) but had a greater diameter and height growth than loblolly or slash pine at 28 years old (Outcalt 1993). Longleaf pine growth on extended rotations may surpass loblolly pine on the more drought-prone soils, such as those found in the South Carolina sandhills (Schmidtling 1987, Outcalt 1993, Boyer 1997). This expectation of greater growth over time, added to the greater resistance of longleaf pine to diseases and insect damage (Wahlenberg 1946, Hodges 1974, Friedenberg et al. 2007), makes longleaf pine a preferred species for reforestation of the South Carolina sandhills when managed for longer rotations. Even on the somewhat better soils of the current study, where a finer textured soil horizon is close to the soil surface, longleaf pine may equal the growth of loblolly pine given sufficient time (Schultz 1997).

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