ROOT-ZONE TEMPERATURE AND WATER AVAILABILITY AFFECT EARLY ROOT GROWTH OF PLANTED LONGLEAF PINE[1]

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Abstract— Longleaf pine seedlings from three seed sources were exposed to three root-zone temperatures and three levels of water availability for 28 days. Root growth declined as temperature and water availability decreased. Root growth differed by seed source. Results suggest that subtle changes in the regeneration environment may influence early root growth of longleaf pine and that root proliferation may vary by seed source.

INTRODUCTION

Since 1800, the area occupied by longleaf pine, *Pinus palustris* Mill., in the South has decrease from 60 million acres to less than 5 million acres (Sirmon and Dennington 1989). Sensitivity to competition for light; susceptibility to brown-spot disease, caused by *Mycosphaerella dearnessii* Barr.; and a prolonged grass stage have prevented longleaf pine from becoming a species of choice for artificial regeneration (Barnett and Dennington 1992; Barnett and others 1990; Guldin 1982; Loveless and others 1989; Sirmon and Dennington 1989).

Longleaf pine establishment is improved by planting high-quality seedlings and by using optimum site preparation methods (Boyer 1985; Loveless and others 1989). The size and root morphology of planted longleaf pine seedlings are major determinants of establishment success (Hatchell 1987; Hatchell and Muse 1990; Lauer 1987; White 1981). The key characteristic used to quantify seedling size is root collar diameter, which should be at least 1.1 cm (Lauer 1987; White 1981). Longleaf pine planting guidelines also recommend a minimum quantity of primary lateral and fibrous roots (Hatchell 1987; Hatchell and Muse 1990).

Unfortunately, the establishment success of operationally-planted longleaf pine seedlings remains low. For example, first-year survival of longleaf pine planted on National Forest System land in the 1991-92 planting season was 66 percent; whereas that of loblolly and slash pine were 83 and 81 percent, respectively (Hessel 1994). Furthermore, a survey of 75 percent of the land in Louisiana that was regenerated with longleaf pine during the 1992-93 planting season indicated that first-year survival was only 44 percent; whereas, that of loblolly and slash pine were both 79 percent (State of Louisiana 1994).

The proliferation of primary lateral roots and new root tips by *Pinus* species is strongly influenced by root-zone temperature, water availability and their interaction (Andersen and others 1986; Brissette and Chambers 1992; Carlson 1986; Nambiar and others 1979). Furthermore, seed source influences the root system morphology within *Pinus* species (Carlson 1986; Hallgren and others 1993; Nambiar and others 1982; Sword and Brissette 1993). The unique stem and root system morphology of longleaf pine (Brown 1964), as well as the responsiveness of this species' root system to lateral root pruning in the nursery (Hatchell 1987; Shoulders 1963), suggests that the longleaf pine root system may be very sensitive to environmental and genetic stimuli and their interaction.

This experiment was conducted as our initial effort to study the new root growth of longleaf pine in response to root zone temperature, water availability, and seed source. Observations were made with container-grown seedlings and provide a basis for future investigation of root system response to environment and seed source, and the impact of this response on longleaf pine establishment.

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MATERIALS AND METHODS

Container-grown longleaf pine seedlings were produced outdoors using the recommendations of Barnett and Brissette (1986). Six-month-old seedlings of uniform size were chosen, stem diameters were measured at the root collar, the growth medium was washed from root systems, and new roots (≥ 5 mm) were excised.

Seedlings were planted in the seedling growth system described by Sword and Brissette (1993) in which water baths were used to maintain three root-zone temperatures: 13, 18, and 23 °C. This 10-degree range is representative of the soil temperature (15 cm) in central Louisiana during winter and early spring (figure 1). Within water baths, three water availability treatments were applied using the method of Brissette and Chambers (1992). Atmospheric temperature was maintained at 20 °C and seedlings received ambient light.

This experiment was done first in December 1993 and repeated in January 1994, using a split plot, randomized block design. Initiation of halves of each repetition were staggered by 1 week. Week of initiation represented blocks in the experimental design. Root-zone temperature (13, 18, and 23 °C) was the whole-plot treatment. Water stress and seed source were subplot treatments and were randomly assigned to seedling planting locations within whole plots. Water stress treatments were a well-watered condition, mild water stress, and moderate water stress. Seed sources were bulk collections from seed orchards in Florida and Mississippi, and a general forest area in north Alabama.

Twenty-eight days after planting, the predawn xylem water potential (Ψ_{pd}) of one mature needle from the mid-shoot area of each seedling was measured in a pressure chamber (PMS Instrument Co., Corvallis, OR). Sand was washed from root systems. New roots, defined as white or light in color and at least 5 mm long, were excised and counted. The excised roots were darkly stained and their projected surface area was measured with a Delta-T area meter (Decagon Devices, Inc., Pullman, WA). The older portion of each root system was dried for 48 hours at 70 °C and weighed.

Stem diameters were subjected to an analysis of variance. With stem diameter as a covariate, all other variables were subjected to an analysis of covariance. Unless noted otherwise, main and interaction effects were considered significant at $P \leq 0.05$. Treatment means were compared using the Least Significant Difference test at $P \leq 0.05$.

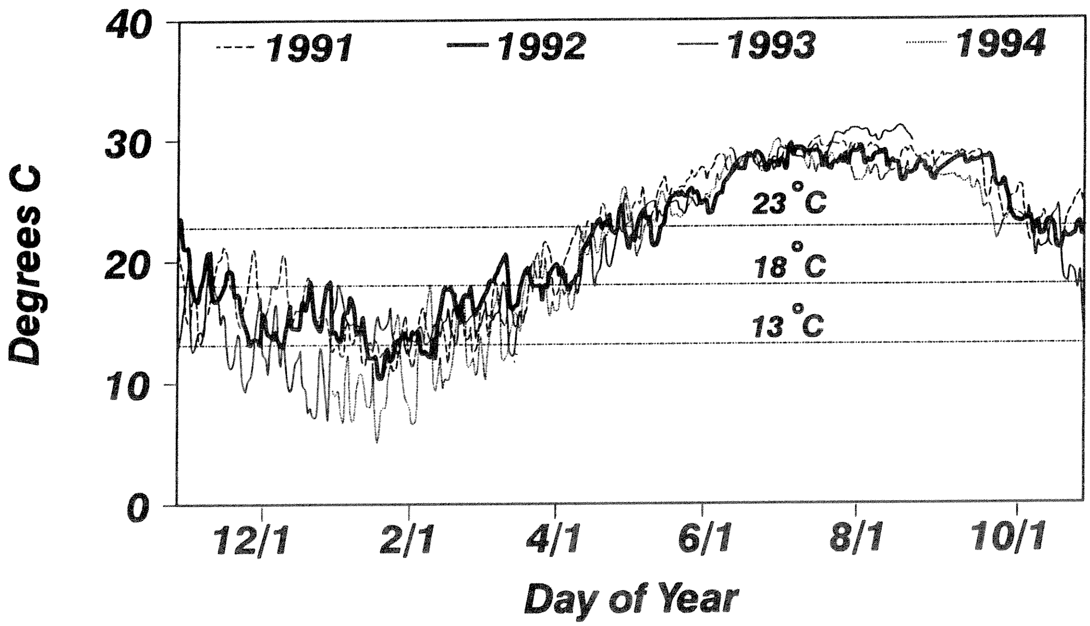

Figure 1--Daily 12:00 pm soil temperature (15 cm) at an open-field location on the Palustris Experimental Forest, Rapides Parish, Louisiana, between January 1991 and September 1994.

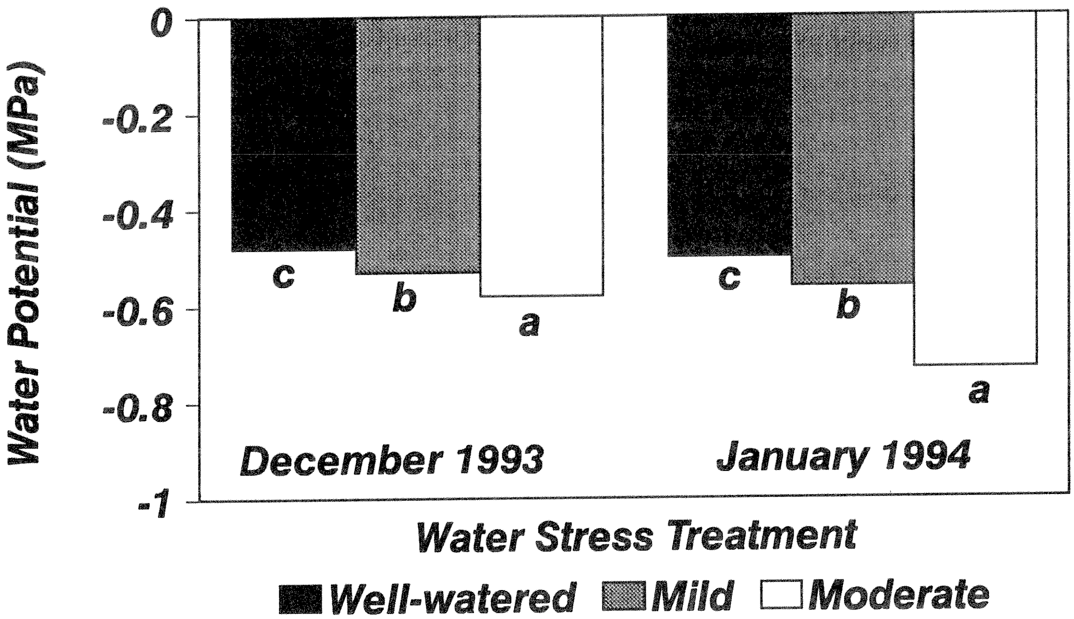

Figure 2--Mean predawn needle xylem water potential, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to water stress treatments for 28 days. In each repetition, means associated with different letters are significantly different at $P \leq 0.05$ by the LSD test.

RESULTS

In both repetitions, water stress significantly reduced Ψ_{pd} after 28 days (table 1). In December, mild and moderate water stress resulted in 0.05 and 0.1 MPa decreases, respectively, in Ψ_{pd}; whereas, in January, decreases of 0.06 and 0.23 MPa, respectively, were found (figure 2). In December, number of new roots was significantly decreased by mild and moderate water stress (23 and 30 percent, respectively) (figure 3). In January, number of new roots was significantly decreased by moderate water stress (35 percent). New root projected surface area was similarly affected (figure 4).

Root growth was significantly affected by the 10-degree root-zone temperature range in this study (table 1). In December and January, an increase in root-zone temperature from 13 to 18 °C caused approximately 6- and 12-fold increases in number and projected surface area of new roots, respectively (figures 5 and 6). Elevation of the root-zone temperature from 18 to 23 °C caused approximately 1.8-fold increases in both the number and projected surface area of new roots in both repetitions.

In January, number of new roots was significantly affected by an interaction between water stress and root-zone temperature (table 1). At 13 °C, water stress did not affect number of new roots; however, at 18 °C, moderate water stress reduced number of new roots when compared to the well-watered condition (figure 7). At 23 °C, number of new roots was less under moderate water stress when compared to both the well-watered condition and mild water stress. Although not significant, a similar trend was observed with new root surface area in January. In December, number of new roots and new root projected surface area were not significantly affected by an interaction between water stress and root-zone temperature.

Seed source significantly affected new root growth (table 1). In both repetitions, the north Alabama source had significantly more new roots than the Florida and Mississippi sources (table 2). In December, the north Alabama source had a significantly larger new root projected surface area than the Florida and Mississippi sources; and in January, had a significantly larger new root projected surface area than the Mississippi source.

Table 1--Analysis of covariance for evaluation of the effects of root-zone temperature, water availability, and seed source on longleaf pine seedling root characteristics using a split plot, randomized block design with initial stem diameter as a covariate[a]

Source of Variation	Predawn Needle Ψ_{pd} (Mpa)			Old root dry weight (g)			New roots (#)			New root area index (cm_2)		
	df	MS	Pr>F	df	MS	Pr>F	df	MS	Pr>F	df	MS	Pr>F
December 1993 replicate												
diameter	1	0.476	0.3100	1	4.055	0.0001	1	338.8	0.3490	1	2134.3	0.3373
block	1	1.331	0.7883	1	1.587	0.0106	1	5181.1	0.1473	1	30371.7	0.1754
temperature (T)	2	7.576	0.6519	2	0.001	0.9263	2	68741.8	0.0139	2	410144.1	0.0171
block x T	2	14.186	0.0001	2	0.017	0.6721	2	972.3	0.0819	2	7146.7	0.0470
water availability (W)	2	23.463	0.0001	2	0.349	0.0200	2	4316.4	0.0018	2	14610.7	0.0397
seed source (S)	2	10.844	0.0016	2	0.452	0.0077	2	5189.5	0.0007	2	31692.5	0.0021
W x S	4	4.880	0.0151	4	0.113	0.2340	4	393.1	0.5653	4	2173.2	0.7004
W x T	4	2.332	0.1556	4	0.016	0.9254	4	1178.3	0.0924	4	4229.3	0.3924
S x T	4	1.599	0.3144	4	0.076	0.4241	4	1577.4	0.0374	4	6609.1	0.1887
W x S x T	8	1.060	0.5830	8	0.033	0.8885	8	245.3	0.8648	8	919.2	0.9807
block x W x S x T	24	1.273	0.4807	24	0.075	0.0184	24	521.3	0.1291	24	3947.2	0.0231
sampling error	265	1.286		268	0.043		268	384.9		268	2310.2	
January 1994 replicate												
diameter	1	11.039	0.0134	1	7.070	0.0046	1	281.5	0.4197	1	576.1	0.6207
block	1	148.502	0.0040	1	1.047	0.3237	1	96.4	0.6778	1	4927.6	0.5409
temperature (T)	2	30.347	0.0195	2	1.663	0.2719	2	101455.7	0.0041	2	526267.0	0.0172
block x T	2	0.604	0.7127	2	0.621	0.4893	2	416.0	0.3823	2	9224.9	0.0208
water availability (W)	2	158.968	0.0001	2	2.514	0.1083	2	6183.6	0.0024	2	20555.5	0.0146
seed source (S)	2	3.376	0.4415	2	2.354	0.1234	2	3763.9	0.0180	2	15393.2	0.0369
W x S	4	0.212	0.9944	4	0.571	0.6978	4	114.5	0.9634	4	1111.9	0.8917
W x T	4	11.662	0.0421	4	1.275	0.3213	4	2601.8	0.0274	4	7533.0	0.1507
S x T	4	4.207	0.4004	4	1.592	0.2208	4	1659.0	0.1117	4	10193.7	0.0681
W x S x T	8	1.221	0.9563	8	0.875	0.5695	8	263.0	0.9443	8	1124.1	0.9672
block x W x S x T	24	3.990	0.0011	24	1.030	0.2525	24	788.5	0.0120	24	4054.3	0.0209
sampling error	269	1.781		268	0.867		268	431.0		268	2346.9	

[a] "block x T" is the error term for whole plot effects. "block x W x S x T" is the error term for subplot effects.

Immediately prior to the start of each repetition, stem diameter was significantly affected by seed source (table 3). Specifically, the stem diameter of the Mississippi source was significantly larger than that of the north Alabama and Florida sources (table 2). After the December repetition, dry weights of the old portion of seedling root systems of the Mississippi and north Alabama sources were significantly larger than that of the Florida source. A similar, but not significant trend was observed after the January repetition.

An interaction between seed source and root-zone temperature significantly affected number of new roots (table 1). In December, at 13 and 18 °C, number of new roots was not affected by seed source; however, at 23 °C, the north Alabama and Florida sources had more new roots than the Mississippi source (figure 8). A similar but not significant trend was observed with new root projected surface area in December. In January, this interaction affected new root projected surface area (P = 0.0681). Specifically, at 13 and 18 °C, new root projected surface area was not affected

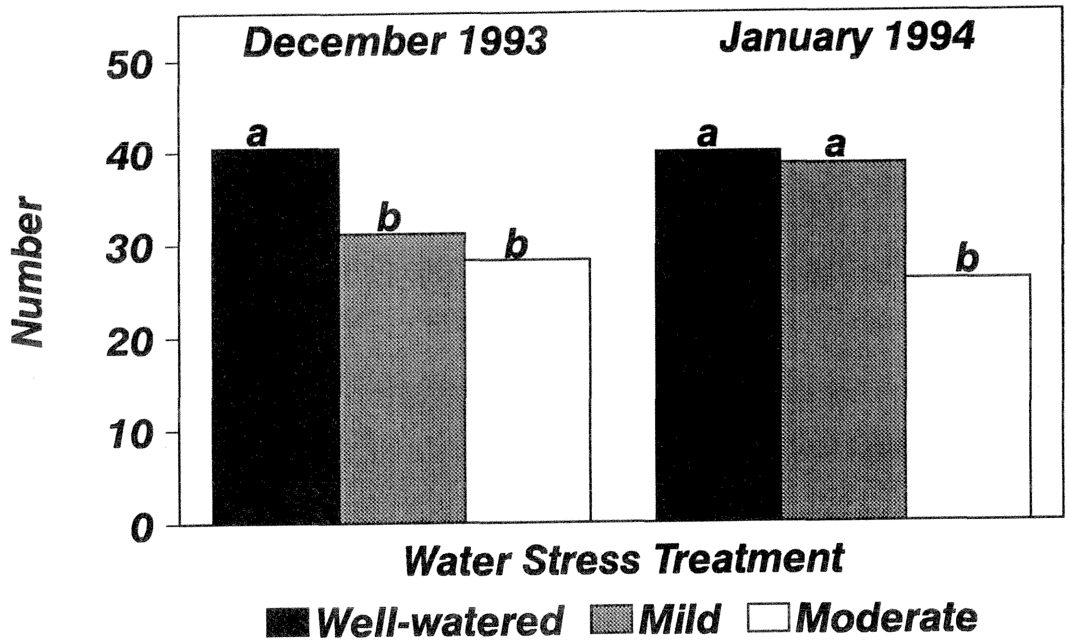

Figure 3--Mean number of new roots, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to water stress treatments for 28 days. In each repetition, means associated with different letters are significantly different at P ≤ 0.05 by the LSD test.

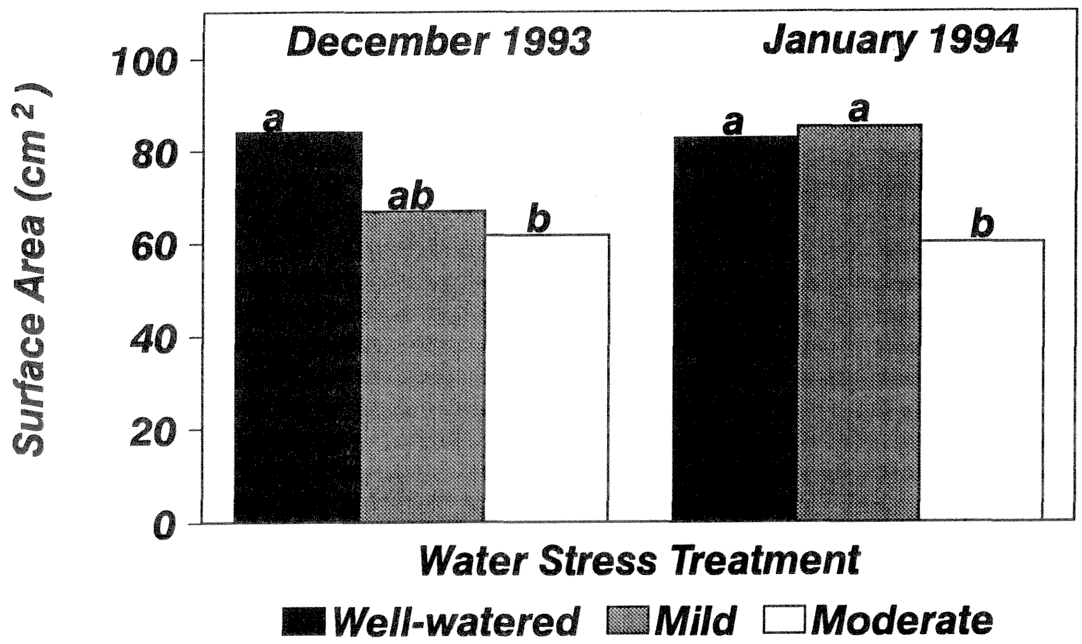

Figure 4--Mean new root projected surface area, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to water stress treatments for 28 days. In each repetition, means associated with different letters are significantly different at P ≤ 0.05 by the LSD test.

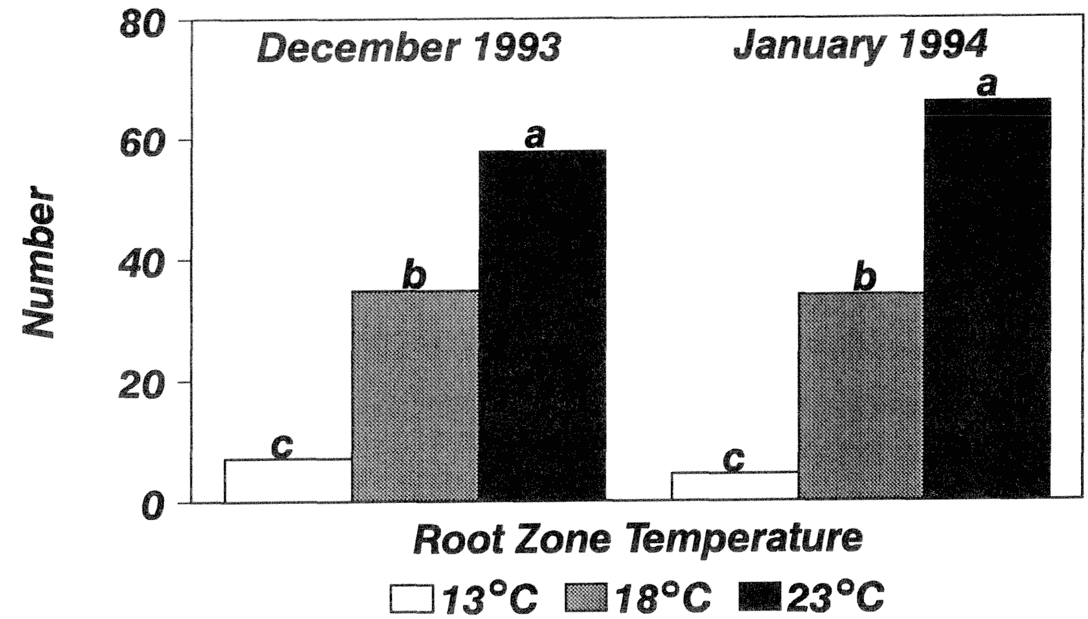

Figure 5--Mean number of new roots, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to three root-zone temperatures for 28 days. In each repetition, means associated with different letters are significantly different at $P \leq 0.05$ by the LSD test.

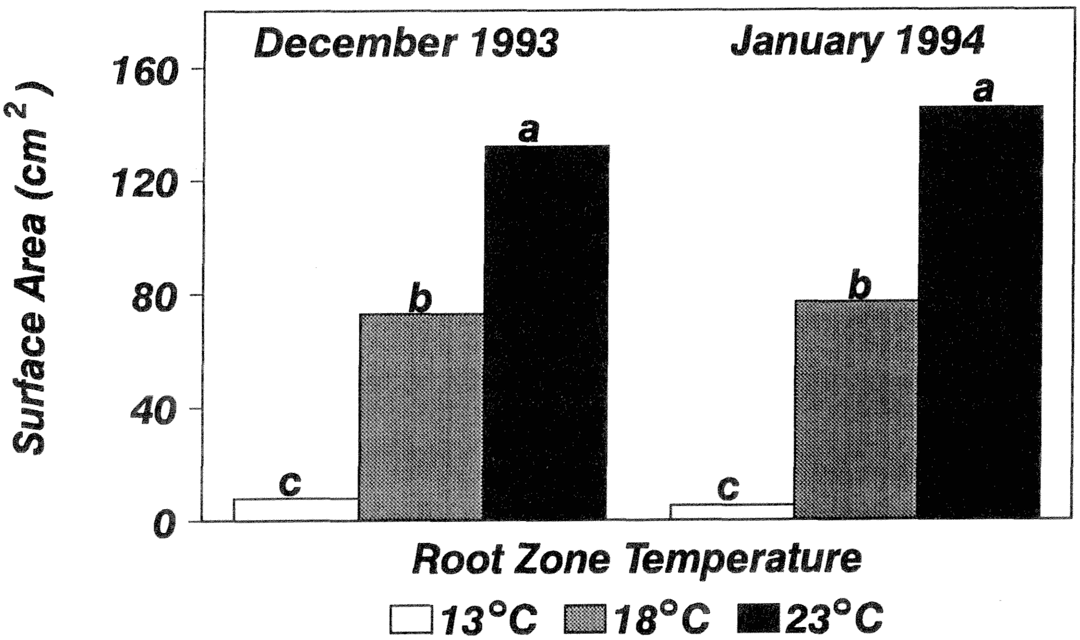

Figure 6--Mean new root projected surface area, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to three root-zone temperatures for 28 days. In each repetition, means associated with different letters are significantly different at $P \leq 0.05$ by the LSD test.

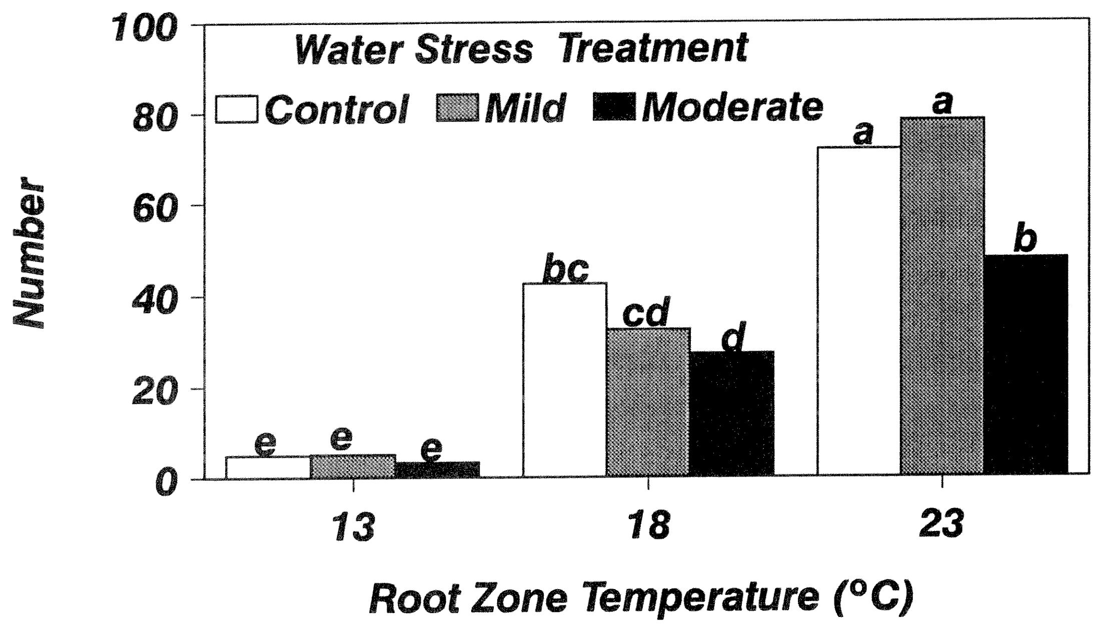

Figure 7--Mean number of new roots, adjusted by initial stem diameter, of container-grown longleaf pine seedlings after exposure to root-zone temperature and water stress treatments for 28 days in January 1994. Means associated with different letters are significantly different at $P \leq 0.05$ by the LSD test.

Table 2--Mean initial stem diameter and adjusted means[a] of root characteristics of three seed sources of container-grown longleaf pine seedlings after exposure to three root-zone temperatures for 28 days in December 1993 and January 1994

Repetition and seed source	Stem diameter (mm)	New roots (#)	New root surface area (cm^2)	Old root dry wt. (g)
December 1993				
North Alabama	5.8 b[b]	40.6 a	90.4 a	1.09 a
Florida	5.9 b	32.8 b	66.4 b	0.98 b
Mississippi	6.3 a	26.1 c	55.6 b	1.10 a
January 1994				
North Alabama	7.7 b	41.7 a	89.7 a	1.54 a
Florida	7.8 b	32.2 b	72.2 ab	1.44 a
Mississippi	8.4 a	30.4 b	65.7 b	1.75 a

[a] Mean root characteristics adjusted by initial stem diameter.
[b] Within repetitions and columns, means associated with different letters are significantly different at $P \leq 0.05$ by the LSD test.

Table 3--Analysis of variance for evaluation of the effect of seed source on longleaf pine seedling stem diameter using a completely random design

Source of Variation	df	MS	Pr>F
--------December 1993 replicate--------			
week (W)	1	3.4434	0.0076
seed source (S)	2	7.7413	0.0001
W x S	2	0.1882	0.6741
sampling error	317	0.4766	
--------January 1994 replicate--------			
week (W)	1	12.2349	0.0001
seed source (S)	2	12.9559	0.0001
W x S	2	3.2398	0.0123
sampling error	317	0.7266	

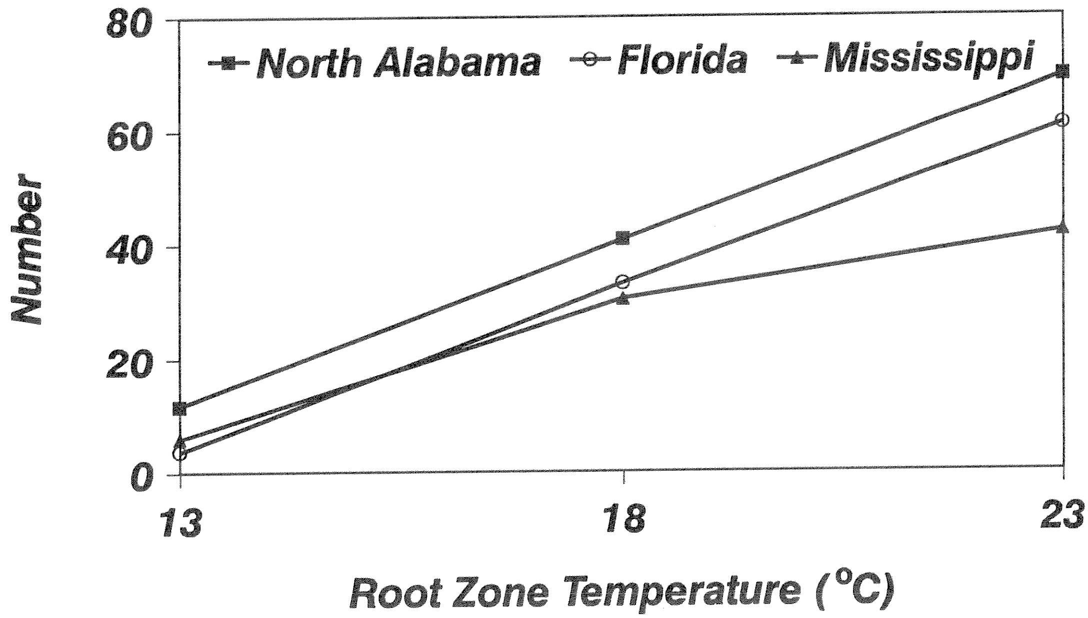

Figure 8--Mean number of new roots, adjusted by initial stem diameter, of three seed sources of container-grown longleaf pine seedlings after exposure to three root-zone temperatures for 28 days in December 1993. At 23°C, new root initiation of north Alabama and Florida sources was significantly greater than that of the Mississippi source by the LSD test ($P \leq 0.05$).

by seed source; however, at 23 °C, that of the north Alabama source was greater than that of the Florida and Mississippi sources. A similar but not significant trend was observed with number of new roots in January.

DISCUSSION

The new root growth of transplanted longleaf pine seedlings was 1.8-fold greater at 23 °C than at 18 °C. Nambiar and others (1979) found a 1.3-fold increase in the new root length of Monterey pine, *Pinus radiata* D. Don, seedlings in response to an increase in root-zone temperature from 15 to 20 °C, 32 days after transplanting. Similarly, Andersen and others (1986) found that an increase in root-zone temperature from 16 to 20 °C caused a 1.4-fold increase in the new root length of transplanted red pine, *Pinus resinosa* Ait., seedlings.

We also found that reduced water availability decreased longleaf pine root growth after transplanting. Furthermore, results from the January repetition indicated that the negative effect of water stress became more pronounced as root-zone temperature increased. Similarly, Brissette and Chambers (1992) reported that the positive response of root growth to increased soil temperature was reduced as water became more limiting to shortleaf pine, *Pinus echinata* Mill., seedlings.

Seedling establishment was not evaluated in the present study. Therefore, we cannot develop relationships between our results and the field performance of planted longleaf pine. However, successful seedling establishment is dependent on the development of a network of new roots after planting (Brissette and Chambers 1992; Carlson 1986; Johnson and Cline 1991). Furthermore, the root-zone temperature and water availability treatments imposed in our study were representative of possible soil conditions during winter and spring in central Louisiana. Since our results characterize initial root responses to the soil environment after planting, they provide a sound basis for making hypotheses about relationships between the root-zone environment, root growth, and field performance of planted longleaf pine.

Root growth was strongly stimulated by an increase in root-zone temperature; however, this positive response was sensitive to water stress. Water availability is a key factor affecting southern pine seedling survival after planting (Gholz and Boring 1991; McGrath and Duryea 1994). Perhaps manipulation of the regeneration environment to maximize soil temperature immediately after planting would increase early root growth. Any gain in new root growth during winter and early spring could reduce the negative effect of early or gradual decreases in water availability as the growing season progressed.

Walker and McLaughlin (1989) found that a black, perforated polyethylene mulch applied at the base of loblolly pine seedlings caused a 5 °C increase in spring soil temperature at 5 cm. Site preparation methods that elevate soil temperature in the root zone of planted longleaf pine may accelerate root growth in late winter and early spring.

In the present study, root growth of longleaf pine was affected by seed source. Similarly, other investigations have demonstrated that root growth of pine species differs by genotype (Carlson 1986; Hallgren and others 1993; Nambiar and others 1982). This information suggests that seed source may influence the root growth of longleaf pine seedlings immediately after planting.

We found that at 13 and 18 °C, root growth did not differ by seed source; however, at 23 °C, root growth of the Mississippi source was less than that of the north Alabama source. Since the duration of this experiment was short and field performance was not evaluated, conclusions about the adequacy of early root growth after planting these seed sources cannot be made. However, our information does suggest that seed sources may differ in the rapidness of their root growth response to increases in temperature as the soil warms in spring.

A positive relationship exists between the root collar diameter and root system size of southern pine seedlings (Hatchell 1987; Hatchell and Muse 1990; Johnson and others 1985). However, negative correlations between the stem diameter and root system fibrosity of longleaf pine seedlings have been reported (Hatchell 1987; Hatchell and Muse 1990). In the present study, we found that the Mississippi source had a larger stem diameter, but less new root growth, when compared to the north Alabama source. The new root initiation of seed sources in this study may be related to their adaption to different planting zones. However, just as carbon partitioning between the shoot and root system of loblolly pine seedlings was found to differ by seed source (Bongarten and Teskey 1987), our results suggest it is possible that carbon partitioning between the tap and fibrous roots of longleaf pine may differ by seed source.

Our results indicate that the new root growth of container-grown longleaf pine is sensitive to subtle shifts in soil temperature and water availability immediately after planting. Furthermore, negative effects of water stress may become more pronounced as root-zone temperature increases. Further research is warranted to determine if soil temperature in the regeneration environment can be manipulated to stimulate early root growth before water limitations occur during the growing season. Our results also suggest that seed source affects longleaf pine root growth responses to changes in soil environments. The aggressiveness of early root growth after planting, and the field performance of longleaf pine seed sources should be evaluated. Moreover, the effect of seed source on carbon partitioning between tap and fibrous roots should be studied.

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