New Forests (2005) 30:253–272
DOI 10.1007/s11056-005-7481-x © Springer 2005

# Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting

MARY ANNE SWORD SAYER[1,*], JOHN C. BRISSETTE[2] and JAMES P. BARNETT[1]
*[1]USDA Forest Service, Southern Research Station, 2500 Shreveport Highway, Pineville, LA 71360, USA; [2]USDA Forest Service, Northeast Research Station, Durham, NH 03824, USA; *Author for correspondence (e-mail: msword@fs.fed.us; phone: + 1-318-473-7275; fax: + 1-318-473-7273)*

Received 21 June 2004; accepted in revised form 6 May 2005

**Key words:** *Pinus echinata, Pinus palustris, Pinus taeda,* Root surface area, Seed source, Water transport

**Abstract.** Comparison of the root system growth and water transport of southern pine species after planting in different root-zone environments is needed to guide decisions regarding when, and what species to plant. Evaluation of how seed source affects root system responses to soil conditions will allow seed sources to be matched to planting conditions. The root growth and hydraulic conductivity of three sources each of shortleaf, loblolly and longleaf pine seedlings were evaluated for 28 days in a seedling growth system that simulated the planting environment. Across species, an increase in root-zone temperature alleviated limitations to root growth caused by water stress. In the coldest temperature, longleaf pine maintained a higher hydraulic conductivity compared to shortleaf and loblolly pine. Without water limitation, the root growth and hydraulic conductivity of shortleaf and loblolly pine were superior to that of longleaf pine, but as water availability decreased, the root growth of longleaf pine surpassed that of loblolly pine. Hydraulic conductivities of the seed sources differed, and differences were attributed to either new root growth, or an increase in the efficiency of the root system to transport water.

## Introduction

The pine forests of the southern United States are primarily composed of mixed and pure stands of the four major pine species in the South: loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* Engelm.), longleaf pine (*Pinus palustris* P. Mill.), and shortleaf pine (*Pinus echinata* P. Mill.). The productivity of these forests is largely due to artificial regeneration programs, initiated after World War II, that continue today (Dougherty and Duryea 1991). Past regeneration efforts focused on the establishment of loblolly and slash pine with bare-root seedlings (Mexal and South 1991; Schultz 1997). At that time, the production of high-quality bare-root longleaf pine seedlings was difficult and management practices and site conditions precluded longleaf pine establishment (Barnett et al. 1990; Barnett and Dennington 1992; Outcalt 2000). The regeneration of shortleaf pine has often been accomplished by direct seeding (Baker 1992; Barrett 1995). However, because shortleaf pine seed crops are

highly variable (Wittwer and Shelton 1992), planted seedlings are frequently used to regenerate this species (Barrett 1995; Smith 1992; Walker 1992).

Unlike the production and establishment of bare-root loblolly pine, the artificial regeneration of bare-root shortleaf and longleaf pine remains difficult (Brissette and Carlson 1986; Hallgren and Tauer 1989; Walker 1992; Barnett and Dennington 1992; Barnett et al. 1990). Because container-grown seedlings are exposed to less root system disturbance than bare-root seedlings (Barnett and McGilvray 1997; Barnett 2002), shortleaf and longleaf pine are now successfully established as containerized stock (Barnett and Brissette 2004; Barnett and McGilvray 1997).

After planting, the absorption and conductance of water is critical to seedling establishment. During this time, water is primarily supplied by new roots, and seedling survival depends on rapid root growth after planting (Wakeley 1954; Carlson 1986; Larsen et al. 1986; Hallgren and Tauer 1989). Root system expansion after planting is greatly influenced by edaphic factors such as soil temperature, and water and light availabilities (Andersen et al. 1986; Barnes 2002; Bongarten and Teskey 1987; Brissette and Chambers 1992; Carlson 1986; Jose et al. 2003; Nambiar et al. 1979). Genotype also influences the southern pine seedling root system (Barnes 2002; Bongarten and Teskey 1987; Hallgren and Tauer 1989; Hallgren et al. 1993; Samuelson 2000). For example, Hallgren and Tauer (1989) evaluated the root growth of 12 open-pollinated seed orchard families of shortleaf pine from Oklahoma and Arkansas and concluded that root growth potential was a good indicator of family field performance (Hallgren et al. 1993).

With the technology to now grow high-quality container-grown loblolly, shortleaf, and longleaf pine seedlings, more than one species may be practical to plant. Knowledge of how the root system of southern pine seedlings responds to soil conditions after planting will help guide decisions regarding when, and what species to plant. Within a species, evaluation of how seed source affects the response of root growth to edaphic conditions will allow seed source to be matched to unique planting environments. We hypothesize that shortleaf, loblolly, and longleaf pine root growth and hydraulic conductivity during early establishment differ depending on edaphic conditions, and that these relationships are affected by seed source. The first objective of our study was to evaluate and compare the root growth and hydraulic conductivity of container-grown shortleaf, loblolly, longleaf pine seedlings after 28 days of exposure to a range of root-zone environments that may be encountered during establishment in the southern United States. Our second objective was to assess how root growth and hydraulic conductivity are affected by seed source within a species.

## Materials and methods

In each of three consecutive years between 1991 and 1993, seed from three seed sources of either shortleaf, loblolly, or longleaf pine were grown outdoors in

Ray Leach Single Cells (115 $cm^3$ volume) (Stuewe and Sons, Inc., Corvallis, OR) containing a 1:1 commercial blend of peat moss and vermiculite using the recommendations of Barnett and Brissette (1986). Shortleaf and loblolly pine were grown for 8 months and longleaf pine was grown for 6 months. Seedlings received a soluble fertilizer applied through the irrigation system. Approximately 2 months before the end of the cultural period, water and fertilizer applications were reduced to encourage hardening. Seedlings remained outdoors, and by the time of the experiment, most seedlings had set bud. At the end of the 1991 cultural period, 324 shortleaf pine seedlings from each of three seed sources and of uniform size were chosen. Similarly, at the end of the 1992 and 1993 cultural periods, 216 loblolly and longleaf pine seedlings from each of three seed sources and of uniform size were chosen. Uniformity was defined as within one standard deviation of the mean root collar diameter (RCD) of 100 randomly selected seedlings.

Shortleaf pine sources were two open-pollinated half-sib seed orchard families from the Texas Forest Service seed orchard (TX1 half-sib and TX2 half-sib), and a woods-run collection from Texas (TX3 woods-run). Loblolly pine sources were a Texas full-sib cross (TX full-sib), a southern Mississippi full-sib cross (MS full-sib), and a bulk collection from a Louisiana and Texas general forest area (LA-TX GFA). Longleaf pine sources were bulk collections from seed orchards in Florida (FL orchard mix) and Mississippi (MS orchard mix), and a general forest area in northern Alabama (AL GFA).

The selected shortleaf pine seedlings were randomly partitioned into three subsets. Each subset was used for one repetition of the experiment in December 1991, January 1992, or March 1992. Similarly in 1992, the selected loblolly pine seedlings, and in 1993, the selected longleaf pine seedlings were partitioned into two subsets and evaluated in repetitions during December and January.

The experiment was conducted in a seedling growth system in a greenhouse. Two water baths, 1.5 × 1.5 × 0.6 m, were used to maintain each of three root-zone temperatures: 13, 18, and 23 °C. One set of baths maintained at the three root-zone temperatures was permanently housed on either the east or west side of the greenhouse. Location in the greenhouse represented experimental blocks. Root-zone temperature was regulated by injecting cold water into the water circulation path of each bath and heating water that was currently circulating. Each bath contained 54 water columns. Water availability was controlled using a modification of the design described by Brissette and Chambers (1992), which was adapted from a system presented by Snow and Tingey (1985). Seedlings were potted in masonry sand in polyvinyl chloride (PVC) containers, 20 cm in height (9.8 cm outer diameter), and the sand surface was sprayed with an anti-transpirant to reduce evaporation. The PVC containers were sealed at the base with nylon filter cloth (20 $\mu$m). Potted seedlings were placed on water columns composed of four floral foam blocks stacked in a 45 cm length of PVC pipe (10.8 cm outer diameter) so that the nylon filter cloth was in contact with the upper foam block. Soil water availability was controlled by the distance between root systems and the water level in the

stacked foam blocks. Water was supplied from irrigation reservoirs through plastic tubing to the base of each column. The elevation of irrigation reservoirs determined the amount of water transported through the plastic tubing and, therefore, the level of water in the columns. For each block of baths, one irrigation reservoir was maintained at one of three elevations which corresponded to three levels of water availability. Levels of water availability were: (1) well-watered so that seedlings were exposed to no water stress, (2) less water availability so that seedlings were exposed to mild water stress, and (3) least water availability so that seedlings were exposed to moderate stress.

Each month, the establishment of potted seedlings in the seedling growth system was done in four phases. In each of two consecutive weeks, the selected seedlings that were hardened and maintained outdoors were processed, potted and placed on the water columns in one of two blocks of baths. Weekly processing was staggered with the first half of seedlings potted two days before the second half. Processing consisted of measuring RCD (mm) and shoot length between the root collar and tip of the terminal shoot (cm) for shortleaf and loblolly pine and RCD alone for longleaf pine. Before potting, the growth medium was washed from root systems and new roots (≥5 mm) were excised. The influence of excision on root branching (Mexal and South 1991) during the experiment was considered negligible because the number of new roots removed from the hardened seedlings was minimal and similar among seedlings. In the greenhouse, air temperature was maintained at 20 °C and seedlings received ambient light.

After 28 days in the experimental environment, the predawn xylem water potential ($\Psi_{pd}$) 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. Root system hydraulic conductivity ($L_R$) was measured by applying hydrostatic pressure to the root system of decapitated seedlings using the method of Brissette and Chambers (1992). Shoots were severed from root systems about 25 mm above the first primary lateral root on the taproot. Stems were inserted through a rubber stopper seated in the removable lid of a pressure vessel so that 12 root systems were suspended inside the vessel. With the lid secure, tap water was pumped through the vessel (20 ± 0.5 °C, 0.13 l/s, 300 ± 0.5 kPa). After a 15 min equilibration period, water exuded from the cut surface of seedling stems was collected in pre-weighed wicks over five consecutive 5 min periods and weighed. Stem area was calculated with RCD measurements, and $L_R$ values were averaged by seedling and expressed as $\mu$mol water/s/mm$^2$ of stem area.

New roots, defined as light in color and at least 5 mm long, were excised and counted (NRNO). Excised roots were stained with Paragon multiple stain (Rietveld 1989), and their projected surface area (NRSA), expressed as mm$^2$, was measured with a Delta-T area meter (Decagon Devices, Inc., Pullman, WA). The older portion of each root system was dried to equilibrium at 70 °C, weighed, and expressed as g dry weight (ORDW).

For each species, measurements taken during repetitions of the experiment were averaged. The normal distribution of each variable was evaluated by the Shapiro-Wilk statistic (SAS Institute 1991), and data were transformed accordingly. Absolute values of $\Psi_{pd}$ were expressed as natural logarithms, and NRNO, NRSA and $L_R$ were either expressed as natural logarithm (ln) or square root values. The main and interaction effects of species, root-zone temperature, and water availability were evaluated by analyses of variance using a randomized complete block split plot in space and time design with two blocks (Steel and Torrie 1980). Root-zone temperature maintained by water baths was the space whole plot effect, species was the time whole plot effect, and water availability was the subplot effect. The year-to-year variation in greenhouse environment was negligible. The main effect of seed source and interaction effects between seed source and both root-zone temperature and water availability were analyzed by analyses of covariance using a randomized complete block split plot design with root-zone temperature as the whole plot effect, seed source and water availability as subplot effects and RCD as the covariate. Main and interaction effects were considered significant at $p \leq 0.05$ and significantly different treatment means were compared with the least significant difference test at $p \leq 0.05$.

Linear regression analyses with $\Psi_{pd}$ as the independent variable were used to determine species and family responses to water availability. Relationships between $L_R$ and both NRSA and ORDW were also evaluated by linear regression analyses. To linearize relationships, absolute values of $\Psi_{pd}$ and values of NRSA were transformed to natural logarithms before analyses. Mean square errors ($s^2$) of pairs of regression lines were assessed for homogeneity by the Bartlett test for equality of variances, and only pairs of regression lines having constant $s^2$ were evaluated by the general linear test approach and the $F$ statistic (Neter and Wasserman 1974).

## Results

### *Species response*

Loblolly pine shoot length (25.6 ± 0.2 cm) was significantly greater than that of shortleaf pine (22.7 ± 0.1 (±standard error)). Values of RCD were also significantly different among the species (loblolly pine: 4.39 ± 0.02 mm; shortleaf pine: 3.99 ± 0.01 mm; longleaf pine: 6.97 ± 0.05 mm). The ORDW of the three species were similar and averaged 1.21 ± 0.07 g. Interaction between root-zone temperature and water availability significantly affected RCD with a small but significant increase (2%) in RCD at 18 and 23 °C as water availability decreased from no water stress to moderate water stress.

Root-zone temperature, water availability and their interaction significantly affected $\Psi_{pd}$, NRNO, NRSA, and $L_R$ (Table 1). Interaction between root-zone temperature and water availability indicated that the effect of water availability

*Table 1.* Probabilities of a greater *F*-value (Pr > *F*) in the analyses of variance of $\Psi_{pd}$ (predawn xylem water potential), number of new roots (NRNO), new root surface area (NRSA), and root hydraulic conductivity ($L_R$) of shortleaf, loblolly, and longleaf pine seedlings in response to root-zone temperature and water availability for 28 days in a greenhouse.

| Source | $\Psi_{pd}$ | | NRNO | | NRSA | | $L_R$ | |
|---|---|---|---|---|---|---|---|---|
| | df | Pr > *F* | df | Pr > *F* | df | Pr > *F* | df | Pr > *F* |
| Block (*B*) | 1 | 0.03050 | 1 | 0.10550 | 1 | 0.10160 | 1 | 0.03710 |
| Temperature (*T*) | 2 | 0.01310 | 2 | 0.00020 | 2 | 0.00070 | 2 | 0.00270 |
| Error ($T \times B$) | 2 | | 2 | | 2 | | 2 | |
| Species (*S*) | 2 | 0.13020 | 2 | 0.29580 | 2 | 0.13760 | 2 | 0.65940 |
| Error ($S \times$ B) | 2 | | 2 | | 2 | | 2 | |
| $S \times T$ | 4 | 0.09200 | 4 | 0.01210 | 4 | 0.01700 | 4 | 0.00930 |
| Error ($S \times T \times B$) | 4 | | 4 | | 4 | | 4 | |
| Water stress (*W*) | 2 | 0.00001 | 2 | 0.00001 | 2 | 0.00001 | 2 | 0.00001 |
| $W \times T$ | 4 | 0.04700 | 4 | 0.00002 | 4 | 0.00005 | 4 | 0.00255 |
| Error ($W \times B$) + ($W \times T \times B$) | 6 | | 6 | | 6 | | 6 | |
| $S \times W$ | 4 | 0.03550 | 4 | 0.37190 | 4 | 0.00130 | 4 | 0.08980 |
| $S \times W \times T$ | 8 | 0.28410 | 8 | 0.97480 | 8 | 0.34740 | 8 | 0.75010 |
| Error ($S \times W \times B$) + ($S \times W \times T \times B$) | 12 | | 12 | | 12 | | 12 | |

df, degrees of freedom.

on $\Psi_{pd}$, NRNO, NRSA and $L_R$ differed depending on root-zone temperature. Values of NRNO and $L_R$ were unaffected as water availability decreased from no water stress to mild water stress at 23 °C (Figure 1). At 18 °C, however, NRNO and $L_R$ decreased significantly as mild water stress occurred. We also observed that although root growth at all levels of water availability was reduced at 13 °C compared to 18 and 23 °C, $L_R$ at 13 °C with no water stress was similar to that at 18 °C with either mild or moderate water stress.

Significant interactions between root-zone temperature and species were found for NRNO and NRSA (Table 1). Species did not affect NRNO or NRSA at 13 °C. At 23 °C, however, the NRNO and NRSA of loblolly pine were significantly greater compared to shortleaf and longleaf pine (Figure 2). A similar relationship was seen at 18 °C for NRSA. In addition, NRNO and NRSA responses to increased root-zone temperature differed in magnitude by species with a greater increase in the root growth of loblolly pine compared to shortleaf and longleaf pine as root-zone temperature increased from 18 to 23 °C.

A significant interaction between root-zone temperature and species was also found for $L_R$ (Table 1). At 23 °C, the $L_R$ of loblolly pine was significantly greater than those of shortleaf and longleaf pine (Figure 2). At 13 °C, the $L_R$ of longleaf pine was 64% greater than those of shortleaf and longleaf pine.

A significant interaction between water availability and species was apparent for $\Psi_{pd}$ and NRSA (Table 1). Because the $\Psi_{pd}$ of the three species at each level of water availability differed, it is likely that the intensity of water stress among the species was different (Figure 3). Interaction between water availability and species, therefore, was evaluated by linear regression of $\ln(-\Psi_{pd})$ and $\ln(\text{NRSA}+1)$. Significant linear relationships between these variables were

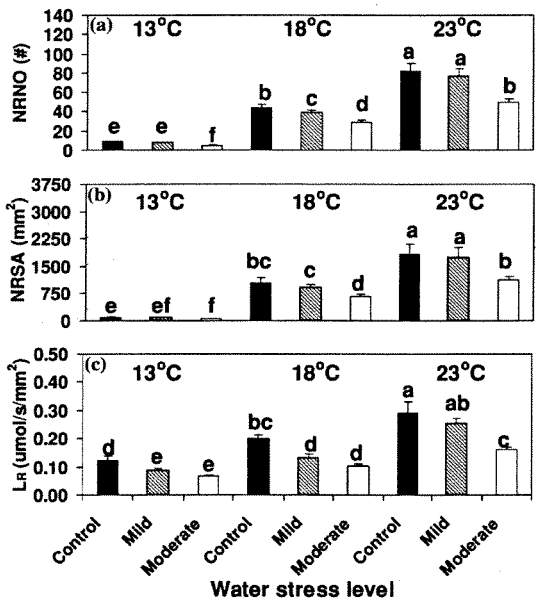


*Figure 1.* New root number (NRNO) (a), new root surface area (NRSA) (b), and hydraulic conductivity ($L_R$) (c), averaged across species, in response to three levels each of root-zone temperature (13, 18, and 23 °C) and water availability (control: no water stress, mild water stress, and moderate water stress) for 28 days in a greenhouse. Error bars represent one standard error of the mean. Means associated with a different letter are significantly different at $p \leq 0.05$ by the least significant difference test.

found for shortleaf pine (18 °C: $R^2 = 0.3368$, root mean square error ($S_{y \cdot x}$) = 0.67 mm$^2$; 23 °C: $R^2 = 0.3291$, $S_{y \cdot x} = 0.65$ mm$^2$), loblolly pine (13 °C: $R^2 = 0.3797$, $S_{y \cdot x} = 1.26$ mm$^2$; 18 °C: $R^2 = 0.6423$, $S_{y \cdot x} = 0.57$ mm$^2$; 23 °C: $R^2 = 0.0.6880$, $S_{y \cdot x} = 0.50$ mm$^2$), and longleaf pine (13 °C: $R^2 = 0.0427$, $S_{y \cdot x} = 1.64$ mm$^2$; 18 °C: $R^2 = 0.3063$, $S_{y \cdot x} = 0.81$ mm$^2$; 23 °C: $R^2 = 0.2215$, $S_{y \cdot x} = 0.67$ mm$^2$).

Because little new root growth occurred at 13 °C, evaluation of the relationship between ln ($-\Psi_{pd}$) and ln(NRSA + 1) among species excluded data collected at 13 °C. The relationship between ln($-\Psi_{pd}$) and ln(NRSA + 1) for longleaf pine appeared different from those of shortleaf and loblolly pine (Figure 4a–c). The $s^2$ of regression lines among species were significantly different according to the Bartlett test for equality of variances, and therefore, regression lines could not be evaluated by the $F$ statistic (shortleaf pine $s^2 = 0.50$ mm$^2$; loblolly pine $s^2 = 0.41$ mm$^2$; longleaf pine $s^2 = 0.68$ mm$^2$). Slopes, however, suggest that the ln($-\Psi_{pd}$) – ln(NRSA + 1) relationship differed among species (Figure 5a). We attribute this distinction to greater variation in the ln(NRSA + 1) of longleaf pine compared to the other two

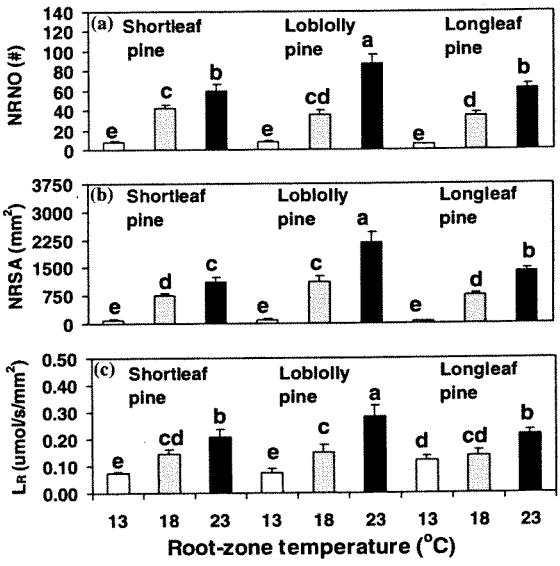


*Figure 2.* New root number (NRNO) (a), new root surface area (NRSA) (b), and hydraulic conductivity ($L_R$) (c) of shortleaf, loblolly, and longleaf pine seedlings in response to three root-zone temperatures (13, 18, and 23 °C) for 28 days in a greenhouse. Error bars represent one standard error of the mean. Means associated with a different letter are significantly different at $p \leq 0.05$ by the least significant difference test.

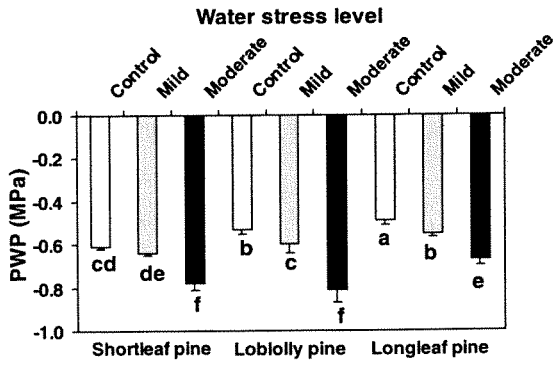


*Figure 3.* Predawn needle xylem water potential (PWP) of shortleaf, loblolly, and longleaf pine seedlings in response to three levels of water availability (control: no water stress, mild water stress, and moderate water stress) for 28 days in a greenhouse. Error bars represent one standard error of the mean. Means associated with a different letter are significantly different at $p \leq 0.05$ by the least significant difference test.

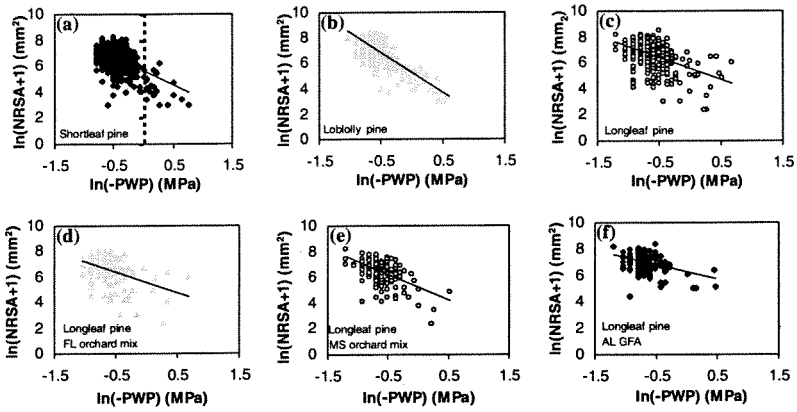


*Figure 4.* Linear relationship between the natural logarithms of new root surface area plus one (ln(NRSA + 1)) and the absolute value of predawn xylem water potential (ln(−PWP)) for (a) shortleaf, (b) loblolly, and (c) longleaf pine, and three seed sources of longleaf pine: (d) FL orchard mix, (e) MS orchard mix, and (f) AL GFA, after exposure to root-zone temperatures of both 18 and 23 °C for 28 days in a greenhouse.

species. Also, among the longleaf pine sources, the relationship between $\ln(-\Psi_{pd})$ and ln(NRSA + 1) for the AL GFA source appeared different from those of the FL and MS orchard mix sources (Figure 4d–f). Significantly different $s^2$ among the longleaf pine sources precluded their comparison by the $F$ statistic (FL orchard mix $s^2 = 0.863$ mm$^2$; MS orchard mix $s^2 = 0.680$ mm$^2$; AL GFA source $s^2 = 0.383$ mm$^2$). Clearly, however, the slope and Y-intercept for the $\ln(-\Psi_{pd})$ – ln(NRSA + 1) relationship of the AL GFA source differed from those of the other two longleaf pine sources (Figure 5b). Non-transformed values of $\Psi_{pd}$ and NRSA suggest that with adequate water, the NRSA of loblolly pine exceeded that of the AL GFA longleaf pine source (Figure 6a). As $\Psi_{pd}$ became more negative, however, the NRSA of the AL GFA longleaf pine source exceeded that of loblolly pine (Figure 6b).

For all three species, linear regressions of $L_R$ and NRSA were significant at root-zone temperatures of 18 and 23 °C. The largest coefficient of determination occurred for loblolly pine at 23 °C ($R^2 = 0.4741$, $S_{y \cdot x} = 0.13\,\mu$mol/s/mm$^2$). All other coefficients of determination ranged between $R^2 = 0.0454$ ($S_{y \cdot x} = 0.14\,\mu$mol/s/mm$^2$) for shortleaf pine at 23 °C and $R^2 = 0.1945$ ($S_{y \cdot x} = 0.12\,\mu$mol/s/mm$^2$) for longleaf pine at 23 °C. Linear relationships between $L_R$ and ORDW for all species and root-zone temperatures were not significant.

### *Seed source response*

Shortleaf pine seedling size was significantly affected by seed source (Table 2), with smaller TX2 half-sib seedlings compared to those of the other two

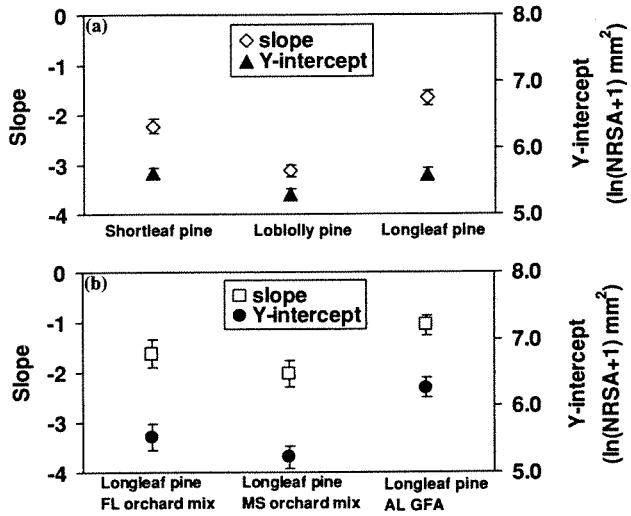


*Figure 5.* Regression parameters (slope and Y-intercept) for the linear relationship between the natural logarithms of new root surface area plus one (ln(NRSA + 1)) and the absolute value of predawn xylem water potential (ln(−PWP)) of (a) shortleaf, loblolly, and longleaf pine, and (b) three sources of longleaf pine after exposure to root-zone temperatures of both 18 and 23 °C for 28 days in a greenhouse. Error bars represent ±1 standard error of the mean.

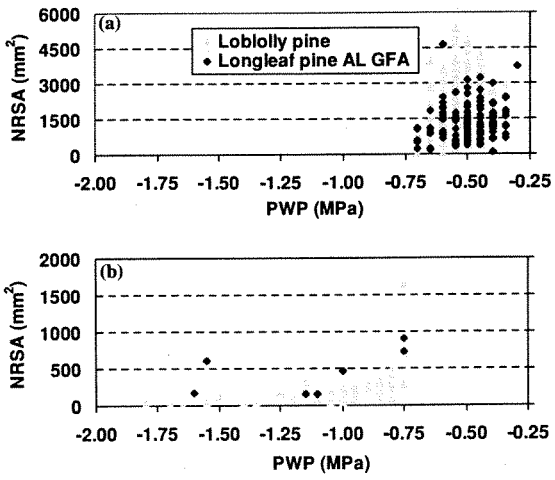


*Figure 6.* Scatter plot of new root surface area (NRSA) and predawn xylem water potential (PWP) of loblolly pine and the AL GFA longleaf pine source (a) at PWP values greater than −0.75 MPa and (b) at PWP values less than or equal to −0.75 MPa after exposure to root-zone temperatures of both 18 and 23 °C for 28 days in a greenhouse.

*Table 2.* Mean morphological characteristics of three seed sources each of shortleaf, loblolly, and longleaf pine seedlings in response to root-zone temperature and water availability for 28 days in a greenhouse.

| Seed source | Height (mm) | RCD (mm) | ORDW (g) |
|---|---|---|---|
| *Shortleaf pine* | | | |
| TX1 half-sib | 22 b[1] | 4.0 a | 1.3 a |
| TX2 half-sib | 20 c | 3.9 a | 1.1 c |
| TX3 woods-run | 25 a | 4.1 a | 1.2 b |
| *Loblolly pine* | | | |
| TX full-sib | 25 b | 4.2 b | 1.1 b |
| MS full-sib | 25 b | 4.3 b | 1.1 b |
| LA-TX GFA | 27 a | 4.6 a | 1.3 a |
| *Longleaf pine* | | | |
| FL orchard mix | – | 6.8 b | 1.2 a |
| MS orchard mix | – | 7.3 a | 1.4 a |
| AL GFA | – | 6.8 b | 1.3 a |

RCD, root collar diameter; ORDW, old root system dry weight.
[1]Means within a variable and species followed by a different letter are significantly different at $p \leq 0.05$ by the least significant difference test.

shortleaf pine sources. The LA-TX GFA loblolly pine seedlings and the MS orchard mix longleaf pine seedlings were significantly larger than seedlings from the other two seed sources of each species.

Shortleaf pine root growth was unaffected, but $L_R$ was significantly influenced by seed source (Table 3). Significant interaction between seed source and root-zone temperature indicated that at 18 °C, the $L_R$ of the TX2 half-sib source (0.20 $\mu$mol/s/mm$^2$) was greater than those of the TX1 half-sib (0.10 $\mu$mol/s/mm$^2$) and TX3 woods-run sources (0.13 $\mu$mol/s/mm$^2$). At 23 °C, the $L_R$ of the TX2 half-sib source (0.26 $\mu$mol/s/mm$^2$) was greater than that of the TX1 half-sib source (0.16 $\mu$mol/s/mm$^2$).

Loblolly pine source had a significant effect on NRNO but not NRSA (Table 3). Significant interaction between seed source and root-zone temperature indicated that the NRNO of the LA-TX GFA source (13 °C: 11 new roots; 18 °C: 39 new roots) was greater than that of the MS full-sib source at 13 °C (seven new roots) and 18 °C (33 new roots), but this effect was not apparent at 23 °C. Loblolly pine $L_R$ was also significantly affected by seed source with a greater $L_R$ of the TX full-sib source (0.19 $\mu$mol/s/mm$^2$) compared to the MS full-sib source (0.16 $\mu$mol/s/mm$^2$) across all three root-zone temperatures.

For longleaf pine, seed source also had a significant effect on root growth (Table 3). The NRSA of the AL GFA source (899 mm$^2$) was 38% greater than that of the FL and MS orchard mix sources. Significant interaction between seed source and root-zone temperature indicated that at 13 °C, values of NRNO for the AL GFA (eight new roots) and MS orchard mix sources (six new roots) were greater than that of the FL orchard mix source (three new roots). At 18 and 23 °C, values of NRNO for the AL GFA source (18 °C: 41

*Table 3.* Probabilities of a greater *F*-value (Pr > *F*) in the analyses of covariance of $\Psi_{pd}$ (predawn xylem water potential), number of new roots (NRNO), new root surface area (NRSA), and root hydraulic conductivity ($L_R$) of three seed sources each of shortleaf, loblolly, and longleaf pine seedlings in response to root-zone temperature and water availability treatments for 28 days in a greenhouse.

| Source | $\Psi_{pd}$ | | NRNO | | NRSA | | $L_R$ | |
|---|---|---|---|---|---|---|---|---|
| | df[1] | Pr > *F* | df | Pr > *F* | df | Pr > *F* | df | Pr > *F* |
| *Shortleaf pine* | | | | | | | | |
| RCD(covariate) | 1 | 0.8014 | 1 | 0.4920 | 1 | 0.8955 | 1 | 0.8463 |
| Block (*B*) | 1 | 0.0367 | 1 | 0.0947 | 1 | 0.1359 | 1 | 0.0262 |
| Temperature (*T*) | 2 | 0.1290 | 2 | 0.0032 | 2 | 0.0172 | 2 | 0.0141 |
| Error (*T* × *B*) | 2 | | 2 | | 2 | | 2 | |
| Water (*W*) | 2 | 0.0001 | 2 | 0.0001 | 2 | 0.0028 | 2 | 0.0009 |
| Seed source (*S*) | 2 | 0.1422 | 2 | 0.5439 | 2 | 0.5686 | 2 | 0.0067 |
| *W* × *S* | 4 | 0.8266 | 4 | 0.8773 | 4 | 0.9989 | 4 | 0.2492 |
| *W* × *T* | 4 | 0.5010 | 4 | 0.6965 | 4 | 0.0614 | 4 | 0.0339 |
| *T* × *S* | 4 | 0.2030 | 4 | 0.4957 | 4 | 0.5395 | 4 | 0.0016 |
| *W* × *T* × *F* | 8 | 0.6285 | 8 | 0.8670 | 8 | 0.8483 | 8 | 0.0878 |
| Error (MSE) | 23 | | 23 | | 23 | | 23 | |
| *Loblolly pine* | | | | | | | | |
| RCD (covariate) | 1 | 0.4052 | 1 | 0.1527 | 1 | 0.7308 | 1 | 0.0239 |
| Block (*B*) | 1 | 0.7647 | 1 | 0.2630 | 1 | 0.2659 | 1 | 0.1451 |
| Temperature (*T*) | 2 | 0.0622 | 2 | 0.0024 | 2 | 0.0039 | 2 | 0.0051 |
| Error (*T* × *B*) | 2 | | 2 | | 2 | | 2 | |
| Water (*W*) | 2 | 0.0001 | 2 | 0.0001 | 2 | 0.0001 | 2 | 0.0001 |
| Seed source (*S*) | 2 | 0.0995 | 2 | 0.0225 | 2 | 0.4187 | 2 | 0.0108 |
| *W* × *S* | 4 | 0.5065 | 4 | 0.4560 | 4 | 0.4675 | 4 | 0.4695 |
| *W* × *T* | 4 | 0.0371 | 4 | 0.3183 | 4 | 0.0001 | 4 | 0.5172 |
| *T* × *S* | 4 | 0.5053 | 4 | 0.0186 | 4 | 0.4503 | 4 | 0.1679 |
| *W* × *T* × *F* | 8 | 0.9550 | 8 | 0.9832 | 8 | 0.4263 | 8 | 0.9824 |
| Error (MSE) | 23 | | 23 | | 23 | | 23 | |
| *Longleaf pine* | | | | | | | | |
| RCD (covariate) | 1 | 0.2635 | 1 | 0.4777 | 1 | 0.0384 | 1 | 0.2707 |
| Block (*B*) | 1 | 0.1440 | 1 | 0.1331 | 1 | 0.2992 | 1 | 0.2091 |
| Temperature (*T*) | 2 | 0.3090 | 2 | 0.0021 | 2 | 0.0116 | 2 | 0.0151 |
| Error (*T* × *B*) | 2 | | 2 | | 2 | | 2 | |
| Water (*W*) | 2 | 0.0001 | 2 | 0.0001 | 2 | 0.0027 | 2 | 0.0001 |
| Seed source (*S*) | 2 | 0.0560 | 2 | 0.0001 | 2 | 0.0007 | 2 | 0.0401 |
| *W* × *S* | 4 | 0.4031 | 4 | 0.9008 | 4 | 0.6563 | 4 | 0.1703 |
| *W* × *T* | 4 | 0.1297 | 4 | 0.7734 | 4 | 0.1616 | 4 | 0.0300 |
| *T* × *S* | 4 | 0.9379 | 4 | 0.0007 | 4 | 0.0752 | 4 | 0.6152 |
| *W* × *T* × *F* | 8 | 0.4976 | 8 | 0.8386 | 8 | 0.9239 | 8 | 0.5866 |
| Error (MSE) | 23 | | 23 | | 23 | | 23 | |

Root collar diameter (RCD) was the covariate.
df, degrees of freedom.

new roots; 23 °C: 75 new roots) were greater than those of the MS orchard mix source (18 °C: 31 new roots; 23 °C: 48 new roots). The AL GFA source (0.17 $\mu$mol/s/mm$^2$) also had a significantly greater $L_R$ than the MS orchard mix source (0.14 $\mu$mol/s/mm$^2$).

For the three seed sources of each species, linear relationships between $L_R$ and ORDW were not significant, but those between $L_R$ and NRSA were significant with the largest coefficient of determination for the MS full-sib loblolly pine source ($R^2$ = 0.5901, $S_{y \cdot x}$ = 0.09 $\mu$mol/s/mm$^2$). All other coefficients of determination ranged between $R^2$ = 0.1563 ($S_{y \cdot x}$ = 0.11 $\mu$mol/s/mm$^2$) for the FL orchard mix longleaf pine source and $R^2$ = 0.5461 ($S_{y \cdot x}$ = 0.12 $\mu$mol/s/mm$^2$) for the TX full-sib loblolly pine source.

Relationships between $L_R$ and NRSA suggested that the response of $L_R$ to NRSA differed by seed source for shortleaf and loblolly pine (Figure 7a–f). The $L_R$-NRSA regressions among the shortleaf and loblolly pine sources were characterized by dissimilar $s^2$, and therefore, could not be compared by the $F$ statistic (shortleaf pine: TX1 half-sib $s^2$, 0.005 $\mu$mol/s/mm$^2$; TX2 half-sib $s^2$, 0.017 $\mu$mol/s/mm$^2$; TX3 woods-run $s^2$, 0.012 $\mu$mol/s/mm$^2$; loblolly pine: TX full-sib $s^2$, 0.015 $\mu$mol/s/mm$^2$; MS full-sib $s^2$, 0.008 $\mu$mol/s/mm$^2$; LA-TX GFA $s^2$, 0.011 $\mu$mol/s/mm$^2$). Slopes of the $L_R$-NRSA regressions among the three sources each of shortleaf and loblolly pine suggested, however, that the TX2 half-sib shortleaf pine source and the TX full-sib loblolly pine source conducted more water per unit of NRSA compared to the remaining two sources of each species (Figure 8a, b).

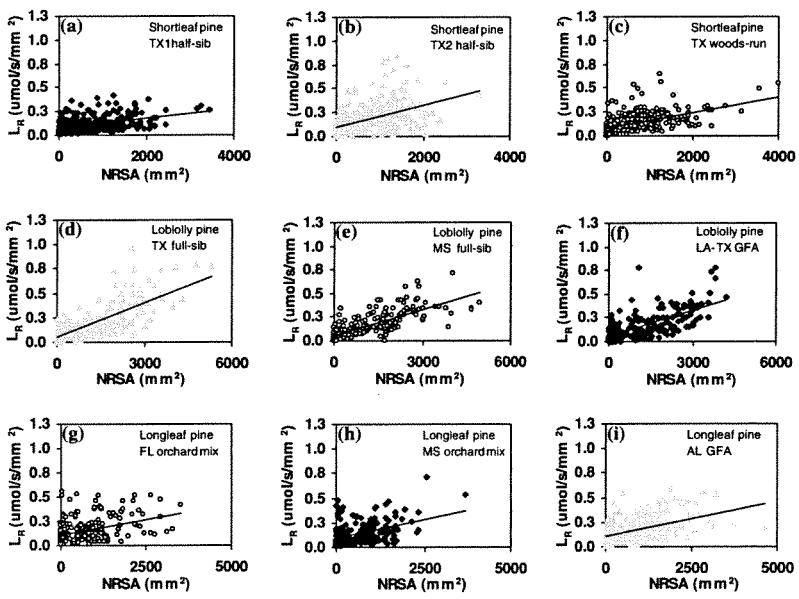


*Figure 7.* Linear relationship between hydraulic conductivity ($L_R$) and new root surface area (NRSA) for three seed sources each of (a–c) shortleaf, (d–f) loblolly, and (g–i) longleaf pine after exposure to root-zone temperatures of 13, 18, and 23 °C for 28 days in a greenhouse.

## Discussion

### *Species response*

Root-zone temperatures in our study are representative of those during the November through March planting window and subsequent period of maximum pine root growth in the South (USDA Forest Service 1989; Sword Sayer and Tang 2004). For example, container-grown seedlings planted on the Palustris Experimental Forest, Rapides Parish, LA between November and March were exposed to average midday surface soil temperatures ranging between 4 and 17 °C over a 10-year period (Figure 9). As the soil warmed between March and June, midday surface soil temperature ranged between 16 and 26 °C.

Dalton and Messina (1994) reported that the mean $\Psi_{pd}$ between April and October of loblolly pine seedlings planted in January was −0.4 MPa. Extreme $\Psi_{pd}$ at these Texas sites occurred in late summer with values of −1.2 MPa in shelterwood and −2.0 to −2.4 MPa in clearcut environments. With potted loblolly pine seedlings, Barnes (2002) defined moderate water stress as $\Psi_{pd}$ of −0.8 MPa, and no water stress as $\Psi_{pd}$ of −0.45 MPa. Seiler and Johnson (1985) reported that well-watered and water stressed 1-year-old loblolly pine seedlings had mean $\Psi_{pd}$ of −0.9 and −1.4 MPa, respectively. In our study, $\Psi_{pd}$

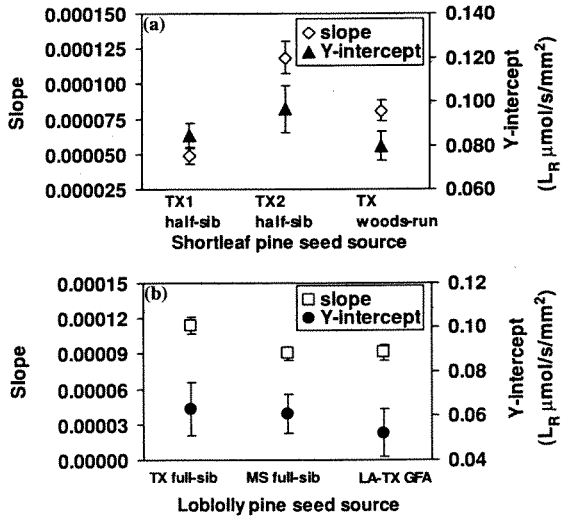


*Figure 8.* Regression parameters (slope and Y-intercept) for the linear relationship between hydraulic conductivity ($L_R$) and new root surface area (NRSA) of three sources each of (a) shortleaf pine and (b) loblolly pine after exposure to root-zone temperatures of 13, 18, and 23 °C for 28 days in a greenhouse. Error bars represent ±1 standard error of the mean.

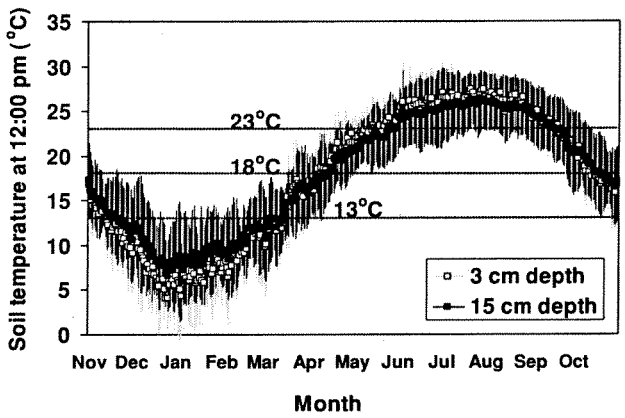


*Figure 9.* Mean midday (12:00 pm CST) soil temperatures at the 3 and 10 cm depths between January 1994 and December 2003 in an open field on the Palustris Experimental Forest, Rapides Parish, LA. Error bars represent ±1 standard deviation of the mean.

of shortleaf, loblolly, and longleaf pine seedlings exposed to moderate, mild, and no water stress ranged between −0.78 and −0.61 MPa, −0.81 and −0.53 MPa, and −0.67 and −0.49 MPa, respectively. These $\Psi_{pd}$ values represent subtle water deficits that might occur due to site characteristics, climate, site preparation methods, or planting time.

Root growth responses in our study support previous research results indicating that pine seedling root growth is positively related to root-zone temperature and negatively related to water stress (Nambiar et al. 1982; Andersen et al. 1986; Carlson 1986; Brissette and Chambers 1992). We found 86%, and 80% increases in NRNO and NRSA, respectively, in response to a root-zone temperature increase from 18 to 23 °C, and a progressive decrease in root growth as water became less available.

Consistent with past research results (Brissette and Chambers 1992; Calrson 1986), we found that the effects of root-zone temperature and water availability on root growth were reflected in $L_R$. Carlson (1986) also reported that across a range of root volumes, loblolly pine seedling $L_R$ was a function of old root system volume. In contrast, we found no relationship between $L_R$ and ORDW for any species. Absence of a relationship between $L_R$ and ORDW may be attributed to the narrow range of seedling size in our study. By selecting seedlings within one standard deviation of the mean RCD of 100 randomly selected seedlings, we reduced the possibility of observing a relationship between $L_R$ and ORDW.

In addition to maximizing root growth, higher root-zone temperature mitigated negative effects of water stress on NRNO and $L_R$. At 18 °C, NRNO and $L_R$ decreased significantly with the occurrence of mild water stress. However, at

23 °C, a significant decrease in NRNO and $L_R$ did not occur until moderate water stress was reached. Regeneration guidelines recommend that southern pine be planted when conditions favor root growth, before the onset of seasonal water deficits (Barnett and Brissette 1986; USDA Forest Service 1989). Our results indicate that maintenance of $L_R$ under mild water stress will likely be gained by following this recommendation. Furthermore, site preparation methods and adjustments in planting time that elevate soil temperature may stimulate root growth and maintain $L_R$ after planting. This effect was demonstrated by Balisky and Burton (1997) who found that management-induced increases in soil temperature stimulated the root growth of planted lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.).

Although the $L_R$ and root growth of all three species responded positively to an increase in root-zone temperature, species differed in the magnitude of these responses. At 13 °C, for example, root growth was minimal for all species, but the $L_R$ of longleaf pine was 63% greater than those of shortleaf and loblolly pine. Furthermore, the $L_R$ of longleaf pine at 13 °C was similar to that at 18 °C. With adequate water, longleaf pine may be uniquely adapted to maintain $L_R$ in cool soils. This adaptation could be beneficial to naturally regenerated longleaf pine because, unlike shortleaf and loblolly pine seed which germinate in spring, longleaf pine seed germinates immediately after dispersing in fall (Derr and Mann 1971; US Department of Agriculture 1974). Because soil temperatures in spring and early summer are favorable for root growth, it is likely that the $L_R$ of newly germinated shortleaf and loblolly pine seedlings is maintained. If the root growth of newly germinated longleaf pine is limited by cool fall and winter soil temperatures, an inherent maintenance of $L_R$ ensures some survival of naturally regenerated seedlings.

We also observed that the magnitude of increase in $L_R$ and root growth was greater for loblolly pine compared to shortleaf and longleaf pine as root-zone temperature increased from 18 to 23 °C. Regeneration success is closely correlated with root growth (Wakeley 1954; Carlson 1986; Larsen et al. 1986; Hallgren and Tauer 1989). As the soil warms, therefore, loblolly pine may outperform shortleaf and longleaf pine during establishment.

Our study describes a range of xylem water potential for newly planted shortleaf, loblolly, and longleaf pine in which $L_R$ and root growth respond positively to an increase in soil temperature up to 23 °C. Specifically, shortleaf, loblolly, and longleaf pine were exposed to water stress levels corresponding to $\Psi_{pd}$ of −0.61 to −0.78 MPa, −0.53 to −0.81 MPa, and −0.49 to −0.67 MPa, respectively. Therefore, an increase in soil temperature will be advantageous to the root growth and $L_R$ of these species even when water limitations yield $\Psi_{pd}$ as low as −0.8 MPa for shortleaf and loblolly pine and −0.7 MPa for longleaf pine.

When water availability is sub-optimal, however, the species of choice may change. With data for root-zone temperatures of 18 and 23 °C combined, the response of NRSA to $\Psi_{pd}$ differed among species and among longleaf pine sources. Comparison of slope and Y-intercept values of $\ln(-\Psi_{pd}) - \ln(\text{NRSA} + 1)$ linear regressions suggests that in the absence of water stress, the NRSA of

loblolly pine exceeded that of the AL GFA longleaf pine source. As $\Psi_{pd}$ decreased, however, the NRSA of the AL GFA longleaf pine source surpassed that of loblolly pine. This information provides a rationale for planting longleaf pine rather than loblolly pine during multiple-year drought, on sites that are prone to drought, or when seedlings are planted late and there is a risk of exposure to seasonal drought.

*Seed source response*

In addition to root-zone temperature and water availability, seed source significantly affected the root growth and $L_R$ of all three species. Two patterns of seed source effect were observed. First, the TX2 half-sib shortleaf pine source had a greater $L_R$ compared to the other two shortleaf pine sources. Because NRNO and NRSA were unaffected by seed source, greater $L_R$ of the TX2 half-sib source could not be attributed to higher amounts of root growth. The TX full-sib loblolly pine source behaved similarly. Comparison of slopes associated with the $L_R$-NRSA relationship of the shortleaf and loblolly pine sources suggests that the TX2 half-sib shortleaf pine source and the TX full-sib loblolly pine source transported more water per unit of NRSA compared to the other two sources of each species. Further research is warranted to determine the potential benefit of selecting seed sources based on the amount of water they conduct relative to their root growth after planting.

We observed a second type of seed source effect on $L_R$ characterized by simultaneous increases in root growth and $L_R$. The NRSA, and $L_R$ of the AL GFA longleaf pine seedlings were greater than those of the MS orchard mix longleaf pine seedlings, but the $L_R$-NRSA relationships among the longleaf pine sources did not differ. It appears as though the larger $L_R$ of the AL GFA source compared the MS orchard mix source was primarily a function of root growth.

The AL GFA longleaf pine seedlings were characterized by more root growth and a larger $L_R$, but had a smaller RCD compared to the MS orchard mix longleaf pine seedlings. It is recommended that high-quality container-grown longleaf pine seedlings have a RCD of at least 6.4 mm (Barnett et al. 2002). However, if container size becomes limiting to longleaf pine root growth during seedling production, and the taproot continues to grow so that the RCD greatly exceeds 6.4 mm, root growth and therefore, $L_R$ after planting may not reach their maximum potential. After longleaf pine reaches a threshold size, field performance may be more a function of cultural conditions rather than stock size.

## Conclusions

It is apparent that across the range of water availabilities in our study, southern pine seedling root system growth and water transport are stimulated by soil

temperatures up to and perhaps above 23 °C. Because the limitations that water stress imparted on root growth were tempered by an increase in root-zone temperature, we suggest that regeneration practices that elevate soil temperature without decreasing water availability are optimum in the South.

Our comparison of three southern pine species presents two rationales for species selection in distinct planting environments. Specifically, longleaf pine seems better adapted to avoid desiccation in cold soil than shortleaf and loblolly pine. This may represent an advantage of longleaf pine over the other two species when the duration between planting in fall or winter and the onset of soil warming in spring is great. We also found that although the root growth and water transport of loblolly pine was greater than that of longleaf pine in the absence of water limitations, the root growth of one source of longleaf pine surpassed that of loblolly pine as water availability decreased. On dry sites or where water deficits are anticipated, therefore, the establishment of longleaf pine may be superior to that of loblolly pine.

Finally, seed source affected the new root growth and $L_R$ of all three species. For longleaf pine, the transport of water by different longleaf pine sources was closely associated with the production of new roots. In contrast, one source each of shortleaf and loblolly pine were characterized by greater $L_R$ without a comparable effect of seed source on root production. Further research is needed to determine if water conductance per unit of new root growth after planting is a useful variable to screen seed sources for planting on sites where water deficit limits root growth.

## Acknowledgements

The authors express great appreciation to John McGilvray, Dan Andries, and Chuck Stangle for the development and maintenance of the seedling growth system used in this study, and for their dedication to seedling production, experimental, and laboratory phases of this study. Further acknowledgement is extended to J.C. Goelz for assistance with linear regression analyses.

## References

Andersen C.P., Sucoff E.I. and Dixon R.K. 1986. Effects of root zone temperature on root initiation and elongation in red pine seedlings. Can. J. For. Res. 16: 696–700.

Baker J.B. 1992. Natural regeneration of shortleaf pine. In: Proceedings of the Shortleaf Pine Regeneration Workshop; Little Rock, Arkansas; October 29–31, 1991. USDA Forest Serv., Southern Forest Experiment Sta., New Orleans, Louisiana Gen. Tech. Rep. SO-90, pp. 102–112.

Balisky A.C. and Burton P.J. 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. New For. 14: 63–82.

Barnes A.D. 2002. Effects of phenology, water availability and seed source on loblolly pine biomass partitioning and transpiration. Tree Physiol. 22: 733–740.

Barnett J.P. and Dennington R.W. 1992. Return to longleaf. Forest Farmer 52: 11–12.

Barnett J.P., Lauer D.K. and Brissette J.C. 1990. Regenerating longleaf pine with artificial methods. In: Proceedings of the Symposium on the Management of Longleaf Pine. USDA Forest Serv., Southern Forest Experiment Sta., New Orleans, Louisiana Gen. Tech. Rep. SO-75, pp. 72–92.

Barnett J.P. 2002. Longleaf pine: Why plant it? Why use containers? In: Barnett J.P., Dumroese R.K. and Moorhead D.J. (eds), Proceedings of Workshops on Growing Longleaf Pine in Containers – 1999 and 2001. USDA Forest Serv., Southern Research Sta., Asheville, North Carolina Gen. Tech. Rep. SRS-56, pp. 5–7.

Barnett J.P., Hainds M.J. and Hernandez G.A. 2002. Interim guidelines for growing longleaf seedlings in containers. In: Barnett J.P., Dumroese R.K. and Moorhead D.J. (eds), Proceedings of Workshops on Growing Longleaf Pine in Containers – 1999 and 2001. USDA Forest Serv., Southern Research Sta., Asheville, North Carolina Gen. Tech. Rep. SRS-56, pp. 27–29.

Barnett J.P. and Brissette J.C. 1986. Producing Southern Pine Seedlings in Containers. USDA Forest Serv., Southern Forest Experiment Sta., New Orleans Louisiana Gen. Tech. Rep. SO-59, 71 p.

Barnett J.P. and Brissette J.C. 2004. Stock type affects performance of shortleaf pine planted in the Ouachita Mountains through 10 years. In: Connor K.F. (ed), Proceedings of the 12th Biennial Southern Silvicultural Research Conference; Biloxi, Mississippi, February 24–28, 2003. USDA Forest Serv., Southern Research Sta., Asheville North Carolina Gen. Tech. Rep. SRS-71, pp. 420–422.

Barnett J.P. and McGilvray J.M. 1997. Practical guidelines for producing longleaf pine seedlings in containers. USDA Forest Serv., Southern Research Sta., Asheville, North Carolina. Gen. Tech. Rep. SRS-14, 28 p.

Barrett J.W. 1995. Regional Silviculture of the United States. 3rd edn. John Wiley & Sons, New York, 643 p.

Bongarten B.C. and Teskey R.O. 1987. Dry weight partitioning and its relationship to productivity in loblolly pine seedlings from seven sources. For. Sci. 33: 255–267.

Brissette J.C. and Carlson W.C. 1986. Effects of nursery bed density and fertilization on the morphology, nutrient status, and root growth potential of shortleaf pine seedlings. In: Proceedings of the 4th Biennial Southern Silvicultural Research Conference; Atlanta, Georgia; November 4–6, 1986. USDA Forest Serv., Southeastern Forest Experiment Sta. Asheville, North Carolina Gen. Tech. Rep. SE-42, pp. 198–205.

Brissette J.C. and Chambers J.L. 1992. Leaf water status and root system water flux of shortleaf pine (*Pinus echinata* Mill.) seedlings in relation to new root growth after transplanting. Tree Physiol. 11: 289–303.

Carlson W.C. 1986. Root system considerations in the quality of loblolly pine seedlings. South. J. Appl. For. 10: 87–92.

Dalton C.T. and Messina M.G. 1994. Water relations and growth of loblolly pine seedlings planted under a shelterwood and in a clear-cut. Tree Physiol. 15: 19–26.

Derr H.J. and Mann W.F. Jr. 1971. Direct-Seeding Pines in the South. USDA Forest Serv., Washington, D.C Agriculture Handbook No. 391, 68 p.

Dougherty P.M. and Duryea M.L. 1991. Regeneration: An overview of past trends and basic steps needed to ensure future success. In: Duryea M.L. and Dougherty P.M. (eds), Forest Regeneration Manual. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 3–7.

Hallgren S.W. and Tauer C.G. 1989. Root growth potential, first-year survival, and growth of shortleaf pine seedlings show effects of lift date, storage, and family. South. J. Appl. For. 13: 163–169.

Hallgren S.W., Tauer C.G. and Weeks D.L. 1993. Cultural, environmental, and genetic factors interact to affect performance of planted shortleaf pine. For. Sci. 39: 478–498.

Jose S., Merritt S. and Ramsey C.L. 2003. Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water, and nitrogen. For. Ecol. Manage. 180: 335–344.

Larsen H.S., South D.B. and Boyer J.M. 1986. Root growth potential, seedling morphology and bud dormancy correlate with survival of loblolly pine seedlings planted in December in Alabama. Tree Physiol. 1: 253–263.

Mexal J.G. and South D.B. 1991. Bareroot Seedling Culture. In: Duryea M.L. and Dougherty P.M. (eds), Forest Regeneration Manual. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 89–115.

Nambiar E.K., Bowen G.D. and Sands R. 1979. Root regeneration and plant water status of *Pinus radiata* D. Don seedlings transplanted to different soil temperatures. J. Exper. Bot. 30: 1119–1131.

Nambiar E.K., Cotterill P.P. and Bowen G.D. 1982. Genetic differences in the root regeneration of radiata pine. J. Exper. Bot. 33: 170–177.

Neter J. and Wasserman W. 1974. Applied Linear Statistical Models Regression, Analysis of Variance, and Experimental Designs. Richard D. Irwin Inc, Homewood, IL, 842 p.

Outcalt K.W. 2000. The longleaf pine ecosystem of the south. Native Plants J. 1: 42–53.

Rietveld W.J. 1989. Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. North. J. Appl. For. 6: 99–107.

Samuelson L.J. 2000. Effects of nitrogen on leaf physiology and growth of different families of loblolly and slash pine. New For. 19: 95–107.

SAS Institute Inc. 1991. SAS Procedures Guide, Release 6.03 Edition. SAS Institute, Cary, NC, 441 p.

Schultz R.P. 1997. Loblolly pine, the ecology and culture of loblolly pine (*Pinus taeda* L.). Agricultural Handbook 713. USDA Forest Serv., Washington, D.C, 494 p.

Seiler J.R. and Johnson J.D. 1985. Photosynthesis and transpiration of loblolly pine seedlings as influenced by moisture-stress conditioning. For. Sci. 31: 742–749.

Smith O.D. Jr. 1992. Historical perspectives on regeneration in the Ouachita and Ozark Mountains – The Ozark National Forest. In: Proceedings of the Shortleaf Pine Regeneration Workshop; Little Rock, Arkansas; October 29–31, 1991. USDA Forest Serv, Southern Forest Experiment Sta., New Orleans, Louisiana. Gen. Tech. Rep. SO-90, pp. 7–11.

Snow M.D. and Tingey D.T. 1985. Evaluation of a system for the imposition of plant water stress. Plant. Physiol. 77: 602–607.

Sword Sayer M.A. and Tang Z. 2004. Long-term root growth response to thinning, fertilization, and water deficit in plantation loblolly pine. In: Proceedings of the 12th Biennial Southern Silvicultural Research Conference; Biloxi, MS; February 24–28, 2003. USDA Forest Serv. Southern Research Sta., Asheville, North Carolina. Gen. Tech. Rep. SRS-71, pp. 458–464.

Steel R.G.D. and Torrie J.H. 1980. Principles and Procedures of Statistics A Biometrical Approach. 2nd ed. McGraw-Hill, New York, pp. 633

US Department of Agriculture 1974. Seeds of Woody Plants in the United States. USDA Agriculture Handbook No. 450, Washington D.C, 883 p.

USDA Forest Service 1989. A Guide to the Care and Planting of Southern Pine Seedlings. USDA Forest Service Man. Bull R8-MB39. USDA Forest Serv. Atlanta, GA, pp. 44

Wakeley P.C. 1954. Planting the southern pines, USDA Monogr. 18. USDA Forest Serv. 233 p.

Walker W.D. 1992. Historical perspectives on regeneration in the Ouachita and Ozark Mountains – The Ozark National Forest. In: Proceedings of the Shortleaf Pine Regeneration Workshop; Little Rock, Arkansas; October 29–31, 1991. USDA Forest Serv., Southern Forest Experiment Sta., New Orleans, Louisiana. Gen. Tech. Rep. SO-90, pp.12–17.

Wittwer R.F. and Shelton M.G. 1992. Seed production in natural shortleaf pine stands. In: Proceedings of the Shortleaf Pine Regeneration Workshop; Little Rock, Arkansas; October 29–31, 1991. USDA Forest Serv. Southern Forest Experiment Sta., New Orleans, Louisiana. Gen. Tech. Rep. SO-90, pp. 113–123.