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# Competition-Induced Reductions in Soil Water Availability Reduced Pine Root Extension Rates

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## ABSTRACT

**The relationship between soil water availability, root extension, and shoot growth of loblolly pine seedlings (*Pinus taeda* L.) was evaluated in a rhizotron sand mixture in the absence and presence of crabgrass (*Digitaria* spp.) competition. Heights and diameters of seedlings grown with crabgrass were reduced 33 and SO%, respectively, compared with seedlings grown in pine monoculture. Furthermore, survival of seedlings was reduced by 16% in the mixed species treatments compared with pine monoculture cells. Soil water contents at all depths were at least 50% lower in mixed species treatments compared with pine monocultures during a dry-down cycle. Maximum loblolly pine root extension rate was 0.10 m $wk^{-1}$ in pine monoculture compared with 0.02 m $wk^{-1}$ in the presence of grass. Pine seedling root extension ceased in the presence of grass during prolonged periods of induced water stress. Crabgrass roots extended at a rate of 0.6 m $wk^{-1}$, a rate largely unaffected by watering regime or differences in water content within the rhizotron. Pine root distributions, at the end of one growing season, were different for seedlings grown with grass than for those in pine monoculture; however, when seedlings of similar size were compared, root distributions were not different. Our results indicate that competition-induced reductions in soil water availability reduced the rate of pine root extension and thus the volume of soil exploited, thereby reducing resource availability and tree growth.**

Evidence from field experiments suggests that water stress is directly responsible for much of the shoot growth reduction associated with competitive interference in young pine plantations (Carter et al., 1984; Shribbs and Skroch, 1985; South and Barnett, 1986; Elliott and White, 1987). Water stress resulting from competitor use of available soil water has both immediate effects on gas exchange and C fixation as well as long-term impacts on physiological processes and seedling development. A strong positive correlation between soil moisture and growth of loblolly pine has been demonstrated (Wenger, 1952; Zahner, 1962; Stransky and Wilson, 1964; Kaufman. 1968; Morris et al., 1993). Reductions in nutrient availability can occur coincident with reduced water availability (Elliott and White, 1987; Morris et al., 1993); however, direct competition for limiting nutrients in young plantations appears more important than water limitations only on sites where high water tables are within the rooting zone and water stress is minimal (Neary et al., 1990).

Distribution of roots within the solum will affect the water and nutrient pool accessible to the tree. Most evidence suggests that after an initial period of free interpenetrating root growth, alterations in seedling root growth patterns occur due to soil water or nutrient depletion by neighboring vegetation (Spurway, 1980). These changes in root distribution may determine the ability of a seedling to compete for spatially stratified water and nutrient resources during subsequent water stress periods. In this regard, both direct effects of reduced soil water potential and indirect effects associated with increased soil resistance to penetration can alter root distribution. Torreano (1992) found that in the absence of growth-limiting physical resistance, controlled reductions in soil water potential affected only root elongation rates and had little effect on pine seedling root distribution. Whether this result can be generalized to include pine root response to patterns of water depletion from competitor withdrawals is unknown.

In this study, we had four objectives: (i) to quantify aboveground and belowground growth response of loblolly pine and a grass competitor to drought, (ii) to evaluate the relationship between soil water depletion and root elongation rates of loblolly pine seedlings, (iii) to determine if localized use of soil water by a grass competitor would alter pine root distribution compared with that found in a similar monoculture environment, and (iv) to evaluate the effectiveness of mycorrhizal inoculation in reducing drought stress.

## MATERIALS AND METHODS

The influences of grass competition and mycorrhizal inoculation on growth of loblolly pine seedlings were evaluated under controlled rhizotron conditions during the summer of 1991. The work was conducted in the University of Georgia Whitehall Experimental Forest rhizotron described by Torreano (1992). The experimental design was a factorial combination of two competition treatments (pine alone and pine grown in mixture with crabgrass) and two ectomycorrhizal inoculation treatments (noninoculated and inoculated with *Pisolithus tinctorius* Pers. Coker and Couch) replicated in three complete blocks.

The rhizotron consisted of 16 individual 1 by 1 by 2 m (length by width by depth) cells with a tempered-glass plate installed at a 7” angle as the inner wall. Rhizotron cells were filled with an artificial soil medium of washed sand (no. 10 fine masonry sand, Curtis Brothers, Watkinsville, GA) and fritted clay (Terra Green Soil Conditioner, Southern Turf Co., Norcross, GA) in a 5:1 ratio by volume. The mixture had a sandy loam texture, provided minimal structural impedance (maximum cone resistance of $<0.5$ MPa), excellent aeration. and uniform nutrient and moisture distribution throughout the cell depth. Nutrient-holding capacity of the mixture was relatively low, allowing easy manipulation of labile nutrient concentrations. Soil nutrient analyses were performed using a double-acid extract (0.05 $M$ HCl plus 0.025 $M$ $H_2SO_4$). Initial concentrations of NH,-N, P, K, Ca, and Mg were 5. 13, 116, 220. and 65 mg $kg^{-1}$, respectively. with measured acidity of pH 5.1 (1:1 soil/water mixture). These conditions were within the range of acidic, nutrient-poor conditions found in southern forest soils (Pritchett and Fisher, 1987).

Union Camp Corporation (Prattville, AL) provided loblolly pine seeds (Family 0225–10–0005-AA) that were germinated

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and planted in Ray Leach tubes filled with the rhizotron soil. Twelve-week-old loblolly pine seedlings were transplanted into the rhizotron and grown for 20 wk as pine monocultures or as mixed species with crabgrass. Four seedlings were planted in each cell to monitor root systems from two seedlings at each rhizotron window. Seedlings were planted 0.25 m apart at 0.17- and 0.42-m distances from the window. Crabgrass seed was purchased from Azline Weed Seed Co. (Leland, MS) and sown 4 wk after seedlings were planted at a rate of 4.2 g, or approximately 7300 large grass seeds, per competition treatment cell.

Vegetative inoculum of the ectomycorrhizal fungus *Pisolithus tinctorius* (Pers.) Coker and Couch (Pt) was provided by Mycorr Tech, Inc. (Pittsburgh, PA). A 100-mL beaker was used to measure commercially prepared vegetative inoculum, which was added to a core of rhizotron soil as the seedlings were transplanted. The inoculum consisted of fungal mycelia grown on a vermiculite-peat moss-nutrient medium substrate, so the hyphae permeated the vermiculite particles. Inoculum that had been killed by steam sterilization was used as the noninoculated control.

Rhizotron cells were well watered for 2 wk while the crabgrass established. For the duration of the experiment, natural rainfall was excluded by rainfall shields moved over the rhizotron cells before precipitation events began. Seedlings were subjected to three dry-down cycles by withholding watering (Weeks 3–4, 5-7, and 10–11). All rhizotron cells were wetted to field capacity when soil water potentials approached -1.5 MPa at 0.30-m depth in the driest rhizotron cell and measured predawn xylem pressure potential was less than -0.3 MPa. All rhizotron cells were kept at field capacity during the fall to monitor root recovery from the previous droughts. Rhizotron cells were watered with a complete nutrient mix of Miller's Special Greenhouse Formula 20-20-20 at the beginning of each drying and recovery period for a total of six fertilizations. Total additions of elemental N, P, and K to each treatment cell were 68, 29, and 56 g, respectively. Micronutrient additions per treatment cell included Fe (0.34 g); Cu, Mn, and Zn (0.17 g each); B (0.1 g); and Mo (0.002 g).

Soil water content was monitored using time domain reflectometry (Topp et al., 1982). Pairs of stainless steel probes were placed at 0.05-, 0.15-, 0.30-, 0.60-, 0.90-, and 1.50-m depths as the rhizotron cells were filled. Coaxial cable was connected to each pair of rods and permanently affixed through cell bottom drain ports to allow easy access. A Tektronix cable tester (Tektronix Model 1502B TDR Cable Tester, Beaverton, OR) was used to measure the reflected signal. Readings were registered in millivolts and related to steel probe length, with a resulting value $k$ used to calculate soil water content using the equation from Topp et al. (1982). Soil water content was evaluated every 2 d throughout the growing season. Soil water characteristic curves, developed using intact cores and Tempe cells, were used to convert soil water content to soil water potential.

Xylem pressure potential (XPP) was measured using a pressure bomb (Scholander et al., 1965) on one fascicle from the main stem of one seedling per rhizotron cell. Predawn measurements were made beginning at 04:00 and were followed by solar noon readings later that day. Each series of readings was completed within 1 h. A steady-state porometer (Model no. LI-1600, LI-COR Inc., Lincoln, NE) was used to measure stomatal conductance and transpiration at least once per week to assess seedling aboveground growth responses. Fascicle leaf area was measured using a portable leaf area meter (LI-COR Model 3000).

Seedling height and diameter were measured weekly. Diameter measurements were made 0.01 m below the cotyledon, and height measurements were recorded as the distance from that mark to the bud tip. Incremental diameter growth was calculated as the change in diameter during a time interval. Aboveground seedling biomass was determined at the end of the experiment. Dry weights (70°C) of stems, branches, and needles were recorded by growth flush to the nearest 0.5 g.

Root tracings were made on Herculene acetate sheets twice weekly for loblolly roots and weekly for grass roots. Physical differences in root appearance of pine and grass simplified identification. Typically, pine roots had suberized and unsuberized lengths that were readily discernible. Pine roots were also generally thicker ($>0.001$ m) and more opaque than grass roots, which were very thin ($<0.0005$ m) and transparent. Roots observed at each window were considered to be viewed within a 3-mm distance of the glass plate (Torreano, 1992), and rooting density was calculated in a volume of soil 1 by 1.85 m by 3 mm (0.00555 $m^3$). Individual lines of all tracings were color coded and dated. Suberized and unsuberized loblolly roots were individually coded for each measurement interval. Grass roots were color coded by measurement period only. At the end of the experiment, individual root tracings were measured using a Lasico linear probe (Model no. 71A-M, Los Angeles, CA), and root extension rates and distribution patterns were determined. Relative root growth was calculated as the proportion of root length grown at a specific water potential per day compared with the maximum root length grown per day.

Soil cores were collected at the end of the experiment in 0.15-m increments to a depth of 1.50 m. For each cell, a subsample of loblolly pine roots totaling between 0.5- and 1.0-m length was examined under a microscope to identify root-infecting fungi. Speciation of ectomycorrhizal fungi was based on morphotype, and populations were recorded as infection percentage and number of tips per 1.0 m of root.

Introducing Pt to the transplanted seedlings was ineffective as a main treatment because native mycorrhizal inoculant was abundant and natural infection of greenhouse-grown seedlings was high. Consequently, the experiment was analyzed as a randomized complete block design with two competition treatments, three blocks, and two replicates. Where appropriate, soil depths were evaluated as splits within main treatment plots. Data on aboveground and belowground parameters were analyzed using appropriate analysis of variance procedures of SAS (SAS Institute, 1985) and reported at the 0.05 level of significance. Duncan's multiple-range test was used to separate means at the 0.05 level of significance. Regression analyses were conducted to evaluate relationships between soil water content and pine root growth.

## RESULTS

Presence of crabgrass in the rhizotron cells corresponded to reductions in soil water content of >50% at each depth in dried mixed-species cells compared with dried pine monoculture cells (Fig. 1). Moisture depletion patterns in pine monoculture cells reflected pine root distribution. Competitor-induced decreases in soil water content were evident as early as 1 wk after grass emergence (Fig. 2A) and were significant ($P > F \leq 0.04$) for all measurements to a depth of 0.90 m during the drying cycles.

Seedling stress, as indicated by predawn XPP, was greater in the mixed-species treatments than the pine monoculture treatment (Fig. 2B). During dry-down cycles, pine seedlings quickly reached a stress level beyond

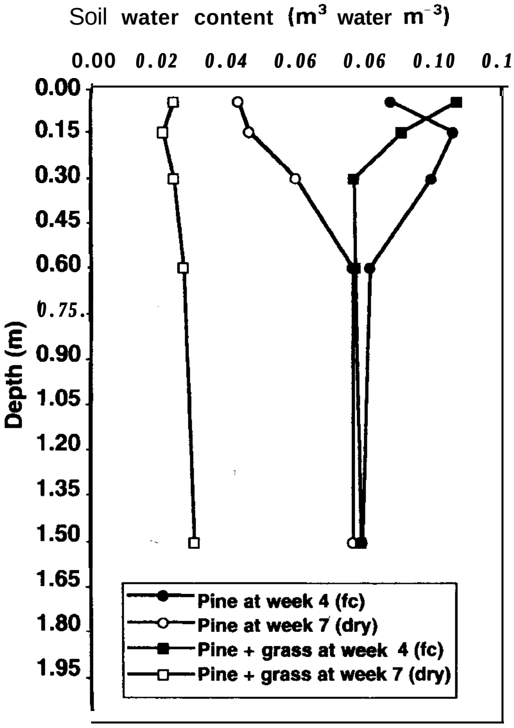

**Fig. 1. Soil water contents for rhizotron profiles of loblolly pine seedlings grown in monocultures or in mixed species, measured at field capacity (fc) and on the 10th day of a dry-down cycle (dry).**

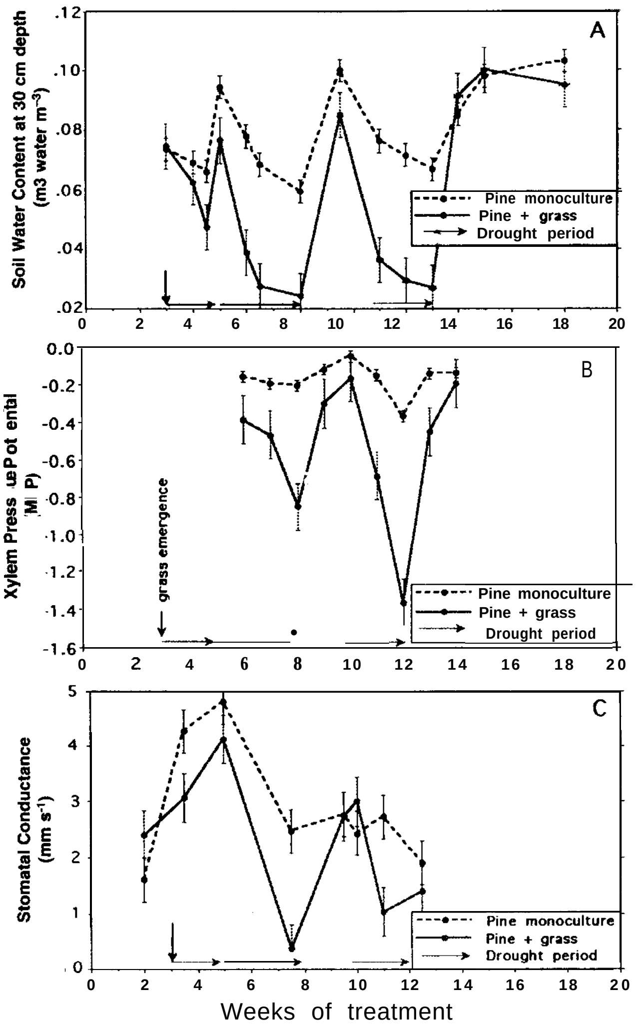

**Fig. 2. Treatment averages of (A) soil water content, (B) xylem pressure potential, and (C) stomatal conductance through time for loblolly pine seedlings grown in monoculture or in mixed species with crabgrass for 20 wk (July-November).**

the expected permanent wilting point of -1.5 MPa. Concurrent decreases in stomatal conductance (Fig. 2C) and transpiration also occurred during dry-down cycles. Mortality was 16% in mixed-species cells after two dry-down cycles.

Reduced water availability translated to decreases in seedling diameter, height, and root growth 1 wk after the first dry-down period. Incremental diameter growth of loblolly pine seedlings was reduced during each dry-down cycle (Fig. 3). Incremental diameter growth of pines grown with grass was significantly lower ($P > F \leq 0.032$) than that of seedlings grown in pine monoculture after Week 3. Final seedling diameters were reduced by 50% when grown with grass, and total heights were reduced 33% (Table 1). These differences translated to a decrease in stem volume of >80%. Tissue dry weight was similarly decreased for pine seedlings grown with grass compared with those grown in pine monoculture (Table 1).

Total density of pine seedling root lengths (m $m^{-3}$) grown in monoculture was 10 times greater than that of seedlings grown with herbaceous competition (Table 1). Crabgrass root length was 44 times that of the stressed loblolly seedlings, which indicates that absorption surfaces of these two species differ greatly. Incremental pine root growth was also significantly different ($P > F \leq 0.0002$) for both competition treatments beginning with the first dry-down period (Fig. 4). Loblolly pine roots grew less in rhizotron cells with grass, which was correlated with reduced soil water content.

Loblolly pine roots in monoculture extended to a depth of 1.50 m in 15 wk at an average rate of 0.10 m $wk^{-1}$. Pine roots grown with competitors extended an average of only 0.02 m $wk^{-1}$ and ceased extension after soil water potential exceeded − 1.5 MPa at 0.30-m depth. Pine root extension resumed 2 wk after available soil water was returned to near field capacity. Decreased rates of root elongation occurred before differences in aboveground growth appeared. During the 20-wk experiment, pine roots at the windows developed obvious first- and second-order laterals but few third- or fourth-order lateral roots.

Crabgrass root extension averaged 0.60 m $wk^{-1}$, with some tips reaching the rhizotron floor within 2 wk of germination. Crabgrass root extension continued at the same rate at all soil water contents, but turnover increased as soil water content decreased. During periods of low soil water content, grass roots would grow, die, and replace themselves in 2-wk cycles.

Total root length at the window was tabulated and the proportion of root growth occurring during each wet and dry-down cycle was calculated (Table 2). New pine root length, number of growing root tips, and root

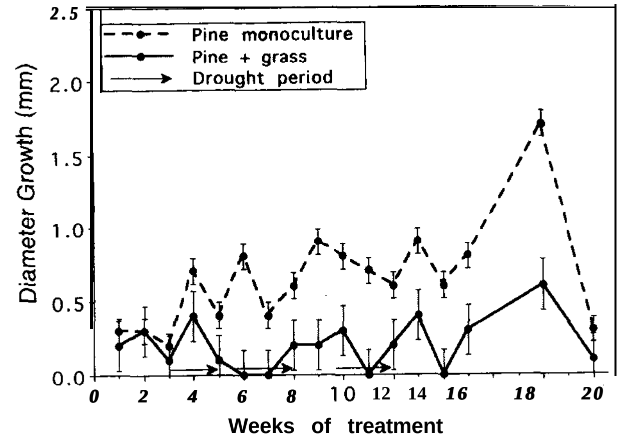

**Fig. 3. Incremental diameter growth of loblolly pine seedlings grown in monoculture or in mixed species with crabgrass for 20 wk (July-November).**

extension rates were almost always lower in the mixed-species treatment than pine monocultures in all measurement periods after the first dry-down cycle (Table 2). Overall, a smaller proportion of total pine roots extended later in the season when seedlings were grown with crabgrass; however, pine root extension rates during the fall (Weeks 12-20) remained similar for both competition treatments (Table 2). Seedling roots in the pine monoculture produced significantly more length ($P > F = 0.0001$) during the final measurement interval as a result of a significantly greater number of actively growing root tips ($P > F = 0.0001$) (Table 2).

When seedlings of similar aboveground size were compared, root distributions were similar. At the end of the experiment, nearly 50% of total roots of seedlings grown with crabgrass were restricted to the upper 0.15 m of soil, compared with 20% in pine monoculture treatments (Fig. 5). Examination of root distributions of seedlings grown with crabgrass (age 32 wk) compared with seedlings of comparable aboveground size in pine monoculture treatments cells (age 19 wk) revealed that loblolly pine root distribution of same-sized seedlings was similar for all treatments, with approximately 50% of the root length concentrated in the upper 0.15 m of soil (Fig. 5).

Seedlings were grown in a greenhouse for 12 wk before inoculation was attempted and root systems had, to a large degree, been infected with the native ***Thelephora terrestris*** Ehrh. ex. Fr. (Tt) by this time. ***Pisolithus tinctorius*** inoculum was added to half of all treatment cells, but multiple species of mycorrhizal infection, including Pt and Tt, were evident in all cells 3 wk after inoculation, thus the inoculation main treatment was never imposed. While total numbers of infected tips and infection percentage of the root systems were not significantly different between inoculation treatments, both values were significantly different ($P > F = 0.02$ and 0.048, respectively) between competition treatments (Table 3). Total mycorrhizal roots and infection percentage were greater in seedlings grown in a pine monoculture; however, infection percentage by Pt was <25% in all treatments. Evaluation of the effectiveness of Pt mycorrhizae in reducing drought stress was not possible.

**Table 1. Average aboveground growth characteristics, biomass?, and root length density for loblolly pine seedlings grown in rhizotron cells as pine monocultures or in mixed species with grass for 20 wk (July-November).**

| Measurement | Pine monoculture | Pine + grass | $P > F$ |
|---|---|---|---|
| Diameter, nun | 1475 | 7.30 | 0.01 |
| Height, nun | 600.00 | 404.00 | 0.01 |
| Needle wt., g seedling-’ | 26.15 | 4.83 | 0.01 |
| Stem wt., g seedling-’ | 14.64 | 3.62 | 0.01 |
| Branch wt., g seedling-.’ | 4.62 | 0.35 | 0.001 |
| Total top, g seedling-’ | 45.37 | 8.80 | 0.01 |
| Pine roots, m m$^{-3}$ | 5024 | 508 | 0.0001 |
| Grass roots, m m$^{-3}$ | 0 | 22 520 | |
| Total roots. m m$^{-3}$ | 5024 | 23 028 | 0.0001 |

† Weights do not include dead seedlings.

## DISCUSSION

Numerous studies have reported pine growth decreases of the magnitude found in this study when pines were grown with herbaceous or woody competitors (Lowenstein et al., 1968; Nelson et al., 1981; Sands and Nambiar, 1984; Bacon and Zedaker, 1987; Morris et al., 1993). The specific mechanism responsible for growth reductions was not generally identified in these studies and probably differs among them; however, reductions in either soil moisture or incident radiation are probably included (Cleary, 1971; Beadle and Jarvis, 1977; Conrad and Radosevich, 1981). In the southeastern USA, the significance of a reduced light environment is generally limited on upland sites during the first growing season following planting (Morris et al., 1993). This observation supports the hypothesis that belowground interactions play an important role in competitive interference.

Decreases in aboveground growth were associated with decreased XPP, stomatal conductance, and transpiration in this study. Others have reported that these measures reflect increasing water stress within the tree resulting from decreasing soil moisture (Kaufman, 1968; Lambert et al., 1972; Nambiar and Zed, 1980; Nelson et al., 1981; Carter et al., 1984; Sands and Nambiar,

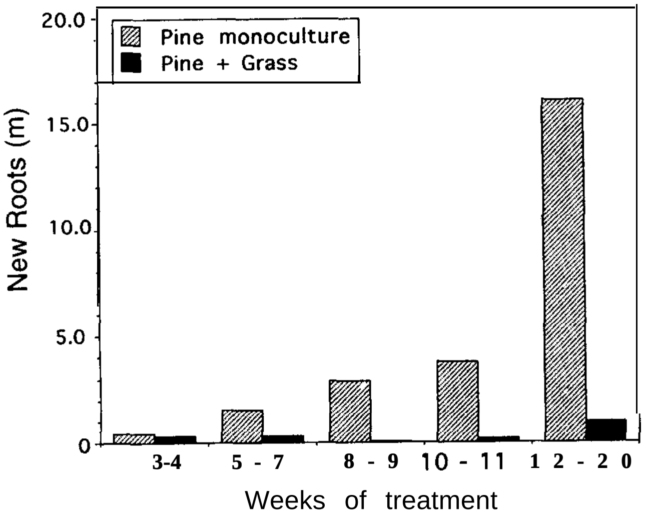

**Fig. 4. Periodic incremental root growth of loblolly pine seedlings grown in monoculture or in competition with crabgrass for 20 wk (July-November).**

**Table 2. Average root growth characteristics during wet and dry-down cycles in rbizotron cells for pine seedlings grown as pine monocultures or in mixed species with grass for 20 wk (July-November).**

| Parameter | Weeks 3–4, dry | Weeks 5-7, dry | Weeks S-9, wet | Weeks 10-11, dry | Weeks 12–20, wet |
|---|---|---|---|---|---|
| New root length, m m$^{3}$ | | | | | |
| Pine monoculture | 73.0 | 302.5 a† | 539.3 a | 767.8 a | 3341.4 a |
| Pine + grass | 122.7 | 100.4 b | 19.3 b | 45.6 b | 219.8 b |
| Grass | 200.4 | 8316.3 | 9605.2 | 2323.0 | 2149.8 |
| Percentage of total length | | | | | |
| Pine monoculture | 1.4 a | 6.0 a | 10.7 a | 15.3 a | 66.5 |
| Pine + grass | 24.1 b | 19.8 b | 3.8 b | 9.8 b | 43.3 |
| Grass | 0.9 | 36.6 | 42.1 | 10.3 | 9.5 |
| Active root tips, no. m$^{-3}$ | | | | | |
| Pine monoculture | 20 | 61 | 155 a | 222 a | 1070 a |
| Pine + grass | 36 | 41 | 9 b | 20 b | 63 b |
| Root extension rate, m d$^{1}$ tip$^{-1}$ | | | | | |
| Pine monoculture | 0.17 | 0.25 a | 0.22 a | 0.25 a | 0.05 |
| Pine + grass | 0.16 | 0.12 b | 0.13 b | 0.16 b | 0.05 |

† Parameter means within time periods followed by different letters are significantly different at the 0.05 level using Duncan's multiple-range test.

1984; Elliott and White, 1987; Walker et al., 1989; Morris et al., 1993).

The greater depletion of soil moisture in mixed species than in pine monoculture treatments demonstrated in this study supports the observations of Shainsky and Radosevich (1986) and Morris et al. (1993). During a 9-d monitoring period, Morris et al. (1993) measured a 62% decrease in volumetric water content at 0.15-m depth in grass plots compared with a 33% decrease in pine monoculture plots. At the same depth in our study, soil water content decreased 76% in mixed-species treatments compared with 50% in pine monoculture.

Results from Torreano (1992) were used to predict root elongation measured against soil water potential. We found this equation consistently overpredicted elongation rates for pine root extension (Fig. 6). Moreover, results from Torreano's study indicate that almost 70% of root growth variation can be explained by soil water potential. Similar regression of our data collected under nearly identical soil conditions indicates that only 49% of the observed variation can be explained by soil water potential.

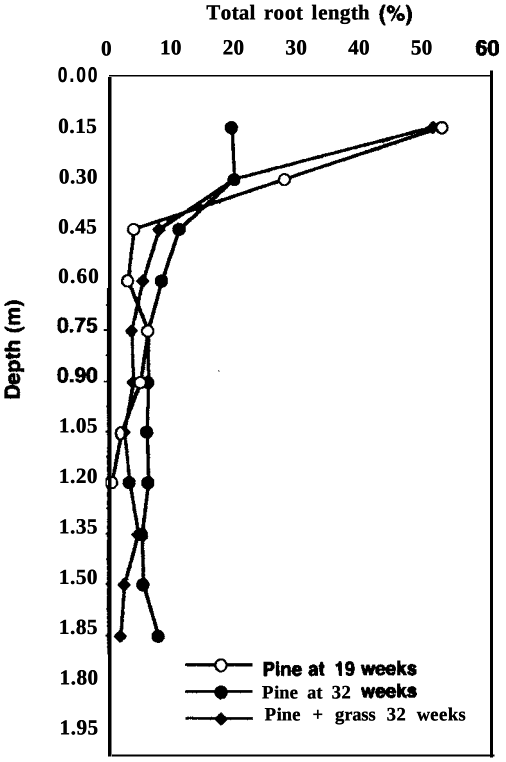

Fig. 5. Distribution by depth of loblolly pine seedling roots grown in rhizotron cells as pine monocultures or in mixed species with grass.

Root response to decreased soil water content will largely determine the growth potential of a seedling. Tree roots may respond to reduced soil water by shifting C allocation and continuing or increasing root growth, ceasing growth, or dying. Such response may result in a change in pine root distribution and, consequently, a shift in uptake patterns. The implications of these different responses are important for future competitiveness.

Comparisons of root characteristics of pine seedlings and competing vegetation emphasize the degree to which competing vegetation dominates the volume of soil surrounding pine roots. In this study, measured root lengths of competitor species averaged 44 times that of the pine root systems after only 20 wk of treatment, while a lo-fold decrease in pine root length occurred in the presence of herbaceous competition. The reduction in absorbing surface is one mechanism for decreased uptake of water and nutrients by pines in competition.

We expected pine root distribution to change as a result of competition; however, when seedlings of similar aboveground size were compared, root distributions were similar. Examination of root distributions of seedlings grown with crabgrass (Week 20) compared with seedlings of comparable aboveground size in pine monoculture treatments cells (Week 7) revealed that lob-

**Table 3. Ectomycorrhizal infection of noninoculated and *Pisolithus tinctorius* (Pt) inoculated loblolly pine seedlings grown in rhizotron cells as pine monocultures or as mixed species with crabgrass for 20 wk.**

| Treatment | Mycorrhizal tips per 1.0-m root | Infection (all types) |
|---|---|---|
| | | % |
| Pine monoculture | | |
| −Pt | 740 a† | 97 a |
| +Pt | 714 a | 97 a |
| Pine + grass | | |
| −Pt | 550 b | 80 b |
| +Pt | 404 b | 53 b |

† Means in a column with dissimilar superscripts are significantly different at the 0.05 level using Duncan's multiple-range test.

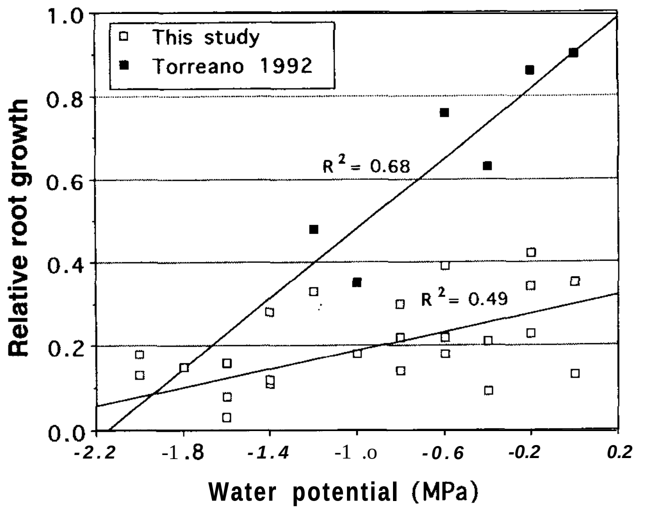

**Fig. 6. Relation between imposed water stress and relative root growth of loblolly pine seedlings grown in a rhizotron under conditions of low resistance to penetration at all soil water potentials.**

lolly pine root distribution of same-sized seedlings was similar for all treatments, with approximately 50% of the root length concentrated in the upper 0.15 m of soil. Crabgrass competition did not alter the rooting distribution patterns of loblolly pine, only the rate at which those roots developed, proliferated, and exploited the rhizotron soil.

The similarities in pine root distribution may be explained in several ways. First, pine root distribution may not respond to water and nutrient availability differences at this stage in development. If physical limitations do not exist (e.g., poor aeration or high soil strength), roots will proliferate throughout the profile in a pattern predetermined by initial root configuration and growth potential. Because root mortality was low, little change in distribution resulted from changes in extension points. Alternatively, saturating the soil with each watering may have reduced overall differences. Finally, the even distribution of crabgrass roots tended to withdraw water and nutrients from the entire rhizotron profile, which led to moderate differences in water and nutrient availability within the profile.

The cessation of root growth observed in this study conserved limited C reserves, but it also set the stage for decreased uptake capacities and put the seedlings at a competitive disadvantage because root length and surface area are generally correlated with water and nutrient uptake (Nye and Tinker, 1977; Bohm, 1979). Our results indicate loblolly roots that ceased to extend during the first drought period never regained the growth rates of roots that were not stressed. During periods of adequate soil water, aboveground growth was noted in all treatments; however, the magnitude was consistently lower in seedlings grown with crabgrass.

These results suggest that the timing and duration of precipitation may be critical to seedling establishment. A dry period early in the growing season that does not result in seedling or root mortality may, nevertheless, reduce growth during an otherwise favorable year. Our results further indicate that competition-induced reductions in soil water availability reduced the rate of pine root extension and thus the volume of soil exploited, thereby reducing resource availability and tree growth. Finally, results suggest it may be possible to predict root volume and distribution for pine seedlings based on aboveground measurements, providing additional tools for managers to evaluate the timing and placement of competition control treatments.

## REFERENCES

Bacon, C.G., and SM. Zedaker. 1987. Third-year growth response of loblolly pine to eight levels of competition control. South. J. Appl. For. 11:(2)91–95.

Beadle, C.L., and P.G. Jarvis. 1977. The effects of shoot water status on some photosynthetic partial processes in Sitka spruce. Physiol. Plant. 41:7–13.

Bohm, W. 1979. Methods of studying root systems. Ecol. Stud. 33. Springer-Verlag, New York.

Carter, G.A., J.H. Miller, D.E. Davis, and R.M. Patterson. 1984. Effect of vegetative competition on the moisture and nutrient status of loblolly pine. Can. J. For. Res. 14:1–9.

Cleary, B.D. 1971. The effects of moisture stress on physiology and establishment of planted Douglas-fir and ponderosa pine seedlings. Ph.D. diss. Oregon State Univ., Corvallis (Diss. Abstr. 7105417).

Conrad, S.G., and S.R. Radosevich. 1981. Photosynthesis, xylem pressure potential, and leaf conductance of three montane chaparral species in California. For. Sci. 27:627–639.

Elliott, K.H., and A.S. White. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. For. Sci. 33:356–366.

Kaufman, M.R. 1968. Water relations of pine seedlings in relation to root and shoot growth. Plant Physiol. 43:281–288.

Lambert, J.L., J.R. Boyle, and W.R. Gardner. 1972. The growth response of a young pine plantation to weed removal. Can. J. For. Res. 2:152–159.

Lowenstein, M., L.P. McConnel, and F.H. Pitkin. 1968. Root development and survival of planted ponderosa pine seedlings as influenced by competing vegetation. Stn. Pap. 5. Univ. of Idaho, College of Forestry, Wildlife and Range Sciences, Moscow.

Morris, L.A., W.S. Garbett, and S.A. Moss. 1993. Competitive interference between selected herbaceous and woody competitors and *Pinus taeda* during two growing seasons following planting. For. Sci. 39:166–187.

Nambiar, E.K.S., and P.G. Zed. 1980. Influence of weeds on the water potential, nutrient content and growth of young radiata pine. Aust. For. Res. 10:279–288.

Neary, D.G., E.J. Jokela, N.B. Comerford, S.R. Colbert, and T.E. Cooksey. 1990. Understanding competition for soil nutrients — the key to site productivity on southeastern Coastal Plain Spodosols. p. 432–450. In S.P. Gessel et al. (ed.) Sustained productivity of forest soils, Proc. 7th N. Am. For. Soils Conf., Vancouver, BC. 24-28 July 1988. Vancouver Forestry Publ., Univ. of Br. Columbia, Vancouver.

Nelson, L.R., R.C. Pedersen, L.L. Autry, S. Dudley, and J.D. Walstad. 1981. Impacts of herbaceous weeds in young loblolly pine plantations. South. J. Appl. For. 5:153–158.

Nye, P.H., and P.B. Tinker. 1977. Solute movement in the soil-root system. Study in Ecol. Vol. 4. Univ. of Calif. Press, Berkeley.

Pritchett, W.L., and R.F. Fisher. 1987. Properties and management of forest soils. 2nd ed. John Wiley & Sons, New York.

Sands, R., and E.K.S. Nambiar. 1984. Water relations of *Pinus radiata* in competition with weeds. *Can.* J. For. Res. 14(2):233–237.

SAS Institute. 1985. SAS user's guide: Statistics. 5th ed. SAS Inst., Cary, NC.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science (Washington, DC) 148:339–346.

Shainsky, L.J., and S.R. Radosevich. 1986. Growth and water relations of *Pinus ponderosa* seedlings in competition regimes with *Arctostaphylos patula* seedlings. J. Appl. Ecol. 23:957–966.

Shribbs, J.M., and W.A. Skroch. 1985. Effect of several ground cover systems on the growth and nutrition of eastern hemlock and white pine. Proc. South. Weed Sci. Soc. Annu. Meet., 38th. Jan. 1985. South. Weed Sci. Soc., Champaign, IL.

South, D.B., and J.P. Barnett. 1986. Herbicides and planting date affect early performance of container-grown and bare-root loblolly pine seedlings in Alabama. New For. 1:17–27.

Spurway, R.A. 1980. Ecophysiological effects of root patterns on the supply of water to plants in mixed communities. .p. 117–187. In D.N. Sen (ed.) Environmental and root behavior. Geobios Int., IX.

Stranskv, J.J.. and D.R. Wilson. 1964. Terminal eloneation of loblollv and shortleaf pine seedlings under moisture stress. Soil Sci. Soc. Am. J. 28:436–438.

Topp, G.C., J.L. Davis, and A.P. Annan. 1982. Electromagnetic determination of soil water using TDR: I. Application to wetting fronts and steep gradients. Soil Sci. Soc. Am. J. 46:672–678.

Torreano, S.J. 1992. Effects of soil water availability, aeration, and soil mechanical impedance on loblolly pine (*Pinus taeda* L.) root development. Ph.D. diss. Univ. of Georgia, Athens (Diss. Abstr. 9224748).

Walker, R.F., D.C. West, S.B. McLaughlin, and C.C. Amundsen. 1989. Growth, xylem pressure potential, and nutrient absorption of loblolly pine on a reclaimed surface mine as affected by an induced *Pisolithus tinctorius* infection. For. Sci. 35:569–581.

Wenger, K.F. 1952. Effect of moisture supply and soil texture on the growth of sweetgum and pine seedlings. J. For. 50:862–864.

Zahner, R. 1962. Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. For. Sci. 8:345–352.