SEASONAL LATERAL ROOT GROWTH OF JUVENILE LOBLOLLY PINE AFTER THINNING AND FERTILIZATION ON A GULF COASTAL PLAIN SITE

Mary Anne Sword, James D. Haywood, and C. Dan Andries[1]

Abstract-h 1989, two levels each of stand density and fertilization were factorially established in an 8-year-old loblolly pine plantation on a P-deficient site. Levels of stand density were nonthinned at 2,732 trees per hectare and thinned at 721 trees per hectare. Fertilizer levels were none or application of 150 kilograms P plus 135 kilograms N per hectare. In 1994, stand basal areas of the nonthinned and thinned plots were 42 and 25 square meters per hectare, respectively, and a second thinning on the previously thinned plots left 15.8 square meters per hectare. The previously fertilized plots were refertilized with 200 kilograms N, 50 kilograms P, and 50 kilograms K per hectare. In 1994 and 1995, tree growth was quantified at the end of the growing season, and lateral root initiation and elongation, soil temperature, and soil water content were measured throughout the growing season. The maximum rate of loblolly pine root growth occurred in May through July with more root growth in the 0- to 5-cm depth than in the 5- to 30-cm depth. A positive relationship between soil water content and root growth was observed. Thinning stimulated root growth 5 years after initial thinning and immediately after rethinning. Fertilization did not affect root growth 5 years after application and refertilization had a limited positive effect on root growth. Although tree growth was not immediately affected by treatment reapplication, a positive relationship was found between current annual tree volume increment and root elongation during peak root growth. We conclude that root system growth is sensitive to environmental variables that affect root metabolism in May through July, and that on the Gulf Coastal Plain, loblolly pine volume gains after silvicultural treatment result, in part, from an increase in soil resource uptake.

INTRODUCTION

The availability of water and mineral nutrients often limits the productivity of southern pine forests on Gulf Coastal Plain sites (Allen 1987, Allen and others 1990, Bassett 1984, Cregg and others 1988, Dougherty 1996, Moehring and Ralston 1967). Low transpiration rates and a high water table during winter result in adequate water availability in the early growing season, but with increased evapotranspiration and reduced precipitation as the growing season progresses, water deficits arise (Knight and others 1994, Moehring and Ralston 1967). In addition, phosphorus (P) and nitrogen (N) deficiencies are common throughout the South (Allen and others 1990, Dougherty 1996), and can produce significant gains in loblolly pine volume (Allen 1987, Fisher and Garbett 1980).

With adequate resource availability, photosynthate is preferentially partitioned to tree branch and foliage, rather than root growth (Dickson 1989, 1991). This phenomenon was demonstrated by Haynes and Gower (1995) after fertilization of 31 -year-old red pine (*Pinus resinosa* Ait.) in Wisconsin. Four years after the start of annual fertilizer amendments, litterfall was increased 49 percent and carbon allocation to root and soil processes was decreased 48 percent. In contrast, long-term water and fertility deficits cause an increase in the proportion of carbon partitioned to the root system (Eissenstat and Van Rees 1994). For example, Keyes and Grier (1981) found that the proportion of biomass partitioned to the root system in two stands of 40-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] was negatively related to soil fertility and site index.

Expansion of tree root systems may be required to offset water and fertility deficits and maximize stand productivity on resource-limited sites in the South. Root growth is affected by growth regulator relations and the availability of carbohydrates, mineral nutrients, and water (Coutts 1987, Dickson 1991, Eissenstat and Van Rees 1994, Klepper 1987). Because these variables are either directly or indirectly influenced by thinning and fertilization, we hypothesize that root system growth and resource uptake can be manipulated by these silvicultural tools. We had two primary objectives in this study: (1) characterize the seasonal root growth and soil environment of plantation loblolly pine (*P. taeda* L.) in response to thinning and fertilization, and (2) evaluate the relationship between tree and root system growth in four stand environments.

MATERIALS AND METHODS

The study was installed in an 8-year-old loblolly pine stand planted at a 1.83meter (m) by 1.83-m spacing on the Palustris Experimental Forest in Rapides Parish, LA. The soil is a Beauregard silt loam (fine-silty, siliceous, thermic. Plinthaquic Paleudult) (Kerr and others 1980). In April 1988, 12 treatment plots-l 3 rows of 13 trees each-were established (Haywood 1994). Thinning and fertilization treatments were randomly assigned to the plots in a 2 by 2 factorial design with three replications. Levels of thinning were: the original stocking [2,732 trees per hectare (ha)], and removal of every other row of trees and every other tree in residual rows in November 1988 (721 trees per ha). Levels of fertilization were: no fertilization and broadcast application of 747 kilograms (kg) per ha diammonium phosphate (135 kg N and 150 kg P per ha) in April 1989. The fertilization rate was based on recommendations for

---

[1] Research Plant Physiologist, Research Forester, and Biological Laboratory Technician, respectively, Southern Research Station, U.S. Department of Agriculture, Forest Service, Alexandria Forestry Center, 2500 Shreveport Highway, Pineville, LA 71380.

In: Waldrop, Thomas A., ed. 1998. Proceedings of the **ninth biennial**
southern silvicultural research **conference;** 1997 **February 25-**
27; Clemson, SC. **Gen.** Tech. Rep. **SRS-20.** Asheville, NC: U.S. **Department**
of **Agriculture,** Forest Service, Southern Research **Station. p.**
194-201.

loblolly pine grown on the nutrient-poor soil in this study (Kerr and others 1980, Shoulders and Tiarks 1983, Tiarks 1982).

Six growing seasons after the initial silvicultural treatments were applied, stand basal areas of the nonthinned and thinned plots were 42 and 25 square meters (m^2) per ha, respectively. In March 1995, the previously thinned plots were thinned from below to 30 percent of maximum stand density index as recommended by Dean and Baldwin (1993), resulting in a residual basal area of 15.8 m^2 per ha. Foliar mineral nutrient concentrations in August 1993 were used to determine a fertilizer recommendation for the previously fertilized plots. Urea, monocalcium phosphate, and potash [200 kg N, 50 kg P, and 50 kg potassium (K) per ha] were broadcast on the previously fertilized plots in March 1995.

Tree heights and diameters at breast height (d.b.h.) were measured quarterly (Haywood 1994) and outside bark stem volume (Baldwin and Feduccia 1987) was calculated. Two replications were chosen as blocks for measurement of root system growth and the soil environment. Blocks were identified based on the influence of topography on soil drainage. At 14-day intervals in May 1994 through January 1995, and June 1995 through January 1996, new roots [≥0.5 centimeters (cm) long] were cumulatively traced onto acetate sheets attached to five vertical Plexiglas rhizotrons (0.3 x 35.4 x 76 cm) per plot (Sword and others 1996). After each measurement period, a computer image file of each acetate tracing was created and the length of the lines contained in each image file was quantified using GSROOT software (PP Systems Inc., Bradford, MA). Net lateral root elongation was calculated by subtraction and expressed as millimeters per square decimeter (mm dm^{-2}) per day. After each measurement period, root initiation was quantified as the number of independently appearing new roots (≥0.5 cm long) in the 0- to 5-, 5- to 15-, and 15- to 30-cm depths, and expressed as number dm^{-2} per day.

Soil temperature (°C) was measured by insulated solid state sensors (Sword and others 1996) inserted in the soil at 5, 15, and 30 cm through ports in the rhitotrons. The water content of the soil (percent volume) was measured by time domain reflectometry with one sensor placed at the 15-cm depth through a port in each of three randomly chosen rhizotrons per plot. Soil temperature and water content were measured at 14-day intervals in May 1994 through January 1995, and June 1995 through January 1996.

Tree height, d.b.h., and stem volume were evaluated by analysis of variance after the 1994 growing season and by analysis of covariance after the 1995 growing season, using a completely random, 2 by 2 factorial experimental design with three replications. Factors were two levels each of fertilization and thinning. Covariates were height, d.b.h., and volume at the end of the 1994 growing season. Net root elongation, soil temperature, and transformed (arcsine of the square root) volumetric soil water content data collected in 1994-95 and 1995-96 were analyzed by a randomized, complete, block-split-plot-in-time design with two blocks. Thinning and fertilization were the whole-plot treatments; time was the subplot treatment. Root initiation in 1994-95 and 1995-96 was analyzed by a randomized, complete, block-split-plot-in-space-and-time design with two blocks. Thinning and fertilization were the whole-plot treatments; time and depth were the subplot treatments. Data were subjected to analyses of variance by measurement date to explain significant time interactions. Together, root growth and soil water content decreased as the growing season progressed. To evaluate this relationship as soil water became less available, Pearson product-moment correlations were calculated for root growth and soil water content in late June through September 1994 (SAS Institute Inc. 1991). Because our time domain reflectometer was inoperable in August through September 1995, we were unable to conduct this analysis in 1995. Main and interaction effects and Pearson correlation coefficients were considered significant at probabilities (Pr) ≤ 0.05 unless otherwise noted, and treatment means were compared with the Least Significant Difference test at Pr ≤ 0.05.

RESULTS

At the end of the 1994 growing season, fertilization significantly increased tree height, and both thinning and fertilization significantly increased d.b.h. and stem volume (table 1). After the 1995 growing season, tree height, d.b.h., and stem volume were not significantly affected by reapplication of the thinning and fertilization treatments.

Maximum rates of root initiation and net root elongation occurred in May through July (figs. 1 and 2). Root initiation was significantly affected by soil depth and by an interaction between time and soil depth in 1994 and 1995 (table 2). Consistently, root initiation in the 0- to 5-cm depth was greater than that at either the 5- to 15-cm or 15- to 30-cm depth; whereas, root initiation at the 5- to 15-cm depth was greater than that at the 15- to 30-cm depth in May and June.

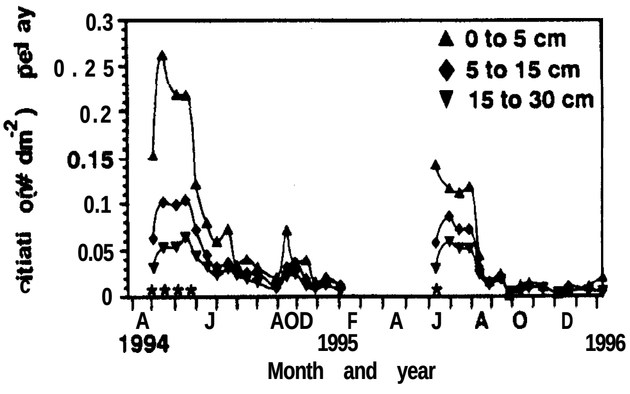

Figure 1 -Seasonal number of roots per decimeter per day initiated at 0 to 5, 5 to 15, and 15 to 30 centimeters in rhizotrons during 1994 and 1995. Asterisks signify measurement intervals associated with significantly more root initiation at 0 to 5 than at 5 to 15 centimeters, and significantly more root initiation at 5 to 15 than at 15 to 30 centimeters, by the LSD lest (Pr ≤ 0.05).

Table 1-Analyses of variance and covariance of juvenile loblolly pine stem growth before and after reapplication of thinning and fertilization on a P-deficient Gulf Coastal Plain site in central Louisiana

Treatment combination	1994—Before treatment reapplication			1995—After treatment reapplication		
	Height	D.b.h.	Volume/tree	Height	D.b.h.	Volume/tree
	m	cm	dm^3	m	cm	dm^3
Not thinned, not fertilized	13.9	13.5	112.5	14.5	13.8	120.6
Not thinned, fertilized	15.0	14.4	140.0	15.9	14.8	161.1
Thinned, not fertilized	13.4	17.4	172.8	14.3	19.0	212.4
Thinned, fertilized	14.7	19.4	229.3	15.6	21.0	277.6

Source of variation	Analyses of variance			Analyses of covariance		
	df[a]	MS	Pr > F-value	df	MS	Pr > F-value
D.b.h. (cm)						
Covariate (C)				1	10.8983	0.0043
Thinning(T)	1	59.9534	0.0001	1	0.8158	0.2932
Fertilization (F)	1	6.1421	0.0054	1	1.1306	0.2228
T x F	1	0.9944	0.1673	1	0.5305	0.3900
(Error)	8	0.4311		7		
Height (m)						
C		.	.	1	2.8209	0.0034
T	1	0.5193	0.1706	1	0.1613	0.3332
F	1	4.3010	0.0025	1	0.0090	0.8131
T x F	1	0.0511	0.6492	1	0.1290	0.3836
(Error)	8	0.2291		7	0.1493	
Volume (dm^3 tree')						
C		.		1	7649.2760	0.0017
T	1	16803.2205	0.0001	1	289.2690	0.3680
F	1	284.9786	0.0033	1	420.7903	0.2838
T x F	1	629.4227	0.1916	1	414.0510	0.2874
(Error)	8	309.3901		7	312.3743	

[a] df = degrees of freedom; MS = mean square; Pr > F-value = probability of a greater F-value.

In 1994, the interaction between time and thinning significantly affected root initiation and elongation (table 2). Thinning was associated with stimulated root initiation in May through June 1994, reduced root initiation in November through December 1994 (fig. 3), and increased root elongation during the 1994 growing season (fig. 2). Root initiation was significantly affected by interactions among time, thinning, and fertilization; and time, thinning, and soil depth. In July through early August 1994, root initiation was greater in the nonthinned, fertilized treatment than in the other treatments, and root initiation at the 0- to 5-cm depth on the nonthinned plots was greater than on the thinned plots.

After silvicultural treatments were reapplied in 1995, thinning resulted in significantly greater root elongation (table 2, fig. 2). Root initiation was significantly affected by interactions between time and fertilization, and among time, fertilization, and thinning. In general, root initiation was stimulated 38 percent by fertilization in June through July 1995. In 1995, a significant positive correlation was observed between current annual stem volume increment and mean root elongation in early June through July (r = 0.6228, Pr = 0.0991) (fig. 4).

Soil temperature at the 5-, 15-, and 30-cm depths was significantly increased by thinning in May through September 1994 and 1995. Thinning significantly decreased soil temperature at the 30-cm depth in November through December 1994, and at the 5-, 15-, and 30-cm depths in November 1995 through January 1996 (fig. 5). In 1994, soil temperature at the 30-cm depth was

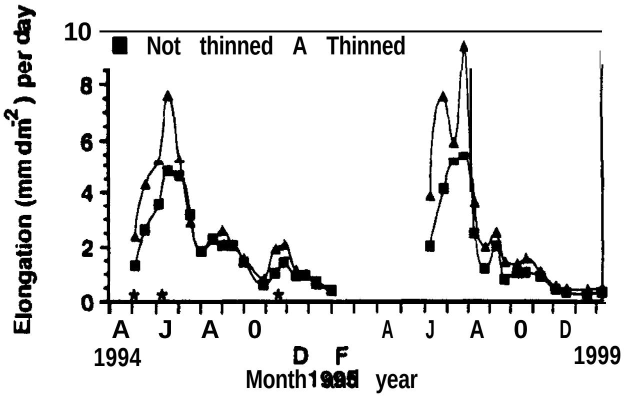

Figure 2—Seasonal net root elongation (millimeters per decimeter) per day in rhizotrons at 0 to 30 centimeters during 1994 and 1995 in response to thinning in November 1988 and March 1995. Asterisks signify measurement intervals in 1994 associated with a significant thinning effect.

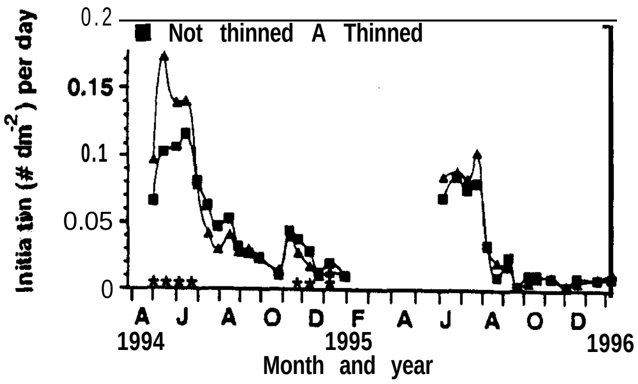

Figure 3-Seasonal number of roots per decimeter per day initiated in rhizotrons at 0 to 30 centimeters during 1994 and 1995 in response to thinning in November 1988 and March 1995. Asterisks signify measurement intervals in 1994 associated with a significant thinning effect.

Table 2-Probability of a greater F-value for the main and interaction treatment effects in the analyses of variance of loblolly pine root initiation rate (number dm^{-2}) per day in the 0- to 5-, 5- to 15- and 15- to 30-cm depths, and root elongation rate (mm dm^{-2}) per day in the 0- to 30-cm depth of the soil during the growing seasons before and after reapplication of thinning and fertilization on a P-deficient Gulf Coastal Plain site in central Louisiana

	1994—Before treatment reapplication		1995—After treatment reapplication	
Source of variation	df[a]	Pr > F-value	df	Pr > F-value
Root initiation (number dm^{-2} /day)				
Block (B)	1	0.1300	1	0.0006
Soil depth (D)	2	0.0037	2	0.0066
Thinning (T)	1	0.3261	1	0.3261
Fertilization (F)	1	0.3490	1	0.5468
T x F	1	0.9178	1	0.6346
T x D	2	0.8565	2	0.8983
F x D	2	0.4225	2	0.6471
T x F x D	2	0.8736	2	0.4874
Time	18	0.0001	14	0.0001
Time x D	36	0.0001	28	0.0001
Time x T	18	0.0001	14	0.1108
Time x F	18	0.1058	14	0.0001
Time x T x F	18	0.0143	14	0.0025
Time x T x D	36	0.0001	28	0.7652
Time x F x D	36	0.9717	28	0.1268
Time x T x F x D	38	0.6204	28	0.9709
Root elongation (mm dm^{-2} /day)				
Block (B)	1	0.2433	1	0.2932
Thinning (T)	1	0.2352	1	0.0192
Fertilization (F)	1	0.4912	1	0.3652
T x F	1	0.8296	1	0.1082
Time	17	0.0001	14	0.0001
Time x T	17	0.0286	14	0.0705
Time x F	17	0.3317	14	0.9625
Time x T x F	17	0.1452	14	0.5070

[a] df = degrees of freedom; Pr > F-value = probability of a greater F-value.

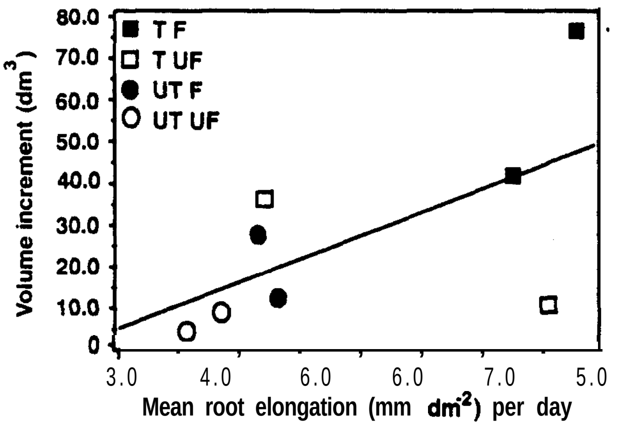

Figure 4—Relationship between the current annual stem volume increment (cubic decimeters) of loblolly pine in 1995 and the mean rate of lateral root elongation (millimeters per decimeter per day) between late June and early August 1995 (r = 0.6228, Pr = 0.0991).

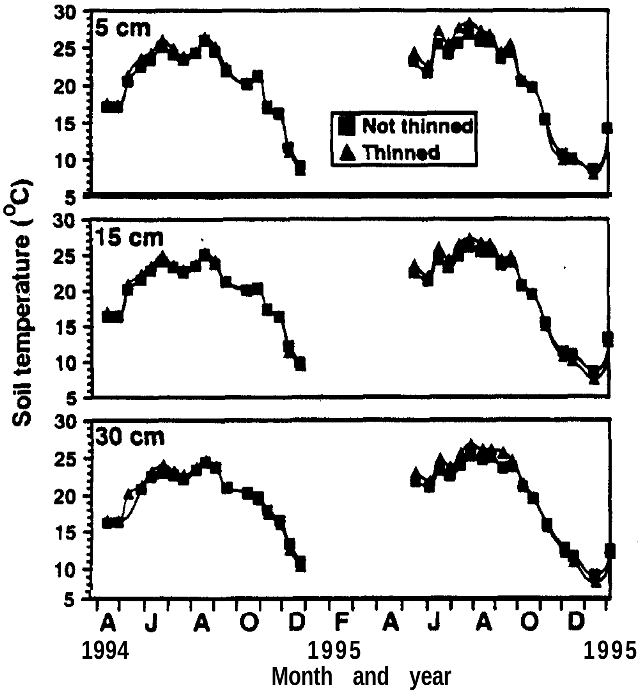

Figure 5—Soil temperature (“C) at 5, 15, and 30 centimeters in rhizotrons during 1994 and 1995 in response to thinning in November 1988 and March 1995.

significantly affected by an interaction between thinning and fertilization. In May through July 1994, soil temperature at the 30-cm depth was 1.0 °C greater on the thinned, nonfertilized plots compared with the other plots. In November through January 1994, soil temperature at the 30-cm depth was 0.7 °C greater on the nonthinned, fertilized plots compared with the other plots.

In 1994, interaction between time and thinning had a significant effect (Pr = 0.0895) on soil water content at the 15-cm depth, with a tendency for greater soil water content at 15-cm in response to thinning (fig. 6). Soil water content at the 15-cm depth in the 1994 growing season was significantly affected by an interaction among time, thinning, and fertilization. In November through December 1994, soil water content at 15-cm was less (14 percent) in response to the nonthinned, nonfertilized treatment compared with the other treatments. In 1995, soil water content at the 15-cm depth was significantly affected by an interaction between time and thinning, with periodic increases in soil water content throughout 1995 on the thinned plots.

Significant positive correlations were found between root elongation and initiation, and soil water content at the 15-cm depth in late June through September 1994. On the nonthinned plots, soil water content at the 15-cm depth was significantly correlated with root initiation at the 0- to 5-cm depth (r = 0.5796, Pr = 0.0005). On the thinned plots, soil water content at the 15-cm depth was significantly correlated with root elongation at the 0- to 30-cm depth (r = 0.5786, Pr = 0.0005), and root initiation at the 0- to 5- (r = 0.6014, Pr = 0.0005), 5- to 15- (r = 0.6032, Pr = 0.0003) (fig. 7), and 15- to 30- (r = 0.6514, Pr = 0.0001) cm depths.

DISCUSSION

In two consecutive years, we observed that new root growth of planted loblolly pine was greatest in May through July, and continued at a reduced rate in August through January. We also found more root growth near the soil surface than deeper in the soil profile. (Sword and others, in press) observed a similar pattern of seasonal root growth at this study site in 1993. Soil temperature, fertility, and moisture availability influence root system growth and development (Eissenstat and Van Rees 1994, Klepper 1987, McMichael and Burke 1996). Therefore, the expansion of loblolly pine root systems may be more sensitive to the surface soil environment in May through July than in other months of the year, and adverse soil environmental conditions in May through July could reduce root system function and soil resource uptake.

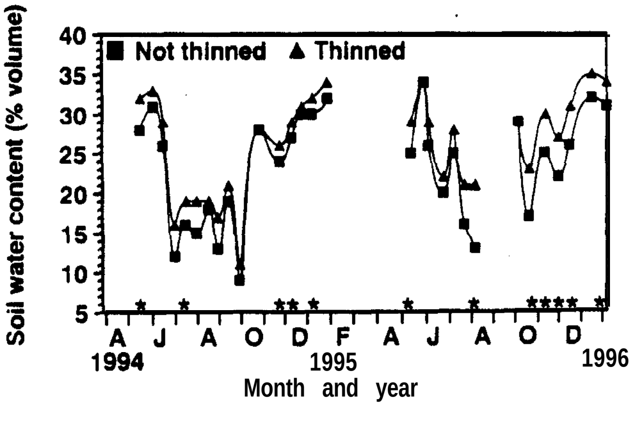

Figure 6—Soil water content (percent volume) at 15 centimeters in rhizotrons during 1994 and 1995 in response to thinning in November 1988 and March 1995. Asterisks signify measurement intervals associated with a significant thinning effect.

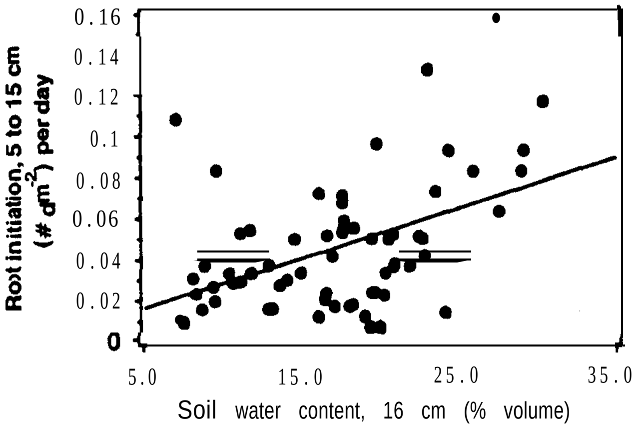

Figure 7--Relationship between the number of roots per decimeter per day initiated in rhizotrons at 5 to 15 centimeters, and soil water content at 15 centimeters (percent volume) during late June through September 1994 on the thinned plots ($r = 0.6032$, $Pr = 0.0003$).

In 1993, we observed a midsummer decrease in root elongation and initiation that corresponded to reduced soil water content (Sword and others, in press). Between June and September 1994, we found that soil water content decreased 68 percent and root growth and soil water content were significantly correlated. Midsummer water deficits are common in the southern pine region (Allen and others 1990, Dougherty 1996), and if severe enough, water deficits reduce root growth (Brissette and Chambers 1992, Sword 1995). In our study, therefore, water availability after July may have been a regulator of the duration of peak root growth.

We observed more root elongation and initiation on plots maintained at a lower stand density. A similar root growth response was observed at the same site in 1993 (Sword and others, in press). In 1993, light availability in the lower canopy was greater at the lower stand density (Gravatt 1994, Sword and others, in press). Root metabolism depends on glucose derived from either starch stored in root parenchyma or current photosynthate translocated to the root system (Dickson 1991). Thus, we conclude that thinning increased light in the canopy which increased the availability of carbohydrates for root metabolism and, therefore, root growth.

Root elongation on the thinned plots continued to be stimulated after reapplication of the thinning treatment. The positive effect of reduced stand density on root initiation was discontinued, however, by the second thinning. This suggests that the proliferation, but not the elongation of new roots in a forest stand is affected by the number of trees remaining after thinning. Auxin produced in branch apical meristems and translocated to the root pericycle regulates new root initiation (Charlton 1996, Coutts 1987). In our study, tree removal reduced the number of branch apical meristems on the site and, therefore, may have reduced the translocation of auxin to the root pericycle and hindered new root initiation.

In 1993, fertilization did not affect root initiation and only stimulated root elongation on plots that were thinned five growing seasons earlier (Sword and others, in press). By the end of 1994, fertilization had no effect on either root initiation or elongation. Fertilization increases carbon fixation and growth by enlarging leaf area (Teskey and others 1994, Vose and Allen 1988). However in 1994, Yu (1996) observed that 6 years after application, fertilization had no effect on leaf area per tree at this study site. One year earlier, Gravatt (1994) found that foliar concentrations of N on the fertilized and nonfertilized plots averaged 11.0 and 13.0 grams (g) per ha; P averaged 0.90 and 0.58 g per ha. These concentrations approach the boundary between mineral nutrient deficiency and sufficiency for loblolly pine (Allen 1987). We hypothesize that the benefits of N and P fertilization on new root growth subsided after six growing seasons because N and P amendments were either depleted or unavailable. Thus, the leaf area per tree and, therefore, the amount of photosynthate translocated to the root system, was no longer increased by fertilization.

Similar to our observations in 1994, we did not observe a strong positive root growth response to reapplication of fertilizer in early 1995. Starch metabolized in spring originates from photosynthate produced in fall and winter of the previous year (Dickson 1989, Gholz and Cropper 1991). As starch is depleted in roots, current photosynthate sustains root growth (Dickson 1989). Because the fascicle density of first-flush internodes is determined during terminal bud development in the previous year (Stenberg and others 1994), and first-flush fascicle expansion is dependent on starch previously stored in branch parenchyma and current photosynthate (Dickson 1989), the availability of carbohydrates for root metabolism in 1995 had been determined before refertilization. Therefore, a strong root growth response to fertilization in 1995 was not expected. At this study site, Haywood (1994) also found that the tree growth response to the initial fertilization was delayed 1 year.

We observed one root growth response that was inconsistent with our conclusion that root growth was not immediately affected by fertilization. Specifically, fertilization significantly increased root initiation during June through July 1995 by 38 percent. Others have documented an increase in lateral root branching in response to localized areas of high soil fertility (Eissenstat and Van Rees 1994, Mou and others 1995, Pregitzer and others 1993). The isolated increase in new root initiation we observed in response to N, P, and K application may have been caused by a pulse of mineral nutrient availability after fertilization.

A strong positive relationship exists between leaf area and productivity of loblolly pine stands (Stenberg and others 1994, Vose and Allen 1988). In 1995, we found that root elongation during peak root growth was positively related to current annual tree volume increment. We cannot specify whether volume gains were caused by greater root growth, or whether both tree volume and root growth were stimulated by foliage production and carbon fixation. However, the tree volume and root growth responses of the four treatment combinations in our study intimate that this relationship is regulated, in part, by soil fertility and light availability in the lower crown. We hypothesize that on resource-limited Gulf Coastal Plain sites, positive stand growth responses to fertilization are a result of increased leaf area and carbon fixation together with greater root growth and soil resource uptake. However, these responses to fertilization require a canopy environment and structure conducive to increased carbon fixation.

LITERATURE CITED

Allen, H.L. 1987. Forest fertilizers: nutrient amendment, stand productivity, and environmental impact. Journal of Forestry. 85: 37-46.

Allen, H.L.; Dougherty, P.M.; Campbell, R.G. 1990. Manipulation of water and nutrients-practice and opportunity in Southern U.S. pine forests. Forest Ecology and Management. 30: 437-453.

Baldwin V.C.; Fedducia, D.P. 1987. Loblolly pine growth and yield prediction for managed West Gulf plantations. Gen. Tech. Rep. SO- 236. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 27 p.

Bassett, J.R. 1964. Tree growth as affected by soil moisture availability. Soil Science Society of America Proceedings. 28: 436438.

Brissette, J.C.; 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 Physiology. 11: 289-303.

Charlton, W.A. 1996. Lateral root initiation. In: Wiasel, Y.; Eshel, A.; Kafkafi, U., eds. Plant roots, the hidden half. New York: Marcel Dekker, Inc.: 149-173.

Coutts, M.P. 1987. Developmental processes in tree root systems. Canadian Journal of Forest Research. 17: 761-767.

Cregg, B.M.; Dougherty, P.M.; Hennessey, T.C. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climate factors. Canadian Journal of Forest Research. 18: 851-858.

Dean, T.J.; Baldwin, V.C., Jr. 1993. Using a density management diagram to develop thinning schedules for loblolly pine plantations. Res. Pap. SO-275. New Orleans, LA: US. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 7 p.

Dickson, R.E. 1989. Carbon and nitrogen allocation in trees. In: Dreyer, E.; Aussenac, G.; Bonnett-Masimbert, M. [and others], eds. Forest tree physiology. Paris: Elsevier/INRA: 631s-647s. Annales des Sciences Forestieres. 46 supplement.

Dickson, R.E. 1991. Assimilate distribution and storage. In: Raghavendra, AS., ed. Physiology of trees. New York: John Wiley & Sons: 51-85.

Dougherty, P.M. 1996. Response of loblolly pine to moisture and nutrient stress. In: Fox, S.; Mickler, R., eds. Impact of air pollutants on southern forests. New York: Springer Verlag, Inc.: 173-195. Series: Ecological studies: analysis and synthesis 118.

Eissenstat, D.M.; Van Rees, K.C.J. 1994. The growth and function of pine roots. Ecological Bulletin. 43: 76-91.

Fisher, R.F.; Garbett, W.S. 1980. Response of semimature slash and loblolly pine plantations to fertilization with nitrogen and phosphorus. Soil Science Society of America Journal. 44: 850-854.

Gholz, H.L.; Cropper, W.P., Jr. 1991. Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. Canadian Journal of Forest Research. 21: 1742.1747.

Gravatt, D.A. 1994. Physiological variation in loblolly pine (*Pinus taeda* L.) as related to crown position and stand density. Baton Rouge, LA: Louisiana State University. 199 p. Ph.D. dissertation.

Haynes B.E.; Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiology. 15: 317-325.

Haywood, J.D. 1994. Seasonal and cumulative loblolly pine development under two stand density and fertility levels through four growing seasons. Res. Pap. SO-283. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 5 p.

Kerr, A., Jr.; Griffis, B.J.; Powell, J.W. [and others]. 1980. Soil survey of Rapides Parish, Louisiana. U.S. Department of Agriculture, Soil Conservation Service and Forest Service. 86 p. In cooperation with: Louisiana State University, Louisiana Agricultural Experiment Station.

Keyes M.R.; Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research. 11: 599-605.

Klepper, B. 1987. Origin, branching and distribution of root systems. In: Root development and function. Cambridge: Cambridge University Press: 103-124. Society of Experimental Biology Seminar Series 30.

Knight, D.H.; Vose, J.M.; Baldwin, V.C., Jr. [and others]. 1994. Contrasting patterns in pine forest ecosystems. Ecological Bulletin. 43: 9-19.

McMichael, B.L.; Burke, J.J. 1996. Temperature effects on root growth. In: Wiasel, Y.; Eshel, A.; Kafkafi, U., eds. Plant roots, the hidden half. New York: Marcel Dekker, Inc.: 1383-1396.

Moehring, D.M.; Ralston, C.W. 1967. Diameter growth of loblolly pine related to available soil moisture and rate of soil moisture loss. Soil Science Society of America Proceedings. 31: 560-562.

Mou, P.; Jones, R.H.; Mitchell, R.J.; Zutter, B. 1995. Spatial distribution of roots in sweetgum and loblolly pine monocultures and relations with above-ground biomass and soil nutrients. Functional Ecology. 9: 689-699.

Pregitzer, K.S.; Hendrick, R.L.; Fogel, R. 1993. The demography of fine roots in response to patches of water and nitrogen, New Phytologist. 125: 575-580.

SAS Institute Inc. 1991. SAS/STAT User's Guide, Release 6.03. Cary, NC: SAS Institute. 1028 p.

Shoulders, E.; Tiarks, A.E. 1983. A continuous function design for fertilizer rate trials in young pine plantations.

In: Jones, E.P., Jr., ed. Proceedings of the second biennial southern silvicultural research conference; 1982 November 4-5; Atlanta, GA. Gen. Tech. Rep. SE-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 352-356.

Stenberg, P.; Kuuluvainen, T.; Kellomäki, S. [and others]. 1994. Crown structure, light interception and productivity of pine trees and stands. Ecological Bulletin. 43: 20-34.

Sword, *M.A.* 1995. Root-zone temperature and water availability affect early root growth of planted longleaf pine. In: Edwards, MB., Jr., ed. Proceedings of the eighth biennial southern silvicultural research conference; 1994 November l-3; Auburn, AL. Gen. Tech. Rep. SRS-1. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 343-353.

Sword, M.A.; Chambers, J.C.; Gravatt, D.A.: Haywood, J.D. [in press]. Ecophysiological responses of managed loblolly pine to changes in stand environment. In: Mickler, R.A., ed. The productivity and sustainability of southern forest ecosystems in a changing environment. New York: Springer Verlag, Inc.

Sword, M.A.; Gravatt, D.A.; Faulkner, P.L.; Chambers, J.L. 1996. Seasonal root and branch growth of 13-year-old loblolly pine five years after fertilization. Tree Physiology. 16: 899-904.

Teskey, R.O.; Gholz, H.L.; Cropper, W.P., Jr. 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. Tree Physiology. 14: 1215-1227.

Tiarks, A.E. 1982. Phosphorus sorption curves for evaluating phosphorus requirements of loblolly pine (*Pinus taeda).* Communications in Soil Science and Plant Analysis. 13: 619-631.

Vose, J.M.; Allen, H.L. 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. Forest Science. 34: 547-563.

Yu, S. 1996. Foliage and crown characteristics of loblolly pine (*Pinus* taeda L.) six years after thinning and fertilization, Baton Rouge, LA: Louisiana State University. 77 p. M.S. thesis.