LONG-TERM ROOT GROWTH RESPONSE TO THINNING, FERTILIZATION, AND WATER DEFICIT IN PLANTATION LOBLOLLY PINE

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Abstract—High water deficits limit the new root growth of loblolly pine (*Pinus taeda* L.), potentially reducing soil resource availability and stand growth. We evaluated new root growth and stand production in response to thinning and fertilization in loblolly pine over a 6-year period that consisted of 3 years of low water deficit followed by 3 years of high water deficit. We found that new root growth exhibited a distinct seasonal pattern, with the timing of maximum root growth affected by water deficit. The magnitude of root growth was affected by both water deficit and thinning. For the 3-year period of high water deficit, we observed an inverse relationship between stemwood production and root growth among the treatment combinations. We hypothesize that by the third year of high water deficit, absorbing roots had migrated deeper into the soil profile; as a result, deep soil water became available for the high rates of stand production observed.

INTRODUCTION

Past research has shown that new loblolly pine (*Pinus taeda* L.) root growth is modal, with a maximum in midspring through midsummer (Farrish 1991, Sword and others 1998). Low soil water potential and high soil strength reduce root growth (Kaufmann 1968, Torreano and Morris 1998, Wraith and Wright 1998). Because these soil properties become more adverse as soil dries, the depletion of plant-available water inhibits new root growth. Loblolly pine root growth peaks during periods of high evaporative demand (Allen and others 1990), which suggests that water availability may be closely related to the production of new loblolly pine roots.

New root growth is needed for the absorption of soil resources that maintain tree physiology and growth. The effects of water deficit on new root growth, therefore, could limit stand production. Forest management activities such as thinning and fertilization may also interact with water deficit to affect new root growth. The objectives of this study were to summarize the new root growth of plantation loblolly pine over a 6-year period that included a period of high annual water deficit, and to assess new loblolly pine root growth responses to thinning and fertilization during this same time period. Choosing current annual stemwood biomass increment (CAI) as a variable representative of stand production, we evaluated the relationship between CAI and new root growth over the 6-year period.

MATERIALS AND METHODS

Study Establishment

The study is located in Rapides Parish, LA, on the Palustris Experimental Forest. The soil is a moderately well drained, very gently sloping Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudults) (Kerr and others 1980). Plant available water to a 1-m depth is 183 mm. Average annual rainfall is 156 cm, and average daily air temperature in summer and winter are 27.4 °C and 11.4 °C, respectively. We determined monthly and annual water balances for the 6-year period between 1993 and 1998 (Thornthwaite and Mather 1955). Rainfall was monitored electronically in an open field adjacent to the study area. Air temperature was obtained from the Louisiana State University Agricultural Center's Dean Lee Research Station located 37 km east of the study.

In May 1981, container-grown loblolly pine seedlings from a woods-run source were planted by U.S. Department of Agriculture Forest Service personnel in the experimental forest at 1.8 by 1.8 m. In 1988, 12 treatment plots (0.06 ha), 13 rows of 13 trees each, were established, and the interior 49 trees were delineated as measurement plots (0.016 ha). Woody vegetation was mowed from the plots, and 2 percent aqueous glyphosate was applied as needed to control grass and herbaceous plants during the study.

In 1988, two levels of thinning (none—2,990 trees/ha, thinned—749 trees/ha), and in 1989, two levels of broadcast fertilization with diammonium phosphate [none and 135 kg nitrogen (N) plus 150 kg phosphorus (P) per ha], were randomly applied to the treatment plots in a factorial design (Haywood 1994). In 1995, the previously thinned plots were rethinned from below so that mean basal area was reduced from 18.2 m^2/ha to 15.4 m^2/ha, and the fertilized plots were refertilized with a broadcast application of urea, monocalcium phosphate, and potash [200 kg N, 50 kg P, and 50 kg potassium (K) per ha]. In 1993, we chose two replications as blocks for intensive root growth measurements. Blocks were chosen by the influence of topography on soil drainage.

Measurements

During the dormant season of every year between 1993 and 1998, we measured total tree height and diameter at breast height (d.b.h.). Inside-bark dry stem mass per tree was predicted by an equation from Baldwin and Feduccia (1987). We calculated CAI for each measurement plot and year as the difference between the megagrams (Mg) of

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standing stem mass at the beginning of the growing season and the Mg of standing stem mass at the end of the growing season plus the Mg of stem mass that was lost during the year from thinning or mortality. Values of CAI are expressed as Mg/ha/year.

In 1993, we installed three Plexiglas rhizotrons (3 by 35.4 by 76 cm) vertically in the soil at three random locations in each measurement plot (Sword and others 1998). Between 1994 and 1998, two more Plexiglas rhizotrons were installed. Rhizotrons were relocated in January and February of each year. At 2- to 5-week intervals beginning in April, the elongation of new roots $\geq$ 5 mm in the 0- to 30-cm depth of rhizotrons was traced with permanent markers onto acetate sheets (21.6 by 30 cm) attached to either side of rhizotrons.

We recorded observations cumulatively. A computer image file of each acetate sheet was created by measurement interval, and the length of lines contained in each image file was quantified using GSROOT software (PP Systems, Inc., Bradford, MA). Net root elongation was calculated by subtraction. Net root initiation at the 0- to 5-cm, 5- to 15-cm, and 15- to 30-cm depths was quantified by counting the number of newly emerged roots $\geq$ 5 mm in rhizotrons during each measurement interval. Root elongation rate was expressed as mm/dm^2/day, root initiation rate was expressed as number/dm^2/day, and mean monthly root elongation and initiation rates were calculated. Annual peak root elongation and initiation were calculated as the average of root elongation and initiation rates between May and October. Amounts of root elongation and initiation that accumulated in rhizotrons since June were calculated for each month between June and October. Cumulative root elongation and initiation were expressed as mm/dm^2 and number/dm^2, respectively.

Statistical Analyses

Monthly root elongation and initiation rates were transformed to square root values to insure that the data were normally distributed. Data were analyzed by analysis of variance using a randomized complete block, split plot design with two blocks. Whole plots were levels of thinning and fertilization, and subplots were month of year. Peak root elongation and initiation were analyzed by analysis of variance using a randomized complete block, split plot design with two blocks. Whole plots were levels of thinning and fertilization, and subplots were years. Values of CAI between 1993 and 1998 were analyzed by analysis of variance using a randomized complete block design with two blocks. Treatments were levels of thinning and fertilization. Main and interaction effects were considered significant at $P \leq 0.05$ unless otherwise noted, and significantly different treatment means were compared with the least significant difference test at $P \leq 0.05$.

Linear relationships between cumulative root elongation and initiation between June and October and annual water deficit, and cumulative root elongation and initiation between June and October and CAI were evaluated by ordinary least squares regression. The slopes of the regression equations were considered significant at $P \leq 0.05$.

RESULTS

Between 1993 and 1998, annual water deficit ranged between 91 mm in 1995 and 343 mm in 1998. Mean annual water deficit in 1996 through 1998 was 1.2 times higher than that in 1993 through 1995. Root elongation and initiation rates differed significantly by month of year (tables 1 and 2). Peak rates of root elongation at the 0- to 30-cm depth occurred during May through July in 1993–97 and August through October in 1998 (fig. 1). Peak rates of root initiation at the 0- to 5-cm, 5- to 15-cm, and 15- to 30-cm depths occurred during May through July in 1993-96, June through August in 1997, and August through October in 1998, respectively.

Root elongation rate at the 0- to 30-cm depth and root initiation rates at the 0- to 5-cm and 15- to 30-cm depths were significantly affected by thinning (tables 1 and 2), with greater rates of root growth on the thinned plots than on the unthinned plots. For root initiation rate at the 0- to 5-cm depth, the significant interaction between month of year

Table 1—Analysis of variance of mean monthly loblolly pine root elongation rate (mm per dm^2 per day) at the 0- to 30-cm depth in response to thinning and fertilization in a loblolly pine plantation in central Louisiana, 1993 to 1998

Source of variation	df	SS	MS	F-value	Pr > F
Block	1	0.0159	0.0159	0.16	0.6954
Month of year	53	118.16	2.2295	21.8	0.0001
Error a	53		0.1022		
Thinning	1	4.2119	4.2119	41.9	0.0001
Fertilization	1	1.6536	1.6536	16.4	0.0001
T x F	1	0.8706	0.8706	8.65	0.0037
T x M	53	4.9764	0.0939	0.93	0.6061
F x M	53	5.0442	0.0952	0.95	0.5830
T x F x M	53	5.0378	0.0951	0.94	0.5852
Error b	162		0.1006		

df = degrees of freedom; SS = sum of squares; MS = mean square; Pr > F = probability of a greater F-value; M = month of year; T = thinning; F = fertilization.

Table 2—Analyses of variance of mean monthly loblolly pine root initiation rate (number per dm² per day) at the 0- to 5-, 5- to 15-, and 15- to 30-cm depths between 1993 and 1998 in response to thinning and fertilization

Source of variation	df	SS	MS	F-value	Pr > F
			0- to 5-cm depth		
Block	1	0.0424	0.0424	0.84	0.3634
Month of year	61	66.741	1.0941	21.6	0.0001
Error a	61		0.0506		
Thinning	1	0.2379	0.2379	5.47	0.0205
Fertilization	1	0.0044	0.0044	0.10	0.7520
T x F	1	0.0086	0.0086	0.20	0.6463
T x M	61	4.7404	0.0777	1.79	0.0017
F x M	61	3.2340	0.0531	1.22	0.1580
T x F x M	61	2.3240	0.0381	0.88	0.7239
Error b	186		0.0435		
			5- to 15-cm depth		
Block	1	0.0027	0.0027	0.09	0.7599
Month of year	61	27.990	0.4588	15.7	0.0001
Error a	61		0.0292		
Thinning	1	0.0491	0.0491	2.18	0.1416
Fertilization	1	0.0205	0.0205	0.91	0.3411
T x F	1	0.0286	0.0286	1.27	0.2614
T x M	61	1.3965	0.0229	1.02	0.4565
F x M	61	2.1569	0.0354	1.57	0.0118
T x F x M	61	1.1686	0.0192	0.85	0.7678
Error b	186		0.0225		
			15- to 30-cm depth		
Block	1	0.0636	0.0636	2.84	0.0973
Month of year	61	17.035	0.2793	12.5	0.0001
Error a			0.2243		
Thinning	1	0.1766	0.1766	9.58	0.0023
Fertilization	1	0.0847	0.0847	4.60	0.0334
T x F	1	0.0815	0.0815	4.43	0.0368
T x M	61	0.9873	0.0162	0.88	0.7181
F x M	61	1.5989	0.0262	1.42	0.0384
T x F x M	61	1.0672	0.0175	0.95	0.5836
Error b	61		0.0184		

df = degrees of freedom; SS = sum of squares; MS = mean square; Pr > F = probability of a greater F-value; M = month of year; T = thinning; F = fertilization.

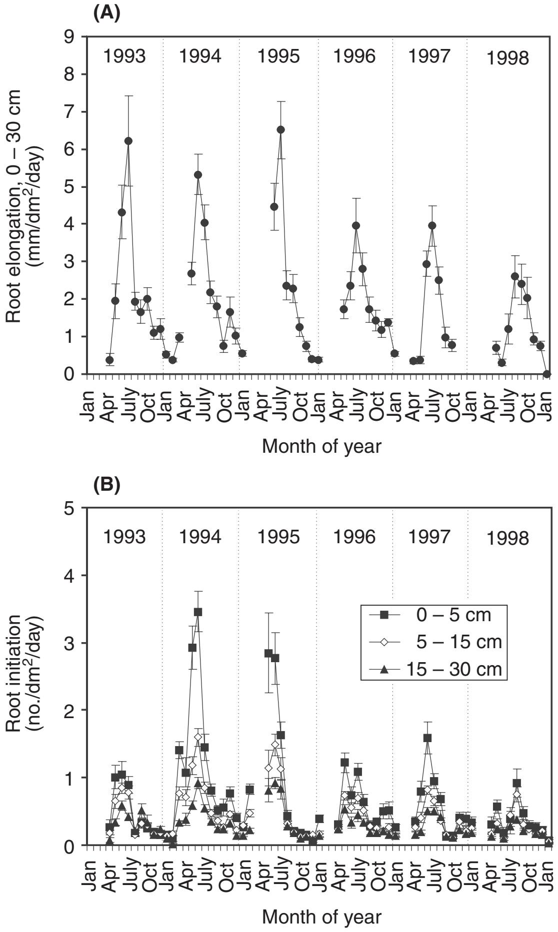

Figure 1—Mean monthly loblolly pine root elongation (A) and initiation (B) rates of loblolly pine in a loblolly pine plantation in central Louisiana, 1993–98.

and thinning was due to higher monthly root initiation rates in response to thinning in 1993, 1994, 1995, and 1997, but not in 1996 and 1998.

Root elongation rate at the 0- to 30-cm depth and root initiation rate at the 15- to 30-cm depth were significantly affected by an interaction between thinning and fertilization (tables 1 and 2). On the unthinned plots, lower rates of root growth were observed in response to fertilization, whereas on the thinned plots, root growth rates were not significantly affected by fertilization. A significant interaction between month of year and fertilization was observed for root initiation rates at the 5- to 15-cm and 15- to 30-cm depths. Root initiation in response to fertilization at the 5- to 15-cm and 15- to 30-cm depths in June and July of 1995 was greater than in all other months during the 6-year period.

Peak root elongation rate during May through October was significantly affected by year (*P* = 0.0586) (table 3), with higher rates of root elongation in 1993 through 1995 than in 1996 through 1998 (fig. 2). Similarly, the peak rate of root initiation was significantly affected by year, with the greatest root initiation rate in 1994 and 1995 and the lowest root initiation rate in 1998. We found that the peak root elongation rate at the 0- to 30-cm depth and root initiation rates at the 0- to 5-cm and 15- to 30-cm depths were significantly affected by thinning, with 45-percent and 22-percent greater root elongation and initiation rates, respectively, on the thinned plots than on the unthinned plots. We also found that a significant interaction between year and fertilization for peak root initiation rate at the 5- to 15-cm depth was due to a 38-percent higher rate of root initiation in response to fertilization in 1995.

Table 3—Probabilities of a greater F-value in the analyses of variance of peak loblolly pine root elongation rate (mm/dm²/day) at the 0- to 30-cm depth, root initiation rate (number/dm²/day) at the 0- to 5-, 5- to 15-, and 15- to 30-cm depths, and current annual stemwood biomass increment (Mg/ha/year) in response to thinning and fertilization in a loblolly pine plantation in central Louisiana, 1993 to 1998

		Elongation rate	Initiation rate			
		0–30 cm	0–5 cm	5–15 cm	15–30 cm	CAI
Source of variation	df	Pr > F				
Block	1	0.7962	0.2948	0.3047	0.8384	0.0752
Year	5	0.0586	0.0007	0.0025	0.0334	0.0214
Thinning	1	0.0005	0.0100	0.2054	0.0069	0.0001
Fertilization	1	0.0793	0.7112	0.9574	0.1074	0.0001
T x F	1	0.3247	0.9986	0.6801	0.9875	0.9880
T x Y	5	0.2906	0.1294	0.3196	0.7882	0.0920
F x Y	5	0.4049	0.0805	0.0376	0.0702	0.4656
T x F x Y	5	0.5374	0.8071	0.2128	0.7983	0.9414

CAI = current annual stemwood biomass increment; df = degrees of freedom; Pr > F = probability of a greater F-value; Y = year; T = thinning; F = fertilization.

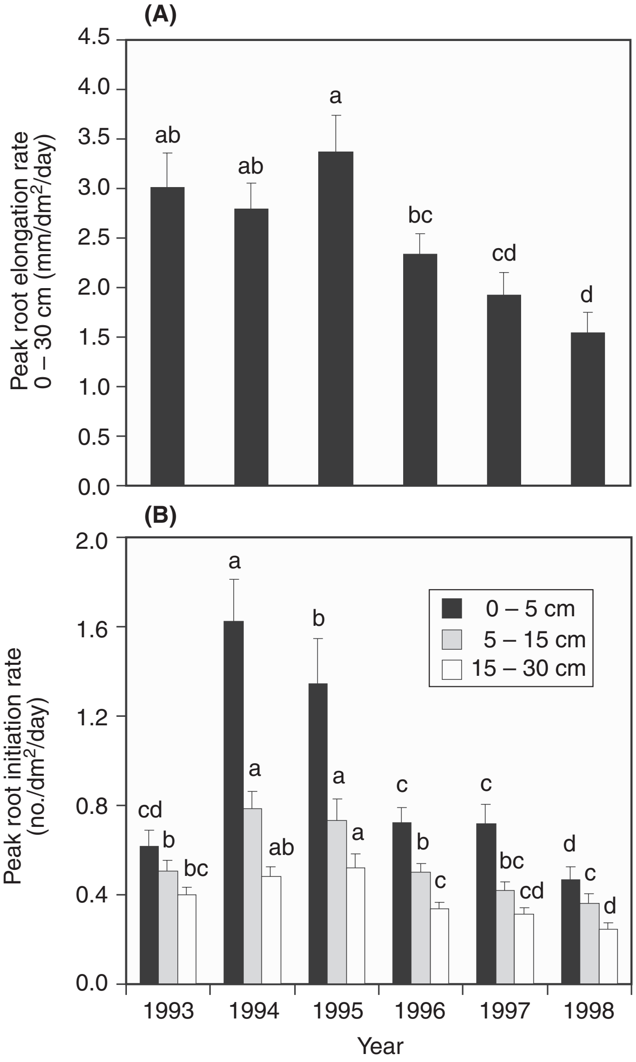

Figure 2—Peak loblolly pine root elongation rate at 0- to 30-cm (A) and initiation (B) rates in a loblolly pine plantation in central Louisiana, 1993–98. Means within a depth interval followed by a different letter are not significantly different at $P \leq 0.05$ by the least significant difference test.

Values of CAI differed significantly by year (table 3). The highest values of CAI were in 1994 (10.2 Mg/ha/year) and 1998 (9.9 Mg/ha/year), and the lowest values of CAI were in 1996 (5.7 Mg/ha/year) and 1997 (6.6 Mg/ha/year). Values of CAI in 1993 (7.5 Mg/ha/year) and 1995 (8.0 Mg/ha/year) were intermediate among the 6 years. Thinning and fertilization significantly affected CAI, with a 34-percent reduction in CAI in response to thinning and a 51-percent increase in CAI in response to fertilization.

We found significant linear relationships between peak root elongation rate and annual water deficit, and between peak root initiation rates at 5- to 15-cm and 15- to 30-cm and annual water deficit (fig. 3). These relationships suggest that root growth was directly and inversely related to annual water deficit.

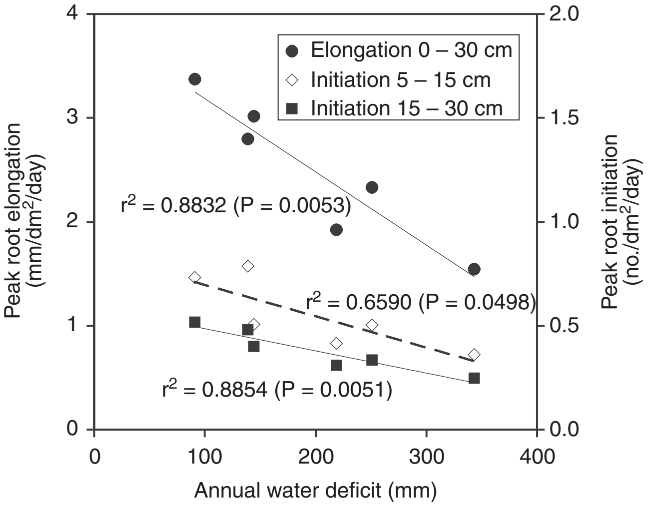

Figure 3—Relationships between peak loblolly pine root elongation and annual water deficit, and peak loblolly pine root initiation and annual water deficit in a loblolly pine plantation in central Louisiana, 1993–98. Values of r^2 are coefficients of determination.

When plot-level data for all years between 1993 and 1998 were combined, the relationship between CAI and cumulative root elongation between June and October was significant but was associated with a low coefficient of determination (table 4). When the relationships between CAI and cumulative root growth between June and October were evaluated for the 3 years of low water deficit (1993–95), significant relationships between CAI and both root elongation and root initiation at the 15- to 30-cm depth were found. The coefficient of determination and slope associated with this relationship indicates that these variables were directly and inversely related (fig. 4).

Relationships between plot-level CAI and cumulative root growth for the 3 years of high water deficit (1996–98) were not significant (table 4). For the 3-year period between 1996 and 1998, however, the chronological relationship between CAI and both cumulative root elongation and cumulative root initiation at the 15- to 30-cm depth between June and October were consistent among the four treatment combinations. Specifically, values of CAI increased and cumulative root growth between June and October decreased over time (fig. 5).

Table 4—Linear relationships between current annual stemwood biomass increment and cumulative root elongation (mm/dm²/day) and initiation[a] (number per dm² per day) during June through October in a loblolly pine plantation in central Louisiana, 1993 to 1998

Time	n	b_1[b]	b_2	Pr > F	r^2
		Root elongation, 0 to 30 cm			
1993–1998	48	10.8	-0.0071	0.0108	0.1331
1993–1995	24	14.58	-0.0126	0.0010	0.3974
1996–1998	24	10.24	-0.0088	0.0688	0.1427
		Root initiation, 0 to 5 cm			
1993–1998	48	7.08	0.0074	0.3878	0.0163
1993–1995	24	7.14	0.0095	0.3871	0.0342
1996–1998	24	9.33	-0.022	0.3321	0.0428
		Root initiation, 5 to 15 cm			
1993–1998	48	7.02	0.012	0.5267	0.0088
1993–1995	24	8.28	0.003	0.9152	0.0005
1996–1998	24	7.94	-0.0087	0.8223	0.0023
		Root initiation, 15 to 30 cm			
1993–1998	48	10.05	-0.037	0.1150	0.0531
1993–1995	24	13.70	-0.076	0.0399	0.1782
1996–1998	24	10.74	-0.075	0.0701	0.1414

CAI = current annual stemwood biomass increment; Pr > F = probability of a greater F-value; r^2 = coefficient of determination.

[a] Cumulative root elongation and initiation were measured in rhizotrons as the sum of root elongation and initiation since June for the months between June and October.

[b] Model: $Y = b_1 + b_2 (X)$ where Y = CAI, X = root elongation at 0 to 30 cm or root initiation at 0 to 5 cm, 5 to 15 cm or 15 to 30 cm, and b_1, and b_2 are coefficients estimated from the data.

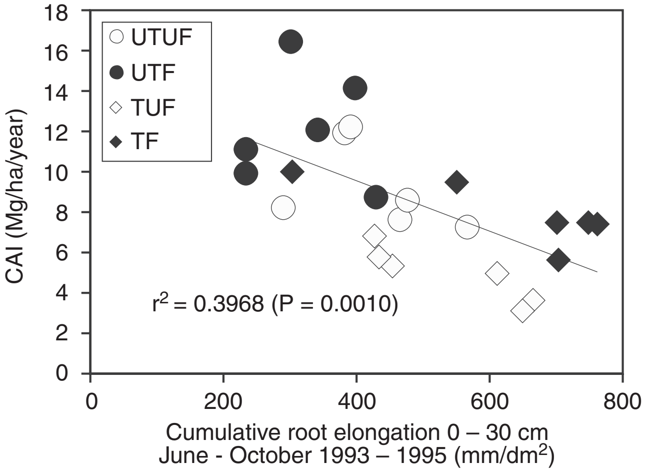

Figure 4—Relationship between current annual stemwood biomass increment (CAI) and cumulative root elongation between June and October 1993–95 in a loblolly pine plantation in central Louisiana. Treatment combinations are unthinned and unfertilized (UTUF), unthinned and fertilized (UTF), thinned and unfertilized (TUF), and thinned and fertilized (TF), and r^2 is the coefficient of determination.

DISCUSSION

The seasonal pattern of loblolly pine root elongation and initiation was multimodal, with a large peak in May through October and smaller intermittent peaks in September through December. This distinct seasonal pattern suggests that annual expansion of the loblolly pine absorbing root network is dependent on new root growth within a relatively narrow window of the growing season.

During this window of root growth, the soil conditions next to the growing roots may influence the magnitude of annual root system expansion. For example, Gulf Coastal Plain soils are commonly characterized by the formation of a winter water table within 200 cm of the soil surface (Soil Survey Staff 1998). An extended period of soil saturation in spring could limit the availability of oxygen for root metabolism early in the period of peak new root growth (Sword and Tiarks 2002). On the other hand, because summer droughts are common on the Gulf Coastal Plain (Allen and others 1990, Dougherty 1996), reductions in soil water content that result in high soil strength may inhibit root elongation later during peak new root growth (Sword and Tiarks 2002).

The relationships we found between annual water deficit and root growth during our 6-year study suggest that water availability greatly influenced root system expansion. For example, we found that new root growth decreased as annual water deficit increased. Since soil water potential and soil strength become more root-growth-limiting as the soil dries (Bennie 1996, Kaufmann 1968, Torreano and Morris 1998), the depletion of soil water associated with high annual water deficit may have created soil environmental conditions that limited new root growth. Also, although maximum root growth occurred in May through July, in years of high water deficit this peak was delayed until precipitation occurred. This response suggests that a surge of new root growth occurs when the conditions that limit new loblolly pine root growth are alleviated.

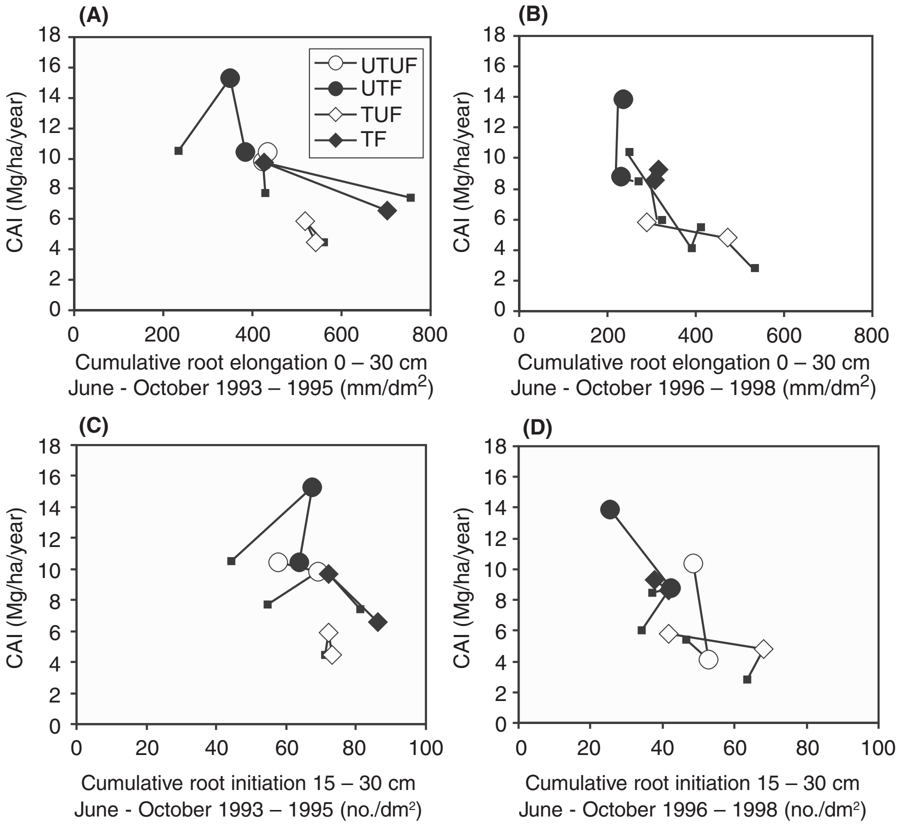

Figure 5—Relationships between current annual stemwood biomass increment (CAI) and cumulative loblolly pine root growth for the 3 years of low water deficit (A and C) and the 3 years of high water deficit (B and D) in a loblolly pine plantation in central Louisiana, 1993–98. Treatment combinations are unthinned and unfertilized (UTUF), unthinned and fertilized (UTF), thinned and unfertilized (TUF), and thinned and fertilized (TF). The beginning of the age sequence for each treatment combination is noted with the small square symbol.

Over the 3-year period of high water deficit, declines in new root growth became more severe. At the same time, progressive decreases in predawn needle water potential and net photosynthesis occurred.[2] In addition to root-growth-limiting soil properties, therefore, negative effects of high water deficit on crown physiology and the availability of carbohydrates for root metabolism may have inhibited new root growth as the 3-year period of high water deficit progressed.

Throughout the 6-year study period, we observed consistently higher rates of root growth in response to thinning. Regardless of water deficit, therefore, light availability in the crown appeared to consistently influence new root growth. In contrast, root growth responses to fertilization were limited to 1995. In early 1995, foliar P concentrations reached deficient values for loblolly pine (1.0 mg/g) (Allen 1987), on both the unfertilized (0.67 mg/g) and fertilized (0.96 mg/g) plots.[3] Since P nutrition strongly affects root growth (Marschner 1986), greater root growth rates immediately after refertilization may have been caused by the alleviation of P limitations to root growth.

During the 3-year period of low annual water deficit between 1993 and 1995, we observed a negative relationship between plot-level CAI and cumulative root growth. Past research has shown that as the availability of essential resources decreases, carbon (C) is preferentially allocated to belowground rather than aboveground growth (Haynes and Gower 1995; Keyes and Grier 1981; Santantonio and Santantonio 1987; Vogt and others 1983, 1987). The CAI and cumulative root growth data from 1993-95 reflect this relationship. On the unthinned plots, however, low rates of net photosynthesis in the lower crown due to light limitations (Gravatt and others 1997, Tang and others 1999) and subsequent reductions in the amount of C allocated for root metabolism may have interfered with the fundamental relationship between resource availability, CAI, and cumulative root growth.

We did not find any consistent relationships between CAI and cumulative root growth among the treatment combinations during the 3-year period of high annual water deficit. As the 3 years of high water deficit progressed, however, a consistent relationship between CAI and cumulative root growth was observed among the treatment combinations. Specifically, cumulative root growth decreased or was unchanged, while CAI increased. We hypothesize that water deficit limited root growth in the 0- to 30-cm depth but

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[2] Tang, Z. Unpublished data.

[3] Sword-Sayer, M.A. Unpublished data.

stimulated root growth below 30 cm. As C was allocated for the metabolism and growth of deep roots, water became less limiting to CAI. Absorbing roots may have migrated deeper in the soil profile so that by the third year of high water deficit, adequate water was supplied for high rates of stemwood production.

In summary, the new root growth of loblolly pine at our study site was characterized by a distinct maximum that occurred over a 3-month period between May and October. Water deficit altered both the magnitude of new root growth and the timing of the peak period of root growth. Furthermore, regardless of water deficit, root growth was closely associated with light availability in the canopy. As we learn more about how soil conditions and carbohydrate availability affect new root growth, this information will improve our ability to manage root system growth and predict the supply of soil resources for stand production. We also found an inverse relationship between CAI and cumulative root growth during the 3-year period of low water deficit, which suggests that C was preferentially allocated to aboveground growth rather than belowground growth along a gradient of stand conditions. This relationship was absent during the 3-year period of high annual water deficit. At this time, however, a consistent inverse relationship between CAI and cumulative root growth was observed among the treatment combinations, which may indicate that by the third year of high annual water deficit, the growth of absorbing roots had adapted so that adequate water was available for high rates of stemwood growth.

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