REAPPLICATION OF SILVICULTURAL TREATMENTS IMPACTS PHENOLOGY AND PHOTOSYNTHETIC GAS EXCHANGE OF LOBLOLLY PINE

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Abstract—A loblolly pine (*Pinus taeda* L.) plantation, established in 1981, was thinned and fertilized in 1988. Thinning and fertilization treatments were applied again in early 1995. The morphology of current flushes and needles were measured between March and October in 1995 through 1997. Physiological responses were monitored in the upper and lower crowns. Needle-fall was collected biweekly, and annual needle biomass was estimated. Although refertilization had little impact on needle-level physiology, it shifted bud burst 1 week earlier and significantly enhanced flush and needle growth. The fertilized trees produced more leaf area per shoot than the unfertilized trees. Refertilization increased tree-level and plot-level annual needle-fall biomass production. Rethinning increased leaf area per fascicle and annual needle-fall biomass per tree. As light level and crown exposure were increased after rethinning, rates of photosynthesis and transpiration of lower crown foliage on the thinned plots rose considerably, but daytime needle water potential remained unaffected.

INTRODUCTION

Forest growth and productivity depend, in part, on the availability of site resources. Nutrient deficiency and drought significantly reduce aboveground and belowground productivity of conifers (Albaugh and others 1998, Sword and others 1998, Teskey and others 1994). Light availability affects canopy structure, branch physiology, and tree growth (Ginn and others 1991, Sheriff 1996, Tang and others 1999). Forest management activities such as thinning and fertilization increase site quality and stand production (Jokela and Martin 2000). Growth responses to silvicultural treatments have been shown to persist for several years. For instance, Brix (1983) found that nitrogen (N) fertilization and thinning increased annual growth of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees for 3 to 5 years. At a Louisiana site, fertilization with N and phosphorous (P) stimulated stem volume increment of loblolly pine (*Pinus taeda* L.) saplings for 4 years (Haywood 1994).

In general, the effects of forest management on relationships between site quality and growth response are not well understood. Studies of tree responses to repeated cultural practices are needed to understand when to implement intensive management for maximizing the productivity that is associated with canopy processes and carbon dynamics (Jokela and Martin 2000, Leverenz and Hinckley 1990, Maier and others 2002, Samuelson and others 2001). This study is part of a long-term project that assesses the impacts of silvicultural manipulations on loblolly pine productivity. The objectives of the study were to (1) quantify flush and foliage growth of 14- to 16-year-old trees 3 years after the second thinning and fertilization, and (2) evaluate physiological performance under different treatment conditions.

MATERIALS AND METHODS

Study Site

The study was conducted on the U.S. Department of Agriculture, Forest Service, Southern Research Station, Palustris Experimental Forest in Louisiana, where the soil was moderately well drained Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudults). In 1981, the plantation was established by planting 3-month-old seedlings at 1.8 x 1.8 m spacing. A factorial combination of two levels each of thinning (thinned or unthinned) and fertilizing (fertilized or unfertilized) treatments, replicated 3 times, was applied to 12 plots (0.57 ha each) in late 1988. On the thinned plots, a row thinning was done with 721 trees ha^{-1} remaining. The unthinned plots had nearly 2,900 trees ha^{-1}. In early 1989, diammonium phosphate (134 kg N and 150 kg P ha^{-1}) was broadcast on the fertilized plots. Thinning and fertilization treatments were reapplied in early 1995. The previously thinned plots were cut again to approximately 510 trees ha^{-1} (16 m^2 ha^{-1}) representing 30 percent of maximum stand density index for loblolly pine grown on Gulf coastal sites (Dean and Baldwin 1993). Stand density of the unthinned plots was 2,860 trees ha^{-1} (42 m^2 ha^{-1}). Urea, triple super phosphate and potash (200 kg N, 50 kg P, and 50 kg K ha^{-1}) were broadcast on the plots that had been fertilized before. Understory hardwoods and shrubs on the plots were removed with a rotary mower, and glyphosate herbicide was sprayed to control weed competition.

Field Measurements

From 1995 to 1997, flush and needle growth were measured in the upper and lower crown of two treatment replications (four plots per replication). At each crown position, four first-order branches each on the south and north side of tree crowns (16 branches per plot) were randomly selected in February. These branches were situated in four to six interior trees on each plot. On the

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branch, one first flush per terminal or adjacent shoot was sampled and flush shoot length was recorded biweekly from March to October. Three needle fascicles on the sample flush were marked randomly and their needle length (from the tip to the edge of the leaf sheath) was measured biweekly between April and October. Similar measurements were made on the subsequent flushes (second and third) of the same sample shoot as trees grew multiple flushes throughout the growing season. Additionally, needle fascicle density (fascicles per cm of the foliated flush shoot) was determined in November 1997.

Each October, two fascicles per sample flush shoot were randomly chosen in the upper and lower crown of six trees per plot, and totally 192 fascicles were removed from the eight plots and examined in the laboratory. Each fascicle was cut at the edge of the leaf sheath. Needle length and volume per fascicle were measured. Leaf surface area per fascicle was estimated from needle length and volume (Johnson 1984). Leaf area per flush was calculated as the product of flush length, fascicle density, and leaf area per fascicle. Number of flushes per shoot was calculated by adding numbers of multiple flushes (first, second, and so forth) that grew on each sample shoot throughout the growing season. Annual flush shoot length was the sum of the length of the measured flushes on the sample shoot, and leaf area per shoot was the sum of the leaf area of the measured flushes on the sample shoot.

Four litter traps (0.92 m^2 each) were randomly installed inside each of the eight plots. Needle-fall was collected biweekly from 1995 to 1998, oven-dried to a constant mass, weighed, and expressed on a plot-area basis. Annual needle-fall biomass per plot was calculated for a phenological year by adding needle dry mass from April to March. Annual foliage biomass per tree was determined by dividing annual needle-fall biomass per plot by number of trees per plot.

On sunny days, needle gas exchange was measured in the upper and lower crown of the interior trees in two replications (eight plots) where shoot and needle morphology were also measured. Gas exchange measurements were taken nearly twice each month from June to October in 1995. The same measurements were made between April and October in 1996 and 1997. During each period, we randomly sampled four plots in one replication on the first day and the other four plots the next day. On a sampling day, three fascicles each from the upper and lower crown (six fascicles per plot) were detached before daylight and their predawn leaf water potentials (Ψ_{pd}) were determined with a pressure chamber (PMS Instrument Co., Corvallis, OR). Photosynthetic measurements were performed between 0930 and 1130 h, using a LI-6200 infrared gas analyzer (closed system) equipped with a 250-mL leaf chamber (Li-Cor, Inc., Lincoln, NE). At each crown position, three branches, each from the south side of three different trees, were selected. Two fully-expanded needle fascicles in the mid-section of the terminal or nearby lateral shoot were placed in the leaf chamber and their net CO_2 exchange (P_n), transpiration (E), and stomatal conductance to water vapor (g_w) were recorded *in situ* under the natural environment. Photosynthetic photon flux density (PPFD), air temperature (T_a), and vapor pressure deficit (VPD) were monitored with the gas analyzer. Needle water potentials (Ψ_{md}) of the sample fascicles were determined using the pressure chamber after each P_n measurement.

Volumetric soil water content (SWC) at the 15-cm depth was measured nearly twice a month at three locations in the interior of each plot with a time domain reflectometer (Soil Moisture Equipment Corp., Santa Barbara, CA).

Statistical Analyses

To test the effects of repeated thinning and fertilization on flush and needle growth, morphological data of each October were analyzed using the analysis of variance for a complete random split-plot design. Thinning and fertilization were considered as the main treatments, sampling year as the subplot and crown position as the sub-subplot. Similar analysis was done on physiology, soil water, and needle-fall data. Main and interactive effects on flush shoot growth, needle-fall biomass production and gas exchange were considered statistically significant at $P \leq 0.10$. All data analyses were conducted with the SAS software package (SAS Institute Inc., Cary, NC).

RESULTS

Shoot and Needle Phenology

Bud burst occurred in the first week of March. By mid-March, 64 and 47 percent of the sample shoots on both fertilized and unfertilized plots, respectively, had bud burst. First flushes expanded rapidly in the early growing season (figs. 1A to 1C). Overall, first-flush shoot elongation averaged 4.0 cm $week^{-1}$ in March, declined to 1.6 cm $week^{-1}$ in April and terminated by the end of May. First-flush needles began elongating in late March and averaged 1.1 cm $week^{-1}$ in May and June. Second flushes grew from May to August, and their needles continued growing through September. The third flushes were observed only in the upper crown and grew between midJuly and October.

Flush and needle morphology positively responded to fertilization (table 1). Over all 3 years, thinning treatments and crown levels, mean shoot length and leaf area per first flush were significantly greater on the fertilized plots than on the unfertilized plots (table 2). Mean shoot length and leaf area per second flush were also greater for the fertilized plots as compared with the unfertilized plots. There was a significant interaction between fertilization and crown position on annual production of multiple flushes. In addition to the first flush, both fertilized and unfertilized trees grew one second and one third flush per shoot in the upper crown. In the lower crown of the fertilized plots, however, one second flush was found for all sample shoots and one third flush for 67 percent of the sample shoots. In contrast, only 8 percent of the sample shoots in the lower crown of the unfertilized trees had one second flush, and no third flush was found in the same crown level. First-flush and second-flush fascicles had significantly greater needle length and leaf area per fascicle for the fertilized trees than for the unfertilized trees (table 2). Annual flush shoot length was increased consistently for the 3 years after refertilization (fig. 2A). Relative to the unfertilized plots, flush shoots of the fertilized trees possessed significantly more leaf area per shoot in 1995 and 1996 (fig. 2B). Moreover, the

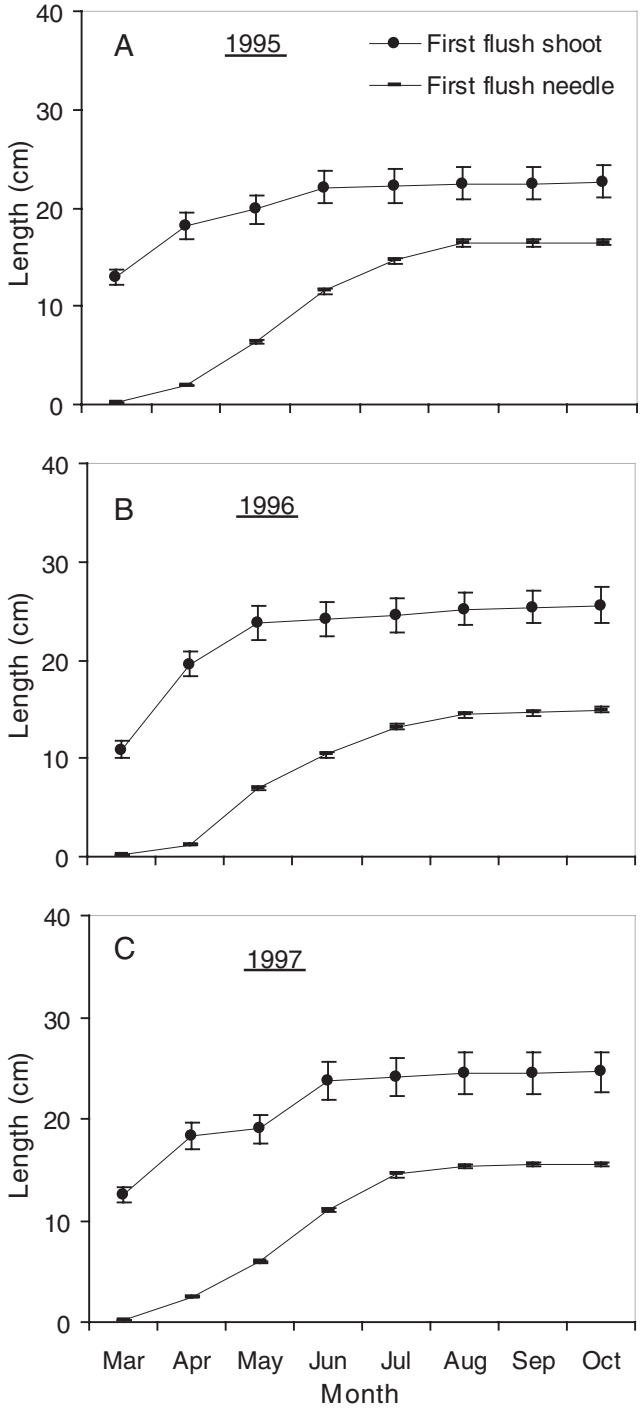

Figure 1—Mean length of first flushes and first-flush needles of 14- to 16-year-old loblolly pine trees 3 years after reapplication of thinning and fertilization. Each mean is the average of biweekly measurements across rethinning and refertilization treatments and crown positions.

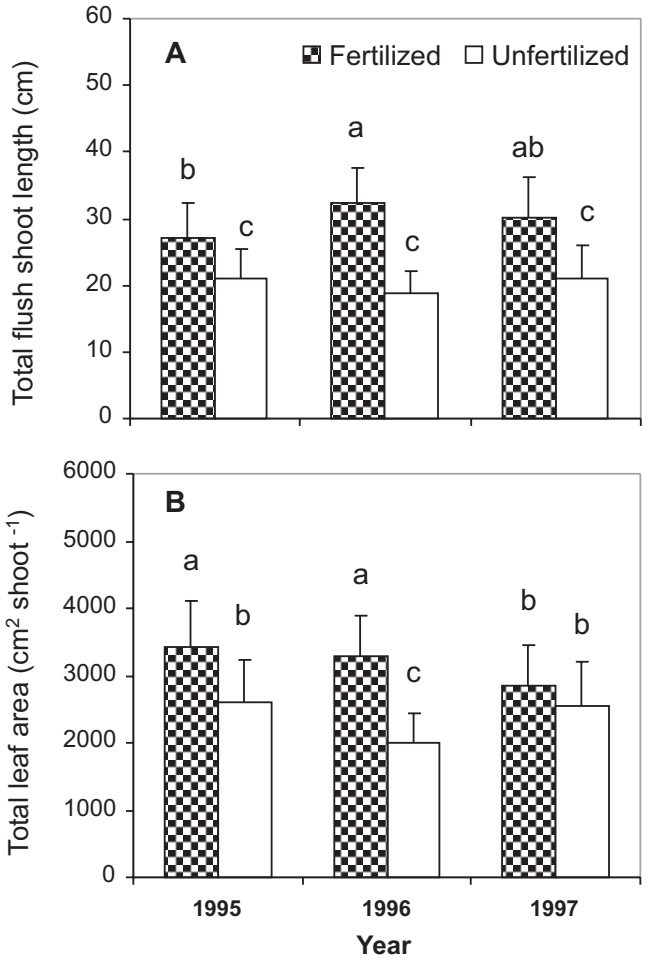

Figure 2—Mean annual flush shoot length and leaf area per shoot of 14- to 16-year-old loblolly pine trees 3 years after refertilization. Each mean is the average of biweekly measurements across rethinning treatments and crown positions. Bars followed by the same letters do not differ significantly at $P \leq 0.10$.

fertilized plots had more annual needle-fall biomass per tree and per plot than the unfertilized plots during the 3-year period (figs. 3A and 3B).

Rethinning significantly increased first-flush fascicle size and leaf area in the upper and lower crown (table 1). Mean needle length and leaf area of the first-flush fascicles were greater on the thinned plots than on the unthinned plots. A significant interaction between thinning and crown position indicated that shoot length and leaf area of upper-crown first flushes were larger on the unthinned plots compared to the thinned plots. Annual flush shoot length positively responded to rethinning, with more flushes per shoot in the lower crown of the thinned trees than those in the same crown level of the unthinned trees. Annual shoot length was 39, 35, 16, and 11 cm for the unthinned-upper, thinned-upper, thinned-lower, and unthinned-lower crown combinations, respectively. Leaf area per shoot was 4,691, 3,838, 1,459, and 1,157 cm^2 for the thinning-by-crown position combinations. Annual foliage production was enhanced by stand density reduction. Needle-fall biomass per tree on the unthinned plots remained identical over the 3 years after rethinning (fig. 3C). However, the thinned trees significantly increased needle-fall production each year. In 1997, needle-fall biomass per tree was 221 percent more on the thinned plots than on the unthinned plots. However, annual needle-fall biomass per plot was lower for the thinned plots (fig. 3D) relative to the unthinned plots because of fewer trees remaining after rethinning.

Table 1—Probability of F-test for the effects of repeated thinning and fertilization treatments and crown position on October flush and needle characteristics of 14- to 16-year-old loblolly pine trees 3 years after treatment in Louisiana

Source of variation	df	FFLG	FFLA	FFNL	FFNA	SFLG	SFLA	SFNL	SFNA	MFPS	FSLG	FSNA
T	1	0.8619	0.3318	0.0426	0.0095	0.5563	0.5843	0.6865	0.3938	0.2508	0.8458	0.3066
F	1	0.0118	0.0407	0.0035	0.0013	0.0219	0.0752	0.0246	0.0160	0.0352	0.0057	0.0279
T x F	1	0.2938	0.3866	0.6036	0.1335	0.1041	0.2368	0.2634	0.1616	0.0890	0.1130	0.7219
Error a	4											
SY	2	0.1621	0.1612	0.0034	0.0001	0.1122	0.0681	0.0030	0.0016	0.3628	0.6141	0.2388
SY x T	2	0.3771	0.5044	0.1227	0.0910	0.8307	0.6948	0.6320	0.5645	0.3628	0.4867	0.4321
SY x F	2	0.1017	0.3399	0.0186	0.0016	0.5379	0.1336	0.0970	0.0441	0.6927	0.1738	0.1427
SY x T x F	2	0.1828	0.3903	0.2692	0.2373	0.1886	0.2095	0.7046	0.6682	0.6927	0.1891	0.2291
Error b	8											
C	1	0.0001	0.0001	0.6909	0.0001	0.0357	0.0279	0.6709	0.8640	0.0875	0.0071	0.0061
C x F	1	0.0038	0.3749	0.2531	0.0322	0.5615	0.9673	0.6793	0.5588	0.0010	0.0306	0.3980
C x T X F	1	0.5071	0.6392	0.1222	0.2069	0.4421	0.4498	—	—	0.0092	0.9079	0.9280
Error c	20											

T = thinning; F = fertilization; SY = sampling year; C = crown; df = degree of freedom; FFLG = first-flush length; FFLA = leaf area per first flush; FFNL = first-flush needle length; FFNA = leaf area per first-flush fascicle; SFLG = second-flush length; SFLA = leaf area per second flush; SFNL = second-flush needle length; SFNA = leaf area per second-flush fascicle; MFPS = numbers of multiple flushes per shoot; FSLG = annual flush shoot length; FSNA = leaf area per flush shoot.

Table 2—Mean values of the October flush and needle characteristics of 14- to 16-year-old loblolly pine trees in response to repeated thinning and fertilization treatments and crown positions 3 years after treatment in Louisiana

Measured variable	T	UT	F	UF	UC	LC
First flush shoot						
Flush length (*cm*)	18.2 a	18.5 a	21.4 a	15.3 b	26.5 a	10.3 b
Leaf area per flush (cm^2)	2,162 a	2,370 a	2,548 a	1,985 b	3,340 a	1,193
Fascicle needle length (*cm*)	16.6 a	15.1 b	17.4 a	14.3 b	15.9 a	15.8 a
Leaf area per fascicle (cm^2)	16.2 a	14.0 b	16.9 a	13.3 b	15.9 a	14.2 b
Second flush shoot						
Flush length (*cm*)	5.6 a	5.1 a	6.7 a	4.1 b	8.6 a	2.2 b
Leaf area per flush (cm^2)	478 a	526 a	601 a	404 b	889 a	115 b
Fascicle needle length (*cm*)	12.5 a	12.4 a	13.5 a	10.7 b	12.6 a	12.0 b
Leaf area per fascicle (cm^2)	12.5 a	12.4 a	13.6 a	10.7 b	12.7 a	11.3 b
Annual flush shoot						
Multiple flushes per shoot	2.8 a	2.6 a	2.8 a	2.5 b	3.0 a	2.3 b
Flush shoot length (*cm*)	25.3 a	24.9 a	29.9 a	20.3 b	37.1 a	13.0 b
Leaf area per shoot (cm^2)	2,648 a	2,924 a	3,184 a	2,389 b	4,265 a	1,308 b

T = thinned plot; UT = unthinned plot; F = fertilized plot; UF = unfertilized plot; UC = upper crown; LC = lower crown.
Means followed by the same letters for each variable within thinning or fertilization treatments or crown positions do not differ significantly at $P \leq 0.10$.

Needle-level Physiology

Photosynthetic gas exchange of foliage did not vary significantly with year (table 3). Across all treatments and crown levels, mean P_n, based on a needle surface area, was 3.5 μmol m^{-2} s^{-1}. Mean g_w and E were significantly higher in 1995 than in 1997. Differences in g_w and E were associated with a significant difference in Ψ_{pd} and SWC between the 2 years. Mean Ψ_{pd} and SWC were -0.56 MPa and 25.9 percent by volume, respectively, in 1995 and -0.72 MPa and 21.5 percent in 1997. Mean Ψ_{md} in late morning was significantly different among the years with more negative values (-1.23 and -1.28 MPa) in 1995 and 1997 than the value (-1.09 MPa) in 1996.

Large variation in light intensity was found vertically within the canopy of the unthinned plot (fig. 4A). Low light limited

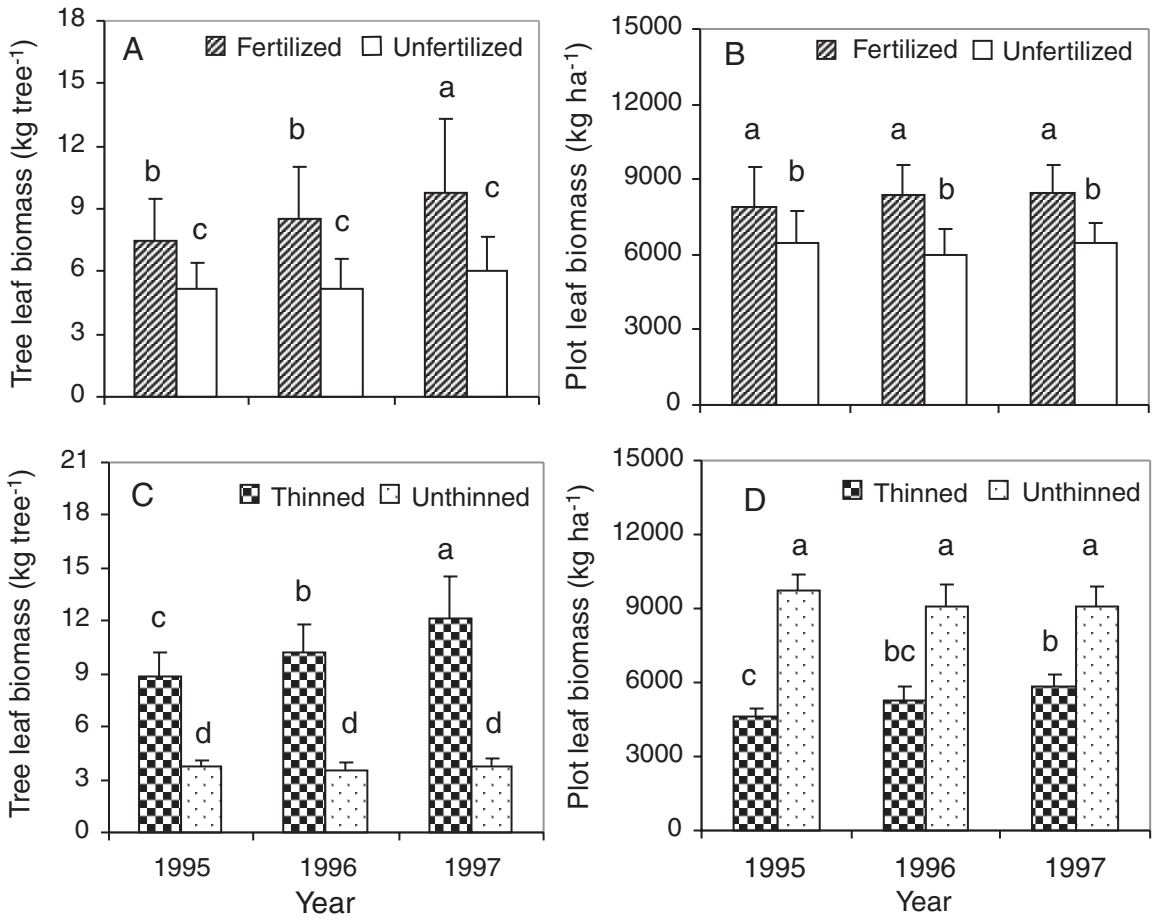

Figure 3—Mean annual needle-fall biomass per tree and per plot 3 years after refertilization and rethinning. Bars followed by the same letters do not differ significantly at $P \leq 0.10$.

Table 3—Probability of F-test for the effects of repeated thinning and fertilization treatments and crown position on the physiological variables of 14- to 16-year-old loblolly pine trees 3 years after treatment in Louisiana

Source of variation	df	P_n	g_w	E	Ψ_{md}	Ψ_{pd}
T	1	0.0253	0.2112	0.0688	0.1206	0.0597
F	1	0.2320	0.4722	0.7108	0.0454	0.0121
T x F	1	0.5577	0.8266	0.9428	0.4988	0.3054
Error a	4					
SY	2	0.1909	0.0001	0.0071	0.0012	0.0001
SY x T	2	0.1219	0.5342	0.6074	0.9554	0.4054
SY x F	2	0.6700	0.9580	0.6792	0.3976	0.3617
SY x T x F	2	0.6454	0.6186	0.5921	0.9571	0.5858
Error b	8					
C	1	0.0001	0.0005	0.0004	0.0003	0.2951
C x T	1	0.0045	0.0055	0.0102	0.0333	0.3750
C x F	1	0.4497	0.4000	0.5766	0.9849	0.6269
C x T x F	1	0.2150	0.4080	0.2906	0.4743	0.6313
Error c	276					

df = degree of freedom; P_n = photosynthesis; g_w = stomatal conductance to water vapor; E = transpiration; Ψ_{md} = daytime needle water potential; Ψ_{pd} = predawn needle water potential; T = thinning; F = fertilization; SY = sampling year.

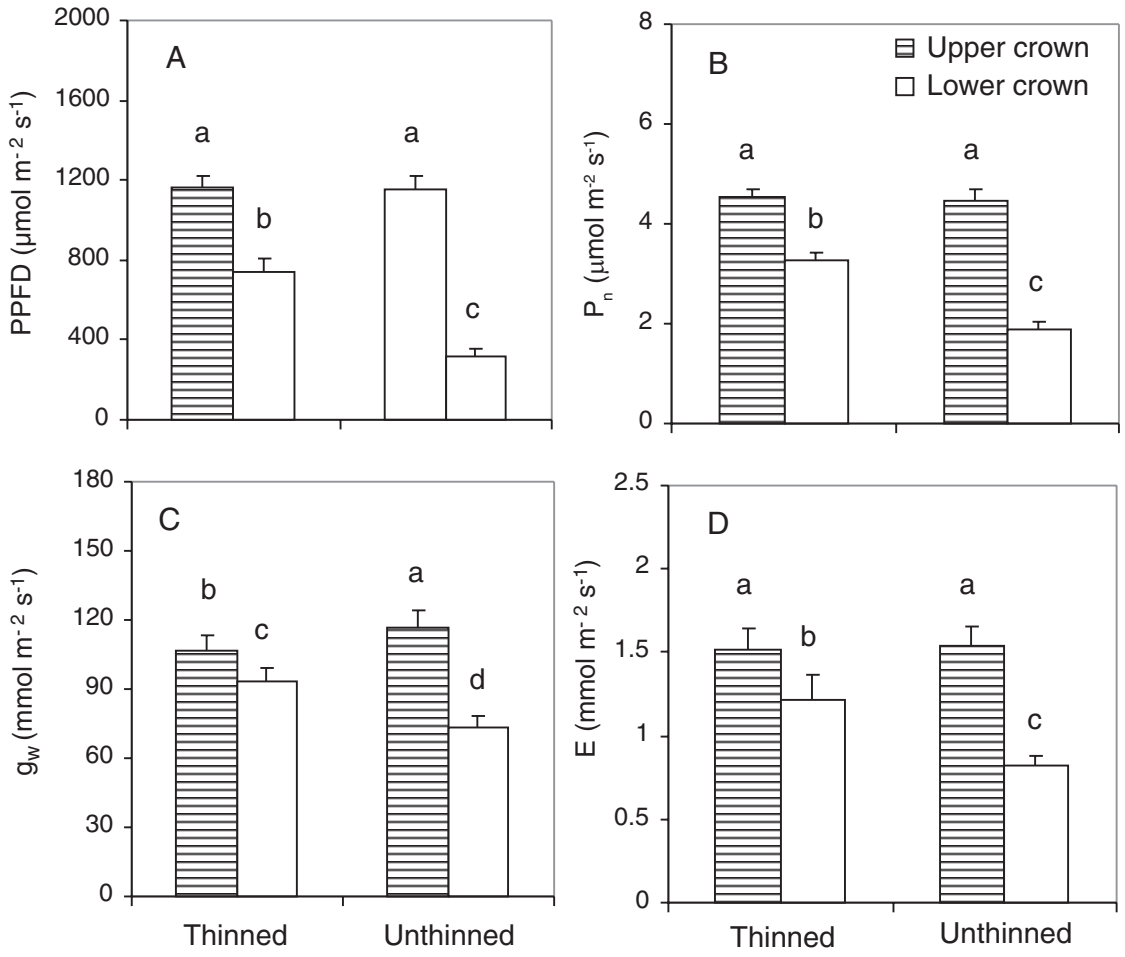

Figure 4—Mean photosynthetic photon flux density (PPFD), photosynthesis (P_n), stomatal conductance (g_w) and transpiration (E) of 14- to 16-year-old loblolly pine trees 3 years after rethinning. Bars followed by the same letters do not differ significantly at $P \leq 0.10$.

photosynthetic activity of lower crown foliage of the unthinned trees. Rethinning significantly increased light penetration and crown exposure, and, therefore, P_n and E of the thinned trees (tables 3 and 4). Across the 3 years, mean PPFD in the lower crown rose 133 percent on the thinned plots in comparison with the unthinned plots. Lower-crown needle P_n on the thinned plots increased 73 percent (fig. 4B). The thinned trees also had higher g_w and E rates (figs. 4C and 4D) and more negative Ψ_{md} in the lower-crown needles. Mean SWC and Ψ_{pd} were slightly and significantly higher on the thinned plots than on the unthinned plots.

Table 4—Mean values of the physiological characteristics of 14- to 16-year-old loblolly pine trees in response to repeated thinning and fertilization and crown positions 3 years after treatment in Louisiana

Measured variable	T	UT	F	UF	UC	LC
P_n (mmol m^{-2} s^{-1})	3.88 a	3.20 b	3.68 a	3.40 a	4.53 a	2.56 b
g_w (mmol m^{-2} s^{-1})	101 a	96 a	97 a	100 a	113 a	83 b
E (mmol m^{-2} s^{-1})	1.37 a	1.20 b	1.29 a	1.27 a	1.55 a	1.02 b
Ψ_{md} (MPa)	-1.22 a	-1.17 a	-1.16 a	-1.24 b	-1.29 b	-1.11 a
Ψ_{pd} (MPa)	-0.61 a	-0.64 b	-0.60 a	-0.65 b	-0.63 a	-0.62 a

T = thinned; UT = unthinned; F = fertilized; UF = unfertilized; UC = upper crown; LC = lower crown; P_n = photosynthesis; g_w = stomatal conductance to water vapor; E = transpiration; Ψ_{md} = daytime needle water potential; Ψ_{pd} = predawn needle water potential. Means followed by the same letters within thinning or fertilization treatments or crown positions do not differ significantly at $P \leq 0.10$.

Refertilization did not have a significant effect on needle P_n, g_w, and E (tables 3 and 4). Mean Ψ_{pd} and $_{md}$ were more negative on the unfertilized plots than on the fertilized plots, but SWC was unaffected by refertilization. Statistically, there was no two-way or three-way interaction among thinning, fertilization and crown position on the physiological attributes.

DISCUSSION

Yu and others (1999) found that maximum increases in annual ring width and stem volume occurred in the third year following the first thinning at our study site. In 1995, 6 years after treatment, however, annual volume growth in response to thinning already decreased to the same level before the first thinning. Prior to rethinning, we observed that crown closure began to take place on the thinned plots. Photosynthetic photon flux density (PPFD) and P_n in the lower crown were only 24 and 28 percent higher, respectively, on the thinned plots compared to the unthinned plots (Tang and others 1999). At that time, differences in shoot and leaf area growth no longer existed between thinned and unthinned plots (Yu and others, in press).

The most important thinning-related change found in this study was the increase in solar radiation on the thinned plots. Over 3 consecutive years after rethinning, PPFD and P_n in the lower crown of the thinned trees rose 133 and 73 percent, respectively. The magnitude of increases in PPFD and P_n in response to rethinning was similar to the magnitude reported by Ginn and others (1991) and Peterson and others (1997) who examined the thinning effects on gas exchange rates of juvenile loblolly pine in Virginia. Our data show that P_n responses to repeated thinning can attain the level following first thinning.

We also found that rethinning stimulated leaf area per fascicle in the lower crown and needle-fall biomass production per tree. Positive responses in both leaf area growth and photosynthesis per unit leaf area could result in a substantial increase in whole-tree carbon uptake. With the advantage of more carbon uptake, thinned-plot trees may have maintained more optimal stem volume growth over the age of the stand than if only first thinning was done (Brix 1983, Sheriff 1996, Yu and others 1999). Commercial thinning of loblolly pine stands in the South is repeated as often as every 10 years for enhancing merchantable saw timber production (Schultz 1997). However, our study suggested that subsequent thinning may be needed sooner than 10 years to increase net photosynthesis rate, leaf area growth and foliage production for maximum volume increment.

Positive P_n responses to fertilization appeared to be inconsistent. On a site low in N and P, for instance, Sheriff and others (1986) found that P, but not N, addition was positively correlated with P_n rates of 7-year-old radiata pine (*Pinus radiata* Don). Thompson and Wheeler (1992) reported a positive relationship between foliar N concentration and carbon uptake of 14-year-old radiata pine. But this relationship was only evident outside the growing season when g_w was less than 75 mmol m^{-2} per second. Teskey and others (1994) observed that N fertilization together with other micro- and macro-nutrients did not alter P_n rates of 23-year-old slash pine (*Pinus elliottii* Engelm.). However, the supply with micro- and macro-nutrients increased light-saturated P_n of 9-year-old loblolly pine on a nutrient-poor soil in North Carolina 2 years after treatment (Murthy and others 1996). Four years later, at the same site, Maier and others (2002) found little fertilization effect on gas exchange. At our site, N and P levels were inherently low in the Beauregard silt loam soil (Tiarks and Haywood 1986). Initial N and P fertilization improved soil fertility and increased volume growth for 4 post-treatment years (Yu and others 1999). For this study, we hypothesized that a fertilization-induced increase in tree growth was partly caused by increases in carbon uptake rates. However, P_n was not different between both fertilized and unfertilized plots. Similarly, Zhang and others (1997) evaluated 4-year-old loblolly pine trees on a southeastern Oklahoma site and revealed no impact of N fertilization on photosynthetic rates. Their results suggest that N-induced increases in foliar chlorophyll concentrations and P_n rates of shaded foliage may only be apparent on sites where leaf chlorophyll and N levels are extremely low. Consistent with the suggestion of Zhang and others (1997), several other researchers have found that a more than 30 percent increase in foliar N concentration of pines grown on nutrient-poor sites was related to an increase in carbon fixation (Beets and Whitehead 1996, Fife and Nambiar 1997).

Low nutrient availability at our site reduced foliage production on the unfertilized plots (Sword and others 1998). Reapplication of N-P-K fertilizers persistently enhanced flush shoot and needle growth. We observed that the fertilized trees annually produced more flushes per shoot, longer flush shoots and greater leaf area per shoot. These findings agree with the measurements reported by Maier and others (2002), who found a 38 percent increase in branch leaf area of 13 year old loblolly pine 5 years after fertilization on a nutrient-poor site in North Carolina. We also observed that tree-level and plot-level needle-fall biomass production was increased by refertilization during the study. The advantage in flush growth and foliage production on the fertilized plots could be one of the major factors for increasing intercepted radiation within the canopy and tree productivity (Albaugh and others 1998, Leverenz and Hinckley 1990, Samuelson and others 2001). Continued assessment of the effects of site factors and cultural practices on canopy physiology and growth response is necessary for a better understanding of the productivity of southern pines in relation to forest management and the changing environment.

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