

Thinning, fertilization, and crown position interact to control physiological responses of loblolly pine

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Summary To examine physiological responses to thinning, fertilization, and crown position, we measured net photosynthesis (P_n), transpiration (E), vapor pressure difference (VPD), stomatal conductance (g_s), and xylem pressure potential (Ψ_1) between 0930 and 1130 h under ambient conditions in the upper and lower crowns of a 13-year-old loblolly pine (*Pinus taeda* L.) plantation six years (1994) after the treatments were applied. Photosynthetic photon flux density (PPFD) and air temperature (T_a) within the canopy were also recorded. Needle P_n of thinned trees was significantly enhanced by 22–54% in the lower crown, because canopy PPFD increased by 28–52%. Lower crown foliage of thinned plots also had higher E and g_s than foliage of unthinned plots, but thinning had no effect on needle Ψ_1 and predawn xylem pressure potential (0430–0530 h; Ψ_{pd}). Tree water status did not limit P_n , E and g_s during the late-morning measurements. Fertilization significantly decreased within-canopy PPFD and T_a . Needle Ψ_1 was increased in fertilized stands, whereas P_n , E and g_s were not significantly altered.

Upper crown foliage had significantly greater PPFD, P_n , VPD, g_s , E , and more negative Ψ_1 than lower crown foliage. In both crown positions, needle P_n was closely related to g_s , PPFD and T_a ($R^2 = 0.77$ for the upper crown and 0.82 for the lower crown). We conclude that (1) silvicultural manipulation causes microclimate changes within the crowns of large trees, and (2) needle physiology adjusts to the within-crown environmental conditions.

Keywords: photosynthesis, *Pinus taeda*, PPFD, stomatal conductance, temperature, transpiration, water status.

Introduction

Physiological and morphological characteristics of forest tree foliage may be associated with differences in stand growth and are influenced by environmental changes and cultural manipulations (Brix 1983, Nelson and Ehlers 1984, Teskey et al. 1987, Dickmann et al. 1990). Net photosynthesis and stomatal conductance of conifer trees are closely related to changes in nutrient concentration, water status, CO_2 concentration, and light availability (Brix 1972, Seiler and Johnson 1985, Teskey

et al. 1986, Smolander and Oker-Blom 1989, Teskey et al. 1994, Murthy et al. 1996, Sheriff 1996). Several seedling studies of forest species have provided basic knowledge of growth, carbon fixation, water relations, and other metabolic processes in response to changing environment and silvicultural manipulations (van den Driessche 1972, Reid et al. 1983, Seiler and Johnson 1985, Teskey et al. 1987). However, there is little information on how foliage of large loblolly pine (*Pinus taeda* L.) trees respond physiologically to cultural treatments, because of (i) difficulties in accessing live crowns of large trees; (ii) lack of effective measurement techniques for use under ambient field conditions; (iii) limitations of monitoring instrumentation for collecting microclimate data; and (iv) economic constraints. Field experiments with older trees are needed to characterize foliar responses within the crown to silvicultural practice, because foliage of older trees may differ physiologically, morphologically, and phenologically from that of seedlings and saplings (Cregg et al. 1989). Nowak et al. (1990) and Ginn et al. (1991) reported that, in loblolly pine, needle net photosynthesis and stomatal conductance in the lower crown increased in response to thinning three years after treatment. In contrast, Gravatt et al. (1997) did not find significant differences in foliar gas exchange and water relations between thinned and unthinned loblolly stands during the fifth year after thinning. Fertilizer application may also have variable effects. In some studies, fertilization increases net photosynthesis and water use efficiency of conifer species (Brix 1983, Smolander and Oker-Blom 1989, Murthy et al. 1996), whereas in other cases it has no effect on photosynthetic activities (Brix and Ebell 1969, Sheriff et al. 1986, Teskey et al. 1994, Zhang et al. 1997).

The objectives of the present study were: (1) to investigate needle gas exchange and water loss of a 13-year-old loblolly pine stand in response to thinning, fertilization, and crown position six years after cultural treatments, and (2) to relate physiological responses to microenvironment within the stand during the growing season. We tested the hypothesis that gas exchange processes of current-year foliage are adjusted within the crown in response to thinning and fertilization.

Materials and methods

Study location and cultural treatments

The study site is a 0.93 ha area situated in the Palustris Experimental Forest of Rapides Parish, Louisiana, USA (31°11' N, 92°41' W). The soil at the planting site is a Beauregard silt loam with a gentle slope and well drained. Containerized seedlings were transplanted to the site at a spacing of 1.8 by 1.8 m in May 1981.

At the end of 1987, tree survival was 97%, with similar-sized trees throughout the site (Haywood 1994). Twelve treatment plots were established in spring 1988. Each plot was 23.8 by 23.8 m. Thinning and fertilization were used in a 2 x 2 factorial design with three replications and randomly applied to the 12 plots. Two thinning treatments (unthinned and thinned) were established in November 1988, with plots that either remained uncut at a density of 2990 trees ha⁻¹ or had every other row of trees and every other tree in the remaining rows removed, leaving the residual trees at a 3.7 by 3.7 m spacing and a density of 731 trees ha⁻¹. Fertilization was completed in April 1989 and consisted of two treatments (fertilized and unfertilized). Fertilized plots were broadcast with diammonium phosphate at a rate of 744 kg ha⁻¹ (134 kg N ha⁻¹ and 150 kg P ha⁻¹) (cf. Shoulders and Tiarks 1983). The associated understory hardwoods, shrubs, and vines were destroyed with a rotary mower. During the post-treatment growing seasons, weed competition was controlled with glyphosate herbicide mixed with 2,4-D, dicamba and dichloroprop. Stand characteristics and post-treatment growth during the four-year period (1989–1992) were reported by Haywood (1994). Generally, thinning significantly increased diameter growth and decreased height growth during that period, whereas fertilization stimulated growth in height, diameter and basal area. Fertilization also interacted with thinning to enhance diameter growth during the four-year period. At the end of 1992, thinned trees had larger diameters but were shorter than unthinned trees, whereas trees in fertilized plots had greater heights, diameters and basal areas than trees in unfertilized plots.

During summer 1991, steel radio towers were established and extended upward above the tree crowns in eight plots (representing two replications of the treatment combinations). Wooden walkways were constructed between these towers in the upper and lower halves of the live crowns to gain partial or full access to crowns of at least eight to ten trees per plot. A computer-based data acquisition system was used to monitor within-crown microenvironmental conditions. The system consisted of a central computer and software program known as SKYLAB (Version 1.1, Agricultural Center, Louisiana State University, Baton Rouge, LA), and individual Keithley data loggers (Model 576, Keithley Instruments, Inc., Taunton, MA) installed in each of the four treatment plots within one replication. Each data logger was connected with four photosynthetically active radiation (PAR) sensors and two shielded solid-state temperature sensors placed at each of the six positions adjacent to selected sample branches that represented the south and north side on each crown level (a total of 12 positions per treatment). Ambient temperature (T_a) and multidirectional

photosynthetic photon flux density (PPFD) in four directions within the canopy were continuously recorded and averaged at 15-min intervals.

Physiological measurements

Photosynthetic data were collected on 13-year-old trees twice each month from June through November 1994 (the sixth growing season after treatment). Three south-facing branches in each of the upper and lower crown were randomly selected from three trees per plot. Different trees were used for measurements. Two healthy fascicles of current-year foliage from the middle portion of the first flush on the terminal or adjacent lateral shoots were measured such that a total of 12 fascicles from six branches were measured per plot. Eight plots (two replications) accessible by the tower systems and walkways were used for photosynthetic measurements, with the four plots of replication one being measured on one day, and the other four plots in replication two measured the next day.

Predawn xylem pressure potentials (Ψ_{pd}) of fascicles removed from the upper- and lower-crown branches between 0430 and 0530 h were measured with a pressure chamber (PMS Instrument Corp., Corvallis, OR, USA). Net photosynthesis (P_n), transpiration (E), stomatal conductance to water vapor (g_s), CO_2 concentration, and vapor pressure difference (VPD) from the intercellular air space of needles to atmosphere were measured between 0930 and 1130 h on sunny days. A portable photosynthesis system (Model 6200, Li-Cor, Inc., Lincoln, NE) with a 250-ml leaf chamber was used. Before each measurement, the system was equilibrated with field conditions and calibrated following standard calibration and testing procedures. During each measurement, middle portions of needles of two fascicles per branch were enclosed in the leaf chamber and measured in their natural orientations on the branch under within-crown ambient conditions. A flow rate of dry air to the leaf chamber was controlled and well stirred to maintain the relative humidity change within 1% in the leaf chamber. Rates of gas exchange were monitored and recorded as changes in CO_2 concentration in the leaf chamber over a time interval of 10–50 s. When the photosynthetic measurement was completed, the needles were detached from the branch and xylem pressure potentials (Ψ_1) of the needles were measured in the field. The needles were then placed and sealed in plastic bags, and taken to the laboratory for leaf area measurements. Needle lengths and volumes per fascicle were recorded, as described by Johnson (1984). Photosynthesis, transpiration and stomatal conductance are expressed on a total needle surface area basis.

Statistical analyses

Monthly means of the microenvironmental and needle physiological parameters were computed from data collected during the growing season. These means were analyzed for a 2 x 2 factorial split-plot design with two replications. Whole-plot factors were thinning and fertilization, whereas crown position (upper and lower) was considered as a subplot factor. The SAS software (SAS Institute Inc., Cary, NC) was used for all data analyses. Main effects of thinning and fertilization and their

interactions, and differences between the two crown positions within each treatment combination were tested for statistical significance at $P \leq 0.10$ (Steel and Torrie 1980). The 0.10 probability level of significance was used because of the high variation expected under natural environmental conditions within large tree canopies. This level of significance was assumed to be sufficient for capturing relationships between cultural treatments at the ground level and within-canopy physiological and micrometeorological changes. When significant treatment or crown effects on a microenvironmental and physiological variable were determined, Least Significant Difference (LSD) tests were conducted to compare differences between the treatment or crown means for that variable. The GLM procedure was utilized for the multiple regression analysis.

Results

Thinning significantly influenced canopy irradiance and air temperature (Table 1). Multidirectional PPFd was higher in thinned stands than in unthinned stands in August, September and October (Figure 1A). Thinned plots had lower mean T_a within the canopy than unthinned plots in September, October and November (Figure 1B).

Needle gas exchange activities of the first-flush foliage in the lower crown were significantly affected by thinning (Table 1). Mean P_n in the lower crown of thinned trees was higher than that of unthinned trees in September through November (Figure 2A). Lower-crown foliage of thinned plots had significantly higher E in September, and greater g_s from August to November than lower-crown foliage of unthinned plots (Figures 2B and 2C). However, needle Ψ_1 and Ψ_{pd} and VPD in the upper and lower crowns were not significantly changed by thinning. In both thinned and unthinned stands, mean Ψ_1 during the late morning (0930 to 1130 h) remained above -1.50 MPa, and, as a result of frequent rainfall, predawn Ψ_{pd} values varied only from -0.57 to -0.70 MPa during the growing season.

Fertilization had significant effects on light availability and temperature within the canopy (Table 1). Mean PPFd and T_a

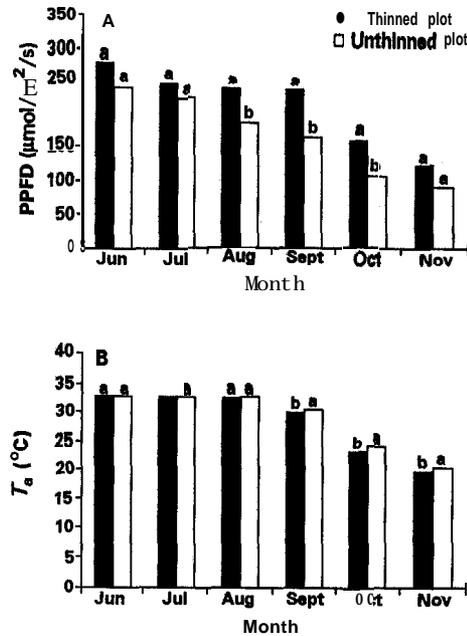


Figure 1. Thinning effects on seasonal changes of (A) multidirectional photosynthetic photon flux density (PPFD) and (B) temperature (T_a) within a loblolly pine plantation. Bars not followed by the same letters in a given month differ at $P \leq 0.10$. Each bar is a mean of daily measurements (0900-1200 h) with 24 light sensors for PPFd and 12 temperature sensors for T_a in each month.

were consistently lower in fertilized stands than in unfertilized stands throughout the growing season (Figure 3A and 3B). However, fertilization did not significantly affect whole-crown needle physiology except xylem water pressure potential, although fertilized trees had lower mean P_n , E , and g_s than unfertilized trees (Figures 3C-3E). More negative Ψ_1 values were observed in unfertilized plots than in fertilized plots in August and October (Figure 3F). Interactions between fertilization and thinning and crown position were not significant for the microclimate and gas exchange measurements.

Table 1. Probability of F-test for the effects of thinning and fertilization on microenvironment and needle physiology within a loblolly pine plantation in 1994.

Source	df	PPFD'	T_a	VPD	P_n	E	g_s	Ψ_1	Ψ_{pd}
Thinning (T)	1	0.0612* ²	0.0308*	0.7664	0.4026	0.9813	0.7974	0.4272	0.3714
Fertilization (F)	1	0.0761*	0.0017*	0.3561	0.4548	0.2739	0.4321	0.0096*	0.2953
T × F	1	0.5617	0.0198*	0.3092	0.7830	0.6437	0.9464	0.1197	0.3744
Crown (C)	1	0.0001'	0.2363	0.0027*	0.0008*	0.0001*	0.0001*	0.0003*	0.2745
T × C	1	0.5511	0.6279	0.4459	0.0436*	0.0068*	0.0059*	0.8393	0.1236
F × C	1	0.2803	0.7458	0.7633	0.3969	0.2492	0.3911	0.3474	0.3858
T × F × C	1	0.6644	0.8734	0.3967	0.7853	0.1347	0.0651*	0.5526	0.5724

¹ Abbreviations: PPFd = multidirectional, photosynthetic photon flux density; T_a = air temperature; VPD = vapor pressure difference; P_n = needle net photosynthesis; E = transpiration; g_s = stomatal conductance to water vapor; Ψ_1 = xylem pressure potential; and Ψ_{pd} = predawn xylem pressure potential.

² An asterisk indicates significance at $P \leq 0.10$.

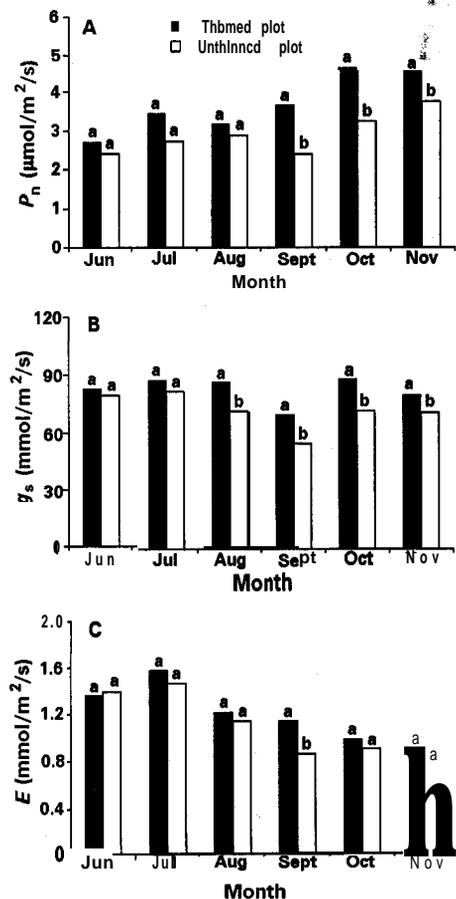


Figure 2. Thinning effects on seasonal patterns of lower crown (A) needle net photosynthesis (P_n), (B) stomatal conductance (g_s) and (C) transpiration (E) within a loblolly pine plantation. Bars not followed by the same letters in a given month differ at $P \leq 0.10$. Each bar is a mean of 12 measurements for a given variable in each month.

Both PPFD and needle physiological responses (except for Ψ_{pd}) differed significantly between the upper and lower crown positions across both thinning and fertilization treatments (Table 1). The upper crown had greater mean PPFD than the lower crown in June through November (Figure 4A). Current-year first flush foliage of the upper crown consistently maintained higher needle P_n than the lower-crown foliage between June and November (Figure 4B). Higher VPD in the upper crown than in the lower crown was associated with greater E and g_s , and more negative Ψ_1 (Figures 4C–4F).

To examine functional relationships between the measured microclimate variables and gas exchange performance of trees in the thinned and unthinned treatments, a regression analysis was conducted. Variance components as a percent of the total variability in needle net photosynthesis were estimated for the environmental and physiological variables. Multidirectional PPFD and T_a within the canopy were significantly correlated with mean P_n and accounted for 65–84% of the total variation in P_n in both thinned and unthinned plots (Table 2). In the upper crown, T_a explained the largest amount of variation in P_n , whereas P_n of the lower crown foliage appeared to be most

limited by low PPFD. There was greater variability in lower-crown P_n in thinned plots than in unthinned plots. Needle g_s was significantly related to P_n . The best model for predicting mean P_n in the upper and lower crowns included PPFD, T_a and g_s (Table 3). The equations were found to fit the measurement data well ($R^2 = 0.77$ for P_n in the upper crown and 0.82 for P_n in the lower crown). Needle Ψ_1 and Ψ_{pd} were not closely coupled with P_n (except Ψ_1 in the lower crown of unthinned plots) and only accounted for 0–1% of the variation in P_n .

Discussion

When measured in saturating light, mean maximum rate of needle net photosynthesis (on a total needle surface area basis) is approximately $6.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ in loblolly pine trees (Fites and Teskey 1988, Murthy et al. 1996). In the present study, averaged over both thinning and fertilization treatments for the entire growing season, P_n of mature first-flush foliage was $4.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the upper crown and $3.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the lower crown. These two values represent 77% (upper crown) and 55% (lower crown) of the light-saturated P_n documented in the literature for this species. Significant variability in light availability and air temperature was observed in the upper and lower crowns during the 1994 growing season. The first-flush foliage in the upper crown maintained significantly higher needle P_n and E , greater g_s , and lower Ψ_1 (more negative) than foliage in the lower crown, because of higher canopy PPFD (Figures 4A–4F and Table 3). Six years after the thinning treatment, thinned plots were beginning to exhibit large differences in needle gas exchange measurements between the two crown levels, because crown closure had started to occur.

Most studies have revealed that conifer stands exhibit responses in net photosynthesis and water relations within the first three years after cultural treatment (Brix 1981, Linder and Axelsson 1982, Brix and Mitchell 1986, Clegg et al. 1990, Liu and Teskey 1995, Murthy et al. 1996). For example, positive relationships between gas exchange and increased PPFD within forest stands after thinning have been reported for loblolly pine (Teskey et al. 1986). Lower-crown gas exchange and stomatal conductance may attain values comparable to those of the upper crown during the first three years after thinning, because irradiance in the lower crown increases after thinning to reach values similar to that in the upper crown (Nowak et al. 1990, Ginn et al. 1991). However, little information is available on how long the impact of silvicultural manipulation on crown physiology persists. We found a significant interaction between thinning and crown position on PPFD and needle gas exchange performance in the lower crown during the sixth year after thinning. Multidirectionally averaged PPFD in thinned stands was 28–52% greater than that in unthinned stands during the growing season (September–November) and, as a result, lower-crown P_n of thinned trees was 22–54% higher than that of unthinned trees during the period. This observation is consistent with the findings of Nowak et al. (1990), Ginn et al. (1991), and Peterson et al. (1997) who carried out similar thinning studies on the same species. Recently, Yu (1996) reported that lower-crown needle surface area per tree was 130% greater in thinned stands than

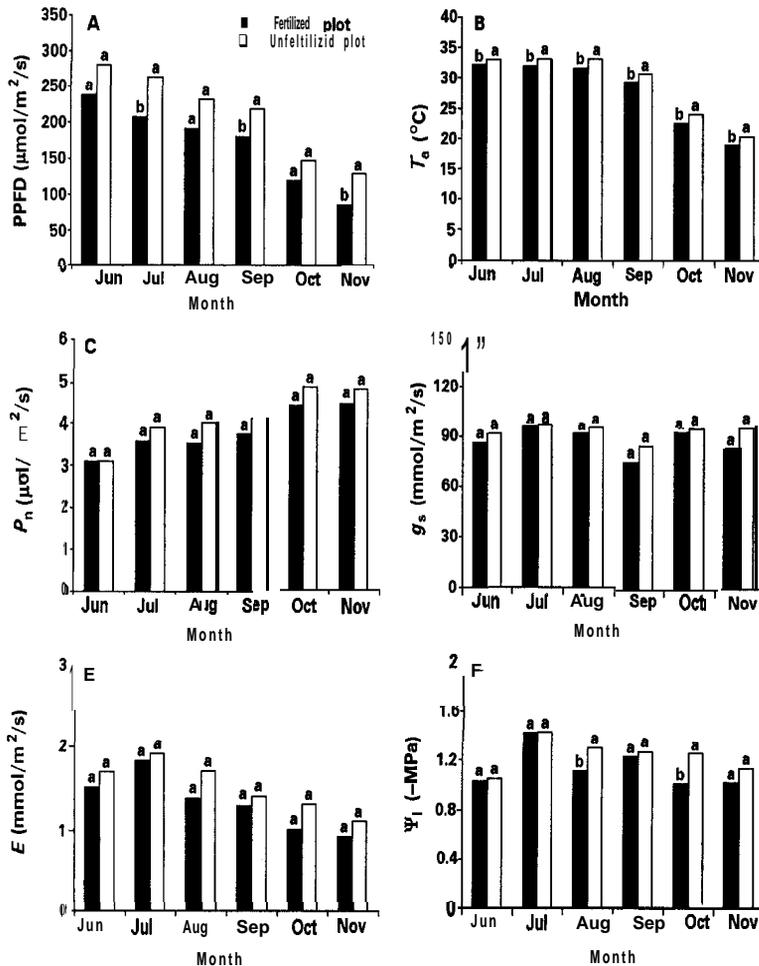


Figure 3. Fertilization effects on seasonal changes of (A) multidirectional, photosynthetic photon flux density (PPFD), (B) temperature (T_a), (C) needle net photosynthesis (P_n), (D) stomatal conductance (g_s), (E) transpiration (E) and (F) xylem pressure potential (Ψ_1) within a loblolly pine plantation. Bars not followed by the same letters in a given month differ at $P < 0.10$. Each bar is a mean of daily measurements with 24 light sensors for PPFD, 12 temperature sensors for T_a , and 24 measurements for a given needle gas exchange variable in each month.

in unthinned stands. Thus, the thinning-induced increase in lower-crown photosynthetic production could be associated with both increasing leaf area and gas exchange per unit of needle surface area. Differences in carbon fixation of lower-crown foliage between thinned and unthinned trees have also been related to variability in photosynthate allocation (Nelson and Isebrands 1983, Dickson 1986, Sword et al. 1996).

Thinned plots had higher g_s and E in the lower crown than unthinned plots, whereas mean Ψ_1 was not significantly different between the two treatments. Stomatal conductance remained relatively high ($94\text{--}113\text{ mmol m}^{-2}\text{ s}^{-1}$ in the upper crown and $54\text{--}87\text{ mmol m}^{-2}\text{ s}^{-1}$ in the lower crown) throughout the year and no stomatal closure was observed in the upper or lower crown foliage during the measurement period (0930–1130 h). The highest g_s and E and lowest Ψ_1 occurred in July. Thereafter, needle E and g_s decreased and Ψ_1 increased toward the end of the growing season. There was no correlation between needle P_n and Ψ_1 or Ψ_{pd} , indicating that needle P_n was not limited by Ψ_1 or Ψ_{pd} after thinning (Table 2). Sufficient precipitation and adequate soil water supply on the site contributed to the apparent lack of relationship between P_n and Ψ_1 and Ψ_{pd} . Other authors have reported similar results in plant water relations in response to thinning (Cregg et al. 1990, Nowak et al. 1990).

Photosynthetic responses of conifer species to fertilizer application have been reviewed recently by Teskey et al. (1994) and Sheriff (1996). Foliar nitrogen content is commonly reported to be positively correlated with net photosynthesis (Smolander and Oker-Blom 1989, Thompson and Wheeler 1992, Mitchell and Hinckley 1993). Murthy et al. (1996) reported that fertilization significantly increased foliar nitrogen concentrations of loblolly pine by 2534% and light-saturated photosynthesis by 20–24% in low basal area stands on dry sites. However, other studies show that fertilization has little effect on gas exchange performance of pine trees (Sheriff et al. 1986, Teskey et al. 1994, Sheriff 1996, Zhang et al. 1997). In the present study, we observed that fertilized stands consistently had lower mean PPFD and T_a than unfertilized stands during the growing season, indicating that mutual leaf shading within the canopy increased in fertilized plots as a result of the rapid production of foliage after fertilization (Sword et al. 1996, Yu 1996). Fertilized trees tended to have lower P_n , E , and g_s and higher Ψ_1 (less negative) than unfertilized trees, but the differences in these physiological measurements between the two treatments were not statistically significant. These results support the close relationship between foliage production and tree growth in response to fertilization (Vose and Allen 1988, Haywood 1994, Yu 1996).

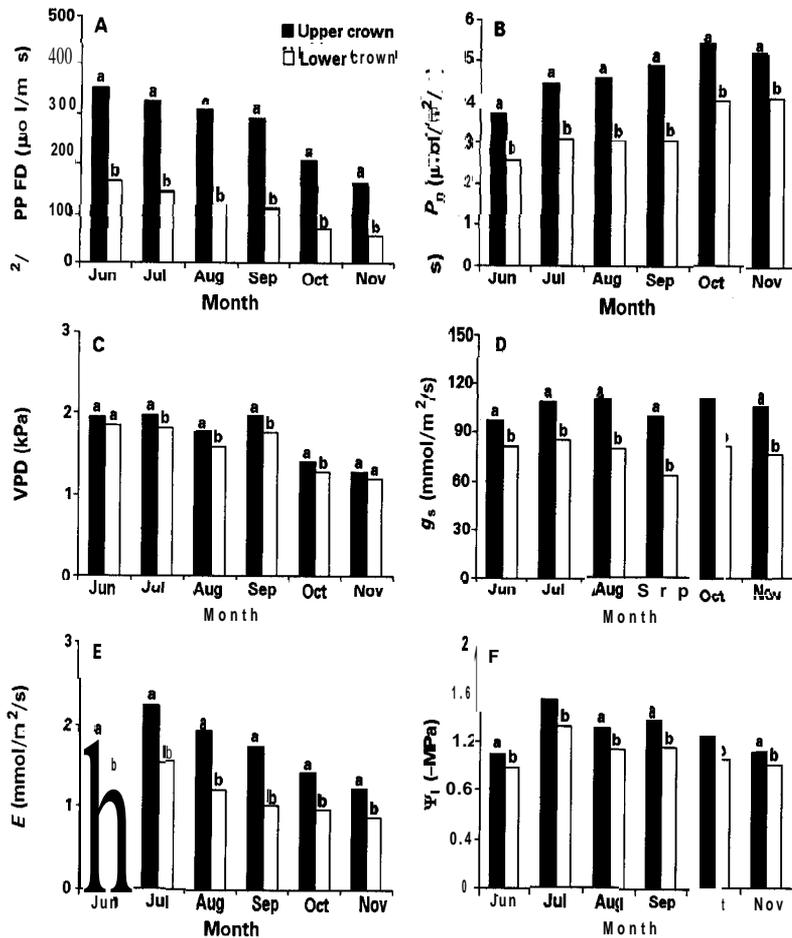


Figure 4. Crown position effects on seasonal changes of (A) multidirectional, photosynthetic photon flux density (PPFD), (B) needle net photosynthesis (P_n), (C) vapor pressure difference (VPD), (D) stomatal conductance (g_s), (E) transpiration (E) and (F) xylem pressure potential (Ψ_1) within a loblolly pine plantation. Bars not followed by the same letters in a given month differ at $P \leq 0.10$. Each bar is a mean of daily measurements with 24 light sensors for PPFD and 24 measurements for a given gas exchange variable in each month.

Table 2. Relative size of variance component of the variables correlated with needle net photosynthesis of loblolly pine in response to thinning.

Measured variable ¹	Relative size of variance component as a % of the total variance of P_n			
	Thinned-upper	Unthinned-upper	Thinned-lower	Unthinned-lower
PPFD	3.160 (30)* ²	1.559 (19)*	11.485 (73)*	9.510 (52)*
T_a	5.299 (50)*	3.981 (46)*	1.699 (11)*	5.094 (28)*
CO_2	0.698 (7)*	0.294 (3)	0.009 (0)	0.000 (0)
VPD	0.003 (0)	1.063 (12)*	0.425 (3)	0.813 (4)*
g_s	1.302 (13)*	1.643 (19)*	1.842 (12)*	1.733 (10)*
Ψ_1	0.048 (0)	0.066 (1)	0.002 (0)	1.046 (6)*
Ψ_{pd}	0.039 (0)	0.011 (0)	0.257 (1)	0.055 (0)
Total	10.549 (100)	8.616 (100)	15.718 (100)	18.251 (100)

¹ Abbreviations: PPFD = multidirectional, photosynthetic photon flux density; T_a = air temperature; CO_2 = ambient CO_2 concentration; VPD = vapor pressure difference; g_s = stomatal conductance to water vapor; Ψ_1 = xylem pressure potential; and Ψ_{pd} = predawn xylem pressure potential.

² An asterisk indicates significance at $P \leq 0.10$.

In summary, under the field conditions of this study, needle gas exchange was highly correlated with light, temperature and stomatal conductance in the upper and lower crowns ($R^2 = 0.77$ and 0.82 , respectively). There was a significant interaction between thinning and crown position in increasing needle P_n , E and g_s in the lower crown foliage as a result of increased PPFD. Light availability was the most important factor limiting needle net photosynthesis in the lower crown. Because

irradiance increases after thinning, the lower crown foliage is able to increase whole-crown photosynthetic production of remaining trees and contribute to total stand carbon fixation. Tree water status was not altered after thinning, which is in agreement with the results reported from other thinning studies. Needle Ψ_1 and Ψ_{pd} did not limit needle g_s , P_n and E during the late morning measurements in either the thinned or unthinned plots. On the other hand, fertilization significantly

Table 3. Relationships between needle net photosynthesis and stomatal conductance and microenvironmental variables within a loblolly pine plantation ($n = 48$).

Equation ¹	R^2	$P_r > F$
Upper crown		
$P_n = 0.003(\text{PPFD}) - 0.077(T_a) + 0.018(g_s) + 3.144$	0.77	0.0001
Lower crown		
$P_n = 0.005(\text{PPFD}) - 0.082(T_a) + 0.029(g_s) + 1.790$	0.82	0.0001

¹ Abbreviations: P_n = needle net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); PPFD = multidirectional, photosynthetic photon flux density ($\mu\text{mol mm}^{-2} \text{s}^{-1}$); T_a = air temperature ($^{\circ}\text{C}$); and g_s = stomatal conductance to water vapor ($\text{mmol m}^{-2} \text{s}^{-1}$).

decreased PPFD and T_a six years after application, but it had little effect on needle physiology adjustment. The more complex interactions among thinning, fertilization, crown development and needle physiology need further investigation. The long-term response under extreme drought stress also needs to be studied to understand fully the effects of silvicultural practices on crown carbon fixation and stand growth.

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References

- Brix, H. 1972. Nitrogen fertilization and water effects on photosynthesis and earlywood-latewood production in Douglas-fir. *Can. J. For. Res.* 2:467-478.
- Brix, H. 1981. Effects of nitrogen fertilizer source and application rates on foliar nitrogen concentration, photosynthesis, and growth of Douglas-fir. *Can. J. For. Res.* 11:775-780.
- Brix, H. 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. *Can. J. For. Res.* 13: 167-175.
- Brix, H. and L.F. Ebell. 1969. Effects of nitrogen fertilization on growth, leaf area and photosynthesis rate in Douglas-fir. *For. Sci.* 15:189-196.
- Brix, H. and A.K. Mitchell. 1986. Thinning and nitrogen fertilization effects on soil and tree water stress in a Douglas-fir stand. *Can. J. For. Res.* 16: 1334-1338.
- Cregg, B.M., J.E. Halpin, P.M. Dougherty and R.O. Teskey. 1989. Comparative physiology and morphology of seedling and mature forest trees. *In* Air Pollution Effects on Forest Vegetation. Eds. R.D. Norle, J.L. Martin and K.F. Jensen. USDA, For. Serv., Northeastern For. Expt. Stn., Broomall, PA, pp 11-18.
- Cregg, B.M., T.C. Hennessey and P.M. Dougherty. 1990. Water relations of loblolly pine trees in southeastern Oklahoma following precommercial thinning. *Can. J. For. Res.* 20:1508-1513.
- Dickmann, D.I., D.A. Michael, J.G. Isebrands and S. Westin. 1990. Effects of leaf display on light interception and apparent photosynthesis in two contrasting *Populus* cultivars during their second growing season. *Tree Physiol.* 7:7-20.

- Dickson, R.E. 1986. Carbon fixation and distribution in young *Populus* trees. *In* Crown and Canopy Structure in Relation to Productivity. Eds. T. Fujimori and D. Whitehead. For. and For. Prod. Res. Inst., Ibaraki, Japan, pp 409-426.
- Fites, J.A. and R.O. Teskey. 1988. CO_2 and water vapor exchange in *Pinus taeda* in relation to stomatal behavior: test of an optimization hypothesis. *Can. J. For. Res.* 18:150-157.
- Ginn, S.E., J.R. Seiler, B.H. Cazell and R.E. Kreh. 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. *For. Sci.* 37: 1030-1040.
- Gravatt, D.A., J.L. Chambers and J.P. Barnett. 1997. Temporal and spatial patterns of net photosynthesis in 12-year-old loblolly pine five growing seasons after thinning. *For. Ecol. Manag.* 97:73-83.
- Haywood, J.D. 1994. Seasonal and cumulative loblolly pine development under two stand density and fertility levels through four growing seasons. USDA, For. Serv., So. For. Expt. Stn. Research Paper SO-283, New Orleans, LA, 5 p.
- Johnson, J.D. 1984. A rapid technique for estimating total surface area of pine needles. *For. Sci.* 30:913-921.
- Linder, S. and B. Axelsson. 1982. Changes in carbon uptake and allocation as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. *In* Carbon Uptake and Allocation in Subalpine Ecosystem as a Key to Management. Ed. R.H. Waring. For. Res. Lab., Oregon State Univ., OR, pp 38-44.
- Liu, S. and R.O. Teskey. 1995. Responses of foliar gas exchange to long-term elevated CO_2 concentrations in mature loblolly pine trees. *Tree Physiol.* 15:351-359.
- Mitchell, A.K. and T.M. Hinckley. 1993. Effects of foliar nitrogen concentration on photosynthesis and water use efficiency in Douglas-fir. *Tree Physiol.* 12:403-410.
- Murthy, R., P.M. Dougherty, S.J. Zarnoch and H.L. Allen. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. *Tree Physiol.* 16:537-546.
- Nelson, N.D. and P. Ehlers. 1984. Comparative carbon dioxide exchange for two *Populus* clones grown in growth room, greenhouse and field environments. *Can. J. For. Res.* 14:924-932.
- Nelson, N.D. and J.G. Isebrands. 1983. Late-season photosynthesis and photosynthate distribution in an intensively cultured *Populus nigra* x *laurifolia* clone. *Photosynthetica* 17:537-549.
- Nowak, J., J.R. Seiler, B.H. Cazell and R.E. Kreh. 1990. Physiological differences in sun and shade foliage in thinned and unthinned loblolly pine. *In* Proc. 6th Biennial Southern Silvicultural Res. Conf., Memphis, TN, pp 541-548.
- Peterson, J.A., J.R. Seiler, J. Nowak, S.E. Ginn and R.E. Kreh. 1997. Growth and physiological responses of young loblolly pine stands to thinning. *For. Sci.* 43:529-534.
- Reid, C.P.P., E.A. Kidd and S.A. Ekwebelam. 1983. Nitrogen nutrition, photosynthesis and carbon allocation in ectomycorrhizal pine. *Plant Soil* 71:415-432.
- Seiler, J.R. and J.D. Johnson. 1985. Photosynthesis and transpiration of loblolly pine seedlings as influenced by moisture stress conditioning. *For. Sci.* 31:742-749.
- Sheriff, D.W. 1996. Responses of carbon gain and growth of *Pinus radiata* stands to thinning and fertilizing. *Tree Physiol.* 16:527-536.
- Sheriff, D.W., E.K.S. Nambiar and D.N. Fife. 1986. Relationship between nutrient status, carbon assimilation and water use in *Pinus radiata* (D. Don) needles. *Tree Physiol.* 2:73-88.
- Shoulders, E. and A.E. Tiarks. 1983. A continuous function design for fertilizer rate trials in young pine plantations. *In* Proc. 2nd Biennial Southern Silv. Res. Conf., Gen. Tech. Rep. SE-24. USDA For. Serv., SE For. Exp. Stn., Asheville, NC, pp 352-356.

- Smolander, H. and P. Oker-Blom. 1989. The effect of nitrogen content on the photosynthesis of Scots pine needles and shoots. *Ann. Sci. For. Suppl.* 46:473s-475s.
- Steel, R.B. and J.H. Torrie. 1980. Principles and practices of statistics. McGraw-Hill Book Co., Inc., New York, NY, 633 p.
- Sword, M.A., D.A. Gravatt, P.L. Faulkner and J.L. Chambers. 1996. Seasonal branch and line root growth of juvenile loblolly pine five growing seasons after fertilization. *Tree Physiol.* 16:899-904.
- Teskey, R.O., J.A. Fites, L.J. Samuelson and B.C. Bongarten. 1986. Stomatal and non-stomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. *Tree Physiol.* 2:131-142.
- Teskey, R.O., B.C. Bongarten, B.M. Cregg, P.M. Dougherty and T.C. Hennessey. 1987. Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine (*Pinus taeda* L.). *Tree Physiol.* 3:41-61.
- Teskey, R.O., H.L. Gholz and W.P. Cropper, Jr. 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. *Tree Physiol.* 14:1215-1227.
- Thompson, W.A. and A.M. Wheeler. 1992. Photosynthesis by mature needles of field-grown *Pinus radiata*. *For. Ecol. Manag.* 52:225-242.
- van den Driessche, R. 1972. Different effects of nitrate and ammonium forms of nitrogen on growth and photosynthesis of slash pine seedlings. *Aust. For.* 36:125-137.
- Vose, J.M. and H.L. Allen. 1988. Leaf area, stemwood growth and nutritional relationships in loblolly pine. *For. Sci.* 34:547-563.
- Yu, S. 1996. Foliage and crown characteristics of loblolly pine (*Pinus taeda* L.) six years after thinning and fertilization. M.S. Thesis. School of Forestry, Wildlife and Fisheries, Louisiana State University, Baton Rouge, LA, 77 p.
- Zhang, Z., T.C. Hennessey and R.A. Heinemann. 1997. Acclimation of loblolly pine (*Pinus taeda*) foliage to light intensity as related to leaf nitrogen availability. *Can. J. For. Res.* 27:1032-1040.