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ORIGINAL ARTICLE

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# Seasonal photosynthesis and water relations of juvenile loblolly pine relative to stand density and canopy position

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**Abstract** To assess the effects of stand density and canopy environment on tree physiology, we measured gas exchange responses of the same needle age class of 16-year-old loblolly pines (*Pinus taeda* L.) in thinned (512 trees ha$^{-1}$) and non-thinned treatment plots (2,863 trees ha$^{-1}$) in central Louisiana. Physiological data were collected in the upper and lower canopy positions on 26 sunny days between July 1996 and June 1997 (one-half of the leaf life span). Mean net photosynthesis was highest (4.3 μmol m$^{-2}$ s$^{-1}$) in the spring and closely corresponded with light intensity in the canopy. Photosynthesis in the winter was nearly 3.0 μmol m$^{-2}$ s$^{-1}$, indicating that loblolly pine enables substantial carbon fixation all year around in the Gulf Coastal Plain region. Mean transpiration and stomatal conductance were highest in the summer and lowest in the winter. With increased light availability after thinning, needle photosynthesis, transpiration and stomatal conductance rose 84, 40 and 23%, respectively, in the lower canopy of the thinned-treatment trees. Light-saturated photosynthetic capacity of the lower canopy needles was 5.2 μmol m$^{-2}$ s$^{-1}$ for the thinned treatment and 4.2 μmol m$^{-2}$ s$^{-1}$ for the non-thinned treatment. It is concluded that thinning-induced light penetration through the canopy enhances physiological activities in the lower canopy foliage of residual trees, and that light availability is the only significant variable for predicting needle-level photosynthesis rates.

**Keywords** Photosynthetic response · *Pinus taeda* · Stomatal conductance · Thinning · Transpiration

## Introduction

Loblolly pine (*Pinus taeda* L.) is extensively planted for timber and fiber production in the southern United States due to its rapid growth and responsiveness to forest management practices (Schultz 1997). Forest researchers have revealed that tree growth (stem diameter and volume and fine roots) of the species responds substantially to thinning manipulations (Dean and Baldwin 1996; Sword et al. 1998; Yu et al. 1999). Positive growth responses are chiefly attributed to increasing live crown ratio, foliage growth and site resource availability (Brix 1983; Snowdon and Waring 1995; Peterson et al. 1997). However, the physiological mechanisms that govern post-thinning growth responses are poorly understood.

Leaf gas exchange sensitivity to climate change has been investigated for commercially important conifers such as radiata pine (*P. radiata* D.) (Whitehead et al. 1996), Scots pine (*P. sylvestris* L.) (Irvine et al. 1998) and slash pine (*P. elliottii* Engelm.) (Teskey et al. 1994). Several studies have also reported that loblolly pine responded physiologically to elevated $CO_2$ and air temperature (Teskey 1997) and components of environmental change (Ellsworth 2000). These studies have been conducted mainly on Carolina piedmont and eastern Gulf Coastal Plain sites. However, seasonal physiological responses of loblolly pine in relation to environmental variation and stand density are not fully investigated in the western Gulf Coastal Region where the climate is characterized by abundant rainfall, hot summers and mild winters. Experiments are needed to better understand how forest management practices affect the physiological processes of loblolly pine trees.

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Recently, research efforts have been made to model stand growth relationships with carbon dynamics and resource availability (Wang and Jarvis 1990; Baldwin et al. 2000). Application of forest models suggests that the accurate prediction of carbon gain and stand productivity requires an understanding of variability in canopy physiology in response to natural environment and forest management practices (Johnsen et al. 2000). The purpose of this study was (1) to determine seasonal physiological responses of the same needle age class of 16-year-old loblolly pine trees after repeated thinning treatments, and (2) to evaluate relationships between net $CO_2$ exchange and canopy environment at two stand densities. Our hypothesis was that canopy position and thinning manipulation could affect seasonal photosynthetic responses and water relations of loblolly pine trees. Response equations were developed to estimate net photosynthesis rates of loblolly pine needles.

## Materials and methods

This experiment was carried out in a loblolly pine plantation (31°11'N, 92°41'W) located about 20 km southwest of Alexandria, Louisiana. The soil was a Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudults), moderately drained and poor in available nutrients (Shoulders and Tiarks 1983). Mean annual temperature was 19°C and annual precipitation was approximately 1,500 mm. In May 1981, the plantation was established at a spacing of 1.8×1.8 m with 14-week-old containerized seedlings. In November 1988, eight research plots (13 rows x13 trees each) were installed for this experiment. Two levels of thinning were randomly applied to those plots in a completely random design with four replications. In the thinned treatments, 75% of trees were removed by mechanically cutting every other row of trees and every other tree in remaining rows, leaving 721 trees $ha^{-1}$. The non-thinned treatments remained at the original density of 2,990 trees $ha^{-1}$. In early 1995, the initially thinned treatments were rethinned to 512 trees $ha^{-1}$. The non-thinned treatments remained unthinned and had 2,860 trees $ha^{-1}$. Herbicides were periodically used to control understorey vegetation. Forty-eight access towers were permanently erected to facilitate ecophysiological data collection in the canopy. Wooden walkways were constructed in the upper canopy (approximately 13 and 14 m high from the ground in the thinned and non-thinned treatments, respectively) and the lower canopy (nearly 9 and 12 m high in the thinned and non-thinned treatments).

During July 1996, needle gas exchange in the upper and lower canopy positions was measured in the expanding fascicles of first flush shoots that were initiated in April 1996. Thereafter, the physiological measurements continued approximately every 2 weeks through December 1996. Similar measurements were made in the same needle age class in February 1997 and continued in April through June 1997. A Li-6200 photosynthesis system (Li-Cor, Lincoln, Neb., USA) associated with a 250-ml leaf chamber (pine needle type) was used for data collection. In order to examine diurnal variability of gas exchange, we conducted the physiological measurements between 0930 and 1130 hours and between 1300 and 1500 hours. The measured variables were net photosynthesis ($P_n$), transpiration ($T_r$) and stomatal conductance to water vapor ($g_s$). Meanwhile, photosynthetic photon flux density (PPFD), air temperature ($T_a$) and vapor pressure deficit from leaf to air (VPD) in the canopy were also monitored. An instrument service in January and overcast weather conditions in March prevented sampling during these months.

Two of the four treatment-plot replications (two thinned and two non-thinned plots) were sampled daily. The sampling scheme was that on the first day of each period, upper canopy needles were measured followed by lower canopy needles. On the second day, the sampling order was reversed for the two canopy positions. At the beginning of each sampling day, three south-side branches per canopy position were randomly selected from three interior trees in each treatment. On each branch, two needle fascicles in the middle section of the terminal first-flush shoot were enclosed in the leaf chamber and the physiological variables of the sample were measured in their natural orientation in the canopy. Forty-eight measurements per day were made. The physiological variables were expressed on a needle surface area basis.

Needle water status was determined with a pressure chamber (PMS Instruments, Corvallis, Ore., USA). Predawn xylem pressure potential ($\Psi_{pd}$) was measured in conjunction with daytime physiological measurements. Three fascicles per canopy position per plot, each from three branches of the interior trees, were detached before dawn (0430 and 0530 hours) and placed in a plastic bag for $\Psi_{pd}$ determinations. Daytime xylem pressure potentials ($\Psi_d$) of the excised fascicles were recorded 5 min following each gas exchange measurement. Three time domain reflectometer sensors (Soil Moisture Equipment, Santa Barbara, Calif., USA) were installed horizontally at the 15-cm soil depth in each plot and soil volumetric moisture content (SMC) was measured twice each month.

The data set consisted of 1,248 observations and grouped into four seasons: summer (July–August 1996 and June 1997), autumn (September–November 1996), winter (December 1996–February 1997) and spring (April–May 1997). The effects of thinning (thinned and non-thinned), season (summer, autumn, winter and spring), canopy position (upper and lower) and diurnal period (morning and afternoon) on gas exchange physiology were determined statistically at $P\leq0.05$, using an analysis of variance (SAS 2000). General additive models were constructed to evaluate interrelationships between $P_n$ and environmental variables. The regression models were tested for statistical differences between the thinning treatments and canopy positions at $P\leq0.05$.

## Results

$P_n$ (per unit needle surface area) averaged 3.5 μmol $m^{-2}$ $s^{-1}$ over the study period. Needle physiology significantly varied with season (Table 1). Mean $P_n$ was lowest in the winter and highest in the spring (Fig. 1A). Winter $P_n$ rates were 70% of the annual peak during the spring. Differences in $T_r$ and $g_s$ were significant among the seasons, with the highest rates in the summer and the lowest rates in the winter (Fig. 1B, C). Winter PPFD in the canopy was lowest of the four seasons and represented 60% of the spring value (Fig. 1D). Mean $T_a$ and VPD in the canopy were highest during the summer and lowest during the winter (Fig. 1E, F). Mean SMC and needle $\Psi_{pd}$ and $\Psi_d$ varied seasonally (Fig. 2A–C), but no significant correlation was found among SMC, $\Psi_{pd}$, $\Psi_d$, $P_n$ and $T_r$.

Physiological attributes were statistically different vertically in the canopy (Table 1). The upper canopy needles had higher mean $P_n$, $T_r$, and $g_s$ rates and more negative $\Psi_d$ than the lower canopy needles. Diurnal measurements showed that the trees maintained significantly higher needle $T_r$ and lower $\Psi_d$ in the afternoon compared to the values in the morning (Table 2). With a significant increase in PPFD, afternoon $T_a$ in the canopy was 5°C higher and VPD doubled over the morning values. However, there was no significant difference in $P_n$ and $g_s$ rates between the morning and afternoon measurements.

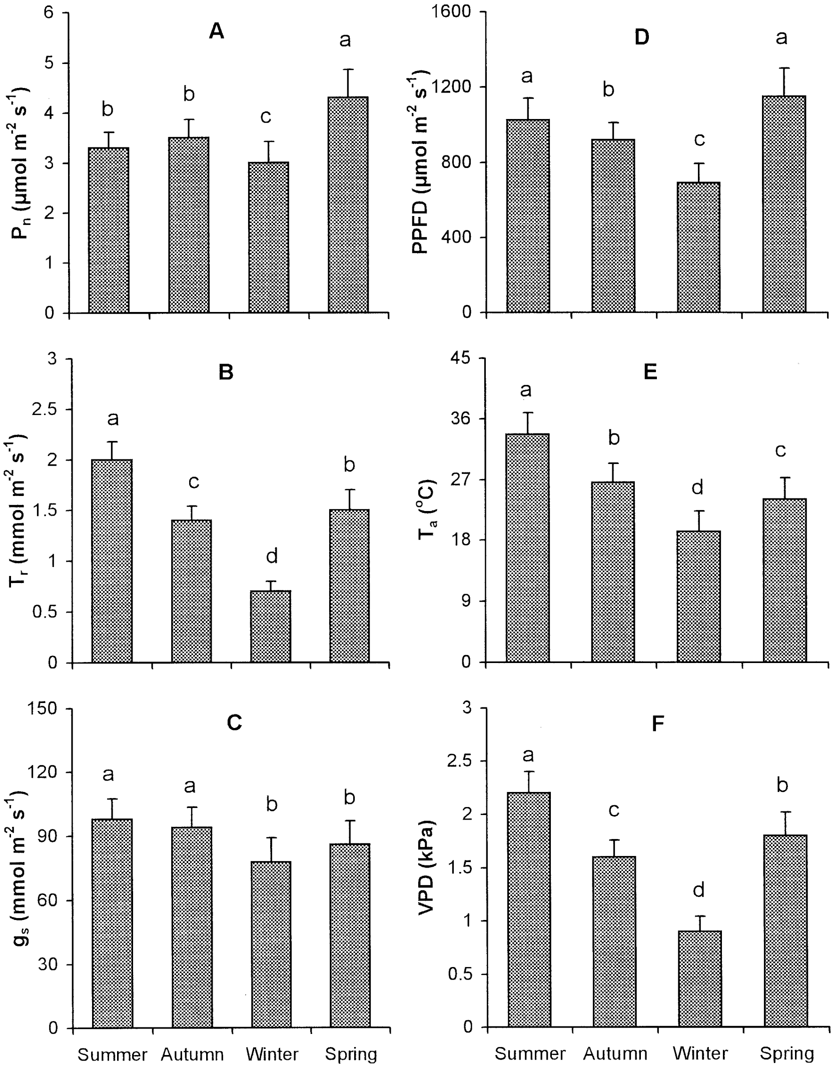

**Fig. 1** Seasonal photosynthesis (*$P_n$*), transpiration (*$T_r$*), stomatal conductance (*$g_s$*), photosynthetic photon flux density (*PPFD*), air temperature (*$T_a$*), and vapor pressure deficit (*VPD*) in a 16-year-old loblolly pine plantation. Means followed by the same letter do not differ significantly at $P \leq 0.05$

**Table 1** Probability associated with *F*-tests for the physiological attributes of 16-year-old loblolly pine trees studied in 1996 and 1997 ($n$=1,248). [$P_n$ net photosynthesis (µmol m$^{-2}$ s$^{-1}$), $T_r$ transpiration (mmol m$^{-2}$ s$^{-1}$), $g_s$ stomatal conductance (mmol m$^{-2}$ s$^{-1}$), $\Psi_d$ daytime xylem pressure potential (MPa), $\Psi_{pd}$ predawn xylem pressure potential (MPa)]

| Source | *df* | $P_n$ | $T_r$ | $g_s$ | $\Psi_d$ | $\Psi_{pd}$ |
|---|---|---|---|---|---|---|
| Season (S) | 3 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| Thinning (T) | 1 | 0.002 | 0.041 | 0.297 | 0.734 | 0.155 |
| S × T | 3 | 0.590 | 0.014 | 0.164 | 0.878 | 0.891 |
| Canopy position (C) | 1 | 0.001 | 0.001 | 0.001 | 0.001 | 0.885 |
| C × T | 1 | 0.001 | 0.006 | 0.007 | 0.022 | 0.733 |
| C × S | 3 | 0.003 | 0.001 | 0.003 | 0.074 | 0.013 |
| C x T x S | 3 | 0.089 | 0.029 | 0.078 | 0.511 | 0.475 |
| Diurnal period (D) | 1 | 0.163 | 0.001 | 0.103 | 0.001 | |
| D × T | 1 | 0.649 | 0.197 | 0.679 | 0.685 | |
| D × S | 3 | 0.513 | 0.001 | 0.018 | 0.005 | |
| D × T × S | 3 | 0.586 | 0.886 | 0.901 | 0.524 | |
| D × C | 1 | 0.008 | 0.775 | 0.095 | 0.564 | |
| D × C × T | 1 | 0.386 | 0.274 | 0.709 | 0.524 | |
| D × S × C | 3 | 0.133 | 0.253 | 0.631 | 0.095 | |

Thinning produced a significant effect on needle physiology (Table 1). Overall, mean $P_n$ was 3.9 µmol m$^{-2}$ s$^{-1}$ for the trees in the thinned treatment, a 26% increase over the $P_n$ rate (3.1 µmol m$^{-2}$ s$^{-1}$) for the trees in the non-thinned treatment. Mean $T_r$ was significantly higher in the thinned treatment than in the non-thinned treatment, but needle $\Psi_{pd}$ and $\Psi_d$ did not differ statistically between the two treatments. A significant thinning-by-canopy position interaction was found for the physiological variables. Needle $P_n$, $T_r$, $g_s$ and $\Psi_{pd}$ in the upper canopy position was the same for the thinned-treatment and non-thinned-treatment trees (Table 2). However,

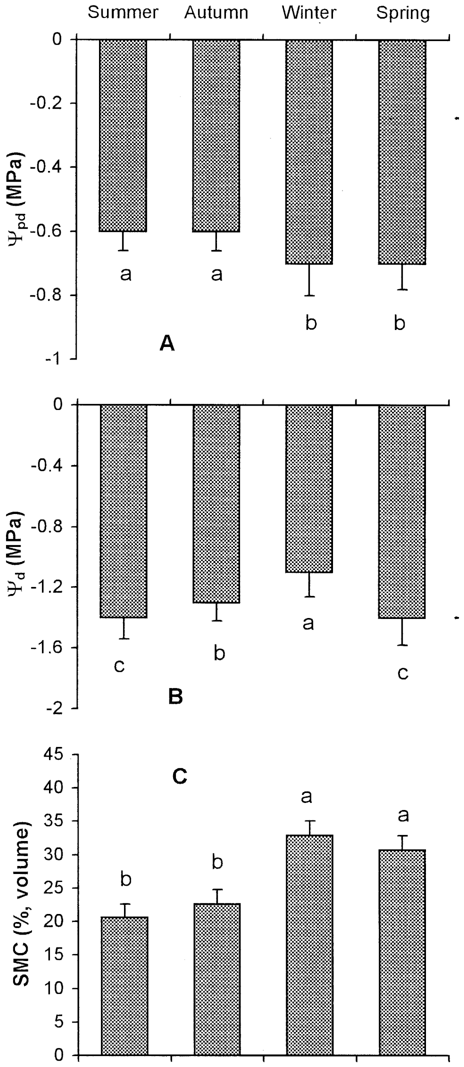

**Fig. 2** Seasonal predawn and daytime xylem pressure potential ($\Psi_{pd}$ and $\Psi_d$) and soil volumetric moisture content (SMC) in a 16-year-old loblolly pine plantation. Means followed by the same letter do not differ significantly at $P \leq 0.05$

lower canopy needle $P_n$, $T_r$, and $g_s$ in the thinned treatment were 85, 50 and 23%, respectively, greater than the rates in the same canopy position of the non-thinned treatment. Needle $\Psi_d$ of the lower canopy foliage was more negative in the thinned-treatment trees relative to the non-thinned-treatment trees. The observed physiological responses coincided with a significantly higher PPFD in the lower canopy of the thinned treatment.

The $P_n$ response pattern was similar for all thinning-by-canopy position combinations (thinned-upper, non-thinned-upper, thinned-lower and non-thinned-lower canopy). Non-thinned-lower canopy needles had little $P_n$ increase above PPFDs of 600 μmol $m^{-2}$ $s^{-1}$. For other combinations, no additional $P_n$ increase was observed as PPFD exceeded 1,000 μmol $m^{-2}$ $s^{-1}$. In order to predict $P_n$ responses, we chose the uppermost 5% of the PPFD-$P_n$ data points for multivariate regression analyses. The results indicated that the regressions differed significantly for the upper and lower canopy positions ($P$=0.006). PPFD at both upper and lower canopy positions was positively correlated with $P_n$ rates and explained 71–79% of the total variation in $P_n$ for the thinning-by-canopy position combinations (Table 3). The light-saturated $P_n$ was significantly higher for the upper canopy position than for the lower canopy. Needles of the thinned-lower canopy had a significantly higher light-saturated $P_n$ compared to the needles in the non-thinned-lower canopy. However, apparent quantum efficiency of photosynthesis (Φ, initial slope of $P_n$ response curve) was not statistically different among the thinning-by-canopy position combinations. $T_a$ and VPD in the canopy were not significant covariates for $P_n$.

## Discussion

Data from this study indicate that in July, the $P_n$ rate (3.9 μmol $m^{-2}$ $s^{-1}$) of young needles (3 months old) in the upper canopy had already attained 65% of light-saturated $P_n$ (6.0 μmol $m^{-2}$ $s^{-1}$). Sword et al. (1996) found that on Gulf Coastal Plain sites, new fascicle needles of loblolly

**Table 2** Physiological attributes of 16-year-old loblolly pine trees studied in 1996 and 1997 ($n$=1,248). [$P_n$ Net photosynthesis (μmol $m^{-2}$ $s^{-1}$), $T_r$ transpiration (mmol $m^{-2}$ $s^{-1}$), $g_s$ stomatal conductance (mmol $m^{-2}$ $s^{-1}$), $\Psi_d$ daytime xylem pressure potential (MPa), $\Psi_{pd}$ predawn xylem pressure potential (MPa) measured between 0430 and 0530 hours. Means ±SE followed by the same letter for each variable in each row do not differ significantly at $P \leq 0.05$]

| Variable | Thinned upper canopy | Thinned lower canopy | Non-thinned upper canopy | Non-thinned lower canopy |
|---|---|---|---|---|
| Morning measurements (0930–1130 hours) | | | | |
| $P_n$ | 4.2 (0.09) a | 3.4 (0.09) b | 4.4 (0.10) a | 1.7 (0.08) c |
| $T_r$ | 1.3 (0.04) a | 1.1 (0.04) a | 1.3 (0.05) a | 0.7 (0.03) b |
| $g_s$ | 105 (2.9) ab | 90 (2.6) b | 111 (2.9) a | 72 (2.8) c |
| $\Psi_d$ | −1.27 (0.02) d | −1.07 (0.01) b | −1.19 (0.01) c | −1.01 (0.01) a |
| $\Psi_{pd}$ | −0.62 (0.01) a | −0.64 (0.01) a | −0.68 (0.01) a | −0.67 (0.01) a |
| Afternoon measurements (1300–1500 hours) | | | | |
| $P_n$ | 4.2 (0.08) a | 3.8 (0.10) a | 4.2 (0.10) a | 2.2 (0.09) b |
| $T_r$ | 2.2 (0.08) a | 2.1 (0.08) a | 2.1 (0.07) a | 1.5 (0.06) b |
| $g_s$ | 95 (2.3) ab | 90 (2.4) b | 99 (2.9) a | 70 (2.2) c |
| $\Psi_d$ | −1.57 (0.02) c | −1.45 (0.02) b | −1.57 (0.02) c | −1.39 (0.02) a |

**Table 3** Regression models and associated statistics for needle photosynthesis of 16-year-old loblolly pine trees in response to light availability in the canopy. [$P_n$ Needle net photosynthesis ($\mu$mol m$^{-2}$ s$^{-1}$), *PPFD* photosynthetic photon flux density ($\mu$mol m$^{-2}$ s$^{-1}$), $P_{\max}$ light-saturated photosynthesis ($\mu$mol m$^{-2}$ s$^{-1}$), $\Phi$ apparent quantum efficiency of photosynthesis, $R^2$ the coefficient of determination]

| Model | $P_{\max}$ | $\Phi$ | $N$ | $R^2$ | CV (%) | $P_r>F$ |
|---|---|---|---|---|---|---|
| Thinned – Upper canopy | | | | | | |
| $P_n=2.100\mathrm{L_n(PPFD)}-8.742$, ($0<\mathrm{PPFD}\le 1{,}000$) | 5.8 | 0.011 | 18 | 0.72 | 17.3 | 0.0001 |
| Non-thinned – Upper canopy | | | | | | |
| $P_n=2.124\mathrm{L_n(PPFD)}-8.937$, ($0<\mathrm{PPFD}\le 1{,}000$) | 5.7 | 0.010 | 18 | 0.79 | 14.6 | 0.0001 |
| Thinned – Lower canopy | | | | | | |
| $P_n=1.527\mathrm{L_n(PPFD)}-5.320$, ($0<\mathrm{PPFD}\le 1{,}000$) | 5.2 | 0.020 | 20 | 0.78 | 17.3 | 0.0001 |
| Non-thinned – Lower canopy | | | | | | |
| $P_n=1.159\mathrm{L_n(PPFD)}-3.157$, ($0<\mathrm{PPFD}\le 600$) | 4.2 | 0.025 | 12 | 0.71 | 17.7 | 0.0001 |

pine begin elongating in early April and achieve 75% of annual maximum needle elongation by the end of June. The photosynthetic capacity of developing foliage and rapid leaf area expansion early in the growing season may allow loblolly pine to take advantage of spring and early-summer field conditions that appear to be optimal for carbon uptake and tree growth.

Hot, humid summers and mild winters are common in the Gulf Coastal Plain region. When light is not limiting, water stress associated with periodic droughts can reduce carbon gain substantially by limiting foliar growth and photosynthesis rates (Teskey et al. 1987). Ellsworth (2000), examining the crown physiology of 12-year-old loblolly pine trees for three years, reported that summer drought caused the largest year-to-year variation in gas exchange rates during the growing season and that drought-induced water deficit decreased daily carbon assimilation by 45% on sunny days. In our study, $\Psi_{\mathrm{pd}}$ and SMC data suggest that no significant drought stress occurred over the study period. Thus, as young needles continued expanding in summer and became mature in autumn, their $P_{\mathrm{n}}$ rates kept increasing gradually (Fig. 1A). After maturity, the same needle age class had the lowest $P_{\mathrm{n}}$ in winter. Teskey et al. (1986) observed high $P_{\mathrm{n}}$ rates in loblolly pine needles at 20°C. It is unlikely that winter $T_{\mathrm{a}}$ (19.3±1.5°C) in our study area caused the 15% decline in $P_{\mathrm{n}}$ between autumn and winter. However, winter PPFD (690 μmol m$^{-2}$ s$^{-1}$) was 24% below the autumn level and 40% below the optimal level (1,000 μmol m$^{-2}$ s$^{-1}$), leading to the significant decrease in winter $P_{\mathrm{n}}$. The highest $P_{\mathrm{n}}$ was observed in the spring, when ambient conditions were most favorable. The photosynthate exported from 1-year-old foliage during that period may have been one of the major carbon sources for flush shoot elongation and needle growth (Dickson 1989; Sword et al. 1996). During the early growing season, therefore, tree carbon balance could be significantly affected by non-optimal environmental conditions.

This experiment presents strong evidence that loblolly pine growing on western Gulf Coastal Plain sites can sustain considerable carbon fixation throughout mild winters. The winter $P_{\mathrm{n}}$ from this study is comparable with the rates of the same needle age class reported by Murthy et al. (1996) and Ellsworth (2000) for trees grown on Carolina piedmont sites. However, our winter $P_{\mathrm{n}}$ rate is almost twice as high as the winter $P_{\mathrm{n}}$ found by Teskey et al. (1994) for 23-year-old slash pine in Florida and much higher than the rates documented by Schaberg et al. (1995) for red spruce in Vermont. In a related study at our site, Kuehler et al. (1999) reported that the root starch concentration of trees increased from November through March. High carbon fixation of foliage in late autumn through winter may be responsible for the continued winter accumulation in root starch (Ford and Deans 1977; Kuhns and Gjerstad 1991). Additionally, Maier et al. (1998) found that branch and stem maintenance respiration of 9-year-old loblolly pine ranged from 0.4 to 1.0 μmol m$^{-2}$ s$^{-1}$ in winter (November-February). Compared to their rates, our winter $P_{\mathrm{n}}$ should be sufficient to meet these respiration costs and maintain carbon gain for starch accumulation during mild winters.

Our study provides insight to understanding spatial variability in canopy environment and gas exchange physiology of southern pines in response to silvicultural management practices. The photosynthetic response models illustrate that PPFD below the light saturation is the most significant factor that controls carbon uptake. The light saturation level and maximum photosynthetic capacity were substantially low in the lower-canopy needles of non-thinned-treatment trees, a characteristic of shade foliage adapted to a light-limiting environment (Cregg et al. 1993; Zhang et al. 1997). In contrast, PPFD in the lower canopy of the thinned treatment increased drastically after thinning. As a result, the $P_{\mathrm{n}}$ rate of the lower canopy needles increased 85% in the thinned treatment (Table 2). The light-saturated $P_{\mathrm{n}}$ of the lower canopy foliage also increased significantly in the thinned-treatment trees, which could make a substantial contribution to whole-tree carbon fixation. Thus, we conclude that as light availability in the canopy of thinned treatments rises, the photosynthetic activity of lower canopy foliage is greatly enhanced.

Needle $T_{\mathrm{r}}$ and $\Psi_{\mathrm{d}}$ were significantly different with season, chiefly due to incident PPFD in the canopy. The increase in solar radiation during the spring and summer led to higher $T_{\mathrm{a}}$, VPD and $T_{\mathrm{r}}$, and more negative $\Psi_{\mathrm{d}}$ relative to other seasons (Figs. 1, 2). We also observed that the upper and lower canopy foliage significantly increased needle $T_{\mathrm{r}}$ and decreased $\Psi_{\mathrm{d}}$ in the afternoon in response to increased solar radiation and $T_{\mathrm{a}}$ and reduced relative humidity. However, $g_s$ and $P_n$ were not different between the morning and afternoon measurements, suggesting that stomatal closure of the upper or lower canopy needles did not occur during the measurement period. A significant interaction of thinning by canopy position on needle physiology demonstrates that non-thinned-treatment trees had greater $T_r$ and $g_s$ in the upper canopy needles than in the lower canopy needles, whereas, in the thinned treatments, $T_r$ and $g_s$ were similar for needles of both canopy positions (Table 2). After thinning, more solar radiation was intercepted by the lower canopy foliage in the thinned treatments and resulted in a significant increase in $T_r$ and $g_s$ rates of the lower canopy needles. Our results of needle $T_r$ and $g_s$ are consistent with the findings reported by Cregg et al. (1990) and Gravatt et al. (1997), who found a positive relationship between light penetration, crown exposure and tree water relations in response to thinning practice.

We used a generalized additive model to predict $P_n$ responses to stand density and canopy environmental variability. Within-canopy PPFD was the only significant variable for the $P_n$ rate of 1-year-old needles (Table 3). Our response equations strongly suggest that process models must be developed separately for managed and non-managed pine stands. However, we found no significant correlation between net photosynthesis and air temperature, vapor pressure deficit, and soil water content. This result, however, should be further verified including environmental extremes over a more extensive geographic range of loblolly pine.

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