Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine

Zhenmin Tang, Mary A. Sword Sayer, Jim L. Chambers, and James P. Barnett

Abstract: Few studies have examined the combined effects of nutrition and water exclusion on the canopy physiology of mature loblolly pine (*Pinus taeda* L.). Understanding the impacts of forest management on plantation productivity requires extensive research on the relationship between silvicultural treatments and environmental constraints to growth. We studied the physiological responses of 18-year-old loblolly pine trees exposed to a combination of fertilization (fertilizer or no fertilizer) and throughfall (normal throughfall or throughfall exclusion). Gas exchange variables were measured in the upper and lower crown between 0900 and 1700 h from May to November in 1999. Needle fall was collected to estimate foliage mass and leaf area. Summer drought and throughfall exclusion significantly decreased predawn xylem pressure potential. Needle-level photosynthesis, transpiration, and stomatal conductance declined during the drought and were significantly lower in the throughfall exclusion treatment. Throughfall exclusion also reduced annual foliage mass and daily whole-crown photosynthesis and transpiration. In the normal throughfall treatment, fertilization had no effect on needle-level physiology, but increased annual foliage mass and whole-crown photosynthesis by 26% and 41%, respectively. With the exclusion of throughfall, however, annual foliage mass and daily whole-crown photosynthesis exhibited little response to fertilization. We conclude that greater nutrient availability enhances the carbon uptake of mature loblolly pine trees by stimulating foliage production, but the positive effects of fertilization on leaf area and carbon fixation are limited by low water availability.

Key words: foliage mass, photosynthesis, *Pinus taeda*, seasonal trend, transpiration, xylem pressure potential.

Résumé : Peu d'études ont examiné les effets combinés de la nutrition et de l'exclusion de l'eau sur la physiologie de la canopée du pin à encens (*Pinus taeda* L.). La compréhension des impacts de l' aménagement forestier sur la productivité des plantations nécessite une recherche extensive sur les relations entre les traitements sylvicoles et les contraintes environnementales s'exerçant sur la croissance. Les auteurs ont étudié les réactions physiologiques de pins à encens âgés de 18 ans, exposés à une combinaison et de fertilisations (avec et sans fertilisant) de précipitations (précipitation normale ou précipitation exclue). Ils ont mesuré les échanges gazeux au sommet et à la base du houppier, entre 0900 et 1700 h, de mai à novembre en 1999. La litière d'aiguille à été récoltée pour évaluer la masse et la surface foliaire. La sécheresse estivale et l'exclusion de la précipitation diminuent significativement la pression potentielle du xylème avant l'aube. La photosynthèse au niveau des aiguilles, la transpiration et la conductance stomatale diminuent au cours de la sécheresse, et sont significativement plus faibles dans le traitement où les précipitations sont exclues. L'exclusion des précipitations réduit également la masse foliaire annuelle, ainsi que la photosynthèse et la transpiration quotidiennes de l'ensemble du houppier. Dans le traitement avec précipitation normale, la fertilisation est sans effet sur le niveau d'activité physiologique des aiguilles, mais augmente la masse foliaire annuelle et la photosynthèse de l'ensemble du houppier de 26 % à 41 %, respectivement. Cependant, avec l'exclusion des précipitations, la masse foliaire annuelle et la photosynthèse quotidienne, pour l'ensemble du houppier, ne montrent que peu de réaction à la fertilisation. Les auteurs concluent qu'une disponibilité accrue aux nutriments augmente l'absorption du carbone du pin à encens, en stimulant la production de feuillage, mais les effets positifs de la fertilisation sur la surface foliaire et la fixation du carbone sont limités par la disponibilité de l'eau.

Mots clés : masse foliaire, *Pinus taeda*, tendance saisonnière, transpiration, pression potentielle du xylème.

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Introduction

Loblolly pine (*Pinus taeda* L.) is the most extensively planted commercial pine species in the southern United States, because of its adaptability to diverse sites and favorable wood properties (Schultz 1997). Site factors such as fertility and water availability affect tree growth and biomass production in loblolly pine stands (Allen et al. 1990; Dougherty et al. 1994; Albaugh et al. 1998). Plantation productivity is also commonly manipulated by silvicultural practices (e.g., site preparation, fertilization, and weed control) that optimize resource availability (Miller et al. 1999; Jokela and Martin 2000; Haywood et al. 2003). Understanding the impacts of forest management on sustained plantation productivity requires extensive assessment of relationships between silvicultural treatments and environmental constraints on growth.

In general, levels of nitrogen and phosphorus are inherently low in loblolly pine plantations throughout the southern United States (Shoulders and Tiarks 1983; Allen et al. 1990). On sites of poor fertility, nutrient deficiencies reduce the production of aboveground biomass considerably (Vose and Allen 1988; Retzlaff et al. 2001; Samuelson et al. 2001). Fertilization is increasingly used for ameliorating low soil fertility and therefore, increasing stand productivity. For example, Albaugh et al. (1998) reported a 152% increase in stem volume growth and a 99% increase in the total biomass of loblolly pine trees 4 years after fertilization. Jokela and Martin (2000) found that annual nutrient addition enhanced the aboveground biomass of loblolly pine by 197%. The positive effects of fertilization on tree growth, however, may be constrained by drought, because water deficit limits tree productivity significantly (Dougherty et al. 1995; Sword et al. 1998; Haywood et al. 2003). Reduced productivity in response to drought is primarily attributed to a decrease in foliage retention, leaf area index, and carbon uptake (Vose and Allen 1988; Hennessey et al. 1992; Ellsworth 2000). However, Sword et al. (1996) observed that summer drought caused a 94% reduction in the fine root initiation of juvenile loblolly pine, suggesting that drought effects on productivity could also be associated with reduced soil resource uptake.

The interactive effects of nutrient and water availability on the canopy physiology and growth of mature loblolly pine trees are poorly understood. A better understanding of relationships among site factors, carbon fixation, and plantation productivity is needed to guide effective management activities. Previous research has documented that fertilization stimulates the foliage growth of loblolly pine (Vose and Allen 1988; Albaugh et al. 1998; Yu et al. 1999; Xiao et al. 2002). In a loblolly pine stand on unfertile soil, for example, Maier et al. (2002) found that foliage biomass and leaf area nearly doubled in response to fertilization. However, fertilization effects on photosynthetic rates vary by site. In some studies, fertilization significantly increased canopy-level photosynthetic capacity by stimulating the production of leaf area (Murthy et al. 1996), but in other studies, nutrient additions had little impact on needle-level photosynthetic rates (Zhang et al. 1997; Samuelson et al. 2001). A needle-level photosynthetic response to fertilization may be dependent on inherent site fertility (Samuelson et al. 2001) or the amount of mutual leaf shading in the canopy (Zhang et al. 1997).

Most studies of the effects of water stress on the physiology of loblolly pine have taken advantage of natural drought or irrigation (Teskey et al. 1986; Groninger et al. 1996; King et al. 1999). Ellsworth (2000) observed that natural drought resulted in a substantial reduction in canopy carbon fixation by young loblolly pine stands. Albaugh et al. (1998) and Murthy et al. (1996) reported that fertilization and irrigation together increased the maximum photosynthetic rate and stem volume growth efficiency of loblolly pine by 24% and 30%, respectively. Fertilization or irrigation alone, however, stimulated volume growth efficiency by only 21% and 9%, respectively. Samuelson et al. (2001) found that irrigation alone or in combination with fertilization enhanced the aboveground biomass of pine saplings by 45% and 85%, respectively, while these treatments had no effect on photosynthetic rates. Larger amounts of aboveground biomass were closely associated with greater amounts of foliage production and leaf area in tree crowns. Few comparative studies have been done to evaluate carbon fixation by loblolly pine in response to combinations of nutrient and water availabilities (Gebre et al. 1998; Tschaplinski et al. 1998). Canopy-level ecophysiology studies of mature trees are necessary to understand relationships between resource availability, carbon fixation, and stand productivity in southern pine forests. Such assessments will help link ecophysiological process models to growth models for future management applications.

This study was designed to (1) characterize the seasonal and diurnal physiology of 18-year-old loblolly pine trees in relation to a combination of fertilization and throughfall exclusion treatments, (2) examine the interactive effects of nutrient and water regimes on foliage production, and (3) quantify daily whole-tree photosynthesis and transpiration under different nutrient and water regimes. Based on previously reported findings (Murthy et al. 1996; Maier et al. 2002), we hypothesized that fertilization enhances the physiological activity and leaf area of mature trees at both high and low water availability. Our extensive measurements of canopy physiology allowed examination of the effects of seasonal drought and different levels of water stress on the needle-level and crown-level carbon fixation of field-grown trees.

Materials and methods

Study area and treatments

Four 0.06-ha treatment plots were selected in a loblolly pine plantation in the Palustris Experimental Forest, about 20 km southwest of Alexandria, Louisiana. The soil is a Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudults) that is moderately well-drained and low in nitrogen and phosphorus (Kerr et al. 1980; Shoulders and Tiarks 1983). The climate is subtropical and humid, with mean monthly temperatures of 8 and 28 °C in January and July, respectively. Mean annual precipitation is 1560 mm, with 970 mm occurring from March to November. The plantation was established in 1981 by planting genetically unimproved, 14-week-old containerized seedlings at 1.8 m × 1.8 m. In November 1988, two levels of thinning, and in January 1989, two levels of fertilization were factorially applied to two replications of four plots. Thinning consisted of mechanically removing every other row of trees and every other tree in the remaining rows, leaving the residual trees at a spacing of 3.7 m × 3.7 m and a density of 732 trees·ha^{-1}. Fertilization consisted of broadcast application of diammonium phosphate (134 kg·ha^{-1} N and 150 kg·ha^{-1} P). In early 1995, the thinning and fertilization treatments were reapplied. The four thinned plots were rethinned from below to produce a density of 534 trees·ha^{-1}. The fertilized plots received 200 kg·ha^{-1} N, 50 kg·ha^{-1} P, and 50 kg·ha^{-1} K as urea, monocalcium phosphate, and potash, respectively.

In April 1999, each of the four thinned plots was divided into two equal subplots for throughfall manipulation. On each plot, one subplot was randomly chosen, and a tarp system that covered the subplot area was installed beneath the canopy. The other subplot was left to receive normal throughfall. The tarp system contained plastic tarps hung from steel cables between two rows of trees in a “V” shape. Bottom edges of the tarps were linked to drain troughs about 0.6–1.4 m above the ground. The drain troughs between tree rows were connected to large aluminum troughs that drained intercepted throughfall from the study site. Polyethylene sheets were used to cover the intertree gaps within tree rows where the edges of the tarps met. To prevent windblown precipitation from entering the throughfall exclusion subplots, additional tarps were hung vertically around the row of border trees. Understory vegetation was treated with glyphosate herbicide as needed. Steel towers were erected to support wooden walkways in the upper and lower one-third of the canopy of each subplot. The walkways in the upper and lower canopy were approximately 15 and 11 m from the ground, respectively.

Water relations measurements

Water content (SWC, *v*/*v*) in the upper 100 cm of the soil profile was measured with a time domain reflectometer (Soil Moisture Equipment Corp., Santa Barbara, California). In the interior of each subplot, eight sensors were installed at four depths: 0–20, 21–33, 33–53, and 60–100 cm. Soil water content was recorded at 6-h intervals from May to November 1999. During that period, the predawn xylem pressure potential (Ψ_{pd}) of needles was measured weekly using a pressure chamber (PMS Instruments, Corvallis, Oregon). Predawn measurements were made on four fascicles per tree that were removed from the mid-crown branches of two interior trees per subplot. In an open field adjacent to the site, precipitation was measured hourly with a rain gauge at a weather station (Omnidata International, Inc., Logan, Utah).

Gas exchange measurements

In situ net photosynthesis (P_{n}), transpiration (E), and stomatal conductance to water vapor (g_{s}) were measured diurnally in the canopy each month from May to November. A portable photosynthesis system (Li-6200, LI-COR, Inc., Lincoln, Nebraska) equipped with a 250-mL leaf chamber was used for gas exchange measurements. Photosynthetic photon flux density (PPFD), air temperatures (T_{a}), and vapor pressure deficit (VPD) were measured concurrently with gas exchange. Prior to daily measurements, the photosynthesis system was calibrated and equilibrated to field conditions. During each measurement, two fascicles (six needles) of the terminal mature shoot were randomly chosen, enclosed in the leaf chamber, and monitored under within-canopy ambient conditions for net CO_2 exchange over a short period of time (10–60 s). Mean PPFD in the canopy ranged from 925 to 1130 μmol·m^{-2}·s^{-1}. The mean CO_2 concentration in the canopy ranged from 362 to 365 ppm. The relative humidity in the leaf chamber was maintained by adjusting the flow rate of dry air from a tube of fresh desiccant ($Mg(ClO_4)_2$) attached to the photosynthesis system and stirred by a small fan inside the chamber. Between two consecutive measurements, the leaf chamber was left open in the shade, with its small fan running to keep the chamber at equilibrium with ambient conditions. The xylem pressure potential (Ψ_{day}) of the sampled fascicles was determined following each gas exchange measurement. The expression of P_{n}, g_{s}, and E was based on leaf surface area calculated from needle length and volume (Johnson 1984). Water use efficiency (WUE) was calculated by dividing P_{n} by E.

Gas exchange measurements were performed in the upper and lower one-third of the crown at 0900, 1100, 1300, 1500, and 1700 h on sunny days. At each crown level, three branches (one each facing south, east, and north) from one interior tree per subplot were selected. Time constraints associated with the magnitude of diurnal and within-canopy measurements prevented sampling more than one tree per subplot during the 2-h interval. Gas exchange measurements were made over a 2-d sampling period. On the first day, measurements were conducted on the subplots within the fertilized plots and on the second day, measurements were conducted on the subplots within the unfertilized plots. Sampling periods were as follows: (1) 19 and 20 May, (2) 9 and 17 June, (3) 22 and 28 June, (4) 22 and 23 July, (5) 28 and 29 July, (6) 17 and 19 August, (7) 15 and 16 September, (8) 22 and 23 September, (9) 13 and 14 October, (10) 20 and 21 October, (11) 4 and 5 November, and (12) 16 and 17 November. Data on the fertilized plots were also collected on 25 August. Sampling dates in each month were selected to maintain uniform environmental conditions. We sampled 1-year-old needles of the first flush of 1998 in May and June. In July–November, we measured current year needles of the first flush of 1999.

Needle-fall collections

Four 0.92-m^2 litter traps were randomly placed on each subplot. To estimate annual foliage production and peak leaf area, needle fall was collected monthly, oven-dried at 70 °C to a constant mass, and weighed. Foliage biomass produced in 1999 was calculated by adding monthly needle-fall collections for one phenological year (April 2000 – March 2001) and expressing values on a subplot basis (Hennessey et al. 1992; Dougherty et al. 1995). Under the assumption that loblolly pine retains its needles for 2 years (Hennessey et al. 1992), foliage mass at peak area was expressed as the sum of needle-fall collections from two consecutive years (April 1999 – March 2001). Total foliage mass at peak leaf area was expressed per subplot and then estimated per tree by dividing the subplot values by the number of trees per subplot. Yu (1996) determined that upper crown foliage accounted for 28% and 31% of tree leaf area on the fertilized and unfertilized plots, respectively, at our study site. These percentages were used to calculate upper and lower crown foliage mass at peak leaf area per tree for the fertilized and unfertilized plots. Peak leaf area per tree was obtained by multiplying foliage mass per tree by specific leaf areas of the upper and lower crown, which was measured on each subplot in October 1999.

Whole-tree carbon uptake

To estimate daily whole-crown P_n and E between 0900 and 1700 h, diurnal P_n (μmol·m^{-2}·s^{-1}) and E (mmol·m^{-2}·s^{-1}) rates (900, 1100, 1300, and 1500 h) of the upper and lower crown were multiplied by the peak leaf area (m^2) of each crown level and then a 2-h interval (7200 s). Daily P_n per crown level was expressed as grams of CO_2 per day, and daily E per crown level was expressed as kilograms of H_2O per day. The diurnal values of the upper and lower crown levels were summed to determine whole-crown P_n and E.

Statistical analyses

Monthly precipitation was calculated as the sum of hourly measurements in each month. The physiological data, collected on the same sample trees throughout the study, were averaged by subplot, replication, crown level, month, and time of day. The data were subjected to a repeated measures analysis of variance in a split-split-plot design, with fertilization as the whole-plot effect, throughfall exclusion as the sub-plot effect, crown position as the sub-sub-plot effect, and month and time of day as the repeated measures. The PROC MIIXED was used for the repeated measures analysis (Littell et al. 1996).

The majority of loblolly pine roots occur in the upper portion of the soil profile (Farrish 1991; Sword et al. 1996). To partition the SWC data by its influence on water availability, therefore, SWC data were grouped into two depths (0–33 and 33–100 cm). Values of SWC and needle Ψ_{pd} were averaged by subplot, replication, and month and analyzed using a repeated measures split-plot design, with fertilization as the whole-plot effect, throughfall exclusion as the sub-plot effect, and month as the repeated measure. Annual foliage mass and daily whole-crown carbon uptake were analyzed using a split-plot design, with fertilization as the whole-plot effect and throughfall exclusion as the sub-plot effect. All main and interaction effects were significant at $p \leq 0.10$. Least significant difference tests at $p \leq 0.10$ were used to separate treatment means (Steel and Torrie 1980).

After combining the data for all treatments, replications, months, and crown levels, linear response equations were developed to assess the relative importance of the microenvironmental factors affecting P_n, g_s, and E. The independent variables included PPFD, T_a, and VPD, and their partial regression coefficients were examined. Values of Ψ_{day} and Ψ_{pd} were also included in the equations to evaluate their potential effects on P_n, g_s, and E. The SAS statistical package (SAS Institute Inc., Cary, North Carolina) was used for all data analyses.

Results

Seasonal trends

Total precipitation was 214 mm in May–June 1999, and 72 mm in August– September 1999 (Fig. 1A). These values are 18% and 66% less than the 30-year average (1971–2000) for these periods, indicating that a drought had occurred in 1999. Volumetric SWC and VPD corresponded with seasonal precipitation. Across all treatments, values of SWC in the 0–33 and 33–100 cm of the soil profile were significantly higher in May–June than in August–September (Tables 1 and 2), whereas VPD followed a reverse pattern during these periods (Fig. 1B). There was a significant throughfall × month interaction on SWC, illustrating that throughfall exclusion reduced SWC in the upper 33 cm of the soil profile in June –November (Fig. 1C). A significant fertilization × month interaction effect on SWC was due to the fertilized plots having higher values of SWC in the 0–33 cm depth in August and October and in the 33–100 cm depth in May, June, and October than the unfertilized plots. Values of needle Ψ_{pd} fell from –0.74 MPa in May to –1.0 MPa in September and were significantly less negative in the normal throughfall treatment relative to the throughfall exclusion treatment in August and September (Tables 1 and 2, Fig. 1D).

Overall, the throughfall exclusion treatment exhibited significantly lower rates of P_n, g_s, and E than the normal throughfall treatment (Tables 3 and 4). Significant interactions between throughfall exclusion and month indicate that in May–July, the normal throughfall treatment maintained higher values of g_s and E compared with the throughfall exclusion treatment (Figs. 2A and 2B). The normal throughfall treatment also had significantly higher values of WUE and Ψ_{day} in July than did the throughfall exclusion treatment (Figs. 2C and 2D). The upper crown needles exhibited higher P_n and E and more negative Ψ_{day} than the lower crown needles (Tables 3 and 4). However, values of P_n, g_s, E, Ψ_{pd}, and Ψ_{day} did not differ statistically between the fertilized and unfertilized plots. No significant interaction between fertilization and throughfall treatments was found for the measured gas exchange attributes.

Diurnal trends

Gas exchange varied with time of day over all treatments (Tables 3 and 4). Significant interactions between throughfall treatment and time of day and between month and time of day were found, indicating that diurnal trends of gas exchange attributes were altered by throughfall exclusion or varied by month. The physiological rates of both normal throughfall and throughfall exclusion treatments are presented for June (nondrought) and August (drought) to show the interactive effects on diurnal gas exchange (Fig. 3). These rates represent the responses across fertilization treatments, crown levels, and sampling dates in each month. In June, the P_n and g_s of trees receiving normal throughfall climbed in the morning (1100 h) and declined in the afternoon (1300–1700 h), whereas in the throughfall exclusion treatment, a late-morning (1100 h) decrease in g_s and a midday (1300 h) decrease in P_n and g_s were observed. Trees under throughfall exclusion also exhibited a late-afternoon (1700 h) reduction in P_n in June. In addition, the June values of E in the normal throughfall treatment rose for most of the day (0900–1500 h) and fell in late afternoon (1700 h), but E in the throughfall exclusion treatment rose until midday (1300 h) and declined afterward (1500–1700 h). Values of Ψ_{day} in both throughfall treatments fell sharply in the morn-

Fig. 1. (A) Monthly precipitation, (B) vapor pressure deficit (VPD), (C) volumetric soil water content (SWC) in the upper 33 cm of the soil profile, and (D) predawn xylem pressure potential (Ψ_{pd}) in an 18-year-old loblolly pine plantation in response to throughfall treatments in 1999.

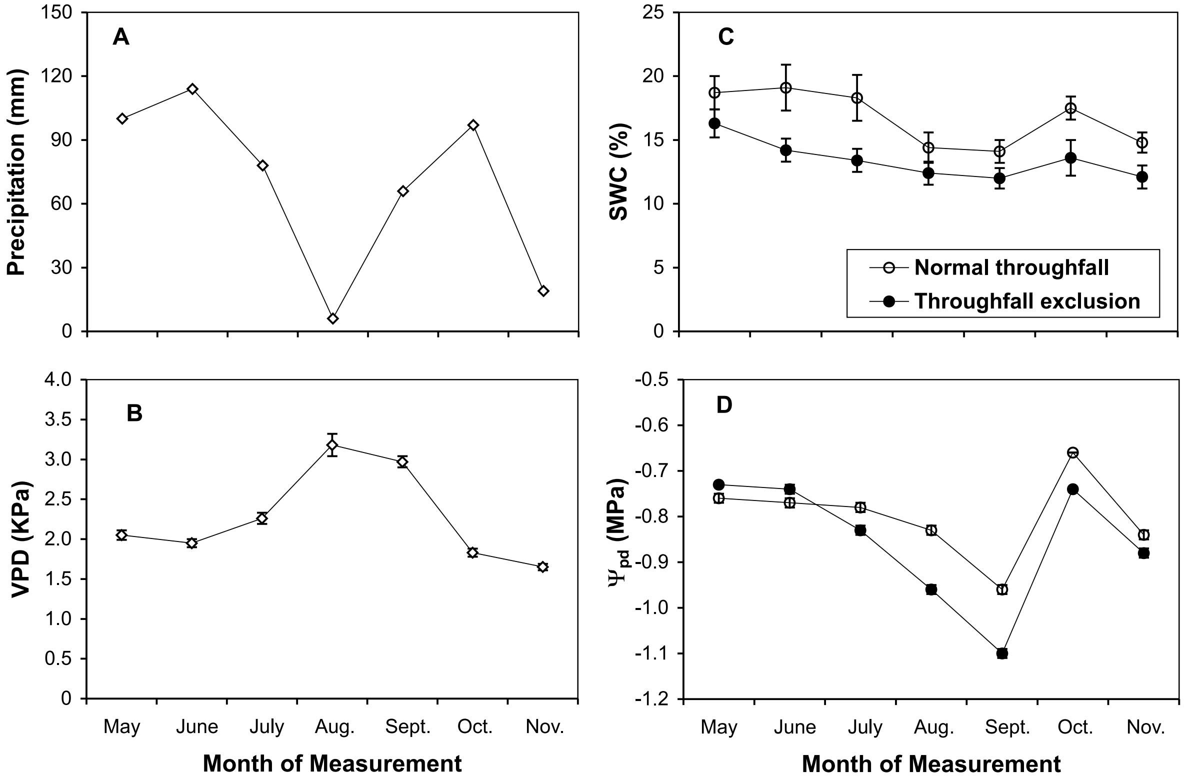


Table 1. Probabilities of a greater *F* value for the effects of fertilization, throughfall, and sampling month on volumetric soil water content (SWC) at depths of 0–33 and 33–100 cm and predawn xylem pressure potential (Ψ_{pd}) in an 18-year-old loblolly pine plantation.

Source	df	SWC at 0–33 cm	SWC at 33–100 cm	Ψ_{pd}
Fertilization	1	0.8608	0.5521	0.7024
Throughfall	1	0.1306	0.7461	0.0619
Throughfall × Fertilization	1	0.6689	0.3114	0.4166
Month	6	0.0001	0.0001	0.0018
Month × Fertilization	6	0.0810	0.0113	0.2466
Month × Throughfall	6	0.0236	0.1084	0.0001
Month × Throughfall × Fertilization	6	0.4471	0.9319	0.0001

Note: df, degrees of freedom.

ing (0900–1300 h) and began recovering in mid-afternoon (1500 h).

In August, compared with June, values of P_n and g_s in the normal throughfall treatment were significantly lower and decreased between morning (0900 h) and late afternoon (1700 h). Similarly, the August P_n and g_s under the throughfall exclusion treatment were lower than the June values. The August values of P_n and g_s were also lower in the throughfall exclusion treatment relative to the normal throughfall treatment. While the August *E* under the normal throughfall treatment increased diurnally for most of the day (0900–1500 h), the *E* under the throughfall exclusion treatment declined between late morning (1100 h) and late afternoon (1700 h). The largest throughfall exclusion effect on *E* was a 53% mid-afternoon (1500 h) reduction. The August values of Ψ_{day} in both throughfall treatments fell from morning (0900 h) to afternoon (1500 h). However, trees receiving throughfall exclusion had an earlier recovery of Ψ_{day} (1300 h) than those receiving normal throughfall (1500 h).

There was also a significant interaction between fertilization, month, and time of day on diurnal gas exchange attributes (Table 3). These responses resulted from different diurnal values with sampling month and fertilization treatment. In October, for example, the P_n value of mid-afternoon (1500 h) was 2.4 and 3.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on the fertilized and unfertilized plots, respectively. During that time, g_s was 45 and 66 $mmol \cdot m^{-2} \cdot s^{-1}$, and *E* was 1.0 and 1.8 $mmol \cdot m^{-2} \cdot s^{-1}$ for the fertilized and unfertilized plots, respectively.

Table 2. Means (±SE) of volumetric soil water content (SWC) at depths of 0–33 and 33–100 cm and predawn xylem pressure potential (Ψ_{pd}) in an 18-year-old loblolly pine plantation in relation to fertilization and throughfall treatments and sampling month in 1999.

Source	SWC at 0–33 cm (%)	SWC at 33–100 cm (%)	Ψ_{pd} (MPa)
Sampling month			
May	17.5 (0.9)a	19.4 (0.7)a	–0.74 (0.00)ab
June	16.6 (1.3)ab	18.3 (0.4)b	–0.76 (0.01)ab
July	15.9 (1.3)b	17.6 (0.4)c	–0.81 (0.00)b
August	13.4 (0.8)c	15.4 (0.3)d	–0.89 (0.01)c
September	13.0 (0.7)c	14.5 (0.4)e	–1.00 (0.01)d
October	15.5 (1.1)b	15.7 (0.4)d	–0.70 (0.00)a
November	13.5 (0.7)c	14.8 (0.3)e	–0.86 (0.01)c
Fertilization			
Fertilized	15.3 (0.6)	16.9 (0.5)	–0.82 (0.1)
Unfertilized	14.9 (0.6)	16.2 (0.3)	–0.84 (0.1)
Throughfall			
Normal	16.7 (0.6)	16.7 (0.3)	–0.79 (0.1)a
Exclusion	13.4 (0.4)	16.4 (0.5)	–0.85 (0.1)b

Note: Means followed by different letters within a column differ significantly by the least significant difference test at $p \leq 0.10$.

Table 3. Probabilities of a greater *F* value for the effects of fertilization and throughfall treatments, sampling month, crown level, and time of day on net photosynthesis (P_n), stomatal conductance (g_s), transpiration (*E*), water use efficiency (WUE) and daytime xylem pressure potential (Ψ_{day}) of 18-year-old loblolly pine trees.

Treatment	df	P_n	g_s	E	WUE	Ψ_{day}
Fertilization	1	0.5435	0.3567	0.2751	0.5086	0.1708
Throughfall	1	0.0756	0.0623	0.0189	0.3492	0.6496
Throughfall × Fertilization	1	0.5342	0.3117	0.4399	0.4011	0.6401
Month	6	0.0020	0.0024	0.0001	0.2841	0.0001
Month × Fertilization	6	0.9630	0.9480	0.6834	0.9441	0.3272
Month × Throughfall	6	0.7695	0.0001	0.0001	0.0183	0.0136
Month × Throughfall × Fertilization	6	0.3822	0.5419	0.8336	0.2432	0.2675
Crown	1	0.0260	0.1606	0.0685	0.5135	0.0190
Crown × Fertilization	1	0.1818	0.3743	0.3908	0.4240	0.2820
Crown × Throughfall	1	0.1155	0.1682	0.4368	0.0436	0.9307
Crown × Throughfall × Fertilization	1	0.1396	0.5208	0.8814	0.1429	0.0072
Crown × Month	6	0.0079	0.0183	0.0005	0.5664	0.0001
Crown × Month × Fertilization	6	0.5024	0.2891	0.3221	0.1542	0.4138
Crown × Month × Throughfall	6	0.1537	0.1012	0.0651	0.9309	0.0943
Crown × Month × Throughfall × Fertilization	6	0.7294	0.8273	0.9730	0.9948	0.7237
Day	4	0.0118	0.0001	0.0050	0.0001	0.0001
Day × Fertilization	4	0.8890	0.0676	0.6513	0.1754	0.2604
Day × Throughfall	4	0.7371	0.0232	0.0011	0.0522	0.0447
Day × Throughfall × Fertilization	4	0.9070	0.3926	0.3653	0.6111	0.5939
Day × Month	24	0.0001	0.0004	0.0001	0.0001	0.0001
Day × Month × Fertilization	24	0.0202	0.0002	0.0001	0.0001	0.0001
Day × Month × Throughfall	24	0.9731	0.3354	0.2043	0.4415	0.7991
Day × Month × Throughfall × Fertilization	24	0.5448	0.9296	0.8079	0.6122	0.9473
Day × Crown	44	0.0001	0.0078	0.0007	0.2856	0.0001
Day × Crown × Fertilization	4	0.4003	0.7551	0.0868	0.8854	0.8736
Day × Crown × Throughfall	4	0.0358	0.7038	0.1058	0.6924	0.1216
Day × Crown × Throughfall × Fertilization	4	0.2314	0.4472	0.1381	0.5363	0.6855
Day × Crown × Month	24	0.2864	0.4792	0.7401	0.0824	0.7164
Day × Crown × Month × Fertilization	24	0.6657	0.6647	0.5708	0.2112	0.5531
Day × Crown × Month × Throughfall	24	0.9772	0.6715	0.4809	0.7962	0.9934
Day × Crown × Month × Throughfall × Fertilization	24	0.9915	0.7269	0.3806	0.9654	0.9999

Note: df, degrees of freedom.

Table 4. Means (±SE) of net photosynthesis (P_{n}), stomatal conductance (g_{s}), transpiration (E), xylem pressure potential (Ψ_{day}), and water use efficiency (WUE) in an 18-year-old loblolly pine plantation in relation to fertilization and throughfall treatments, crown level, sampling month, and time of day in 1999.

Treatment	P_{n} (μmol·m^{-2}·s^{-1})	g_{s} (mmol·m^{-2}·s^{-1})	E (mmol·m^{-2}·s^{-1})	Ψ_{day} (MPa)	WUE (mg CO_2·g· H_2O^{-1})
Sampling month					
May	3.3 (0.10)a	72 (3.2)ab	1.53 (0.09)a	–1.72 (0.04)bc	7.72 (0.50)
June	3.5 (0.09)a	91 (2.4)a	1.74 (0.05)a	–1.65 (0.02)b	5.67 (0.21)
July	2.9 (0.08)ab	79 (2.6)ab	1.56 (0.06)a	–1.76 (0.02)c	6.01 (0.35)
August	1.7 (0.12)c	37 (2.8)c	1.00 (0.07)bc	–1.77 (0.03)c	5.66 (0.41)
September	2.2 (0.08)bc	29 (1.1)c	0.79 (0.03)cd	–1.77 (0.01)c	7.24 (0.21)
October	2.9 (0.10)ab	61 (1.7)b	1.07 (0.04)b	–1.48 (0.02)a	8.08 (0.36)
November	2.4 (0.11)b	42 (1.9)c	0.69 (0.03)d	–1.53 (0.01)a	7.88 (0.34)
Fertilization					
Fertilized	2.5 (0.06)	52 (1.4)	1.01 (0.03)	–1.62 (0.01)	7.26 (0.18)
Unfertilized	2.8 (0.05)	64 (1.5)	1.32 (0.03)	–1.77 (0.01)	6.76 (0.18)
Throughfall					
Normal	2.9 (0.06)a	63 (1.3)a	1.29 (0.03)a	–1.68 (0.02)	6.84 (0.17)
Exclusion	2.5 (0.05)b	54 (1.5)b	1.06 (0.03)b	–1.71 (0.02)	7.16 (0.19)
Crown level					
Upper	3.3 (0.05)a	66 (1.4)	1.37 (0.03)a	–1.81 (0.01)b	7.16 (0.17)
Lower	2.2 (0.05)b	51 (1.3)	0.98 (0.02)b	–1.57 (0.01)a	6.85 (0.19)
Time of day					
0900	2.7 (0.09)a	71 (2.2)a	0.70 (0.02)b	–1.24 (0.01)a	11.0 (0.38)a
1100	3.4 (0.08)a	69 (2.3)a	1.28 (0.04)a	–1.67 (0.02)b	7.77 (0.23)b
1300	2.9 (0.07)a	58 (2.1)b	1.50 (0.05)a	–1.87 (0.01)c	5.68 (0.17)c
1500	2.7 (0.07)a	52 (1.9)b	1.48 (0.06)a	–1.92 (0.02)c	5.36 (0.16)c
1700	1.7 (0.09)b	39 (2.2)c	0.93 (0.04)b	–1.68 (0.02)b	4.42 (0.21)d

Note: Means followed by different letters within a column differ significantly by the least significant difference test at $p \leq 0.10$.

Whole-crown carbon fixation

Overall, fertilization produced 21% more foliage mass in 1999 (Tables 5 and 6). Relative to the normal throughfall treatment, the throughfall exclusion treatment produced 12% less foliage mass in 1999. A significant interaction between fertilization and throughfall treatments was found for foliage mass. The fertilized–normal throughfall treatment combination grew 26% more annual foliage mass than the unfertilized–normal throughfall treatment combination (control), whereas the fertilized–throughfall exclusion and unfertilized–throughfall exclusion treatment combinations produced similar foliage masses compared with the control treatment.

Values of daily whole-crown P_{n} and E decreased 25% and 31%, respectively, in response to throughfall exclusion, whereas fertilization significantly enhanced whole-crown P_{n} (Tables 5 and 6). There was a significant interaction between fertilization and throughfall treatments for whole-crown carbon fixation. Compared to the control treatment, daily whole-crown P_{n} rose 41% in the fertilized–normal throughfall treatment combination, remained unchanged in the fertilized–throughfall exclusion treatment combination, and declined 24% in the unfertilized–throughfall exclusion treatment combination. However, there was no significant main effect of fertilization or interaction effect between fertilization and throughfall treatments on daily whole-crown E.

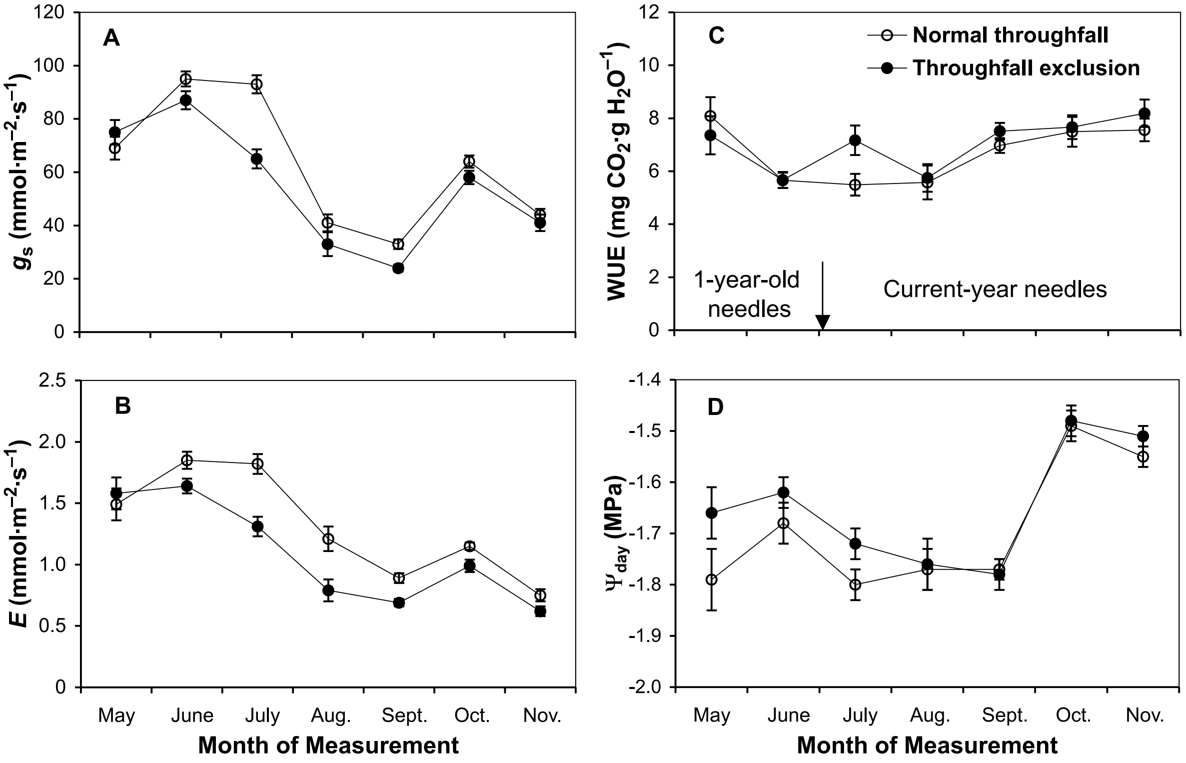
Gas exchange – environment relations

Regression analysis showed that needle-level P_{n}, g_{s}, and E responded positively to Ψ_{pd} and PPFD and negatively to VPD (Table 7). Both PPFD and VPD within the canopy explained 54% and 22% of the total variation in P_{n}, 11% and 10% of that in g_{s}, and 18% and 3% of that in E, respectively. Needle Ψ_{pd} accounted for 4%, 13%, and 23% of the variation in P_{n}, E, and g_{s}, respectively. Air temperature was correlated with needle g_{s} and E and responsible for 21% and 27% of the total variation in g_{s} and E, respectively. This indicated that rates of g_{s} and E linearly increased with rising T_{a} in the canopy. Needle Ψ_{day} was not a significant covariate for P_{n}, g_{s}, and E.

Discussion

Our study of diurnal gas exchange responses to fertilization and throughfall treatments is a unique approach to quantifying the physiological responses of mature loblolly pine trees to nutrient and water availabilities. We found that under water deficit, the gas exchange responses were closely correlated with Ψ_{pd}. Values of P_{n}, g_{s}, and E declined appreciably as Ψ_{pd} fell below –0.8 MPa in August and September. This is consistent with the direct relationship between Ψ_{pd} values less than or equal to –0.9 MPa and decreases in the P_{n} of mature slash pine (*Pinus elliottii* Engelm.) found by

Fig. 2. Seasonal trends of (A) needle stomatal conductance (g_s), (B) transpiration (E), (C) water use efficiency (WUE), and (D) xylem pressure potential (Ψ_{day}) of 18-year-old loblolly pine trees in response to throughfall treatments in 1999. The gas exchange measurements were made on 1-year-old needles in May–June and current year needles in July–November. Each data point represents the mean across fertilization treatments, crown levels, sampling dates in each month, and time of day.



Teskey et al. (1994). These results show that Ψ_{pd} is an important indicator of the water status and physiological activity of field-grown southern pine trees.

Four levels of water stress were experienced in our study. In May–July, normal throughfall and throughfall exclusion created little and mild water stress, respectively. In August – September, normal throughfall and throughfall exclusion created moderate and severe water stress, respectively. Values of P_n, g_s, and E in May–July and August–September were directly related to these levels of water stress. This observation may be explained by the differences in rooting zone between the water exclusion regimes. For example, using a split root system, Kosola and Eissenstat (1994) found that water deficiency in the top pot of citrus seedlings led to a greater fraction of total fine root mass in the bottom pot than when water was sufficient in both the top and bottom pots. Partial drought did not affect predawn leaf water potential or whole plant mass, suggesting that the shift in rooting zone led to an adequate supply of water for seedling growth. This phenomenon was also observed by Torreano and Morris (1998), who found that the fine root growth of loblolly pine seedlings was closely coupled with the vertical distribution of water in the soil profile. At our study site, higher soil water content was maintained at the 33–100 cm depth than at the 0–33 cm depth, although soil water was depleted in both depth increments of the soil profile as water limitations progressed between May and September. Consequently, we hypothesize that throughout the growing season, gas exchange was maintained, in part, by the migration of new fine root growth vertically to access water stored deeper in the soil profile. A similar scenario was proposed by Grulke and Retzlaff (2001), who attributed the physiological activity of mature ponderosa pine (*Pinus ponderosa* Laws.) during drought to the acquisition of water by roots within interstices of cracked bedrock at a 1 m depth. However, where we found that gas exchange on the throughfall exclusion treatments was reduced between June and August, deep root growth and, therefore, soil water acquisition may have been limited physically by soil strength (Bennie 1996, Wraith and Wright 1998). Furthermore, because throughfall exclusion resulted in 25% less daily whole-crown P_n, root growth may have been limited metabolically by carbon allocation to the root system. The acquisition of deep soil water and its effect on the physiological activity of large loblolly pine trees is an important area for further research.

Ellsworth (2000), examining the canopy physiology of loblolly pine for 3 years on a North Carolina site, found that drought caused a large year-to-year variation in P_n and reduced whole-crown carbon uptake by 45%. Consistent with this study, we found that drought reduced daily whole-crown P_n substantially. It is apparent that the carbon uptake of large trees on our Louisiana site is sensitive to water deficit. Loblolly pine produces multiple growth flushes throughout the year (Dougherty et al. 1994). In spring, photosynthate exported from mature foliage is used primarily for the growth of new shoots and needles (Dickson 1987; Cregg et al. 1993). Thus, high P_n of 1-year-old needles in spring is necessary for rapid expansion of the first flush and subsequent

Fig. 3. Diurnal trends of needle net photosynthesis (P_n), stomatal conductance (g_s), transpiration (E), and xylem pressure potential (Ψ_{day}) of 18-year-old loblolly pine trees in response to throughfall treatments in June (no drought) and August (drought) 1999. The gas exchange measurements were made on 1-year-old needles in May–June and current year needles in July–November. Each data point represents the mean across fertilization treatments, crown levels, and sampling dates in each month.

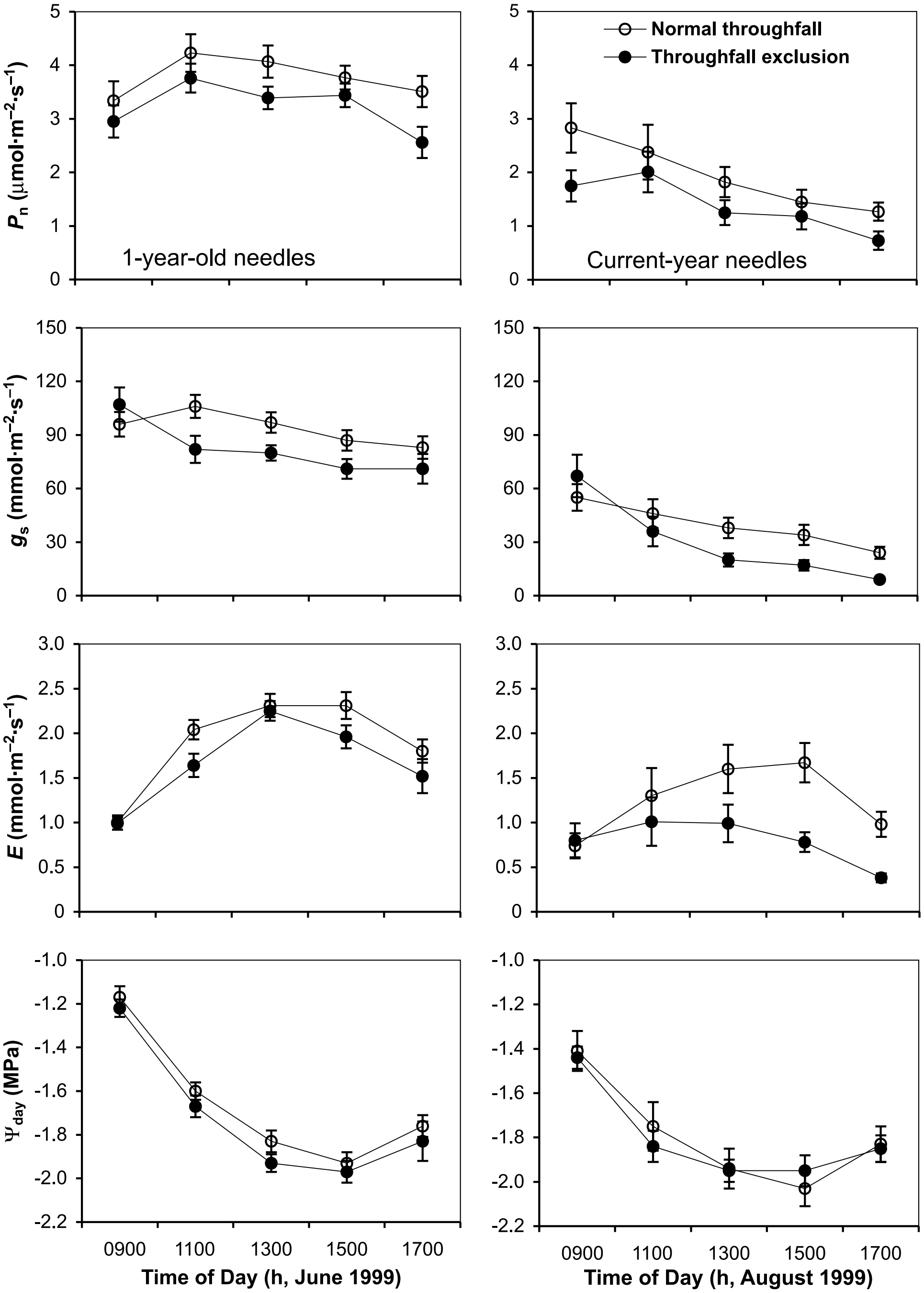


Table 5. Probabilities of a greater F value for the effects of fertilization and throughfall treatments on annual foliage mass and daily whole-crown photosynthesis (P_n) and transpiration (E) of 18-year-old loblolly pine trees in 1999.

Source	df	Annual foliage mass	Whole-crown P_n	Whole-crown E
Fertilization	1	0.0269	0.0602	0.4245
Throughfall	1	0.0004	0.0050	0.0259
Throughfall × Fertilization	1	0.0880	0.0885	0.3829

Note: df, degrees of freedom.

Table 6. Means (±SE) of annual foliage mass and daily whole-crown photosynthesis (P_n) and transpiration (E) of 18-year-old loblolly pine trees in response to fertilization and throughfall treatments.

Treatment	Annual foliage mass ($kg \cdot ha^{-1}$)	Whole-crown P_n ($g\ CO_2 \cdot d^{-1}$)	Whole-crown E ($kg\ H_2O \cdot d^{-1}$)
Fertilization			
Fertilized	5549 (171)a	297 (19.3)a	48.5 (4.7)a
Unfertilized	4597 (105)b	216 (14.9)b	39.8 (3.5)a
Throughfall			
Normal	5395 (202)a	295 (18.8)a	52.1 (4.5)a
Exclusion	4751 (126)b	220 (16.2)b	36.2 (3.1)b
Fertilization × throughfall			
Fertilized, normal	6012 (220)a	346 (23.7)a	57.7 (7.3)
Fertilized, exclusion	5085 (125)b	253 (23.9)b	39.2 (5.0)
Unfertilized, normal	4778 (133)bc	245 (20.9)b	46.4 (5.4)
Unfertilized, exclusion	4416 (142)c	186 (18.9)c	33.1 (3.7)

Note: Values represent the responses across crown levels and sampling months in 1999. Means followed by different letters within a column differ significantly by the least significant difference test at $p \leq 0.10$.

Table 7. Linear relationships of needle-level photosynthesis (P_n), stomatal conductance (g_s), and transpiration (E) of 18-year-old loblolly pine trees with predawn xylem pressure potential (Ψ_{pd}, MPa), light (PPFD, $\mu mol \cdot m^{-2} s^{-1}$), air temperature ($T_a$, °C), and vapor pressure deficit (VPD, kPa) within the canopy ($n = 104$).

Equation	R^2	p >F
Photosynthesis rate (P_n, $\mu mol \cdot m^{-2} \cdot s^{-1}$)		
$P_n = 0.002PPFD - 0.622VPD + 1.785\Psi_{pd} + 3.519$	0.81	0.0001
Stomatal conductance (g_s, $mmol \cdot m^{-2} \cdot s^{-1}$)		
$g_s = 0.028PPFD + 2.902T_a - 29.759VPD + 44.414\Psi_{pd} + 46.26$	0.64	0.0001
Transpiration rate (E, $mmol \cdot m^{-2} \cdot s^{-1}$)		
$E = 0.001PPFD + 0.052T_a - 0.190VPD + 1.106\Psi_{pd} - 0.332$	0.62	0.0001

Note: R^2 is the coefficient of multiple determination and $p > F$ is the probability of a greater F value.

flushes that are produced during the current growing season. In the western Gulf coastal plain region, drought occurs from year to year (Allen et al. 1990; Hennessey et al. 1992; Dougherty 1996). With the potential rise in future temperature and reduction in future precipitation predicted by general circulation models, drought is likely to occur more frequently and more severely in the southern United States (Cooter 1998). As demonstrated in our study, spring drought could significantly limit carbon fixation, causing a reduction in the growth of multiple flushes and foliage and ultimately tree productivity (Leverenz and Hinckley 1990).

Past studies are inconsistent regarding the relationship between fertilization and carbon fixation on sites of low fertility. In a nutrient-deficient loblolly pine plantation in North Carolina, Murthy et al. (1996) observed that both light-saturated P_n and foliar nitrogen concentration increased 20% and 30%, respectively, after application of micro- and macro-nutrients. Four years later at the same site, Maier et al. (2002) found that the response of P_n to fertilization no longer existed. Other researchers reported that an appreciable rise in the P_n of pines growing on nutrient-poor sites required more than a 30% increase in foliar nitrogen concentration (Beets and Whitehead 1996; Fife and Nambiar 1997). On a site that was low in both nitrogen and phosphorus, Sheriff et al. (1986) also noted that applied phosphorus, but not nitrogen, was positively related to the P_n of radiata pine (*Pinus radiata* Don.). The silt loam soil at our study site is inherently low in nitrogen and phosphorus (Shoulders and Tiarks 1983). We tested the hypothesis that fertilization would increase needle P_n and total leaf area. Contrary to our hypothesis, we found that needle P_n was not different between the fertilized and unfertilized plots 4 years after the second fertilization. In an earlier study at this site, Gravatt (1994) found that P_n at 13 years of age was not affected by supplemental nitrogen and phosphorus applied 5 years earlier. At this time, however, foliar nitrogen concentrations averaged 11.1 and 12.6 $g \cdot kg^{-1}$, and foliar phosphorus concentrations averaged 0.90 and 0.58 $g \cdot kg^{-1}$, on the fertilized and unfertilized plots, respectively. Because concentrations of foliar nitrogen and phosphorus of 11.0 and 1.0 $g \cdot kg^{-1}$, respectively, denote the onset of deficiency in loblolly pine (Allen 1987), it is likely that the benefits of nitrogen and phosphorus additions were gone by 13 years of age. Perhaps the positive response of P_n to nitrogen and phosphorus occurs immediately after fertilization when foliar concentrations are high. As nitrogen and phosphorus are diluted in growing plant tissue and their concentrations approach critical levels, the positive effect of fertilization on P_n is lost.

Although fertilization did not affect P_n, it enhanced the total leaf area of individual trees, leading to a 38% increase in daily whole-crown carbon uptake. Because nutrient availability influences biomass allocation between foliage and roots (King et al. 1999), increases in the leaf area of the fertilized trees could be attributed to an increase in biomass allocation to shoot length and leaf area per shoot (Tang et al. 1999). Similarly, Albaugh et al. (1998) found that field-grown loblolly pine allocated more biomass to foliage than roots in response to fertilization. In an earlier study at our site, Yu et al. (1999) observed that for the first 3 years after the second fertilization, annual volume growth increased with larger leaf areas on fertilized plots compared with unfertilized plots. Thereafter, volume growth declined as the positive effect of fertilization on leaf area diminished. Other studies have revealed that more biomass is partitioned to the aboveground components (stem, branch, and foliage) of fertilized loblolly pine trees compared with unfertilized trees (Vose and Allen 1988; Jokela and Martin 2000). Furthermore, positive relationships between leaf area, carbon gain, and stand productivity have been reported elsewhere for other conifers (Brix 1983; Leverenz and Hinckley 1990; Fife and Nambiar 1997; Xiao et al. 2002). It is apparent that leaf area is a very important factor affecting canopy carbon uptake within a window of time after fertilization.

One of our objectives was to determine whether water and nutrient availabilities interact to affect the carbon fixation of individual trees. We found that at the needle level, P_n did not respond to fertilization in either throughfall exclusion or normal throughfall treatments. At the tree level, however, fertilization increased daily whole-crown P_n on plots receiving normal throughfall, but had little effect on whole-crown P_n where throughfall was excluded. Whole-crown P_n did not respond to fertilization where throughfall was excluded, because total leaf area was unaffected by fertilization on these water deficient plots. Our results agree with the findings reported by Ibrahim et al. (1998), who investigated the interactive effects of water and nitrogen on the carbon allocation of poplar (*Populus* spp.) hybrids. They found that under nitrogen deficiency, trees experiencing water stress had a lower P_n, less leaf area, and a smaller aboveground biomass than well-watered trees. As suggested in the present study and in other studies, fertilization may not be effective to optimize carbon fixation of large trees on sites where severe drought occurs periodically. A combination of fertilization and irrigation, however, can achieve greater leaf area, crown-level carbon fixation, and tree productivity (Albaugh et al. 1998; Samuelson et al. 2001).

In conclusion, under the field conditions of the present experiment, the combined effects of summer drought and throughfall exclusion caused the lowest rates of gas exchange. Throughfall exclusion also interacted with fertilization to affect annual foliage mass. As a result, whole-tree carbon uptake responded positively to fertilization when a higher amount of water was available, but exhibited little response to fertilization when a lower amount of water was available. Our findings provide important insight into how the whole-tree carbon fixation and plantation productivity of loblolly pine respond to fertilization on sites that either differ by water availability or experience periodic drought.

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