Transpiration and Canopy Stomatal Conductance of 5-Year-Old Loblolly Pine in Response to Intensive Management

Lisa J. Samuelson and Thomas A. Stokes

Abstract: The influence of weed control only (W) versus weed control plus irrigation (WI) and weed control plus irrigation and fertigation (WIF) on canopy stomatal conductance (G_S) and transpiration expressed on a ground (E) and leaf area (E_L) basis was examined over 1 year in 5-year-old loblolly pine (*Pinus taeda* L.) to determine whether increased leaf area index (L) in response to intensive silviculture resulted in regulation of G_S, whole-tree hydraulic conductance per unit sapwood area (G), or the ratio of transpiring leaf area to conducting sapwood area (A_L:A_S) to minimize the gradient in water potential from soil to leaf ($\Delta\Psi$). Values of E were as high as 3.9 mm d^{-1} and increased from a total of 357 mm in the W treatment to 529 and 565 mm in the WI and WIF treatments, respectively. Values of E_L did not vary with treatment and were, on average, 0.8 mm d^{-1} in summer and 0.4 mm d^{-1} in winter. Increasing management intensity increased L by as much as 76% and sapwood area up to 68%, but had no influence on $\Delta\Psi$, G, G_S, or leaf specific hydraulic conductance. High L values realized by intensive management resulted in regulation of A_L:A_S to maintain $\Delta\Psi$ with increasing canopy development. FOR. SCI. 52(3):313–323.

Key Words: Hydraulic conductance, leaf area to sapwood area ratio, fertilization, irrigation, sap flow.

A REVIEW OF LONG-TERM PRODUCTION dynamics of loblolly pine (*Pinus taeda* L.) stands in the southern United States identified soil nutrient availability as the most important driver of loblolly pine productivity (Jokela and Dougherty 2004). Two-fold gains in productivity in response to fertilization, competition control, and superior genotypes (Borders and Bailey 2001) have been achieved largely by increases in leaf area. As an example, in a study of loblolly pine under intensive management since planting, maximum aboveground net primary production and leaf area index (L) increased with management intensity to 25 Mg ha^{-1} yr^{-1} and 5.8 m^2 m^{-2}, respectively, at only age 4, with L reaching a theoretical maximum for loblolly pine (Samuelson et al. 2004a). Intensive silviculture may greatly increase L and accelerate stand development, but the influence of intensive management practices on the balance between hydraulic properties and growth in rapidly growing stands is unclear. Stand evaporation has been shown to be proportional to stand growth (LeMaitre and Versfeld 1997), but high L values may result in regulation of canopy stomatal conductance (G_S), transpiration per unit leaf area (E_L), whole-tree hydraulic conductance per unit sapwood area (G), or the ratio of transpiring leaf area to conducting sapwood area (A_L:A_S) to maintain the gradient in water potential from soil to leaf ($\Delta\Psi$) within narrow limits (Whitehead 1998).

The relationship between plant form and plant water relations in aerodynamically coupled canopies can be described by

$$A_L/A_S = (G \cdot \Delta\Psi)/(G_S \cdot D), \tag{1}$$

where G is whole-tree conductance per unit sapwood area and D represents bulk air vapor pressure deficit (Whitehead et al. 1984a, b, Ewers et al. 2005). Changes in stomatal conductance have also been shown to be proportional to changes in leaf specific hydraulic conductance (G_L) by

$$G_S = (G_L \cdot \Delta\Psi)/D, \tag{2}$$

under steady-state conditions and high boundary layer conductance (Hubbard et al. 2001), although the mechanism by which stomata sense perturbations in G and G_L is unclear (Buckley 2005). The close relationship between transpiring leaf area and stem conducting area indicates that increased leaf area production requires a proportional increase in sapwood area, increased G, or reductions in G_S and G_L to avoid damaging leaf water potentials (Whitehead and Beadle 2004). For example, structural adaptation to transpiration demand was demonstrated in Scots pine (*Pinus sylvestris* L.) by proportional increases in leaf area and sapwood area with little change in leaf water potential 14 years after thinning (Whitehead et al. 1984b), and by decreasing A_L:A_S with a warmer, drier climate (Mencuccini and Grace 1995). In plantation ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws) subjected to severe drought during the growing season, increasing A_L:A_S with tree height was possible only if

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G_S decreased (Simonin et al. 2006). An approximate doubling of L in loblolly pine by fertilization was associated with lower G_S and G_L, and less stem growth than in fertilized + irrigated trees with similar L values (Ewers et al. 1999, 2000). Pataki et al. (1998) also showed a strong positive relationship between G_S and G in loblolly pine.

The objective of this study was to investigate the influence of intensive management on hydraulic properties, transpiration, and G_S of 5-yr-old loblolly pine to better understand processes controlling maximum production. Large increases in productivity in response to increasing management intensity were reported by age 5 in this plantation (Samuelson et al. 2004a). We explored relationships described by Equations 1 and 2 to gain insight into regulation of hydraulic properties and growth in rapidly growing stands. Transpiration and G_S were measured over 1 year in stands treated with irrigation and irrigation plus fertigation (irrigation with a fertilizer solution). We could not test relationships directly, but hypothesized that high L values realized from intensive silviculture would result in regulation of water transport capacity to maintain $\Delta\Psi$, and that management intensity would not influence G_S, E_L, and WUE (amount of stem wood produced per unit of water transpired).

Materials and Methods

Site and Study Description

The 15-ha research plantation was established by International Paper, Inc., in the Upper Coastal Plain 22 km west of Bainbridge, GA, and was previously described by Samuelson et al. (2004a). Average yearly precipitation and mean temperature for the region are 1,257 mm and 18.9°C, respectively (Ruffner 1980). Soils were classified as a Grossarenic Paleudult, a sandy clay loam of the Troup series. The site was previously used for soybean farming. Before planting, the site was ripped to a 45-cm depth with a single shank subsoiler and disk-harrowed in Aug. and Nov. 1994. Residual herbaceous vegetation was removed and 1-yr-old bareroot loblolly pine seedlings were hand-planted in Jan. 1995 using a 2.4 m × 3.7 m spacing. The measurement plot was a 0.05 ha subplot with 28 trees within a 0.20 ha treatment plot. Seedlings were from an open-pollinated, improved, second-generation family of loblolly pine. Treatment plots were arranged in a randomized complete block design and two blocks were studied. The following treatments were applied since plantation establishment and randomly assigned to treatment plots within the blocks:

W.—Complete weed control of all competition using a broadcast application of sulfometuron (0.1 kg active ingredient ha^{-1}) and several directed applications of glyphosate (1.5% solution in water) throughout the summer.

WI.—Weed control plus drip irrigation (Netafim WI, Inc., Altamonte Springs, FL), and in 1999 and 2000 approximately 1,280 mm of water was added each year (monthly additions during the study are given in Figure 1).

WIF.—Weed control plus drip irrigation (described above) and fertigation with a fertilizer solution of NH_4NO_3 and urea (79 kg N ha^{-1} yr^{-1} in 1999 and 2000), H_3PO_4 (20 kg P ha^{-1} yr^{-1} in 1999 and 2000), and K_2O (79 kg K ha^{-1} yr^{-1} in 1999 and 2000) applied from May to Sept.

Stand biometric data (height, dbh, biomass, current annual increment, L, and A_L:A_S) were from Samuelson et al. (2004a) and measured in Dec. 1999 with the exception of L, which was measured in Sept. 1999. At age 5, dbh, basal area, stem biomass, current annual increment, and L increased with increasing management intensity (Table 1). Leaf area index increased 76% from 2.1 m^2 m^{-2} in W stands to 3.7 m^2 m^{-2} in WIF stands, and basal area was 68% higher in WIF stands than in W stands.

Environmental Data

Relative humidity and air temperature were recorded hourly with a relative humidity and temperature self-contained datalogger (Telog Instruments, Inc., Victor, NY) placed in an open field adjacent to the study site and D was calculated based on Buck (1981). January data were not collected because of instrument malfunction. Photosynthetically active radiation (PAR) in the open field was measured using a quantum sensor (LI-190, LI-COR, Inc., Lincoln, NE) and average hourly values stored by a datalogger (LI-1000, LI-COR, Inc., Lincoln, NE). Precipitation was measured on site by International Paper, Inc. Potential evapotranspiration (PET) data were obtained from a weather station located at the Attapulgus Research Farm approximately 21 km from the study site (Georgia Automated Environmental Monitoring Network (http://www.griffin.peachnet.edu/aemn/cgi-bin/AEMN.pl?site=GAAT. June, 2003). Soil moisture was not monitored in this study, but data collected from June 2000 through June 2001 are available in Samuelson et al. (2004b) and indicate a more than doubling of soil moisture in response to irrigation treatments.

Transpiration

Thermal dissipation probes (Dynamax, Inc., Houston, TX) based on Granier (1987) of a 30 mm length were inserted into the sapwood approximately 1.5 m above groundline at a north and south aspect in two trees in each plot in two blocks (12 trees total). Probes were inserted by removing the outer bark and drilling small holes (1.6 mm in diameter) into the sapwood. Silicon was placed around the probes to seal out water, and the stem was wrapped with a porous insulation around the probes to reduce thermal gradients. Dendrometer bands were placed on each measurement tree near sensor height to monitor diameter and sapwood area. Two additional trees per plot of similar diameter were cored 1.5 m aboveground in June 2000 to determine sapwood area by ultraviolet light. Each tree was 100% sapwood at the probe location. Sample trees represented average plot level height and diameter (Table 1) with no forks or surrounding gaps from missing trees.

Sap flux (q, m s^{-1}, as defined by Reid et al. (2005)) was recorded every 30 seconds, averaged every 30 min, and

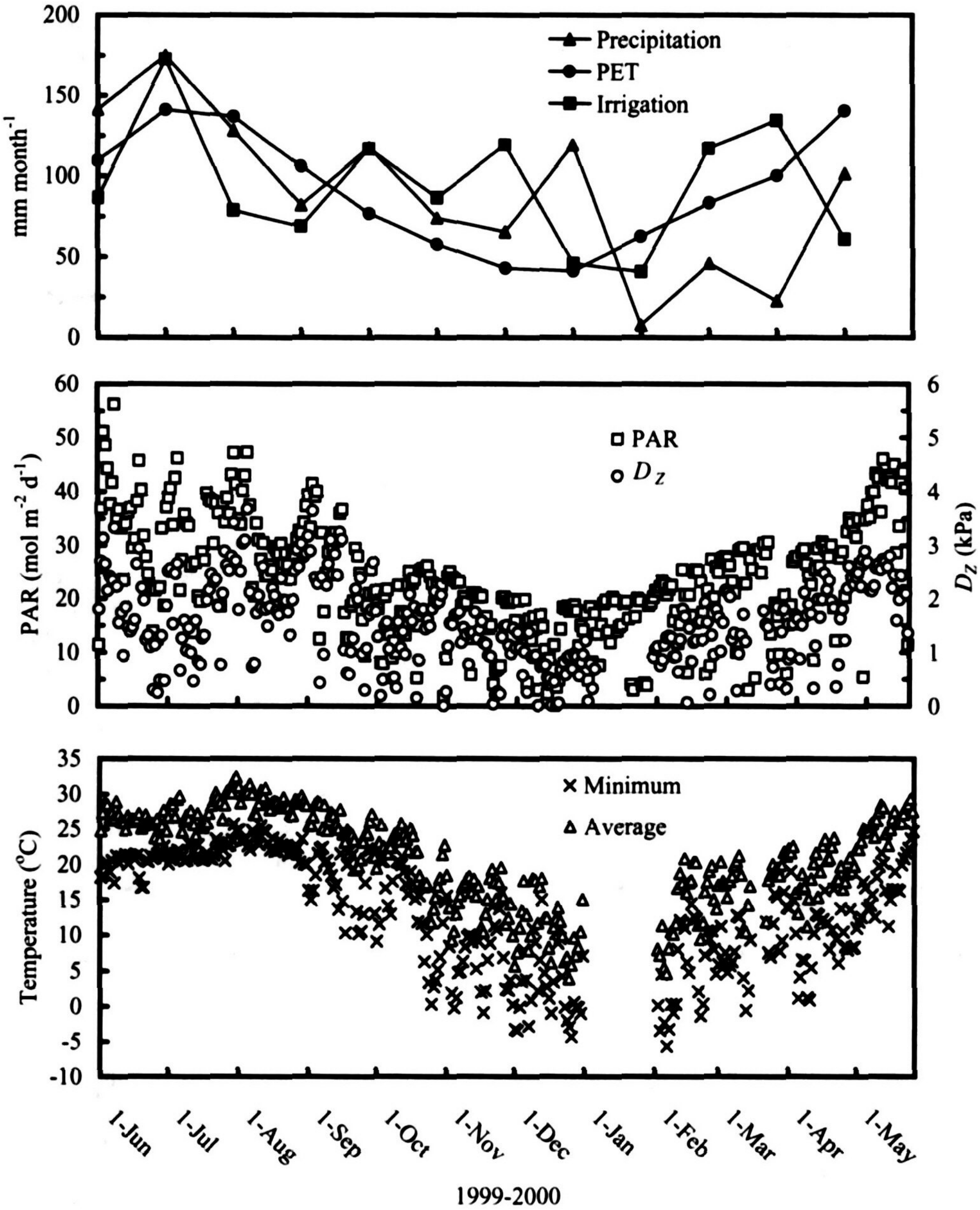

Figure 1. Monthly precipitation, potential evapotranspiration (PET), and irrigation; daily sum of photosynthetically active radiation (PAR) and daily average vapor pressure deficit during daylight hours (D_Z); and minimum and average 24-h temperatures over the study period for the 5-yr-old loblolly pine research plantation in Bainbridge, Georgia.

stored by a datalogger (DL2e, Delta-T Devices, Ltd., Cambridge, UK). Measurements were recorded from June 1999 through May 2000 with the exception of Nov. 1999 because of power failure. Data were averaged by hour and across aspect of each sample tree. Sap flow (Q, volume flow per unit time in kg h^{-1}, as defined by Reid et al. (2005)) was calculated as the product of q and sapwood area (Granier 1987) assuming uniform flow across the sapwood cross-sectional area. Transpiration on a ground area basis (E) was estimated by averaging Q across the two sample trees in a plot, dividing by plot area, and scaling up using the ratio of plot basal area to average sample tree basal area in each plot. The scaling ratio was considered appropriate because stands were even-aged with a limited range in tree size (Čermák et al. 2004). Transpiration was calculated on a leaf area basis (E_L) for each sample tree by dividing Q by individual tree leaf area determined using allometric equations (Samuelson et al. 2004a) and adjusting by seasonal changes in leaf area development and senescence reported in the literature (Kinerson et al. 1974).

The 30-mm probes measured 52, 43, and 40% of the average plot-level sapwood cross-sectional area per tree in the W, WI, and WIF treatments, respectively (Table 1). Because radial variation in sap flow was not measured, we estimated the potential reduction in total E and E_L from radial variation with sapwood depth based on correction factors derived from 10-yr-old maritime pine (*Pinus pinaster* Ait.), a species that begins producing mature wood at the

Table 1. Mean (SE) height, dbh, sample tree dbh, basal area, stem biomass, current annual increment (CAI), leaf area index (L), the ratio of leaf area to cross-sectional sapwood area (A_L:A_S), total transpiration expressed on a ground (E) and leaf area basis (E_L) and adjusted for potential radial variation, and water use efficiency (WUE) of 5-yr-old loblolly pine in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments

	W	WI	WIF	$P > F$
Height (m)	6.7 (0.3) b	8.0 (0.2) a	8.1 (0.2) a	<0.001
Dbh (cm)	11.6 (0.5) c	14.0 (0.5) b	14.9 (0.4) a	<0.001
Sample tree dbh (cm)	11.7 (0.6) b	13.5 (0.7) b	15.5 (0.1) a	0.027
Basal area ($m^2\ ha^{-1}$)	10.8 (0.9) c	15.4 (1.3) b	18.2 (1.0) a	<0.001
Stem biomass ($Mg\ ha^{-1}$)	17.7 (1.7) c	27.1 (2.7) b	32.6 (2.0) a	<0.001
CAI ($Mg\ ha^{-1}\ yr^{-1}$)	8.8 (0.7) c	12.9 (1.5) b	17.4 (1.8) a	<0.001
L ($m^2\ m^{-2}$)	2.1 (0.2) c	3.1 (0.3) b	3.7 (0.2) a	<0.001
A_L:A_S ($m^2\ cm^{-2}$)	0.194 (0.002) c	0.202 (0.002) b	0.206 (0.001) a	<0.001
Total E (mm)	357 (60) b	529 (12) a	565 (20) a	0.052
Adjusted total E (mm)	355 (58) b	503 (11) a	528 (16) a	0.071
Total E_L (mm)	236 (22.2)	229 (0.4)	190 (1.1)	0.207
Adjusted total E_L (mm)	235 (20.9)	221 (2.6)	178 (0.1)	0.128
WUE (g stem C kg^{-1} H_2O)	0.59 (0.08)	0.47 (0.04)	0.81 (0.03)	0.118

Observed probability values for treatment effects are shown. Different letters indicate significant treatment differences.

13th ring (Delzon et al. 2004). Other published relationships for older loblolly pine were not applicable as they were based on stems consisting of both juvenile and mature wood with a large reduction in q at the transition zone (Phillips et al. 1996). Juvenile wood usually occurs until the 7th to 10th ring from the pith in loblolly pine (Megraw 1985), and Phillips et al. (1996) attributed the source of reduced q with sapwood depth in 12-yr-old loblolly pine to 40% lower hydraulic conductivity in juvenile wood relative to mature wood. Correction factors based on average plot diameters were applied to hourly estimates of Q, and adjusted E and E_L totals were estimated to help the reader understand potential uncertainties in the up-scaled data. Water use efficiency (WUE) over the study period was calculated for sample trees by dividing the amount of carbon produced in stem wood estimated from diameter increment and allometric equations (Samuelson et al. 2004a) by the amount of water transpired.

Canopy Stomatal Conductance

G_S was calculated using the following equation from Monteith and Unsworth (1990):

$$G_S = (\lambda \cdot E_L \cdot \gamma)/(\rho \cdot c_p \cdot D), \quad (3)$$

where λ is the latent heat of vaporization of water (2,465 J g^{-1}), γ the psychometric constant (65.5 Pa K^{-1}), ρ the density of air (1,225 g m^{-3}), c_p the specific heat of air (1.01 J g^{-1} K^{-1}), and E_L is in g m^{-2} s^{-1}. In calculating G_S we assumed that the atmosphere and canopy were well coupled and hydraulic capacity was negligible. Values were converted from m s^{-1} to mmol m^{-2} s^{-1} following Nobel (1991). Mean midday G_S was calculated as the average from 11:00 am to 12:00 pm eastern standard time and only when $D \geq 1.0$ kPa to reduce errors from instrument limitations (Ewers and Oren 2000).

Hydraulic Conductance

Whole-tree hydraulic conductance per unit sapwood area (G) and leaf specific hydraulic conductance (G_L) were calculated by the slope of the linear relationship between tree level Q expressed on a sapwood or leaf area basis, respectively, and leaf water potential (Ψ_L) (Wullschleger et al. 1998). Ψ_L was measured using a pressure chamber (PMS Instrument Corporation, Corvallis, OR) on one fascicle collected from the upper crown of each sample tree at 5:00, 9:00, and 11:00 am, and 1:00 and 3:00 pm eastern standard time on June 22–23, July 29–30, and Aug. 18–19, 1999. One block was randomly selected and measured over 1 day and treatment plots were randomly selected for order of measurement within a block. The gradient in water potential between the soil and leaf ($\Delta\Psi$) was calculated as the difference in Ψ_L between 5:00 am and 1:00 pm.

Statistical Analyses

All data were averaged across the two sample trees in each plot and individual treatment plots were considered the experimental unit. The experimental design was a randomized complete block with two blocks. Analysis of variance (ANOVA) with block and treatment as main effects was used to examine treatment effects on E, E_L, adjusted E, and adjusted E_L summed over the 11 months. Duncan's Multiple Range Test was used to separate treatment means. Multivariate repeated measures analysis (Von Ende 1993) was used to examine the influence of treatment and season on the mean daily sum of E_L and mean midday (11:00 am–2:00 pm) G_S averaged across summer (June, July, and Aug.) and winter (Dec. and Feb.) months. The effects of treatment and measurement month on predawn Ψ_L, $\Delta\Psi$, G, and G_L were examined in the same way. Linear and nonlinear relationships (Ewers et al. 2005) between the daily sum of E_L and the daily sum of PAR or daily average D vapor pressure deficit during daylight hours (D_Z) were explored over one summer and one winter month to determine whether potential treatment effects on relationships varied with season. Similarly, the response of G_S to PAR and D was examined over one randomly selected clear day in summer (July 30, 1999) and winter (Feb. 22, 2000). The effects of treatment and season on parameter estimates were tested using multivariate repeated measures analysis. Because of the low power of this study to detect treatment effects, effects were considered significant at the $P \leq 0.10$ level.

Results

Growing Conditions

Precipitation ranged between 8 and 175 mm month^{-1} and totaled 1,080 mm over the measurement year (Figure 1). Total PET during the measurement period was 1,097 mm. Daily PAR and D_Z were generally lower in the nongrowing season than in summer, and average daily sum of PAR and D_Z were 32.2 mol m^{-2} d^{-1} and 1.9 kPa in summer, respectively, and 15.5 mol m^{-2} d^{-1} and 0.9 kPa in winter, respectively (Figure 1). The average temperature during summer months was 27.7°C (Figure 1). During the winter months of Dec. and Feb., average temperature was 12.5°C, with 19 days below a minimum temperature of 0°C.

Effects of Intensive Management on Transpiration

E was as high as 3.9 mm d^{-1} (Figure 2) and averaged over the summer months of June, July, and Aug. was 1.5, 2.0, and 2.4 mm d^{-1} for W, WI, and WIF treatments,

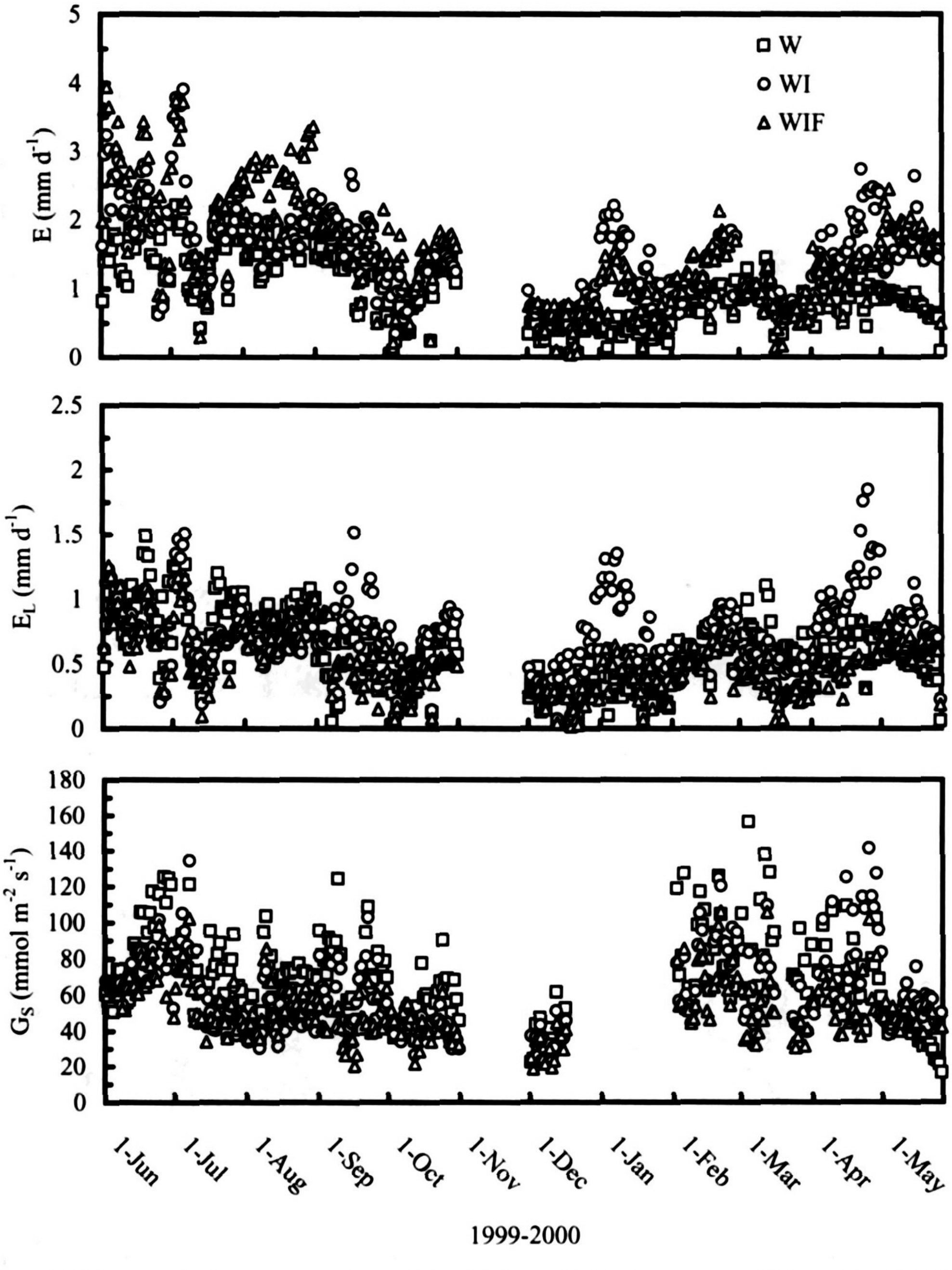

Figure 2. Daily transpiration on a ground area (*E*) and leaf area (E_L) basis and mean midday canopy stomatal conductance (G_S) in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments in 5-yr-old loblolly pine from June 1999 through May 2000.

respectively (Figure 3). Averaged over the winter months of Dec. and Feb., E decreased to 0.5, 1.0, and 0.9 mm d^{-1} for W, WI, and WIF treatments, respectively. Repeated measures analyses of daily E averaged over winter and summer indicated significant season and treatment effects but no significant interaction effect (Table 2). For both seasons, daily E was higher in the WI and WIF treatments than in the W treatment but similar between WI and WIF treatments (Figure 3). Totaled over the 11 months of the study, E was 357, 529, and 565 mm for W, WI, and WIF treatments, respectively, and significantly higher in the WI and WIF treatments than the W treatment and similar between WI and WIF stands (Table 1). Total E adjusted for potential radial variation was reduced by less than 1% in W stands, 5% in WI stands, and only 7% in WIF stands (Table 1). Adjusted total E was also significantly greater in WI and WIF than W stands and similar between WI and WIF treatments. No significant effect of treatment on WUE was

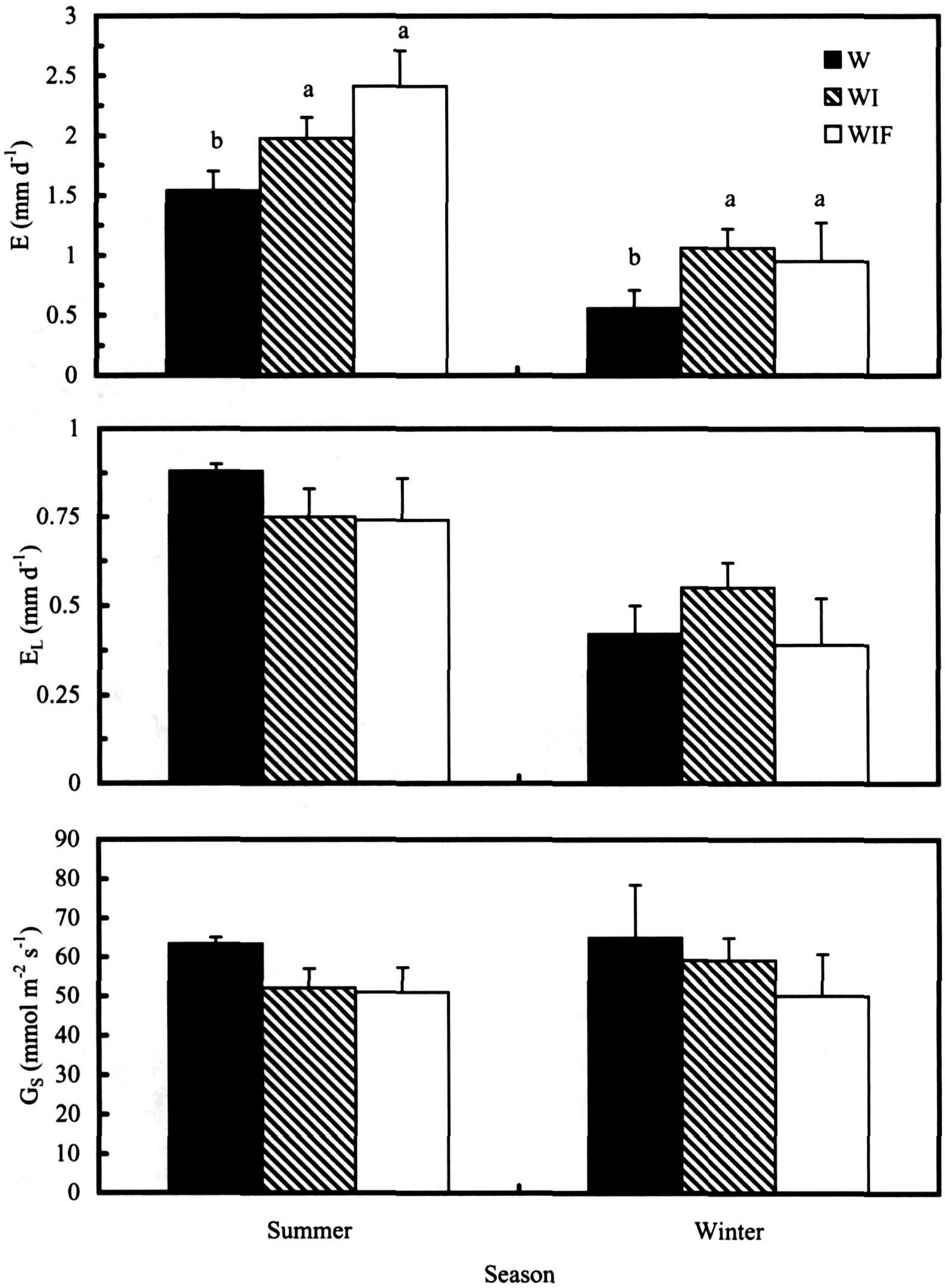

Figure 3. Daily transpiration on a ground (E) and leaf area (E_L) basis and mean midday canopy stomatal conductance (G_S) averaged by season in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments in 5-yr-old loblolly pine. Different letters indicate significant treatment differences and stand error bars represent variation between blocks.

Table 2. Observed probability values for repeated measures analyses of time (season or month) and management treatment effects on daily transpiration on a ground (E) and leaf (E_L) area basis, mean midday canopy stomatal conductance (G_S), whole-tree hydraulic conductance (G), leaf specific hydraulic conductance (G_L), predawn leaf water potential (Ψ_L), and the gradient in water potential between the soil and leaf ($\Delta\Psi$) in 5-yr-old loblolly pine

Variable	Treatment $P > F$	Time $P > F$	Treatment × time $P > F$
E	0.031	0.017	0.639
E_L	0.216	0.043	0.619
G_S	0.214	0.828	0.903
G	0.763	0.427	0.261
G_L	0.488	0.278	0.948
Ψ_L	0.743	0.523	0.722
$\Delta\Psi$	0.538	0.241	0.856

detected and average WUE was 0.62 g stem C kg^{-1} H_2O transpired (Table 1).

In contrast, no significant treatment differences in total E_L or adjusted total E_L were observed and E_L was on average 218 mm for the 11 months (Table 1). Adjusted total E_L was reduced by less than 1% in W stands, 4% in WI stands, and only 6% in WIF stands compared to unadjusted E_L totals (Table 1). A significant effect of season on daily E_L was observed but no treatment or interaction effects were detected (Table 2). E_L was as high as 1.8 mm d^{-1} (Figure 2) and on average 0.8 and 0.4 mm d^{-1} during summer and winter, respectively (Figure 3). The nonlinear model ($E_L = a^*(1 - e^{-bD_Z})$) describing the relationship between daily E_L and D_Z resulted in the best fit both months, with R^2 ranging from 88 to 97% (Figure 4 and Table 3). Repeated measures analyses of parameter estimates indicated a significant effect of month on parameter a, with the ultimate maximum value of E_L higher in July than Feb., but no significant treatment or treatment by month interaction effects (Table 4).

Effects of Intensive Management on Canopy Stomatal Conductance

Mean midday G_S was as high as 156 mmol m^{-2} s^{-1} (Figure 2) and on average 56 mmol m^{-2} s^{-1} over summer months and 58 mmol m^{-2} s^{-1} over the two winter months (Figure 3). No significant treatment, season, or interaction effects on mean midday G_S were observed (Table 2). Average winter estimates were based mainly on the higher values in Feb. because of limited data in Dec. and no data from Jan. (Figure 2).

The nonlinear model ($G_S = a * (1 - e^{-b\mathrm{PAR}})$) describing the relationship between G_S and PAR resulted in the best fit

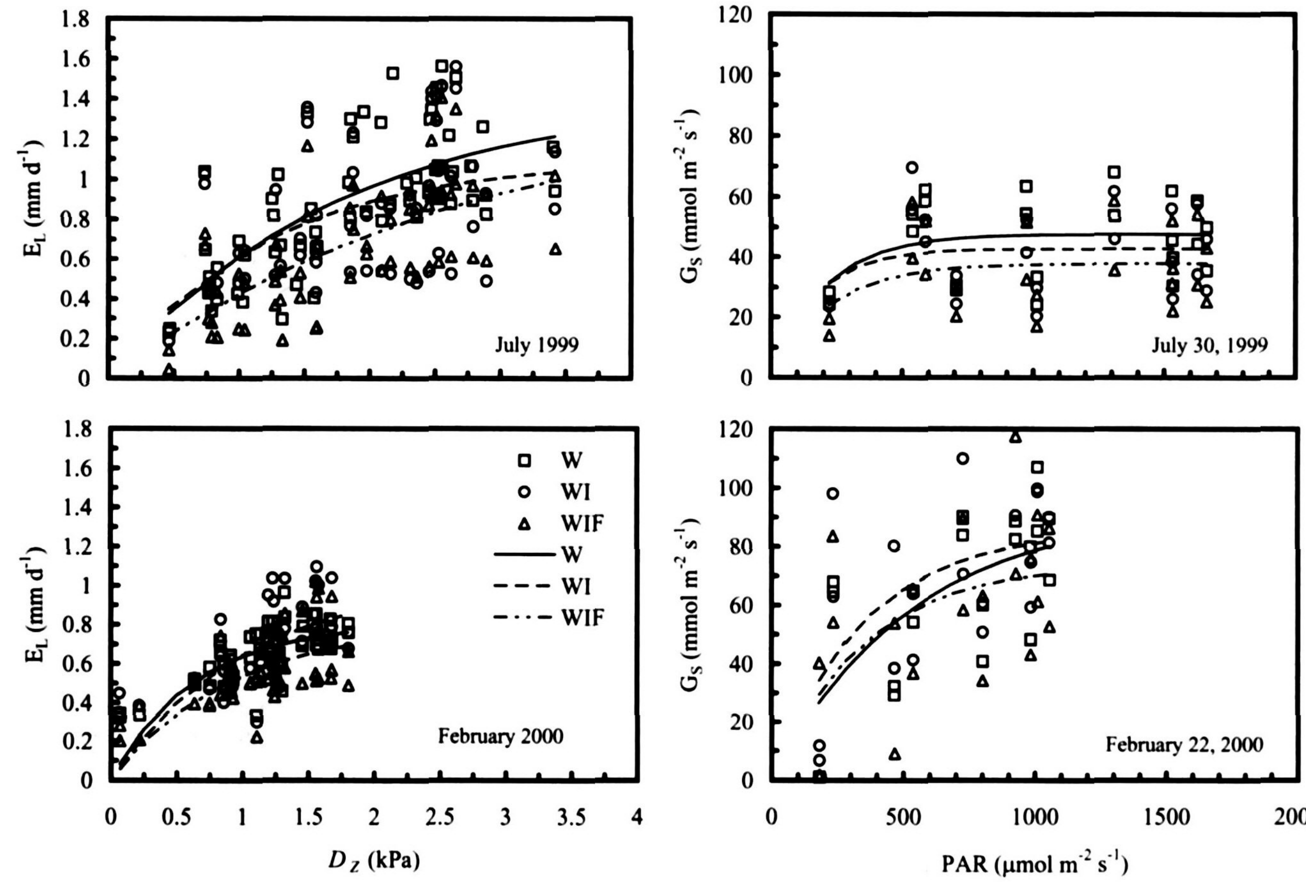

Figure 4. Relationship between daily transpiration per unit leaf area (E_L) and daily average vapor pressure deficit during daylight hours (D_Z) measured in July and Feb., and between canopy stomatal conductance (G_S) and photosynthetically active radiation (PAR) measured on one day in July and Feb. of 5-yr-old loblolly pine in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments. Each data point represents a measurement for one block-treatment combination on one sampling day (E_L) or hour (G_S).

Table 3. Parameters for nonlinear models describing relationships between transpiration on a leaf area basis (E_L, mm d^{-1}) and daily average vapor pressure deficit during daylight hours (D_Z, kPa) and between canopy stomatal conductance (G_S, mmol m^{-2} s^{-1}) and photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) for 5-yr-old loblolly pine in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments

Model and Date	Treatment	*a*	*b*	d.f.	R^2
$E_L = a \cdot (1 - e^{-bD_Z})$					
Jul. 1999	W	1.43	0.54	62	0.93
	WI	1.10	0.82	62	0.88
	WIF	1.42	0.36	62	0.90
Feb. 2000	W	0.81	1.56	53	0.97
	WI	1.04	0.95	53	0.94
	WIF	0.80	1.11	53	0.93
$G_S = a \cdot (1 - e^{-b\mathrm{PAR}})$					
Jul. 30, 1999	W	47.75	0.005	22	0.93
	WI	42.78	0.006	22	0.91
	WIF	37.81	0.005	22	0.89
Feb. 22, 2000	W	93.27	0.002	19	0.91
	WI	86.18	0.003	19	0.90
	WIF	74.65	0.003	19	0.86

Table 4. Observed probability values for repeated measures analyses of time (month or day) and management treatment effects on parameters for nonlinear models describing relationships between transpiration on a leaf area basis (E_L, mm d^{-1}) and daily average vapor pressure deficit during daylight hours (D_Z, kPa) and between canopy stomatal conductance (G_S, mmol m^{-2} s^{-1}) and photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) for 5-yr-old loblolly pine

Model and Parameter	Treatment $P > F$	Time $P > F$	Treatment × time $P > F$
$E_L = a \cdot (1 - e^{-bD_Z})$			
a	0.861	0.050	0.866
b	0.556	0.141	0.615
$G_S = a \cdot (1 - e^{-b\mathrm{PAR}})$			
a	0.513	0.005	0.431
b	0.754	0.053	0.735

for both days, with R^2 ranging from 86 to 93% (Table 3, Figure 4). Repeated measures analyses of parameter estimates for the nonlinear models indicated a significant effect of day on parameters *a* and *b* but no significant treatment effects or interactions between treatment and day (Table 4). The instantaneous slope of G_S for any value of PAR (parameter *b*) was higher in July than Feb., but the ultimate maximum value of G_S (parameter *a*) was greater in Feb. than in July (Table 3).

Effects of Intensive Management on Hydraulic Capacity

No significant main or interaction effects of treatment and measurement month were observed for G, G_L, predawn Ψ_L, or $\Delta\Psi$ (Table 2). Averaged across treatment and month, G was 3.0 mol m^{-2} s^{-1} MPa^{-1} and G_L was 1.3 mmol m^{-2} s^{-1} MPa^{-1} (Figure 5). Predawn Ψ_L and $\Delta\Psi$ were maintained across treatments and measurement months, and were, on average, −0.77 MPa and 0.86 MPa, respectively (Figure 5). Small (4–6%) but significant increases in the A_L:A_S ratio were observed with increasing management intensity (Table 1). The A_L:A_S ratio increased from 0.194 m^2 cm^{-2} in W stands to 0.202 m^2 cm^{-2} and 0.206 m^2 cm^{-2} in WI and WIF treatments, respectively.

Discussion

Rapid early growth and increased L in response to intensive management resulted in an increase in average daily E during summer months from 1.5 mm d^{-1} in W stands to an average 2.2 mm d^{-1} in WI and WIF stands. In natural stands of loblolly pine ranging in age from 6 to 10 years and with sapwood area between 12 and 24 m^2 ha^{-1}, E was similar at 1.5–2.5 mm d^{-1} (Phillips and Oren 2001). Ewers et al. (1999) reported 0.7, 0.7, and 1.8 mm d^{-1} in response to control, irrigation, and irrigation + fertilization treatments, respectively, in 12-yr-old loblolly pine with similar sapwood area (9.0–21.9 m^2 ha^{-1}) and L (1.8–3.6 m^2 m^{-2}). Higher transpiration rates have been documented in 16-yr-old *Pinus radiata*, as much as 6.8 mm d^{-1} in stands with an L value of 6.6 m^2 m^{-2} (Teskey and Sheriff 1996). During the winter months of Dec. through Feb., E was, on average, 1.0 mm d^{-1} in WI and WIF stands and lower than the average 1.8 mm d^{-1} reported for 15-yr-old loblolly pine in Florida (Martin 2000). However, basal area in the Florida study was more than double ours, at 40.5 m^2 ha^{-1}.

Compared to studies with similar stand structure, E (357–565 mm) summed over the 11-month study period and adjusted for potential radial decline (355–528 mm) was within the range reported for loblolly pine and fast-growing hardwoods. For example, in 6- to 10-yr-old natural loblolly

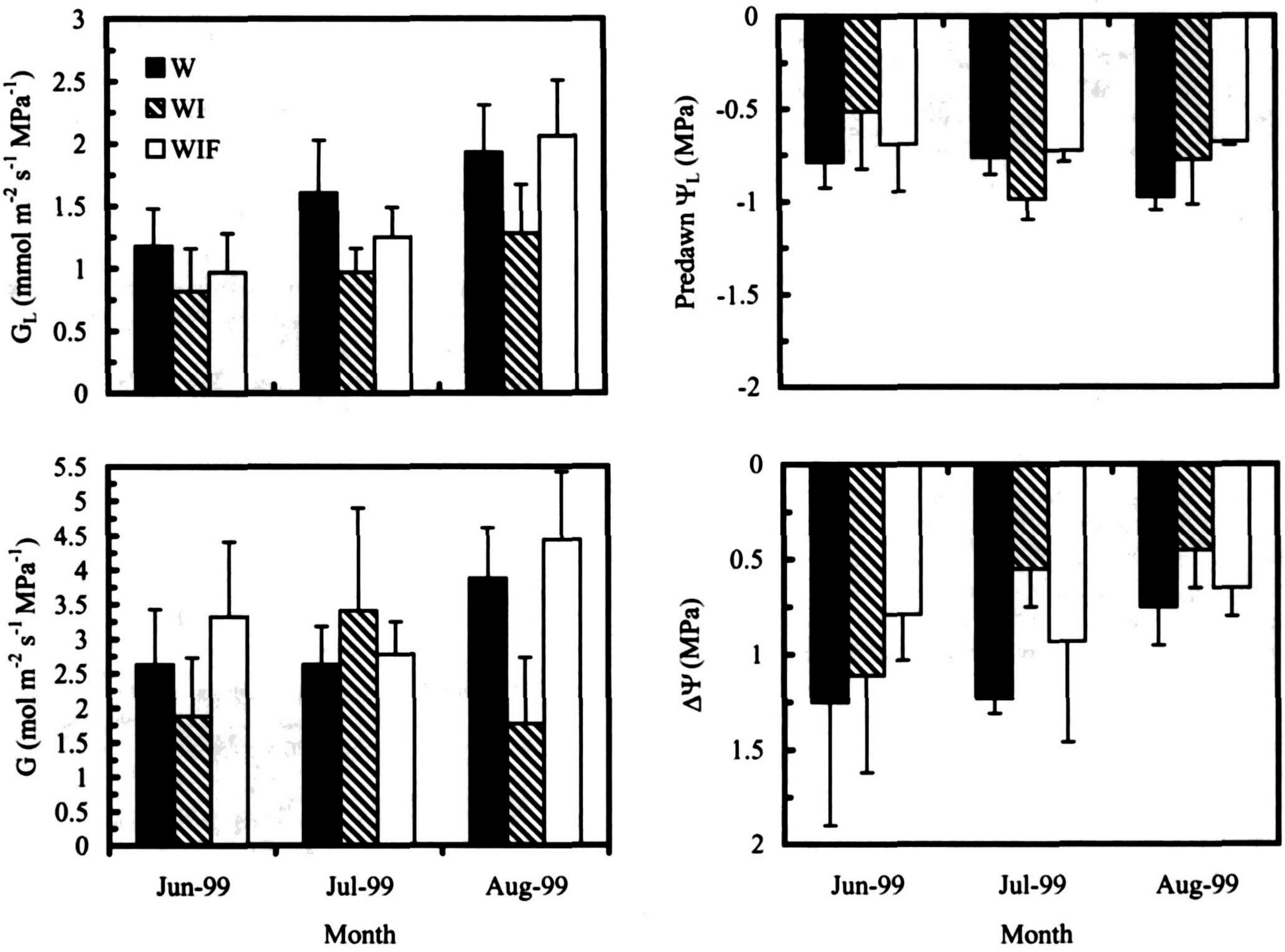

Figure 5. Leaf specific hydraulic conductance (G_L), whole-tree hydraulic conductance per unit sapwood area (G), predawn leaf water potential (Ψ_L), and the gradient in water potential from leaf to soil ($\Delta\Psi$) in 5-yr-old loblolly pine in response to weed control (W), weed control + irrigation (WI), and weed control + irrigation + fertigation (WIF) treatments measured in June, July, and Aug. Stand error bars represent variation between blocks.

stands, E ranged from 323 to 410 mm yr^{-1} (Phillips and Oren 2001). In 12-yr-old plantation loblolly pine stands, E was 331 mm yr^{-1} in the control versus 581 mm yr^{-1} in response to irrigation + fertilization (Ewers et al. 2001). E was approximately 545 mm yr^{-1} in 12-yr-old sweetgum stands with a sapwood area of 24 m^2 ha^{-1} and L of 6 m^2 m^{-2} (Wullschleger and Norby 2001). Fertilization of fast-growing *Eucalyptus* increased L by 33% to 6 m^2 m^{-2} and E also by 33%, from 302 mm yr^{-1} to 401 mm yr^{-1} (Hubbard et al. 2004). Higher E in response to intensive management was a function of increased leaf area, because no treatment effects on E_L were observed. Leaf area index and total E were increased by WI and WIF treatment on average by 62% and 53%, respectively, over the control. Likewise, maximum productivity over the life of the plantation was also a function of management effects on leaf area (Samuelson et al. 2004a). Crown closure and an upward shift in the live crown in WI and WIF stands were observed at age 5 (Samuelson et al. 2004a), but light availability was not likely limiting to overall carbon gain up to this point, because WUE was similar among treatments (Köstner et al. 2002, Hubbard et al. 2004) and current annual increment at age 5 was highest in WIF stands (Table 1).

We hypothesized that increased L would be associated with physiological or structural changes that limit water loss and minimize $\Delta\Psi$ (Whitehead 1998). Equations 1 and 2 indicate that increased leaf area production requires a proportional increase in sapwood area, increased G, or reduced G_S and G_L to avoid damaging leaf water potentials (Whitehead and Beadle 2004). In support of this hypothesis, $\Delta\Psi$, predawn Ψ_L, and E_L were similar among treatments, but the 76% increase in L in WIF stands was not accompanied by a comparable increase in G or decrease in G_S. We observed strong nonlinear relationships between E_L and D_Z, and G_S and PAR similar to those reported by Ewers et al. (2001) for loblolly pine, and Ewers et al. (2001) also detected no influence of irrigation or irrigation + fertilization on these relationships. Increasing leaf area and E did not reduce G_L, and average G_L (1.3 mmol m^{-2} s^{-1} MPa^{-1}) was similar to the 0.5–1.1 mmol m^{-2} s^{-1} MPa^{-1} reported for loblolly pine (Ewers et al. 2000, Hacke et al. 2000). In 15-yr-old loblolly pine fertilization nearly doubled L, increased A_L:A_S by 18%, and had no influence on $\Delta\Psi$, but the increase in L was offset by decreased G_S and G_L relative to control stands (Ewers et al. 2000). When irrigation was supplied with fertilization, enhancement of sapwood growth was 47% greater than with fertilization alone and because of greatly increased sapwood area, a 107% increase in L in response to irrigation + fertilization relative to control stands resulted in no decline in G_L, G_S, and $\Delta\Psi$ (Ewers et al. 2000). Likewise, in our study, large increases in L were balanced by large increases in sapwood area rather than by comparable changes in G, G_S, or G_L. However, our small sample size and low statistical power may have limited our ability to detect small changes in hydraulic traits that may be related to the 4% and 6% increase in A_L:A_S in WI and WIF stands, respectively.

This is the first study we are aware of to document seasonal variability in water use and G_S in rapidly growing loblolly pine under continuous intensive management. It is interesting to note that G_S was high in Feb. and strongly related to PAR in winter as well as summer. Gough et al. (2004) found similar photosynthetic capacities year-round and that PAR and D rather than temperature explained on average 63% of the variation in net photosynthesis of 14-yr-old loblolly pine during the nongrowing season (Nov.–Mar.), despite below freezing night temperatures and measurement temperatures as low as 12°C. Winter carbon fixation in loblolly pine is facilitated by climate and seasonal changes in the temperature optimum for photosynthesis (Teskey et al. 1986, Gough et al. 2004). When incident shortwave radiation is favorable, autumn and winter may be important periods for carbon uptake in loblolly pine because cooler temperatures reduce respiration more than photosynthesis (Lai et al. 2002, Sampson et al. 2006). From 15% (Ellsworth 2000) to over 20% (Gough et al. 2004) of annual carbon fixation of loblolly pine was estimated to occur during the nongrowing season in North Carolina. Based on similar G_S between summer and winter, and winter net photosynthesis rates 45% of maximum in this plantation at age 4 (Samuelson et al. 2001), we concur with Martin (2000) that considerable carbon gain takes place during winter in loblolly pine. We suggest that the contribution of photosynthesis during the nongrowing season to annual carbon gain is greater than 20% in loblolly pine's most southern range.

In conclusion, water use by fast-growing loblolly pine stands was a function of management effects on leaf area. High forest productivity has been attributed to increases in A_L:A_S and G (White et al. 1998, Tyree 2003), but we observed only a 4 to 6% increase in A_L:A_S and no change in G or G_L. High L was balanced by large increases in sapwood area and $\Delta\Psi$ was maintained with increasing canopy development. Although soil nutrient availability is most limiting to loblolly pine productivity (Jokela and Dougherty 2004), these results and Ewers et al. (2000) indicate that exceptionally high L and productivity realized in this young plantation was possible because irrigation was supplied with fertilization and water availability was not limiting to stem growth.

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