

Water availability and genetic effects on water relations of loblolly pine (*Pinus taeda*) stands

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Summary The effect of water availability on water relations of 11-year-old loblolly pine stands was studied over two growing seasons in material from two contrasting seed sources. Increasing soil water availability via irrigation increased transpiration rate, and maximum daily transpiration rate on irrigated plots was similar for both seasons, reaching values of 4.3 mm day⁻¹. Irrigation also changed soil water extraction patterns. In the rain-fed control plots, 73% of the average daily transpiration was extracted from the upper 0.75 m of the soil profile. Under irrigated conditions, 92% of transpired water was extracted from the upper 0.75 m of soil, with 79% of transpired water coming from the upper 0.35 m of the profile; only 10% of total transpiration in this treatment was extracted from the soil below 1 m. There was an irrigation × seed source interaction in the response of canopy conductance to water vapor (G_C) to vapor pressure deficit (D). Under water-limited conditions, trees from the South Carolina seed source (SC) had stronger stomatal control than trees from the Florida seed source (FL), but this difference was not present when water was not limiting. The transpiration-induced water potential gradient from roots to shoots ($\Delta\Psi$) was relatively constant across treatments ($P = 0.52$) and seed sources ($P = 0.72$), averaging 0.75 MPa. This reflects strong stomatal control that maintains relatively constant $\Delta\Psi$ but at the same time allows leaf water potential (Ψ_l) to fluctuate dramatically in synchrony with soil water potential (Ψ_s). The two seed sources evaluated also showed differences in foliar N and $\delta^{13}C$, possibly reflecting differences in adaptation to ambient humidity and water availability regimes in their respective ranges. These differences among seed sources under different water availability scenarios may be informative to natural resource managers and breeders as they design tree improvement and genetic deployment programs for future climate scenarios. For example, the increased stomatal control of SC under decreased soil moisture availability may make this taxon a more conservative deployment choice than FL under future, drier climate scenarios but perhaps at the risk of lower productivity.

Keywords: canopy conductance, hydraulic conductance, irrigation, sap flow density radial profile, soil water uptake, transpiration, $\delta^{13}C$.

Introduction

Loblolly pine (*Pinus taeda* L.) is the most commercially important timber species in the southeastern USA, accounting for more than 84% of seedlings planted (McKeand et al. 2003). Loblolly pine is also one of the fastest growing pines and thrives on various sites from east Texas to southern Missouri to north Florida to south New Jersey.

Water availability is one of the main factors controlling tree growth and species distribution (Lambers et al. 1998). Water supply to leaves is needed to sustain photosynthesis and can influence the characteristics of the secondary xylem (wood) formed during the growing season (Panshin and de Zeeuw 1980). Plant primary production requires substantial amounts of water, and this water loss is an unavoidable consequence of photosynthesis when stomata are open for carbon assimilation (Lambers et al. 1998, Gartner and Meinzer 2005). Plants regulate water loss in response to water deficits by closing stomata to avoid irreversible cavitation (Sperry and Ikeda 1997, Sperry 2000, Tyree 2003). Hydraulic conductance is the change in flow rate of liquid water through the system per change in hydraulic pressure driving the flow (Sperry 2000). It can limit the maximum rate of gas exchange and carbon gain (Tyree 2003). Plants with high hydraulic conductance tend to have higher growth rates and are more vulnerable to embolism than plants with lower hydraulic conductance (Tyree and Zimmermann 2002). Low values of hydraulic conductance reduce the ability to maintain stomatal conductance as evaporative demands increase at low soil moisture content (Wullschlegel et al. 1998, Wang et al. 2003). The water potential at which stomatal closure occurs has been shown to be closely related to the water potential level at which xylem cavitation becomes significant (Sperry

and Ikeda 1997). In other words, regulation of stomatal conductance and water loss appears to have evolved so that catastrophic xylem embolism is avoided (Sperry 2000).

Many studies have investigated loblolly pine water relations (e.g., Pataki et al. 1998, Ewers et al. 1999, 2000, Ewers and Oren 2000, Hacke et al. 2000, Martin 2000, Samuelson et al. 2001, Samuelson and Stokes 2006), but few have investigated stand-level water relations of contrasting seed sources in a fully replicated experiment. The overall objective of this study was to investigate the influence of soil water availability and seed source on stand transpiration, soil water use, canopy conductance and whole-tree hydraulic conductance in an 11-year-old loblolly pine experiment, with the aim to understand the degree that varying seed sources differ in water relations behavior. Given the high genetic variability inherent in loblolly pine (Sierira-Lucero et al. 2002), the overriding ecological and economic importance of the species (Schultz 1997) and the potential for changing precipitation and temperature regimes in the region (Solomon et al. 2007), it is important to understand the tradeoffs and risks associated with adaptations to limiting water supply and atmospheric water demand by different loblolly pine taxa. We hypothesize (i) water extraction patterns will change due to water availability limitations, so irrigated trees will take up water mostly from upper soil layers; (ii) due to water availability limitations, whole-tree hydraulic conductance (K_{S-wt}) will be decreased in control versus irrigated treatments because of cavitation of water-conducting tracheids and (iii) due to natural selection between sites with differences in native moisture conditions, trees from a 'wet' climate will have a smaller degree of stomatal control in response to water stress, reflected in smaller adjustments in canopy conductance (G_C) under water-stressed conditions. Water availability was controlled through an irrigation treatment applied to two fast-growing seed sources that received extra irrigation water input since plantation establishment.

Materials and methods

Site and stand description

The study took place in an irrigation and genetics experiment established in January 1995 by International Paper, Inc. in the Upper Coastal Plain 22 km west of Bainbridge, GA (30°48' N latitude and 84°39' W longitude). Soils at this location were classified as well-drained Grossarenic Paleudults, with 0.5 m sandy loam over sandy clay loam (Samuelson 1998).

The study consisted of two water availability treatments and two genetic entries (seed sources) in factorial combination, repeated three times in a split-plot randomized complete block design (12 plots total), with irrigation as the whole plot and genetic entry (seed source) as the subplot. This experiment represented a subset of the whole study, which also in-

Table 1. Mean annual maximum (Tmax), mean (Tmean) and minimum (Tmin) temperatures, average seasonal (M–S, May to September; O–A, October to April) potential evapotranspiration (PET) and precipitations (pp) for source sites (FL, Marion County, Florida, SC, Georgetown County, South Carolina) and study site (GA, Decatur County, Georgia).

	Site		
	FL	SC	GA
Tmax (°C)	22.4	19.6	20.8
Tmean (°C)	17.2	14.6	15.2
Tmin (°C)	11.9	9.7	9.6
pp M–S (mm)	777.4	588.2	567.3
PET M–S (mm)	835.5	821.9	861.6
pp O–A (mm)	505.1	597.2	731.1
PET O–A (mm)	699.9	534.6	636.1

Mean annual temperatures and precipitation were obtained at <http://cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl>.

Long-term (1951–1998) PET was obtained from United States Geological Survey Hydro-Climatic Data Network (HCDN) at <http://daac.ornl.gov/cgi-bin/search/hcdn.pl?d=810>.

cluded two additional seed sources, fertilization and pest control treatments. The measurement plots had an area of 0.026 ha, containing 28 sample trees planted at a 2.4 × 3.7 m spacing and surrounded by two buffer rows. The seed sources were obtained from industrial tree improvement seed orchards and consisted of (1) FL, a mixture of north-central Florida half-sib families (primarily from Marion County), and (2) SC, a single half-sib family from the South Carolina Coastal Plain (Georgetown County). The water treatments included an irrigated (6.25 mm day⁻¹ on drip irrigation from July to November in 2005 and from March to October in 2006) and a nonirrigated control treatment. Samuelson (1998) and Samuelson et al. (2001, 2008) reported additional site and experimental details.

The long-term environmental characteristics of the originating location of each seed source compared to the study site is presented in Table 1. FL has around 2–3 °C higher annual maximum, mean and minimum temperatures than SC. During the warmer growing season (May to September), potential water deficit, expressed as the ratio between potential evapotranspiration (PET) and precipitation (pp), is larger in SC compared with FL (1.39 and 1.07, respectively), but during cooling months (October to April), this trend is reversed, and SC has no potential water deficit (PET is 10.5% lower than pp), while FL had 38.5% larger PET than pp, indicating that FL had greater water availability during the growing season compared with SC.

Meteorological and soil moisture measurements

Meteorological data were recorded from June 2005 to January 2007 with an automatic weather station located in an open area adjacent to the stand. Precipitation in both measurement years was below historic averages but evenly dis-

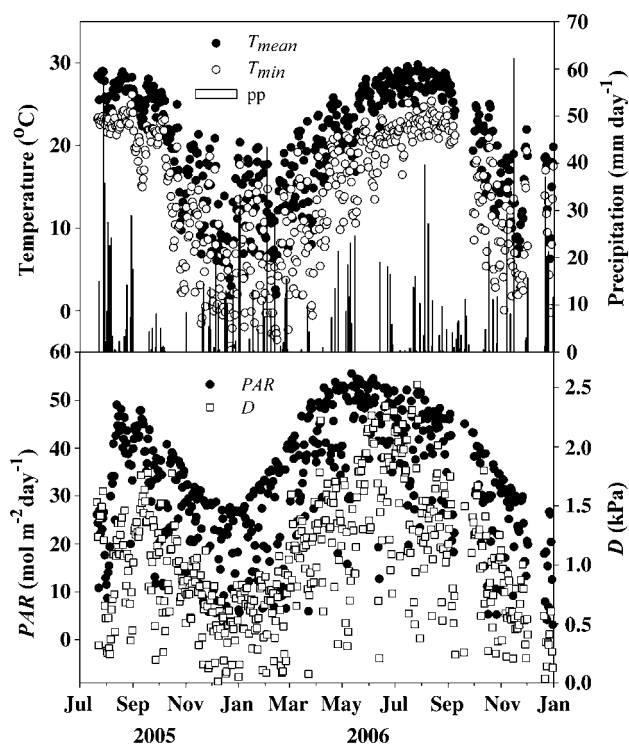


Figure 1. Environmental conditions through study period. (A) Daily mean (T_{mean}) and minimum (T_{min}) temperatures and total precipitation; (B) daily sum of photosynthetically active radiation (PAR) and daily average of vapor pressure deficit (D) during daylight hours over the study period.

tributed throughout the year. Total precipitation from July to December was 463 and 467 mm for seasons 2005 and 2006, respectively, corresponding to ~28% lower rainfall than the 30-year average for Bainbridge (<http://cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl>, May 2008). In 2006, total precipitation from January to December was 902 mm, 36% lower than the long-term average. For 2006, mean daily temperature during summer was very uniform, averaging 24.3 °C; mean daily temperature during winter was 13.6 °C (Figure 1). Potential evapotranspiration was calculated from weather station data using the Priestley–Taylor equation (Priestley and Taylor 1972).

Vertically oriented, 200-mm-long capacitive soil moisture probes (EC-20, Decagon Devices, Pullman, WA, USA) were used to estimate volumetric soil water content (θ_v). The manufacturer's probe installation kit, consisting of a custom-shaped blade to make the insertion in the soil and a tool to place the probe into the insertion point, was used to install the probes. For deeper installations, an auger was used to reach the desired depth, and then the installation kit with extension rods was used to install the probe. The soil volume measured by the probe was not disturbed.

In June 2005, two probes were installed at 0.2 m depth (midpoint of probe installed at 0.1–0.3 m soil depth) on each plot into within and between planting row positions. Reported values of θ_v at 0.2 m corresponded to the average of

measurements at both positions for each plot. In March 2006, one additional probe was installed at 0.5 m depth (midpoint of probe installed at 0.4–0.6 m soil depth) in the center of each plot to measure changes in volumetric water content in deeper portions of the soil profile. At the same time, in order to evaluate the dynamics of soil water extraction under rain-fed conditions, probes were installed at 1.0, 1.5 and 2.0 m depth in each replicate of the nonirrigated FL seed source plots. The estimations of water content of each probe were extrapolated to the midpoint distance between sensors. Soil-specific calibrations were developed from soil samples taken 0.5 m away from each probe; soil samples were collected from the same depth where the probes were installed. Soil-specific calibrations were not significantly different ($P = 0.78$ and 0.79 for intercept and slope, respectively) from the manufacturer's default calibration which transformed sensor outputs (mV) to volumetric water content: $\theta_v = -0.24508 + 0.0007958 \cdot \text{mV}$.

Total water content from the top 0.75 m of the soil profile (WC, mm) was calculated for each plot as the summation of the product between θ_v and the corresponding soil layer depth (z) that was assumed as the distance from the midpoint between two contiguous soil moisture probes (e.g., for a soil moisture probe installed at 0.5 m, a soil layer depth of 0.4 m was assumed, representing a soil layer between 0.35 and 0.75 m, because above and below this probe there were sensors installed at 0.2 and 1.0 m depth). Available soil water (ASW) was calculated for each plot and day by analyzing the limits of wetting and drying of the soil through the entire study period. Drained upper limits (DUL) and lower limits of water extraction (LL) were determined for each plot and depth; ASW was calculated using the formula proposed by Ritchie (1981):

$$\text{ASW} = 1 - \frac{\text{DUL} - \text{WC}}{\text{DUL} - \text{LL}}$$

The same procedure was carried out to estimate WC and ASW at deeper soil layers in nonirrigated FL seed source plots where deeper probes were installed.

Soil physical parameters

The relationship between θ_v and soil matric potential (Ψ_s) was quantified by constructing soil water release curves using the filter paper method (Deka et al. 1995, Ophori and Maharjan 2000, Marinho and Oliveira 2006) on soils sampled close to each soil moisture probe installation point in each control-FL plots. The relationship between θ_v and Ψ_s was obtained by fitting the model proposed by Warren et al. (2005).

For the same samples used to develop the water release curves, particle size distribution was determined using the hydrometer method (Gee and Bauder 1986). Soil bulk density (ρ_s) was determined using a soil core sampler (0200, Soil Moisture Equipment Corp, Santa Barbara, CA, USA) on samples at <1.0 m depth because of difficulty in extracting intact cores below that depth. Three samples per plot and

depth were extracted, and the average was used for further analysis. Particle size distribution changed with soil depth, increasing clay content as increasing soil depth. For 0.1–0.3, 0.4–0.6, 0.9–1.1, 1.4–1.6 and 1.9–2.1 m depth, the average sand and clay content were 80.7, 76.2, 63.3, 68.4 and 67.4% and 6.8, 11.8, 22.7, 23.8 and 23.8%, respectively. For ρ_s estimations below 1.0 m depth, data were obtained from the Natural Resources Conservation Service-US Department of Agriculture soil survey for the study area (<http://soildatamart.nrcs.usda.gov>, April 2008). Saturated soil hydraulic conductivity (k_{sat}) and unsaturated hydraulic conductivity as a function of θ_v (k_θ) were determined for each plot and depth using a computer program based on pedotransfer functions (Schaap et al. 2001; ROSETTA version 1.2, US Salinity Laboratory ARS-UDA, Riverside, CA, USA).

Water extraction at different soil depths

The local water balance method (Oren et al. 1998, Ewers et al. 1999) was used to estimate the proportion of daily water use associated with daily changes in soil water content for each plot and depth. An expression for infiltration rate (I) was estimated by the equation (Hillel 1998):

$$I = -k_\theta \cdot z$$

For each depth and for days without rain (Ewers et al. 1999), changes in water content (Δ_s) were determined using the formula presented by Oren et al. (1998):

$$\Delta_s = \Delta_\theta \cdot z$$

where Δ_θ is daily change in volumetric water content. Daily water uptake by trees from each layer was computed as the difference between Δ_s and net infiltration (I_{net}), which was calculated as the difference between I from the layer above and I to the layer below. No lateral water movement was assumed (terrain slope <5%).

Tree selection

Sap flux density in the stem xylem was measured on a subset of eight trees per plot in all evaluated plots (96 trees in total) using Granier-type heat dissipation probes (Granier 1985, 1987) from June 2005 to January 2007. The measurement trees were chosen from across the range of tree sizes using ‘quantiles of total’, a stratification scheme which weights the selection of large trees more heavily (Hatton et al. 1995, Martin et al. 1997, Čermák et al. 2004). By selecting measurement trees using this method, a sample size of eight trees per plot was sufficient to control estimation error on sap flow determinations (Hatton et al. 1995).

Leaf area index

Using a Canopy Area Analyzer (LAI2000, Li-Cor Inc., Lincoln, NE, USA), projected leaf area index (LAI) was measured in October 2005. This instrument may not yield

Table 2. Diameter at breast height (DBH) and number of variable length sap flow probes (in parenthesis) installed on FL seed source trees.

	DBH (mm)		
	Small	Medium	Large
Control	167 (6)	196 (7)	230 (8)
Irrigated	172 (6)	209 (7)	271 (8)

Maximum depths reached with six, seven and eight probes were 80, 100 and 120 mm for small, medium and large trees, respectively.

highly accurate absolute estimates of LAI in conifer stands with clumped foliage (Law et al. 2001, Sampson and Allen 1995), but our primary intent was to detect relative differences among treatments. To determine daily LAI for each plot, we fitted a third-order polynomial to an average annual time series of LAI, normalized to the maximum annual LAI value, derived from LAI2000 measurements collected from January 2002 to January 2005 (Samuelson et al. 2008; L. Samuelson, unpublished data). Then we used the polynomial function to extrapolate our point measurements to a daily time series.

Sap flow measurements

Twenty-millimeter-long Granier-type heat dissipation probes were installed on the north side of the stem in all 96 sample trees at 1.8–2.0 m above ground and were used to measure sap flux density (J_s). This method has been used widely and described elsewhere (Lu 1997, Braun and Schmid 1999, Clearwater et al. 1999, Ewers and Oren 2000, Lu et al. 2004).

To account for radial patterns in J_s (Hatton et al. 1990, James et al. 2003, Ford et al. 2004), variable length sap flow probes, as described by James et al. (2002), were installed in a subset of three trees (small, medium and large diameter) on both irrigated and control plots on the FL seed source in one replicate (Table 2). Sample trees were also selected using the stratification method from across the range of tree diameters. Probes were installed at 1.8–2.0 m height and inserted at 10 mm depth intervals, with the tip of the 10 mm probes reaching 10, 20, 30, 40, 60, 80, 100 and 120 mm depths (assumed to measure sap flux density in discrete depths, e.g., 0–10, 10–20, ..., 110–120 mm). The probe for the outermost position was installed on the north side of the stem, and subsequent probes were installed clockwise around the stem at 45° intervals until the depth of the stem pith was reached, which was at 80, 100 and 120 mm for small, medium and large trees, respectively (Table 2).

For the radial profile sample trees, total tree sap flow (Q) was calculated following Hatton et al. (1990), as the sum of all individual sap flow estimations determined for each sensor along the xylem radius, where each 30-min J_s was converted to Q by weighting each sap flux density measured at each depth by the sapwood area containing the annulus

corresponding to each probe. For each time step, sap flow for the whole tree (Q_T) was calculated by summing all individual flows for all n individual annuli in each tree following [Nadezhdina et al. \(2002\)](#):

$$Q_T = \sum_{i=1}^n J_i \cdot A_i$$

where J_i and A_i correspond to sap flux density and area for each individual annulus, respectively. Single-point sensor sap flow was estimated by calculating sap flow for the outermost two rings (Q_{20}), assuming that this estimation corresponded with regular 20 mm Granier-type sap flow probes:

$$Q_{20} = J_1 \cdot A_1 + J_2 \cdot A_2$$

where J_1 and J_2 correspond to sap flux density measured at 10 and 20 mm depth, and A_1 and A_2 are the areas of corresponding annuli. For each day and tree, a relationship between Q_T and Q_{20} was fitted. A strong relationship between Q_{20} and Q_T ($P < 0.001$, $R^2 = 0.93$) was observed in all trees and days analyzed. Changes in the slope of that relationship for different days were highly correlated with changes in environmental conditions affecting sap flow and radial profile in sap flux density. Using multiple linear regression, vapor pressure deficit (D , kPa), global radiation (RAD, W m^{-2}) and θ_v of the top 0.1–0.3 m were incorporated into the model, in order to account for changes in the slope of the relationship between Q_{20} and Q_T . The final model used to transform sap flow values estimated with regular 20-mm Granier-style probes to whole sap flow using radial profile information was: $Q_T = 1.09186Q_{20} + 1.54759A_s + 0.00089165D + 0.00001125\text{RAD} - 0.28217\theta_v$. The model explained 97% of the variation in Q_T . Daily total sap flow per tree was calculated after the summation of all Q_T across all day and multiplying by the corresponding time and volume factors.

In all measured trees, at the same point as the sap flow probes, bark depth was measured with a bark gauge, and sap wood thickness was measured using 5-mm diameter wood cores. Color differences and changes in water content were used to identify sapwood and heartwood boundaries for each tree. During the two seasons of measurements, changes in tree sapwood area (A_s) were determined from monthly measurements of stem diameter at breast height (DBH) and a regression relating DBH to A_s , after log-transformation of both variables ($P < 0.001$, $R^2 = 0.98$). The same linear model was used for all treatments ($P > 0.05$): $\ln(A_s) = 15.347 + 2.185 \ln(\text{DBH})$. This equation was applied to the DBH measured for all trees in the study plots each month, resulting in $A_{s\text{-plot}}$. Plot level sapwood area was then estimated for each plot and day using linear extrapolation between measurement dates. Land-level sapwood area was calculated as $A_{s\text{-plot}}$ multiplied by a scaling factor per plot calculated as the ratio between total land area and total sapwood area per plot. Tree-level sap flow data were integrated to the stand-level transpiration per ground area per plot (E) after summing all eight daily total sap flow per tree per plot and multiply-

ing by land-level sapwood area per plot. Stand transpiration per unit leaf area (E_L) was calculated after dividing E by the corresponding LAI per plot at each time step. Mean daily E was expressed as a proportion of PET for each treatment in order to assess the effect of evaporative demand on E across measurement period.

Canopy conductance

Canopy stomatal conductance for water vapor (G_C , $\text{mmol}_{\text{water}} \text{m}^{-2}_{\text{leaf area}} \text{s}^{-1}$) was calculated as in [Granier and Loustau \(1994\)](#) from the inverted Penman–Monteith equation, using E_L transformed to corresponding units and meteorological data as inputs ([Monteith and Unsworth 2007](#)). To reduce error due to instrument limitations on relative humidity measurements, G_C was calculated only when $D \geq 0.6$ kPa ([Ewers and Oren 2000](#)). A reference G_C ($G_{C\text{ref}}$) was calculated at $D = 1$ kPa ([Granier et al. 1996](#), [Oren and Pataki 2001](#)). The response of G_C to D was quantified using boundary line analysis ([Schäfer et al. 2000](#), [Ewers et al. 2001a](#)). The upper boundary line for each plot was derived by binning G_C data into 0.2 kPa D intervals (from 0.6 to 4.6 kPa) and then selecting the highest 95% G_C for any interval. For each plot, all upper G_C values in each D interval were related to the natural logarithm of D ([Granier et al. 1996](#)):

$$G_C = G_{C\text{ref}} - m \cdot \ln D$$

where m is the slope of the regression fit, representing stomatal sensitivity to D (i.e., $dG_C/d\ln D$). Using diurnal values of G_C ([Phillips and Oren 1998](#)), diurnal average G_C ($G_{C\text{day}}$) was calculated. Leaf-specific $G_{C\text{day}}$ ($G_{C\text{la}}$) was calculated dividing $G_{C\text{day}}$ by daily leaf area of each plot. For the same 6-month period used for soil water extraction analysis, half-hourly G_C data were conditionally selected to minimize photosynthetically active radiation (PAR) or D constraints on G_C ($\text{PAR} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $D < 1.4$ kPa). Relative daily canopy conductance ($G_C\%$) was calculated as daily means of control plots normalized by daily means of irrigated (well-watered) $G_{C\text{la}}$ for each seed source within each replicate (Figure 5), and using a logistic model, $G_C\%$ was fitted to available soil water ([Lecoeur and Sinclair 1996](#)). It should be noted that there is a degree of uncertainty in G_C absolute values due to potential errors in LAI determinations.

Whole-tree hydraulic conductance

Whole-tree sapwood-specific hydraulic conductance ($K_{S\text{-wt}}$, $\text{mol}_{\text{water}} \text{m}^{-2}_{\text{sapwood}} \text{s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) was computed following the regression technique ([Wullschlegel et al. 1998](#)) and calculated as ([Phillips et al. 2002](#), [Franks 2004](#)):

$$K_{S\text{-wt}} = \frac{E_s}{\Psi_l - \Psi_s - \rho_w \cdot g \cdot h}$$

where E_s is transpiration rate per unit sapwood area ($\text{mol}_{\text{water}} \text{m}^{-2}_{\text{sapwood}} \text{s}^{-1}$), Ψ_l and Ψ_s are leaf and soil water potentials at 0.1–0.3 m depth (MPa), respectively, ρ_w is the

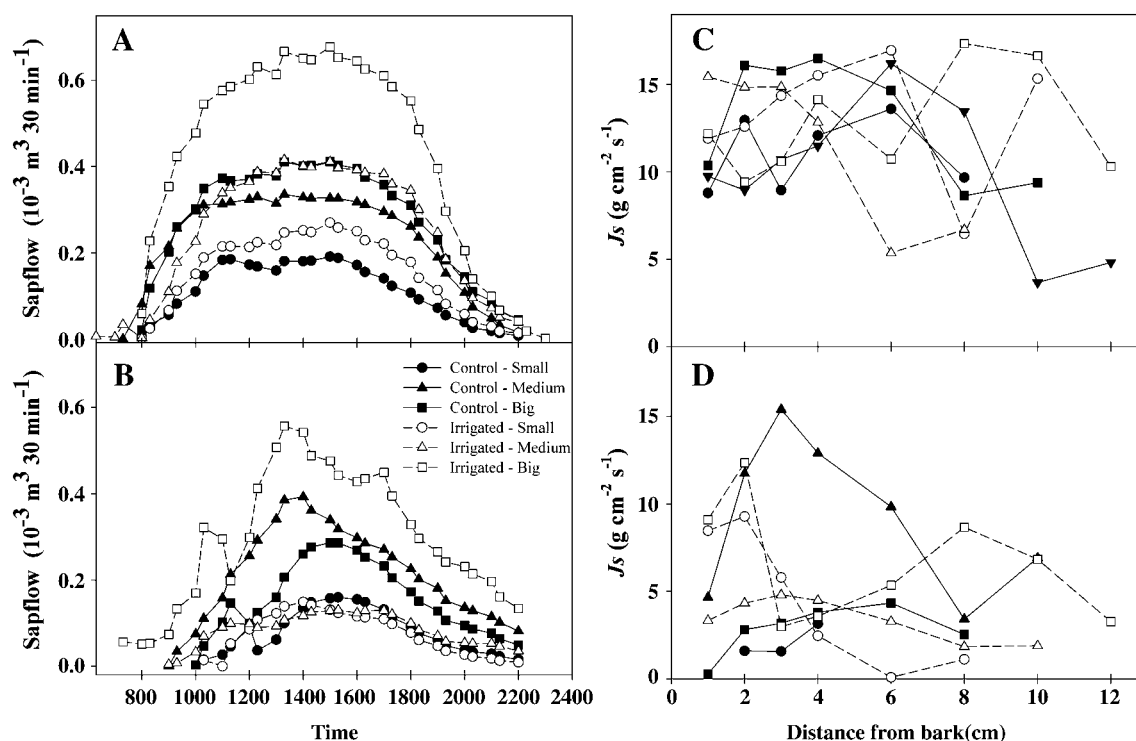


Figure 2. Diurnal variation in weighted sap flow (A, B) and radial profile in sap flux density at noon (C, D) for six selected trees of FL seed source on two contrasting days during 17 August 2006 (A, C) and 15 November 2006 (B, D).

density of liquid water (kg m^{-3}), g is the acceleration due to gravity (m s^{-2}) and h is tree crown height (m). Tree height was measured on December 2005, 1 month after water potential measurements (15 November 2005). As h is the vertical distance from soil to sites of evaporation in crown needles, and sampling tissue for water potential measurements was extracted from the upper fifth of the crown in branches fully exposed to light, h was assumed to be four-fifths of total tree height. Ψ_1 was measured using a portable pressure chamber (PMS 1000, MPS Instrument Co., Corvallis, OR, USA) on one shoot tip consisting of the terminal bud plus 20 to 30 fascicles from pre-dawn (5:30–6:00) to late afternoon at 2-h intervals, completing four to five measurements per tree throughout the day. Samples were collected on a subset of four trees per plot (on which sap flow was measured) on all 12 measurement plots. Each measurement was completed within 3 min after shoot excision, covering the sample with wet towels inside a plastic bag and stored inside an insulated box to minimize desiccation. Shoot sampling was carried out using a self propelled telescopic lifting machine and pole pruner. Hydraulic conductance was then calculated for each of the four measurement trees per plot which were then averaged to the plot level for statistical analysis.

Foliar analysis

Foliar sampling was carried out in December 2005 on the same 48 trees measured for water potential in November 2005. Needles from the last flush with fully elongated nee-

dles were collected by excising tips of branches from the top fifth of the crown and were stored on ice for transport to the lab. Carbon isotope composition ($\delta^{13}\text{C}$) was measured using a mass spectrometer, and nitrogen concentration (N) was measured using a Europa Scientific ANCA-SL Stable Isotope Analysis System (Europa Scientific, Crewe, UK) at the Cornell Boyce Thompson Institute Stable Isotope Laboratory. All-sided specific leaf area (SLA) was determined using the ratio between surface area and dry weight of needles. Individual needle surface area was calculated according to Murthy and Dougherty (1997) and Niinemets et al. (2001) from needle radius and length measured with a $\times 10$ scaled magnifier and a digital caliper (CD-6, Mitutoyo, Kawasaki, Japan), respectively, on 10 needles per tree. After surface area was determined, the needles were oven-dried for 48 h at 75°C and weighed to the nearest 0.0001 g (XA-100, Denver Instruments, Denver, CO, USA).

Statistical analysis

Analysis of variance (ANOVA) was used to analyze effects of irrigation and seed source in water relation traits, including Bonferroni adjustments for differences in least square means (PROC MIXED, SAS Inc., Cary, NC, USA). The linear model for the analysis was:

$$Y_{ijk} = \mu + b_i + I_j + F_{k(j)} + (IF)_{k(j)} + (bI)_{ij} + (bF)_{ik(j)} + (bIF)_{ik(j)} + \varepsilon_{ijk}$$

where Y_{ijk} is the parameter value of the plot of the k th seed source nested in the j th irrigation treatment in the i th replicate; $i = 1, 2$ and 3 for replications; $j = \text{control and irrigated}$; $k = \text{FL and SC}$; and

μ : population mean,

b_i : random variable of replication $\sim \text{NID}$, normally and independently distributed $(0, \sigma_b^2)$,

I_j : fixed effect of irrigation (control or irrigated),

$F_{k(j)}$: fixed effect of seed source (FL or SC) nested within irrigation,

$(IF)_{k(j)}$: fixed effect of irrigation \times seed source (irrigation) interaction,

$(bI)_{ij}$: random variable for replication \times irrigation interaction $\sim \text{NID}(0, \sigma_{bI}^2)$,

$(bF)_{ik(j)}$: random variable for replication \times seed source (irrigation) interaction $\sim \text{NID}(0, \sigma_{bF}^2)$,

$(bIF)_{ik(j)}$: random variable for replication \times irrigation \times seed source (irrigation) interaction $\sim \text{NID}(0, \sigma_{bIF}^2)$,

ijk : error term $\sim \text{NID}(0, \sigma^2)$

Repeated measures analysis was used to analyze time series data.

Results

Sap flow

The relationship between J_s and distance from bark had no distinctive shape, changing the pattern of variation in J_s during the year, depending on environmental conditions and tree size (Figure 2). For example, on summer days with high D and θ_v (as 17 August, Figure 1), diurnal variation in J_s for maximum conductivity xylem zones was similar between different tree sizes, with and without irrigation. However, late in the season, on days when D was low and θ_v on control plots was also low (as 15 November, Figure 1), this pattern varied depending on tree size and irrigation treatment (Figure 2). In terms of radial variation in J_s , for the same example days, large trees reached maximum midday J_s between 20 and 60 mm xylem depth for nonirrigated trees between 80 and 100 mm xylem depth for irrigated trees on 17 August and 15 November, respectively (Figure 2).

After correcting sap flow estimations using Granier-type probes with the model that accounts for radial profile and environmental conditions, sap flow was determined for each plot for all the measurement period (June 2005 to January 2007). After the irrigation treatment started (June 2005), θ_v and E time series clearly separated for control and irrigated treatments in both seed sources (Figure 3). The maximum daily E was similar for both seasons, reaching a maximum of 4.3 mm day^{-1} on irrigated plots. In 2006 on control plots, the maximum E only reached 2.6 mm day^{-1} . On rain-fed control plots, E was highly dependent on rainfall events (Figures 3 and 5); monthly average daily E was 1.8 and 3.2 mm day^{-1} for summer months on control and irrigated

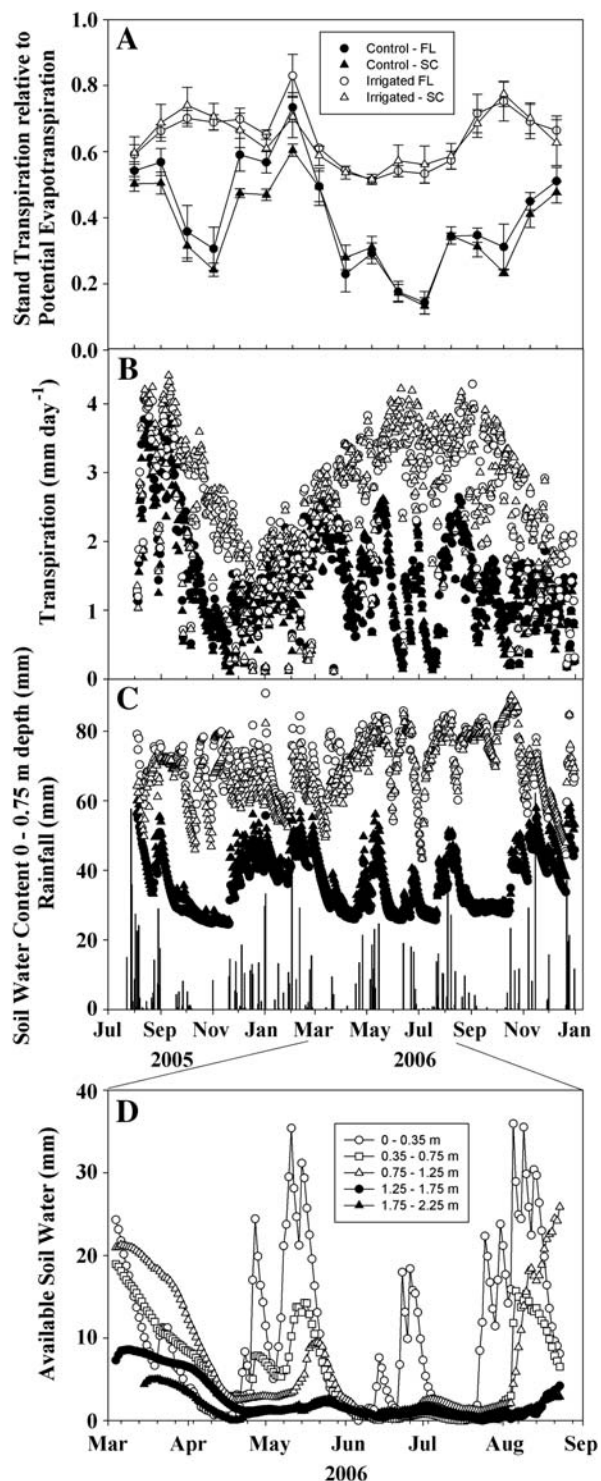


Figure 3. Seasonal pattern in stand transpiration to potential evapotranspiration ratio (A), stand transpiration (B), soil water content and rainfall (C) for loblolly pine stands under irrigation treatment (control and irrigated) including two different seed sources (FL and SC) and available soil water for five different soil layers on nonirrigated FL seed source plots for a 6-month period in 2006 (D). Each symbol is the mean of three replicate plots.

Table 3. Mean diameter at breast height (DBH), height, basal area (BA) and leaf area index (LAI) for irrigation \times seed source (SS) treatments.

	Control		Irrigated		$P > F^*$		
	FL	SC	FL	SC	Irrigation	SS	Irrigation \times SS
DBH (mm)	185	189	203	207	0.026	0.018	0.527
Height (m)	13.8	14.5	15.8	16.4	< 0.01	0.019	0.895
BA ($\text{m}^2 \text{ha}^{-1}$)	31.2	29.4	35.8	36.1	0.0452	0.525	0.406
LAI ($\text{m}^2 \text{m}^{-2}$)	4.2	4.5	4.6	4.4	0.348	0.597	0.083

Means at Age 10 when the study started (June 2005), LAI was measured in October 2005.

FL, Florida seed source; SC, South Carolina Coastal Plain seed source. * P -values using mixed model procedure for split-plot design.

plots, respectively. The average annual E during the 2005 measurement season (163 days) was 248 and 369 mm for control and irrigated plots, respectively, corresponding to a 49% increase ($P = 0.03$ for irrigation effect). There was no effect of seed source ($P = 0.29$) and no seed source by irrigation interaction ($P = 0.09$). In 2006, irrigated plots transpired 89% more than control plots (490 versus 930 mm for control and irrigated plots, respectively); there was no effect of seed source ($P = 0.68$) or interaction of seed source with irrigation treatment ($P = 0.41$). Total rainfall during measurement seasons 2005 and 2006 was 463 and 902 mm, respectively, resulting in average total E for control plots representing 53.5 and 54.3% of total rainfall for each season. Assuming an average daily irrigation input of 6.25 mm day^{-1} , and discounting a total of 26 and 29 days of malfunctioning system during seasons 2005 and 2006, respectively, average total E for irrigated plots represented 28.0 and 31.0% of total water input (rainfall plus irrigation) for seasons 2005 and 2006, respectively.

Monthly daily average transpiration rate (E_{day}) was positively correlated to G_{Cday} in control plots ($P < 0.001$, $R^2 = 0.72$) but not correlated to G_{Cday} in irrigated plots (data not shown). Using multiple linear regression, including monthly average total daily global radiation ($\text{W m}^2 \text{day}^{-1}$), monthly average daylight D (kPa) and monthly average daily soil water content up to 0.35 m, variation in E_{day} in control plots was explained principally by total daily radiation (partial $R^2 = 0.859$; $P < 0.001$) and to a much lesser extent by G_{Cday} , soil water content and D (partial $R^2 = 0.070$, 0.014 and 0.008, respectively); under irrigated conditions, variation in E_{day} was explained only by changes in radiation ($R^2 = 0.98$; $P < 0.001$). After pooling all monthly averages of control and irrigated plots, variation in E_{day} was explained by changes in soil water content (partial $R^2 = 0.92$; $P < 0.001$) and to a lesser extent by radiation (partial $R^2 = 0.03$; $P < 0.001$); the model also indicates that there was a slight, but significant, effect of seed source, decreasing E_{day} by 0.12 mm day^{-1} for the SC trees under the same soil moisture and radiation conditions.

When monthly total E was expressed as a proportion of monthly total PET (E/PET), a strong effect of time (month) and irrigation ($P < 0.001$) but no effect of seed source ($P = 0.49$) was observed on E/PET . Average E/PET across measurement period was 0.39 and 0.65 for nonirrigated and irrigated plots, respectively (Figure 3A). Interaction between

E/PET and time was significant ($P < 0.001$) for each irrigation treatment. There were differences in E/PET between control and irrigated plots during October and November 2005 and from April to November 2006 ($P < 0.001$). Within irrigated plots, changes in E/PET were highly negatively correlated to total incoming radiation ($P < 0.001$; $r = -0.94$; data not shown), reaching higher values between 0.70 and 0.76 during September and October and showing lower values between 0.50 and 0.55 from April to July. Stomatal regulation due to high D during summer days reduced E away from PET even when there was no restriction in soil water supply.

Leaf area index

No differences between treatments were observed in LAI measured on 15 October 2005 (Table 3). Average projected LAI for irrigated and control plots was 4.35 and $4.5 \text{ m}^2 \text{m}^{-2}$, respectively ($P = 0.35$); at the seed source level, LAI for FL and SC seed sources was 4.4 and $4.5 \text{ m}^2 \text{m}^{-2}$, respectively ($P = 0.59$).

Soil moisture

Soil water content was highly affected by irrigation treatment (drip-irrigation treatment in 2005, which ran from June to November; during season 2006, irrigation started in March and finished in October). On nonirrigated plots, the 0- to 0.35-m soil layer remained at the minimum extractable soil water values for long periods in both seasons (Figure 3C); seasonal θ_v average for control and irrigated plots, including nonsystem functioning periods, was 10.9 and 17.7% in 2005 and 11.3 and 17.1% in 2006, respectively.

Relative water use from individual layers in the upper 2 m was determined from late February to late August 2006 for the FL seed source only on nonirrigated plots (Figure 3D). Analysis of soil water movement and transpiration rate indicates that, across the season, daily transpiration rate matched with soil water extraction up to 2.0 m depth ($P = 0.11$; paired t -test) on nonirrigated plots. Average daily water uptake from the 0- to 0.75-m depth corresponded to 92 and 73% of the average daily transpiration rate for irrigated and control plots, respectively. Day-to-day variation in transpiration rate followed a similar pattern to changes in ASW in the upper 0.35 m of soil (Figure 3B and C). A little more than half

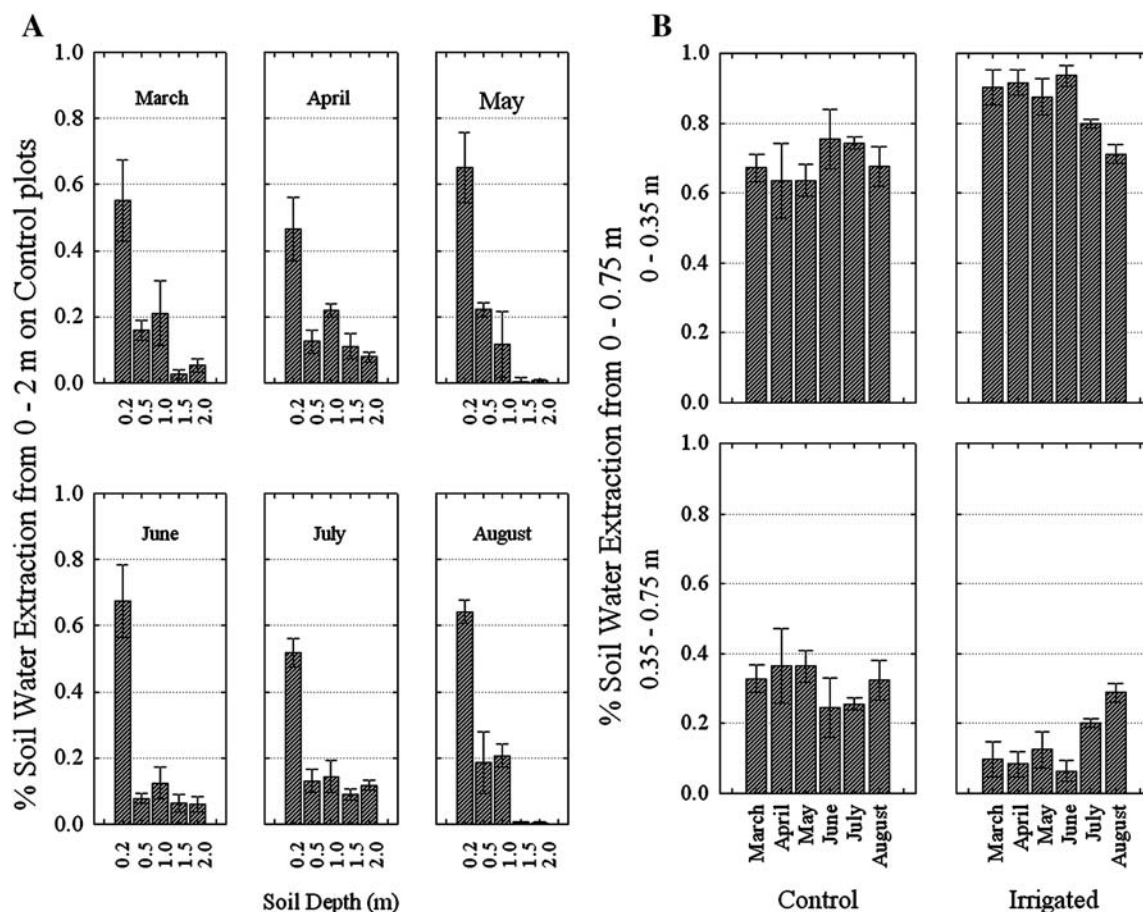


Figure 4. Proportion of soil water extraction used for transpiration from the 0–2 m soil depth on nonirrigated plots (A) and from 0–0.75 m depth on control and irrigated plots for FL seed source plots (B).

of the water used for transpiration was taken from the upper 0.35 m depth, averaging across the season 58, 15, 17, 5 and 5% for the 0–0.35, 0.35–0.75, 0.75–1.25, 1.25–1.75 and 1.75–2.25 m depths, respectively (Figure 4A). Interaction between relative uptake from each layer and time (month) was significant only for water uptake at 0–0.35 m depth between April and June ($P = 0.012$).

In order to investigate the effect of irrigation, the same analysis was performed for irrigated and control plots, but only for 0.1–0.3 and 0.4–0.6 m depth probes, because no deeper sensors were installed on irrigated plots. From the amount of water extracted from the first 0.75 m, 67 and 86% were taken from the upper 0.35 m for control and irrigated plots, respectively (Figure 4B). There was no significant time \times irrigation interaction ($P > 0.05$), indicating that the average extraction pattern did not change during the evaluation period.

Canopy conductance

Canopy conductance to water vapor was highly affected by the irrigation treatment (Figure 5, $P = 0.0001$ and 0.0099 for seasons 2005 and 2006, respectively). There was no irrigation \times seed source interaction in average G_C ($P > 0.28$ in all cases and seasons). For each year, there was an irrigation

\times time interaction ($P < 0.001$) associated with interruptions in the irrigation treatment.

There was irrigation \times seed source interaction in the response of G_C to vapor pressure deficit (Table 4). Under water-deficit conditions (control), G_C sensitivity to D ($dG_C/d\ln D$) and G_C at $D = 1$ kPa (G_{Cref}) for the South Carolina Coastal Plain seed source (SC) were smaller than the north Florida source (FL) ($P = 0.01$ and 0.03 , respectively). Under non-water-limited conditions (irrigated), the seed sources were not different in $dG_C/d\ln D$ and G_{Cref} ($P = 0.08$ and 0.44 , respectively). The FL seed source had the same $dG_C/d\ln D$ and G_{Cref} under control and irrigated conditions ($P = 0.97$ and 0.81 , respectively). There were differences between seed sources and irrigation treatment in D_{max} (D when G_C equals zero). G_{Cmin} , the minimum G_C at any given D above 2 kPa, was higher on irrigated than on control plots ($P < 0.001$). At high D values (above 2 kPa), the minimum G_C observed was always higher on irrigated than on control plots ($P < 0.001$).

Whole-tree hydraulic conductance

There was a strong effect of irrigation and no effect of seed source or their interaction on average K_{S-wt} , Ψ_{pred} and Ψ_{min} (Table 4). Control and irrigated treatments had average K_{S-wt}

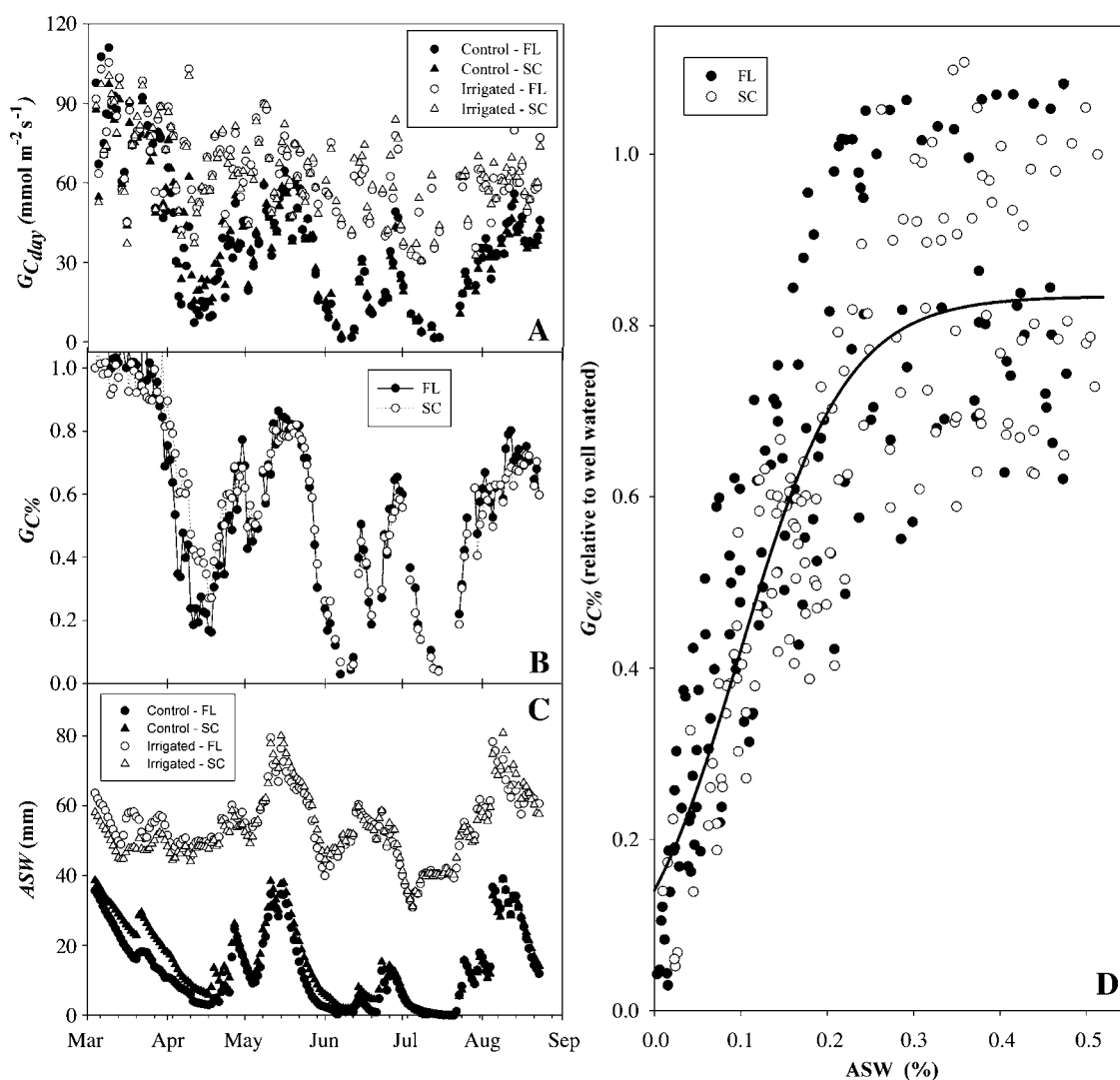


Figure 5. (A) Mean daily canopy conductance (G_{Cday}), (B) normalized canopy conductance ($G_{C\%}$), (C) available soil water (ASW) for 0–0.75 m depth and (D) the relationship between ASW and normalized canopy conductance for a 6-month period in 2006 for loblolly pine under irrigation treatment (control and irrigated) for two different seed sources (FL and SC).

Table 4. Mean $dG_C/d\ln D$, G_{Cref} , G_{Cmin} , D_{max} , K_{S-wt} , Ψ_{pred} , Ψ_{min} , $\Delta\Psi$, SLA, $N\%$ and $\delta^{13}C$ for irrigation \times seed source (SS) treatments.

	Control		Irrigated		$P > F^*$		
	FL	SC	FL	SC	Irrigation	SS	Irrigation \times SS
G_{Cref}	136.57	111.59	135.98	148.64	0.309	0.188	0.008
$-dG_C/d\ln D$	82.70	66.62	79.67	83.80	0.572	0.158	0.042
D_{max}	5.24	5.34	5.69	5.96	0.230	0.484	0.737
G_{Cmin}	0.72	1.14	15.89	15.97	0.0002	0.772	0.845
K_{S-wt}	0.843	0.824	2.918	2.825	0.029	0.779	0.855
Ψ_{pred}	-1.172	-1.122	-0.677	-0.660	0.021	0.111	0.366
Ψ_{min}	-1.939	-1.916	-1.404	-1.389	<0.0001	0.537	0.889
$\Delta\Psi$	0.766	0.793	0.727	0.729	0.522	0.727	0.764
SLA	109.48	100.62	108.20	100.97	0.108	0.786	0.635
$N\%$	1.36	1.42	1.45	1.52	0.005	0.024	0.836
$\delta^{13}C$	-29.57	-29.07	-30.12	-29.62	0.041	0.036	0.997

FL, Florida seed source; SC, South Carolina Coastal Plain seed source. * P -values using mixed model procedure for split-plot design.

of 0.83 and 2.87 mol m⁻² s⁻¹ MPa⁻¹, respectively. Average Ψ_{pred} for control and irrigated plots was -1.15 and -0.67 MPa, respectively. Average Ψ_{min} on the control plots reached as low as -1.92 MPa, while on irrigated plots Ψ_{min} was -1.39 MPa. The maximum leaf water potential gradient ($\Delta\Psi$, MPa), calculated as the difference between Ψ_{min} and Ψ_{pred} , was not different between irrigation and seed source treatments (Table 4).

Foliar analysis

There was a strong effect of irrigation and seed source, but no interaction, on foliar *N* concentration and $\delta^{13}\text{C}$ (Table 4). There was no difference in all-sided SLA between treatments. Irrigated trees had higher foliar *N* concentration ($P = 0.005$) and higher discrimination against ^{13}C (more negative $\delta^{13}\text{C}$; $P = 0.041$) than nonirrigated trees. At a genetic level, the SC source showed higher *N* concentration and less discrimination against ^{13}C than FL source ($P = 0.02$ and 0.03 , respectively).

Discussion

Loblolly pine has a large natural distribution range, a high degree of genetic variation, and significant phenotypic plasticity (Schultz 1997, Sierra-Lucero et al. 2002, Martin et al. 2005). Breeding programs and genetic deployment strategies are relatively sophisticated for this species (McKeand et al. 2003), but it is uncertain to what degree our current knowledge of family-level performance will translate to future climate scenarios. This study was designed to increase our understanding of how stand-level water relations of loblolly pine taxa originating from contrasting environments respond to soil water availability. Mechanistic insight into water relations variation among taxa should be helpful as managers consider how to alter breeding and deployment programs for changing climate conditions.

Phillips et al. (1996) reported that daily J_s in the outer 20 mm of xylem was 59% larger than at 20–40 mm depth in 12-year-old loblolly pine. Ford et al. (2004) found a Gaussian shape in the J_s radial profile in mature loblolly pine, with maximum midday J_s occurring in the outer 4 cm of sapwood and decreasing towards the heartwood. In contrast, Jimenez et al. (2000) also reported that radial profiles of sap flow were highly variable in all measured laurel trees, not finding distinguishable groups based on quantitative differences, and Wullschlegel and King (2000) found no relationship between sapwood thickness and fraction of functional sapwood in yellow poplar trees. The nonuniform changes in radial profile in J_s described in Figure 2 were similar to those presented by Nadezhdina and Čermák (2000). They reported that after changes in θ_v , the radial profile in J_s changed nonhomogeneously across the radius, decreasing more drastically, as soil drought, in zones of higher J_s (see Figure 3 on Nadezhdina and Čermák 2000). Phillips et al. (1996) also reported

changes in radial profile in sap flow due to changing soil moisture. These findings are indicators of interactions between environment and radial profile in J_s , related to differences in vulnerability to cavitation (Domec and Gartner, 2003) or to differences in water potential gradient (Domec et al. 2005) at different depths into the conductive xylem. This evidence supports our approach not to use a single model that only accounts for differences in radial profile at mid-day at a particular time.

The maximum E was similar for both measurement years, reaching a maximum as high as 4.3 mm day⁻¹ for irrigated plots; this value is concordant with Samuelson and Stokes (2006), who reported for the same plots at age 5 a maximum transpiration rate of 3.9 mm day⁻¹. On irrigated plots, regression analysis indicated that E_{day} was controlled primarily by PAR, while in the control treatment E_{day} was a function of G_{Cday} , θ_v and D in addition to PAR. These relationships are consistent with the Jarvis and McNaughton (1986) concept of decoupling, which states that as the magnitude of G_c becomes larger relative to boundary layer conductance, transpiration will become increasingly dependent on radiation and less dependent on, or less 'coupled' to, D . While needle-leaved conifers are generally considered to be highly coupled due to their relatively low stomatal conductance and high boundary layer conductances (Jarvis and McNaughton 1986, Ewers and Oren 2000), variation in the relative size of these conductances in response to the environment will cause temporal variation in coupling (Wullschlegel et al. 2000, Martin et al. 2001, Bracho et al. 2008).

For both 2005 and 2006, most of the water used for transpiration (58%) was extracted from the upper 0.35 m soil depth under rain-fed conditions. On average, only 10% of total transpiration was sustained from water below 1 m depth. This result is highly variable, depending on site characteristics, but several authors confirmed the trend that most of the water extraction in loblolly pine plantations comes from upper soil layers (Oren et al. 1998, Ewers et al. 1999 and Retzlaff et al. 2001a). Average relative water uptake from 0 to 0.35 m depth showed interaction with time only between April and June ($P = 0.012$), and for the rest of soil layers and periods evaluated, there was no time effect on relative water uptake, meaning that the proportion of water uptake used for transpiration was constant across the season.

Using water release curves developed for each soil layer, Ψ_s for soil below 1 m was always below -1.2 MPa on all 173 days where Ψ_s was estimated, reaching values below -1.5 MPa from April until late August (data not shown). Hacke et al. (2000) measured vulnerability to cavitation in loblolly pine roots, indicating that at -1.5 MPa, 50 and 75% of loss in conductivity due to cavitation is reached for loam and sandy soils, respectively. Ewers et al. (2000) reported 80% loss of conductivity in roots of 14-year-old loblolly pine when xylem water potential reached -1.5 MPa. Assuming similar patterns of cavitation vulnerability on our site, we can surmise that loss of conductivity was much higher than 50% during most of the season for roots found below

100 cm depth. Several authors have indicated that most of fine roots biomass is confined to top 0.2–0.5 m soil (Ewers et al. 2000, Hacke et al. 2000, Retzlaff et al. 2001b), so the small amount of fine roots present in loblolly pine stands below 1 m, together with the low water potential present during most of the season, can help to explain the soil water extraction pattern at this site. Throughout the measurement period, the frequency of days when Ψ_s was below -1.2 MPa on the rain-fed plots was 50, 49 and 58% for 0.1–0.3, 0.4–0.5 and 0.9–1.1 m soil depth, respectively. Taking into account the values of vulnerability to cavitation reported by Ewers et al. (2000) and Hacke et al. (2000), it is clear that trees in the rain-fed treatments experienced substantial water stress during the study.

Canopy conductance to water vapor was highly affected by soil water availability (Figure 5). This response has been widely reported for loblolly pine at the leaf level under greenhouse (Bongarten and Teskey 1986, Teskey et al. 1986) and field-growing conditions (Samuelson 1998) and also at the canopy level (Oren et al. 1998).

There was a significant interaction between water availability and seed source ($G \times E$) in the response of G_C to D . This $G \times E$ interaction implies that under water-limited conditions, the SC seed source trees had stronger stomatal control than FL trees, but this difference was not present when water was not limiting. In an analysis of four provenances of loblolly pine, including Atlantic Coastal Plain (ACP, geographically equivalent to the SC seed source) and Central Florida (CF) sources, Sierra-Lucero et al. (2002) reported that, although CF yielded 10% more average volume per land area than ACP sources at age 10, there was a large $G \times E$ interaction of families within the Florida provenance, and ACP families were more stable across sites than CF. In a study of physiological traits of loblolly pine seedlings comparing ACP families with xeric families from East Texas carried out under dry field conditions, Grissom and McKeand (2001) found no differences in midday light saturated net photosynthesis but significant differences in midday stomatal conductance (g_s); ACP families had lower g_s and higher intrinsic water use efficiency than xeric provenance. Differences in G_C sensitivity to D between SC and FL under water-limited conditions can be related to the fact that FL trees originate in an environment with more summer rainfall, less summer moisture deficit and extended growing season compared to the SC seed source (Table 1). When they are exposed to low soil moisture conditions, the FL seed source shows less stomatal regulation to D compared with well-watered conditions. At D values above 2 kPa, the minimum G_C observed was always higher on irrigated than on control plots ($P < 0.001$). This implies that, while water availability does not affect G_C sensitivity to D or G_{Cref} , when PAR and temperature restrict G_C , stomata remain slightly open if θ_v does not reach a critical value. These differences in productivity and physiological response to drying soil between SC and FL are analogous to previous observations that loblolly pine from very dry seed sources (such as east Texas or Arkansas/

Oklahoma) had greater drought resistance but lower productivity than Atlantic Coastal Plain sources (Wells and Wakeley 1966, Wells 1983, Lambeth et al. 1984). However, the differences between SC and FL are more subtle and may allow flexibility in deploying seed sources in future, drier climates without the large sacrifices in productivity that would attend deployment of seed from very dry source areas.

The sensitivity of G_{Cday} to soil water content was not different between seed sources, and the same response curve can be used for both seed sources (Figure 5D) because all parameters of the logistic model were not significantly different ($P > 0.40$ for all three parameters). The response of canopy conductance to soil moisture was expressed in relative terms using a logistic model $G_C\% = (0.834)/(1 + (4.935) * \exp(-(16.147)*ASW))$. In our study, G_C response to θ_v was a sigmoid shape with two characteristic response zones. When $ASW > 30\%$, there was no effect on G_C ; when $ASW < 30\%$, G_C decreased linearly until it reached minimum values between 2 and 18% of well-watered plots and when ASW was zero (Figure 5D). This nonzero y -axis intercept was explained because ASW was calculated from the upper 0.75 m soil depth, from where 73 and 90% of transpiration water on control and irrigated plots, respectively, so water uptake could theoretically continue if ASW in the upper 0.75 m reaches zero. Similar threshold responses of transpiration or leaf or canopy conductance to ASW have been reported for a wide range of species, including pea (Lecoeur and Sinclair 1996), *Arabidopsis* and maize (Wahbi and Sinclair 2007), loblolly pine (Oren et al. 1998) and diverse perennial tree species (Sinclair et al. 2005). Bréda et al. (1993) reported for mature *Quercus petraea*, a drought-resistant species, a strong decrease in relative evapotranspiration when ASW was below a threshold of 40%, but transpiration decreased linearly only when ASW was below 15%. Ewers et al. (2001b) reported for a 12-year-old loblolly pine plantation no differences in G_C response to decreasing θ_v between irrigated and control trees. Our findings reflect the soundness of the response of canopy conductance to changes in θ_v .

Whole-tree sapwood-specific hydraulic conductivity (K_{S-wt}) was similar to those reported by Samuelson and Stokes (2006) for the same study site at age 4.5 years. No differences in K_{S-wt} , Ψ_{pred} and $\Delta\Psi$ were found at that time between control and irrigated plots, suggesting that the treatment differences found in our study were caused by in situ xylem cavitation rather than tracheid morphological changes resulting from higher water availability. After expressing the difference between K_{S-wt} of irrigated and control plots relative to K_{S-wt} of irrigated plots as a surrogate of percentage loss of conductivity (PLC, %) (Tyree et al. 1992) and using Ψ_{pred} as an index of Ψ_s of rooting zone, a strong relationship ($P = 0.008$) appears between PLC and Ψ_{pred} (Figure 6B). For the range of data, reductions in Ψ_{pred} explained 86% of the variability in PLC. When Ψ_{pred} for control plots reached -1.3 MPa, K_{S-wt} was only 20% of well-watered trees; this result is comparable with vulnerability curves measured on roots of the same species by Ewers et al. (2000), where PLC

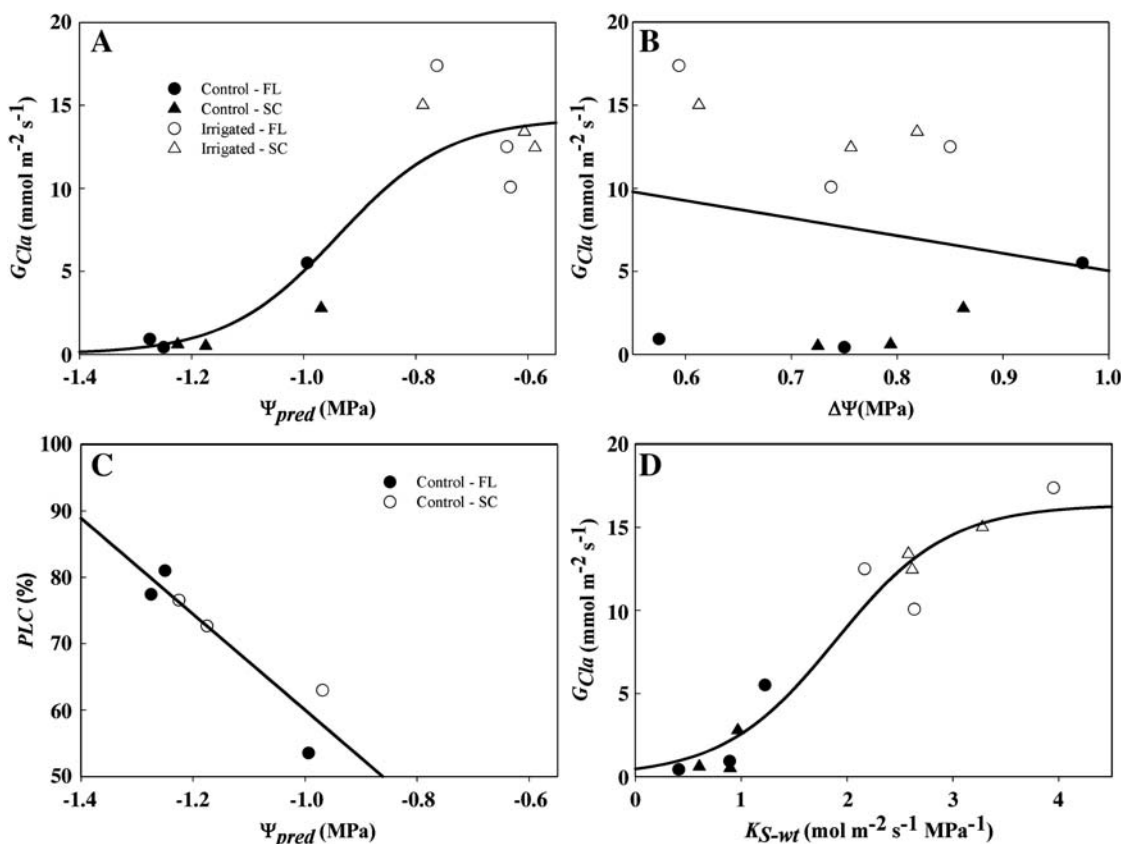


Figure 6. Relationships between mean daily canopy conductance (G_{Cla}) and pre-dawn water potential (Ψ_{pred}) (A), maximum daily water potential gradient ($\Delta\Psi$) (B) and whole-tree sapwood-specific hydraulic conductance (K_{S-wt}) (D) for two loblolly pine seed sources (FL and SC) under control and irrigation treatments. The loss of conductivity of control in relation to irrigated plots (PLC) is presented including both seed sources (C). All data were calculated with data collected the same day (15 November 2005).

was 80% at -1.5 MPa. In a recent study on 4-year-old loblolly pine, Samuelson et al. (2008) concluded that irrigation had no influence on hydraulic traits. It should be noted that Ψ_{pred} in the Samuelson et al. (2008) study was not different between control and irrigated plots with no significant time \times irrigation interaction (Ψ_{pred} measured between June and August). This result implies that irrigation had no effect on soil moisture in their study, likely due to high rainfall during the summer. Under these conditions, we would anticipate little or no difference in water relation traits between treatments.

The maximum transpiration-induced water potential gradient from roots to shoots ($\Delta\Psi$) was relatively constant across treatments ($P = 0.52$) and seed source ($P = 0.72$), averaging 0.75 MPa. This relatively constant $\Delta\Psi$ is similar to that reported by Samuelson and Stokes (2006) and Samuelson et al. (2008), which was maintained across treatments during summer months on an average value of 0.86 and 0.75 MPa, respectively. On the other hand, minimum daily xylem water potential (Ψ_{min}) was different between control and irrigated trees ($P < 0.001$), being, on average, 0.5 MPa lower for control trees. This response in leaf water potential corresponds to that presented by Franks et al. (2007) as 'isohydrodynamic', where a strong stomatal control maintains relatively constant

$\Delta\Psi$ (Table 4; $P = 0.52$) but at the same time allowed Ψ_{leaf} to fluctuate dramatically in synchrony with Ψ_s (Table 4; between control and irrigated plots, $P = 0.02$ and < 0.001 for Ψ_{pred} and Ψ_{min} , respectively). For the day of leaf water potential measurement, average canopy conductance per unit leaf area (G_{Cla}) was highly correlated with Ψ_{pred} and K_{S-wt} , following a sigmoid curve shape (Figure 6A and D). Teskey et al. (1986) reported that g_s declined slightly until xylem pressure potential reached a threshold point of ~ -1.0 MPa, after which g_s declines rapidly and total stomatal closure occurs at -2.0 MPa; visual analysis of their results indicate that $\sim 50\%$ of loss of g_s is reached around -1.2 MPa. In our study, above $\Psi_{pred} \sim -1.1$ MPa, G_{Cla} increased linearly until plateauing above -0.6 MPa (Figure 6A). The relationship between G_{Cla} and K_{S-wt} follows the same pattern, with negligible increment in G_{Cla} if K_{S-wt} is higher than, ~ 3.0 mol m⁻² s⁻¹ MPa⁻¹. G_{Cla} was very stable within water availability treatments and was not correlated with $\Delta\Psi$ (Figure 6B; $P = 0.61$).

Carbon isotope composition ($\delta^{13}C$) is an indicator of the relationship between stomatal conductance and photosynthesis rate (Farquhar et al. 1989). Increases in $\delta^{13}C$ (less negative value) can be a result of lower stomatal conductance, higher photosynthetic capacity or both. $\delta^{13}C$ was highly affected for both irrigation and seed source; this response to

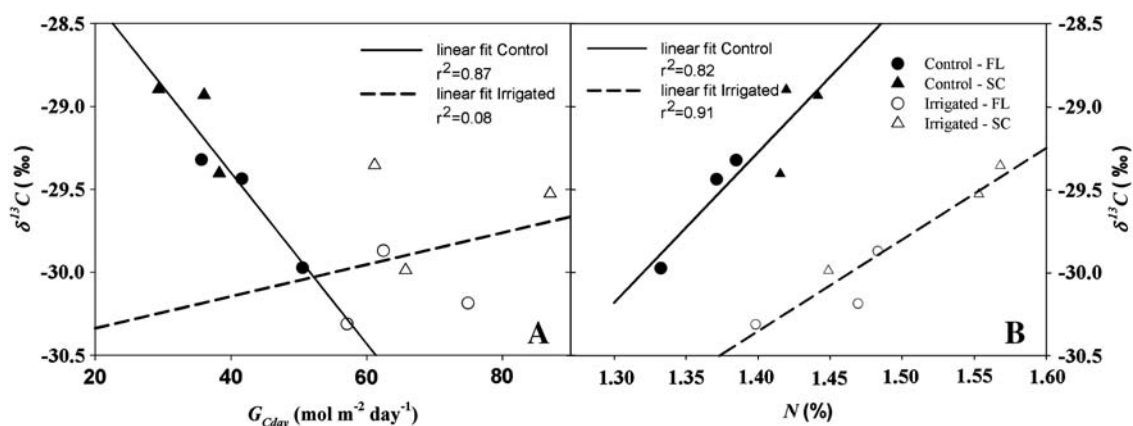


Figure 7. Relationships between mean daily canopy conductance (G_{Cla}) (A) and foliar nitrogen concentration (N) (B) with $\delta^{13}C$ for control and irrigated plots.

water availability was comparable to that reported for the same species by Yang et al. (2002) and for *Pinus radiata* (Korol et al. 1999) and *Eucalyptus globulus* (Macfarlane et al. 2004). In our study, at the seed source level, higher foliar N and less negative $\delta^{13}C$ on the SC trees were indicators of higher water use efficiency of this seed source in comparison to the FL source. This is consistent with the reduced stomatal control we observed in the FL seed source compared with SC. $\delta^{13}C$ was strongly negatively correlated with mean daily canopy conductance (calculated as the mean value of daylight canopy conductance for the period between irrigation treatment start, on June 2005, to foliar sampling day, in December 2005) on control plots but not on irrigated plots ($P = 0.007$ and 0.58 , respectively; Figure 7A). $\delta^{13}C$ was strongly positively correlated with foliar N concentration on both the control and irrigated plots (Figure 7B), and the slope of this relationship was not significantly different between treatments ($P = 0.13$), but trees under water stressed conditions showed, for the same $\delta^{13}C$, lower foliar N concentration compared with irrigated; the difference in intercept of this relationship (Figure 7B) is presumably caused by reduced G_C in control plots.

As foliar N was higher on irrigated compared with the control plots ($P = 0.005$) (similar to Yang et al. 2002 and Albaugh et al. 2004), for irrigated trees, variability in $\delta^{13}C$ could be explained by changes in photosynthetic capacity, while for water-stressed trees, changes in $\delta^{13}C$ could be explained by both variation in stomatal conductance and photosynthetic capacity. As higher foliar N levels are generally associated with increased photosynthetic capacity (McGarvey et al. 2004), the positive correlation between $\delta^{13}C$ and foliar N could indicate higher water use efficiency in plots with both higher foliar N and $\delta^{13}C$. Yang et al. (2002) argued that the higher foliar N concentration on irrigated plots could be an effect of reductions in fine root system growth due to drought; in our study site, Samuelson et al. (2008) reported that total root biomass was significantly higher in irrigated plots, and Fabião et al. (1995) also reported significant incre-

ment in fine roots of 6-year-old irrigated *E. globulus*, but additional research is needed in order to establish a causal relationship.

Conclusion

In an 11-year-old loblolly pine plantation, increasing water availability via irrigation increased transpiration rate and canopy stomatal conductance for water vapor (G_C), and whole-tree water conduction efficiency (K_{S-wt}) was maintained at high levels due to avoidance of xylem embolism. Loblolly pine tends to maintain constant water potential gradient from roots to shoots at a cost of loss of conductivity under water-limited conditions. The two seed sources evaluated showed differences in G_C sensitivity to D under water-limited conditions, foliar N and $\delta^{13}C$, perhaps reflecting differences in adaptation to ambient humidity and water availability in their native environments. Given predictions of altered precipitation and temperature regimes for the southeastern USA, considerations of stand-level water relations traits of different taxa is critical. While the logistics of this study limited our measurements and therefore our direct inferences to only two taxa, the correspondence of our results with previous tree-level studies in other loblolly pine taxa from the same regions suggests that our data may apply more broadly. The observations in this study may prove informative to natural resource managers and breeders as they design tree improvement and genetic deployment programs for future climate scenarios. For example, the decreased G_{Cref} of SC under decreased soil moisture availability may make this taxon a more conservative deployment choice than FL under future, drier climate scenarios but perhaps at the risk of lower productivity.

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References

- Albaugh, T.J., H. L. Allen, P. M. Dougherty and K. H. Johnsen. 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192:3–19.
- Bongarten, B.C. and R.O. Teskey. 1986. Water relations of loblolly pine seedlings from diverse geographic origins. *Tree Physiol.* 1:265–276.
- Bracho, R., T.L. Powell, S. Dore, J.H. Li, C.R. Hinkle and B.G. Drake. 2008. Environmental and biological controls on water and energy exchange in Florida scrub oak and pine flatwoods ecosystems. *J. Geophys. Res.-Biogeosci.* 113:G02004.
- Braun, P. and J. Schmid. 1999. Sap flow measurements in grapevines (*Vitis vinifera* L.) 2. Granier measurements. *Plant Soil* 215:47–55.
- Bréda, N., H. Cochard, E. Dreyer and A. Granier. 1993. Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann. Sci. For.* 50:571–582.
- Čermák, J., J. Kučera and N. Nadezhdina. 2004. Sap flow measurements with two thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees Struct. Func.* 18:529–546.
- Clearwater, M.J., F.C. Meinzer, J.L. Andrade, G. Goldstein and N.M. Holbrook. 1999. Potential errors in measurement of non uniform sap flow using heat dissipation probes. *Tree Physiol.* 19:681–687.
- Deka, R.N., M. Wairiu, P.W. Mtakwa, C.E. Mullins, E.M. Veenendaal and J. Townend. 1995. Use and accuracy of the filter-paper technique for measurement of soil matric potential. *Eur. J. Soil. Sci.* 46:233–238.
- Domec, J.C. and B.L. Gartner. 2003. Relationship between growth rates and xylem hydraulic characteristics in young, mature, and old-growth Ponderosa pine trees. *Plant Cell Environ.* 26:471–483.
- Domec, J.C., M.L. Pruyn and B.L. Gartner. 2005. Axial and radial profiles in conductivities, water storage and native embolism in trunks of young and old growth ponderosa pine trees. *Plant Cell Environ.* 128:1103–1113.
- Ewers, B.E. and R. Oren. 2000. Analysis of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. *Tree Physiol.* 20:579–589.
- Ewers, B.E., R. Oren, T.J. Albaugh and P.M. Dougherty. 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. *Ecol. Appl.* 9:513–525.
- Ewers, B.E., R. Oren and J.S. Sperry. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* 23:1055–1066.
- Ewers, B.E., R. Oren, K.H. Johnsen and J.J. Landsberg. 2001a. Estimating maximum mean canopy stomatal conductance for use in models. *Can. J. For. Res.* 31:198–207.
- Ewers, B.E., R. Oren, N. Phillips, M. Strömberg and S. Linder. 2001b. Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*. *Tree Physiol.* 21:841–850.
- Fabião, A., M. Madeira, E. Steen, T. Kätterer, C. Ribeiro and C. Araújo. 1995. Development of root biomass in an *Eucalyptus globulus* plantation under different water and nutrient regimes. *Plant Soil.* 168–169:215–223.
- Farquhar, G.D., J.R. Ehleringer and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Mol. Biol.* 40:503–537.
- Ford, C.R., M.A. McGuire, R.J. Mitchell and R.O. Teskey. 2004. Assessing variation in the radial profile of sap flux density in *Pinus* species and its effect on daily water use. *Tree Physiol.* 24:241–249.
- Franks, P.J. 2004. Stomatal control and hydraulic conductance, with special reference to tall trees. *Tree Physiol.* 24:865–878.
- Franks, P.J., P.L. Drake and R.H. Froend. 2007. Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. *Plant Cell Environ.* 30:19–30.
- Gartner, B.L. and F. C. Meinzer. 2005. Structure-function relationships in sapwood water transport and storage. In *Vascular Transport in Plants*. Eds. M. Zwieniecki and N.M. Holbrook. Elsevier/Academic Press, Oxford, UK, pp 307–318.
- Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. In *Methods of soil analysis*. Part 1. Ed. A. Klute 2nd ed. Agron. Mongr. 9. ASA and SSSA, Madison, WI, pp. 383–411.
- Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3:309–320.
- Granier, A. and D. Loustau. 1994. Measuring and modeling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71:61–81.
- Granier, A., P. Biron, N. Breda, J.-Y. Pontailler and B. Saugier. 1996. Transpiration of trees and forests: short and long-term monitoring using sapflow methods. *Global Change Biol.* 2:265–274.
- Grissom, J.E. and S.E. McKeand. 2001. Comparative physiology of contrasting genotypes of loblolly pine under dry field conditions. *Proceedings, 26th Biennial SFTIC*, Athens, GA 122–124.
- Hacke, U.G., J.S. Sperry, B.E. Ewers, D.S. Ellsworth, K.V.R. Schäfer and R. Oren. 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124:495–505.
- Hatton, T.J., E.A. Catchpole and R.A. Vertessy. 1990. Integration of sapflow velocity to estimate plant water use. *Tree Physiol.* 6:201–209.
- Hillel, D. 1998. *Environmental Soil Physics*. Academic Press, San Diego, 771 p.
- James, S.A., M.J. Clearwater, F.C. Meinzer and G. Goldstein. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol.* 22:277–283.
- James, S.A., F.C. Meinzer, G. Goldstein, D. Woodruff, T. Jones, T. Restom, M. Mejia, M. Clearwater and P. Campanello. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134:37–45.
- Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15:1–49.
- Jimenez, M.S., N. Nadezhdina, J. Ěermak and D. Morales. 2000. Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol.* 20:1149–1156.
- Korol, R.L., M.U.F. Kirschbaum, G.D. Farquhar and M. Jeffreys. 1999. Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. *Tree Physiol.* 19:551–562.
- Lambeth, C.C., P.M. Dougherty, W.T. Gladstone, R.B. McCullough and O.O. Wells. 1984. Largescale planting of North Carolina loblolly pine in Arkansas and Oklahoma: a case of gain versus risk. *South. J. Appl. For.* 82:736–741.

- Lambers, H., F.S. Chapin III and T.L. Pons. 1998. Plant Physiological Ecology. Springer, New York, 540 p.
- Law, B.E., S. Van Tuyl, A. Cescatti and D.D. Baldocchi. 2001. Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. *Agric. For. Meteorol.* 108:1–14.
- Lecoeur, J. and T.R. Sinclair. 1996. Field pea transpiration and leaf growth in response to soil water deficits. *Crop Sci.* 36: 331–335.
- Lu, P. 1997. A direct method for estimating the average sap flux density using a modified Granier measuring system. *Aust. J. Plant Physiol.* 24:701–705.
- Lu, P., L. Urban and P. Zhao. 2004. Granier's Thermal Dissipation Probe (TDP) method for measuring sap flow in trees: theory and practice. *Acta Bot. Sin.* 46:631–646.
- Macfarlane, C., M.A. Adams and D.A. White. 2004. Productivity, carbon isotope discrimination and leaf traits of trees of *Eucalyptus globulus* Labill. in relation to water availability. *Plant Cell Environ.* 27:1515–1524.
- McKeand, S., T. Mullin, T. Byram and T. White. 2003. Deployment of genetically improved loblolly and slash pine in the South. *J. For.* 101:32–37.
- Marinho, A.M. and O.M. Oliveira. 2006. The filter paper method revisited. *Geotech. Test. J.* 39:9.
- Martin, T.A. 2000. Winter season tree sap flow and stand transpiration in an intensively-managed loblolly and slash pine plantation. *J. Sust. For.* 10:155–163.
- Martin, T.A., K.J. Brown, J. Cermak, R. Ceulemans, J. Kucera, F.C. Meinzer, J.S. Rombold, D.G. Sprugel and T.M. Hinckley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. *Can. J. For. Res.* 27:797–808.
- Martin, T.A., K.J. Brown, J. Kucera, F.C. Meinzer, D.G. Sprugel and T.M. Hinckley. 2001. Control of transpiration in a 220-year-old *Abies amabilis* forest. *For. Ecol. Manage.* 152:211–224.
- Martin, T.A., P.M. Dougherty, M.A. Topa and S.E. McKeand. 2005. Strategies and case studies for incorporating ecophysiology into southern pine tree improvement programs. *South. J. Appl. For.* 29:70–79.
- McGarvey, R.C., T.A. Martin and T.L. White. 2004. Integrating within-crown variation in net photosynthesis in loblolly and slash pine families. *Tree Physiol.* 24:1209–1220.
- Monteith, J.L. and M. Unsworth. 2007. Principles of Environmental Physics Third Edition. Academic Press, New York, 440 p.
- Murthy, R. and P.M. Dougherty. 1997. Estimating foliage area of loblolly pine shoots. *For. Sci.* 43:299–303.
- Nadezhkina, N. and J. Čermák. 2000. Responses of sap flow rate along tree stem and coarse root radii to changes of water supply. In *The supporting roots of trees and woody plants: form, function and physiology. Developments in plant and soil sciences*. Ed. A. Stokes, Kluwer, Dordrecht, vol 87; 227–238.
- Nadezhkina, N., J. Čermák and R. Ceulemans. 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiol.* 22:907–918.
- Niinemets, U., D.S. Ellsworth, A. Lukjanova and M. Tobias. 2001. Site fertility and the morphological and photosynthetic acclimation of *Pinus sylvestris* needles to light. *Tree Physiol.* 21: 1231–1244.
- Ophori, D.U. and B. Maharjan. 2000. First approximations of soil moisture retention curves using the filter-paper method. *Hydrol. processes.* 14:1131–1138.
- Oren, R. and D.E. Pataki. 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. *Oecologia* 127:549–559.
- Oren, R., B.E. Ewers, P. Todd, N. Phillips and G. Katul. 1998. Water balance delineates the soil layer in which moisture affects canopy conductance. *Ecol. Appl.* 8:990–1002.
- Panshin, A.J. and C. de Zeeuw. 1980. Textbook of wood technology 4th edn. McGraw-Hill, New York, 722 p.
- Pataki, D.E., R. Oren and N. Phillips. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *J. Exp. Bot.* 49:871–878.
- Phillips, N. and R. Oren. 1998. A comparison of two daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. *Ann. Sci. For.* 55:217–235.
- Phillips, N., R. Oren and R. Zimmermann. 1996. Radial trends in xylem sap flow in non-, diffuse- and ringporous species. *Plant Cell Environ.* 19:983–990.
- Phillips, N., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiol.* 22:205–211.
- Priestley, C.H.B. and R.J. Taylor. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Mon. Weather Rev.* 100:81–82.
- Retzlaff, W.A., G.K. Blaisdell and M.A. Topa. 2001a. Seasonal changes in water source of four families of loblolly pine (*Pinus taeda* L.). *Trees Struct. Func.* 15:154–162.
- Retzlaff, W.A., J.A. Handest, D.M. O'Malley, S.E. McKeand and M. A. Topa. 2001b. Whole-tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda* L.): influence of genetics and fertilization. *Can. J. For. Res.* 31:960–970.
- Ritchie, J.T. 1981. Soil water availability. *Plant Soil* 58:327–338.
- Sampson, D.A. and H.L. Allen. 1995. Direct and indirect estimates of leaf area index (LAI) for lodgepole and loblolly pine stands. *Trees* 9:119–122.
- Samuelson, L.J. 1998. Influence of intensive culture on leaf net photosynthesis and growth of sweetgum and loblolly pine seedlings. *For. Sci.* 44:308–316.
- Samuelson, L.J. and T.A. Stokes. 2006. Transpiration and canopy stomatal conductance of 5-year-old loblolly pine in response to intensive management. *For. Science* 52:313–323.
- Samuelson, L.J., T. Stokes, T. Cooksey and P. McLemore III. 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. *Tree Physiol.* 21:369–376.
- Samuelson, L.J., J. Butnor, C. Maier, T. Stokes, K. Johnsen and M. Kane. 2008. Growth and physiology of loblolly pine in response to long-term resource management: defining growth potential in the southern United States. *Can. J. For. Res.* 38:721–732.
- Schaap, M.G., F.J. Leij and M.Th. Van Genuchten. Rosetta: a computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. *J. Hydrol.* 251:163–176.
- Schäfer, K.V.R., R. Oren and J.D. Tenhunen. 2000. The effect of tree height on crown-level stomatal conductance. *Plant Cell Environ.* 23:365–377.
- Schultz, R.P. 1997. The Ecology and Culture of Loblolly Pine (*Pinus taeda* L.). USDA Forest Service, Washington, DC, 493 pp.
- Sierra-Lucero, V., S.E. McKeand, D.A. Huber, D.L. Rockwood and T.L. White. 2002. Performance differences and genetic parameters for four coastal provenances of loblolly pine in the southeastern United States. *For. Sci.* 48:732–742.

- Sinclair, T.R., N.M. Holbrook and M.A. Zwieniecki. 2005. Daily transpiration rates of woody species on drying soil. *Tree Physiol.* 25:1469–1472.
- Solomon, S., D. Qin, M. Manning et al. 2007. Technical summary. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* Eds. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller. Cambridge University Press, Cambridge, 74 pp.
- Sperry, J.S. 2000. Hydraulic constraints on plant gas exchange. *Agr. For. Meteorol.* 104:13–23.
- Sperry, J.S. and T. Ikeda. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiol.* 17:275–280.
- Teskey, R.O., J.A. Fites, L.J. Samuelson and B.C. Bongarten. 1986. Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. *Tree Physiol.* 2:131–142.
- Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. *Trees* 17:95–100.
- Tyree, M.T. and M.H. Zimmermann. 2002. Xylem structure and the ascent of sap. Second Edition. Springer, Berlin, 283 pp.
- Tyree, M.T., J. Alexander and J.L. Machado. 1992. Loss of hydraulic conductivity due to water stress in intact juveniles of *Quercus rubra* and *Populus deltoides*. *Tree Physiol.* 10:411–415.
- Wahbi, A. and T.R. Sinclair. 2007. Transpiration response of Arabidopsis, maize and soybean to drying of artificial and mineral soil. *Env. Exp. Bot.* 59:188–192.
- Wang, T., S.N. Aitken and K.L. Kavanagh. 2003. Selection for improved growth and wood quality in lodgepole pine: effects on phenology, hydraulic architecture and growth of seedlings. *Trees* 17:269–277.
- Warren, J.M., F.C. Meinzer, J.R. Brooks and J.C. Domec. 2005. Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Agric. For. Meteorol.* 130:39–58.
- Wells, O.O. 1983. Southwide pine seed source study-loblolly pine at 25 years. *South. J. Appl. For.* 7:63–71.
- Wells, O.O. and P.C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. *For. Sci. Monogr.* 11:40.
- Wullschlegel, S.D. and A.W. King. 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiol.* 20:511–518.
- Wullschlegel, S.D., F.C. Meinzer and R.A. Vertessy. 1998. A review of whole-plant water use studies in trees. *Tree Physiol.* 18:499–512.
- Wullschlegel, S.D., K.B. Wilson and P.J. Hanson. 2000. Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. *Agr. For. Meteorol.* 104:157–168.
- Yang, W.Q., R. Murthy, P. King and M.A. Topa. 2002. Diurnal changes in gas exchange and carbon partitioning in needles of fast- and slow-growing families of loblolly pine (*Pinus taeda*). *Tree Physiol.* 22:489–498.