

Water availability and genetic effects on wood properties of loblolly pine (*Pinus taeda*)

C.A. Gonzalez-Benecke, T.A. Martin, A. Clark III, and G.F. Peter

Abstract: We studied the effect of water availability on basal area growth and wood properties of 11-year-old loblolly pine (*Pinus taeda* L.) trees from contrasting Florida (FL) (a mix of half-sib families) and South Carolina coastal plain (SC) (a single, half-sib family) genetic material. Increasing soil water availability via irrigation increased average whole-core specific gravity (SG) and latewood percentage (LW%) by 0.036 and 6.93%, respectively. Irrigation did not affect latewood SG or wood stiffness, but irrigated FL and SC trees had more latewood due to a 29 day longer growing season. Irrigation did not affect the length of corewood production, but irrigated trees had earlier transition ages, producing outerwood ~3 years before rainfed trees. The increase in whole-core SG and LW% was moderate because irrigation promoted earlywood growth in corewood formed before canopy closure, but after year 7, rain-fed and irrigated trees had similar earlywood growth but irrigated trees had more latewood growth, increasing ring SG and LW%. The SC half-sib family had higher SG and greater LW% than trees from FL independent of irrigation due to greater yearly latewood growth. Thus, absence of soil water stress extended seasonal diameter cessation date but did not change latewood SG or wood stiffness.

Résumé : Nous avons étudié l'effet de la disponibilité en eau sur la croissance en surface terrière et les propriétés du bois de tiges de pin à encens (*Pinus taeda* L.) âgées de 11 ans et dont le matériel génétique provenait soit de la Floride (FL) (un mélange de descendances uniparentales), soit de la plaine côtière de la Caroline du Sud (CS) (une seule descendance uniparentale). L'augmentation de la disponibilité en eau par l'irrigation a augmenté la gravité spécifique (GS) moyenne du bois de cœur et le pourcentage de bois final (BF) de respectivement 0,036 et 6,93%. L'irrigation n'a influencé ni la GS du bois final ni la rigidité du bois, mais les tiges FL et CS irriguées avaient plus de bois final parce que leur saison de croissance durait 29 jours de plus. L'irrigation n'a pas influencé la durée de la production de bois de cœur mais l'âge de transition arrivait plus tôt chez les arbres irrigués qui produisaient du bois d'aubier environ trois ans avant les arbres alimentés en eau par la pluie. L'augmentation de la GS et du pourcentage de BF du bois de cœur était modérée parce que l'irrigation favorisait la croissance du bois initial dans le bois de cœur formé avant la fermeture du couvert. Mais après sept ans, la croissance du bois initial était semblable chez les arbres alimentés en eau par la pluie et les arbres irrigués alors que la croissance du bois final était plus prononcée chez les arbres irrigués, ce qui augmentait la GS et le pourcentage de BF des cernes. La descendance uniparentale de la CS avait une GS et un pourcentage de BF plus élevés que les arbres de la FL indépendamment de l'irrigation à cause d'une plus forte croissance annuelle du bois final. Par conséquent, l'absence de stress hydrique a repoussé la date de la croissance saisonnière en diamètre mais n'a changé ni la GS du BF, ni la rigidité du bois.

[Traduit par la Rédaction]

Introduction

The southeastern United States has more than 13 million ha of southern pine plantations (Fox et al. 2007) from which about 58% of total US timber is harvested (Jordan et al. 2007), constituting the largest timber production zone in the world (McKeand et al. 2003; Allen et al. 2005). In this region, loblolly pine (*Pinus taeda* L.) thrives on various sites from east Texas to southern Missouri to north Florida to south New Jersey and is one of the fastest growing pine species, accounting for more than 84% of planted seedlings in the United States (McKeand et al. 2003).

Tree improvement and silvicultural research programs are key components of the success of the loblolly pine forest in-

dustry (McKeand et al. 2003; Fox et al. 2007). These improvement programs have focused primarily on volume growth, stand management, disease resistance, tree form, and, more recently, wood properties. Specific gravity (SG) and modulus of elasticity (MOE) are important wood properties affecting the performance of solid and engineered wood products manufactured from loblolly pine (Panshin and de Zeeuw 1980; Jordan et al. 2008). SG and fiber tensile strength are also important determinants of paper strength (Courchene et al. 2006; Jordan et al. 2008). Because small increases in SG or wood stiffness by tree improvement (genotype) and silviculture (environment) can have large impacts on wood production and value (Panshin and de Zeeuw 1980), the measurement of wood stiffness

Received 11 May 2010. Accepted 17 August 2010. Published on the NRC Research Press Web site at cjfr.nrc.ca on 5 November 2010.

C.A. Gonzalez-Benecke,¹ T.A. Martin, and G.F. Peter. School of Forest Resources and Conservation, P.O. Box 110410, University of Florida, Gainesville, FL 32611, USA.

A. Clark III. USDA Forest Service, Southern Research Station, Athens, GA 30602, USA.

¹Corresponding author (e-mail: cgonzabe@ufl.edu).

Table 1. Mean annual maximum (T_{\max}), mean (T_{mean}), and minimum (T_{\min}) temperatures and average seasonal (M–S, May–September; O–A: October–April) precipitation (pp) and potential evapotranspiration (PET) for genetic material source sites (FL, Marion County, Florida; SC, Georgetown County, South Carolina) and study site (GA, Decatur County, Georgia).

	Site		
	FL	SC	GA
T_{\max} (°C)	22.4	19.6	20.8
T_{mean} (°C)	17.2	14.6	15.2
T_{\min} (°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

Note: Mean annual temperatures and precipitation were obtained at lwf.ncdc.noaa.gov/oa/climate/normal/usnormals.html. Long-term (1951–1998) evapotranspiration was obtained from the USGS Hydro-Climatic Data Network at daac.ornl.gov/cgi-bin/search/hcdn.pl?d=810.

and SG is becoming an important component of many tree breeding and silvicultural research programs (Li et al. 2007; Roth et al. 2007; Cherry et al. 2008; Kumar et al. 2008).

Region-wide surveys demonstrate that SG tends to increase with decreasing latitude (Megraw 1985; Larson et al. 2001; Jordan et al. 2008). It is hypothesized that this regional trend is due to growing season length, with a longer season producing more latewood. The general trend of decreasing SG from south to north and east to west is coincident with seasonal rainfall patterns and length of the growing season (Clark and Saucier 1989; Larson et al. 2001). Dougherty et al. (1994) indicated that diameter growth cessation date depends on soil moisture content and transpiration rate, and Cregg et al. (1988) concluded that among-year differences in SG and latewood percentage (LW%) correlated with summer rainfall patterns, with years of high summer rainfall having higher SG and LW% compared with dry summers. However, provenance studies grown on common sites show that the Florida provenance (e.g., Gulf Hammock and Marion County) had lower SG compared with the more northerly Atlantic coastal provenance, suggesting that genetic control can be more important than environmental control (Jett et al. 1991; Jayawickrama et al. 1997).

Wood quality characteristics are likely influenced by traits that have evolved to maintain water supply to transpiring leaves under water stress (Panshin and de Zeeuw 1980). Plants regulate water loss in response to water deficits by closing stomata, and the water potential at which stomatal closure occurs has been shown to be closely related to the water potential at which xylem cavitation becomes significant (Sperry and Ikeda 1997; Tyree 2003). Thus, regulation of stomatal conductance and water loss appears to have evolved so that catastrophic xylem embolism is avoided (Sperry 2000). Wood SG depends on the proportion and density of latewood, which in pines averages twice the den-

sity of earlywood (Jordan et al. 2008). The adaptive importance of latewood is thought to be twofold. The smaller lumen diameters are more resistant to cavitation and therefore provide protection against embolism at reduced soil water potentials (Tyree 2003; Pittermann et al. 2006a), and the thicker walls are more resistant to implosion if an embolism occurs (Hacke et al. 2001; Pittermann et al. 2006b).

In this study, we examined the effect of water availability and genetic material on radial growth and wood properties of a midrotation loblolly pine plantation. Water availability was controlled by an irrigation treatment of trees from two fast-growing genetic materials that received extra water input since plantation establishment. Given the high genetic variability inherent in loblolly pine (Sierra-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 interaction between stem secondary xylem growth and adaptations to limiting water supply by different loblolly pine taxa. We hypothesize that (i) the date of diameter growth cessation depends on soil moisture conditions and transpiration rate, (ii) irrigation treatments will extend the period of xylem growth, resulting in higher LW% and higher SG, mimicking effects observed in wetter years, (iii) the cambial transition age from corewood to outerwood will start earlier in irrigated treatments due to the effect on LW% and SG, and (iv) genetic material from Florida will have wood quality characteristics in response to irrigation different from those of Atlantic coastal plain material.

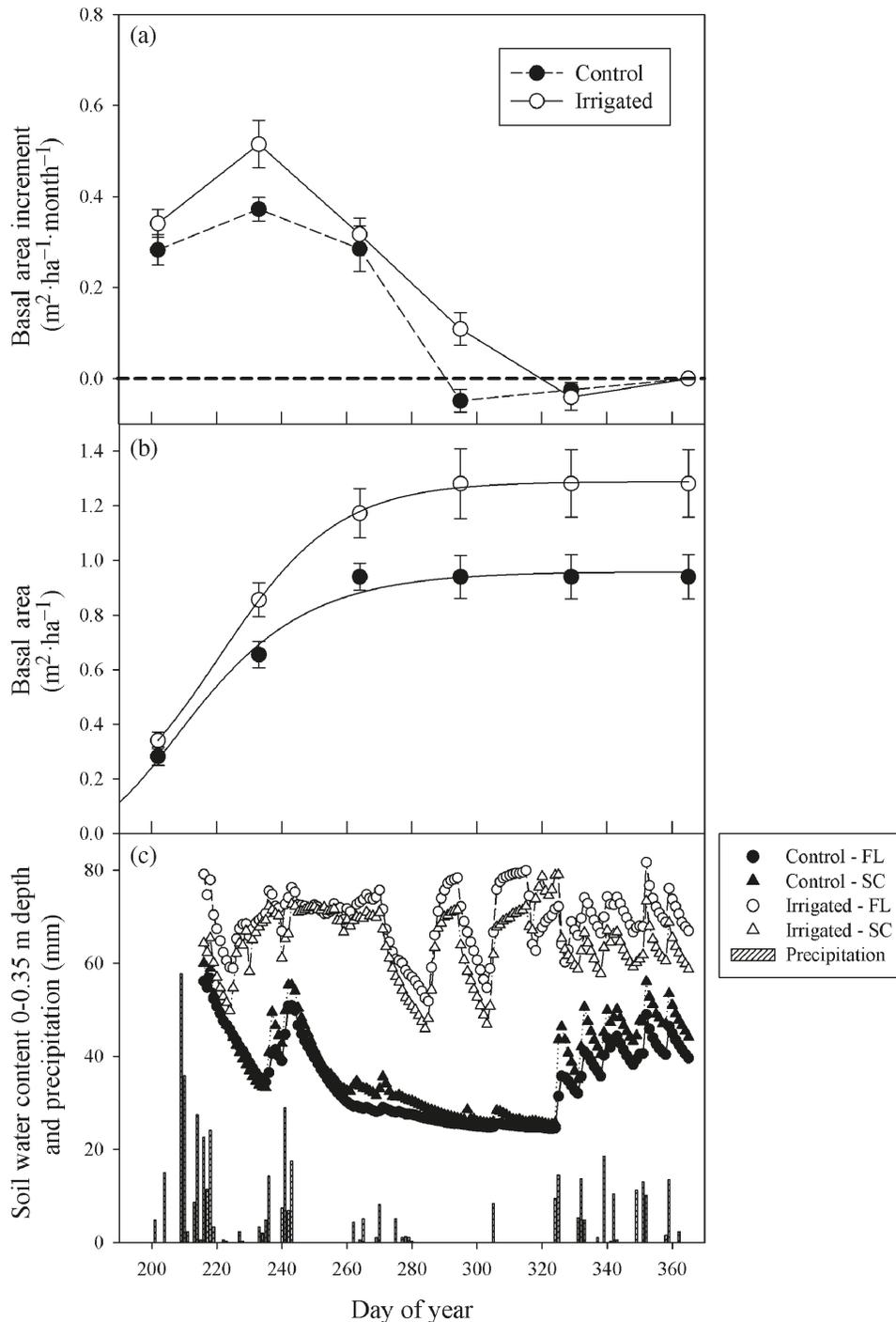
Materials and methods

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, Georgia (30°48'N, 84°39'W). Soils at this location were classified as well-drained Grossarenic Paleudults, with 0.5 m sandy loam over sandy clay loam (Samuelson 1998).

For this study, two water availability treatments and two genetic material entries in factorial combination were selected. The experimental design contained three replicates in a split-plot randomized complete block (12 plots total) with irrigation as the whole plot and genetic entry as the subplot. This study represented a subset of the whole study, which included additional genetic materials and treatments. The measurement plot areas were 0.026 ha containing 28 sample trees planted at 2.4 m × 3.7 m spacing and surrounded by two buffer rows. The genetic material was obtained from industrial tree improvement seed orchards and consisted of FL, a mixture of north-central Florida half-sib families (primarily from Marion County), and SC, a single half-sib family from the South Carolina coastal plain (Georgetown County). The study included a water-irrigated treatment (6.25 mm·day⁻¹ on drip irrigation from July to November; total seasonal water addition was 631 mm) and a nonirrigated control treatment (Samuelson 1998; Gonzalez-Benecke and Martin 2010). Additional site and experimental details are reported in Samuelson et al. (2004 and 2008).

Fig. 1. Daily average precipitation and soil water content and basal area in 2005. (a) Average monthly basal area growth and (b) cumulative basal area accretion for irrigated and control plots. Nonlinear fitting for cumulative basal area corresponds to the Chapman–Richards model. (c) Soil water content for the 0–0.35 m depth and precipitation for the irrigated and control treatments with two different genetic materials, Florida family mix (FL) and South Carolina coastal plain half-sib family (SC). Measurements started in early June and ended in late December.



Comparison of the native environment of the SC family and the open-pollinated FL families shows that FL has 2–3 °C higher annual maximum, mean, and minimum temperatures than SC (Table 1). During the warmer growing period (May–September), potential water deficit, expressed as the ratio between potential evapotranspiration and precipitation, is greater in SC compared with FL (1.39 and 1.07, respec-

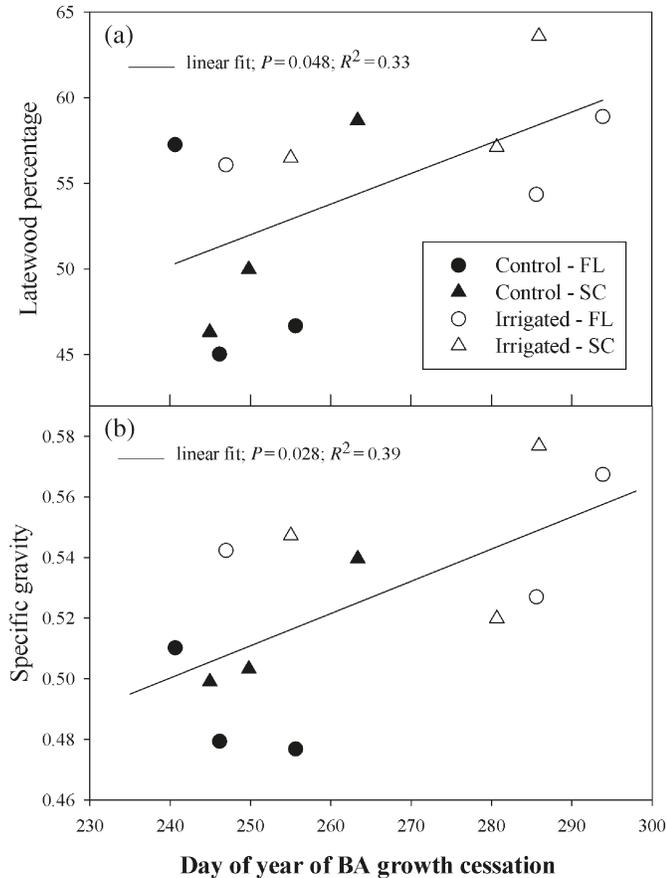
tively), but during the cooling months (October–April), this trend is reversed and SC has no potential water deficit (evapotranspiration is 10.5% lower than precipitation), while FL has 38.5% larger evapotranspiration than precipitation, indicating that the FL material evolved with greater water availability during the growing period compared with the SC material.

Table 2. Age 11 mean diameter at breast height (DBH), height, basal area (BA), and leaf area index (LAI) for irrigation \times genetic treatments.

	Control		Irrigated		<i>P</i> > <i>F</i>		
	FL	SC	FL	SC	Irrigation	Genetic	Irrigation \times genetic
DBH (mm)	200.8	209.7	213.1	228.2	<0.001	0.004	0.577
Height (m)	15.4	16.0	17.2	17.8	<0.001	0.186	0.939
BA (m ² ·ha ⁻¹)	34.0	32.9	39.7	39.8	0.003	0.707	0.654
LAI (m ² ·m ⁻²)	4.2	4.5	4.6	4.4	0.348	0.597	0.083

Note: Means at age 11 (December 2005); LAI was measured in October 2005. FL, Florida family mix; SC, South Carolina coastal plain half-sib family. *P* values used the mixed model procedure for split-plot design.

Fig. 2. Relationship between the cessation of basal area growth and (a) latewood percentage and (b) specific gravity for irrigated and control plots that included trees from the Florida family mix (FL) and South Carolina coastal plain half-sib family (SC) in 2005. A linear fit was significant for both cases (*P* = 0.028 and *P* = 0.048 for latewood percentage and specific gravity, respectively).



Meteorological and soil moisture measurements

Meteorological data were recorded with an automatic weather station located in an open area adjacent to the stand. The sensors were measured every 30 s with an automatic datalogger (CR10, Campbell Scientific, Logan, Utah) and were stored as 30 min averages. Long-term meteorological measurements from stand establishment (January 1995) until the beginning of our measurements (June 2005) were obtained from a weather station installed by International Paper, Inc. in an area close to the study site (30°49'N, 84°37'W).

To assess the effectiveness of irrigation application, vertically oriented 200 mm long capacitive soil moisture probes (EC-20, Decagon Devices, Pullman, Washington) were used to measure volumetric soil water content (θ_v) (cubic metres per cubic metre). The manufacturer's probe installation blade was used to install the probes. The soil volume measured by the probe was not disturbed. Details of soil water content determinations are reported in Gonzalez-Benecke and Martin (2010).

Diameter and basal area growth

During the 2005 growing season, monthly changes in diameter at breast height (DBH) (millimetres) and basal area (BA) (square metres per hectare) were measured on eight trees per plot previously selected for sapflow measurements (see Gonzalez-Benecke and Martin 2010). To estimate BA, plot-specific expansion factors were determined by measuring all of the trees of all plots at the beginning and at the end of the study. For each plot, cumulative BA growth was plotted against time, and BA cessation day was determined as the date (day of year) when 95% of the total growth was attained (Hanover 1963; Jayawickrama et al. 1998) using a nonlinear fit with the Chapman-Richards model (PROC NLIN; SAS Inc., Cary, North Carolina):

$$[1] \quad BA = a(1 - e^{-b \times \text{day}})^c$$

where *a*, *b*, and *c* are curve-fitting parameters and "day" corresponds to day of year of the Julian calendar.

Wood properties

In April 2006, 12 mm increment wood cores that crossed from bark to bark (passing through the pith) were extracted at breast height on the same trees used for DBH measurements. The whole cores were split at the center of the pith and two radii cores were obtained per tree sampled. Wood cores were labeled and dried at 50 °C and conditioned to an equilibrium moisture content of ~8%. One radius was stored as a backup for further analysis and the other was sent to the USDA Forest Service Forestry Sciences Laboratory in Athens, Georgia, for X-ray densitometry analysis (Hoag and Krahmer 1991; Clark et al. 2006b) (QTRS-01X; Quintek Measurement Systems, Knoxville, Tennessee). Latewood SG (SG_L), earlywood SG (SG_E), latewood width (W_L) (millimetres), earlywood width (W_E) (millimetres), ring width (W_R) (millimetres), LW%, and whole-ring SG (SG_R) were determined for each ring on all 96 sample trees.

SG is the dimensionless ratio of the weight of a wood sample in relation to the weight of an equal volume of water

Fig. 3. Annual (a and b) latewood percentage, (c and d) latewood specific gravity, (e and f) ring specific gravity, and (g and h) annual total rainfall and water added by drip irrigation from 1995 through 2005 for (a, c, e, and g) water availability and (b, d, f, and h) genetic material (Florida family mix (FL) and South Carolina coastal plain half-sib family (SC)) treatments. Thirty-year rainfall mean for the site (1408 mm) is indicated with a line in Figs. 3g and 3h.

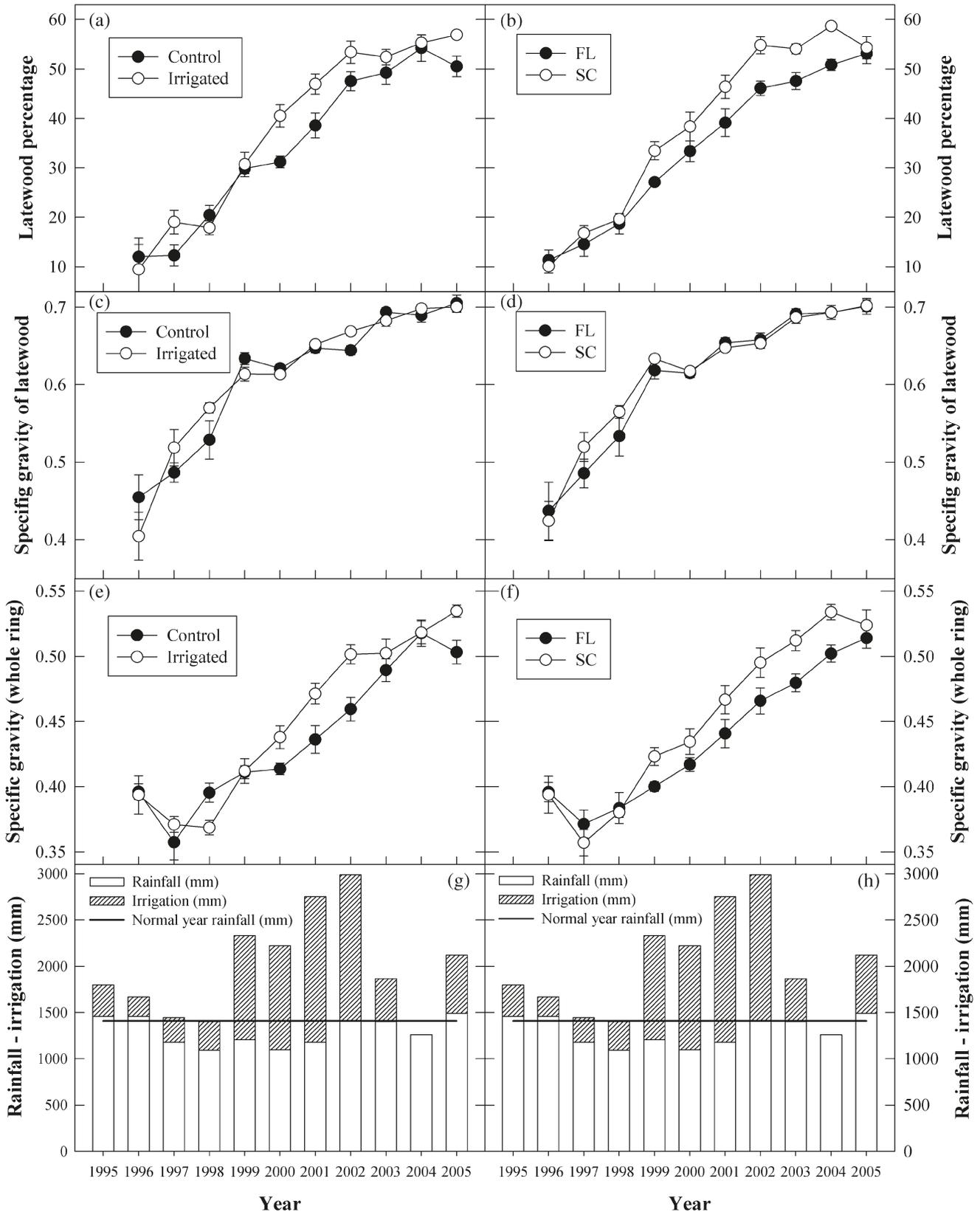


Table 3. Time series analysis ANOVA for wood properties on rings formed between 1998 and 2005 for irrigation × genetic treatments.

Trait	<i>P</i> > <i>F</i>							
	Irrigation	Genetic	Irrigation × genetic	Year	Irrigation × year	Genetic × year	Irrigation × year × genetic	
SG _E	0.582	0.300	0.286	<0.001	<0.001	0.493	0.016	
SG _L	0.863	0.877	0.868	<0.001	<0.001	0.155	0.528	
SG _R	0.036	0.027	0.845	<0.001	0.010	0.153	0.286	
LW%	0.015	0.002	0.864	<0.001	<0.001	0.001	0.023	
A _E	0.008	0.893	0.696	<0.001	<0.001	0.024	0.954	
A _L	<0.001	0.003	0.952	<0.001	0.014	0.876	0.072	
A _R	0.001	0.155	0.658	<0.001	<0.001	0.072	0.640	
V _E ²	0.121	0.722	0.110	<0.001	0.111	0.106	0.999	
V _L ²	0.193	0.646	0.098	<0.001	0.204	0.824	0.238	
V _R ²	0.063	0.219	0.109	<0.001	0.023	0.034	0.582	
MOE _E	0.149	0.319	0.247	<0.001	0.0005	0.094	0.849	
MOE _L	0.405	0.709	0.422	<0.001	0.089	0.746	0.327	
MOE _R	0.004	0.092	0.418	<0.001	0.014	0.053	0.597	

Note: SG, specific gravity; LW%, latewood percentage; A, area; V², stiffness; MOE, modulus of elasticity; E, earlywood; L, latewood; R, whole-ring. *P* values used the mixed model procedure for split-plot design.

at a standard temperature (Larson et al. 2001). SG of earlywood and latewood from each annual ring for each radial strip was determined at 60 µm intervals. An SG value of 0.48 was used to distinguish earlywood from latewood (Clark et al. 2006b; Jordan et al. 2007). LW% was calculated for each ring as the percentage of latewood area to total growth ring area (Jayawickrama et al. 1997).

Wood stiffness (dynamic longitudinal stiffness or MOE) was estimated using the longitudinal wave velocity (*V*) (kilometres per second) and the density of the wood (*ρ*) (kilograms per cubic metre) from X-ray densitometry using the following equation (Lindström et al. 2004; Roth et al. 2007; Mora et al. 2009):

$$[2] \quad \text{MOE} = V^2 \rho$$

V was determined with a contact ultrasonic system (Out of Plane Ultrasonic System; Sonisys, Inc., Atlanta, Georgia) on the same 96 samples on which SG was measured. *V* was measured in the longitudinal direction of the radial strips on the cross-sectional face.² Stiffness of earlywood and latewood was determined at 1 mm intervals on each annual ring of the outer 70 mm of xylem on each sample.

Transition between corewood and outerwood was determined by fitting a four-parameter logistic function on yearly ring SG (SG_R) or LW% profiles on each tree. The model was selected after comparing different sigmoidal functions and had the form

$$[3] \quad X = y_0 + \frac{a - y_0}{1 + e^{(\text{age} - x_0)/b}}$$

where *X* is the wood property evaluated (SG_R or LW%), “age” is tree age after planting assigned to the corresponding ring, *y*₀ is the lower asymptote as age → -∞, *a* is the upper asymptote as age → ∞, *x*₀ is the inflection point, and *b* is the scale parameter (Pinheiro and Bates 2000).

The criteria of Mora et al. (2007) were used to demarcate corewood and outerwood: corewood is the area between ring number 1 (age 3) and the ring where the maximum rate in change in LW% was observed (*t*_{max}). Transition wood starts at *t*_{max} and ends at the ring at which the rate of change in LW% was <0.01 unit (*t*_{min}); LW% is quite constant in successive rings. Outerwood starts at *t*_{min}. The areas of corewood and outerwood were determined using the corresponding BAs at breast height. Diameter of juvenile core and percentage of corewood produced at breast height were calculated from previously determined demarcation points (Mora et al. 2007).

Whole-ring SG, V², and MOE (i.e., SG_R, V_R², and MOE_R) were determined for each ring as the sum of the product of each wood property trait (early and latewood) by the corresponding early or latewood ring area and divided by total whole-ring area. Weighted whole-core SG, LW%, V², and MOE were calculated as the sum of the product of each wood property trait on each ring (early and latewood) by the corresponding ring BA and divided by total tree BA (Jordan et al. 2007).

Statistical analysis

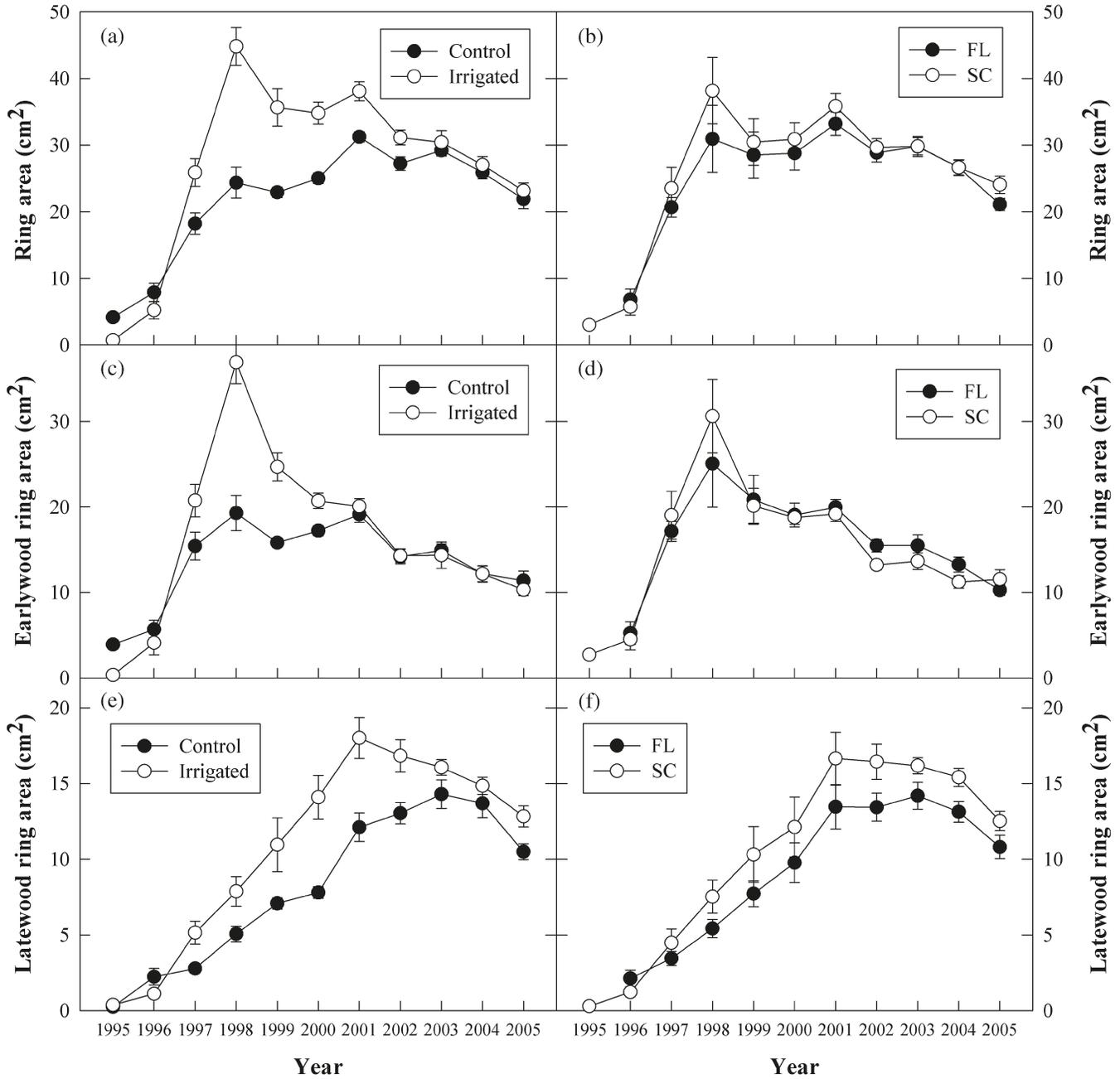
ANOVA was used to analyze effects in wood property traits of irrigation and genetic material, including Bonferroni adjustments for differences in least square means (PROC MIXED; SAS Inc., Cary, North Carolina). The linear model for the analysis was

$$[4] \quad Y_{ijk} = \mu + b_i + I_j + F_{k(j)} + (IF)_{k(j)} + (bI)_{ij} + (bF)_{ik(j)} + (bIF)_{ik(j)} + \varepsilon_{ijk}$$

where *Y*_{ijk} is the parameter value of the plot of the *k*th genetic material nested in the *j*th irrigation treatment in the *i*th replicate where *i* = 1, 2, and 3 for replications, *j* is control or irrigated, and *k* = FL or SC, *μ* is the population mean, *b*_{*i*} is the random variable of replication ~ NID(0, σ_{*b*}²), (NID, nor-

²G.F. Peter, C. Habeger, and L.R. Schimleck. A rapid high resolution ultrasonic method for measuring wood specific stiffness, modulus of elasticity and estimating cellulose microfibril angle. Submitted.

Fig. 4. Annual growth in (a and b) ring area, (c and d) earlywood area, and (e and f) latewood area during each year from 1995 through 2005 for (a, c, and e) water availability and (b, d, and f) genetic material (Florida family mix (FL) and South Carolina coastal plain half-sib family (SC)) treatments.



mally and independently distributed), I_j is the fixed effect of irrigation (control or irrigated), $F_{k(j)}$ is the fixed effect of genetic material (FL or SC) nested within irrigation, $(IF)_{k(j)}$ is the fixed effect of the irrigation \times genetic material (irrigation) interaction, $(bI)_{ij}$ is the random variable for the replication \times irrigation interaction $\sim \text{NID}(0, \sigma_{bI}^2)$, $(bF)_{ik(j)}$ is the random variable for the replication \times genetic material (irrigation) interaction $\sim \text{NID}(0, \sigma_{bF}^2)$, $(bIF)_{ik(j)}$ is the random variable for the replication \times irrigation \times genetic material (irrigation) interaction $\sim \text{NID}(0, \sigma_{bIF}^2)$, and ε_{ijk} is the error term $\sim \text{NID}(0, \sigma_\varepsilon^2)$.

Repeated measures analysis was used to analyze time ser-

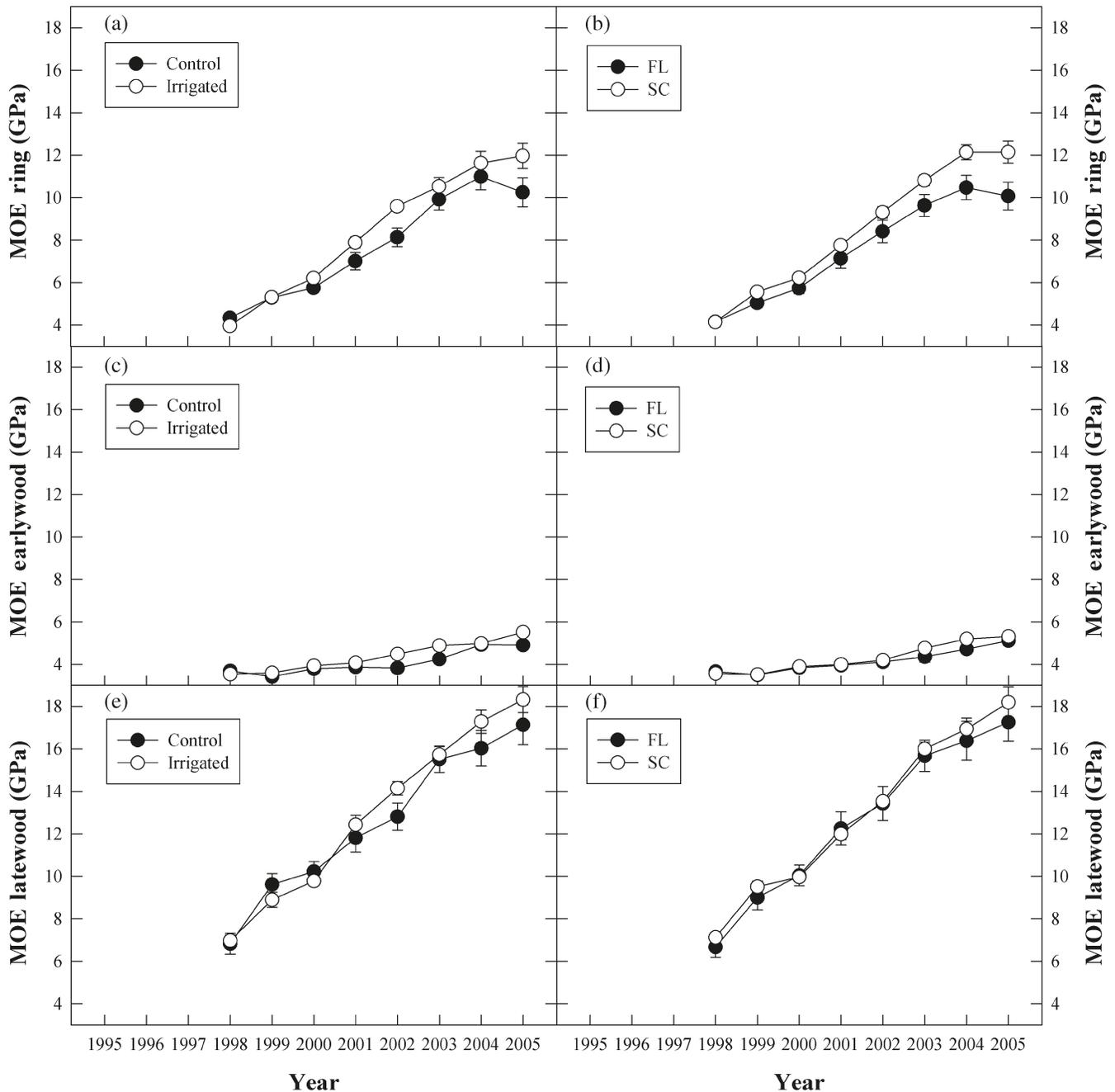
ies data. Several covariance structure models were used for the time series analysis (power, heterogeneous first-order autoregressive, compound symmetry, heterogeneous Toeplitz, unstructured, and uncorrelated models) and the model with the lowest Schwartz's Bayesian information criterion was selected for each variable analyzed (Littell et al. 1996).

Results

Environmental and soil moisture conditions

Soil water content was highly affected by the irrigation

Fig. 5. Annual (a and b) ring MOE, (c and d) earlywood MOE, and (e and f) latewood MOE during each year from 1998 through 2005 for (a, c, and e) water availability and (b, d, and f) genetic material (Florida family mix (FL) and South Carolina coastal plain half-sib family (SC)) treatments.



treatment. Seasonal θ_v average for the control was 10.9% and 17.7% for the irrigated plots during the 2005 growing season (Fig. 1).

In 2005, precipitation (1490 mm) was evenly distributed throughout the year and was 5.8% higher than historic averages (1409 mm). Total precipitation from July to December 2005 was 574.8 mm, 4.3% higher than the 30-year average for Bainbridge, Georgia. However, from 1 September to 19 November (79 days), only 36 mm of precipitation occurred as rain (Fig. 1). Yearly rainfall records from 1995 to 2006 indicate that precipitation was in most cases lower than nor-

mal, being between 15% and 22% lower from 1997 to 2001 and slightly higher, between 3.5% and 5.8%, in 1995, 1996, and 2005.

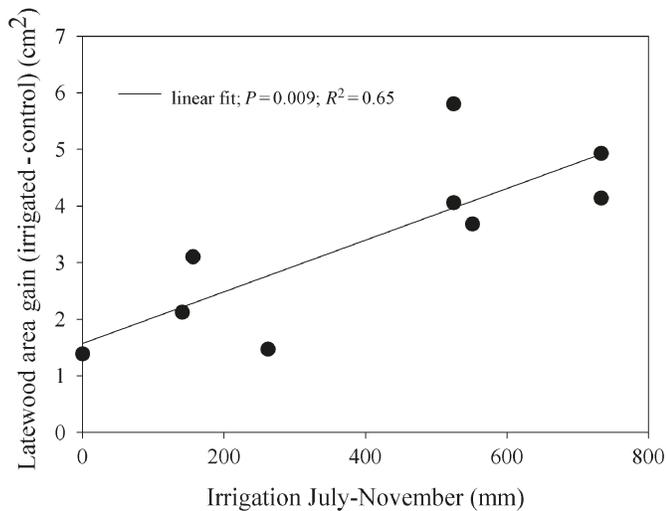
Diameter and BA growth and day of growth cessation

At age 11, BA was significantly greater in the irrigated plots ($P = 0.003$) (Table 2) for both genetic materials. On an individual tree basis, significant effects for both DBH (outside bark) measured in December 2005 and cumulative ring width using the whole wood core (tree radius without bark) were found for irrigation ($P = 0.0003$ and $P = 0.0002$,

Table 4. Least square means for whole-core area-weighted wood properties on rings formed between 1998 and 2005 for irrigation \times genetic treatments.

Trait	Control		Irrigated		$P > F$		
	FL	SC	FL	SC	Irrigation	Genetic	Irrigation \times genetic
SG	0.446	0.465	0.451	0.472	0.407	0.018	0.912
LW%	37.65	42.92	39.44	44.49	0.224	0.003	0.933
V^2	14.41	16.30	15.36	15.45	0.905	0.223	0.083
MOE	6.78	8.27	7.56	8.01	0.524	0.113	0.227
A_E	123.21	125.39	155.81	151.38	0.003	0.880	0.662
A_L	74.08	93.42	102.14	120.83	0.0002	0.001	0.928

Note: FL, Florida family mix; SC, South Carolina coastal plain half-sib family; SG, specific gravity; LW%, latewood percentage; V^2 , stiffness ($\text{km}^2\text{-s}^{-2}$); MOE, modulus of elasticity (GPa); A_E , earlywood area (cm^2); A_L , latewood area (cm^2). P values used the mixed model procedure for split-plot design.

Fig. 6. Relationship between mean latewood area difference between irrigated and nonirrigated plots and the amount of water added through irrigation during July–November for 1997–2005.

respectively) and taxa ($P = 0.039$ and $P = 0.039$, respectively) with no significant interactions ($P = 0.58$ and $P = 0.76$, respectively). The fact that the FL and SC materials differed in individual tree DBH but not in BA is explained by the greater mortality observed for SC (14.9%) compared with FL (5.4%) ($P = 0.004$).

The day of growth cessation was prolonged significantly ($P = 0.031$), with irrigated plots growing 29 days longer than the control plots (Fig. 1). Growth cessation date did not differ between genetic material ($P = 0.72$) and no irrigation by genetic material interaction ($P = 0.18$) was observed. On average, irrigated plots reached 95% of total BA growth at day 275 (1 October). In 2005, BA growth cessation day was correlated with LW% and SG ($P < 0.05$) (Fig. 2), explaining 33.5% and 39.6% of the variation, respectively.

Wood properties

The first two growth years (1995 and 1996) were eliminated from the analysis for two reasons: because wood cores were sampled at 1.4 m and only 29% of the trees reached that height in year 1, and even though around 94% of the trees showed a growth ring in the sampled wood core in 1996 (for 65% of the trees that was the first “ring”), those rings were mostly pith-associated wood (Larson et al. 2001).

Irrigation significantly affected ring SG and LW% for both taxa with no irrigation \times genetic material interactions ($P = 0.84$ and $P = 0.86$, respectively) (Fig. 3; Table 3). These wood properties depended on year of growth ($P < 0.001$) (Table 3), with a significant year of growth \times irrigation interaction for SG_R and LW%; the year of growth \times genetic material interaction was not significant for SG_R but was for LW% (Table 3). In contrast with SG and LW%, no effect of treatments or interaction with year of growth was observed for earlywood and latewood V^2 (Table 3). Only whole-ring V^2 was affected by irrigation and genetic material, but that effect was due to greater LW% on irrigated and SC plots and not to a direct effect of treatments on V^2 . MOE followed a similar trend as SG, increasing from pith to bark (Fig. 4; Table 3), reflecting the small effect of treatments on V^2 . Average MOE_E and MOE_L increased from 3.5 and 7.0 GPa at age 4 up to 5.5 and 18.0 GPa at age 11, respectively. MOE_R , on the other hand, increased from 4 GPa at age 4 to 12 GPa at age 11 (Fig. 4).

During the 2003 (when the irrigation system was working only intermittently) and 2004 (when the system was not functioning) (L.Samuels, personal communication) growing seasons, irrigated and control plots did not differ in SG_R ($P = 0.57$ and 0.46, respectively) or LW% ($P = 0.11$ and 0.60, respectively). However, in 2005 when irrigation was reactivated in June, a significant effect of irrigation on SG_R and LW% ($P = 0.004$ and 0.002, respectively) was observed (Fig. 3). From age 5 in 1999, the SC family had higher SG_R and LW% than the FL family mix, and those differences were maintained even when irrigation was suspended ($P < 0.001$) (Figs. 3 and 5). In 2005 at age 11, LW% was not significantly different between FL and SC ($P = 0.556$). SG_L was not affected by irrigation ($P = 0.708$) or taxa ($P = 0.421$) and no irrigation \times genetic material interaction was detected ($P = 0.919$). SG_L increased from initial values of about 0.43 in 1995 (similar to SG_R at the same age) to a maximum of ~ 0.70 between ages 9 and 11 (Fig. 3). This trend to reach a maximum SG_L between ages 9 and 11 was not attained for V_L^2 , which continued increasing at a more or less constant yearly rate, at least until age 11, when our sampling was carried out (data not shown).

In terms of whole-core weighted wood properties (Table 4), irrigation showed no effect on SG and LW% ($P = 0.40$ and 0.22, respectively), averaging across genetic materials values of 0.455 and 0.461 in whole-core weighted SG and values of 40.28% and 42.24% in whole-core

Table 5. Least square means for four parameters of the fitted logistic model and demarcation points for corewood and outerwood for irrigation × genetic treatments.

	Control		Irrigated		<i>P</i> > <i>F</i>		
	FL	SC	FL	SC	Irrigation	Genetic	Irrigation × genetic
<i>a</i>	50.62	55.92	52.19	58.19	0.314	0.0017	0.670
<i>b</i>	1.208	1.184	0.787	0.834	0.126	0.944	0.836
<i>x</i> ₀	7.06	5.86	5.69	5.55	0.006	0.016	0.04
<i>y</i> ₀	20.89	15.33	15.78	18.39	0.781	0.637	0.231
<i>t</i> _{max}	6.50	5.67	5.90	5.43	0.093	0.021	0.415
<i>t</i> _{min}	14.37	13.30	10.47	10.77	0.016	0.727	0.538
<i>t</i> _{min} – <i>t</i> _{max}	7.87	7.63	4.57	5.33	0.023	0.795	0.628

Note: FL, Florida family mix; SC, South Carolina coastal plain half-sib family; *a*, upper asymptote; *b*, rate of change; *x*₀, inflection point; *y*₀, lower asymptote; *t*_{max}, corewood demarcation age; *t*_{min}, outerwood demarcation age; *t*_{max} – *t*_{min}, transition zone. *P* values used the mixed model procedure for split-plot design. Model: $LW\% = y_0 + (a - y_0)/(1 + e^{(age-x_0)/b})$.

weighted LW% for control and irrigated trees, respectively. The SC material had higher whole-core SG and LW% than the FL material (*P* = 0.018 and 0.003, respectively). There was no effect of irrigation or genetic material on whole-core *V*² (*P* = 0.90 and 0.22, respectively) and MOE (*P* = 0.52 and 0.11, respectively).

Annual ring growth

After excluding rings from 1995 and 1996, irrigation significantly affected annual ring (*A*_R), earlywood (*A*_E), and latewood ring area (*A*_L) (square centimetres) (Table 3; Fig. 5); however, the response to water availability depended on the year of growth (*P* < 0.014 for year × irrigation interaction). Irrigated and control plots did not differ in *A*_R growth in 2002, 2003, and 2004 (in these two last years, the stand received scarce or no irrigation). In the case of *A*_E, the irrigation treatments differed only between 1997 and 1999 (*P* < 0.001). The amount of irrigation applied between July and November was positively and strongly related to the difference in *A*_L (*P* = 0.009, *R*² = 0.65) (Fig. 6). The effects of irrigation on *A*_L were maintained until 2002 (*P* < 0.05), 3 years longer than *A*_R. Then, during 2003 and 2004, when irrigation was intermittent or turned off, no difference in latewood production was detected, but during 2005, when irrigation was restarted, the effect of water supply on *A*_L was significant again (*P* = 0.0016) (Fig. 5e). At a genetic material level, even though SC tended to produce more *A*_R than FL (Fig. 5b), only in 1998 and 2005 was that difference significant (*P* < 0.025). There was no difference in *A*_E between taxa (*P* = 0.88). *A*_L was significantly higher in SC during most irrigated years since 1999 and was not associated with precipitation during each year indicated by a relatively constant difference in *A*_L, independent of rainfall or irrigation (Fig. 5f). Only during 2004, when irrigation was not applied, was the effect of genetic material not significant (*P* = 0.13). Irrigated trees had both larger whole-core total *A*_E and *A*_L (*P* = 0.003 and *P* < 0.001, respectively) (Table 4). No irrigation × genetic material interaction was detected for any variable measured (Tables 3 and 4).

Demarcation points between corewood and outerwood and proportion of corewood

As the irrigation response in the two genetic materials was related to changes in LW% rather than intrinsic changes

in SG or MOE, demarcation points for corewood and outerwood were determined using LW% as the dependent variable in a logistic function. The estimated values of demarcation points as well as the four parameters of the fitted logistic model are given in Table 5. Irrigation did not affect parameter *a* (upper asymptote), but the SC trees reached outerwood with 5%–6% higher asymptotic values of LW% (*P* = 0.0017) (Table 5) independent of water availability conditions (no irrigation × genetic material interaction). The parameter *x*₀ (inflection point or age when LW% reached half of *a*) was affected by both irrigation and taxa, with a significant irrigation × genetic material interaction (*P* = 0.04). Under water-deficient conditions, *x*₀ differed between FL and SC (*P* = 0.006), averaging 7.1 and 5.9 years for FL and SC, respectively, but under irrigated conditions, the families were the same (*P* = 0.63), averaging *x*₀ ≈ 5.6 years. For SC, *x*₀ was not affected by water availability (*P* = 0.31), whereas FL showed different *x*₀ when there was no water deficit (*P* = 0.003). The parameters *b* (scale parameter) and *y*₀ (lower asymptote) were not affected by treatments (Table 5).

The corewood demarcation point (*t*_{max}) was not affected by water availability (*P* = 0.094) but differed between taxa (*P* = 0.021) (Table 5); SC started producing transition wood 0.65 year before FL. For irrigated trees, transition wood zone (*t*_{min} – *t*_{max}) was 2.8 years shorter than for rain-fed trees (*P* = 0.022) for both FL and SC genetic materials. There was no effect of genetic material on the outerwood demarcation point. Outerwood started to be produced at age 10.6 and 13.8 in irrigated and rainfed conditions, respectively (*P* = 0.016).

Discussion

While numerous observational studies suggest that water relationships and length of growing season interact to affect tree wood properties (Larson 1963; Antonova and Shebeko 1986; Cregg et al. 1988; Myers and Talsma 1992; Dougherty et al. 1994; Jayawickrama et al. 1998; Rozenberg et al. 2002; Sánchez-Vargas et al. 2007; Gruber et al. 2010), this is the first study to our knowledge to comprehensively test these hypotheses by experimentally manipulating soil water availability. After crown closure, increasing summer and fall water availability (via irrigation from June to Novem-

ber) increased SG and LW% by extending the length of the growing season. These results suggest that limiting water availability in the fall likely affects the timing of the onset of vascular cambial meristem dormancy. Bassett (1964) concluded that diameter growth cessation depended on soil moisture and evaporation demand and, in the absence of drought, diameter growth can continue until late in the season when other factors, such as temperature and (or) photoperiod, trigger cessation. In our study, variability in the date of BA cessation through irrigation was well correlated with variability in SG and LW%. The positive and strong relationship between the amount of water applied through irrigation between July and November and the gain in latewood area was concordant with the results of Cregg et al. (1988), where loblolly pine with higher SG and LW% occurred in years with high compared with years with low summer rainfall.

Samuelson et al. (2004) reported that in the first 4 years of the experiment investigated here, irrigation treatments increased leaf area index (LAI) (3.8 versus 2.0 m²·m⁻² in irrigated and control plots, respectively). After age 4, LAI in the control plots continued to increase steadily until age 6 when the LAI of control and irrigated treatments was the same, and between ages 8 and 10, Samuelson et al. (2008) reported no differences in peak LAI between control and irrigated plots, which is consistent with our LAI measurements in October 2005 at age 10 (Table 2). Our results show that the early age responses to irrigation that promoted LAI led to increases in A_R and A_E (Fig. 5). After this initial effect of water availability on LAI up to age 6, A_E was not different between irrigated and control trees (Fig. 5c).

Independent of the irrigation effect on earlywood formation, more latewood was produced each year when irrigation was applied. In contrast with our findings, Albaugh et al. (2004) reported no effect of irrigation on BA, SG_R , and LW% in 10- to 12-year-old irrigated loblolly trees grown on an infertile and somewhat excessively drained sandy soil. As Larson et al. (2001) pointed out, earlywood and latewood are independently related to SG, so annual growth in A_E and A_L determinations (Fig. 5) can help to understand SG patterns. The dynamics in earlywood and latewood production response to water availability explains the marginal effect of irrigation on whole-core-weighted SG. Larson et al. (2001) indicated that irrigation throughout the whole season will promote more earlywood and latewood with negligible final effects on SG, but as soil moisture is most commonly limiting during late-season growth, irrigation should promote latewood formation increasing SG (in our site, on average between 1995 and 2005, 35% of total yearly rain fell between January and March when the trees were not growing).

Trees under nonlimiting soil water conditions started to produce outerwood ~3 years before rain-fed trees, even though corewood demarcation age was not affected by irrigation. Our results for nonirrigated conditions are concordant with demarcation ages reported by Mora et al. (2007) and Tassisa and Burkhart (1998). These authors also pointed out that early intensive silviculture treatments (Mora et al. 2007) and thinning (Tassisa and Burkhart 1998) have no effect on outerwood transition age. Planting density and site preparation have also been reported to not change outer-

wood transition age (Clark and Saucier 1989; Clark and Edwards 1999). Jordan et al. (2008) and Clark et al. (2006a) also found that, besides genetic variation, most of the variability in demarcation age was associated with differences in the geographic area where Gulf coastal plain sites had earlier ages of corewood demarcation. In our study, a constant increase in LW% of irrigated trees was reflected in a shortened transition from corewood to outerwood, producing corewood at age 10.6 instead of age 13.8, for rain-fed trees. Thus, sites within the same geographical region with higher soil water availability during summer and fall produce more latewood each year and reach outerwood-type wood at younger ages. Even though the age at which outerwood production started was not different between taxa, the outerwood demarcation point was approximately 1 year sooner for the SC than for the FL material in rain-fed conditions.

Several authors indicate that loblolly pine latewood initiation is under genetic control. Cregg et al. (1988) found that 70% of the 10-year-old loblolly pine trees that initiated latewood formation early in a dry year also initiated latewood formation earlier in a wet year. Jayawickrama et al. (1997) reported that Atlantic coastal plain loblolly pine (ACP, the provenance of our SC family) transitioned from earlywood to latewood 10–20 days earlier than North Florida provenance trees. The same authors also reported higher average SG and LW% for ACP than FL source trees. Interestingly, bud break started during the same week in all of the families and provenances, suggesting that ACP and FL provenances did not vary in the day of height growth initiation (Jayawickrama et al. 1998). Here, genetic material differences in SG were related to the fact that SC had greater latewood areas (SG of latewood and earlywood was similar between taxa). This difference in latewood growth was not related, at least during the 2005 season, to differences in growing period cessation, since both taxa averaged similar BA growth cessation day. Thus, this difference between taxa could be related to higher growth rates of SC during latewood formation and (or) earlier transition from earlywood to latewood production for the SC genetic material. Interestingly, the FL material evolved with greater water availability during the growing period compared with the SC material, with an evapotranspiration to precipitation ratio of 1.07 versus 1.39, suggesting that the SC family may be better adapted to water deficits because of its ability to make more latewood.

No effect of irrigation was observed for V^2 or MOE in contrast with the significant effects reported for fertilization (Clark et al. 2004; Antony et al. 2009), fertilization combined with weed control (Clark et al. 2004; Roth et al. 2007), and initial plantation density (Roth et al. 2007; Lasserre et al. 2009). The stability of wood stiffness to different water availability shows that changes in V^2 are not related to LW% and are consistent with the observation that differences in V^2 are due predominately to changes in cellulose microfibril angle.² The irrigation-induced changes in transition age observed with LW% and not for MOE indicate that these properties change independently during cell differentiation, similar to the findings reported by Clark et al. (2006a). Thus, as reported by others, the transition age depends on genetic and environmental factors.

Conclusion

After the fast initial response to irrigation associated with increased LAI development, long-term responses of wood quality traits to water availability are primarily related to an extended growing season and associated increase in latewood production. Trees from the South Carolina coastal plain half-sib family produced more latewood than trees from the north-central Florida family mix. Soil moisture limitations constrain latewood growth on loblolly pine plantations, reducing both SG and LW%, and eventually extending the period to reach mature outerwood as defined by SG. The two genetic materials differed in the amount of carbon allocated to latewood, perhaps reflecting differences in adaptive traits related with ambient humidity and water availability that promote differences in growth period length. These findings from juvenile wood need to be evaluated in older trees to confirm the trends of water availability and genetic material effects on mature outerwood properties of loblolly pine. It will also be important to expand analyses to include a wider range of genetic material, which will allow broader genetic inference than could be achieved in this study.

Acknowledgements

The authors thank International Paper, Inc. for access to the study site, Dr. Michael Kane and Mr. Mark Register for project assistance and maintenance of the irrigation treatment, and Mr. Cristóbal González for his help with V^2 measurements. Funding was provided by the USDA Forest Service, National Science Foundation award No. 0344029, and the Forest Biology Research Cooperative at the University of Florida.

References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., and Johnsen, K.H. 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manag.* **192**(1): 3–19. doi:10.1016/j.foreco.2004.01.002.
- Allen, H.L., Fox, T.R., and Campbell, R.G. 2005. What is ahead for intensive pine plantation silviculture in the South? *South. J. Appl. For.* **29**: 62–69.
- Antonova, G.F., and Shebeko, V.V. 1986. Influence of environment on the secondary wall development of Scots pine tracheids. *Lesovedenie*, **2**: 72–76.
- Antony, F., Jordan, L., Daniels, R.F., Schimleck, L.R., Clark, A., III, and Hall, D.B. 2009. Effect of midrotation fertilization on growth and specific gravity of loblolly pine. *Can. J. For. Res.* **39**(5): 928–935. doi:10.1139/X09-021.
- Bassett, J.R. 1964. Diameter growth of loblolly pine trees as affected by soil-moisture availability. *U.S. For. Serv. Res. Pap. SO-9*.
- Cherry, M.L., Vikram, V., Briggs, D., Cress, D.W., and Howe, G.T. 2008. Genetic variation in direct and indirect measures of wood stiffness in coastal Douglas-fir. *Can. J. For. Res.* **38**(9): 2476–2486. doi:10.1139/X08-087.
- Clark, A., III, and Edwards, E.M. 1999. Effect of six site-preparation treatments on piedmont loblolly pine wood properties at age 15. *In Proceedings of the Tenth Biennial Southern Silvicultural Research Conference, Shreveport, La, 16–18 February 1999. Edited by J.D. Haywood. U.S. For. Serv. Gen. Tech. Rep. SRS 30. pp. 316–320.*
- Clark, A., III, and Saucier, J.R. 1989. Influence of initial planting density, geographic location, and species on juvenile wood formation in southern pine. *For. Prod. J.* **39**: 42–48.
- Clark, A., III, Borders, B.E., and Daniels, R.F. 2004. Impact of vegetation control and annual fertilization on wood properties of loblolly pine at age 12. *For. Prod. J.* **54**: 90–96.
- Clark, A., III, Daniels, R.F., and Jordan, L. 2006a. Juvenile–mature wood transition in loblolly pine as defined by annual ring specific gravity, proportion of latewood, and microfibril angle. *Wood Fiber Sci.* **38**: 292–299.
- Clark, A., III, Daniels, R.F., Miller, J.H., and James, H. 2006b. Effect of controlling herbaceous and woody competing vegetation on wood quality of planted loblolly pine. *For. Prod. J.* **56**: 40–46.
- Courchene, C.E., Peter, G.F., and Litvay, J. 2006. Cellulose microfibril angle as a determinant of paper strength and hygroexpansivity in *Pinus taeda* L. *Wood Fiber Sci.* **38**: 112–120.
- Cregg, B.M., Dougherty, P.M., and Hennessey, T.C. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climate factors. *Can. J. For. Res.* **18**(7): 851–858. doi:10.1139/x88-131.
- Dougherty, P.M., Whitehead, D., and Vose, J.M. 1994. Environmental influences on the phenology of pine. *Ecol. Bull.* **43**: 64–75.
- Fox, T.R., Jokela, E.J., and Allen, H.L. 2007. The development of pine plantation silviculture in the southern United States. *J. For.* **105**: 337–347.
- Gonzalez-Benecke, C.A., and Martin, T.A. 2010. Water availability and genetic effects on water relations of loblolly pine (*Pinus taeda*) stands. *Tree Physiol.* **30**(3): 376–392. doi:10.1093/treephys/tpq118. PMID:20071360.
- Gruber, A., Strobl, S., Veit, B., and Oberhuber, W. 2010. Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiol.* **30**(4): 490–501. doi:10.1093/treephys/tpq003. PMID:20197285.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., and McCulloh, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia (Berl.)*, **126**(4): 457–461. doi:10.1007/s004420100628.
- Hanover, J.W. 1963. Geographic variation in ponderosa pine leader growth. *For. Sci.* **9**: 86–95.
- Hoag, M.L., and Kraemer, R.L. 1991. Polychromatic X-ray attenuation characteristics and wood densitometry applications. *Wood Fiber Sci.* **23**: 23–31.
- Jayawickrama, K.J.S., McKeand, S.E., Jett, J.B., and Wheeler, E.A. 1997. Date of earlywood–latewood transition in provenances and families of loblolly pine, and its relationship to growth phenology and juvenile wood specific gravity. *Can. J. For. Res.* **27**(8): 1245–1253. doi:10.1139/cjfr-27-8-1254.
- Jayawickrama, K.J.S., McKeand, S.E., and Jett, J.B. 1998. Phenological variation in height and diameter growth in provenances and families of loblolly pine. *New For.* **16**: 11–25.
- Jett, J.B., McKeand, S.E., and Weir, R.J. 1991. Stability of juvenile wood specific gravity of loblolly pine in diverse geographic areas. *Can. J. For. Res.* **21**(7): 1080–1085. doi:10.1139/x91-148.
- Jordan, L., Schimleck, L.R., Clark, A., III, Hall, D.B., and Daniels, R.F. 2007. Estimating optimum sampling size to determine weighted core specific gravity of planted loblolly pine. *Can. J. For. Res.* **37**(11): 2242–2249. doi:10.1139/X07-085.
- Jordan, L., Clark, A., III, Schimleck, L.R., Hall, D.B., and Daniels, R.F. 2008. Regional variation in wood specific gravity of planted loblolly pine in the United States. *Can. J. For. Res.* **38**(4): 698–710. doi:10.1139/X07-158.
- Kumar, S., Burdon, R.D., and Stovold, G.T. 2008. Wood properties

- and stem diameter of *Pinus radiata* in New Zealand: genetic parameter estimates of clonal and seedling material. *N.Z. J. For. Sci.* **38**: 88–101.
- Larson, P.R. 1963. The indirect effect of drought on tracheid diameter in red pine. *For. Sci.* **9**: 52–62.
- Larson, P.R., Kretschmann, D.E., Clark, A., III, and Isenbrands, J.G. 2001. Juvenile wood formation and properties in southern pine. U.S. For. Serv. Gen. Tech. Rep. FPL-GTR-129.
- Lasserre, J.P., Mason, E.G., Watt, M.S., and Moore, J.R. 2009. Influence of initial planting spacing and genotype on microfibril angle, wood density, fiber properties and modulus of elasticity in *Pinus radiata* D. Don corewood. *For. Ecol. Manag.* **258**(9): 1924–1931. doi:10.1016/j.foreco.2009.07.028.
- Li, X., Huber, D.A., Powell, G.L., White, T.L., and Peter, G.F. 2007. Breeding for improved growth and juvenile corewood stiffness in slash pine. *Can. J. For. Res.* **37**(10): 1886–1893. doi:10.1139/X07-043.
- Lindström, H., Harris, P., Sorensson, C.T., and Evans, R. 2004. Stiffness and wood variation of 3-year old *Pinus radiata* clones. *Wood Sci. Technol.* **38**: 579–597. doi:10.1007/s00226-004-0249-1.
- Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. D. 1996. SAS® system for mixed models, SAS Institute Inc., Cary, N.C.
- McKeand, S., Mullin, T., Byram, T., and White, T. 2003. Deployment of genetically improved loblolly and slash pine in the South. *J. For.* **101**: 32–37.
- Megraw, R.A. 1985. Wood quality factors in loblolly pine. The influence of tree age, position in tree, and cultural practice on wood specific gravity, fiber length, and fibril angle. Tappi Press, Atlanta, Ga.
- Mora, C.R., Allen, H.L., Daniels, R.F., and Clark, A., III. 2007. Modeling corewood–outerwood transition in loblolly pine using wood specific gravity. *Can. J. For. Res.* **37**(6): 999–1011. doi:10.1139/X06-250.
- Mora, C.R., Schimleck, L.R., Isik, F., Mahon, J.M., Jr., Clark, A., III, and Daniels, R.F. 2009. Relationships between acoustic variables and different measures of stiffness in standing *Pinus taeda* trees. *Can. J. For. Res.* **39**(8): 1421–1429. doi:10.1139/X09-062.
- Myers, B.J., and Talsma, T. 1992. Site water balance and tree water status in irrigated and fertilized stands of *Pinus radiata*. *For. Ecol. Manag.* **52**(1–4): 17–42. doi:10.1016/0378-1127(92)90494-T.
- Panshin, A.J., and de Zeeuw, C. 1980. Textbook of wood technology. 4th ed. McGraw-Hill, New York.
- Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-plus. Springer Series in Statistics and Computing. Springer-Verlag, New York.
- Pittermann, J., Sperry, J.S., Hacke, U.G., Wheeler, J.K., and Sikkema, E. 2006a. Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. *Am. J. Bot.* **93**(9): 1265–1273. doi:10.3732/ajb.93.9.1265.
- Pittermann, J., Sperry, J.S., Wheeler, J.K., Hacke, U.G., and Sikkema, E.H. 2006b. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant Cell Environ.* **29**(8): 1618–1628. doi:10.1111/j.1365-3040.2006.01539.x. PMID:16898022.
- Roth, B.E., Li, X., Huber, D.A., and Peter, G.F. 2007. Effects of management intensity, genetics and planting density on wood stiffness in a plantation of juvenile loblolly pine in the southeastern USA. *For. Ecol. Manag.* **246**(2–3): 155–162. doi:10.1016/j.foreco.2007.03.028.
- Rozenberg, P., Van Loo, J., Hannrup, B., and Grabner, M. 2002. Clonal variation of wood density record of cambium reaction to water deficit in *Picea abies* (L.) Karst. *Ann. For. Sci.* **59**(5–6): 533–540. doi:10.1051/forest:2002038.
- 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., Johnsen, K., and Stokes, T. 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to six years of intensive management. *For. Ecol. Manag.* **192**(1): 59–70. doi:10.1016/j.foreco.2004.01.005.
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T., Johnsen, K., and Kane, M. 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**(4): 721–732. doi:10.1139/X07-191.
- Sánchez-Vargas, N.M., Sánchez, L., and Rozenberg, P. 2007. Plastic adaptive response to weather events: a pilot study in a maritime pine tree ring. *Can. J. For. Res.* **37**(11): 2090–2095. doi:10.1139/X07-075.
- Schultz, R.P. 1997. The ecology and culture of loblolly pine (*Pinus taeda* L.). USDA Forest Service, Washington, D.C.
- Sierra-Lucero, V., McKeand, S.E., Huber, D.A., Rockwood, D.L., and White, T.L. 2002. Performance differences and genetic parameters for four coastal provenances of loblolly pine in the southeastern United States. *For. Sci.* **48**: 732–742.
- Solomon, S., Qin, D., Manning, M., Alley, R.B., Berntsen, T., Bindoff, N.L., Chen, Z., Chidthaisong, A., Gregory, J.M., Hegerl, G.C., Heimann, M., Hewitson, B., Hoskins, B.J., Joos, F., Jouzel, J., Kattsov, V., Lohmann, U., Matsuno, T., Molina, M., Nicholls, N., Overpeck, J., Raga, G., Ramaswamy, V., Ren, J., Rusticucci, M., Somerville, R., Stocker, T.F., Whetton, P., Wood, R.A., and Wratt, D. 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. Edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller.* Cambridge University Press, Cambridge, U.K., and New York.
- Sperry, J.S. 2000. Hydraulic constraints on plant gas exchange. *Agric. For. Meteorol.* **104**(1): 13–23. doi:10.1016/S0168-1923(00)00144-1.
- Sperry, J.S., and Ikeda, T. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiol.* **17**(4): 275–280. PMID:14759867.
- Tassisa, G., and Burkhart, H.E. 1998. Juvenile-mature wood demarcation in loblolly pine trees. *Wood Fiber Sci.* **30**: 119–127.
- Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. *Trees (Berl.)*, **17**: 95–100.