



## Ecophysiological comparison of 50-year-old longleaf pine, slash pine and loblolly pine

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### ARTICLE INFO

#### Article history:

Received 15 December 2011

Received in revised form 13 February 2012

Accepted 19 February 2012

Available online 29 March 2012

#### Keywords:

*Pinus palustris*

*Pinus elliotii*

*Pinus taeda*

Water use efficiency

Photosynthesis

Leaf water potential

### ABSTRACT

Longleaf pine (*Pinus palustris* Mill.), a species that once dominated the southeastern USA, is considered to be more drought tolerant than the principle plantation species in the South, loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliotii* Engelm.), and so is predicted to better cope with increases in drought frequency associated with climate change. To determine if longleaf pine displays a more conservative water use strategy than the other two southern pine species, we examined diurnal patterns in leaf light-saturated photosynthesis, stomatal conductance, water use efficiency and leaf water potential ( $\Psi_L$ ) over one growing season in a 50-year-old replicated field experiment. Short-term photosynthetic response to temperature was examined in August. No consistent differences among species in leaf gas exchange rates were observed, but  $\Psi_L$  was higher in longleaf pine compared to loblolly and slash pine across the growing season. Foliar  $\delta^{13}C$  measured at the end of the growing season was higher in longleaf pine than in loblolly pine but not slash pine. No temperature optimum of photosynthesis was observed in any species and photosynthesis did not respond to changing temperature. Based on leaf physiological traits, these results do not support the contention that longleaf pine has a more conservative leaf water use strategy than the other two pine species. The results do suggest that differences in hydraulic architecture or hydraulic efficiency may account for higher  $\Psi_L$  and perhaps greater drought tolerance in longleaf pine.

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### 1. Introduction

Planted pine forests in the southeastern USA produce more timber than any other country and approximately 16% of the global industrial wood supply (Prestemon and Abt, 2002; Wear and Gries, 2002). Loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliotii* Engelm.), are the dominant plantation species in the South (Sheffield and Knight, 1982; Sheffield et al., 1983; Schultz, 1997). However, prior to European settlement, longleaf pine (*Pinus palustris* Mill.) forests occupied from 24 to 36 million ha in the Gulf and Atlantic Coastal Plains of the southern USA (Stout and Marion, 1993), but because of land use changes, difficulties in seedling establishment, fire suppression and conversion to other southern pines, longleaf pine now occupies 3–5% of its original expanse (Brockway and Lewis, 1997; Gilliam and Platt, 1999). There is a renewed interest in restoring longleaf pine for high value wood products, pine straw production, wildlife and biodiversity benefits and carbon sequestration (South, 2006). In addition, increasing the acreage of longleaf pine has been proposed as a path toward climate change adaptation in southern forests (Diop et al., 2009).

The percentage of area in the southeastern USA experiencing drought has increased since the 1970s and continued warming with longer intervals between rainfall events is predicted for the southeastern USA through the end of this century (Trenberth, 1998; Karl et al., 2009). Higher temperatures will influence plant physiological processes directly as well as increase soil evaporation and plant transpiration, and thus increase the frequency, duration and intensity of drought (Karl et al., 2009) and perhaps, southern forest productivity (McNulty et al., 1996; Noormets et al., 2010). Longleaf pine has been suggested as a species that can contribute to climate change mitigation, because of long rotations and long-term carbon storage combined with greater resistance to insects, diseases and wind damage, less energy inputs relative to the more intensively managed loblolly pine and slash pine (Stanturf et al., 2007; Johnsen et al., 2009), and superior tolerance to both drought and low soil nutrition, which has been largely assumed based on success of longleaf pine on highly well-drained sandy sites. Longleaf pine has generally been considered a slower growing southern pine, but over longer rotations, growth of longleaf pine may exceed that of loblolly pine (Schmidtling, 1987). Given the resurgence of interest in restoring longleaf pine by federal and state agencies and private landowners, there is a basic need for information on longleaf pine physiology, and in particular drought and high temperature tolerance, relative to other southern pines.

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The objective of this research was to compare leaf physiological characteristics among 50-year-old trees of longleaf pine, loblolly pine and slash pine in a long-term, replicated field experiment in southern MS. Diurnal patterns in light-saturated photosynthesis ( $A_{\text{sat}}$ ), stomatal conductance ( $g_s$ ), water use efficiency (WUE) and leaf water potential ( $\Psi_L$ ) were examined from May through September of one year and short-term photosynthetic response to controlled temperature change was measured in August. We tested the hypotheses that: (1) longleaf pine would employ a more conservative water-use strategy defined by lower  $g_s$ , increased WUE and avoidance of low  $\Psi_L$ , whereas the other pines would employ a more prodigal water-use strategy defined by higher  $g_s$  and tolerance of lower  $\Psi_L$  (Donovan et al., 2000), and (2) because all three species are exposed to long, hot summers with extremes frequently exceeding 38 °C (Baker and Langdon, 1990; Boyd, 1990; Lohrey and Kossuth, 1990), the photosynthetic temperature optimum would not vary among species.

## 2. Materials and methods

### 2.1. Experimental site

The research site is located in the USDA Forest Service Harrison Experimental Forest near Saucier, MS in the DeSoto National Forest located 32 km north of Gulfport, MS (30.65N, 89.04W, elevation 50 m). The experiment was established in 1960 for growth and genetics studies on longleaf, loblolly, and slash pine (Schmidtling, 1973). The climate is temperate-humid subtropical with average annual precipitation of 1651 mm distributed evenly throughout the year (Adams et al., 2004). Soils are well-drained, fine sandy loams in the Poarch series and the Saucier–Susquehanna complex and low in nutrients. The site is in the Gulf Coastal Plain within the historic range of longleaf pine. The site was not used for agriculture and the original longleaf pine forest was clear cut in 1900 and naturally regenerated. Prior to plantation establishment the area was stocked with second growth longleaf pine which was cut in 1959 (Schmidtling, 1973). Weather data for 2010 was obtained from the National Oceanic and Atmospheric Administration (<http://www1.ncdc.noaa.gov/pub/data/cirs/>).

The study was designed as a randomized complete block with split plots and five cultivation–fertilization treatments, three species, two specific gravity seed sources and four replicates, for a total of 120 plots (Johnsen et al., 2009). Whole plots within a block represented the species treatment and consisted of 10 (two specific gravity treatments  $\times$  five cultivation–fertilization treatments) 100-tree plots. Five treatments were established: (1) no cultivation or fertilization, (2) cultivated with no fertilization, (3) cultivated with a single application of 112 kg ha<sup>-1</sup> of NPK fertilizer, (4) cultivated with a single application of 224 kg ha<sup>-1</sup> of NPK fertilizer, and (5) cultivated with a single application of 448 kg ha<sup>-1</sup> NPK fertilizer. Cultivated plots were disked prior to planting, disked three times each season for the next three years and mowed in years 4 and 5 to reduce competition. Fertilizer was applied one year after planting. Loblolly, longleaf and slash pine seedlings were grown in a nursery using local seed and grouped by two levels of wood specific gravity, low and high. Plots were planted with 100 one-year-old bare root seedlings on a 3.05  $\times$  3.05 m spacing in February and March of 1961. No thinnings were conducted.

Previous studies reported no differences in growth between the specific gravity groups within species so the two noncontiguous plots were combined (Schmidtling, 1973; Clark and Schmidtling, 1988). There were no differences in basal area between the fertilizer levels (treatments 3, 4 and 5) prior to Hurricane Katrina, which struck the site in August 2005 (Johnsen et al., 2009). An inventory in 2006 indicated differences in storm damage between loblolly

**Table 1**

Characteristics of plots selected for measurements at age 50 including survival, basal area (BA), and density, and range in diameter at breast height (DBH) of the three sample trees selected within a plot.

	Survival (%)	BA (m <sup>2</sup> ha <sup>-1</sup> )	Density (trees ha <sup>-1</sup> )	DBH (cm)
<b>Block 1</b>				
Loblolly pine	25	18.1	269	32.5–34.9
Longleaf pine	24	18.2	258	33.9–39.1
Slash pine	16	15.6	172	33.6–35.4
<b>Block 2</b>				
Loblolly pine	25	18.6	269	31.5–35.4
Longleaf pine	37	24.5	398	32.7–35.1
Slash pine	41	21.1	441	30.5–35.2
<b>Block 3</b>				
Loblolly pine	22	18.5	237	35.3–40.2
Longleaf pine	33	19.0	355	31.1–32.3
Slash pine	26	18.5	280	32.3–33.5

pine and longleaf pine with loblolly pine suffering more storm related mortality than longleaf pine (Johnsen et al., 2009).

Plots within blocks were selected based on treatment and basal area (Table 1). Only plots receiving cultivation and a level of fertilization (112, 224 or 448 kg ha<sup>-1</sup> NPK fertilizer) were chosen. Plot selections were based on stand structure (Table 1) rather than the same level of fertilization since previous studies showed a significant difference between fertilized and unfertilized plots but not between the different levels of fertilizer (Clark and Schmidtling, 1988; Johnsen et al., 2009). One plot per species was selected in each block and only blocks 1–3 from the original study were used. Three dominant trees were selected in each plot based on diameter at breast height (1.37 m, DBH) (Table 1). The range of DBH values for the selected trees was from 31.5 to 40.2 cm. Prescribed fire was applied to the site on February 17, 2010. No crown scorching was observed in any of the selected plots one month after the fire. The experiment was 50 years-old at the start of data collection.

### 2.2. Leaf physiological measurements

Light-saturated leaf net photosynthesis,  $g_s$ , WUE ( $A_{\text{sat}}$ /transpiration) and  $\Psi_L$  were measured May 12–14, June 15–17, July 13–15, and September 13–15, 2010 on fascicles from each of the three trees of each species in a plot. Measurements were made at 830, 1200, and 1500 h and one block was randomly selected and measured a day. Leaf gas exchange measurements were made at a photosynthetically active radiation (PAR) level of 1800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , CO<sub>2</sub> concentration of 400 ppm and at ambient temperature and leaf to air vapor pressure deficit ( $D$ ) using a portable gas exchange system (LICOR 6400, Li-Cor, Inc., Lincoln, NE, USA). During measurements, average air temperature and  $D$  were 34.9 °C and 2.9 kPa in May, 33.1 °C and 2.1 kPa in June, 34.6 °C and 2.5 kPa in July, and 31.7 °C and 2.5 kPa in September, respectively.

Shoots were detached from trees using a shotgun and fascicles measured within 3 min following detachment (Samuelson et al., 2001; Maier et al., 2002). One-year-old needles were measured in May and the first current year flush was measured in June, July and September. After gas exchange measurements, needle length and diameter were measured and dry mass determined. Needle gas exchange rates were calculated on a total area basis (Samuelson et al., 1992). Specific leaf weight (SLW) was determined as needle dry mass per total area. Leaf water potential was measured on a fascicle from each tree using a pressure chamber (PMS Instrument Co., Corvallis, OR). Soil moisture was measured at the 830 h measurement session in each plot using time domain reflectometry (Trace System I, Soil Moisture Equipment Corp., Santa Barbara,

CA, USA). Soil moisture was measured at a north and south aspect of each tree 1 m from the base and values averaged across aspect.

To determine the duration of time that stomata would remain open following the detachment of shoots and during measurement of photosynthetic response to controlled temperature,  $g_s$  was compared between needles *in situ* in the crown and on detached shoots from the same branch on May 11, 2010. Stomatal conductance of attached shoots and detached shoots placed in water was measured using two portable gas exchange systems (Li-6400, Li-Cor Inc., Lincoln, NE, USA). We compared cut and *in situ* paired branches to determine the duration of time stomata remained open following detachment. A bucket truck was used to access the crowns of one tree of each species on the edge of three plots. Six pairs per tree, consisting of a detached and attached shoot from the same main branch, were monitored over time. Measurements were made from 900 until 1600 h. Results are shown in Fig. 1 and indicate that  $g_s$  of detached shoots remained stable for up to 5 h. Temperature response curves were measured on August 10–12, 2010 on one detached shoot, approximately 30 cm in length, from each tree. Shoots were re-cut underwater and the cut-ends kept in water for the duration of sampling. The first current year flush was measured. Leaf gas exchange was measured at a PAR of  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $\text{CO}_2$  concentration of 400 ppm. The gas exchange systems were fitted with temperature control kits (LICOR 6400–88, Li-Cor Inc., Lincoln, NE, USA) to increase the temperature range in the leaf chamber. Detached shoots were placed in a growth chamber for the duration of measurements and exposed to each temperature for 30 min. The growth chamber and leaf cuvette were set at 20 °C, 30 °C, and 40 °C. Actual average leaf temperature at the set air temperatures was 23.6 °C, 30.5 °C and 37.6 °C, respectively. Because of the extended period of time needed to cool the leaf cuvette following a high temperature, measurements were made from lowest to highest temperature. Water was added to the soda lime to maintain  $D$  at 1–2 kPa and average  $D$  at 20 °C and 30 °C was 1.3 kPa and 1.6 kPa, respectively, but at 40 °C  $D$  increased to an average of 3.0 kPa. The first measurements were made 2 h after detachment and final measurements were completed within 4 h of detachment. One block was randomly selected and measured a day.

### 2.3. Foliar $\delta^{13}\text{C}$ and nitrogen analyses

Needles used in the September sampling were used for measurements of foliar  $\delta^{13}\text{C}$  and nitrogen concentration. Samples were pooled by plot. Needles were oven-dried to a constant mass at 65 °C and ground for 4 min using a ball mill grinder (Spex 8000, SPEX SamplePrep LCC, Metuchen, NJ, USA). Foliar N concentration was determined using a Carlo-Erba analyzer (NA 1500 Series I, Carlo Erba Instrumentation, Milan, Italy). For foliar  $\delta^{13}\text{C}$  measurements, samples were analyzed for the  $^{13}\text{C}:^{12}\text{C}$  ratio using the Duke University, Phytotron SIRA Seriea II isotope ratio mass spectrometer (Micromass, Manchester, UK) operated in automatic trapping mode after combustion of samples. The reference  $\text{CO}_2$  was standardized against the standard Pee Dee belemnite.

### 2.4. Statistical analyses

Data were averaged by month, block, species, and for diurnal measurements time of measurement. Effects of species and time of measurement, where appropriate, were tested using repeated measures analysis of variance (Proc Mixed, SAS Inc., Cary NC) with block treated as a random factor and species as a fixed factor. In all tests, effects were considered significant at  $\alpha = 0.10$ . Differences between species or temperature were determined using Tukey's paired comparison procedure. Functions describing  $g_s$  or WUE response to  $D$  were fit to each species-block combination using data

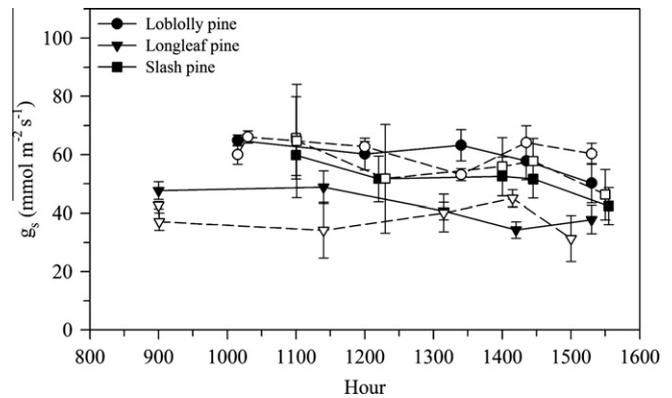


Fig. 1. Mean (SEM) stomatal conductance ( $g_s$ ) of attached (closed symbols) and detached (open symbols) foliage of loblolly pine, slash pine and longleaf pine over time. Each point represents six fascicles.

from current years foliage (June, July and September sessions) for a total of 27 sample points per block and species combination (3 dates, 3 trees, 3 measurement times within a date). Species effects on equation coefficients were tested as described above.

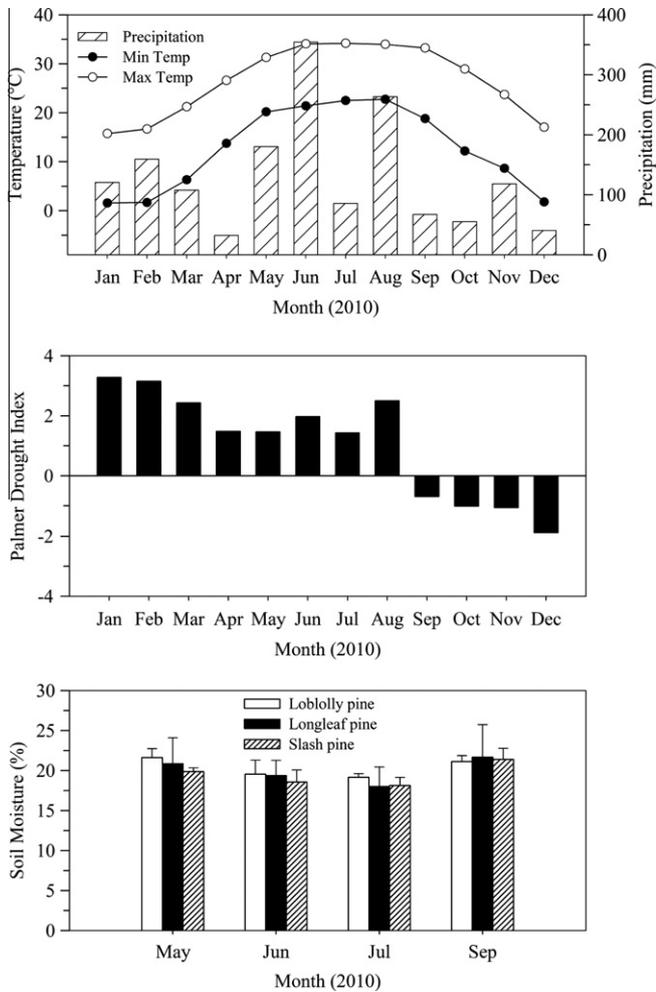
## 3. Results

### 3.1. Climate

Monthly precipitation in 2010 ranged from 32 mm in April to 355 mm in June and totaled 1584 mm for the year (Fig. 2). Average daily maximum temperatures ranged from 15.7 °C to 34.2 °C and minimum temperatures from 1.6 °C to 22.7 °C (Fig. 2). The Palmer Drought Index did not indicate significant drought until October and the last measurement session was mid-September (Fig. 2). Soil moisture measured at 830 h was not significantly different among species in any month (Table 2 and Fig. 2). Averaged across species, soil moisture ranged from 18.4% in July to 21.4% in September.

### 3.2. Leaf physiology

Within a sampling month, no significant time of measurement by species interactions were observed for any variable (Table 2). Time of measurement had a significant effect of  $A_{\text{sat}}$  and  $g_s$  in all months, and for the majority of months leaf gas exchange rates were higher during the morning session than the late afternoon session (Fig. 3). Time of measurement influenced WUE in June and September and in general WUE was lower at 1500 h. Leaf water potential was highest in the morning session in May, July and September (Table 2 and Fig. 4). Significant species effects were detected for  $A_{\text{sat}}$  in June and  $g_s$  in May and September (Table 2). In June, longleaf and slash pine had higher  $A_{\text{sat}}$ , 4.4 and  $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, than loblolly pine ( $3.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Fig. 3). Stomatal conductance was higher in loblolly pine and longleaf pine than in slash pine in May while in September  $g_s$  was lowest in longleaf pine (Fig. 3). With the exception of September when  $\Psi_L$  was high in all species,  $\Psi_L$  was consistently higher, approximately 0.5 MPa, in longleaf pine than in slash pine or loblolly pine (Fig. 4). No significant relationships between leaf gas exchange rates and  $\Psi_L$  or soil moisture were observed for any species (data not shown). An exponential decay relationship between  $g_s$  and  $D$  ( $y = a * e^{(b * D)}$ ) as described by Meinzer et al. (1984) provided the best fit to the data with  $R^2$  ranging from 0.89 to 0.94 (Fig. 5). A linear relationship between WUE and the inverse of  $D$  was significant for all species and blocks with  $R^2$  ranging from 0.30 to 0.61 (Fig. 5). No significant differences between spe-



**Fig. 2.** Monthly precipitation, mean minimum and maximum temperatures and the Palmer Drought Index during the year of the study (2010) and average (SEM) soil moisture by species during leaf gas exchange measurements.

**Table 2**

Observed probability values for the effects of species and time of measurement on leaf net photosynthesis ( $A_{\text{sat}}$ ), stomatal conductance ( $g_s$ ), water use efficiency (WUE), and leaf water potential ( $\Psi_L$ ) measured repeatedly during diurnal measurements and species effects on soil moisture measured at 0830 h.

Month	Variable	Time	Species	Time × species
May	$A_{\text{sat}}$	0.033	0.889	0.555
	$g_s$	0.015	0.064	0.369
	WUE	0.407	0.646	0.876
	$\Psi_L$	<0.001	0.058	0.168
	SM	–	0.749	–
	June	$A_{\text{sat}}$	0.006	0.039
$g_s$		0.029	0.683	0.276
WUE		0.006	0.093	0.302
$\Psi_L$		0.530	0.015	0.944
SM		–	0.792	–
July		$A_{\text{sat}}$	0.055	0.877
	$g_s$	0.010	0.666	0.737
	WUE	0.228	0.194	0.866
	$\Psi_L$	0.018	0.069	0.927
	SM	–	0.789	–
	September	$A_{\text{sat}}$	0.026	0.322
$g_s$		0.002	0.0244	0.137
WUE		0.001	0.701	0.472
$\Psi_L$		0.100	0.139	0.875
SM		–	0.983	–

cies in model coefficients were observed for either function (Table 3).

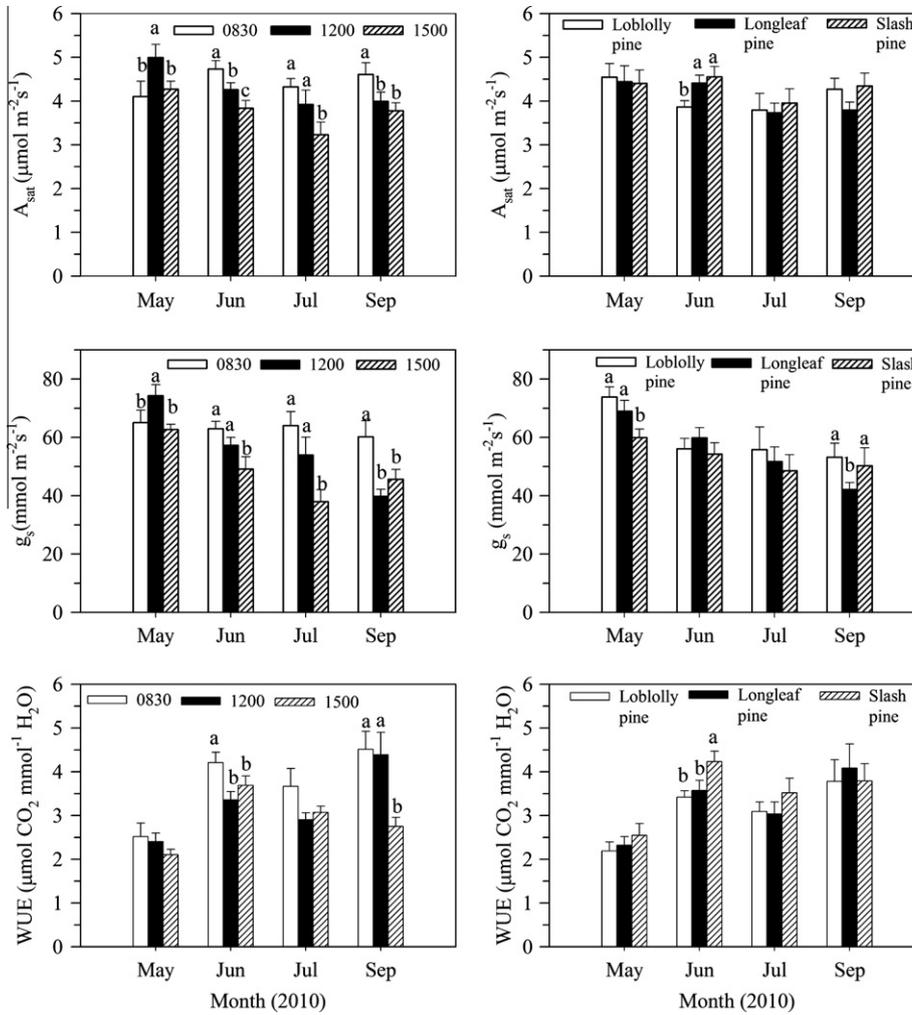
No significant main or interactive effects of temperature and species were observed for  $A_{\text{sat}}$  and  $g_s$  (Table 4). Light-saturated photosynthesis averaged across all temperatures and species was  $3.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $g_s$  was  $48.8 \text{ mmol m}^{-2} \text{s}^{-1}$ . Water use efficiency decreased with increasing temperature but did not vary with species. No significant effects of species on leaf temperature were observed (data not shown).

### 3.3. Foliar $\delta^{13}\text{C}$ and nitrogen concentration

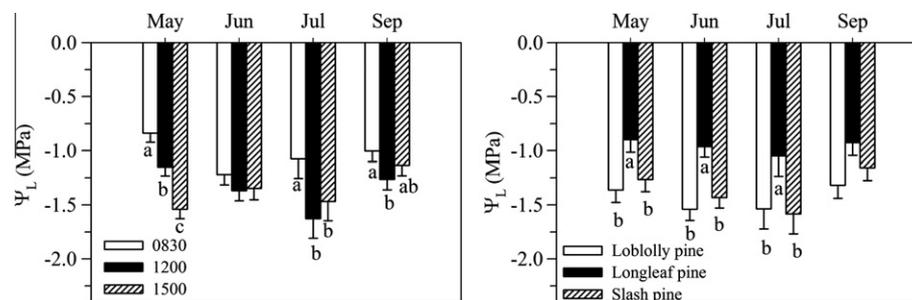
Foliar  $\delta^{13}\text{C}$  was higher (less negative) in longleaf pine than loblolly pine and similar between loblolly pine and slash pine (Table 3). Nitrogen concentration per unit leaf mass was  $10.5 \text{ mg g}^{-1}$  in loblolly pine and higher than in longleaf pine or slash pine (Table 3). Specific leaf weight was higher in slash pine and longleaf pine than loblolly pine (Table 3). When N concentration was expressed per unit leaf area, no species differences were observed.

## 4. Discussion

Although it has been presumed that longleaf pine may be more drought tolerant than the other southern conifers, physiology and growth of longleaf pine has previously been shown to be responsive to water availability (Foster and Brooks, 2001). For example, Ford et al. (2008) reported that longleaf pine productivity in savanna systems was regulated by water table depth. Using tree-ring chronologies, Henderson and Grissino-Mayer (2009) determined that the Palmer Drought Severity Index and Palmer Hydrological Drought Index had the highest correlation with longleaf pine growth, and precipitation in the spring and summer was also positively related to growth. In separate experiments,  $g_s$  at the leaf and canopy level of mature longleaf pine, slash pine and loblolly pine has been shown to be sensitive to  $D$  (Addington et al., 2006; Domec et al., 2009; Gonzalez-Benecke et al., 2011) and likewise in this study,  $g_s$  of all three species was sensitive to  $D$ . The relationship between  $g_s$  and  $D$  has been commonly described by the function  $g_s = a + b(\ln D)$  for many species including loblolly pine and most often based on crown canopy conductance at high PAR calculated from sap flux measurements (Samuelson et al., 2008; Domec et al., 2009). However, an exponential function of the form  $g_s = a * e^{(b * D)}$  provided the best fit to  $g_s$  and  $D$  in all three species. A similar function was reported for 50-year-old Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) (Lagergren and Lindroth, 2002) and for two tropical coniferous species (Meinzer et al., 1984). We had no measurements of  $g_s$  at  $D < 1.5 \text{ kPa}$  and many measurements at higher  $D$  ( $D > 2.0 \text{ kPa}$ ), not usually encountered in other studies. It is possible that inclusion of measurements at lower  $D$  and correspondingly higher maximum  $g_s$  may have changed the relationship between  $g_s$  and  $D$ . Alternatively, Drake et al. (2010) observed less sensitivity of canopy  $g_s$  to  $D$  with increasing age in loblolly pine trees ranging in age from 14 to 97 years, because of lower maximum canopy  $g_s$  rates at low  $D$  in older trees. Within the ambient range of  $D$  in our study, the hypothetical maximum  $g_s$  ( $a$ ) and the sensitivity of  $g_s$  to  $D$  ( $b$ ) did not vary significantly with species. Likewise, Gonzalez-Benecke et al. (2011) reported no differences in sensitivity of canopy  $g_s$  to  $D$  between co-occurring mature slash pine and longleaf pine but longleaf pine demonstrated greater sensitivity of canopy  $g_s$  to low soil moisture than slash pine when under drought conditions. We observed no relationship between  $g_s$  and soil moisture or  $\Psi_L$  in any species, most likely because of the absence of significant or prolonged soil moisture stress during the study. All three species exhibited an inverse relationship between WUE and  $D$ , as reported



**Fig. 3.** Mean (SEM) light-saturated net photosynthesis ( $A_{\text{sat}}$ ), stomatal conductance ( $g_s$ ) and water use efficiency (WUE) in response to hour of measurement and species by month. Different letters indicate time or species differences based on Tukey tests.

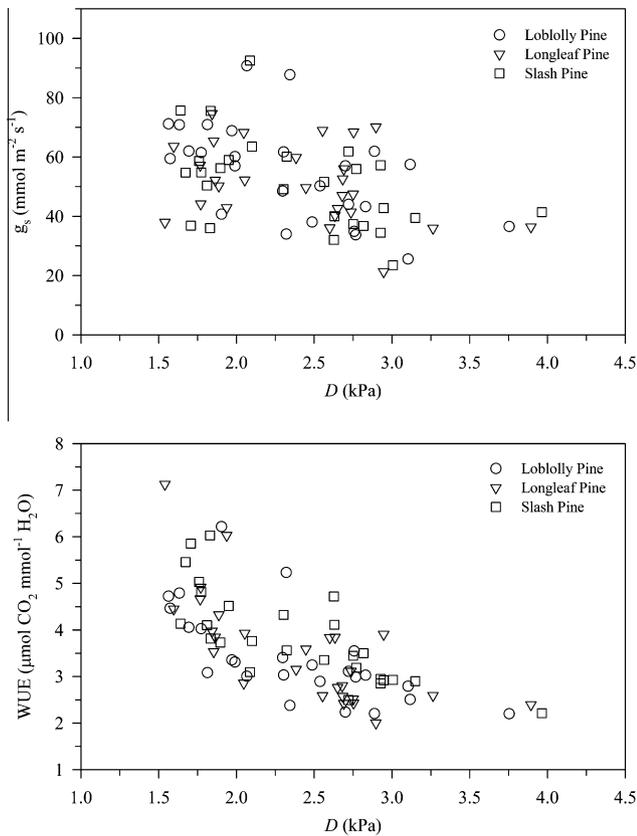


**Fig. 4.** Mean (SEM) leaf water potential ( $\Psi_L$ ) by month in response to hour of measurement and species. Different letters indicate time or species differences based on Tukey tests.

for a variety of forest species (Baldocchi et al., 1987; Law et al., 2002), which indicates a conservative nature when  $D$  is high (Tang et al., 2006) and suggests similar optimization of plant water use among species (Mahrt and Vickers, 2002). Powell et al. (2008) reported a comparable relationship between stand-level WUE and  $D$  in a natural longleaf-slash pine forest that was not altered by drought.

We observed higher foliar  $\delta^{13}\text{C}$ , and presumably greater needle WUE across the growing season, in longleaf pine relative to loblolly pine and consistently higher  $\Psi_L$  in longleaf pine relative to both species, but no consistent differences in leaf  $g_s$  and WUE that

would support a more conservative water use strategy in longleaf pine. Compared to other reports of foliar  $\delta^{13}\text{C}$  in longleaf pine, the average  $\delta^{13}\text{C}$  of  $-29.06\text{‰}$  falls within the range of  $\delta^{13}\text{C}$  ( $-29\text{‰}$  to  $-25\text{‰}$ ) reported for foliage of mature longleaf pine on more water limited sites but is closer to values for foliage under less water stress (Samuelson et al., 2003). Anderson and Johnsen (2009) reported a range in foliar  $\delta^{13}\text{C}$  from  $-28.7\text{‰}$  to  $-26.8\text{‰}$  in mature longleaf pine on a sandhills site which also suggests that soil water was not as limiting in our study. Avoidance of low  $\Psi_L$  in longleaf pine may be due to greater hydraulic efficiency rather than significant differences in leaf-level gas exchange. For example, a higher



**Fig. 5.** Stomatal conductance ( $g_s$ ) and leaf water use efficiency (WUE) in response to leaf to air vapor pressure deficit ( $D$ ) in 50-year-old loblolly pine, slash pine and longleaf pine. Each data point represents a mean of three replicates per block, species, date, and measurement session.

sapwood to leaf area ratio and higher maximum sapwood-specific hydraulic conductivity in roots was observed in mature longleaf pine compared to mature slash pine that may provide longleaf pine with a competitive advantage on drier soils (Gonzalez-Benecke et al., 2010; Gonzalez-Benecke et al., 2011). Addington et al. (2006) compared hydraulic traits and leaf gas exchange of mature longleaf pine between a xeric and mesic site and determined that adjustments in hydraulic architecture such as an increase in the root area to leaf area ratio and increase in conductivity of small roots accounted for similar  $g_s$  between sites. Ford et al. (2008) reported WUE at the whole-tree level based on sap flux measurements that was twofold greater in mature longleaf pine relative to values in the literature for mature loblolly pine (Sun et al., 2000). On well-drained soils, longleaf pine has a large tap root (4 m beneath the soil surface for a 250-year-old tree) and wide spreading root system (up to 23 m) (Heyward, 1933) that may provide greater access to water during drought than in loblolly and slash pine. However, direct comparison of root morphology and depth among species is lacking. It is possible that during severe drought typically associated with longleaf pine habitat, longleaf pine may exhibit a more conservative water use strategy. For

**Table 4**

Mean (SEM) light-saturated net photosynthesis ( $A_{sat}$ ), stomatal conductance ( $g_s$ ) and water use efficiency (WUE) in response to temperature and species and observed probability values for species and temperature effects. Different letters indicate temperature or species differences based on Tukey tests.

	$A_{sat}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$g_s$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol CO}_2$ $\text{mmol}^{-1} \text{H}_2\text{O}$ )
Temperature ( $^{\circ}\text{C}$ )			
20	$3.1 \pm 0.3$	$42.6 \pm 5.5$	$5.85 \pm 0.50$ a
30	$3.1 \pm 0.2$	$51.1 \pm 3.7$	$4.02 \pm 0.24$ b
40	$3.1 \pm 0.2$	$52.8 \pm 8.1$	$2.21 \pm 0.33$ c
$P > F$	0.968	0.458	<0.001
Species			
Loblolly pine	$3.2 \pm 0.2$	$51.7 \pm 5.1$	$3.82 \pm 0.58$
Slash pine	$3.2 \pm 0.2$	$55.5 \pm 5.3$	$3.64 \pm 0.50$
Longleaf pine	$2.8 \pm 0.3$	$39.3 \pm 6.8$	$4.62 \pm 0.77$
$P > F$	0.460	0.170	0.145
Temperature $\times$ species			
$P > F$	0.945	0.996	0.714

example, Lewis et al. (2011) observed similar leaf physiological traits across six *Eucalyptus* species native to xeric and mesic environments and concluded that physiological differences between species were driven by environmental factors associated with habitat rather than inter-specific genetic variation.

Temperature may influence leaf net photosynthesis by affecting processes such as the rate of enzyme kinetics, mitochondrial respiration, photorespiration,  $\text{CO}_2$  solubility and photosynthetic membrane composition (Berry and Björkman, 1980; Jordan and Ogren, 1984; Sage and Kubien, 2007) and, alone or in combination with  $D$ , stomatal opening (Medlyn et al., 2002). Increasing temperature has been shown to increase (Lewis et al., 2001), decrease (Callaway et al., 1994) or have little effect on  $A_{sat}$  (Cunningham and Read, 2002). A distinct temperature optimum for photosynthesis has been observed in a variety of tree species (Battaglia et al., 1996; Man and Loeffers, 1997; Hikosaka et al., 2007; Dreyer et al., 2001) including deciduous species in the southeastern USA (Gunderson et al., 2010). The majority of temperature studies in trees have been conducted on seedlings, often with conflicting results. For example, in loblolly pine seedlings there are reports of: (1) no sensitivity of photosynthesis to temperature (Teskey et al., 1986; Werten et al., 2010), (2) declines in photosynthesis at higher measurement temperatures (Nedlo et al., 2009), and (3) sensitivity of photosynthesis based on growth temperature, with less sensitivity to high temperature in seedlings grown at warmer temperatures (Teskey and Will, 1999). Of the available mature tree studies, no distinct temperature optimum for net photosynthesis has been observed in slash pine or loblolly pine (Ellsworth, 2000; Teskey et al., 1994). Based on work by Werten et al. (2010) with loblolly pine saplings, insensitivity of  $A_{sat}$  to temperature is likely a result of a result of a broad temperature optimum and not acclimation of  $A_{sat}$  to temperature. Similarly, Way and Oren (2010) in a meta-analysis of 58 tree species found little support for acclimation of photosynthetic capacity to increases in temperature. In a temperate climate such as in the southeastern USA with high seasonal and day-to-day variation in temperature, a broad tempera-

**Table 3**

Mean (SEM) specific leaf area (SLW), foliar nitrogen concentration per unit leaf weight ( $N_m$ ) or leaf area ( $N_a$ ), foliar  $\delta^{13}\text{C}$ , and coefficients for equations describing the relationship between stomatal conductance ( $y = a * e^{(b*D)}$ ) or water use efficiency ( $y = c + d(1/D)$ ) and leaf to air vapor pressure deficit ( $D$ ) by species. Observed probability values for species effects are indicated. Different letters indicate species differences based on Tukey tests.

Species	SLW ( $\text{g m}^{-2}$ )	$N_m$ ( $\text{mg g}^{-1}$ )	$N_a$ ( $\text{g m}^{-2}$ )	$\delta^{13}\text{C}$ (‰)	$a$	$b$	$c$	$d$
Loblolly pine	$73.8 \pm 1.9$ b	$10.5 \pm 0.2$ a	$0.77 \pm 0.04$	$-30.66 \pm 0.19$ b	$126.50 \pm 23.0$	$-0.35 \pm 0.11$	$0.64 \pm 0.10$	$6.17 \pm 0.55$
Slash pine	$90.4 \pm 1.6$ a	$9.0 \pm 0.5$ b	$0.82 \pm 0.03$	$-29.98 \pm 0.29$ ab	$97.66 \pm 22.90$	$-0.26 \pm 0.09$	$0.47 \pm 0.56$	$7.68 \pm 1.53$
Longleaf pine	$87.1 \pm 1.8$ a	$9.0 \pm 0.5$ b	$0.78 \pm 0.01$	$-29.06 \pm 0.24$ a	$83.48 \pm 20.48$	$-0.18 \pm 0.11$	$-0.22 \pm 0.76$	$8.55 \pm 1.91$
$P > F$	0.003	0.084	0.684	0.041	0.537	0.635	0.363	0.270

ture optimum would maintain maximum photosynthesis over a wide span of temperatures (Cunningham and Read, 2002).

## 5. Conclusions

In summary, a more conservative water use strategy in longleaf pine defined by lower  $g_s$  and higher WUE relative to loblolly pine and slash pine was not supported, although leaf  $\delta^{13}C$  was higher in longleaf pine than in loblolly pine. Higher  $\Psi_L$  in longleaf pine than in loblolly pine and slash pine suggests possible adaptation to drier environments through hydraulic changes such as in the leaf area to sapwood area ratio, allocation to root versus shoot, and rooting depth, or increases in hydraulic efficiency such as in root conductivity (Addington et al., 2006; Gonzalez-Benecke et al., 2010; Gonzalez-Benecke et al., 2011). Species differences in  $\Psi_L$  do not appear to impact leaf gas exchange but higher  $\Psi_L$  might impact productivity on dry sites via increased leaf turgor pressure and cell volume growth (Johnsen and Major, 1999). No species differences in short-term photosynthetic response to temperature and no photosynthetic temperature optimum was evident which supports the supposition that temperature interactions with other environmental factors such as drought rather than large changes in photosynthesis with temperature may dominate southern pine forest response to climate change (Dillaway and Kruger, 2010; Gunderson et al., 2010; Wertin et al., 2010).

## Acknowledgements

This project was funded by the USDA Forest Service, Southern Research Station and the Center for Longleaf Pine Ecosystems at Auburn University.

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