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

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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 elliottii* 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 (Ψ_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 Ψ_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 Ψ_L and perhaps greater drought tolerance in longleaf pine.

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 elliottii* 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_{sat}), stomatal conductance (g_S), water use efficiency (WUE) and leaf water potential (Ψ_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 Ψ_L, whereas the other pines would employ a more prodigal water-use strategy defined by higher g_S and tolerance of lower Ψ_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.

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^2 ha^{-1})	Density (trees ha^{-1})	DBH (cm)
Block 1				
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
Block 2				
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
Block 3				
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

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 × 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^{-1} of NPK fertilizer, (4) cultivated with a single application of 224 kg ha^{-1} of NPK fertilizer, and (5) cultivated with a single application of 448 kg ha^{-1} 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 × 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 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^{-1} 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_{sat}/transpiration) and Ψ_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 μmol m^{-2} s^{-1}, CO_2 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,