# **Original Article**

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# Specific gravity of slash, longleaf, and loblolly pine growth rings formed in mature trees during periods of drought

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**Abstract:** Studies linking wood properties of the southern pines to climate parameters and/or irrigation treatments have generally used seedlings or mid-rotation age trees, the latter comprised primarily of juvenile wood. To investigate possible drought-induced effects on mature wood physical properties, densitometry data from 50-year-old slash (Pinus elliottii Engelm.), longleaf (Pinus palustris Mill.), and loblolly (taeda L.) pine trees were matched with annual soil moisture values. Each of two growth ring groupings per increment core had a two-year period of ample moisture followed by a two-year period of drought; these were centered at ages of 20 and 38 years. For slash pine, the latewood width was 30% lower (p = 0.011) for the drought period at age 20. Seemingly similar results were obtained for longleaf pine, but the probability (p = 0.051) just exceeded the threshold for significance ( $\alpha$  = 0.05). No differences were observed for either earlywood or total ring widths. Ring specific gravity (SG) values that were 11% lower for slash pine and 7% lower for longleaf pine can be attributed to drought-related reductions in latewood formation. Unlike other studies with younger trees, both percent latewood and ring SG values for mature loblolly pine were unaffected by drought.

**Keywords:** drought; earlywood; latewood; southern yellow pine; specific gravity.

### 1 Introduction

The southern pine forests are the leading timber resource for wood production in the USA with the volume of planted

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As the growing season commences in the spring, earlywood (springwood) formation in the conifers is initiated and continues until higher temperatures and lower moisture availability during the summer months leads into latewood (summerwood) formation. The higher specific gravity (SG) of latewood is imparted by tracheids having smaller lumens, thicker cell walls, and smaller cell sizes (Larson 1969; Zobel and van Buijtenen 1989). Transient increases in tracheid cell wall thickness can occur in the earlywood, triggered by signals similar to those for latewood formation (Gonzalez-Benecke et al. 2015; Marchand and Filion 2012). These narrow bands of tracheids with higher cell wall thicknesses, called false rings (or intraannual density fluctuations), can be distinguished from true growth rings by a gradual decrease in cell wall thickness over time as opposed to the abrupt change in cell wall thickness that occurs between growth rings (Carvalho et al. 2015; Copenheaver et al. 2006; Wimmer et al. 2000).

Trees with fast growth rates, especially at lower ages, are more prone to the formation of false rings (Marchand and Filion 2012). Studies on pines have generally shown false rings to be associated with water stress (Hoffer and Tardif 2009; Marchand and Filion 2012); however, a study with jack pine (*Pinus banksiana*) showed no significant relationship to either precipitation or temperature (Copenheaver et al. 2006). Unlike the pines, perturbations in the cell wall thicknesses of spruce (*Picea abies*, *Picea mariana*) tracheids were found to be more sensitive to temperature than water availability (Franceschini et al. 2012, 2013; Gričar et al. 2015; Hoffer and

Tardif 2009). In another study on P. abies, temperature (and precipitation) did not show any significant relationship to measures of growth (ring width) or latewood formation (Wimmer and Grabner 2000).

For loblolly pine, aside from drought causing reduced growth ring widths (Graham et al. 2012), and the occurrence of false rings (Gonzalez-Benecke et al. 2015), lower proportions of latewood have been reported (Cregg et al. 1988; Hennessey et al. 2004). Accordingly, while the normal seasonal decline in soil moisture (and increase in temperature) leads to latewood formation through the summer and autumn months, drought conditions during this timeframe limit the extent that latewood formation continues to occur, effectively lowering the growth ring SG. Conversely, studies providing ample supplies of water via irrigation, used to mimic wetter years, can result in more latewood formation and higher ring SG (Gonzalez-Benecke et al. 2010; Love-Myers et al. 2010), although this is not always the case (Albaugh et al. 2004). It should be acknowledged that the longer growing season for loblolly pine on the southernmost sites is also a factor in greater latewood formation (Jokela et al. 2004).

In a detailed review by Zahner (1963) on the impacts of moisture stress on wood formation in conifers, limitations to our understanding of the impacts on large trees were twofold. First, findings with seedlings have been extrapolated to large trees, and second, when interpreting growth rings from transverse sections (or increment cores), researchers could only surmise which wood cells were formed as moisture conditions varied throughout the year. Regarding the extrapolation of seeding data to mature trees, young loblolly pine trees (age 3 years) had a higher proportion of latewood under drought than with irrigation (Zahner 1962), which was an opposite finding from those more recently determined for loblolly pine trees at age 10 or older (Cregg et al. 1988; Gonzalez-Benecke et al. 2010; Hennessey et al. 2004). Considering these differences, and observations that wood formed lower in loblolly pine tree boles is impacted more by water stress than higher up (Zahner 1968), it is apparent that wood maturity is highly relevant when assessing the impact of drought on various wood properties.

To date, studies linking the wood properties of the southern pines to annual climate data, and/or irrigation, have used mid-rotation age trees (ca. 10 years) for which the increment cores examined are mostly comprised of juvenile wood (Albaugh et al. 2004; Cregg et al. 1988; Gonzalez-Benecke et al. 2010, 2015). In a study by Hennessey et al. (2004), similar effects of drought were observed in the mature wood growth rings, those being from the last 3 years of data collection for rotation age trees with stand age of 24 years. Opportunities to investigate the

impacts of climate parameters of temperature and/or precipitation on mature wood properties is limited given the current short rotation ages (20-25 years) for loblolly pine sawtimber (Dahlen et al. 2018). Specific to mature loblolly trees (age ca. 50 years), a prior study for trees grown on two mainland USA sites and a Hawaii site provides some insight into the effects of temperature/precipitation on growth (Samuelson et al. 2013). While relationships of growth to monthly and annual climate parameters were assessed, wood properties were averaged to whole core and mature wood only data for between-site comparisons. Interestingly, while the longer growing season at the Mississippi site resulted in more latewood formation than at the North Carolina site, the trees grown in Hawaii, under favorable temperatures over most of the year, had the lowest percent latewood and lowest ring SG, attributable in part to atypical ring density profiles.

Among the three main southern pines, longleaf pine has greater suitability to drier sites compared to loblolly and slash pines (Landers 1991; Lantz 1987); slash pine outperforms loblolly pine on the wettest sites (Borders and Harrison 1989). In a prior study with these three southern pine species, within- and between-species comparisons were conducted to assess the impact of solvent extraction on the wood property data (Eberhardt and Samuelson 2015). In the present study, the X-ray densitometry data from the slash, longleaf and loblolly pine increment cores were matched with annual Palmer Drought Severity Index (PDSI) values to select growth ring groupings formed during periods of above- and below-normal soil moisture. As a meteorological index, the PDSI classifies drought conditions using precipitation and temperature data along with soil type; increasingly negative PDSI values correspond to the increasing severity of the drought. Results presented here now provide direct within- and between-species comparisons of wood property data for mature southern pines, paired by periods of ample soil moisture followed by drought.

# 2 Materials and methods

### 2.1 Study trees and increment core collection

Plantation slash, longleaf, and loblolly pine trees sampled for this study were from a replicated field experiment established in 1960 on the USDA Forest Service's Harrison Experimental Forest (30.65N, 89.04W) within the DeSoto National Forest (Mississippi, USA). Soils there are well-drained, fine-sandy loams in the Poarch series and Saucier-Susquehanna complex. The climate is classified as temperatehumid subtropical (Adams et al. 2004). Soil moisture (PDSI) data (Figure 1, Table 1) from a weather station near the site were obtained

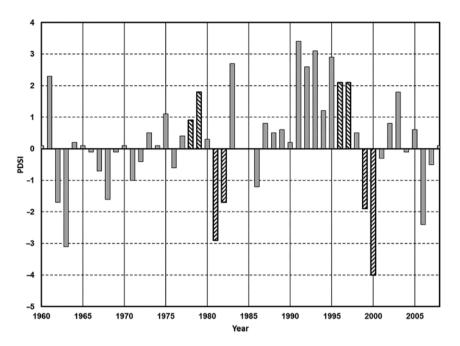


Figure 1: Palmer drought severity index (PDSI) at the study site over the years assigned for the increment cores. Bars with diagonal lines show targeted +PDSI and -PDSI years corresponding to growth rings for wood property comparisons.

from the National Oceanic and Atmospheric Administration (https:// www.ncdc.noaa.gov/cdo-web/). Detailed information about the study design and history of the trees can be found in Samuelson et al. (2012); see also Schmidtling (1973). Using an increment borer, a single pith-tobark increment core (12 mm diameter) was collected in 2010 at breast height (1.37 m) from each of nine dominant trees representing each of the three southern pine species at the study site. This gave a total of 27 increment cores for our analysis. The breast-height diameter ranges for the trees were as follows: slash pine, 30.5-35.4 cm; longleaf pine, 31.1-39.1 cm; loblolly pine, 31.5-40.2 cm. Basal area and stand density data for the study plots sampled can be found in Samuelson et al. (2012). The trees boles had round circumferences; there were no indications of compression wood formation in any of the increment cores removed.

Table 1: Annual PDSI, precipitation and average annual temperature for years selected for comparison of growth rings formed under wet periods (+PDSI) followed by periods of drought (-PDSI).

	PDSI value	PDSI soil moisture condition	Precipitation (cm)	Average (°C)
1978	0.9	Incipient wet	176.5	19.2
1979	1.8	Mild wet	231.2	19.0
1981	-2.9	Moderate drought	136.5	19.7
1982	-1.7	Mild drought	179.2	20.1
1996	2.1	Moderate wet	147.0	19.5
1997	2.1	Moderate wet	201.2	19.6
1999	-1.9	Mild drought	122.8	20.5
2000	-4.0	Severe drought	113.9	20.2

### 2.2 Wood property determinations

The increment cores, 27 in all, were processed into X-ray densitometry specimens as described in Eberhardt and Samuelson (2015). The data used herein are for specimens subjected to exhaustive (i.e., Soxhlet) extraction with acetone, thus eliminating the contribution of extractives to the SG values, especially for longleaf pine wood, known to be resinous. Briefly, wood properties (SG, percent latewood) and ring widths were determined by X-ray densitometry (Model QTRS-01X, Quintek Measurement Systems, Knoxville, TN, USA) using density measurements collected with an interval of 0.06 mm. A SG of 0.480 was used as the threshold between earlywood and latewood zones (Antony et al. 2012; Clark et al. 2006). Densitometer calibration was on a green volume and oven-dried mass basis.

Using the PDSI plot for the study site (Figure 1), specific years were selected to obtain growth rings from years with high and low soil moisture. Two timeframes were selected showing patterns of noticeably +PDSI years followed by -PDSI (i.e., drought) years. At the target zone centered at an age of 20 years, there were two +PDSI years (1978, 1979) followed by two -PDSI years (1981, 1982). The growth ring for 1980, between these growth ring groupings, had normal soil moisture. Likewise, at the target zone centered at an age of 38 years, two +PDSI years (1996, 1997) were followed by two -PDSI years (1999, 2000). The growth ring for 1998, between these growth ring groupings, had normal soil moisture. Paired t-tests were carried out using MS Excel.

### 3 Results and discussion

## 3.1 Growth ring selection by PDSI values

Years representing periods of above normal (+PDSI) and below normal (drought, -PDSI) soil moisture conditions at

the study site were selected from the plotted PDSI data (Figure 1). These periods of time constituted 2 years with +PDSI values being paired with the same number of years with -PDSI values. Annual precipitation and average annual temperature data are provided in Table 1, showing lower precipitation and higher temperature values for the periods of drought paired with the preceding periods of ample soil moisture. While individual years could have been compared, the PDSI data allowed for two years which could compensate for lag phases in tree growth from year to year. Likewise, it was fortuitous that a normal year  $(-0.5 \le PDSI \le 0.5)$  occurred between each wet period and drought period. Since climatic conditions as far back as 2 years prior have the potential to impact current growth in longleaf pine (Meldahl et al. 1999), the normal soil moisture (PDSI) year would seemingly reduce the influence of moisture carry over from wet periods preceding drought periods.

The increment cores used in the present study are unique in that they are from the same site and same age trees, but more importantly, they are from mature trees that are not often studied, especially for loblolly pine, because of short rotation ages typical of intensively managed plantations. Indeed, the age of the loblolly pine trees studied here (50 years) is twice that of stands managed for pulp/lumber. It should also be noted that the juvenile to mature wood transition in loblolly pine occurs near a cambial age of 10 years (Clark et al. 2006, Jordan et al. 2008); based on the inflection points for ring SG and percent latewood data, the transition for longleaf pine may extend out to higher cambial ages, up to even 20 years (Eberhardt et al. 2018, 2019). Thus, with increased tree age

and girth, the volume of latewood is increased, imparting the desired increases in wood SG and mechanical properties that accompany tree maturity. In the present study, the growth ring groupings, each directly comparing +PDSI and -PDSI wood, were centered at ages of 20 and 38 years, providing mature wood data.

In a prior study with loblolly pine alone, a larger sampling allowed us to demonstrate limited correlations between ring width index and intra-annual climate parameter (e.g. monthly precipitation) variations (Samuelson et al. 2013). A different approach was taken in the current study to provide direct comparisons of growth rings near the same age between two-year periods of drought or ample soil moisture, assigned using annual values for PDSI; paired t-tests were deemed appropriate to provide a comparison suited to the limited number of trees sampled, that being nine trees per species. This wood quality assessment is unique in that it allows the comparison of the three most abundant southern pine species from a randomized complete block experimental design (Samuelson et al. 2012) with a specific focus on the mature wood zone.

### 3.2 Ring width data

Results presented in Table 2 provide ring width data that is broken down to the widths of earlywood and latewood. with the percent latewood being the percentage that the latewood width contributes to the (total) ring width. Relative comparisons between the earlier (years 1978–1979 and 1981–1982; centered at age 20 years) and later (1996–1997 and 1999-2000; centered at age 38 years) growth ring

Table 2: Differences in width and percent latewood values for growth rings formed under years assigned to wet periods (+PDSI) followed by periods of drought (-PDSI); probabilities are from paired t-tests.

Pine species		Earlywood width (mm)		Latewood width (mm)		Ring width (mm)		Percent latewood	
	Assigned years	1978-1979 1981-1982	1996-1997 1999-2000		1996-1997 1999-2000		1996-1997 1999-2000		1996-1997 1999-2000
	Age at center year	20	38	20	38	20	38	20	38
Slash	(+PDSI)	0.40 ± 0.43	0.61 ± 0.35	1.51 ± 0.55	1.35 ± 0.46	1.90 ± 0.93	1.97 ± 0.72	82.2 ± 11.2	71.9 ± 15.4
	(-PDSI)	$0.42 \pm 0.34$	$0.66 \pm 0.24$	$1.06 \pm 0.29$	$1.26 \pm 0.30$	$1.48 \pm 0.23$	$1.92 \pm 0.39$	72.5 ± 22.0	65.7 ± 11.7
	Difference	-0.02	-0.05	0.45	0.09	0.42	0.05	9.7	6.2
	<i>p</i> -value	0.891	0.556	0.011	0.486	0.181	0.781	0.226	0.136
Longleaf	(+PDSI)	$0.94 \pm 0.25$	$0.66 \pm 0.31$	$2.17 \pm 1.02$	$1.37 \pm 0.40$	3.11 ± 1.07	$2.03 \pm 0.44$	$67.9 \pm 9.5$	68.0 ± 14.7
	(-PDSI)	$1.04 \pm 0.29$	$0.73 \pm 0.24$	$1.45 \pm 0.43$	$1.20 \pm 0.39$	$2.49 \pm 0.55$	$1.92 \pm 0.48$	$57.6 \pm 9.3$	$62.0 \pm 9.6$
	Difference	-0.10	-0.07	0.72	0.17	0.62	0.11	10.3	6.0
	<i>p</i> -value	0.285	0.357	0.051	0.085	0.102	0.270	0.014	0.170
Loblolly	(+PDSI)	$0.63 \pm 0.50$	$0.76 \pm 0.21$	$1.49 \pm 0.54$	$1.09 \pm 0.53$	$2.12 \pm 0.74$	$1.85 \pm 0.65$	70.7 ± 20.9	56.3 ± 11.3
	(-PDSI)	$0.55 \pm 0.22$	$0.74 \pm 0.22$	$1.27 \pm 0.46$	$0.92 \pm 0.26$	$1.82 \pm 0.54$	$1.66 \pm 0.44$	69.4 ± 12.3	55.5 ± 5.7
	Difference	0.08	0.02	0.22	0.17	0.30	0.19	1.3	0.8
	<i>p</i> -value	0.567	0.291	0.096	0.291	0.088	0.368	0.785	0.834

groupings show that ring widths are generally narrower or the same for the more mature growth rings. There appears to be one exception, that being for the -PDSI ring widths for slash pine where the value for the more mature wood (age 38) is seemingly 0.44 mm wider (Table 2). The same trend was present for the slash pine -PDSI latewood and -PDSI earlywood widths. While the +PDSI earlywood width is also wider for the more mature slash pine growth rings (age 38), this is offset by a narrower +PDSI latewood width, affording seemingly similar +PDSI ring widths between the two ages (20 and 38 years). In the ring width data for loblolly pine, the wider earlywood widths, for both the +PDSI and -PDSI growth rings, were offset by narrower latewood widths. The net results were the more typical narrower growth rings for the more mature wood. Notwithstanding, the objective of the study was not to investigate various anomalies in ring width data, but these observations illustrate how ring widths are the sum of the earlywood and latewood widths, and that these latter two widths can be offsetting values within growth rings.

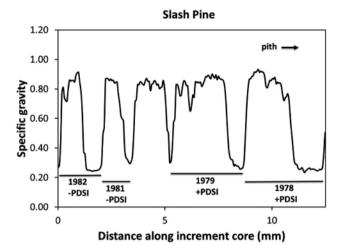
The +PDSI and -PDSI values for the width determinations were compared for the three pine species using paired t-tests and gave a significant difference (p = 0.011) for the slash pine latewood widths at age 20, but not age 38 (p = 0.486). The latewood width data at age 20 seemingly followed the same trend with longleaf and loblolly pines; however, the probability values (longleaf, p = 0.051; loblolly, p = 0.096) were higher than the threshold of statistical significance used ( $\alpha = 0.05$ ). Ring widths generally trend downward with increasing distance from the pith; however, comparing the width values (earlywood, latewood, ring) between ages showed that lower width values occurred only 60% of the time in side-by-side comparisons, that is, within the same species and within the same PDSI grouping (+PDSI or -PDSI). The smaller width values for the more mature growth rings (age 38) may have contributed to the lack of significant differences in comparisons between +PDSI and –PDSI groupings (via paired t-tests). Note that the two years of drought for years 1999 and 2000 were preceded by several years of ample moisture from years 1991 until 1997 (Figure 1). Since climatic conditions as far as 2 years prior were suggested to impact current conditions in longleaf pine (Meldahl et al. 1999), we cannot exclude this protracted wet period from impacting the age 38 +PDSI and -PDSI comparisons via the possibility for accumulated moisture carrying over into the drought years of 1999 and 2000.

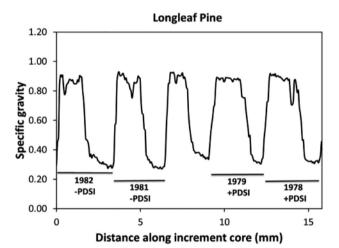
Whereas latewood formation for the southern pines is highly influenced by current moisture conditions, earlywood formation is not (Zahner and Grier 1990). This is especially true in the lower tree bole for which the tree will shift to latewood formation while earlywood formation still

continues for the higher tree bole that is closer to the crown, the source of photosynthates and growth hormones (Larson 1969; Zahner 1963, 1968). For a study on longleaf pine, latewood width provided a more "robust" signal from climate conditions than earlywood width or total ring width (Henderson and Grissino-Mayer 2009). Likewise, August rainfall, undoubtedly occurring in a month during which latewood is formed, was shown to be a better predictor for longleaf pine ring chronologies than any other month (Devall et al. 1991). Our data substantiates these assessments given the significant differences in latewood width (but not earlywood and total ring width) during our comparisons between +PDSI and -PDSI groupings (via paired *t*-tests) at age 20 years.

Data from X-ray densitometry, often averaged/ modeled for a set of increment cores, can afford plots of wood properties against cambial age (ring number) to demonstrate the changes (i.e., from pith to bark) in the growth ring properties, showing trends that unfold with tree maturation. Based on such plots, the juvenile wood to mature wood transition for loblolly pine is generally accepted to occur at a cambial age of 10 years (Clark et al. 2006; Jordan et al. 2008; Larson et al. 2001). Similar results for the study trees have been previously reported, along with SG profiles for individual growth rings (Eberhardt and Samuelson 2015). In studies by others, plots of individual growth rings have been useful for drawing associations between intra-annual ring density fluctuations (false rings) and climate conditions leading to their formation (Bouriaud et al. 2005).

Plots of SG against the distance along the increment core were generated in the present study for the growth rings centered on an age of 20 years (1980) for a single tree from each species (Figure 2). Unlike Bouriaud et al. (2005), that provided density values that corresponded to the day of the year, or a relative intra-ring position, the data presented here parallel our early work (Eberhardt and Samuelson 2015), using only the distance along the increment core. Briefly, the plot for slash pine shows wider latewood band for the +PDSI years (1978-1979) than those for the -PDSI years (1981–1982), matching the significant difference in latewood width (Table 2). The plots for longleaf and loblolly (Figure 2) are also reflective of the data shown in Table 2. Noteworthy from the SG profiles is that the earlywood to latewood transitions are not nearly as abrupt for loblolly pine as they are for slash and longleaf pine. For a given species, there are no apparent differences in said transitions between growth rings formed under different soil moisture conditions (wet vs. dry), here assigned by PDSI values.





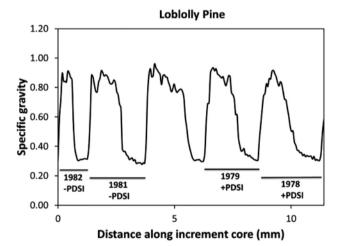


Figure 2: X-ray densitometry profiles for growth rings centered on a cambial age of 20 years and representing 2-year periods of ample moisture (1978–1979, +PDSI) and drought (1981–1982, -PDSI) for slash, longleaf, and loblolly pine increment cores.

### 3.3 Percent latewood and ring SG

The percent latewood value is based on the proportion of the ring width that is contributed by the latewood width. Differentiating between earlywood and latewood in the southern pines is commonly based on a threshold value for SG (e.g., 0.480) which is computationally straightforward with data collected by X-ray densitometry (Antony et al. 2012; Clark et al. 2006; Jordan et al. 2008). Comparison of the +PDSI and -PDSI groupings for percent latewood gave only one significant difference (p = 0.014), that being for longleaf pine at age 20 (Table 2). Since trends in ring SG closely follow the proportions of latewood and earlywood in the southern pine wood (Clark and Saucier 1989; Tasissa and Burkhart 1998), for the corresponding data in Table 3, ring SG for longleaf pine at age 20 was significantly lower (0.606 vs. 0.650; p = 0.007). The ring SG for slash pine was also significantly lower (0.637 vs. 0.717; p = 0.023) despite the absence of a difference for the corresponding percent latewood values. Both percent latewood and ring SG for loblolly pine were seemingly unaffected by drought. This is unlike other studies with loblolly pine that have shown a lower proportion of latewood for growth rings formed during droughts (Cregg et al. 1988; Hennessey et al. 2004). Intuitively, one might expect the ring SG to be lower, reflecting the lower proportion of latewood (Hennessey et al. 2004); however, this is not always the case (Cregg et al. 1988). While latewood SG for a different hard pine, Scots pine (Pinus sylvestris L.), was impacted by moisture (Candel-Pérez et al. 2018), we saw no differences in latewood SG for the three southern pines in our study. Indeed, the latewood SG values between +PDSI and -PDSI groupings (via paired t-tests) for a given age and species are all similar. The same holds true for the earlywood SG values.

### 3.4 Southern pine drought resistance

Longleaf pine is better suited to drier sites when compared to slash and loblolly pines (Landers 1991; Lantz 1987; Hart et al. 2020; Samuelson et al. 2012). Slash pine performs the best on very wet sites (Borders and Harrison 1989; Gibson et al. 1986). Our findings of significant differences in between the + PDSI and -PDSI data for latewood width, percent latewood, and ring SG were with longleaf pine and/or slash pine, for growth rings centered on an age of 20 years. Among the three southern pine species studied herein, these two species are at the extremes of adaptation

Table 3: Differences in specific gravity values for growth rings formed under years assigned to wet periods (+PDSI) followed by periods of drought (-PDSI); probabilities are from paired t-tests.

Pine species		Earlywood specific gravity		Latewood specific gravity		Ring specific gravity	
	Assigned years  Age at center year	1978-1979 1981-1982 20	1996-1997 1999-2000 38	1978-1979 1981-1982 20	1996-1997 1999-2000 38	1978-1979 1981-1982 20	1996–1997 1999–2000 38
Slash	(+PDSI)	0.370 ± 0.061	0.365 ± 0.060	0.798 ± 0.071	0.757 ± 0.069	0.717 ± 0.071	0.634 ± 0.061
	(-PDSI)	$0.348 \pm 0.051$	$0.351 \pm 0.054$	$0.762 \pm 0.077$	$0.784 \pm 0.055$	$0.637 \pm 0.092$	$0.631 \pm 0.074$
	Difference	0.022	0.013	0.036	-0.027	0.080	0.003
	<i>p-</i> value	0.100	0.237	0.126	0.278	0.023	0.907
Longleaf	(+PDSI)	$0.355 \pm 0.027$	$0.367 \pm 0.033$	$0.799 \pm 0.059$	$0.784 \pm 0.054$	$0.650 \pm 0.054$	$0.647 \pm 0.082$
	(-PDSI)	$0.342 \pm 0.023$	$0.364 \pm 0.028$	$0.799 \pm 0.051$	$0.788 \pm 0.041$	$0.606 \pm 0.064$	$0.625 \pm 0.058$
	Difference	0.013	0.003	0.000	-0.004	0.044	0.022
	<i>p-</i> value	0.122	0.771	0.951	0.746	0.007	0.262
Loblolly	(+PDSI)	$0.334 \pm 0.047$	$0.323 \pm 0.018$	$0.746 \pm 0.056$	$0.806 \pm 0.032$	$0.622 \pm 0.095$	$0.596 \pm 0.055$
	(-PDSI)	$0.357 \pm 0.041$	$0.331 \pm 0.021$	$0.756 \pm 0.081$	$0.785 \pm 0.051$	$0.627 \pm 0.051$	$0.579 \pm 0.054$
	Difference	-0.023	-0.008	-0.010	0.021	-0.005	0.017
	<i>p</i> -value	0.367	0.284	0.757	0.142	0.875	0.487

to soil moisture. Drought conditions and irrigation have been shown to impact percent latewood and ring SG for loblolly pine (Cregg et al. 1988; Gonzalez-Benecke et al. 2010; Hennessey et al. 2004); however, the trees used in those studies were young by comparison to the trees used in the present study. Since the +PDSI versus -PDSI wood property differences for slash pine and longleaf pine were significant at age 20 years, but not age 38 years, further studies are needed to determine if the influence of drought truly diminishes with wood maturity. At this point we cannot exclude other factors such as the resolution of the data we captured by X-ray densitometry, and the limited sample sizes available for the study. Altogether, despite accepted adaptations of southern pine species to wet or dry site conditions (e.g., slash pine on wet sites), those adaptations do not seem to carry over to between-species differences in mature wood physical properties from soil moisture extremes (wet vs. drought conditions).

# 4 Conclusions

Comparisons of ring width and physical property data for growth rings from years of ample soil moisture (+PDSI) paired with years of drought (-PDSI) show significant impacts on latewood formation, as evidenced by values for latewood width, percent latewood, and ring SG. It remains to be determined if detectible drought-related reductions in latewood formation manifest in detectible reductions in mechanical wood properties such a bending strength, reducing stem resistance to breakage from wind. Limited impacts of water stress on earlywood formation in established southern pine trees were supported by the absence of significant differences in our data for both earlywood width and earlywood SG. Despite the caveats of sample size and data resolution, results presented here show that while drought can impact wood formation and its physical properties, the magnitude of the differences may decrease with increasing wood maturity. While specific southern pines may be better adapted to drier or wetter sites, these differences in site preference may not manifest in droughts impacting the formation of the mature wood, or its physical properties, for one species over another.

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### References

Adams, M.B., Loughry, L.H., and Plaugher, L.L. (2004). Experimental forests and ranges of the USDA Forest Service. Gen. Tech. Rep. NE-321. Newtown Square, PA: USDA Forest Service, Northeastern Research Station.

- 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: 3-19.
- Antony, F., Schimleck, L.R., and Daniels, R.F. (2012). A comparison of earlywood-latewood demarcation methods - a case study in loblolly pine. IAWA J. 33: 187-195.
- Borders, B.E. and Harrison, W.M. (1989). Comparison of slash pine and loblolly pine performance on cutover site-prepared sites in the coastal plain of Georgia and Florida. South. J. Appl. For. 13: 204-207.
- Bouriaud, O., Leban, J.-M., Bert, D., and Deleuze, C. (2005). Intraannual variation in climate influence growth and wood density of Norway spruce. Tree Physiol. 25: 651-660.
- Candel-Pérez, D., Lo, Y.-H., Blanco, J.A., Chiu, C.-M., Camarero, J.J., de Andrés, E.G., Imbert, J.B., and Castillo, F.J. (2018). Droughtinduced changes in wood density are not prevented by thinning in Scots pine stands. Forests 9: 4.
- Carvalho, A., Nabais, C., Vieira, J., Rossi, S., and Campelo, F. (2015). Plastic response of tracheids in Pinus pinaster in a water-limited environment: adjusting lumen size instead of wall thickness. PLoS One 10: e0136305.
- Clark, A., III, Daniels, R.F., and Jordan, L. (2006). 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, 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.
- Copenheaver, C.A., Pokorski, E.A., Currie, J.E., and Abrams, M.D. (2006). Causation of false ring formation in Pinus banksiana: a comparison of age, canopy class, climate and growth rate. For. Ecol. Manag. 236: 348-355.
- 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 climatic factors. Can. J. For. Res. 18: 851-858.
- Dahlen, J., Auty, D., and Eberhardt, T.L. (2018). Models for predicting specific gravity and ring width for loblolly pine from intensively managed plantations, and implications for wood utilization. Forests 9: 292.
- Devall, M.S., Grender, J.M., and Koretz, J. (1991). Dendroecological analysis of a longleaf pine Pinus palustris forest in Mississippi. Vegetatio 93: 1-8.
- Eberhardt, T.L. and Samuelson, L.J. (2015). Collection of wood quality data by X-ray densitometry: a case study with three southern pines. Wood Sci. Technol. 49: 739-753.
- Eberhardt, T.L., So, C.-L., and Leduc, D.J. (2018). Wood variability in mature longleaf pine: differences related to cardinal direction for a softwood in a humid subtropical climate. Wood Fiber Sci. 50: 323-336.
- Eberhardt, T.L., So, C.-L., and Leduc, D.J. (2019). Wood property maps showing wood variability in mature longleaf pine: does getting old change juvenile tendencies? Wood Fiber Sci. 51: 193-208.
- 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.
- Franceschini, T., Bontemps, J.-D., and Leban, J.-M. (2012). Transient historical decrease in earlywood and latewood density and unstable sensitivity to summer temperature for Norway spruce in northeastern France. Can. J. For. Res. 42: 219-226.

- Franceschini, T., Longuetaud, F., Bontemps, J.-D., Bouriaud, O., Caritey, B.-D., and Leban, J.-M. (2013). Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce Picea abies (L.) Karst. Trees 27: 219-226.
- Gibson, M.D., McMillin, C.W., and Shoulders, E. (1986). Moisture content and specific gravity of the four major southern pines under the same age and site conditions. Wood Fiber Sci. 18:
- Gonzalez-Benecke, C.A., Martin, T.A., Clark, A., III, and Peter, G.F. (2010). Water availability and genetic effects on wood properties of loblolly pine (Pinus taeda). Can. J. For. Res. 40: 2265-2277.
- Gonzalez-Benecke, C.A., Riveros-Walker, A.J., Martin, T.A., and Peter, G.F. (2015). Automated quantification of intra-annual density fluctuations using microdensity profiles of mature Pinus taeda in a replicated irrigation experiment. Trees Struct. Funct. 29: 185-197.
- Graham, J.H., Duda, J.J., Brown, M.L., Kitchen, S., Emlen, J.M., Malol, J., Bankstahl, E., Krzysik, A.J., Balbach, H., and Freeman, D.C. (2012). The effects of drought and disturbance on the growth and developmental instability of loblolly pine (Pinus taeda L.). Ecol. Indicat. 20: 143-150.
- Gričar, J., Prislan, P., de Luis, M., Gryc, V., Hacurová, J., Vavrčik, H., and Čufar, K. (2015). Plasticity in variation of xylem and phloem cell characteristics of Norway spruce under different local conditions. Front. Plant Sci. 6: 730.
- Hart, J., O'Keefe, K., Augustine, S.P., and McCulloh, K.A. (2020). Physiological responses of germinant Pinus palustris and P. taeda seedlings to water stress and the significance of the grass-stage. For. Ecol. Manag. 458: 117647.
- Henderson, J.P. and Grissino-Mayer, H.D. (2009). Climate-tree growth relationships of longleaf pine (Pinus palustris Mill.) in the southeastern coastal plain USA. Dendrochronologia 27: 31-43.
- Hennessey, T.C., Dougherty, P.M., Lynch, T.B., Wittwer, R.F., and Lorenzi, E.M. (2004). Long-term growth and ecophysiological responses of a southeastern Oklahoma loblolly pine plantation to early rotation thinning. For. Ecol. Manag. 192: 97-116.
- Hoffer, M. and Tardif, J.C. (2009). False rings in jack pine and black spruce trees from eastern Manitoba as indicators of dry summers. Can. J. For. Res. 39: 1722-1736.
- Jokela, E.J., Dougherty, P.M., and Martin, T.A. (2004). Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. For. Ecol. Manag. 192: 117-130.
- 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: 698-710.
- Landers, J.L. (1991). Disturbance influence on pine traits in the southeastern United States. In: Hermann, S.M. (Ed.), Proceedings 17th tall timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, FL, pp. 61-98.
- Lantz, C.W. (1987). Which southern pine species is best for your site? For. Farmer 47: 11-12.
- Larson, P.R. (1969). Wood formation and the concept of wood quality. Yale University, School of Forestry Bulletin No. 74. New Haven, CT: Yale University.
- Larson, P.R., Kretschmann, D.E., Clark, A., III, and Isebrands, J.G. (2001). Formation and properties of juvenile wood in the southern pines: a synopsis. Gen. Tech. Rep. FPL-GTR-129. Madison, WI: USDA Forest Service, Forest Products Laboratory.

- Love-Myers, K.R., Clark, A., III, Schimleck, L.R., Dougherty, P.M., and Daniels, R.F. (2010). The effects of irrigation and fertilization on specific gravity of loblolly pine. For. Sci. 56: 484-493.
- Marchand, N. and Filion, L. (2012). False rings in the white pine (Pinus strobus) of the Outaouais Hills, Quebec (Canada), as indicators of water stress. Can. J. For. Res. 42: 12-22.
- Meldahl, R.S., Pederson, N., Kush, J.S., and Varner, J.M., III (1999). Dendrochronological investigations of climate and competitive effects on longleaf pine growth. In: Wimmer, R., and Vetter, R.E. (Eds.), Tree-ring analysis: biological, methodological, and environmental aspects. London: CABI Publishing, pp. 265-285.
- Samuelson, L.J., Eberhardt, T.L., Bartkowiak, S.M., and Johnsen, K.H. (2013). Relationships between climate, radial growth and wood properties of mature loblolly pine in Hawaii and a northern and southern site in the southeastern United States. For. Ecol. Manag. 310: 786-795.
- Samuelson, L.J., Stokes, T.A., and Johnsen, K.H. (2012). Ecophysiological comparison of 50-year-old longleaf pine, slash pine and loblolly pine. For. Ecol. Manag. 274: 108-115.
- Schmidtling, R.C. (1973). Intensive culture increases growth without affecting wood quality of young southern pines. Can. J. For. Res. 3: 565-573.
- Schultz, R.P. (1999). Loblolly the pine for the twenty-first century. N. For. 17: 71-88.
- South, D.B. and Harper, R.A. (2016). A decline in timberland continues for several southern yellow pines. J. For. 114: 116-124.

- Tasissa, G., and Burkhart, H.E. (1998). Modeling thinning effects on ring specific gravity of loblolly pine (Pinus taeda L.). For. Sci. 44: 212-223.
- Wear, D., and Greis, J. (2002). Southern forest resource assessment. Gen. Tech. Rep. SRS-53. Asheville, NC: USDA Forest Service, Southern Research Station.
- Wimmer, R. and Grabner, M. (2000). A comparison of tree-ring features in Picea abies as correlated with climate. IAWA J. 21:
- Wimmer, R., Strumia, G., and Holawe, F. (2000). Use of false rings in Austrian pine to reconstruct early growing season precipitation. Can. J. For. Res. 30: 1691-1697.
- Zahner, R. (1962). Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. For. Sci. 8: 345-352
- Zahner, R. (1963). Internal moisture stress and wood formation in conifers. For. Prod. J. 13: 240-247.
- Zahner, R. (1968). Water deficits and growth of trees. In: Kozlowski, T.T. (Ed.), Water deficits and plant growth. New York: Academic Press, pp. 191-254.
- Zahner, R. and Grier, C.E. (1990). Concept for a model to assess the impact of climate on the growth of the southern pines. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A., and Warren, W.G. (Eds.), Process modeling of forest growth responses to environmental stress. Portland: Timber Press, pp. 383-392.
- Zobel, B.J. and van Buijtenen, J.P. (1989). Wood variation: its causes and control. Berlin: Springer.