



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



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ABSTRACT

Production rates of loblolly pine (*Pinus taeda* L.) in favorable exotic environments indicate that full biological expression of growth potential in loblolly pine has not yet been attained in its native range. In previous work, high productivity in a loblolly pine plantation in Hawaii (HI) was hypothesized to be related to a more favorable climate conducive to year round carbon gain. To better understand the role of climate in limiting loblolly pine growth, relationships between radial growth and climate were examined in mature loblolly pine grown on two sites representing the opposite latitudinal ends of its ecological niche, Mississippi (MS) and North Carolina (NC), and on a third site in Hawaii (HI) representing a more favorable exotic environment. Raw ring widths were detrended and chronologies built for each site. At the northernmost site, ring width index (RWI) was positively correlated to February, April and July temperatures, annual mean temperature of the current and previous year, and annual maximum temperature. In MS trees, the only significant correlation between growth and climate was a positive correlation between RWI and November temperature. Growth at the MS site was likely more impacted by frequent hurricanes. In HI trees, no significant correlations between growth and temperature were observed but RWI was significantly related to precipitation during the dry season, which occurred from May–September. Potential anatomical alterations in the earlywood and latewood transition zones and timing of earlywood and latewood formation were indicated and may account for low ring specific gravity and percent latewood in HI trees. The moderate temperatures at the HI site likely supported high productivity but sensitivity to precipitation in HI trees indicates that reductions in water availability may effect loblolly pine growth even under more moderate temperatures when evaporative demand is low.

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1. Introduction

Loblolly pine (*Pinus taeda* L.) is the dominant plantation species in the southern United States (U.S.) (Schultz, 1999) and over the last 50 years a tripling of productivity has been achieved through improvements in genetics, seedling culture and management of resource availability (Fox et al., 2007). However, production rates of loblolly pine outside its native range in favorable exotic environments indicate that full biological expression of growth potential in loblolly pine in its native range has not yet been attained (Jokela et al., 2004). For example, growth rates of loblolly pine plantations in Brazil and Argentina can be three times that for similar stands on the U.S. mainland (Schultz, 1999). Maximum carrying capacity for closed canopy loblolly pine stands is between 45 and

50 m² ha^{−1} (Jokela et al., 2004), but basal area in a loblolly pine study in Hawaii (HI), known as the Olinda Study (DeBell et al., 1989; Harms et al., 1994, 2000), was 93 m² ha^{−1} at 48 years of age (Samuelson et al., 2010). Higher carrying capacity in the Olinda Study and other favorable exotic environments appears to be related to climate, specifically low evaporative demand, mild year-long temperatures, and longer day lengths (Lanner, 1966) that promote year round carbon gain (Samuelson et al., 2010), support high leaf area (Harms et al., 1994) and reduce competition-related mortality (DeBell et al., 1989). Wallinger (2002) also suggested a longer growing season may explain a tripling of productivity in loblolly pine plantations in Brazil. In contrast, on the mainland in its native range, stem growth and latewood production are dominated by a surge of growth in the spring and slowing of growth in the fall related to temperature and water availability. The more moderate climate of HI may serve as a model of climate conditions supporting optimum productivity in loblolly pine (Samuelson et al., 2010)

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and growth under those climate conditions may provide insight into the potential impact of climate change on loblolly pine productivity.

Continued increases in the rate of warming are predicted to occur in the southeastern U.S. with the greatest projected increases in temperature and evaporative demand during summer months (Karl et al., 2009). In the future, the duration and intensity of summer droughts may increase (Seager et al., 2009) and impact loblolly pine forest productivity (Schmidtling, 1994; Noormets et al., 2010). For example, simulations from a process based ecosystem model indicated reductions in net primary productivity as high as 40% in southern forests in response to drought over the period of 1895–2007 (Chen et al., 2012). Changes in current climate envelopes (Ibáñez et al., 2006) may result in shifts in range limits so that species remain in their ecological or “requirement” niches (Leibold, 1995; Holt, 2009), which will impact forest planation management (Huan et al., 2011). To better understand how changes in climate may influence loblolly pine growth, we explored relationships between climate and stem radial growth in mature loblolly pine grown on two sites representing the opposite latitudinal ends of its ecological niche, Mississippi (MS) and North Carolina (NC), and on a third site representing a more favorable exotic environment in HI (the Olinda Study). We tested the hypotheses that: (1) the relationships between climate and tree ring indicators are of opposite sign in northern and southern sites on the mainland, and (2) because of low intra and inter-annual variation in temperature, there will be no relationship between climate and radial growth of HI trees.

In addition to growth, wood specific gravity (SG) measurements have been correlated with regional climate parameters of precipitation and temperature for both angiosperms (Wiemann and Williamson, 2002) and gymnosperms (Briffa et al., 2002). For example, within a given region, cultivation of *Pinus sylvestris* L. at an elevated temperature impacted earlywood SG (Kilpeläinen et al., 2003) while *Picea abies* (L.) Karst latewood SG showed a greater response to summer temperature (Franceschini et al., 2012) and drought (Bouriaud et al., 2005). Regional variation in wood properties for loblolly pine has been shown (Jordan et al., 2008), with the extended growing seasons in the southernmost latitudes affording greater ring SG as a function of greater latewood formation (Jokela et al., 2004). Antony et al. (2010) determined that stands in the southern Atlantic Plain and Gulf Coastal Plan have the highest SG within the loblolly pine range because of higher summer precipitation, higher mean annual temperature and a longer growing season. In the present study, the HI loblolly pine provided an opportunity to examine trends in ring, earlywood and latewood SG, and percent latewood of mature wood under climate conditions atypical of those found on the mainland.

2. Materials and methods

2.1. Hawaii (HI) site

The 1.6 ha spacing trial was located on Maui at an elevation of 1120 m on the northwest slope of Haleakala (Table 1). The study

was established in January 1961 by the USDA Forest Service and Hawaii State Division of Forestry and Wildlife (Whitesell, 1970) and designed using a Latin Square Design with four replications. Each treatment plot was 0.11 ha with the central square 25 tree plot forming the measurement plot. The square spacing treatments were 1.8 m, 2.4 m, 3.0 m, and 3.7 m. One-year-old seedlings were purchased commercially and the seed source is unknown. Growth has been monitored over the life of the study (Whitesell, 1970; Debell et al., 1989; Harms et al., 1994, 2000; Samuelson et al., 2010). No thinnings were conducted.

A core 12 mm in diameter was removed at breast height (1.37 m) from three randomly selected trees, dominant in the canopy and within 1 standard deviation of average plot DBH, from each plot for a total of 48 cores in January 2009 when trees were 48 years of age. Eight cores were deleted from the data set due to core breakage or absence of pith. At the time of sampling, basal area and volume were similar among spacing treatments and averaged 93 m² ha⁻¹ and 1076 m³ ha⁻¹, respectively (Table 1) (Samuelson et al., 2010). Cores were pooled across treatments to increase the sample size in chronology development.

Monthly precipitation data were obtained from a weather station in Olinda located 1.8 km from the study site (<http://www1.ncdc.noaa.gov/pub/data/>, Olinda #1 332, Coop ID: 517041). The 12 month Standard Precipitation Index (SPI) values for the Olinda station were provided by the state Climatologist (Dr. Pao-Shin Chu, State Climatologist, Dept. of Meteorology, University of HI at Manoa). The SPI is a probability index with an index of zero indicating the median precipitation amount and positive values indicating greater and negative values indicating less than median precipitation (Guttman, 1999). Temperature data were obtained from a station located 3.6 miles from the study site in Kula, HI (<http://www1.ncdc.noaa.gov/pub/data/>, Kula Branch Station 324.5, Coop ID: 515000) beginning in 1979. No data on the Palmer Drought Severity Index (PDSI) were available for the Olinda area. The PDSI includes precipitation, evaporation, runoff and soil moisture in determining drought severity, with negative values indicating greater severity (Guttman, 1999).

2.2. Mississippi (MS) site

The research site was located in the USDA Forest Service Harrison Experimental Forest near Saucier, MS within the DeSoto National Forest 32 km north of Gulfport, MS (elevation 50 m) (Schmidtling, 1973). The experiment was designed as a randomized complete block with five cultivation-fertilization treatments and four blocks (see Johnsen et al., 2009 for a complete description). Five treatments were applied: (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 3 years, and mowed in years 4 and 5 to reduce competition. Fertilizer was applied 1 year after planting. One-year-old bare root seedlings were from local seed were planted with on a 3.05 × 3.05 m spacing in February 1961. No thinnings were

Table 1

Description of loblolly pine stands located in Hawaii (HI), Mississippi (MS) and North Carolina (NC) including mean plot-level diameter at breast height (DBH), height (HT) and basal area (BA), and chronology descriptive statistics including mean sensitivity (ms), expressed population signal (EPS), and between tree correlation (r_{bt}). For the MS site, HT was last measured in 2000 and DBH and BA were measured in 2006. The other sites were measured at the time of coring. The number of tree rings in the NC stand ranged from 49 to 62.

Site	Location	Elevation (m)	Planted	Thinnings	DBH (cm)	HT (m)	BA (m ² ha ⁻¹)	# Cores	ms	r_{bt}	EPS
HI	20.49°N, 156.17°W	1120	1961	None	36.7	30.6	93	38	0.33	0.17	0.88
MS	30.65°N, 89.04°W	50	1961	None	28.8	19.8	18	13	0.43	0.27	0.82
NC	36.00°N, 78.97°W	90	Natural	1980	34.2	31.7	50	30	0.26	0.16	0.85

conducted. Two Category 5 hurricanes struck the site: Hurricane Camille in 1969 and Hurricane Katrina in 2005. Other significant hurricanes that impacted the area include Hurricane Frederic in 1979 (Category 4), Hurricane Elena in 1985 (Category 3) and Hurricane Georges in 1998 (Category 4).

One core 12 mm in diameter per tree was removed at breast height from five trees per plot in three of the blocks and in plots that had received a fertilization treatment, for a total of 15 cores, in June 2011. Basal area before Hurricane Katrina was not significantly different among the three fertilization treatments (treatments 3, 4 and 5) (Johnsen et al., 2009) and plots were selected based on similar remaining basal area following Hurricane Katrina (Table 1). Trees were randomly selected from those within one standard deviation of average plot DBH. Two cores were deleted from the data set due to core breakage or absence of pith.

Monthly temperatures and precipitation were measured at a weather station near the study area (<http://www1.ncdc.noaa.gov/pub/data/>, Saucier Experimental Forest, MS, Coop ID: 227840). The 12 month PDSI and SPI were obtained from the National Oceanic and Atmospheric Administration (<http://www1.ncdc.noaa.gov/pub/data/>; State 22, climate division 10 (Coastal)).

2.3. North Carolina (NC) site

The stand was naturally regenerated and located in Duke Forest in Durham, NC (elevation 90 m). Initial stocking is unknown. In 1944, the original stand was thinned leaving only seed trees and in 1952 the seed trees were harvested. A liberation cut for release was conducted in 1952 and the stand was thinned in 1980 (Marissa Hartzler, program Director of Duke Forest). At the time of coring, the DBH of 100 trees was measured in a 0.10 ha plot and trees within 1 standard deviation of the mean were randomly chosen. One core each from 30 trees was removed at breast height February 2011. The number of rings ranged from 49 to 62.

Temperature and precipitation data were obtained from a weather station located in Durham, NC (<http://www1.ncdc.noaa.gov/pub/data/>, Durham, Coop ID: 312515). The PDSI and SPI were for the Northern Piedmont region (Durham and Orange Counties) (<http://www.nc-climate.ncsu.edu/climate/climdiv.php/>).

2.4. Densitometry

Wood cores were stored under refrigeration until processing. Cores were placed in wooded core holders, dried (50 °C, 24 h), and then permanently glued into place. Mounted specimens were sawn into 2.3 mm thick strips, from bark to pith, leaving the transverse surface of the core exposed and bordered by adhering wood strips remaining from the core holders. To measure wood properties (SG, percent latewood) and ring widths, densitometry was performed using a Quintek Measurement Systems (Knoxville, TN) X-ray densitometer. Specific gravity measurements were determined at 0.06 mm intervals, scanning along the radial direction from bark to pith. A SG of 0.480 was used to differentiate between earlywood and latewood zones (Koubaa et al., 2002; Clark et al., 2006; Antony et al., 2012). Densitometer calibration was on a green volume and oven-dried mass basis. Cores with defects (e.g., missing growth rings because of knots), that could not be compensated for by sample preparation, were not used. A total of 38, 13 and 30 cores were used from the HI, MS and NC sites, respectively. Wood properties and ring widths were weighted by ring basal area to obtain a whole-core value for each tree to include (rings 1–45) and exclude (rings 9–45) juvenile wood (core wood).

2.5. Chronology development

Since the plantation history was known at each site, dating the cores was done visually and matched with the corresponding densitometry data. Typically narrow false rings, often appearing in multiples within a given growth ring, were identified by comparing density trace patterns with accompanying video images. To remove age-related growth trends from the data sets, the raw ring width data were detrended using a spline function with a frequency response of 50% at a wavelength of 0.67 of the series length (Cook and Peters, 1981; Bunn, 2008) in the dendrochronology program library in R (dplR) (Bunn, 2008). The smoothing spline yielded the best results based on visual inspection of each ring-width series. The function was fit to each series individually and a mean value chronology was built for each site using robust bi-weight means of the pre-whitened chronologies to reduce the influence of outliers and remove autocorrelation from the chronologies (Bunn, 2008). The ring width index (RWI) was calculated as the ratio of observed to expected ring width. Three indices were used to characterize the quality of the chronologies: the expressed population signal (EPS), mean sensitivity (ms) and mean between series correlation (r_{br}). The EPS is a measure of chronology reliability or chronology confidence, with 0.85 considered the threshold (Wigley et al., 1984; Briffa, 1995). Mean sensitivity is a measure of sensitivity of trees to yearly changes in growth-limiting factors (Cook et al., 1998) and between series correlation (r_{br}) is a measure of the strength of the common growth signal between trees (Wigley et al., 1984; Briffa and Jones, 1990).

2.6. Statistical analyses

Because geographic variation in growth is confounded by genetics, microclimate, soils and management history, relationships between radial growth and climate were examined separately for each site. Pearson's correlation coefficient was used to test for significant relationships between RWI and climate variables. Climate variables included the sum of precipitation on a monthly and annual basis, a 12-month PDSI and SPI, average monthly temperatures, and the average annual mean, maximum and minimum temperatures. The goal was to identify environmental variables related to growth rather than develop response functions and predictor variables for regressions.

Based on annual patterns in SG at each site and those reported in the literature (Clark and Saucier, 1989; Clark and Schmidting, 1989; Larson et al., 2001; Clark et al., 2006), juvenile wood was defined as the first eight rings of growth. Differences among sites in whole core wood properties were not tested due to lack of true replication; therefore, general trends are discussed and not attributed directly to specific site differences. Representative densitometry traces are shown and discussed in the context of potential changes in growth characteristics in HI trees, but differences in trace characteristics could not be quantitatively assessed.

3. Results

3.1. Climate

Average annual temperatures at HI were more uniform across the years in the chronology, ranging from 17.3 to 18.4 °C, compared to the range of 18.3–20.9 °C at MS and 13.6–17.1 °C at NC (Fig. 1). The HI site was characterized by moderate monthly mean temperatures ranging from 15.9 to 19.6 °C with no marked seasonal trends, in contrast to the mainland sites which demonstrated a range in mean monthly temperature of 10.8–27.5 °C at MS and 3.8–25.5 °C at NC (Fig. 2). Average summer and winter temperatures at HI were

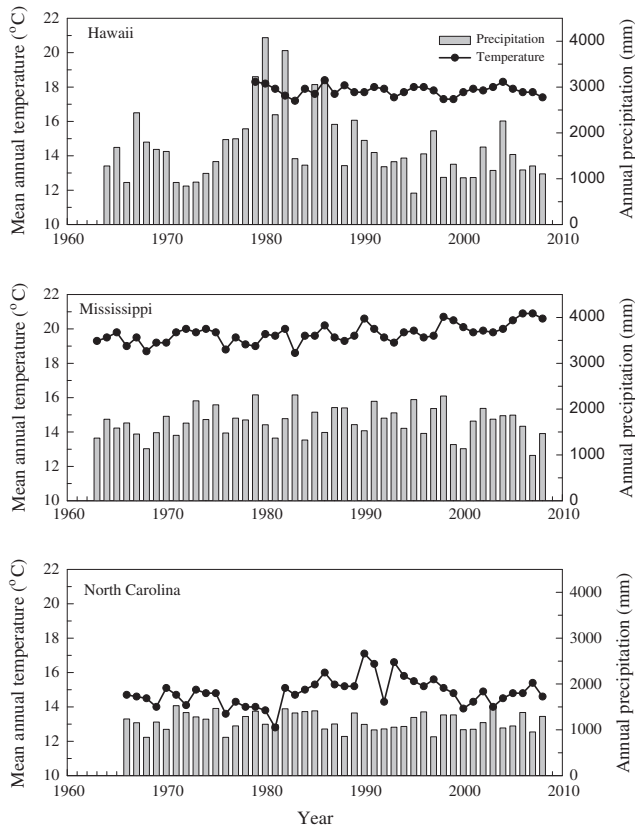


Fig. 1. Mean annual temperature and annual sum of precipitation by site over the years used in the climate correlation analyses.

intermediate to the mainland sites with lower average summer temperatures and higher average winter temperatures at HI (Fig. 2). At HI, annual precipitation averaged across the years in the chronology was $1711 \text{ mm year}^{-1}$ but annual precipitation over the same period varied from 686 to $4078 \text{ mm year}^{-1}$, and a dry season (May–September) was evident over the years of the HI chronology. However, summer precipitation at HI was within the range observed on the mainland sites (Fig. 2). At MS, average annual precipitation over the chronology was $1753 \text{ mm year}^{-1}$ and ranged was from 989 to $2312 \text{ mm year}^{-1}$. Annual precipitation varied from 836 to $1517 \text{ mm year}^{-1}$ and was on average $1187 \text{ mm year}^{-1}$ over the years of the chronology at the NC site. At HI, the SPI indicated drier ($\text{SPI} < -1$) years in 1971, 1972, 1994 and 2008 (Fig. 3). The MS site experienced low (< -2) PDSI in 1962, 1981, 1999–2000 and 2006. At NC, the PDSI fell below -2 only in 2007.

3.2. Radial growth

Chronologies for the three sites are shown in Fig. 4. The EPS values for HI and NC cores reached the 0.85 threshold and the EPS for the MS cores was just below the threshold (0.82) (Table 1). In the NC trees, the EPS reached the threshold in 1966. Mean sensitivity values were within the 0.15–0.3 range previously reported for similar loblolly pine chronologies (Cook et al., 1998) but r_{bt} values were low, perhaps because of heterogeneous site conditions, in particular variation in light. For example, in the HI plantation competition for light varied by density treatment and resulted in a two-tier canopy early in stand development (Debell et al., 1989), and thus the effects of competition for light on growth may exceed the effects of climate variation (Clark et al., 2011). Similarly,

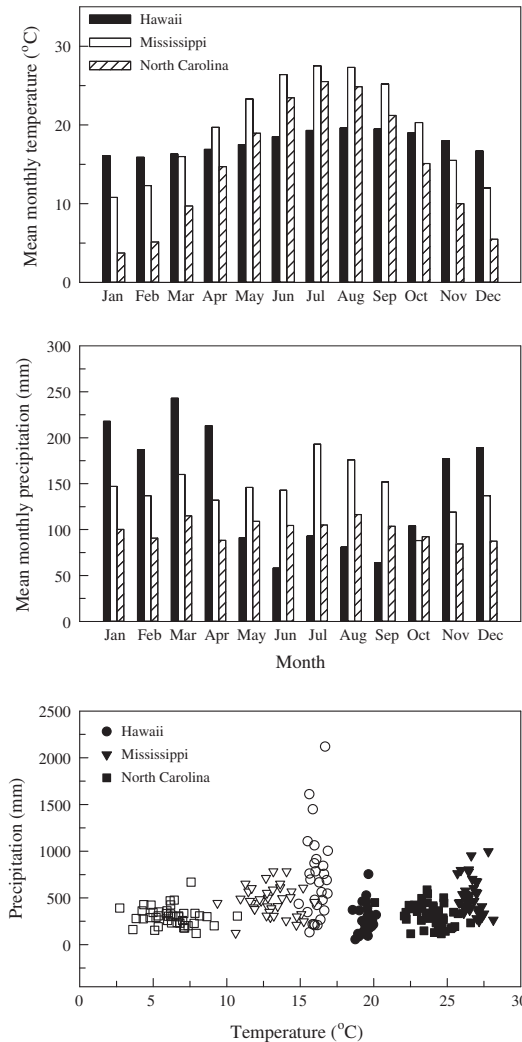


Fig. 2. Mean monthly temperature and precipitation by site, and average summer (closed symbols) and winter (open symbols) temperature and precipitation over the years used in the climate correlation analyses.

spacing in the natural NC stand was not uniform, and hurricanes in the MS study opened up irregular gaps.

No significant correlations between RWI and monthly, seasonal or annual temperatures, or SPI were detected for HI trees, but growth of HI trees was positively correlated to May, September and December precipitation (Figs. 5 and 6). Precipitation at HI was summed for the driest months (May–September) and the sum used in the analyses. Significant correlations between RWI and the sum of precipitation during the dry season of the current year ($p = 0.041$, $r = 0.31$) and previous year ($p = 0.011$, $r = 0.38$) were observed.

At MS, a decline in RWI for three years following the Category 5 hurricane in 1969 was followed by increasing RWI until 1979. In 1980, the year following a Category 4 hurricane, RWI continued to increase until 1983 (Fig. 4). The RWI of MS trees was significantly correlated only to November temperature (Figs. 5 and 6).

In NC, thinning of the stand in 1980 was followed by a 2 year decline in growth and then a 5 year increase in RWI (Fig. 4). The RWI of NC trees was significantly and positively correlated with February, April and July mean temperatures and negatively correlated with June precipitation (Fig. 5). The RWI of NC trees was also positively correlated to mean annual temperature, mean annual maximum temperature and the previous year mean annual

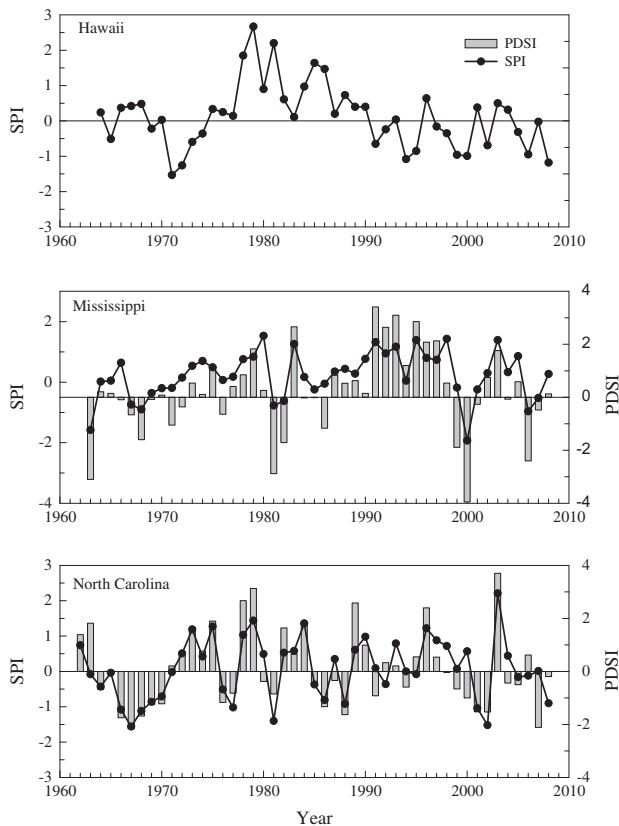


Fig. 3. Annual Standard Precipitation Index (SPI) and Palmer Drought Severity Index (PDSI) by site over the years used in the climate correlation analyses. The PDSI data were not available for the Hawaii site.

temperature and negatively correlated with annual precipitation, SPI and PDSI (Fig. 6).

3.3. Wood properties

At HI, ring SG, latewood SG and percent latewood for mature wood (rings 9–45) trended lower relative to mainland sites (Fig. 7). Corresponding mean whole-core SG values were expectedly lower in HI trees when calculated by excluding or including the first 8 growth rings, designated as being mostly juvenile wood (Table 2). Mean whole-core ring width of HI trees more than doubled upon including data for the first 8 growth rings. In MS trees, ring SG and percent latewood trended similarly across ring numbers (Fig. 7). Mean whole-core ring SG, which thus coincided with percent latewood values, were the highest for the MS site (Table 2). Including the wide juvenile wood rings in the calculation raised the mean whole-core ring width of MS trees from 1.57 to 5.06 mm. In NC trees, ring SG, latewood SG and percent latewood for mature wood were relatively constant along ring numbers (Fig. 7). Mean whole-core values for the mature wood of NC trees were similar to those when including the juvenile wood, and in both cases, the values for whole-core SG and percent latewood were intermediate to those for the HI and MS sites (Table 2).

A densitometry trace from a single radial strip representative for the HI site had atypical growth ring density profiles with multiple peaks of higher SG wood in latewood bands of individual rings (Fig. 8). Transitions from latewood to earlywood were not abrupt, but instead showed gradually declining SG values, especially for juvenile wood growth rings. Densitometry traces representative for the MS and NC sites had typical abrupt SG transitions from latewood to earlywood (Fig. 8). The trace representative of the MS site

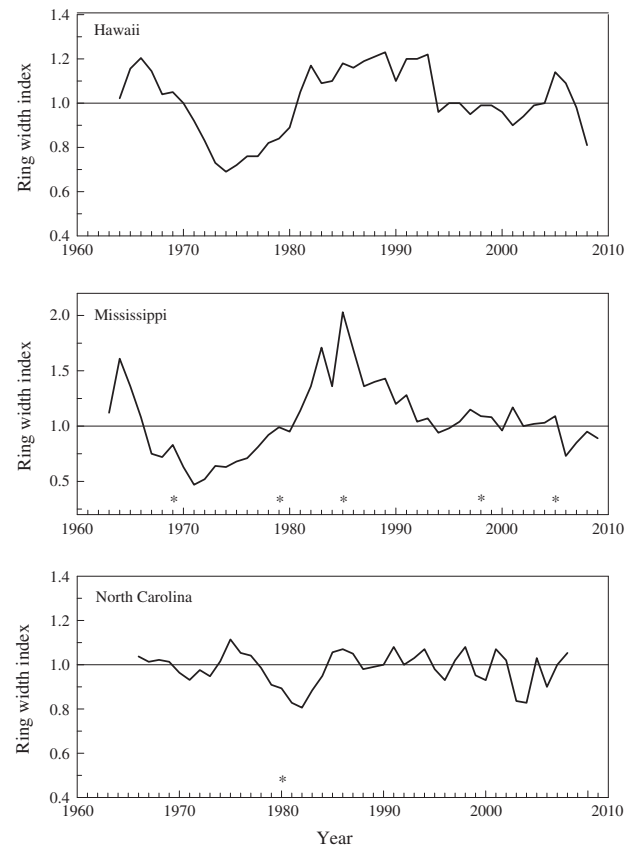


Fig. 4. Standard chronologies for loblolly pine by site. *Indicates years with hurricanes in the Mississippi chronology and a thinning in the North Carolina chronology.

also demonstrated individual ring profiles that were particularly symmetrical in the mature wood (Fig. 8).

4. Discussion

Over the native range of loblolly pine, average annual rainfall varies from 1020 to 1520 mm and mean annual temperatures vary from 13 °C to 24 °C, with an average July temperature of 27 °C and January average between 4 and 16 °C (Baker and Langdon, 1990). Mean annual temperatures in the chronologies fell within this climate envelope, with the NC site bracketing the low end of the temperature range and the MS site the higher end. Because radial growth of trees at their northern range margin is most often limited by temperature (Fritts, 1976; Pederson et al., 2004), we hypothesized that annual ring growth of loblolly pine would be positively related to temperature in the northern portion and negatively related in the southern portion of its native ecological niche. In support of this hypothesis, we observed positive correlations between radial growth and July temperature, annual mean temperature and annual mean maximum temperature at the NC site and negative but non-significant correlations with annual and maximum temperature at the MS site.

Nedlo et al. (2009) proposed that that future increases in temperature may have a positive effect on loblolly pine growth in the northern portion of the range, where temperatures are sub-optimal for photosynthesis, and a negative effect at the extreme southern portion of the range, where temperatures are supra-optimal for photosynthesis, dark respiration rates are high, and drought is more likely due to high evaporative demand. At cooler

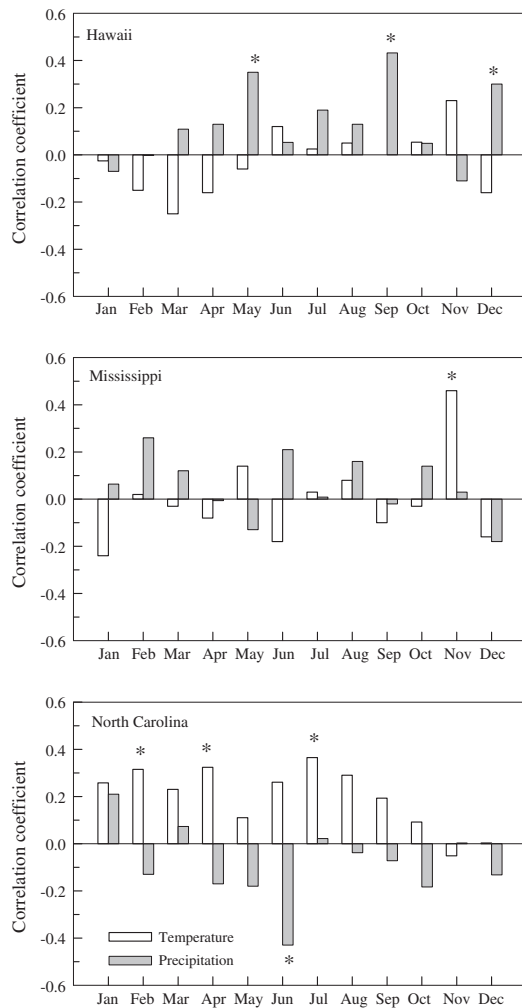


Fig. 5. Correlation coefficients for relationships between ring width index of loblolly pine and average monthly temperature and precipitation by site. *Indicates a significant ($\alpha = 0.05$) correlation.

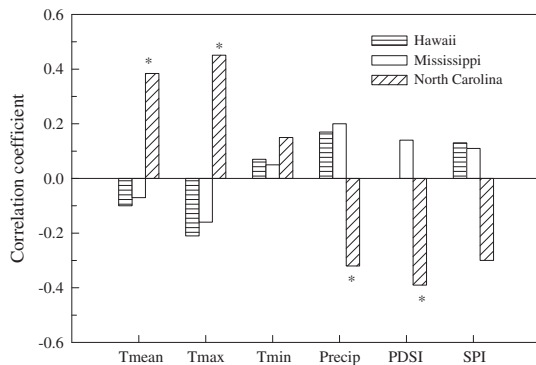


Fig. 6. Correlation coefficients for relationships between ring width index of loblolly pine and annual mean, maximum and minimum temperatures, total annual precipitation, the Palmer Drought Severity Index (PDSI) and the Standard Precipitation Index (SPI) by site. The PDSI was not available for the Hawaii site. *Indicates a significant ($\alpha = 0.05$) correlation.

and moister sites and in regions where temperature is limiting to growth, higher summer temperatures are not always associated with drought and may enhance net photosynthesis (Boisvenue and Running, 2006; Seidling et al., 2012). Similar to our results, Abrams and Black (2000) observed positive correlations between

RWI and mean annual temperature and the previous year's mean temperature in loblolly pine in eastern Virginia.

Growth of trees at the NC site was positively related to mean annual temperature of the previous year, most likely through temperature effects on photosynthesis and subsequent carbohydrate storage, which affect radial growth in spring (Lo et al., 2010; Mölder et al., 2010). Growth of NC trees was also positively correlated to average February and April temperatures, and temperature has been shown to influence cambial reactivation and earlywood tracheid production (Dufour and Morin, 2013) in variety of tree species including loblolly pine in NC (Woods and Debrunner, 1970). Correlations between radial growth and February temperature have been reported for southern pines at their northern latitudinal range margin (Kirwin et al., 2007; Bhuta et al., 2009). Environmental conditions, in particular temperature (Begum et al., 2012), that increase photosynthesis before the resumption of growth are correlated with earlywood formation in temperate zones (Lebourgeois, 2000). The negative correlation between radial growth and June precipitation in NC trees may be related to increases in cloud cover and reduced photosynthesis and subsequently less latewood production when the transition between latewood and earlywood typically occurs (Cregg and Dougherty, 1988). Dufour and Morin (2013) reported that the most important factor controlling tracheid production in black spruce was daytime light intensity and photosynthesis.

Cook et al. (1998) conducted a comprehensive analysis of climate and radial growth in loblolly pine over the years of 1960–1990 and reported positive correlations with temperature at the northern range margin, no correlation with climate in trees growing in coastal MS and correlation with drought only in the western range margin where drought is more common. Similar to Cook et al. (1998), we observed no significant correlations between radial growth and any precipitation or drought indices in MS trees. It should be noted, however, that the lower sample size at the MS site may lead to a general underestimation of climate-growth correlations (Mérian et al., 2013). The climate at the MS site is temperate-humid, subtropical with precipitation distributed evenly throughout the year (Adams et al., 2004), and annual precipitation at the MS site during the years of the chronology was generally higher than the range average of 1020–1520 mm (Baker and Langdon, 1990). In a study of leaf physiological rates of trees in the same plots used in this study, soil moisture was not limiting to leaf carbon gain (Samuelson et al., 2012).

Alternatively, the high frequency of stand level disturbances from hurricanes and subsequent wind damage may have had a bigger impact on growth at the MS site than climate *per se*, due to the shedding of foliage, and thus reduced total carbon gain, and gap creation. Signals that influence ring width include the age-related growth trend, climate variations, disturbances originating from within the forest and disturbance from outside the forest community such as from hurricanes (Cook, 1985). It is unclear how the frequent hurricanes affected mortality since annual plot-level growth and survivorship data are not available. However, the Category 5 hurricane Katrina in 2005 directly killed trees both by downing them and snapping boles (Johnsen et al., 2009). The Category 4 hurricane Camille that struck the site in 1979 was followed by increasing RWI until a peak in RWI in 1985 when a Category 3 hurricane passed over the site. Between 1969 and 1985, tree density on plots used in this study declined 50%, from an average of 970 trees ha^{-1} to 487 trees ha^{-1} , but average basal area was reduced by only 3%, from 22 $\text{m}^2 \text{ha}^{-1}$ to 21.4 $\text{m}^2 \text{ha}^{-1}$, indicating high growth rates in residual trees over that period (unpublished data, John Butnor, personal communication). Competition induced mortality could account for the decline in tree density. In addition, stands were 18 years of age and unthinned when Camille struck and it is likely that the response to wide scale disturbance was

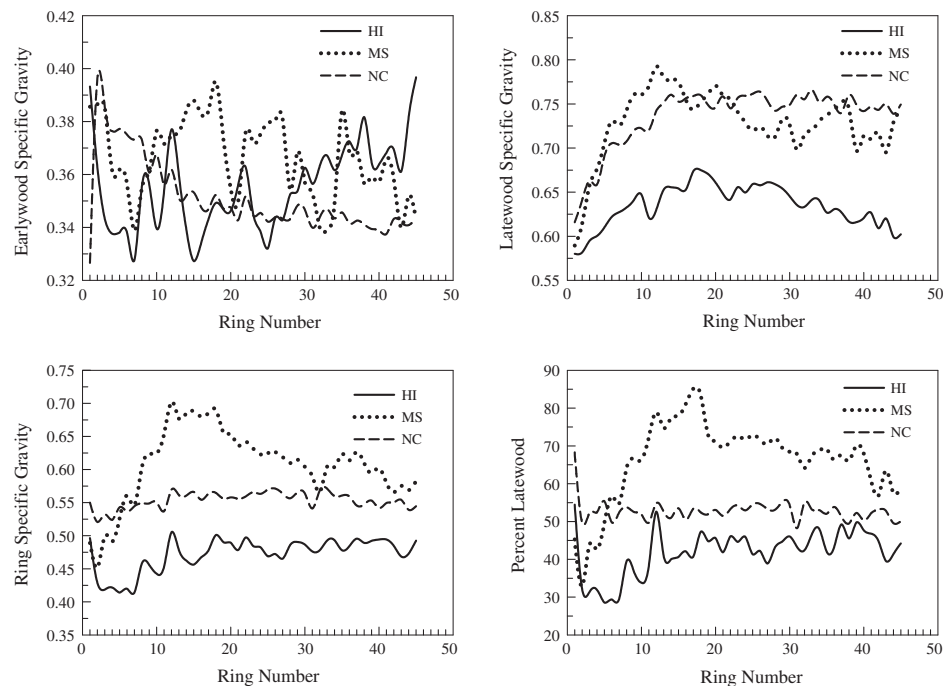


Fig. 7. Mean earlywood, latewood, and ring specific gravity, and percent latewood versus ring number for loblolly pine cores from Hawaii, Mississippi and North Carolina.

Table 2
Mean whole-core wood properties with and without the juvenile core for loblolly pine in Hawaii (HI), Mississippi (MS) and North Carolina (NC).

Ring numbers	Site	Ring SG	Earlywood SG	Latewood SG	Percent latewood	Ring width (mm)
1–45	HI	0.463 (0.038)	0.344 (0.018)	0.642 (0.026)	39.78 (8.54)	5.80 (1.57)
	MS	0.587 (0.035)	0.359 (0.021)	0.735 (0.029)	60.58 (6.30)	5.06 (1.20)
	NC	0.550 (0.031)	0.344 (0.017)	0.742 (0.033)	51.98 (5.34)	2.72 (0.51)
9–45	HI	0.484 (0.039)	0.348 (0.019)	0.654 (0.032)	44.35 (8.36)	2.28 (0.50)
	MS	0.629 (0.053)	0.365 (0.038)	0.748 (0.029)	70.08 (11.51)	1.64 (0.47)
	NC	0.558 (0.036)	0.342 (0.018)	0.755 (0.038)	52.49 (5.81)	2.48 (0.43)

Note: values are means for specified ring numbers with standard deviations in parentheses. SG = specific gravity.

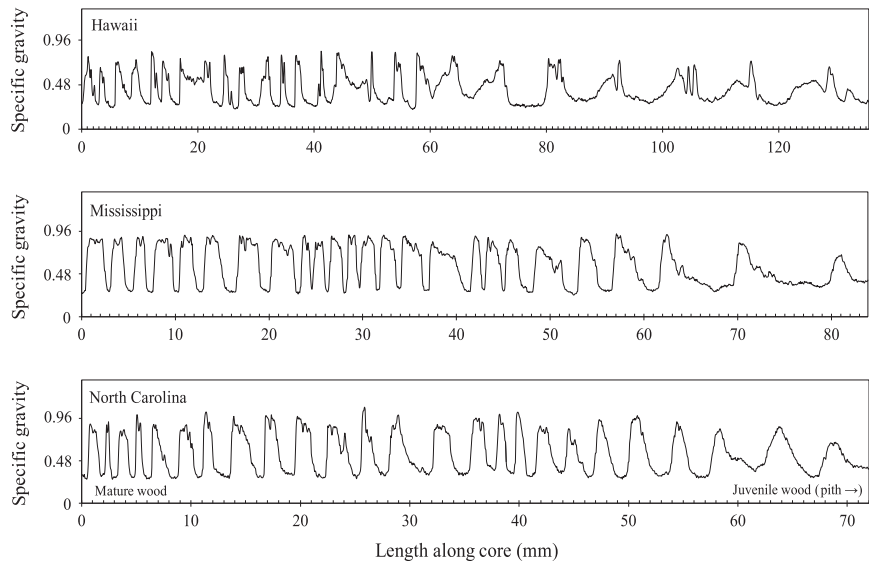


Fig. 8. Representative densitometry scans for individual loblolly pine wood cores from Hawaii, Mississippi and North Carolina . A total of 25 rings were selected, starting near the pith, to show both mature (left) and juvenile (right) wood zones.

greater when stands were younger and capable of rapid growth relative to growth later in stand development.

We hypothesized that annual ring growth of loblolly pine grown in Hawaii would not be correlated to climate and radial growth of HI trees was not correlated to temperature. However, growth of HI trees was sensitive to precipitation in May and September at the beginning and end of the dry season, and precipitation summed for the current and previous year's dry season. The sensitivity of growth to December precipitation is interesting in that bud break and considerable flush development were observed in January 2009 in HI trees and the majority of loblolly pine leaf growth may have occurred during the rainy season rather than in spring and summer, as in its native range (Samuelson et al., 2010). Loblolly pine appears to be vulnerable to drought at the HI site despite a more moderate climate in terms of temperature. Sensitivity of radial growth to precipitation the previous fall has been observed in loblolly pine (Friend and Hafley, 1989). Gonzalez-Benecke et al. (2010) found that irrigation increased ring SG and latewood percent in 11-year-old loblolly pine by extending the seasonal diameter cessation date.

Consistent with the hypothesis that an extended growing season results in greater latewood formation in loblolly pine growing in its native range (Jokela et al., 2004), MS trees relative to NC trees demonstrated positive correlation between growth and November temperature and higher ring SG and percent latewood for the mature wood. High ring SG is associated with a higher proportion of latewood and greater tracheid cell wall thickness (Larson, 1957; Panshin and deZeeuw, 1980). Lignin incorporation in the cell walls of latewood tracheids is temperature sensitive and tracheid maturation may continue over the winter in temperate regions (Nix and Villiers, 1985; Donaldson, 1991). In contrast, HI trees, which appear to have a longer growing season, had lower ring SG. Prior comparisons of the HI cores to mainland loblolly pine data from the literature (Samuelson et al., 2010) showed that whole-core ring SG and percent latewood for the HI loblolly pine were at the high end of the range of values for mainland loblolly pine reported by Jordan et al. (2008). However, the literature data (Jordan et al., 2008) were from plantations with a mean tree age of 23.4 years, which is one half that for the trees from the HI site. In the present study we report whole-core wood properties for the HI loblolly pine and similarly-aged loblolly pine from two mainland sites in its native range.

In HI trees, lack of the typical seasonal variation in temperature found within loblolly pine's native range raises interesting questions concerning possible anatomical alterations in the earlywood and latewood transition zones, as well as the precise timing for the onset both earlywood and latewood formation. As in most studies utilizing X-ray densitometry, demarcation between earlywood and latewood was typically based on the density reading crossing a threshold value (Koubaa et al., 2002), with 0.480 being commonly used for loblolly pine (Jordan et al., 2008; Love-Myers et al., 2009). It is beyond the scope of the present study to redefine the earlywood-latewood and latewood-earlywood transitions for the density profile anomalies observed for HI loblolly pine. Rather, we suggest that future investigations of climate related changes in transitions are warranted. Use of the threshold method here allows an objective comparison of wood property data between sites in the current study and that reported in the literature for loblolly pine. Other demarcation methods have been proposed; however, they are equally arbitrary. For example, Mork's index, a method based measurements of double cell wall thickness and lumen diameter, can be interpreted in more than one manner (Koubaa et al., 2002). Some studies using densitometry data have proposed to redefine earlywood-latewood transitions (but not the latewood-earlywood transitions) through modeling. For example, the earlywood-latewood has been proposed to occur at the inflection point

of the density readings within an individual ring (Koubaa et al., 2002; Antony et al., 2012). Plaguing the validation of such methods are perturbations in growth affording noncompliant false rings (Pernestål et al., 1995; Franceschini et al., 2013). Other modeling studies avoid arbitrarily redefining model-specific delineations of earlywood to latewood transitions by focusing on within ring density variations that may be attributed to climate parameters within a given growing season (Franceschini et al., 2013; Ivković and Rozenberg 2004; Rozenberg et al., 2004).

From the above discussion we acknowledge that there may be some ambiguity when characterizing earlywood-latewood (and latewood-earlywood) transitions for the HI loblolly pine given its growth in an abnormally moderate climate. Indeed, observation of the density traces along the HI loblolly pine cores often showed the SG to gradually decline between growth rings as opposed to the typical abrupt SG drop observed for mainland loblolly pine when coming out of winter dormancy. Our intent in providing densitometry traces is to illustrate the regularity of the growth ring profiles for mainland loblolly pine relative to the Hawaii loblolly pine. The lower latewood SG for the HI trees would appear to be a manifestation of lower maximum latewood SG readings along a latewood band and gradual transitions on either end of the latewood band, both causing the lower cumulative latewood SG values for individual rings. It is plausible that more favorable temperatures support radial expansion all year, which may explain the lower percent latewood and lower ring SG compared to mainland trees. This would contrast with mainland loblolly pine where cell formation typically ceases during winter dormancy; however, photosynthesis continues (Gough et al., 2004) and cell wall thickening occurs in the last formed tracheids (Nix and Villiers, 1985). This study is the first to report on wood properties of mature wood in loblolly pine grown in a more favorable exotic environment that supported long-term maximum productivity.

5. Conclusions

In summary, climate affected radial growth of loblolly pine but its impact varied within its ecological niche. High productivity of loblolly pine in HI was likely due to exposure to a more favorable thermal niche. The photosynthetic optimum for net photosynthesis of loblolly pine during summer months is between 20 and 26 °C, but the ratio of net photosynthesis to leaf dark respiration has been shown to decline linearly from 15 °C to 35 °C in loblolly pine (Werten et al., 2012), indicating lower leaf net carbon gain at higher temperatures. The more moderate temperatures year round (15–20 °C) in HI likely contributed to superior growth, presumably through sustained leaf photosynthesis, reduced dark respiration rates, and continuous radial growth, which may account for low ring SG in HI trees. Sensitivity to precipitation in HI trees, despite exposure to more optimum growth temperatures, indicates that increases in drought frequency and intensity may impact loblolly pine growth even under more salubrious conditions such as low evaporative demand.

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