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Original article

The effects of climatic variability on radial growth of two varieties of sand pine (*Pinus clausa*) in Florida, USA

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Abstract – Total ring, earlywood, and latewood master chronologies were derived for six stands (three of each of the two varieties) of sand pine (*Pinus clausa*) spanning the geographic breadth of the species extant range in Florida, USA. Climate/growth correlations, analysis of extreme growth years, and multiple regression models were developed to relate growing season (current and lagged) monthly temperature and precipitation with interannual variability in sand pine growth increments. Four research hypotheses were evaluated: (1) Sand pine growth is more sensitive to variation in precipitation than variation in temperature. (2) Sand pine growth variation is linked to El Niño-Southern Oscillation warm- vs. cold-phase events. (3) Climate/growth relations are stronger for the peninsular (Ocala; *P. c.* var. *clausa*) variety of sand pine than the panhandle (Choctawhatchee; *P. c.* var. *immuginata*) variety. (4) Climatic signals are stronger for coastal populations (vs. inland) for both varieties. Precipitation (especially in the winter/spring season of current-year growth) was more strongly linked to sand pine growth than temperature, earlywood growth was significantly greater in warm-phase El Niño-Southern Oscillation years in four of the six stands, and climate/growth relationships were stronger in coastal populations. We found no consistent inter-varietal contrasts in the strength of climatic signals, although climate/growth relationships were distinctive in the two inland panhandle stands, where canopy/understory interactions may partially obscure expression of climatic influence. We found greater sensitivity to temperature in inland panhandle stands (especially in latewood series), but consistently strong growth response to precipitation in the other four stands (especially in earlywood and total ring series). Our findings extend the evidence for ENSO influence on terrestrial biophysical phenomena in Florida.

sand pine / dendroclimatology / El Niño-Southern Oscillation / Florida

Résumé – **Effets de la variabilité climatique sur la croissance radiale de deux variétés de pin (*Pinus clausa*) en Floride, USA.** La chronologie des années caractéristiques a été dérivée de la mesure des cernes, du bois initial et du bois final dans 6 peuplements (3 pour chacune des variétés) de *Pinus clausa* représentant toute la gamme géographique de l'espèce en Floride, USA. La corrélation climat/croissance, l'analyse des années de croissance extrême et des modèles de régression multiple ont été développées pour établir les relations entre la température et les précipitations mensuelles au cours de la saison de végétation, et la variabilité inter-annuelle des accroissements de *Pinus clausa*. Quatre hypothèses de recherches ont été évaluées : (1) La croissance de *Pinus clausa* est plus sensible aux variations des précipitations qu'à celles de la température. (2) La variation de croissance de *Pinus clausa* est liée aux oscillations (évènements chauds versus froids de El Niño dans le sud). (3) Les relations climat/croissance sont plus fortes pour la variété péninsulaire (Ocala ; *P. c.* var. *clausa*) que pour la variété Choctawhatchee (*P. c.* var. *immuginata*). (4) Les signaux climatiques sont plus forts pour les

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populations côtières (versus intérieures) pour les deux variétés. Les précipitations (particulièrement celles de la saison hiver-printemps de l'année courante de croissance) sont plus fortement liées à la croissance de *Pinus clausa* que la température. La croissance initiale est significativement plus grande pendant les années de phases chaudes des oscillations de El Niño pour 4 des 6 peuplements, et les relations climat/croissance sont plus fortes pour les populations côtières. Il n'a pas été trouvé de différences consistantes inter-variétales dans la force du signal climatique, bien que les relations climat/croissance soient différentes pour les deux peuplements intérieurs de la variété Choctawhatchee, où les interactions canopées/sous étage ont pu atténuer l'expression des signaux climatiques. Il a été mis en évidence une plus grande sensibilité à la température dans les peuplements intérieurs de Choctawhatchee (en particulier pour le bois final), mais il y a une forte réponse, constante, de la croissance pour les précipitations dans les 4 autres peuplements (en particulier pour le bois initial et l'ensemble des cernes). Ces travaux confirment l'évidence de l'influence de ENSO sur les phénomènes biophysiques terrestres.

***Pinus clausa* / dendroclimatologie / oscillation de El Niño / Floride**

1. INTRODUCTION

Variation in climate/growth relationships exhibited by a single tree species across environmental and geographic gradients provides valuable insights into the integrated response of plants to physical site factors [8, 17, 26] as well as into the reconstruction of past climates [10, 16, 28, 33]. Overlying these physical gradients may be more subtle intraspecific variation imposed by regionally distinctive patterns of stand history and plant demography. Although less commonly examined in tree-ring studies (which generally limit their sample to those trees in a population most likely to experience physical stress), such biotically and historically mediated variability in climate/growth relations may be prominent for some taxa.

The purpose of this study is to document climate/growth relations throughout the range of sand pine (*Pinus clausa*), a species virtually endemic to Florida, USA. By developing a regional network of master chronologies based on total ring, earlywood, and latewood widths, this study offers a comprehensive examination of dendroclimatic variation within this geographically restricted species. Moreover, all trees in mapped stands are sampled, so that there is no systematic bias in tree selection to favor expression of a climatic signal. Sand pine is particularly well suited for examining the effects of both physical gradients and biotic influences on climate/growth relations, because climatic gradients of precipitation and temperature seasonality are well expressed across Florida, and previous work has documented meaningful contrasts in population structure and disturbance dynamics between the two varieties of sand pine [21].

Florida experiences a moist subtropical, grading to near-tropical, climate [4]. Annual precipitation totals are relatively high (ca. 120–180 cm), although drier winters become increasingly pronounced southward on the peninsula. In central Florida, about one-third of the total annual precipitation falls in the six-month period from November to April. Summers are uniformly warm and humid throughout Florida, with a high frequency of convective thundershowers, especially over the interior of the peninsula. Winters exhibit a marked mean temperature gradient; freezes are uncommon (1.5 to 3.5 days per year) in central Florida, but are more common (8 to 20 days per year, depending on coastal proximity) in the Florida panhandle [25]. Growing season ranges from a minimum of about 8 months in the panhandle interior to about 11 months near the southeastern range limit of sand pine. Annual potential evapotranspiration estimates range from about 105 to 120 cm.

In addition to geographic gradients in winter season precipitation and temperature across Florida, climatologists have established strong links between El Niño-Southern Oscillation (ENSO) phase and winter precipitation departures across the southeastern United States [7, 14, 22]. Warm-phase, or El Niño events, are commonly characterized by wetter than normal winters with regional strengthening of the subtropical jet stream. By contrast, cold-phase, or La Niña events, often yield drier than normal winters over Florida, as upper-level support for storm development is weakened.

Sand pine has been taxonomically partitioned into two varieties [18, 32]: Choctawhatchee sand pine (*P. c.* var *immuginata*) is restricted to the Florida panhandle (except for a population on an Alabama barrier island), and Ocala sand pine (*P. c.* var *clausa*) is limited to the Florida peninsula. In general, sand pine is shade-intolerant [5], subsists on sandy, dry, nutrient-poor substrates [9], and possesses a disturbance-dependent regeneration ecology [19].

Our previous research [21] has established significant ecological differences in demographic structure between the two varieties of sand pine. Choctawhatchee sand pine is not fire dependent (and, hence, is generally non-serotinous). Individuals of this variety preferentially regenerate in small canopy gaps triggered by frequent wind damage along the Gulf of Mexico coastal strand. Thirty-five to 65% of trees in sample populations of this variety displayed at least one growth release event linked with wind damage [21]. Population structures are of the reverse-J form [31], with occasional stem recruitment in the understory of most stands. Ocala sand pine is historically dependent on crown fires, and, hence, exhibits a high percentage of serotiny in most populations. Lightning fires are common, especially during drier summers in the Florida peninsula [29]. Before effective fire exclusion, a coarse-grained patch dynamic of stems recruited following fires. Naturally seeded, mature populations of this variety (those we sampled were initiated in the 1920s and 1930s) exhibited relatively little evidence of growth release (10–25% of stems) [21]. Population structures were narrowly even-aged, with recruitment in burned patches ceasing about a decade after crown fire.

Given our knowledge of climatic gradients across Florida and ecological/ demographic contrasts between sand pine varieties, we tested four research hypotheses:

1) **Sand pine is more sensitive to interannual variation in precipitation than temperature.** Restriction of sand pine to xeric substrates imposes a significant likelihood that growth may be curtailed in drought years. Because winters are typically dry (especially southward on the peninsula), sand pine may be particularly sensitive to interannual variability in winter precipitation. By contrast, long growing seasons and warm temperatures impose little direct effect on growth patterns, although temperature may influence climate/growth relations for interior sites in the panhandle, where freeze frequency and duration is higher than elsewhere across Florida.

2) **Sand pine growth anomalies are linked to warm and cold phases of the ENSO.** To the extent that sand pine growth is sensitive to interannual variation in winter precipitation, warm-phase ENSO years should yield greater sand pine growth than cold-phase ENSO years.

3) **Dendroclimatic signals are stronger in Ocala sand pine (the peninsular variety) than Choctawhatchee sand pine (the panhandle variety).** Climatic effects may be muted by varietal contrasts in regeneration ecology. Synchronous recruitment and stand development in fire-initiated patches yield more uniform growth patterns among canopy trees in Ocala sand pine, which should minimize the confounding influence of shading and other forms of competition on growth. By contrast, the multiple-aged structure of Choctawhatchee sand pine promotes growth suppression of understory stems by shading.

4) **Coastal populations of both varieties exhibit stronger dendroclimatic signals than their inland counterparts.** Sand pine populations located on or near the coastal strand often exhibit some degree of stunting, apparently associated with pruning by persistent winds and possibly limited depth of freshwater lenses. Such environmentally imposed physiological stress commonly sharpens the climatic signal embedded in tree-ring records [23, 27].

We employ climate/growth correlations, analysis of extreme growth years, and multiple regression to characterize spatial variability in the dendroclimatic signal of sand pine and to evaluate our research hypotheses. Our study is conceptually distinct from most dendroclimatic reconstructions to date, because we collected cores from all trees in each stand. This permits us to compare the strength of the climatic signal in stands of differing age-structure and canopy/understory competitive effects. In addition, if ENSO phase linkages with sand pine growth emerge, our study will extend the evidence in the southeastern United States of terrestrial biophysical responses to atmospheric teleconnections modulated by ENSO phase, which have heretofore concentrated on fire behavior [1, 24] and agricultural productivity [12, 13].

2. MATERIALS AND METHODS

2.1. Study sites

Three sand pine forest stands were mapped for each variety (*figure 1*). For Choctawhatchee sand pine (panhandle), sites were sampled at Eglin Air Force Base–Scrub Hill (EOS), Gulf Islands National Seashore–Naval Live Oaks (GIN), and St. Joseph Peninsula State Park (STJ). For Ocala sand pine (peninsula), sites were sampled at Highlands Hammock State Park (HHO), Jonathan Dickinson State Park (JDO), and Rock Springs Run State Reserve (RSO). Location of mapped plots was randomized within larger forest stands; plot sizes ranged between 40×40 and 60×60 m, depending on sand pine density. Each stand was strongly dominated by sand pine (>80% of overstory basal area); in addition, substrates and disturbance histories were uniform within each stand.

Sand pine inhabits modern and paleo-dunes associated with marine beach sediments. STJ was located on recently active sand dunes and possessed dune-and-swale topography. JDO, the other coastal stand, also exhibited remnant dunal topography, with a thick veneer of sands (ca. 2–4 m) overlying Pleistocene marine sediments. The remaining four sites were flat to gently sloping (<3°), with a thin veneer of sand (ca. 1–2 m) overlying Pleistocene or older sediments. Surface soils in all stands were sandy (sand fraction = 92–98%, see *table I*), with capillary water estimates in the upper 50 cm of soil of 2.0–2.2 cm [9]. Elevations were low, ranging from 3.5 m above sea level at STJ to 40 m at EOS. Flat topography, excessively drained sands, and low soil nutrient contents (*table I*) provided comparable substrate conditions among sites, although the dunes at STJ lacked older, clay-rich sediments at depth.

All stands were on state or federal reserve lands characterized by passive management (fire exclusion, no logging or grazing) and light recreation. Fires have been absent from stands since, at least, establishment of the oldest stems; hurricanes and extratropical cyclones have exposed all stands to sporadic blowdown events.

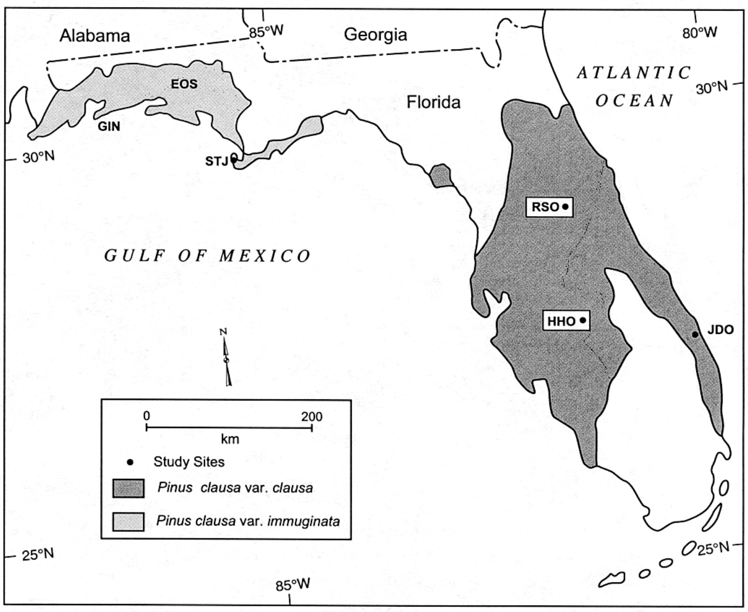

Figure 1. Range map of sand pine with location of study stands.

Table I. Summary of tree-ring data used to develop master chronologies in each stand.

	Period of record	No. cores	No. trees	Mean ± SD of radial increment (mm)		
				Total ring	Earlywood	Latewood
Choctawhatchee sand pine:						
EOS	1897–1994	126	91	1.81 ± 0.90	1.34 ± 0.76	0.48 ± 0.27
GIN	1930–1994	86	62	1.82 ± 0.83	1.38 ± 0.72	0.45 ± 0.25
STJ	1874–1994	63	54	1.08 ± 0.57	0.82 ± 0.47	0.27 ± 0.17
Ocala sand pine:						
HHO	1940–1994	119	81	1.93 ± 1.10	1.40 ± 0.93	0.53 ± 0.30
JDO	1927–1993	91	74	1.62 ± 1.05	1.25 ± 0.91	0.36 ± 0.23
RSO	1939–1994	138	89	2.14 ± 0.99	1.60 ± 0.84	0.54 ± 0.26

2.2. Climatic data

Monthly temperature and precipitation data were summarized by climatic division with data available from the National Climatic Data Center [20]. Florida is partitioned into seven climatic divisions. All three panhandle sites are located in Division 1. The peninsular sites are in Division 3 (RSO) or Division 4 (HHO, JDO) (*figure 2*; the climate diagram for Division 3 is not shown – it differs little from Division 4). Climatic division means were used instead of individual weather stations near study sites because local stations often had missing data and a relatively short period of record. Complete monthly temperature and precipitation records extend back to 1895 for each climatic division.

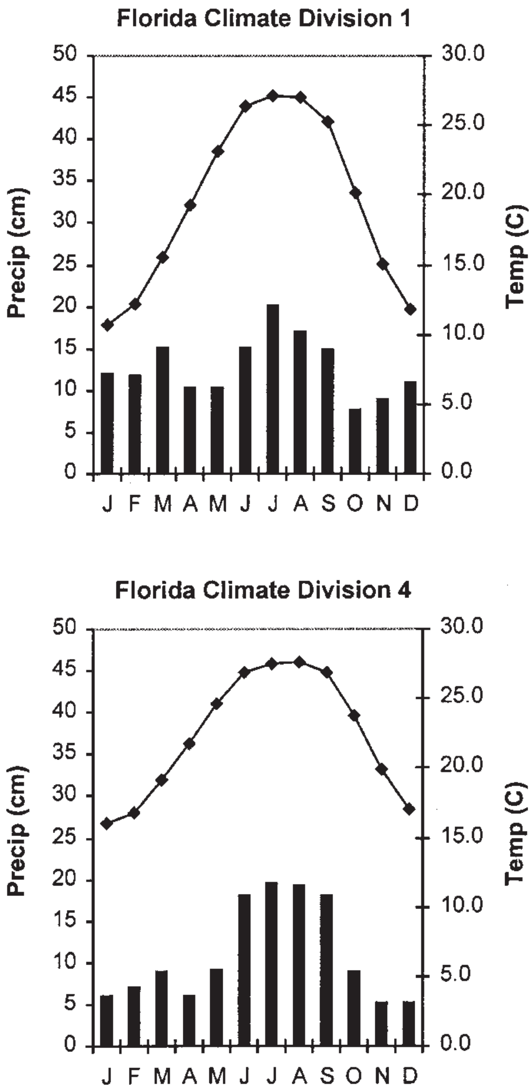

Figure 2. Climate diagrams for Florida Climatic Division 1 (panhandle) and Division 4 (central peninsula). Precipitation is depicted with bars; temperature with a line. Based on the 54-year period of common record for this study (1940–1993).

2.3. Tree core extraction and measurement

Two cores were extracted from all sound trees (i.e., lacking heart rot) > 5 cm diameter at breast height (dbh = 1.4 m). Cores were taken at right angles from one another, 30 cm above the ground. Cores were maintained as distinct records, rather than averaged by tree, because of substantial within-tree variation in growth patterns in some stands. Core processing followed standard protocol [30]. Cores were mounted, sanded with progressively finer-grit sand paper, and measured with a computer-based optical image analysis system (OPTIMAS^{TM}) at an accuracy of 0.008 mm. Transitions between earlywood and latewood in annual increments were determined by darkening of color. Most earlywood-latewood transitions were distinct; where transitions were diffuse, gray-scale values from the image analysis software were available to aid in marking the transition.

2.4. Master chronology development

At least one core from 75 to 95% of trees in each stand was reliably crossdated, as confirmed by COFECHA [15]. Crossdated cores were retained for developing master chronologies. The highest percentage of trees that were not crossdated (20 to 25%) came from the two coastal populations (JDO and STJ). Among the Choctawhatchee sand pine stands, the majority of trees excluded from the master chronology were understory individuals (20 of 29 were <8 cm dbh); by contrast, Ocala sand pine understory trees were rare–none were excluded from the chronology.

Three master chronologies were developed for each stand: total ring width, earlywood, and latewood. To accentuate short-term variance in tree growth that is most likely linked to interannual climatic variability, ring-width series from each core were filtered by three procedures [11]: (1) low frequency variance was removed from the series with a cubic smoothing spline (50% cut-off after 32 years), (2) persistence within the resulting smoothed series was removed by autoregressive modeling–thereby muting temporal carryover in growth signal from year-to-year, and (3) the resultant series was fitted to a negative exponential form to account for the decline in radial growth rates as trees age. Master chronologies for each stand and segment type were expressed as standard normal deviates (*z*-scores) across all years of record.

Master chronologies developed for total ring width, earlywood, and latewood in each stand were correlated with one another to assess the commonality in their growth response. For each annual increment segment (i.e., total ring, earlywood, and latewood), master chronologies were correlated for all stand pairs to assess geographic variability and varietal contrasts in patterns of growth.

2.5. Climate/growth modeling

For each master chronology, bivariate correlations between annual growth increments and monthly mean temperature, and between annual growth and monthly total precipitation were calculated for the 21-month period extending from March of the previous growing season to November of the current growing season, in keeping with unusually long growing seasons in these near-tropical latitudes. To facilitate geographic comparison, these analyses were limited to the 54-year period of record common to all six sites (1940–1993).

As complementary evidence of climatic controls, extreme growth years were analyzed for the same period. For each master chronology, annual growth increments for which $|z| > 1.0$ were segregated into rapid-growth and slow-growth groups. Differences-of-means (Student's t-tests) between rapid- and slow-growth years were calculated for monthly mean temperature and total precipitation data for the same 21-month interval used in bivariate correlations.

For each master chronology, multiple regression models relating annual growth increments to climatic variables were developed for the period of common record (1940–1993). We used ordinary least-squares regression instead of climatic response functions, because regression explicitly permits interaction among regressors, thus providing a better integrative explanatory model than the sets of bivariate correlations on which climate response functions are based. Candidate climatic variables for regression included monthly mean temperature and total precipitation, as well as composite means and sums for multiple consecutive months. For example, the importance of winter and spring precipitation might be incorporated into a model by summing the total precipitation received from January through May in each year of record and entering this as a single variable. Inclusion of multiple-month climatic variables promotes parsimony, both statistically (by limiting the reduction of degrees of freedom in the model) and physically (by emphasizing the aggregate significance of climatic forcing during critical periods).

Following the recommendation of the Center for Ocean-Atmospheric Prediction Studies at Florida State University [2], we adopted the Japan Meteorological Agency (JMA) ENSO index, which is based on observed (1949–present) and reconstructed (1868–1948) mean sea-surface temperature anomalies from the tropical Pacific Ocean. ENSO years were assigned to warm phase, neutral, or cold phase, based on the JMA index. We tested for differences of means of sand pine growth index values between warm- and cold-phase ENSO years for each of the 18 master chronologies.

3. RESULTS

3.1. Summary statistics and master chronologies

Mean radial growth rates were highest for inland Ocala sand pine stands (HHO, RSO). By contrast, the two coastal populations (JDO, STJ) were characterized by the lowest mean growth rates (*table I*).

Serial correlations between the annual increment segment types in each stand revealed that total ring width and earlywood width series were very strongly correlated (0.865–0.981) (*table II*). Latewood width series were uniformly lower in correlation with both total ring and earlywood width series across all stands.

Inter-stand correlations of ring width series produced consistent results: correlations between stands of the

Table II. Correlation among width series within each stand. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Site	Earlywood-Latewood	Earlywood-Total Ring	Latewood-Total Ring
EOS	0.497 ***	0.865 ***	0.583 ***
GIN	0.556 ***	0.937 ***	0.682 ***
STJ	0.563 ***	0.896 ***	0.571 ***
HHO	0.552 ***	0.975 ***	0.709 ***
JDO	0.563 ***	0.971 ***	0.677 ***
RSO	0.686 ***	0.981 ***	0.803 ***

Table III. Inter-stand correlations of growth indices for earlywood, latewood, and total ring width. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	GIN	STJ	HHO	JDO	RSO
Total Ring:					
EOS	0.464 ***	0.539 ***	0.045	0.068	0.151
GIN	___	0.387 **	–0.080	0.104	–0.055
STJ	___	___	0.246	0.214	0.312 *
HHO	___	___	___	0.492 ***	0.499 ***
JDO	___	___	___	___	0.432 **
Earlywood:					
	GIN	STJ	HHO	JDO	RSO
EOS	0.405 **	0.491 ***	0.054	0.129	0.179
GIN	___	0.307 *	–0.055	0.150	–0.085
STJ	___	___	0.262	0.258	0.297 *
HHO	___	___	___	0.474 ***	0.484 ***
JDO	___	___	___	___	0.401 **
Latewood:					
	GIN	STJ	HHO	JDO	RSO
EOS	0.575 ***	0.524 ***	0.246	–0.080	0.267
GIN	___	0.518 ***	0.176	0.002	0.181
STJ	___	___	0.202	0.059	0.322 *
HHO	___	___	___	0.283 *	0.551 ***
JDO	___	___	___	___	0.159

same variety were positive and statistically significant, whereas correlations between stands of different varieties were not statistically significant (*table III*). There were two exceptions to this outcome: JDO and RSO did not exhibit a significant positive correlation for latewood width (although both are from Ocala sand pine) and STJ and RSO exhibited significant positive correlations for all three series types (although they are of differing varieties).

Stand-level master chronologies for all three series types were similar; only total ring width chronologies are displayed (*figure 3*). Years of record characterized by consistent growth anomalies ($|z| > 1.0$) for half or more of the stands include:

– rapid growth–1912*, 1929*, 1947, 1959, 1960, 1966, 1969, 1973, 1975, 1983, and 1991;

– slow growth–1927*, 1932*, 1940, 1951, 1954, 1963, 1967, 1981, and 1985.

Several early years are denoted with an asterisk because they pre-date the period of common record for all six sites and are, therefore, based on fewer chronologies. (Recognition of extreme years based on departures of half or more stands in a given year is arbitrary–too few chronologies are available to employ a more statistically rigorous cut-off.) The period from 1959 to 1975 is distinguished by a high concentration of rapid-growth years (over the entire period of record, 6 of the 11 rapid-growth years occur in this 17-year interval). Slow-growth years were more historically dispersed, although the early-1950s produced two slow-growth years in a 4-year period. Years of anomalous growth were not uniformly expressed by both varieties. Growth anomalies in 1954 (–), 1963 (–), and 1969 (+) were recorded in Choctawhatchee stands but not Ocala stands; conversely, growth anomalies in 1951 (–), 1983 (+), and 1985 (–) were recorded in Ocala stands but not Choctawhatchee sand pine stands.

3.2. Climate/growth correlations

Precipitation was generally positively associated with growth in the current growing season, often significantly so in the period between January and June *(figures 4 and 5*). Indeed, winter and spring precipitation leading into the growing season emerged as the most consistent and

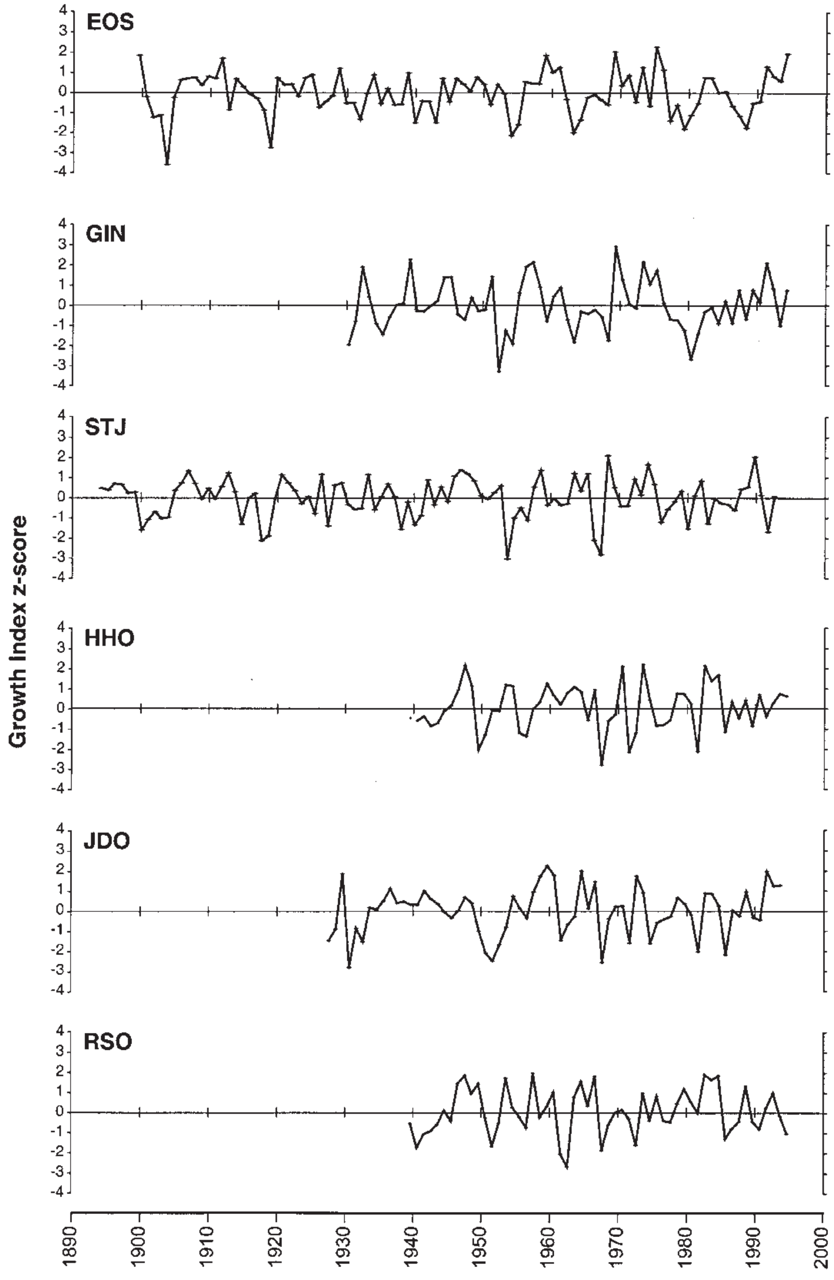

Figure 3. Total ring width master chronologies for each of the six study stands, with the growth index expressed as standard normal deviates.

prominent correlate of sand pine growth patterns across the species' range. Precipitation from the previous growing season exhibited weaker correlations of mixed sign, very few of which were statistically significant.

Precipitation was more strongly correlated with sand pine growth than was temperature in STJ (*figure 4*) and all three of the Ocala sand pine stands (*figure 5*). For the three Ocala stands, temperature correlations with growth series were weak, although there is some evidence of lagged temperature effects from the prior spring in the inland Ocala stands (HHO, RSO) (*figure 5*). For the two inland Choctawhatchee stands (EOS, GIN) temperature and precipitation exhibited comparable levels of

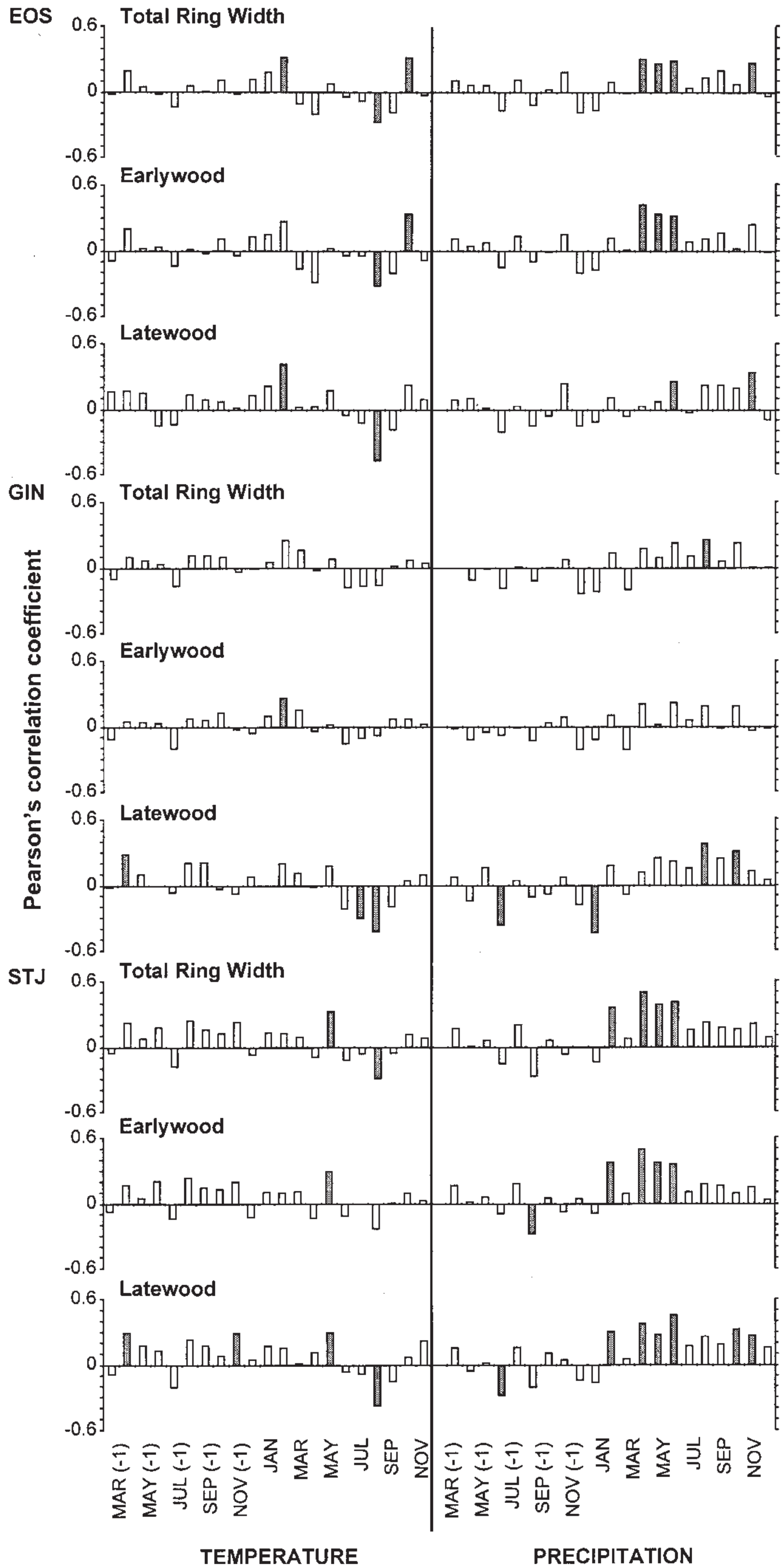

Figure 4. Climate/growth correlations for Choctawhatchee sand pine stands. Pearson product-moment correlation coefficients of monthly mean temperature and total precipitation with annual radial growth are plotted with bars for 21 consecutive months from March of the previous growing season [MAR (–1)] to November of the current growing season. Corelation coefficients that are statistically significant at $p < 0.05$ are depicted with shaded bars.

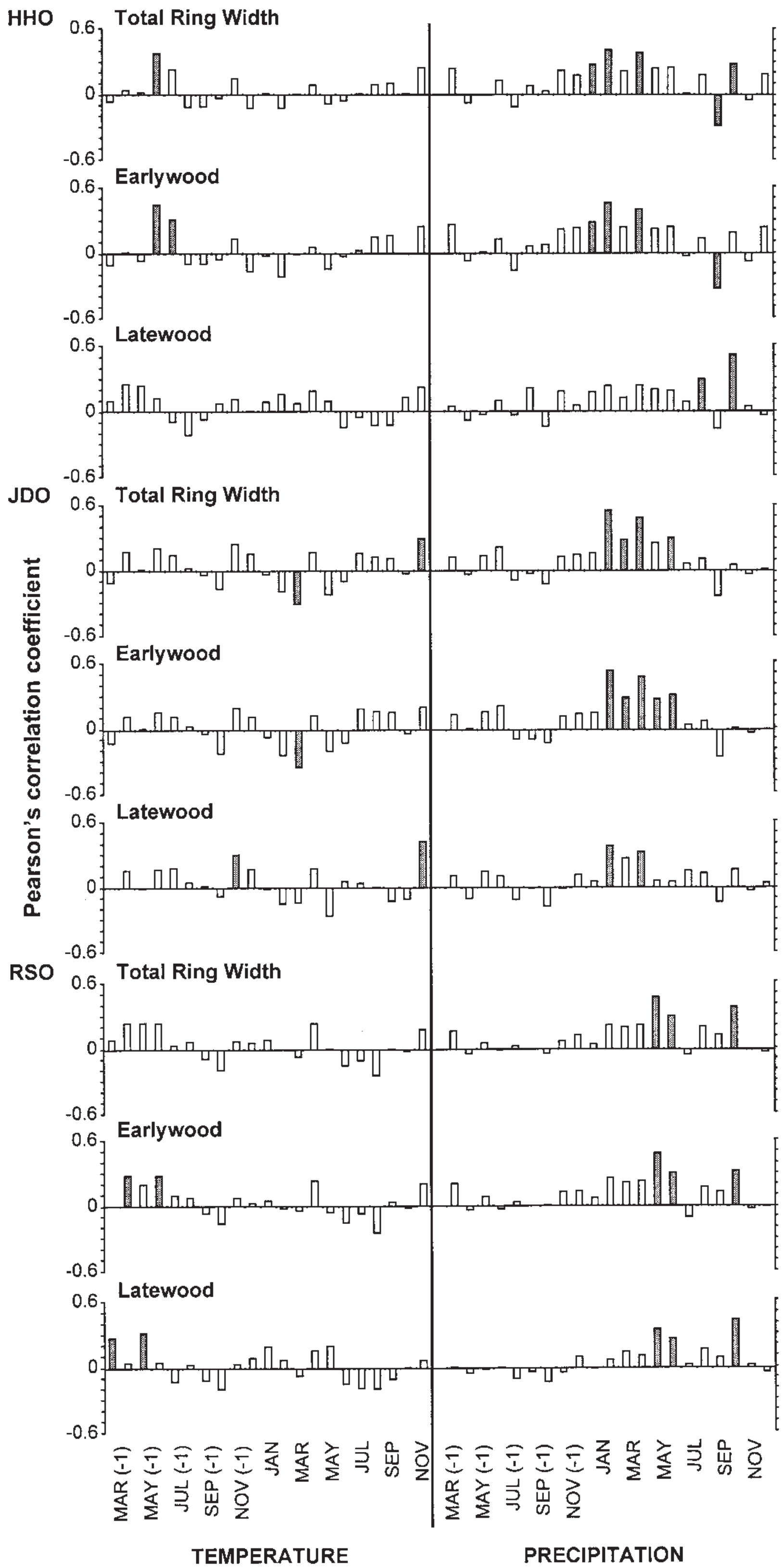

Figure 5. Climate/growth correlations for Ocala sand pine. See legend of *figure 4* for details.

correlation with sand pine growth increments. Temperature correlations in these two stands were generally positive for the early growing season periods (statistically significant only in February), switching to negative in the later months of the growing season (statistically significant only in August).

Among the series types, precipitation is more consistently positively associated with total ring width and earlywood width series. Latewood width series exhibited somewhat greater responsiveness to temperature variables.

3.3. Analysis of extreme years

Examining differences of means between rapid- vs. slow-growth years for the same suite of monthly climatic variables employed in climate/growth correlations revealed similar outcomes. Positive associations of monthly precipitation variables with rapid-growth years were evident for both sand pine varieties (*table IV*). For Choctawhatchee sand pine, there were 21 positive associations of precipitation with rapid growth, as opposed to five negative associations. All of the positive

Table IV. Summary of extreme analyses for monthly precipitation variables during the period of common record (1940–1993). For each time series (site by series type), years in which $|z| > 1.00$ were segregated into rapid- vs. slow-growth groups. Significant difference-of-means outcomes (Student's t-test; $p < 0.05$) are depicted with a + where more rapid growth is associated with greater precipitation and a – where slower growth is associated with greater precipitation.

	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N
	LAG (–1)										NO LAG										
Choctawhatchee sand pine:																					
EOS:																					
Total Ring													+	+	+						
Earlywood									–				+	+	+						
Latewood																					
GIN:																					
Total ring									–						+						
Eearlywood																					
Latewood							–		–	–					+		+				
STJ:																					
Total ring											+		+	+	+		+	+			
Earlywood											+		+	+	+						
Latewood													+		+						
Ocala sand pine:																					
HHO:																					
Total ring											+		+		+						+
Earlywood								+			+		+		+						+
Latewood											+		+						+		
JDO:																					
Total ring											+		+								
Earlywood											+	+	+								
Latewood																					
RSO:																					
Total ring											+			+	+				+		
Earlywood											+		+	+	+						
Latewood														+					+		

associations were from the current growing season, with 18 of the 21 clustered in the winter/spring interval from January to May. Each of the five negative associations fell during the prior autumn (September to December). For Ocala sand pine, the positive association of precipitation with rapid-growth years is even stronger, with 27 positive associations and no negative associations. Twenty- one of the 27 positive associations for Ocala sand pine occurred in the January to May period of the current growing season. For each variety, about 14% of the t-tests were significant at $p < 0.05$, above the 5% of significant outcomes that would be generated by chance.

In keeping with the bivariate climate/growth correlations, temperature was more weakly associated with anomalous growth years than precipitation *(table V)*. For Choctawhatchee sand pine, 8% of the t-tests generated significant values for monthly temperature variables, moderately exceeding the 5% random standard. Ten

Table V. Summary of extreme analyses for monthly temperature variables during the period of common record (1940–1993). For each time series (site by series type), years in which $|z| > 1.0$ were segregated into rapid- vs. slow-growth groups. Significant difference-of-means outcomes (Student's t-test; $p < 0.05$) are depicted with a + where more rapid growth is associated with higher temperatures and a – where slower growth is associated with higher temperatures.

	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N
	LAG (–1)										NO LAG										
Choctawhatchee sand pine:																					
EOS:																					
Total ring																		–			
Earlywood																					
Latewood																		–			
GIN:																					
Total ring																					
Earlywood												+									
Latewood																–					
STJ:																					
Total ring		+					+	+	+							–					
Earlywood		+					+	+													
Latewood								+	+									–			
Ocala sand pine:																					
HHO:																					
Total ring																					
Earlywood				+											–						
Latewood																					
JDO:																					
Total ring																					
Earlywood		+																			
Latewood																					+
RSO:																					
Total ring								–													
Earlywood																					
Latewood			+																		

positive associations of temperature with growth were evident; seven of these ten occurred in the autumn (September to November) of the prior year. By contrast, there were five negative associations of temperature with growth, all clustered during the hottest period of the current growing season (June to August). For Ocala sand pine, only 3% of t-test outcomes for monthly temperature variables were significant, below the 5% random standard.

3.4 Multiple regression analysis

With the exception of GIN, adjusted-R^2 values for models based on total ring width ranged between 0.378 and 0.547, indicative of reasonable levels of explanatory covariance between climatic drivers and sand pine growth response (*table VI*). STJ, the coastal Choctawhatchee site, displayed the highest explained variance for all three series. Earlywood-based regression models were consistently strong for Ocala sand pine stands, with adjusted-R^2 values ranging between 0.407 and 0.487. Earlywood-based models for the two inland Choctawhatchee stands (EOS, GIN) were substantially weaker. Latewood-based regression models were generally characterized by lower explanatory power than total ring width and earlywood-based models. Choctawhatchee sand pine stands exhibited higher adjusted-R^2 values in latewood-based models (0.363–0.446) than Ocala sand pine stands (0.263–0.342).

The rankings of standardized regression coefficients within the various models reveal that a precipitation

Table VI (continued on next page). Summary of regression analyses for each combination of site and series type, based on the period of common record (1940–1993) among all sites. Significance levels of overall F-statistic and individual regression coefficients is indicated as: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Overall F-statistic	R^2	Adjusted R^2	Climatic variable §	Standard regression coefficient	Tolerance
Choctawhatchee sand pine:						
EOS:						
Total ring	13.97***	0.456	0.423	ΣMARMAYP	0.437***	0.999
				AUGT	–0.376***	0.997
				FEBT	0.351**	0.998
Earlywood	13.02***	0.338	0.312	ΣMARMAYP	0.499***	1.000
				AUGT	–0.282*	1.000
Latewood	19.29***	0.431	0.408	AUGT	–0.493***	0.998
				FEBT	0.453***	0.998
GIN:						
Total ring	6.38**	0.200	0.169	ΣMAYJULP	0.360**	1.000
				FEBT	0.269*	1.000
Earlywood	4.50*	0.150	0.117	ΣMAYJULP	0.279*	1.000
				FEBT	0.272*	1.000
Latewood	16.11***	0.387	0.363	ΣJULSEPP	0.516***	1.000
				ΣAPRJUNP	0.337**	1.000
STJ:						
Total ring	22.35***	0.573	0.547	ΣJANMAYP	0.633***	0.961
				MAYT	0.208*	0.951
				ΣJULSEPP	0.193*	0.949
Earlywood	28.88***	0.531	0.513	ΣJANMAYP	0.666***	0.978
				MAYT	0.212*	0.978
Latewood	22.37***	0.467	0.446	ΣJANMAYP	0.516***	0.976
				ΣJULSEPP	0.375***	0.976

Table VI (continued).

	Overall F-statistic	R^2	Adjusted R^2	Climatic variable §	Standard regression coefficient	Tolerance
Ocala sand pine:						
HHO:						
Total ring	17.07***	0.401	0.378	ΣJANMAYP	0.517***	0.955
				JUN(–1)T	0.273*	0.955
Earlywood	19.21***	0.430	0.407	ΣJANMAYP	0.504***	0.955
				JUN(–1)T	0.326**	0.955
Latewood	10.20***	0.380	0.342	SEPP	0.404**	0.933
				ΣJANMAYP	0.258*	0.953
				ΣAPRJUN(–1)T	0.253*	0.974
JDO:						
Total ring	49.82***	0.489	0.480	ΣJANJUNP	0.700***	-----
Earlywood	51.38***	0.497	0.487	ΣJANJUNP	0.705***	-----
Latewood	13.23***	0.342	0.316	ΣJANJUNP	0.409***	0.961
				NOVT	0.345**	0.961
RSO:						
Total ring	16.08***	0.491	0.460	ΣJANMAYP	0.510***	0.990
				ΣJULSEPP	0.337**	0.950
				ΣAPRJUN(–1)T	0.251*	0.943
Earlywood	15.33***	0.479	0.448	ΣJANMAYP	0.521***	0.990
				ΣAPRJUN(–1)T	0.279*	0.943
				ΣJULSEPP	0.273*	0.950
Latewood	10.43***	0.290	0.263	ΣJULSEPP	0.399**	1.000
				ΣJANMAYP	0.369**	1.000

§ Variable-naming protocol: Months are designated by three-letter abbreviations (e.g., MAR = March; SEP = September). If the variable is lagged from the previous year, a (–1) follows the monthly abbreviation (e.g., NOV(–1) = November of the prior year). P or T at the end of the variable name indicates precipitation or temperature, respectively. Σ followed by two month designators indicates that the variable is the sum of these and all intervening months (e.g., ΣJANJUN = sum of January through June).

variable was the primary variable in 17 of 18 models. The EOS latewood model was the exception; it lacked a precipitation variable. This reinforces findings from bivariate correlation and extreme growth analyses, which highlight the primacy of precipitation over temperature in models of sand pine growth responses in most circumstances. All precipitation variables in all regression models were positively related to sand pine growth. The seasonality of these precipitation regressors varied geographically. For Ocala sand pine, sums of precipitation for the January–May or January–June period appeared in all nine models, and were the primary variable in seven of nine. For Choctawhatchee sand pine, the seasonal timing of primary precipitation variables drifts from January–May for the coastal STJ stand, to March–May for EOS, to May–July for earlywood and total ring width series in GIN, to July–September in the GIN latewood width series.

Although temperature variables play a secondary role, they are included in 13 of the 18 regression models. Temperature variables were primary only in EOS latewood. The seasonality of temperature influences varied between varieties. For Choctawhatchee sand pine, monthly temperatures from February and May of the current year were positively related to growth, whereas August temperatures were negatively related to growth. For Ocala sand pine, five of the six models in the two inland stands

(HHO, RSO) incorporated positive responses of growth to lagged temperatures from the spring (April–June) of the prior growing season. JDO, the coastal Ocala stand (and also the southernmost locale in the study) exhibited a positive growth response to November temperatures of the current growing season in the latewood model.

Multiple regression outcomes from the period of common record underscored the strong linkage of earlywood growth to early/mid-season precipitation variables, which were primary variables in all earlywood models from across the entire range of sand pine. Not surprisingly, late-season temperature (August–November) and precipitation (July–September) figured more prominently in latewood regression models.

3.5. Relationship of sand pine growth to ENSO phase

Earlywood width series showed significant differences in growth between warm-phase and cold-phase ENSO years in all three Ocala sand pine stands, as well as in STJ (*table VII*). As expected, warm-phase conditions, which are associated with increased winter precipitation over Florida, fostered more rapid sand pine growth. The two inland Choctawhatchee sand pine stands (EOS, GIN) exhibited no relationship of growth to ENSO phase, in keeping with their muted response to precipitation variability in regression models. Unlike the earlywood width series, latewood widths showed no significant growth relationship to ENSO phase. (Predictably, the response of the total ring width series was similar to earlywood, but was somewhat muted by inclusion of the latewood increment.)

Table VII. Difference-of-means test results for earlywood growth index values compared between warm-phase and cold-phase ENSO years. Tests confirmed equality of variance between the two groups of years in each stand. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Mean ± st. dev. of growth index value		
Site	Cold phase	Warm phase	Student's t
Choctawhatchee sand pine:			
EOS	–0.082 ± 0.931	–0.064 ± 0.997	0.058
GIN	0.451 ± 0.863	–0.025 ± 1.036	1.321
STJ	–0.360 ± 0.952	0.311 ± 0.830	2.527 *
Ocala sand pine:			
HHO	–0.623 ± 0.565	0.499 ± 0.784	4.130 ***
JDO	–0.255 ± 0.913	0.503 ± 0.970	2.091 *
RSO	–0.270 ± 0.625	0.412 ± 0.857	2.341 *

4. DISCUSSION AND CONCLUSIONS

Given the tolerance of sand pine for dry, low nutrient substrates, its growth response to precipitation variability is logical. Precipitation totals in the period just prior to (January and February) and in the early/middle parts of the growing season (March through June) consistently emerged as strong influences on growth across the species range. Temperature variability was a secondary influence on sand pine growth in some areas; it was most prominently expressed in inland Choctawhatchee sand pine stands (EOS, GIN). The Florida panhandle experiences the highest frequency of freeze events of any region within the species' range. These findings supported our first research hypothesis: overall, precipitation is more strongly linked to sand pine growth patterns than is temperature. Nevertheless, our results underscore the importance of spatial variability in climatic controls of tree growth across a species range.

Radial growth patterns of other southern pine species have been linked to precipitation variability elsewhere in the American Southeast ([34] for slash pine (*Pinus elliottii*), [3] for loblolly pine (*Pinus taeda*), [6] for longleaf pine (*Pinus palustris*)). However, these studies identified growth responses to summer or annual precipitation measures and were based on samples from restricted geographic areas. Our range-wide sampling is unique among tree-ring based climate/growth studies of southern pines.

The strong association of sand pine growth with interannual variability of winter/spring precipitation in four stands (the three Ocala sand pine stands plus STJ) conformed with the ENSO/growth findings. In the same four stands, earlywood growth increments were significantly greater in warm-phase ENSO years, years characterized by increased winter precipitation over Florida. Hence, our second research hypothesis was supported: sand pine growth series are sensitive indicators of ENSO phase. This finding extends previous evidence of ENSO effects on biophysical phenomena in the southeastern United States. Simard et al. [24] and Brenner [1] found greater wildfire activity in drier, cold-phase ENSO years. Hansen et al. [12, 13] found links between agricultural productivity and ENSO phase; winter vegetable yields in Florida declined in warm-phase ENSO years, which the authors attributed to increased rainfall, reduced daily maximum temperatures, and reduced solar radiation in these years. We suspect that dendroclimatic reconstructions for other pines and upland hardwood species in peninsular Florida would reveal links to ENSO phase similar to those we reported, although sand pine may be especially sensitive to precipitation, because it occupies unusually dry and nutrient-poor sites, relative to most other tree species in Florida.

For the majority of stands, climate/growth relations were most strongly expressed in total ring width series. Climate/growth relationships were stronger in the earlywood than latewood series of the three Ocala sand pine stand and STJ. In contrast, latewood-based regressions displayed stronger climatic links in the two interior Choctawhatchee sand pine stands (EOS, GIN). As noted above, these were the two stands in which temperature was most often included as a primary variable in our regression models. Our findings reinforce the importance of examining all components of radial growth in dendroclimatic reconstructions. Just as there can be prominent spatial variability in climatic controls across a species range, there also can be pronounced spatial variability in the climatic sensitivity of earlywood vs. latewood increments across a species range.

Each sand pine variety exhibited a distinctive historical pattern of growth, with low inter-varietal correlations among ring series, for the most part. Analysis of extreme growth years reinforced these varietal contrasts; some extreme growth years were only recorded in one of the two varieties. This suggests that, while broader circulation patterns (such as those related to ENSO teleconnections) affect the climate of Florida, sub-regional spatial variability in the expression of drought or excess rains can be expected in some years.

Climate/growth regressions from Ocala sand pine stands were uniformly strong in explanatory power. Each of these stands is characterized by a narrowly even-aged structure, so that all stems are generally responsive to the same climatically mediated growth rhythms. Like Ocala sand pine, the coastal Choctawhatchee sand pine stand (STJ) showed strong climatic linkages to growth, presumably because of the greater physiological stress imposed in this stand situated on recently active dunes and lacking a clay-rich layer at depth (which, if present, would elevate subsurface water supply). By contrast, the two inland Choctawhatchee sand pine stands (EOS, GIN) produced the weakest climate/growth relations. Stand-scale biotic effects may account for some reduction in the strength of climate/growth signal in these stands. On-going sand pine recruitment maintained by wind-induced, gap-phase regeneration in these stands appears to weaken the climatic signal in radial growth records, presumably due to canopy effects on understory growth. In combination with regional contrasts in winter temperature regime, these biotic effects cause distinctive climate/growth relations to emerge for inland Choctawhatchee sand pine stands. Because of the wide variance in climate/growth explanatory power between the inland and coastal Choctawhatchee sand pine stands, we conclude that our third research hypothesis was not supported: we found no consistent varietal differences in the strength of climate/growth relationships.

In general, we found that climate/growth relations were well expressed, even when cores were extracted from all trees in a stand. We screened cores that did not crossdate well with the remainder of cores within a stand, but this eliminated less than 25% of trees, even in Choctawhatchee sand pine stands characterized by strong canopy/understory influences. In dendroclimatic reconstructions, it may not be necessary to impose a systematic bias in tree selection to enhance expression of the climatic signal in a master chronology, at least where site factors ensure some degree of physiological stress. Sampling all possible trees in a stand reduces the likelihood that important climatic signals will be missed in chronology development.

Coastal stands of both sand pine varieties were characterized by reduced growth rates, as their stunted physiognomy suggested. Climate/growth regressions in STJ (coastal Choctawhatchee sand pine) generated the highest explanatory power, irrespective of series type, among all six stands. JDO (coastal Ocala sand pine) was second in climatic explanatory power for the total ring and earlywood width series. In both stands, winter/spring precipitation variables were strongly related to variation in radial growth patterns. Collectively, these results supported our fourth research hypothesis: climate/growth relationships are more strongly expressed in coastal populations than inland populations of sand pine. In future efforts to establish ENSO-based links with productivity of natural vegetation in Florida, coastal strand environments should receive high priority, because their substrates magnify the consequences of interannual variation in winter season precipitation.

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