Climate response of five oak species in the eastern deciduous forest of the southern Appalachian Mountains, USA

James H. Speer, Henri D. Grissino-Mayer, Kenneth H. Orvis, and Cathryn H. Greenberg

Abstract: The climatic response of trees that occupy closed canopy forests in the eastern United States (US) is important to understanding the possible trajectory these forests may take in response to a warming climate. Our study examined tree rings of 664 trees from five oak species (white (*Quercus alba* L.), black (*Quercus velutina* Lam.), chestnut (*Quercus prinus* L.), northern red (*Quercus rubra* L.), scarlet (*Quercus coccinea* Münchh.)) from 17 stands in eastern Tennessee, western North Carolina, and northern Georgia to determine their climatic response. We dated the samples using skeleton plots, measured the cores, and compared the site- and regional-level tree-ring chronologies of each separate species with divisional climate data. The oldest trees in each chronology dated back to 203 years for black oak, 299 years for chestnut oak, 171 years for northern red oak, 135 years for scarlet oak, and 291 years for white oak. We successfully developed climate models via multiple regression analyses with statistically significant ($P < 0.05$) variables representing the Palmer Drought Severity Index and average monthly temperature for most of the site-species chronologies (average $R^2 = 0.15$). All regional climate response models included the Palmer Drought Severity Index from either June or July as the most significant variable in the climate response, suggesting that growing-season drought is the most important factor limiting oak growth in the southeastern US. An increase in temperature and reduction in moisture is likely to reduce their competitiveness in their current locations and force these species to migrate to cooler climates, thereby greatly changing ecosystem health and stability in the southern Appalachians.

Résumé : La réponse climatique des arbres présents dans les forêts à couvert fermé dans l'est des États-Unis est importante pour comprendre l'évolution potentielle de ces forêts en réaction au réchauffement climatique. Nous avons étudié les cernes annuels de 664 arbres appartenant à cinq espèces de chênes (chênes des blanc (*Quercus alba* L.), de noir (*Quercus velutina* Lam.), châtaignier (*Quercus prinus* L.), rouge (*Quercus rubra* L.), écarlate (*Quercus coccinea* Münchh.)) provenant de 17 peuplements dans l'est du Tennessee, l'ouest de la Caroline du Nord et le nord de la Georgie dans le but de déterminer leur réponse climatique. Nous avons daté les échantillons à l'aide de relevés des caractéristiques des cernes, mesuré les carottes et comparé les séries dendrochronologiques de chaque espèce séparément aux données climatiques divisionnaires, à l'échelle de la station et de la région. Les plus vieux arbres dans chaque chronologie avaient 203 ans pour le chêne des teinturiers, 299 ans pour le chêne de montagne, 171 ans pour le chêne rouge, 135 ans pour le chêne écarlate et 291 ans pour le chêne blanc. À l'aide d'analyses de régression multiple, nous avons réussi à développer des modèles climatiques qui comportaient des variables statistiquement significatives ($P < 0,05$) pour la plupart des chronologies des différentes combinaisons d'espèces et de stations (R^2 moyen = 0,15). Ces variables représentaient l'indice de sévérité de sécheresse de Palmer et la température mensuelle moyenne. Dans tous les modèles de réponse climatique régionale, l'indice de sévérité de sécheresse de Palmer des mois de juin ou juillet était la variable la plus significative dans la réponse climatique, indiquant que la sécheresse durant la saison de croissance est le facteur limitant le plus important pour la croissance du chêne dans le sud-est des États-Unis. Une augmentation de la température et une diminution de l'humidité réduira probablement leur compétitivité et leur occupation actuelle du territoire et forcera ces espèces à migrer vers des climats plus frais, ce qui par conséquent affectera sérieusement la santé et la stabilité des écosystèmes dans le sud des Appalaches.

[Traduit par la Rédaction]

Introduction

Global temperatures are predicted to warm from 2.4 to 5.5 °C if atmospheric CO_2 levels reach 650 ppm, according to the 2007 report from the Intergovernmental Panel on Climate Change (IPCC) (Solomon et al. 2007). This warming is likely to be associated with some increase in precipitation, but increased evapotranspiration may counteract that to yield a net decrease in runoff in the southeastern US (Mulholland et al. 1997). Vegetation response to these climatic forcing factors is important in the management of southeastern forests because these forests have some of the highest levels of biodiversity anywhere in the United States (US) (White and Miller 1988). Predictions of vegetation response to moderate climate change suggest a regional expansion of forests, while severe climate change may cause more fires in southeastern forests, resulting in a rapid conversion to savanna grasslands (Bachelet et al. 2004). An understanding of individual species' response to climate is necessary to better understand vegetation dynamics in the face of a warming climate (Graumlich 1993).

Trees that grow in closed-canopy (interior) forests have previously been avoided for dendroclimatic reconstructions because competition for light and episodic disturbances may affect tree growth and mask the tree's response to climatic variations (Fritts 1976). Understanding the climatic response by trees that grow in such locations is desirable, however, because forest management in the eastern US is largely concerned with managing closed-canopy forests and only marginally involved in managing old-growth stands where the most desirable trees for dendroclimatic studies are found.

Natural disturbances are important in the development of the eastern deciduous forest (Pickett and White 1985). High winds and ice storms can cause tree falls and set off a complex process of gap dynamics (Lafon and Speer 2002). Surface fires have burned in deciduous forests, leaving behind a record in buried fire scars on oak and pine trees and causing changes in the successional pathways of the mixed hardwood–pine forests (Sutherland and Smith 2000; DeWeese 2007). These disturbances cause relatively long (5–20 years) suppressions and releases in tree-ring series that may confound the low-frequency climate signal from trees that grow in forest interiors. The climatic response of closed forest canopy trees needs to be examined to evaluate how they respond to climate despite these confounding signals caused by disturbance processes. Understanding how trees have responded to climatic variations during the twentieth century will help improve models that predict changing forest resources and productivity under a constantly changing climate that is likely to be enhanced by pervasive human alterations of the landscape and the atmosphere.

Reconstructions of past climate variations using tree-ring data have been developed around the world and have contributed strongly to our growing understanding of natural climate fluctuations and, subsequently, global climate change (Mann et al. 1998; Stahle et al. 2000; Esper et al. 2002). Examination of the climate response of trees native to the eastern US has been performed on various species, including pines (primarily *Pinus taeda* L. and *Pinus echinata* Mill.) (Friend and Hafley 1989; Grissino-Mayer et al. 1989; Grissino-Mayer and Butler 1993), bald cypress (*Taxodium distichum* (L.) Rich.) (Stahle and Cleaveland 1996), tuliptree (*Liriodendron tulipifera* L.) (Orwig and Abrams 1997; Pan et al. 1997), and white oak (*Quercus alba* L.) (LeBlanc 1993; Rubino and McCarthy 2000). These studies have clearly demonstrated the potential for using southeastern tree species to better understand past trends in climate, but no study has compared the strength and clarity of the climatic response among the multiple oak species that dominate these southeastern forests.

This paper is the first to compare the climatic response of five oak species in the southeastern US. We will also compare the climatic response observed in these five oak species with that observed in white oak tree-ring chronologies developed previously, which mainly show an early to midsummer Palmer Drought Severity Index (PDSI) response. White oak is considered the most important tree species in the southeastern US for providing information on past climate because of its wide geographic range and its proven sensitivity to year-to-year climate fluctuations (Jacobi and Tainter 1988; Rubino and McCarthy 2000; LeBlanc and Terrell 2001). Our work is also valuable because it compares the climatic response of multiple species from the same sites to assess whether site conditions can enhance or dampen the interspecific response to climate. Physiological research has demonstrated that different tree species have different climate responses due to the time of year that growth occurs in various zones of the tree (i.e., root activity, shoot elongation, stem diameter growth) (Krueger and Trappe 1967; Jenkins and Pallardy 1995; Fekedulegn et al. 2002). Dendroclimatologists should be able to use these differing responses to extract climate records tuned to different parts of the year to provide a more complete climate reconstruction for a site. Furthermore, this paper will illustrate the potential of using tree species and sites that have historically been avoided when conducting climate reconstructions because they were located in forest interior conditions.

Our study began with three primary objectives: (1) to document the climatic response of five oak species in the eastern deciduous forest, (2) to compare the growth response among species to determine which species are valuable for climate reconstruction, and (3) to compare this climatic response with that found in white oak, which has been the standard for dendrochronological climate studies with oaks in the eastern US.

Methods

Site description

Our sites were initially established by personnel working with the US Department of Agriculture Forest Service for the study of acorn production (mast) in oak trees to monitor food production for black bears (*Ursus americana*) in the southern Appalachian Mountains (Greenberg 2000; Speer 2001). The Forest Service established 17 permanent plots from 1991 to 1993 in the Chattahoochee National Forest in northern Georgia, the Cherokee National Forest in eastern Tennessee, and the Pisgah National Forest in western North Carolina (Table 1; Fig. 1). Most of the sites are distributed broadly except for seven sites that were clustered in the Bent Creek watershed near Asheville, North Carolina. The

Table 1. Site information.

Site	Latitude (°N)	Longitude (°W)	Elevation (m a.s.l.)	Oak species*
Chattahoochee National Forest, northern Georgia				
Cohutta	34.94	84.78	441	Chestnut (11), scarlet (7), white (7)
Tallulah	34.92	83.46	606	Chestnut (7), red (17), white (8)
Brasstown Work Center	34.93	83.92	755	White (6)
Cherokee National Forest, eastern Tennessee				
Burnett Gap	36.22	82.56	644	Black (6), chestnut (8/16), red (5), scarlet (11), white (9)
Hiawassee cluster B	35.34	84.57	270	White (10)
Hiawassee cluster C	35.34	84.57	481	Black (9), chestnut (10), scarlet (10)
Tellico	35.38	84.33	587	Black (18), chestnut (17), red (18), scarlet (16), white (18)
Pisgah National Forest, western North Carolina				
Bike Trail	35.52	82.63	729	Black (9), red (10), scarlet (7), white (8)
Buell Plot	35.52	82.63	695	Chestnut (19), red (7), scarlet (9), white (8)
Green's Lick	35.52	82.63	910	Black (6), chestnut (21), red (24), white (15)
Hard Times	35.52	82.63	785	Chestnut (18), scarlet (5), white (23)
Hurricane Gap	35.88	82.80	1149	Chestnut (18), red (17), scarlet, white (6)
Jackson Farm	35.97	82.97	481	Black (12), chestnut (14), red (12), scarlet (12), white (12)
Mill Ridge	35.73	82.97	732	Chestnut (11), scarlet (12), white (12)
Old Gate	35.52	82.63	719	Chestnut (9), scarlet (14)
Rice Pinnacle	35.52	82.63	682	Scarlet (19), white (19)
South Ridge	35.52	82.63	828	Chestnut (18), red (13), scarlet (8), white (7)

*The numbers in parentheses are the number of trees sampled of each oak species on each site.

Fig. 1. Locations of study sites, national forests and parks, and climate divisions in the southern Appalachians. Sample sites are numbered 1–11 (black circles): 1, Watauga; 2, Jackson Farm; 3, Burnett Gap; 4, Mill Ridge; 5, Hurricane Gap; 6, Bent Creek experiment forest cluster containing Buell Plot, Bike Trail, Green's Lick, Hard Times, Old Gate, Rice Pinnacle, and South Ridge; 7, Tellico; 8, Hiawassee cluster; 9, Cohutta; 10, Brasstown Work Center; 11, Tallulah. Nine National Oceanic and Atmospheric Administration climate divisions cover the study area: VA 06, Virginia 6; TN 01, Tennessee 1; NC 01, North Carolina 1; NC 02, North Carolina 2; SC 01, South Carolina 1; SC 02, South Carolina 2; GA 01, Georgia 1; GA 02, Georgia 2; and GA 03, Georgia 3. The gray regions designate national forest land and the gray region labeled GSMNP is the Great Smoky Mountains National Park.
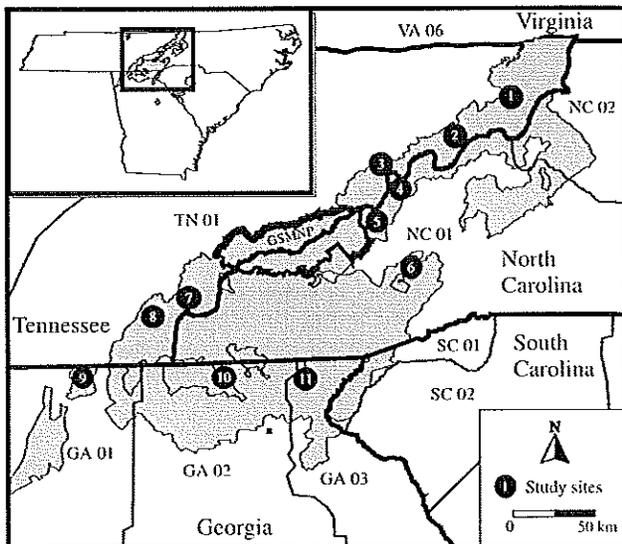
majority of sites are between 400 and 800 m a.s.l. in elevation, with the lowest site at 270 m and the highest at 1149 m.

Vegetation at all sites is classified as Eastern Deciduous Forest Province, Appalachian Oak Forest Section (Bailey 1980). American chestnut (*Castanea dentata* (Marsh.) Borkh.) once dominated this province, but the introduced chestnut blight (*Cryphonectria parasitica* (Murill) Barr) decimated the population. Today, chestnut has been replaced mainly by chestnut oak (*Quercus prinus* L.), northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and tuliptree (Nelson 1955; Woods and Shanks 1959; Young 1996). Oak has become the dominant component of the deciduous forest canopy in the southern Appalachian region.

In the southern Appalachian Mountains, European settlement affected the landscape through farming, logging, and livestock grazing as early as AD 1795 (SAMAB 1996). Varying intensities of logging in the 1800s and 1900s left the study area largely covered with second-growth forest (SAMAB 1996). This relatively recent removal of mature trees through logging and the subsequent regeneration of early-successional forest limits the temporal extent of the dendrochronological record in most areas.

Field methods

Trees and sites were chosen to represent a wide range of tree ages, topographic positions, and site conditions to provide a more comprehensive set of analyses to investigate the spatiotemporal climatic response of trees within the region. For the original study on mast production, USDA Forest Service employees tagged the trees and mapped site locations, enabling the relocation of the 664 trees sampled for this study (Greenberg 2000; Speer 2001). At each of the 17 sites, we took two cores per tree from up to five oak species (black oak (*Quercus velutina* Lam.), chestnut oak,

northern red oak, scarlet oak (*Quercus coccinea* Muenchh.), and white oak). The cores were stored in plastic straws and the straws were labeled with the site name and tree number. Using the site name and tree number, a database maintained by the USDA Forest Service could be accessed to retrieve species information, diameter at breast height (DBH), crown class (dominant, codominant, intermediate, or understory), crown size, aspect, slope angle, terrain shape index, and landform index.

Chronology development

We dried all cores at 65 °C for 24 h, mounted them on wooden core mounts, and surfaced them with a belt sander using progressively finer grits of sandpaper from ANSI 120 grit (105–125 μm) through ANSI 400 grit (20.6–23.6 μm) (Orvis and Grissino-Mayer 2002). For each site, we created skeleton plots from 10 cores to develop a master tree-ring chronology for crossdating purposes (Stokes and Smiley 1968). Crossdating refers to the assignment of the precise calendar year to each tree ring based on recognizable patterns of wide and narrow rings from within a site (Douglass 1941). Skeleton plots facilitate the crossdating process by emphasizing the narrow rings that contribute to the unique pattern of rings (Stokes and Smiley 1968). All tree rings from the remaining cores were crossdated using the patterns from the master skeleton plot.

We then measured the widths of all crossdated tree rings on all cores to 0.01 mm precision using a Velmex measuring system, then used the computer program COFECHA to check our crossdating and measurement accuracy (Holmes 1983; Grissino-Mayer 2002). The primary function of COFECHA is to ensure correct crossdating, and it does so using segmented time series correlation analyses. Shorter segments of each measurement series being tested are compared with the same segment from a chronology computed from all remaining series. If each tested segment is correctly crossdated, the correlation will be statistically significant (usually $P < 0.0001$) and positive. Segments that correlate poorly are flagged by the software and must be reinspected for crossdating and measurement accuracy.

We entered the measurement series into the program ARSTAN to standardize each series to a mean of 1.0 and stabilize the variance, thus ensuring that the majority of the undesirable age-related (i.e., nonclimatic) growth trend was removed (Cook 1985). The flexibility of the cubic smoothing spline used by ARSTAN to standardize the series determines the frequencies of events that can or cannot be analyzed in the final detrended chronology. We determined the best spline to use for our climate response study by trying different cubic smoothing splines (100 year, 60 year, 40 year, 35 year, 30 year, 25 year, 20 year, 15 year, 10 year, and 5 year), then determined which resulting chronology showed maximum correlations with climate variables.

Tree-ring series from individual trees growing within the same stand often vary owing to differential responses caused by competition for light, water, and nutrients, and owing to other more localized disturbances such as individual gap dynamics. Since we sampled 664 trees from five different oak species growing at 17 separate sites, we were able to develop chronologies at two distinct spatial scales. We first de-

veloped site-species chronologies that incorporated all of the trees of one oak species on a site. To develop robust chronologies with little intertree variability, we limited site-species chronologies to stands that included five or more trees of a given species. We constructed 55 site-species chronologies: 15 white oak, 13 chestnut oak, 12 scarlet oak, 9 northern red oak, and 6 black oak. The number of individuals per chronology varied from 5 to 24 trees, with 664 trees included in the final 55-chronology dataset. We also developed five regional-species chronologies by combining all series from each of the five oak species, using the same methods as for the site-species chronologies. These procedures resulted in a set of tree-ring index chronologies for each species that retain the common variance at the site and regional levels throughout our study area in the southern Appalachian Mountains.

Climate–tree growth analyses

The PDSI (Palmer 1965) can better model tree growth than can precipitation or temperature alone because the PDSI serves as a proxy for water availability, which is what often drives tree growth (Cook et al. 1992; Grissino-Mayer and Butler 1993; Rubino and McCarthy 2000). For our climate models, we examined monthly PDSI, precipitation, and temperature data for the nine National Oceanic and Atmospheric Administration climate divisions that cover our study area (Fig. 1). We used divisional climate data because the climate divisions represent a broader level of climate variability, whereas individual weather stations may be more sensitive to microclimatic phenomena that affect the individual meteorological stations. Climate divisions in this region are bounded by topographic barriers that affect air mass movement and orographic effects (Konrad 1996). Thus, divisional data provide a more homogeneous climate variable that has a better potential for meaningful extrapolation beyond the specific site being studied.

To determine the best climatic calibration data set, we compared our five regional-species chronologies against monthly PDSI values for all nine climate divisions. We also defined two aggregate regions: the first by averaging the PDSI values for all nine climate divisions by month, and the second by averaging the monthly PDSI values for Tennessee climate division 1 and North Carolina climate division 1 only. These two divisions cover most of the study area and incorporate the mountainous portion of the southern Appalachian Mountains (Fig. 1). The appropriate climate calibration data set was chosen through correlation of the regional tree-ring chronologies with all of the division and aggregate division data.

We used correlation analysis to test for significant associations between tree growth (as indicated by the tree-ring chronologies) and climate, using monthly PDSI, mean monthly temperature, and total monthly precipitation from January through December for the year in which the tree ring was formed and from the eight lagged months, May through December, of the previous year. The climate data ranged from AD 1895 to 2000. The climate conditions of the months prior to ring formation can affect tree growth through preconditioning of the soil and through formation or depletion of carbohydrate reserves stored in the tree from the previous year (Fritts 1976). The earlywood pores in oak

Table 2. Dating quality of the regional-species chronologies.

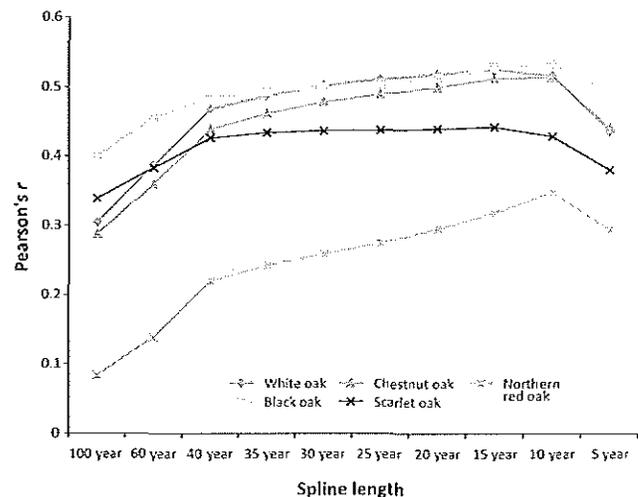| Regional-species chronology	Number of trees	Number of cores	Years	Interseries correlation	Mean sensitivity
Black oak	67	129	203	0.49	0.19
Chestnut oak	182	351	299	0.42	0.19
Northern red oak	49	78	171	0.37	0.19
Scarlet oak	132	257	135	0.44	0.18
White oak	169	332	291	0.44	0.21
Minimum	49	78	135	0.37	0.18
Average	120	229	220	0.43	0.19
Maximum	182	351	299	0.49	0.21
Sum	599	1147			

trees are formed coincident with leaf out; and therefore, their growth must draw from the previous year's stored photosynthates. We developed a summer (May through August) aggregate variable for the climate variables, for both current and previous summers. In all, we correlated 20 single months and two summer seasonal values of PDSI, temperature, and precipitation (66 variables) against our site-species chronologies.

We next used stepwise linear regression in SPSS (version 10) (Norusis 1999) to develop a climate model for each of the five regional-species chronologies. We examined the regression models to determine which significant variables were justified based on climatic and physiological mechanisms and to ensure that we kept our models parsimonious while maximizing the variance explained by climate. To test the climate response of the five oak species in this study, we developed all models using the same climate variables, representing the same two climate divisions that were chosen for the regional-species models. We recognize that at the site-species level, trees are likely to be responding in part to microclimatic effects, but we wished to measure the response to broad-level climate phenomena and, therefore, restricted our analyses to the divisional climate data. The Durbin–Watson (D–W) statistic was used to test for an acceptable level of autocorrelation in our time series (Ostrom 1978), with a range of 1.6 –2.4 considered as acceptable.

Results

Dating quality of the site-species and regional-species chronologies

The 55 site-species chronologies had an average interseries correlation of 0.56 (ranges from 0.45 to 0.70) and an average mean sensitivity (year-to-year variability) of 0.20 (ranges from 0.14 to 0.27). Black oak exhibited the highest interseries correlations among the five species analyzed, while northern red oak had the lowest. Northern red oak yielded significantly lower interseries correlations than scarlet oak ($t = 2.665$, $P \leq 0.05$) and black oak ($t = 2.698$, $P \leq 0.05$). Black oak yielded significantly higher interseries correlations than chestnut oak ($t = 2.083$, $P \leq 0.05$). White oak had the highest mean sensitivity (0.22), while the other four species clustered around 0.19. Chestnut oak and white oak lived the longest (299 and 291 years, respectively), while the other three species lived long enough to extend beyond the modern climate record based on maximum sample age for each species (Table 2).

Fig. 2. Correlation of regional-species chronologies with climate (two-division mean PDSI; see text) as a function of spline length, by species.

The five regional-species chronologies had moderate interseries correlations (average = 0.43) and mean sensitivities (average = 0.19) (Table 2). Higher values at the stand level are expected because all trees in any given stand are growing under similar circumstances and have similar controlling factors, including competition and exposure to site-specific climate history.

Spline choice and chronology development

By analyzing the correlation of each regional-species chronology with climate (specifically July PDSI as explained below), we determined that a 15 year cubic smoothing spline performed the best (Fig. 2). For all five species, the correlation with July PDSI gradually increased as the spline length was shortened. Correlations deteriorated with the 10 and 5 year splines, which suggested the 15 year spline was optimal for all standardization calculations in this study. The 15 year cubic smoothing spline removed low frequency nonclimatic variation and enhanced interannual variation, thus increasing the correlations with climate. The 15 year spline retained 50% of the variance at 15 years and 99% of the variance at 5 years and below. Therefore, noise from confounding factors with a 5 year or longer trend was dampened or removed from the chronology.

Table 3. Statistics for the climate models developed for the regional-species chronologies.

Species	r	r^2	D–W	P value	Climate model
Black oak	0.61	0.37	1.47	<0.001	$\hat{y} = 0.0259PD_{jun} + 0.0084T_{mayp} - 0.0075T_{sep} + 0.961$
Chestnut oak	0.61	0.37	2.10	<0.001	$\hat{y} = 0.0220PD_{jul} - 0.0118PD_{mayp} - 0.0077T_{sep} + 1.515$
Northern red oak	0.48	0.23	1.57	<0.001	$\hat{y} = 0.0121PD_{jun} + 0.0076T_{mayp} - 0.0077T_{sep} + 1.027$
Scarlet oak	0.51	0.26	1.99	<0.001	$\hat{y} = 0.0176PD_{jul} + 0.0062T_{mayp} - 0.0058T_{sep} + 0.987$
White oak	0.60	0.36	1.97	<0.001	$\hat{y} = 0.0219PD_{jul} - 0.0083T_{sep} + 0.0058T_{mayp} + 1.184$

Note: For the climate models, $\hat{y}$ is the tree-ring index value, PD_{jun} is PDSI June, PD_{jul} is PDSI July, PD_{mayp} is PDSI prior May, T_{mayp} is temperature from the prior May, and T_{sep} is temperature for the current September. We used these regional-species chronology responses to determine the monthly climate variables to include in the climate models for the site-species climate analysis.

Our five regional-species chronologies ranged from 134 to 298 years in length (based on the oldest individual in the chronology). The regional white oak chronology was the longest (1701–1999). Of the 55 site-species chronologies we developed, our longest extends back to 1701 while the shortest started in 1958. Most cores were relatively short in length, with the average year of establishment for all trees being 1912.

Analysis of climate response across the landscape

Climate parameters

PDSI, temperature, and precipitation averaged between Tennessee division 1 and North Carolina division 1 correlated the highest with our regional tree-ring index chronologies compared with the other divisional climate data. We averaged the data from these two divisions together to create a combined region that represented climate across the study area. We thereafter used the monthly PDSI, temperature, and precipitation values from this aggregate climate division for the whole of the study. Our chronologies responded most strongly to PDSI, especially growing-season PDSI (Fig. 3). Our oak chronologies showed a negative response to temperature in the summer and current September (Fig. 4). The precipitation response was similar to but weaker than the PDSI response and correlated significantly with the growing season and the previous August (Fig. 5). Because of the similar responses to PDSI and precipitation, we excluded precipitation from the multiple regression analyses to avoid colinearity. We developed statistically significant climate models for all five regional-species chronologies using three monthly PDSI or temperature variables (Table 3). June PDSI or July PDSI were always the first variables chosen for the models, followed by temperature from May of the previous year and September of the current year. Our climate models explained from 23% (northern red oak) to 37% (black and chestnut oak) of the variance in our regional-species chronologies (Table 3). All regional-species chronologies had low autocorrelation (average D–W = 1.821) (Table 3). Significant climate models ($P < 0.05$) were developed for 71% of the site-species chronologies and the climate variables explained 8.3% to 39.0% of the variance.

Species compared

White oak has been the most commonly used eastern North American oak species for climate reconstruction. We examined our results to see whether our white oak chronologies were particularly suited for climate reconstruction using PDSI and temperature variables. In our 55 site-species chronologies, white oak chronologies did not yield significantly higher interseries correlations than the other four oak species studied ($P < 0.005$). However, the white oak chronologies did have a significantly higher mean sensitivity ($P < 0.005$). Assessing all site-species chronologies, we found that chestnut oak correlated best with climate and had more chronologies with relatively high proportions of variance explained by climate (average $R^2 = 0.18$, max $R^2 = 0.35$). Other species ranked, in order of average variance explained, as follows: white oak (average $R^2 = 0.17$, max $R^2 = 0.35$), black oak (average $R^2 = 0.15$, max $R^2 = 0.39$), scarlet oak (average $R^2 = 0.14$, max $R^2 = 0.32$), and northern red oak (average $R^2 = 0.10$, max $R^2 = 0.25$) (Fig. 6).

Discussion

The high interseries correlations and mean sensitivities for the oak chronologies developed in this study suggest that oak trees in the southeastern US respond to coherent regional- and stand-level controls. Our results compare favorably with the descriptive statistics of regional tree species from 84 sites and 16 species throughout the southeastern US, where the average interseries correlation is 0.49 and the average mean sensitivity is 0.26 (Table 4). The average interseries correlation from 48 published oak chronologies located throughout the US is 0.40, while the average mean sensitivity is 0.19. In comparison, our averages (0.56 and 0.20, respectively) would be considered quite good for sites where mesic conditions and closed canopies predominate. Furthermore, our trees were originally chosen for a study of tree masting behavior; neither the sites nor the individual trees were selected specifically for climatic analyses. High values for interseries correlations and mean sensitivities, combined with the significant amount of variance explained by PDSI and temperature, suggest that climate is likely the dominant signal that affects tree growth in these forest interior sites, at both the stand and regional levels.

All five oak species analyzed in this study responded to similar climate variables. Responses to June and July PDSI may reflect moisture stress (or surplus) during the middle of the growing season, and therefore, drought during these months reasonably has the strongest individual correlations with regional-species chronologies. That some species respond better to June PDSI and others to July PDSI may be due to slightly different timing of growth in different species. The positive response to the previous year's May temperature suggests that an increase in the length of the

Fig. 3. The response of the regional-species chronologies to the Palmer Drought Severity Index (PDSI). Black bars denote variables that correlate significantly at the 0.01 level.
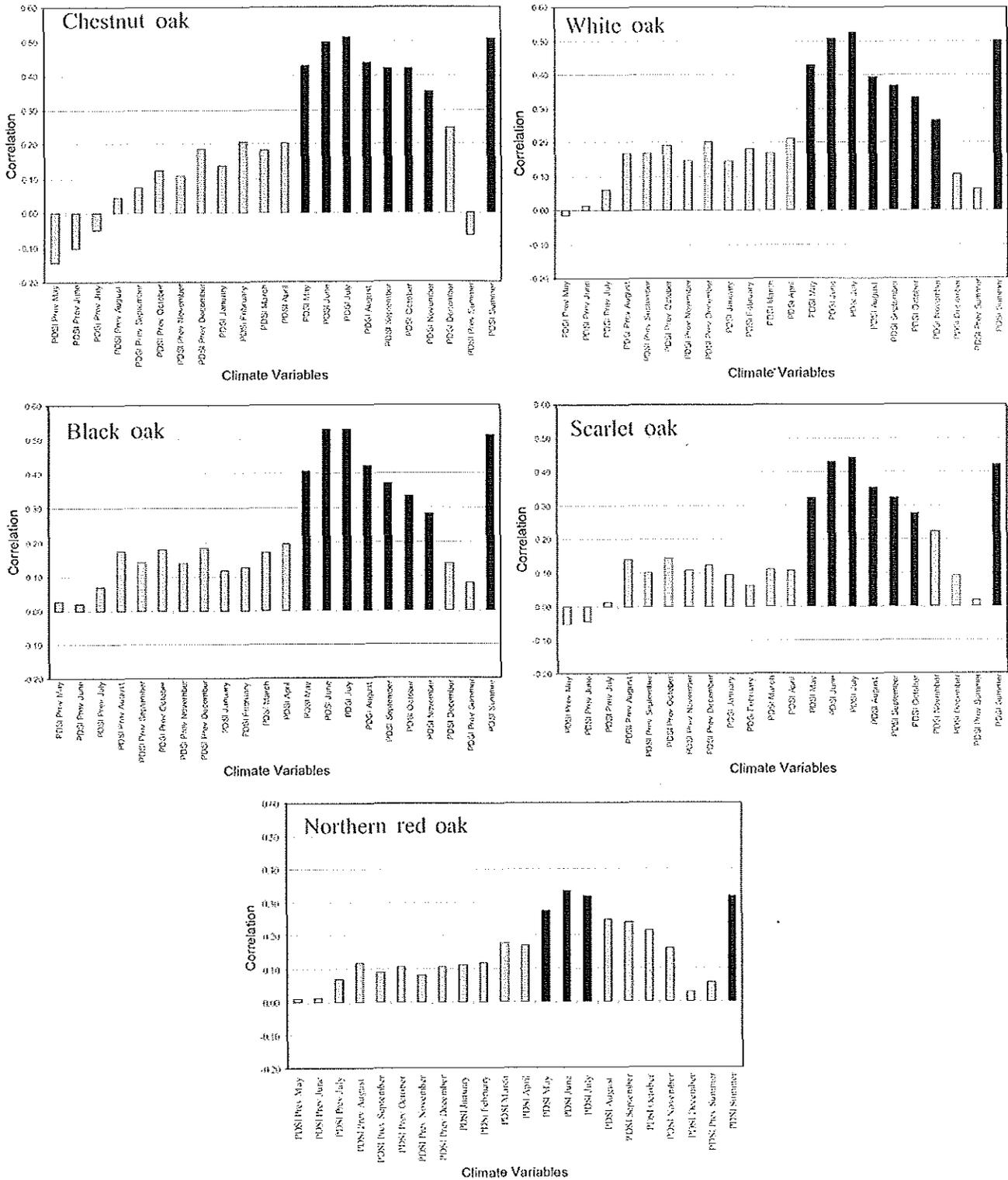
Fig. 4. The response of the regional-species chronologies to temperature. Black bars denote variables that correlate significantly at the 0.01 level.
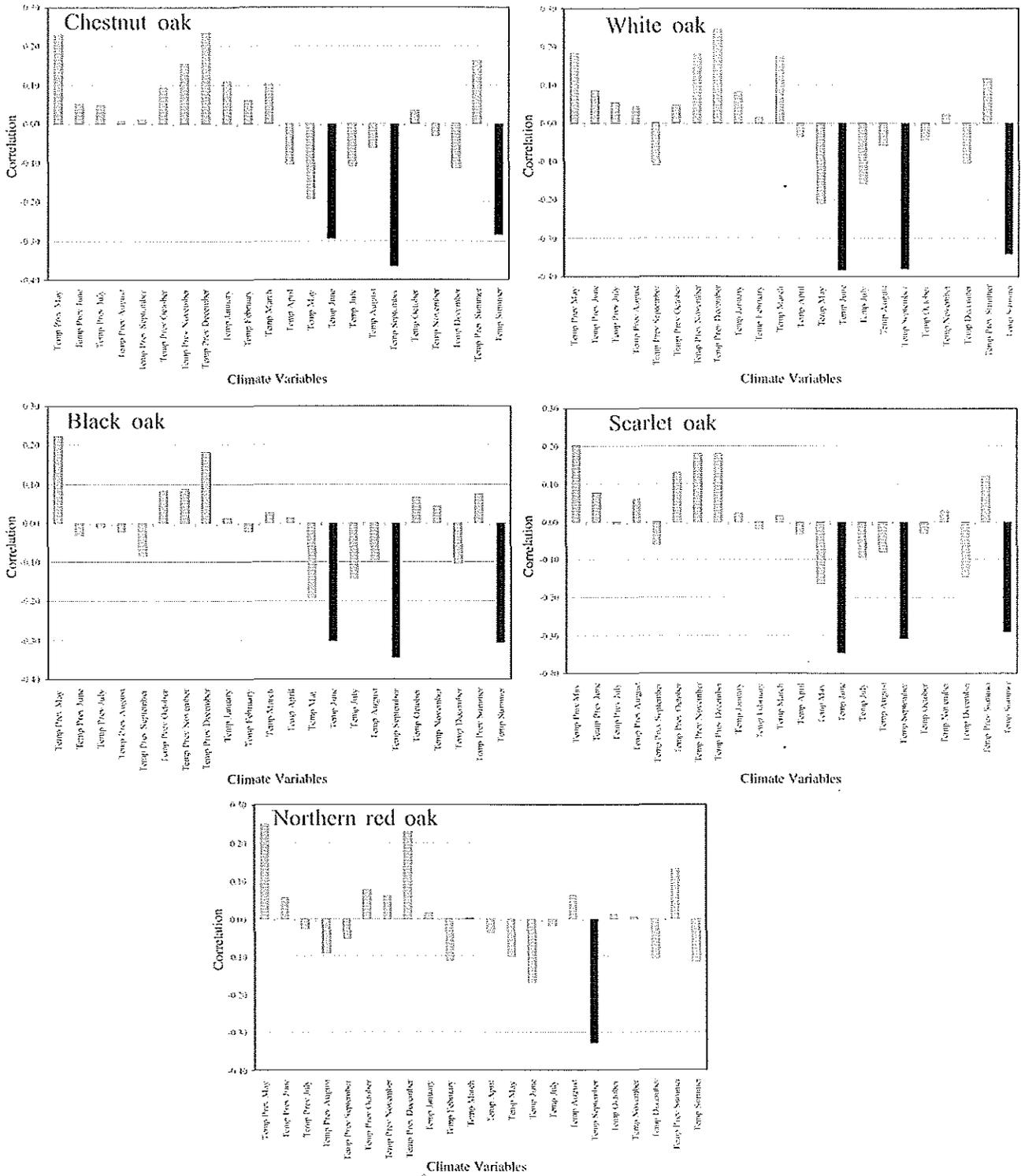
Fig. 5. The response of the regional-species chronologies to precipitation. Black bars denote variables that correlate significantly at the 0.01 level.

Table 4. Comparison of the results of this study with chronology statistics from 84 sites and 16 species developed in the southeastern US.

Species	Number of sites	Series intercorrelation	Average mean sensitivity	Location	Data source[*]
Liriodendron tulipifera	1	0.65	0.37	Tennessee	ITRDB 2000
Picea rubens	2	0.55	0.20	North Carolina	ITRDB 2000
Pinus echinata	1	0.53	0.26	Georgia	ITRDB 2000
Pinus echinata	1	0.76	0.30	Tennessee	ITRDB 2000
Pinus echinata	2	0.42	0.25	North Carolina	ITRDB 2000
Pinus echinata	12	0.48	0.20	Southeastern US	Estes 1970
Pinus palustris	3	0.50	0.28	North Carolina	ITRDB 2000
Pinus taeda	3	0.47	0.24	North Carolina	ITRDB 2000
Quercus alba	5	0.65	0.23	Tennessee	ITRDB 2000
Quercus alba	3	0.40	0.19	Southern Illinois	Robertson 1992
Quercus alba	3	0.52	0.20	North Carolina	ITRDB 2000
Quercus alba	4	0.49	0.14	South Carolina	Jacobi and Tainter 1988
Quercus alba	11	0.32	0.19	Southeastern US	Estes 1970
Quercus lyrata	2	0.37	0.22	Southern Illinois	Robertson 1992
Quercus macrocarpa	1	0.26	0.19	Southern Illinois	Robertson 1992
Quercus michauxii	3	0.29	0.20	Southern Illinois	Robertson 1992
Quercus pagodaefolia	3	0.42	0.17	Southern Illinois	Robertson 1992
Quercus palustris	1	0.38	0.17	Southern Illinois	Robertson 1992
Quercus rubra	2	0.27	0.15	Southern Illinois	Robertson 1992
Quercus shumardii	1	0.45	0.19	Southern Illinois	Robertson 1992
Quercus velutina	9	0.38	0.20	Southeastern US	Estes 1970
Taxodium distichum	1	0.63	0.50	Tennessee	ITRDB 2000
Taxodium distichum	2	0.66	0.58	North Carolina	ITRDB 2000
Taxodium distichum	3	0.66	0.59	Georgia	ITRDB 2000
Tsuga canadensis	1	0.62	0.25	Tennessee	ITRDB 2000
Tsuga canadensis	2	0.55	0.21	North Carolina	ITRDB 2000
Tsuga caroliniana	2	0.64	0.22	North Carolina	ITRDB 2000
Quercus alba	15	0.57	0.22	Southern Appalachians	This study
Quercus coccinea	12	0.58	0.18	Southern Appalachians	This study
Quercus prinus	14	0.54	0.20	Southern Appalachians	This study
Quercus rubra	10	0.52	0.19	Southern Appalachians	This study
Quercus velutina	7	0.61	0.19	Southern Appalachians	This study

[*]The data source shows the published article from which these data were taken, or else ITRDB 2000, which means these values are reported on the internet for the holdings of the ITRDB.

Fig. 6. The proportion of variance explained for each site-species chronology by the Palmer Drought Severity Index (PDSI) models with variables chosen for each species at the regional level.
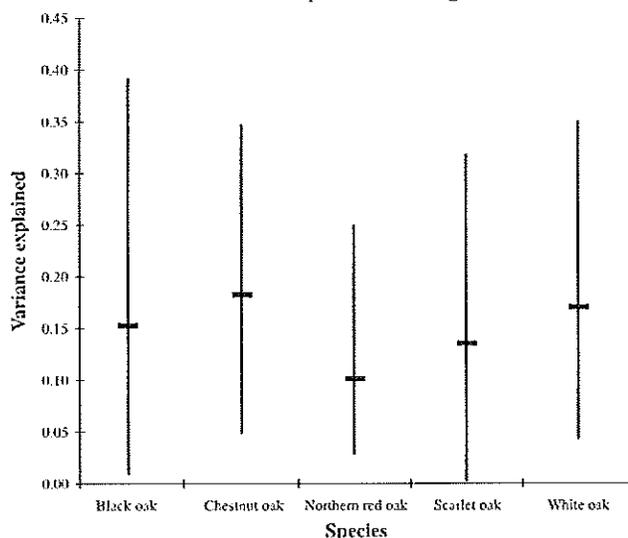
previous year's growing season increases the ability of trees to store nutrients for early spring growth in the following growing season. Repeatedly, September temperature was negatively correlated with ring width in the regional-species chronologies and the site-species chronologies. This suggests that warm temperatures during the end of the growing season stress the tree causing it to shut down growth.

White oak is frequently used for climate reconstructions in eastern North America. Our results show that white oak does not, on average, record a stronger stand- or regional-level climate signal than the other four oak species studied. Its higher mean sensitivity may indicate that it actually has a strong climate signal but that it may be masked by an unaccounted-for noise factor. The stronger climate response found for the chestnut oak chronologies suggests that this species should be used more often for climate reconstruction purposes. Scarlet oak and black oak also demonstrated good chronology statistics and high correlations with temperature and PDSI. Therefore, more research should incorporate chestnut, black, and scarlet oak for future climate reconstructions. Our results show that northern red oak has the weakest chronology statistics of the five species in our study area and did not record climate well on most sites. This last

finding is supported by Fekedulegn et al. (2002) who found that northern red oak has the lowest climate response out of four eastern tree species, including tuliptree, chestnut oak, and red maple, growing in West Virginia.

The length of time that the different oak species live before senescence and death will affect how useful each tree species is for long-term climate reconstructions. The oldest individuals of all five species lived longer than the modern climate record, making them useful for climate reconstructions. Chestnut oak and white oak, however, lived about 100 years longer than the other three oak species, and could provide opportunities for climate reconstructions going back nearly 300 years based on data from forest-interior species. It was interesting that despite the turn of the century logging in this region, we were able to find long-lived individuals in all five oak species.

Because this study is part of a larger project on mast reconstruction, we used a liberal standardization method (a 15 year cubic smoothing spline) to remove signals that were considered to be noise. We would have used a different approach if our primary goal had been to reconstruct climate that included low-frequency (i.e., interdecadal) climate signals. Our approach probably enhanced interannual variability and, thereby, increased statistical response to short-term climatic variability, while obscuring tree growth relationships with long-term climate patterns. This effect on the inferred climate response would be the same across species and would, therefore, not alter our results regarding the abilities of the different species when used in climate reconstruction. For future studies, we recommend that chestnut oak, scarlet oak, and black oak be used as well as white oak for climate reconstruction. Our results demonstrate that sites in closed-canopy oak forests can be useful for climate reconstruction and should be used when circumstances warrant.

Climate change predictions suggest a warming climate in the southeastern US but with little increase in precipitation, in contrast to global predictions (Solomon et al. 2007). These trends of warmer temperature and lower precipitation would result in greater extremes and frequency in drought events that could negatively impact oak growth in the southeastern US. Based on the positive relationship with summer PDSI and the negative relationship with September temperature for these five oak species, the increased moisture stress that is predicted to occur with global warming is likely to decrease the vigor of the extant oak trees in the southeastern US. This change in growing conditions is likely to force oak trees to establish at higher elevations, or migrate to higher latitudes, through seed dispersal. The resultant stress on living oak trees may lead to forest health decline and an increase of damage from a variety of forest pathogens. Forest managers may be left with the circumstance of managing forests that are no longer situated at their climatic optimum.

References

Bachelet, D., Neilson, R.P., Leniham, J.M., and Drapek, R.J. 2004. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystem, 4(3): 164–185. doi:10.1007/s10021-001-0002-7.

Bailey, R.G. 1980. Descriptions of the ecoregions of the United States. USDA Miscellaneous Publication No. 139.

Cook, E.R. 1985. A time series analysis approach to tree ring stan-

dardization. Ph.D. dissertation, The University of Arizona, Tucson, Ariz., USA.

Cook, E.R., Stahle, D.W., and Cleaveland, M.K. 1992. Dendroclimatic evidence from eastern North America. In Climate since A.D. 1500. Edited by R.S. Bradley and P.D. Jones. Routledge Press, London, UK. pp. 331–348.

DeWeese, G.G. 2007. Past fire regimes of Table Mountain pine (Pinus pungens Lamb.) stands in the central Appalachian Mountains, Virginia, U.S.A. Ph.D. dissertation, University of Tennessee, Knoxville, Tenn., USA.

Douglass, A.E. 1941. Crossdating in dendrochronology. J. For. 39(10): 825–831.

Esper, J., Schweingruber, F.H., and Winiger, M. 2002. 1,300 years of climate history for western central Asia inferred from tree-rings. Holocene, 12: 267–277. doi:10.1191/0959683602hl543rp.

Estes, E.T. 1970. Dendrochronology of black oak (Quercus velutina Lam.), white oak (Quercus alba L.), and shortleaf pine (Pinus echinata Mill.) in the central Mississippi Valley. Ecol. Monogr. 40(3): 195–316. doi:10.2307/1942285.

Fekedulegn, D., Hicks, R.R., and Colbert, J.J. 2002. Influence of topographic aspect, precipitation, and drought on radial growth of four major tree species in an Appalachian watershed. For. Ecol. Manage. 177: 409–425. doi:10.1016/S0378-1127(02)00446-2.

Friend, A.L., and Hafley, W.L. 1989. Climatic limitations to growth in loblolly and shortleaf pine (Pinus taeda and P. echinata): a dendroclimatological approach. For. Ecol. Manage. 26(2): 113–122. doi:10.1016/0378-1127(89)90039-X.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York, USA.

Graumlich, L.J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great lakes region. Can. J. For. Res. 23: 133–143. doi:10.1139/x93-020.

Greenberg, C.H. 2000. Individual variation in acorn production by five species of southern Appalachian oaks. For. Ecol. Manage. 132: 199–210. doi:10.1016/S0378-1127(99)00226-1.

Grissino-Mayer, H.D. 2002. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57(2): 205–221.

Grissino-Mayer, H.D., and Butler, D.R. 1993. Effects of climate on growth of shortleaf pine (Pinus echinata Mill.) in northern Georgia: a dendroclimatic study. Southeast. Geogr. 33(1): 65–81.

Grissino-Mayer, H.D., Rosenberger, M.S., and Butler, D.R. 1989. Climatic response in tree rings of loblolly pine from north Georgia. Phys. Geogr. 10(1): 32–43.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43: 69–78.

ITRDB. 2000. Tree-ring data search [online]. Available from http://hurricane.ncdc.noaa.gov/pls/paleo/fm_createpages.treering [accessed August 2000].

Jacobi, J.C., and Tainter, F.H. 1988. Dendroclimatic examination of white oak along an environmental gradient in the Piedmont of South Carolina. Castanea, 53(4): 252–262.

Jenkins, M.A., and Pallardy, S.G. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Can. J. For. Res. 25: 133–143.

Konrad, C.E., II. 1996. Relationships between precipitation event types and topography in the southern Blue Ridge Mountains of the southeastern USA. Int. J. Climatol. 16: 49–62. doi:10.1002/(SICI)1097-0088(199601)16:1<49::AID-JOC993>3.0.CO:2-D.

Krueger, K.W., and Trappe, J.M. 1967. Food reserves and seasonal growth of Douglas-fir seedlings. For. Sci. 12: 192–202.

Lafon, C.W., and Speer, J.H. 2002. Using dendrochronology to identify major ice storm events in oak forests of southwestern Virginia. Clim. Res. 20(1): 41–54. doi:10.3354/cr020041.

LeBlanc, D.C. 1993. Temporal and spatial variation of oak growth–climate relationships along a pollution gradient in the midwestern United States. Can. J. For. Res. 23: 772–782. doi:10.1139/x93-102.

LeBlanc, D., and Terrell, M. 2001. Dendroclimatic analyses using Thornthwaite-Mather-type evapotranspiration models: a bridge between dendroecology and forest simulation models. Tree-Ring Res. 57: 55–66.

Mann, M.E., Bradley, R.S., and Hughes, M.K. 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature, 392: 779–787. doi:10.1038/33859.

Mulholland, P.J., Best, G.R., Coutant, C.C., Hornberger, G.H., Meyer, J.L., Robinson, P.J., Stenberg, J.R., Turner, R.E., Vere-Herrera, F., and Wetzel, R.G. 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. Hydrol. Process. 11(8): 949–970. doi:10.1002/(SICI)1099-1085(19970630)11:8<949::AID-HYP513>3.0.CO;2-G.

Nelson, T.C. 1955. Chestnut replacement in the southern highlands. Ecology, 36(2): 352–353. doi:10.2307/1933248.

Norusis, M.J. 1999. SPSS 9.0 guide to data analysis. Prentice Hall, Upper Saddle River, N.J., USA.

Orvis, K.H., and Grissino-Mayer, H.D. 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. Tree-Ring Res. 58(1/2): 47–50.

Orwig, D.A., and Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees (Berl.), 11: 474–484. doi:10.1007/s004680050110.

Ostrom, C.W. 1978. Time series analysis: regression techniques. Sage University Paper series on Quantitative Application in the Social Sciences. Series Number 07-001. Sage Publishers, Beverly Hills, Calif., USA.

Palmer, W.C. 1965. Meteorological drought. US Weather Bureau Research Paper Number 45. US Weather Bureau, Washington, D.C., USA.

Pan, C., Tajchman, S.J., and Kochenderfer, J.N. 1997. Dendroclimatological analysis of major forest species of the central Appalachians. For. Ecol. Manage. 98(1): 77–88. doi:10.1016/S0378-1127(97)00087-X.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Pres, San Diego, Calif., USA.

Robertson, P.A. 1992. Factors affecting tree growth on three lowland sites in southern Illinois. Am. Midl. Nat. 128: 218–236. doi:10.2307/2426456.

Rubino, D.L., and McCarthy, B.C. 2000. Dendroclimatological analysis of white oak (*Quercus alba* L., *Fagaceae*) from an old-growth forest of southeastern Ohio, USA. J. Torrey Bot. Soc. 127(3): 240–250. doi:10.2307/3088761.

SAMAB (Southern Appalachian Man and the Biosphere). 1996. The southern Appalachian assessment: summary report. Report 1 of 5. USDA Forest Service Southern Region, Atlanta, Ga., USA. R8-TP 25.

Solomon, S., Qin, D., Manning, M., Alley, R.B., Berntsen, T., Bindoff, N.L., Chen, Z., Chidthaisong, A., Gregory, J.M., Hegerl, G.C., Heimann, M., Hewitson, B., Hoskins, B.J., Joos, F., Jouzel, J., Kattsov, V., Lohmann, U., Matsuno, T., Molina, M., Nicholls, N., Overpeck, J., Raga, G., Ramaswamy, V., Ren, J., Rusticucci, M., Somerville, R., Stocker, T.F., Whetton, P., Wood, R.A., and Wratt, D. 2007. Technical summary. *In* Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignorm, and H.L. Miller. Cambridge University Press, N.Y., USA.

Speer, J.H. 2001. Oak mast from dendrochronology: a new technique demonstrated in the southern Appalachian region. Ph.D. dissertation, University of Tennessee, Knoxville, Tenn., USA.

Stahle, D.W., and Cleaveland, M.K. 1996. Large-scale climatic influences on baldcypress tree growth across the southeastern United States. *In* Climatic variations and forcing mechanisms of the last 2000 years. *Edited by* P.D. Jones, R.S. Bradley, and J. Jouzel. NATO ASI Series 141. pp. 125–140.

Stahle, D.W., Cook, E.R., Cleaveland, M.K., Therrell, M.D., Meko, D.M., Grissino-Mayer, H.D., Watson, E., and Luckman, B.H. 2000. Tree-ring data document 16th century megadrought over North America. Eos Trans. AGU, 81(12): 121–125. doi:10.1029/00EO00076.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. The University of Chicago Press, Chicago, Ill., USA.

Sutherland, E.K., and Smith, K.T. 2000. Resistance is not futile: the response of hardwoods to fire-caused wounding. *In* Proceedings of the Workshop on Fire, People, and the Central Hardwoods Landscape, 12–14 March 2000, Richmond, Kentucky. *Edited by* D.A. Yaussy. USDA Forest Service, Northeastern Research Station. Gen. Tech. Rep. NE-274. pp. 111–115.

White, P.S., and Miller, R.I. 1988. Topographic models of vascular plant richness in the southern Appalachian high peaks. J. Ecol. 76: 192–199. doi:10.2307/2260463.

Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology, 40(3): 349–361. doi:10.2307/1929751.

Young, P.J. 1996. A retrospective dendroecology of the American chestnut in a southern Appalachian ecosystem. M.S. thesis, University of Arkansas, Fayetteville, Ark., USA.