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Do High-Elevation Northern Red Oak Tree-Rings Share a Common Climate-Driven Growth Signal?

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Abstract

Six open-canopy high-elevation northern red oak (*Quercus rubra* L.) ring-width records were evaluated along the Southern Appalachian mountain range for a common climate-driven growth signal. Ring-width records show significant correlations over the past two centuries with principal component one (PC-1) accounting for 50% of the common variance. Spectral analysis reveals that the relative variance in ring-width is concentrated at decadal time scales. Ring-width records show positive correlations ($p < 0.05$) with prior fall–early winter and current summer mean temperature, and negative correlations ($p < 0.05$) with prior late summer–winter total precipitation. Yet, temperature-precipitation covariance along the Southern Appalachian mountain range during winter and summer seasons undergoes a significant reversal with intervening spring and fall seasons showing weak association. As a result, ring-width-climate signal strength exhibits time-dependence over the instrumental period, although the temporal change is not statistically significant. This temporal change suggests that both temperature and precipitation can have a marked influence on ring-width variability depending on the degree of seasonal covariance. Finally, obtaining a stable interannual climate-growth calibration for these particular ring-width records remains a foremost challenge, and is a primary consequence of mixed temperature-precipitation signal strength and little power at higher frequencies.

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Introduction

Using a collection of geographically distributed tree-ring records for climatic study requires the assumption that top-down climate processes and patterns influence annual growth ring formation locally (Cook, 1992). The strength of this climatic expression can be gauged by assessing the common growth signal between trees in the same local environment, as well as trees growing several hundred kilometers apart. In continental regions where climate variability exhibits pronounced seasonality and rhythmic behavior such as the desert southwest (Swetnam and Betancourt, 1992; Meko et al., 1993), south-central plains (Stahle, 1990), or the central Pacific Coast (St. George and Ault, 2011), tree-ring records share a high proportion of common growth variance, and faithfully record interannual to decadal variability. Trees growing in mountainous regions near upper- and lower-forest zones also share significant common variance because either cold temperatures or moisture deficits frequently limit growth (LaMarche, 1974; Fritts, 1976; Hughes and Funkhouser, 2003). However, outside of these cardinal dendroclimatic regions, non-climatic factors often complicate the extraction of climate variability from tree-ring records. For example, temperate regions commonly lack pronounced seasonality in precipitation, high-elevation environments that contain temperature-limited trees, and relatively open stands devoid of competition for available resources. Thus, conducting dendroclimatological research in temperate ecosystems primarily yields a weakened common growth signal that reflects increased local-scale noise.

In order to obtain tree-ring records that capture decadal climate variability over eastern North America, efforts must be made to locate open-canopy stands within a region dominated by dense closed-canopy forest (Crawford and Kennedy, 2009). Trees growing within this closed-canopy structure typically experience higher inter-tree competition—an endogenous factor that dampens the common signal (Cook, 1985). This local-scale ecological effect, in the form of tree-level growth suppressions, can significantly override the influence of macro-scale climate variability on ring-width variations (Cook and Briffa, 1990). In contrast, trees growing within a low-density open-canopy forest are more likely to have stronger climate signals because ecological competition is minimal (Fritts et al., 1965; Pilcher, 1990). Open-canopy forests across eastern North America are rare, and this fact has restricted development of dendroclimatic records capable of recording regional climate patterns at decadal time scales. Still, numerous tree-ring records exist for eastern North America (see International Tree Ring Databank contributors, http://www.ncdc.noaa.gov/paleo/treering.html) thanks to advancements in closed-canopy tree-ring standardization (Cook and Peters, 1981).

Northern red oak, a deciduous species that occupies low- to high-elevation sites across the Southern Appalachian mountain range, has received considerable attention in dendroclimatic research (e.g., Tainter et al., 1990; Pan et al., 1997; Fekedulegn et al., 2003; Speer et al., 2009); however, these studies were based on tree-ring records from lower elevation closed-canopy stands where climate is less variable and often markedly differs from higher elevation regions (Konrad, 1996). In this paper, a collection of six open-canopy high-elevation northern red oak (*Quercus rubra* L.) ring-width records are evaluated for the presence of a common climate-driven growth signal across the Southern Appalachian mountain range in the southeastern United States. The first stage of analysis determines whether high-elevation

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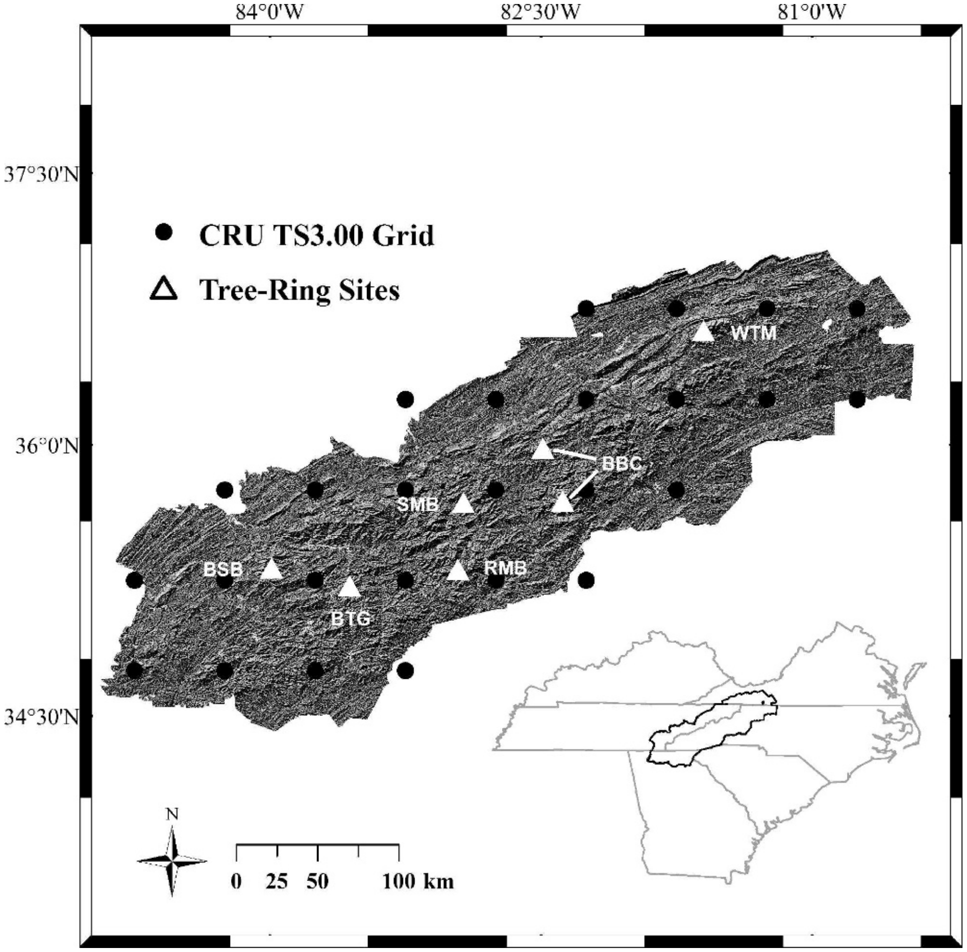

FIGURE 1. Southern Appalachian mountain range, high-elevation northern red oak ring-width records, and CRU TS3.00 temperature and precipitation grid points (0.5° × 0.5°). The Big Bald Craggy (BBC) chronology represents ring-width data combined from two nearby sites to lengthen and increase sample depth.

northern red oak ring-width records share a spatially coherent common growth signal in time and frequency domains, and the second stage test for significant surface temperature and precipitation association.

This study differs from previous dendroclimatic studies on northern red oak from two standpoints. First, living tree-ring records, supplemented by remnant wood, have been collected from open-canopy high-elevation forest environments above 1600 m along a 250 km southwest–northeast transect. Second, these records have been developed at northern red oak's elevational range limit, and comprise the longest set of multi-century northern red oak tree-ring records ever developed from the southeastern United States. This common signal approach allows the determination to be made whether open-canopy high-elevation northern red oak tree-ring records along the Southern Appalachian mountain range record regional climate variability.

Tree-Ring Data and Methods

The Southern Appalachian mountain range is located in the southeastern United States between 34–37°N and 81–84°W (Fig. 1). High-elevation forest stands across the mountain range are reminiscent of the high-latitude boreal-deciduous ecotone (Whittaker, 1956), and include a northern hardwood species assemblage with isolated spruce-fir forest zones. The high-elevation open-canopy northern red oak stands under investigation in this study tend to occur on west and southwest aspects in and around Southern Appalachian grass/heath balds (Crawford and Kennedy, 2009). This southeastern sub-region has a predominantly humid subtropical climate with cooler and wetter conditions occurring with increasing elevation. In general, the winter season (December–February) tends to be cold and snowy with mild-moist summers (June–August). Total annual precipitation can exceed 150 cm across higher elevation regions, but is highly variable across the range resulting from differences in windward (leeward) slope exposure and proximity to Gulf of Mexico (Konrad, 1995, 1996). Annual snowfall varies with valleys receiving 20 cm or less and higher mountain slopes receiving 80+ cm from orographic effects (Perry and Konrad, 2006).

Living tree and remnant wood specimens from six high-elevation (>1600 m) open-canopy northern red oak stands were collected along a southwest–northeast gradient in the Southern Appalachian mountain range (Fig. 1). Between 25 and 40 trees were sampled at each site, and either two cores or one cross section were taken from each tree using an increment borer or chainsaw. Each sample was prepared and processed according to standard dendrochronological techniques (Stokes and Smiley, 1996). Skeleton plotting was used to visually crossdate samples, and each series was measured to the nearest 0.001 mm. Visual crossdating was statistically verified with COFECHA (Holmes, 1983).

Age-related geometrical growth trends for each tree were removed with a deterministic growth curve using ARSTAN (Cook, 1985; Cook and Kairiukstis, 1990). Before detrending, an adaptive power-transformation was applied to each ring-width series to account for any ring-width population skew, improve curve fits, and minimize trend propagation in the final mean chronology calculation (Cook and Peters, 1997). In addition, the variance was stabilized with a 67% n spline and Briffa's r-bar

TABLE 1

High-elevation northern red oak ring-width chronology statistics.

Ring-width chronologies	Elev. (m)	Lat./Long.	Trees (series)	Record Length (*n*)	Median Segment	*r*	ms	First-auto.	eps > 0.85
Whitetop Mountain, VA (WTM)	1684	36.63, −81.60	17 (39)	1671–2006 (336)	199	0.58	0.20	0.65	1675–2006
Big Bald/Craggy Gardens, NC (BBC)	1681	35.98, −82.49	53 (81)	1763–2005 (243)	131	0.57	0.21	0.65	1806–2005
Sandy Mush Bald, NC (SMB)	1600	35.68, −82.93	27 (52)	1729–2007 (279)	124	0.54	0.20	0.66	1814–2007
Rich Mountain Bald, NC (RMB)	1639	35.31, −82.96	30 (59)	1607–2007 (401)	175	0.50	0.18	0.84	1664–2007
Bob-Stratton Bald, NC/TN (BSB)	1628	35.32, −83.99	35 (62)	1763–2007 (243)	140	0.55	0.19	0.67	1778–2007
Burningtown Bald, NC (BTG)	1641	35.22, −83.56	34 (69)	1732–2007 (276)	191	0.53	0.17	0.55	1737–2007

method (Briffa and Jones, 1990). The 67% spline is necessary to appropriately stabilize the radial growth variance in ring-porous species because as *Quercus* spp. mature, their earlywood vessels increase the proportional ring-width variability unrelated to environmental conditions. This tendency has been identified as a "trend in variance" that is biologically dependent and must be removed for confident interpretation of ring-width variation towards the end of time series (e.g., Shiyatov et al., 1990).

A conservative detrending approach was applied to each ring-width series by fitting a horizontal mean line, a negative exponential curve, or a linear regression line with a negative slope. Ring-width chronologies were constructed by dividing the expected ring-width by the actual ring-width to produce a dimensionless index of average growth across all series. Each chronology was estimated by using a bi-robust weighted mean to ensure against the inclusion of outlying ring-width values (Cook, 1985). Autoregressive modeling was used to remove serial autocorrelation and obtain a residual chronology without lower frequency growth persistence, unlike the standard chronology produced from the same series.

Correlation and principal components analysis (PCA) were used to assess the common growth variance between each standardized ring-width chronology in the time domain (e.g., Peters et al., 1981). The period 1800–2005 was selected for comparison because the sample size for each chronology was deemed sufficient using an expressed population signal (EPS) cutoff of 0.85 (e.g., Wigley et al., 1984). Both residual and standard chronologies were subject to this analytical step because each time-series reflects a distinct difference in autocorrelation structure. For the same period, spectral analysis was used to estimate the relative concentration of frequency-dependent variance within each ring-width chronology, followed by a comparison between frequency-stratified variance (LaMarche, 1974). Spectral estimates were computed using the Blackman-Tukey method (Meko, 1992; Chatfield, 2004) and only site-specific standard chronologies were used for this analytical step because the autocovariance structure was preserved during standardization.

Using the Matlab function seascorr (e.g., Meko et al., 2011), Monte-Carlo correlation analysis (1000 simulations) was used to assess the significance between northern red oak ring-width variability and surface temperature and precipitation. Mean monthly temperature and total monthly precipitation were obtained from the University of East Anglia Climate Research Unit TS3.00 $0.5^\circ \times 0.5^\circ$ gridded data set (e.g., Mitchell and Jones, 2005; CRU, 2008), and the four grid points surrounding each site chronology were selected for comparison. In addition, principal component one (hereinafter PC-1) was compared with the twenty-six TS3.00 grid points covering the spatial domain of the Southern Appalachian mountain range (Fig. 1). Monthly and seasonal (2–4 month averages) coefficients for temperature and precipitation were computed across a 14-month window from prior August to current September during 1903–2005. Monthly and/or seasonally significant ring-width-climate associations were tallied for $p < 0.05$ and $p < 0.01$ levels (two-tailed). The temporal stability of each significance coefficient was tested using a split-period approach that separated 1903–2005 into two distinct early (1903–1947) and late (1948–2005) sub-periods. The difference between each sub-period correlation coefficient was calculated and subject to a significance test to determine whether sub-period coefficients were statistically different (e.g., Meko et al., 2011). Although the East Anglia Climate Research Unit's TS3.00 gridded data set accounts for changes in climate station density over time (Mitchell and Jones, 2005), early and late periods were selected because station density was noted to have increased substantially across the Southern Appalachian region after 1948 (e.g., Menne et al., 2009). This pre- and post-1948 change in meteorological observation offered a logical break across 1903–2005 to evaluate climate signal stability.

Results

High-elevation northern red oak ring-width records along the Southern Appalachian mountain range (Table 1 and Fig. 2) are significantly correlated across the past two centuries (Table 2). Slightly stronger correlations were observed between residual variance than autocorrelated variance, and in part reflects site-level southwest–northeast differences in mean sensitivity and biological persistence (Table 1). PCA between standardized ring-width records revealed a strong spatially coherent common growth signal along the mountain range. Each standard ring-width chronology loaded positively with PC-1, and cumulatively, accounted for 50% of the common variance (Table 3). Although PC-2 and PC-3 contributed an additional 34%, the sign of the loadings were different and indicate possible southwest–northeast differences between ring-width records (Table 3); however, because only six sites were evaluated, and the interpretation of lower order components becomes increasingly difficult without *post-hoc* reasoning, PC-2 and PC-3 were excluded from further analysis. PCA on residual variance (not shown) yielded very similar results and contributed no new meaningful information.

Spectral analysis of ring-width records revealed that over the past two centuries, the relative stratification of frequency-dependent ring-width variance has been concentrated at lower frequencies, particularly at decadal time scales. Ring-width variance at frequencies less than 5 years consistently fell below the white noise floor (i.e., null continuum) and indicated no significant variance is present at higher frequencies. Correlation analysis between the frequency-stratified variance (5–20 years) of each ring-width chronology yielded high coefficients (0.66–0.95), and suggests spatial coherence between frequency-dependent variance. Spectral estimates on PC-1 indicated that the common

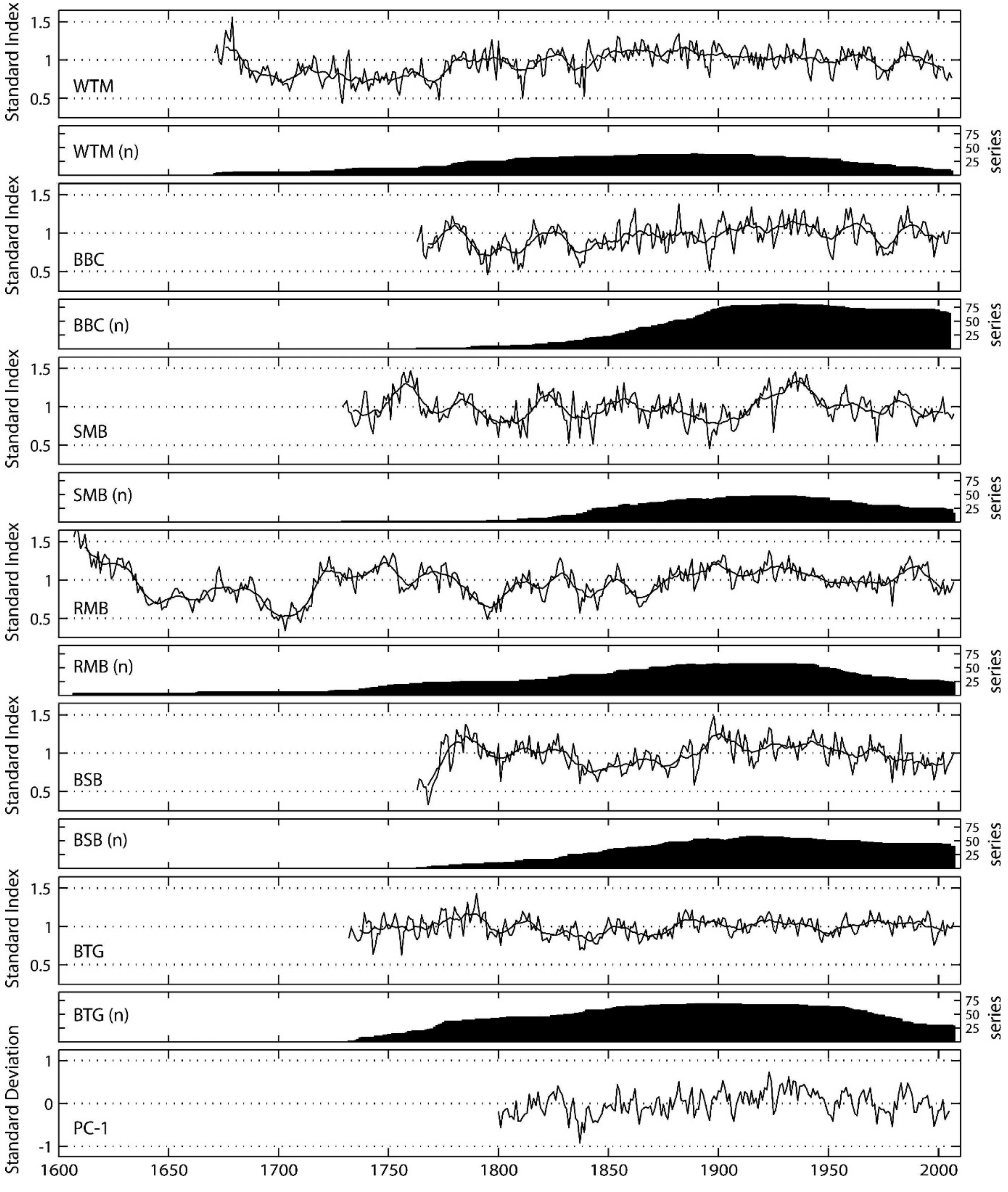

FIGURE 2. Open-canopy high-elevation northern red oak Whitetop Mountain (WTM), Sandy Mush Bald (SMB), Rich Mountain Bald (RMB), Bob-Stratton Bald (BSB), Burningtown Gap (BTG), and principal component one (PC-1) ring-width records with an 11-year moving average to visually emphasize decadal variance.

growth variance also exhibited significance variance at decadal time scales (Fig. 3).

High-elevation northern red oak ring-width records were significantly correlated with mean temperature and total precipitation for 1903–2005 (Table 4). Individual monthly correlations varied by site, but the overall pattern of significance was consistent for prior fall–winter and current summer seasons. For mean temperature, prior October–prior December (positive) and current June–July (positive) were significant, and for total precipitation, prior September–current January (negative) and current June–July (negative) were significant (Table 4). Correlations for standard and residual chronologies did not differ substantially, although

TABLE 2

Time domain correlations between high-elevation northern red oak ring-width records (1800–2005). (A) Residual chronologies; (B) Standardized chronologies.

A

	WTM	BBC	SMB	RMB	BSB	BTG
WTM						
BBC	0.60*					
SMB	0.28*	0.46*				
RMB	0.45*	0.52*	0.54*			
BSB	0.38*	0.42*	0.39*	0.66*		
BTG	0.31*	0.39*	0.45*	0.64*	0.54*	

B

	WTM	BBC	SMB	RMB	BSB	BTG
WTM						
BBC	0.61*					
SMB	0.29*	0.53*				
RMB	0.36*	0.47*	0.33*			
BSB	0.20*	0.31*	0.18*	0.58*		
BTG	0.19*	0.33*	0.21*	0.65*	0.50*	

Significance: $p<0.01$. * (two-tailed).

standard ring-width exhibited a wider seasonal response window with slightly higher coefficients (Table 4).

Ring-width records showed time-dependent correlations with each monthly and/or seasonally significant temperature and precipitation coefficient for early and late sub-periods, but aside from a few notable exceptions, these differences were not statistically significant (Table 4). Examining the seasonal correlations between each site-specific temperature and precipitation CRU TS3.00 grid point (i.e., closest grid to each site by distance) for the 14-month period from prior August to current September revealed a significant seasonal change between temperature-precipitation covariance. For all ring-width sites across the mountain range, two significant seasonal peaks in temperature-precipitation covariance occur during winter (December–March) and summer (June–July) seasons with intervening fall and spring seasons exhibiting weak association (Fig. 4). During the winter season, the covariance between temperature and precipitation is positive, whereas, the relationship is negative for the summer season. This seasonality in covariance indicates a tendency towards warm-wet (cool-dry) winters, and warm-dry (cool-wet) summers. Though synchronous temporal changes in ring-width-climate signals do not occur across early and late periods, there appears to be a possible subtle shift from a prior fall precipitation response at a few sites during the early period to a current summer season precipitation response during the late period (Table 4). For standard ring-width chronologies, only one site (SMB) showed a statistically significant change in prior September precipitation sensitivity, whereas, for residual ring-width chronologies, three sites (WTM, SMB, and BSB) demonstrated a significant change in prior November temperature, prior September precipitation, and current June–July precipitation, respectively (Table 4).

PC-1 demonstrated significant seasonal temperature and precipitation correlations with each CRU TS3.00 grid point across the Southern Appalachian mountain range for 1903–2005 (Fig. 5). Prior October–prior December mean temperature was significant for all grid points, and exhibited a stronger spatial pattern of significance towards the southern portion of the mountain range (Fig. 5, part a). Current June–July mean temperature was only significant for 12 of the 26 grid points, but revealed a spatial pattern of significance towards the northern portion of the Southern Appalachian range (Fig. 5, part b). Prior September–current January total precipitation was significant for 23 of the 26 grid points, and showed a strong spatial pattern of significance for both northern and southern portions of the mountain range (Fig. 5, part c). For PC-1, a significant temporal change in prior fall, winter, and summer season climate signals did not occur between early and late sub-periods.

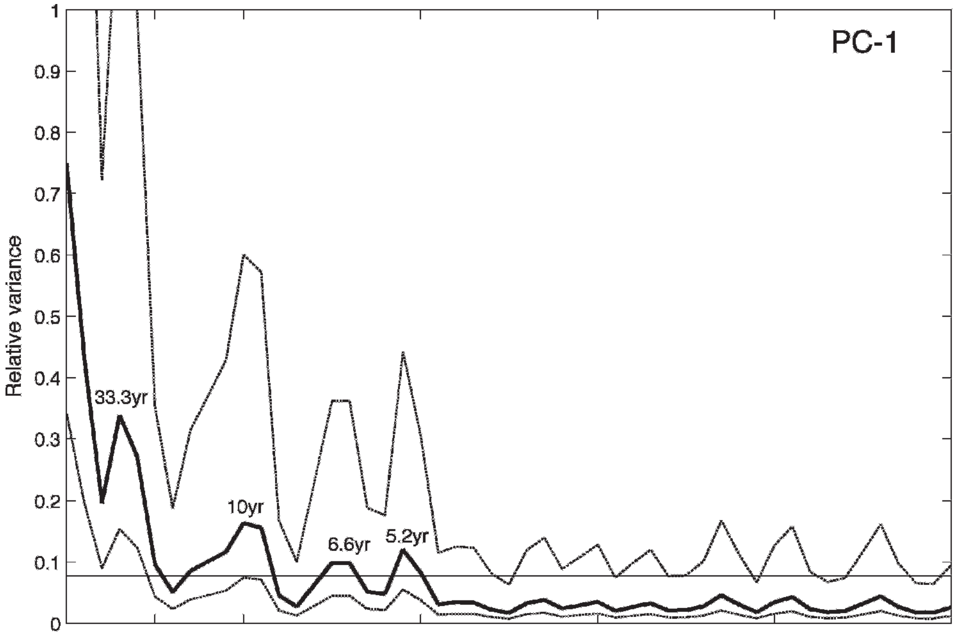

FIGURE 3. Spectral estimates of the common ring-width variance (PC-1) (heavy black line) with 95% confidence intervals (thin dotted lines). The straight line indicates the white noise floor.

TABLE 3

Principal component statistics for high-elevation northern red oak ring-width records.

Loadings	PC-1	PC-2	PC-3
WTM	0.33	0.16	−0.63
BBC	0.53	0.26	−0.38
SMB	0.47	0.56	0.64
RMB	0.43	−0.37	0.02
BSB	0.38	−0.61	0.21
BTG	0.23	−0.27	0.09
Variance (%)	0.50	0.20	0.14
Cumulative (%)	0.50	0.70	0.84

Discussion

ASSESSING THE COMMON GROWTH SIGNAL IN HIGH-ELEVATION NORTHERN RED OAK RING-WIDTH

Open-canopy high-elevation northern red oak ring-width records share significant correlations over the past two centuries, and indicate the presence of a common growth signal across at least 250 km in the Southern Appalachian mountain range of the southeastern United States. Even though intra-site differences in ring-width growth occur, namely mean sensitivity and autocorrelation, PC-1 reflects a clear and strong spatial pattern of common growth variance. Collectively, this common growth signal suggests that a primary regional climate control limits northern red oak growth at its elevational range limits. This finding is consistent with other studies that have also identified significant common growth variance between *Quercus* spp. and other deciduous species at higher latitudes (e.g., Gramulich, 1993; Pederson et al., 2004). In particular, Pederson et al. (2004) found that winter temperature controls regional deciduous tree growth in the Hudson River valley. More broadly, common growth variance between numerous tree-ring chronologies across the western United States has been linked to regional drought variability (e.g., Meko et al., 1993), as well as a warm season temperature signal in high-elevation Great Basin Bristlecone pine (*Pinus longeva*) (e.g., Hughes and Funkhouser, 2003; Salzer et al., 2009).

Spectral estimates on PC-1 indicated that a significant proportion of the total variance is concentrated between 25 and 40 years with a peak at 33.3, and suggest that not only is there a common growth signal, but its variance exhibits decadal persistence. This common signal is possibly tied to the variance

TABLE 4

Significant high-elevation northern red oak ring-width, temperature, and precipitation correlations.

A. Standard Chronologies			Correlation Coefficient and Period				
			Full	Early	Late		
Site	Variable	Month(s)	1903–2005	1903–1947	1948–2005	Coefficient Difference	*p*
WTM	Tmean	ns					
	Precip.	Jun.	−0.30**	−0.20	−0.37	0.196	0.341
		pSept.–pDec.	−0.30**	−0.20	−0.32	0.134	0.526
BBC	Tmean	pNov.	0.20*	0.04	0.33	−0.303	0.140
	Precip.	pOct.–Jan.	−0.27*	−0.10	−0.33	0.243	0.271
SMB	Tmean	ns					
	Precip.	pSept.	−0.32*	−0.50	−0.10	−0.442	0.039*
RMB	Tmean	Jul.	0.32**	0.23	0.37	−0.159	0.456
		pOct.–pDec.	0.31**	0.47	0.14	0.379	0.066
	Precip.	ns					
BSB	Tmean	pJul.–pAug.	−0.30**	−0.32	−0.27	−0.046	0.822
	Precip.	pSept.–pNov.	−0.35**	−0.26	−0.23	−0.032	0.875
BTG	Tmean	pNov.–pDec.	0.30**	0.36	0.25	0.123	0.548
	Precip.	Jan	−0.20*	−0.23	−0.17	−0.065	0.765

B. Residual Chronologies			Correlation Coefficient and Period				
			Full	Early	Late		
Site	Variable	Month(s)	1903–2005	1903–1947	1948–2005	Coefficient Difference	*p*
WTM	Tmean	pNov	0.24*	0.00	0.41	−0.433	0.035*
		Jun.Jul.	0.20*	0.12	0.25	−0.133	0.520
	Precip.	Jun.	−0.31**	−0.16	−0.42	0.281	0.170
		pSept.–pOct.	−0.25**	−0.17	−0.29	0.118	0.570
BBC	Tmean	pAug.	−0.20*	−0.35	−0.10	−0.259	0.207
	Precip.	Jan.	−0.21*	−0.07	−0.32	0.256	0.210
SMB	Tmean	ns					
	Precip.	pSept.	−0.20*	−0.41	0.01	−0.455	0.030*
RMB	Tmean	pDec.	0.30*	0.45	0.17	0.312	0.130
	Precip.	ns					
BSB	Tmean	pJul.–pAug.	−0.36**	−0.32	−0.37	0.056	0.784
	Precip.	Jun.–Jul.	−0.24*	0.07	−0.48	0.596	0.004*
BTG	Tmean	pNov.–pDec.	0.30**	0.37	0.24	0.140	0.496
	Precip.	ns					

Significance: $p < 0.01$ ** (two-tailed).
Significance: $p < 0.05$ * (two-tailed).
ns: not significant.

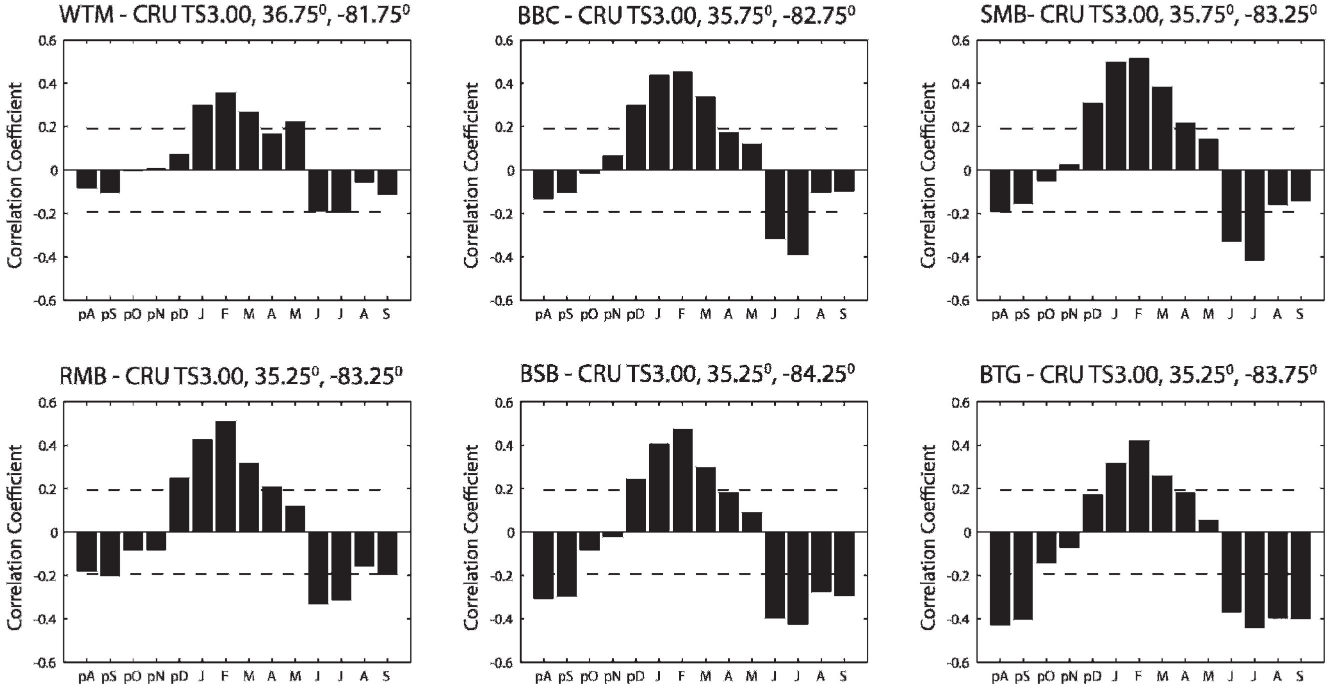

FIGURE 4. Fourteen-month (prior August–current September) seasonal covariance between mean temperature and total precipitation. Correlation coefficients reflect the association between seasonal temperature average and seasonal precipitation sum for the 3 prior months. The dotted line represents the 95% confidence interval.

spectrum of the regional climate growth control, but since much of northern red oak's growth lacks significant high-frequency variability, a frequency-dependent bias may be present within these records making it more challenging to calibrate interannual temperature and precipitation variability with ring-width (e.g., Fonti et al., 2009).

CLIMATE-DRIVEN CONTROL ON NORTHERN RED OAK RING-WIDTH VARIABILITY

Ring-width growth in high-elevation northern red oak along the Southern Appalachian mountain range is evidently favored by warmer mean temperatures and reduced precipitation during the prior fall, winter, and current summer seasons. Northern red oak's positive response to mean temperature indicates that radial growth in these high-elevation mountain environments is limited by cold temperatures (e.g., Fritts, 1976; Tranquillini, 1979; Paulsen et al., 2000; Rossi et al., 2008). Specifically, a positive response to fall–early winter temperature in the year preceding growth possibly indicates that warmer (colder) temperatures reduce (increase) the occurrence of winter xylem embolisms (e.g., Cochard and Tyree, 1990; Sperry and Sullivan, 1992; Sperry et al., 1994; Pederson et al., 2004). Winter xylem embolism damage is common to *Quercus* spp. and disrupts water conductance during spring vesselwood production (Cochard and Tyree, 1990; Sperry and Sullivan, 1992; Sperry et al., 1994) while also influencing whether stored non-structural resources within the tree can be allocated to new cell formation or damaged cell recovery during the following growing season (e.g., Pederson et al., 2004). Correspondingly, a positive response to June–July mean temperature indicates that an early arrival of warmer spring temperatures would initiate an earlier break in dormancy and leaf-out (Bassow and Bazzaz, 1998). For the higher elevations of the Southern Appalachian mountain range, the growing season is shorter and leaf-out often occurs 2–4 weeks later than low-elevation deciduous stands.

Northern red oak is adapted to drier conditions and can withstand moisture deficiencies with deep root structures, water-transport mechanisms, and xeromorphic leaves (Abrams, 1990). A negative response to late summer–winter precipitation preceding growth indicates that wet saturated soils with poor aeration (i.e., waterlogging effect) would reduce respiration capacity and as a result, limit radial growth (Fritts, 1976; Körner, 1998). Northern red oak's determinant strategy for bud scar formation in the prior year increases the likelihood that late-season growing conditions in the prior year will carry over to the next year's growth (e.g., Sander, 1990; Pederson et al., 2004). In a study of northern red oak physiology, Fritts (1976) found that 95% of radial growth was completed by mid-summer, with the remaining seasonal growth production reserved for food resource allocation during the next growing season. Foster and Leblanc (1993) found that *Quercus* spp. radial growth was dependent upon water balance conditions in the prior year's late growing season as well as the current year. Taken together, high-elevation northern red oak ring-width variability registers an aggregated response to seasonal temperature and precipitation in the prior and current year, but more importantly, indicates that growth can be limited by either temperature and/or precipitation.

The temporal stability of each significant temperature and precipitation signal present in high-elevation northern red oak ring-width was evaluated over early and late sub-periods during 1903–2005. A significant change in signal stability was observed at a few sites, but this signal change was not consistent across a particular season, between site-specific standard and residual chronologies, or between sites along the mountain range. This result seems to suggest that any observed change in high-elevation northern red oak climate signal stability is likely related either to local climate variability or to a mixed temperature-precipitation signal that exhibits time-dependence. Tree-ring studies of various species across several geographic regions have noted shifting seasonal climate signals or reduced climate sensitivity over the

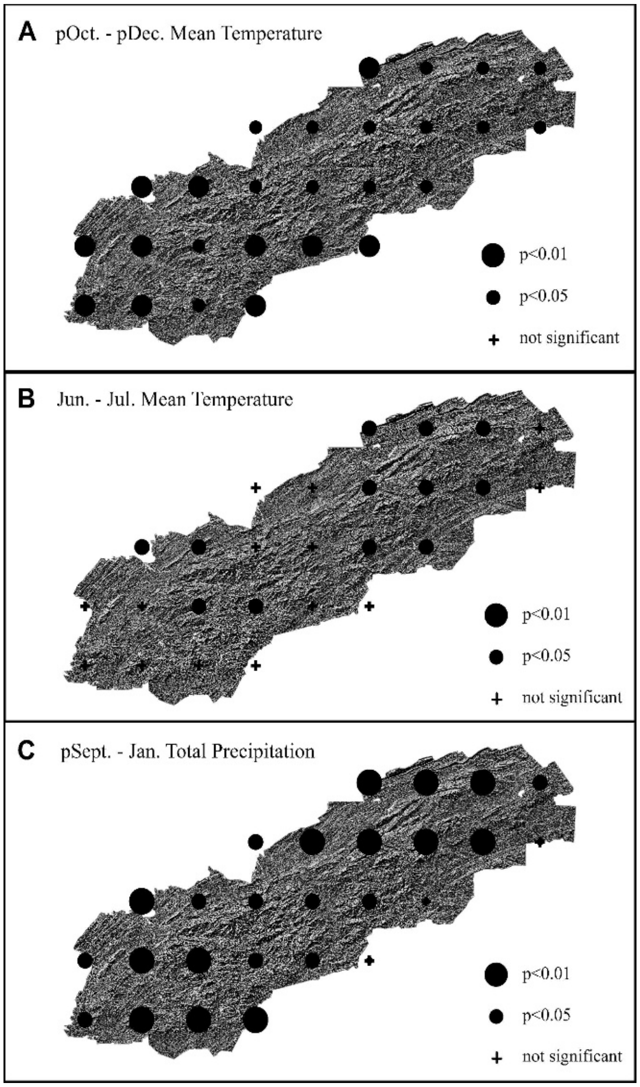

FIGURE 5. Significant correlations between high-elevation northern red oak PC-1 and seasonal mean temperature and seasonal total precipitation for the Southern Appalachian mountain range.

20th century (e.g., Biondi, 2000; Briffa, 1998; Wilmking et al., 2005); nonetheless, it is unclear whether these studies actually tested for a significant difference between time-unstable climate signals as outlined by Meko et al. (2011). Examining temperature and precipitation covariance for the 14-month period from prior August–current September for each ring-width site revealed a significant change between winter and summer seasons. Since ring-width variability is significantly correlated with prior fall–early winter temperature, prior late summer–winter precipitation, and current summer temperature, and the seasonal covariance between temperature and precipitation changes significantly during these growing seasons, a mixed seasonal temperature-precipitation signal is likely embedded within high-elevation northern red oak ring-width variability that fluctuates in strength depending upon seasonal temperature-precipitation covariance.

The common growth signal shared by each high-elevation northern red oak ring-width chronology indicates that ring-width variance carries a regional climate signal. This regional signal appears tuned to prior fall–early winter temperature and prior late summer–winter precipitation with a strong spatial fingerprint across the entire mountain range. A current summer mean temperature signal is present, but it is largely confined to the northern portion of the mountain range and shows much weaker significance regionally. These results contrast with other northern red oak dendroclimatic studies from low- to mid-elevation closed-canopy forest stands across the Southern Appalachian region which have found significant summer drought sensitivity, and indicates that water stress is the dominant control on ring-width variability at lower elevations (e.g., Tainter et al., 1984, 1990; Pan et al., 1997; Speer et al., 2009). On the other hand, at its northern range limits, northern red oak ring-width has shown significant sensitivity to both summer drought (e.g., Tardif and Conciatori, 2006a, 2006b; Tardif et al., 2006) and winter temperature (e.g., Pederson et al., 2004). More importantly, this study is the first to find that open-canopy high-elevation northern red oak ring-width variability is positively controlled by temperature, and negatively controlled by precipitation. This result is consistent with what would be expected for ring-width at high elevations and elevational species range limits (Fritts, 1976; Tranquillini, 1979; Körner, 1998).

Conclusion

Open-canopy high-elevation northern red oak ring-width records share a significant common growth signal along the Southern Appalachian mountain range that exhibits variance at decadal time scales. The primary regional climate signal entrained within these ring-width records corresponds to prior fall–early winter mean temperature and prior late summer–winter total precipitation, though regional climate-growth signal strength appears contingent on the seasonal covariance between temperature and precipitation during winter and summer seasons. Despite a breakdown in climate signal stability during the instrumental period, the temporal change is not significant. Rather, it indicates that both temperature and precipitation can limit growth during the prior fall, winter, and current summer seasons, but that these climate-growth controls may operate jointly or in opposition over time to produce a mixed signal. Equally important to consider is that since a significant proportion of northern red oak's ring-width variance is concentrated at decadal time scales, a frequency-dependent climate response may exist, complicating the goal of developing a stable climate-growth calibration at interannual time scales.

This study provides compelling evidence that in addition to other *Quercus* spp. tree-ring records developed from temperate and Mediterranean regions, open-canopy high-elevation northern red oak tree-ring records hold the potential for evaluating decadal climate variability over the past four centuries across the Southern Appalachian region. Disentangling the apparent time-dependent mixed temperature-precipitation signal retained in high-elevation northern red oak ring-width represents a challenge that will likely require an intra-seasonal examination of vesselwood-latewood variance, especially relationships to seasonal climate variability and/or possible frequency-dependent climate responses contained therein (e.g., Gonzalez and Eckstein, 2003; Fonti et al., 2009). It is important to note that although future hydroclimate change remains uncertain for the southeastern United States in response to climatic warming (e.g., Seager et al., 2009), this study points out that temperature change across the Southern Appalachian region may have differential effects on winter and summer precipitation seasonality, and if so, tree-ring records may have difficulty resolving this change clearly.

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References Cited

Abrams, D. M., 1990: Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, 7: 227–238.

Bassow, S. L., and Bazzaz, F. A., 1998: How environmental conditions affect canopy leaf-level photosynthesis in four deciduous tree species. *Ecology*, 79: 2660–2675.

Biondi, F., 2000: Are climate–tree growth relationships changing in north-central Idaho? *Arctic and Alpine Research*, 32: 111–116.

Briffa, K. R., 1998: Reduced sensitivity of tree-growth to temperature at high northern latitudes. *Nature*, 391: 678–682.

Briffa, K. R., and Jones, P. D., 1990: Basic chronology statistics and assessment. *In* Cook, E. R., and Kairiukstis, L. A. (eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht: Kluwer/IIASA, 137–152.

Chatfield, C., 2004: *The Analysis of Time Series, an Introduction.* Sixth edition. New York: Chapman and Hall/CRC, 333 pp.

Cochard, H., and Tyree, M. T., 1990: Xylem dysfunction in *Quercus*–vessel sizes, tyloses, cavitation and seasonal-changes in embolism. *Tree Physiology*, 6: 393–407.

Cook, E. R., 1985: A time series analysis approach to tree ring standardization. Dissertation, University of Arizona, Tucson.

Cook, E. R., 1992: Using tree rings to study past El Niño/Southern Oscillation influences on climate. *In* Diaz, H. F., and Markgraf, V. (eds.), *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge: Cambridge University Press, 203–214.

Cook, E. R., and Briffa, K. R., 1990: Data analysis. *In* Cook, E. R., and Kairiukstis, L. A. (eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht: Kluwer/IIASA, 97–162.

Cook, E. R., and Kairiukstis, L. A., 1990: *Methods of Dendrochronology: Applications in the Environmental Sciences.* Dordrecht: Kluwer Academic Publishers/IIASA, 394 pp.

Cook, E. R., and Peters, K., 1981: The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree Ring Bulletin*, 41: 45–53.

Cook, E. R., and Peters, K., 1997: Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene*, 7: 361–370.

Crawford, C. J., and Kennedy, L. M., 2009: Spatial and temporal patterns of tree encroachment into a Southern Appalachian grass/heath bald. *Natural Areas Journal*, 29: 500–508.

Fekedulegn, D., Hicks, R. R., and Colbert, J. J., 2003: Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *Forest Ecology and Management*, 177: 409–425.

Fonti, P., Treydte, K., Osenstetter, S., Frank, D., and Esper, J., 2009: Frequency-dependent signals in multi-centennial oak vessel data. *Palaeogeography Palaeoclimatology Palaeoecology*, 275: 92–99.

Foster, J. R., and LeBlanc, D. C., 1993: A physiological approach to dendroclimatic modeling of oak radial growth in the Midwestern United States. *Canadian Journal of Forest Research*, 23: 783–798.

Fritts, H. C., 1976: *Tree Rings and Climate*. Caldwell, New Jersey: The Blackburn Press, 567 pp.

Fritts, H. C., Smith, D. G., Cardis, J. W., and Budelsky, C. A., 1965: Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology*, 46: 394–401.

Gonzalez, I. G., and Eckstein, D., 2003: Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiology*, 23: 497–504.

Gramulich, L. J., 1993: Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*, 23: 133–143.

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

Hughes, M. K., and Funkhouser, G., 2003: Frequency-dependent climate signal in upper and lower forest border tree rings in the mountains of the Great Basin. *Climatic Change*, 59: 233–244.

Konrad, C. E., 1995: Maximum precipitation rates in the southern Blue Ridge Mountains of the southeastern United States. *Climate Research*, 5: 159–166.

Konrad, C. E., 1996: Relationships between precipitation event types and topography in the southern Blue Ridge Mountains of the southeastern USA. *International Journal of Climatology*, 16: 49–62.

Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.

LaMarche, V. C., 1974: Frequency-dependent relationships between tree-ring series along an ecological gradient and some dendroclimatic implications. *Tree-Ring Bulletin*, 34: 1–20.

Meko, D. M., 1992: Spectral properties of tree-ring data in the United States as related to El Niño/Southern Oscillation. *In* Diaz, H. F., and Markgraf, V. (eds.), *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge: Cambridge University Press, 227–241.

Meko, D. M., Cook, E. R., Stahle, D. W., Stockton, C. W., and Hughes, M. K., 1993: Spatial patterns of tree-growth anomalies in the United States and southeastern Canada. *Journal of Climate*, 6: 1773–1786.

Meko, D. M., Touchan, R., and Anchukaitis, K., 2011: Seascorr: a Matlab program for indentifying the seasonal climate signal in an annual tree-ring time series. *Computers and Geosciences*, 37: 1234–1241, doi:10.1016/j.cageo.2011.01.013.

Menne, M. J., Williams, C. N., and Vose, R. S., 2009: The United States Historical Climatology Network Monthly Temperature Data—Version 2. *Bulletin of American Meteorological Society*, 90: 993–1007, doi: 10.1175/2008BAMS2613.1.

Mitchell, T. D., and Jones, P. D., 2005: An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, 25: 693–712, doi:10.1002/joc.1181.

Pan, C., Tajchman, S. J., and Knochenderfer, J. N., 1997: Dendroclimatological analysis of major forest species of the central Appalachians. *Forest Ecology and Management*, 98: 77–87.

Paulsen, J., Weber, U. M., and Körner, C., 2000: Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research*, 32: 14–20.

Pederson, N., Cook, E. R., Jacoby, J. C., Peteet, D. M., and Grifflin, K. L., 2004: The influence of winter temperatures on the annual radial growth of six northern range margin species. *Dendrochronologia*, 22: 7–29.

Perry, L. B., and Konrad, C. E., 2006: Relationships between NW flow snowfall and topography in the Southern Appalachians, USA. *Climate Research*, 32: 35–47.

Peters, K., Jacoby, G. C., and Cook, E. R., 1981: Principal components analysis of tree-ring sites. *Tree Ring Bulletin*, 41: 1–19.

Pilcher, J. R., 1990: Primary data. *In* Cook, E. R., and Kairiukstis, L. A. (eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht: Kluwer/IIASA, 23–96.

Rossi, S., Deslauriers, A., Gricar, J., Seo, J. W., Rathgeber, C. B. K., Anfodillo, T., Morin, H., Levanic, T., Oven, P., and Jalkanen, R., 2008: Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography*, 17: 696–707.

Salzer, M. W., Hughes, M. K., Bunn, A. G., and Kipfmueller, K. F., 2009: Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 20348–20353.

Sander, I. L., 1990: *Quercus rubra* L. Silvics of North America: 2. Hardwoods. *In* Burns, R. M. (ed.), *Agriculture Handbook 654*. Washington D.C.: U.S. Department of Agriculture Forest Service, 727–733.

Seager, R., Tzanova, A., and Nakamura, J., 2009: Drought in the southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *Journal of Climate*, 22: 5021–5045.

Shiyatov, S., Mazepa, V., and Cook, E., 1990: Correcting for trend in variance due to changing sample size. *In* Cook, E. R., and Kairiukstis, L. A. (eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht: Kluwer/IIASA, 133–137.

Speer, J. H., Grissino-Mayer, H. D., Orvis, K. H., and Greenberg, C. H., 2009: Climate response of five oak species in the eastern deciduous forest of the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research*, 39: 507–518.

Sperry, J. S., and Sullivan, J. M., 1992: Xylem embolism in response to freeze-thaw cycles and water-stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology*, 100: 605–613.

Sperry, J. S., Nichols, K. L., Sullivan, J. M., and Eastlack, S. E., 1994: Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*, 75: 1736–1752.

Stahle, D. W., 1990: A tree-ring record of false spring in the south-central USA. Dissertation, Arizona State University, Tempe.

St. George, S., and Ault, T., 2011: Is energetic decadal variability a stable feature of the central Pacific Coast's winter climate? *Journal of Geophysical Research–Atmospheres*, 116: D12102, doi:10.1029/2010JD015325.

Stokes, M. A., and Smiley, T. J., 1996: *An Introduction to Tree-Ring Dating*. Tucson, Arizona: The University Arizona Press, 73 pp.

Swetnam, T. R., and Betancourt, J. A., 1992: Temporal patterns of Southern Oscillation–wildfire teleconnections in the southwestern United States. *In* Diaz, H. F., and Markgraf, V. (eds.), *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge: Cambridge University Press, 259–270.

Tainter, F. H., Fraedrich, S. W., and Benson, D. M., 1984: The effect of climate on growth, decline, and death of northern red oaks in the western North Carolina Nantahala Mountains. *Castanea*, 49: 127–137.

Tainter, F. H., Retzlaff, W. A., Starkey, D. A., and Oak, S. W., 1990: Decline of radial growth in red oaks is associated with short-term changes in climate. *European Journal of Forest Pathology*, 20: 95–105.

Tardif, J. C., and Conciatori, F., 2006a: A comparison of ring-width and event year chronologies derived from white oak (*Quercus alba*) and northern red oak (*Quercus rubra*), southwestern Quebec, Canada. *Dendrochronologia*, 23: 133–138.

Tardif, J. C., and Conciatori, F., 2006b: Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, southwestern Quebec, Canada. *Canadian Journal of Forest Research*, 36: 2317–2330.

Tardif, J. C., Conciatori, F., Nantel, P., and Gagnon, D., 2006: Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Quebec. *Canadian Journal of Biogeography*, 33: 1657–1669.

Tranquillini, W., 1979: *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*. New York: Springer-Verlag, 137 pp.

University of East Anglia Climate Research Unit (CRU) [Phil Jones, Ian Harris], 2008: CRU Time Series (TS) high resolution gridded datasets [Internet]. NCAS British Atmospheric Data Centre. Accessed on 1 June 2011 from http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276.

Whittaker, R. H., 1956: Vegetation of the Great Smoky Mountains. *Ecological Monographs*, 26: 1–80.

Wigley, T. M., Briffa, K. R., and Jones, P. D., 1984: On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23: 201–213.

Wilmking, M., D'Arrigo, R., Jacoby, G. C., and Juday, G. P., 2005: Increased temperature sensitivity and divergent growth trends in circumpolar boreal forests. *Geophysical Research Letters*, 32: L15715, doi:10.1029/2005GL023331.

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