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CLIMATIC RESPONSE OF OAK SPECIES ACROSS AN ENVIRONMENTAL GRADIENT IN THE SOUTHERN APPALACHIAN MOUNTAINS, USA

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ABSTRACT

We investigated the climatic sensitivity of oak species across a wide elevation range in the southern Appalachian Mountains, an area where greater knowledge of oak sensitivity is desired. We developed three tree-ring chronologies for climatic analyses from oak cores taken from the Jefferson National Forest, Virginia, and Great Smoky Mountains National Park, Tennessee. We statistically compared the three chronologies with monthly climatic data from 1930 to 2005. The results of our analyses suggest that oak species in the southern Appalachian Mountains require a cool, moist summer for above average-growth to occur. The climate signal increased in duration from high to low elevational and latitudinal gradients, indicating a strong moisture-preconditioning signal during the previous fall at our lowest elevation site. A notable finding of this research was the degree of responsiveness in oaks that are growing in forest interior locations where strong climate sensitivity would not be expected because of the effects of internal stand dynamics. Furthermore, the relationships between evapotranspiration rates and the geographic factors of elevation, latitude, and aspect influence the climate signals at the three sites. Our research suggests that oaks located in a warm and xeric climate experience more physiological stress and put forth a more varied climatic response.

Keywords: Quercus, dendroclimatology, dendrochronology, tree rings, climate response, southern Appalachian Mountains.

INTRODUCTION

Climatic variables such as precipitation, air temperature, and drought often account for a large portion of annual radial growth variation in trees located in temperate regions. The annual growth increments of trees are an important proxy data source that can be used to evaluate forest health (Cook *et al.* 1987; Swetnam and Betancourt 1998), model past climate conditions (Grissino-Mayer 1996; Cook *et al.* 1999; Díaz *et al.* 2001), and make predictions of the environment of future forests (Pan and Raynal 1995; Tessier *et al.* 1998; Goldblum and Rigg 2005). To investigate this relationship, some dominant factor such as water availability or temperature must limit tree growth (Fritts 1976). Studies in the eastern United States have focused on selecting sites that exhibit the desirable xeric characteristics often used in dendroclimatic investigations (Harrod and White 1999; Lafon and Grissino-Mayer 2007). Other studies conducted in the eastern U.S. have shown that trees growing in more mesic sites can also prove to be climate-sensitive (Stahle *et al.* 1988; Stahle and Cleaveland 1992).

The southern Appalachian Mountains provide suitable environmental conditions for dendrochronological studies, and researchers have focused primarily on such genera as *Abies*, *Picea*, *Pinus*, and *Quercus* (Adams *et al.* 1985; Cook and Johnson 1989; Harrod and White 1999; Armbrister 2002; Lafon and Speer 2002; Webster *et al.* 2004; Hart *et al.* 2008). Since the 1980s, dendrochronological

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research in the southern Appalachian Mountains has largely been concerned with the recurrence frequency of fire in pine ecosystems (Harmon 1982; DeWeese 2007; Lafon and Grissino-Mayer 2007) and drought (Grissino-Mayer and Butler 1993; Cook *et al.* 1988; Cook *et al.* 1999). Other researchers have investigated age structure and changing stand composition (Harrod and White 1999; Hart *et al.* 2008) and masting periods in oak forests (Speer 2001). Cook *et al.* (1999) used oak species as part of a vast network of chronologies in the eastern United States to reconstruct broad-scale spatial patterns of drought across the coterminous US. However, relatively few dendroclimatic studies in the region have tested the site-specific climate response of oak species (Jacobi and Tainter 1988; Orwig and Abrams 1997; Speer *et al.* 2009).

Dendroclimatic studies in the central to southern Appalachian Mountains and Southern United States have largely found that low precipitation and high temperatures limit radial growth in oak species (Pan *et al.* 1997; Bortolot *et al.* 2001; D'Arrigo *et al.* 2001; Stahle *et al.* 2001; Speer 2001). Despite this progress, very little research has investigated the climatic sensitivity of oak species across environmental gradients in the southern Appalachians. Sensitivity of oak species has been previously studied across different soil gradients by Estes (1970) in the Mississippi Valley and Charton and Harmon (1973) in northwest Indiana, with both investigations reporting varying degrees of climatic sensitivity depending on composition and texture of soil. Stahle and Hehr (1984) examined sensitivity of post oak (*Quercus stellata* Wangenh.) across a precipitation gradient in the south-central United States and found oaks to be more sensitive westward toward more arid regions. Jacobi and Tainter (1988) investigated the effects of climate on ring-width variation among white oak (*Quercus alba* L.) chronologies across a gradient of xeric uplands to mesic bottomlands in the South Carolina Piedmont and reported greater climatic sensitivity in oaks located in more xeric sites. The general trend reported in this body of research is that oak species are more climatically sensitive in more xeric locations.

In this study, we developed and analyzed the climate response found in three oak tree-ring chronologies developed from interior forest trees located in xeric pine-oak forests in the mountains of the Jefferson National Forest (JNF), Virginia, US, and the Great Smoky Mountains National Park (GSMNP), Tennessee, US. The three chronologies incorporate multiple species including white oak, black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus montana* Willd.), and blackjack oak (*Quercus marilandica* Muenchh.). Rather than testing the climatic sensitivity of oak along a moisture-based gradient (*i.e.* mesic to xeric) as others have previously done (Stahle and Hehr 1984; Jacobi and Tainter 1988), we sought to compare the climatic sensitivity of xeric-site oaks along elevational and latitudinal gradients. Greater knowledge of environmental factors that affect climate response among the *Quercus* species is necessary for appropriate selecting of study sites for climatic reconstructions involving oak species. The specific objectives of our study were to: (1) quantitatively analyze the influence of monthly climate conditions on year-to-year ring-width variation in forest interior oak trees, and (2) compare sensitivity, temporal duration, and variation of the climate signal between the northerly, higher elevation Virginia sites with the lower elevation, more southerly site in Tennessee.

METHODS

Study Areas

Our study areas fall within the range of the humid subtropical climate of the southeastern United States, which encompasses the lower elevations of the southern Appalachian Mountains. Cold winters and hot summers characterize this climate type (Bailey 1978). The JNF, located in the Blue Ridge Mountains of southwestern Virginia, receives an average of 109.7 cm of precipitation annually (NCDC 2007). The 1930 to 2007 average monthly temperatures range from 1°C in January to 22°C in July (NCDC 2007). GSMNP is located on the border of Tennessee and North Carolina and receives 140 to 216 cm of precipitation annually (NPS 2007). Monthly tem-

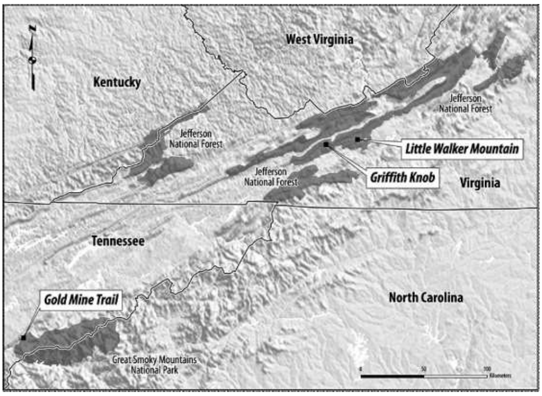

Figure 1. Locations of the three study areas in the southern Appalachian Mountains. Study area abbreviations: Little Walker Mountain (LWM), Griffith Knob (GK), and Gold Mine Trail (GMT).

peratures in the region average 3°C in January to 24°C in July (NCDC 2007).

The JNF and the GSMNP share similar land-use history. Prior to creation of JNF and GSMNP, much of the area's forests were affected by logging and clearing of land for agriculture (Pierce 2000; USDA 2007). The JNF was created by the United States Department of Agriculture in 1936 by combining lands formerly located within the Unaka and Natural Bridge National Forests, as well as other lands obtained by the Clinch and Mountain Lake Purchase Units (USDA 2007). Before the National Forest's creation, much of the area's highland forests were logged for timber and agricultural purposes (USDA 2007). Prior to establishment of GSMNP by Congress in 1934, the majority of the westernmost areas of the park (including our study area) was owned by the Morton Butler Lumber Company with a few private holdings inside the lumber tract (Harmon 1982). However, most of the Morton-Butler tract remained unlogged when the park was established and old-growth stands were left intact (Harmon 1982; Pierce 2000). Biotic and abiotic disturbances that have affected southern Appalachian xeric pine-oak stands during the past century include fire suppression (Harmon 1982; Brose *et al.* 2001), southern pine beetle (*Dendroctonus frontalis* Zimmermann) outbreaks (Lafon and Kutac 2003), and chestnut blight fungal infections (McCormick and Platt 1980).

Table 1. Summary location data of study sites in Virginia and Tennessee, US.

Study Site	Location	Elevation	Aspect
Griffith Knob (GK)	37°01′N 81°13′W	1,100–1,150 m	West
Little Walker Mountain (LWM)	37°03′N 80°56′W	800–920 m	North
Gold Mine Trail (GMT)	35°38′N 83°54′W	460–600 m	South

Our study concentrated on three study sites: Griffith Knob (GK) and Little Walker Mountain (LWM) in the JNF and Gold Mine Trail (GMT) in GSMNP (Figure 1). The different geographic characteristics of the three study sites permitted a comparative study of climatic sensitivity in regards to elevation, aspect, and latitude (Table 1). Vegetation was similar at each site with yellow pine species [Table Mountain pine (*Pinus pungens* Lamb.), shortleaf pine (*Pinus echinata* Mill.), Virginia pine (*Pinus virginiana* Mill.), and pitch pine (*Pinus rigida* Mill.)] and oak species (chestnut, white, and black oaks) dominating the canopy. Black gum (*Nyssa sylvatica* Marsh.), scarlet oak, bear oak (*Quercus ilicifolia* Wangenh.), red maple (*Acer rubrum* L.), and striped maple (*Acer pensylvanicum* L.) occurred less often in the canopy, whereas rosebay rhododendron (*Rhododendron maximum* L.), mountain laurel (*Kalmia latifolia* L.), and blueberry (*Vaccinium* spp.) were commonly found in the understory. Each site exhibited xeric soil characteristics.

Field Methods

Working with USDA Forest Service and National Park Service personnel, we selected study sites with minimal effects from human-related disturbances to reduce the potential of non-climatic "noise" corrupting or masking the climate signal. We established at least three 20 by 50 m study plots at each site. The initial purpose of these plots was to characterize stand composition and history and to analyze the climate response of Table Mountain pine (DeWeese 2007), but the data also afforded us an opportunity to analyze climate response in other hardwood species. Within each plot, two increment cores were collected from each living tree ≥5 cm

Table 2. Descriptive statistics and oak species composition of the three site chronologies developed for this study.

Sites	Number of Series	Range of Years	Interseries Correlation	Mean Sensitivity	Species Composition (% Weight)
Griffith Knob (GK)	43	1889–2003	0.67	0.277	*Q. alba* (2%) *Q. coccinea* (14%) *Q. montana* (79%) *Q. rubra* (2%) *Q. velutina* (2%)
Little Walker Mountain (LWM)	40	1889–2004	0.66	0.268	*Q. coccinea* (5%) *Q. montana* (88%) *Q. rubra* (7%)
Gold Mine Trail (GMT)	37	1836–2005	0.57	0.224	*Q. alba* (38%) *Q. coccinea* (41%) *Q. marilandica* (2%) *Q. montana* (14%) *Q. velutina* (5%)

DBH following customary field practices (Stokes and Smiley 1968).

Laboratory Methods

All increment cores were mounted, sanded and dated according to accepted dendrochronology laboratory methods (Stokes and Smiley 1968; Orvis and Grissino-Mayer 2002). Researchers typically develop oak chronologies from a single species or a grouping of similar species (*e.g.* white oaks or red oaks). However, the chronologies presented here were developed from several oak species each to ensure an adequate sample size was obtained for

Table 3. Comparison of chronologies developed for this study and other area oak chronologies found on the International Tree Ring Data Bank (ITRDB) and those developed by Speer *et al.* (2009).

Species Composition	Interseries Correlation	Mean Sensitivity	Location	Source
Quercus spp. (GK)	0.67	0.277	Virginia	This study
Quercus spp. (LWM)	0.66	0.268	Virginia	This study
Quercus spp. (GMT)	0.57	0.224	Tennessee	This study
Quercus alba	0.57	0.220	Southern Appalachians	Speer *et al.* 2009
Quercus alba	0.61	0.196	Tennessee	ITRDB 2010
Quercus alba	0.53	0.181	Virginia	ITRDB 2010
Quercus alba	0.54	0.164	Virginia	ITRDB 2010
Quercus alba	0.53	0.175	North Carolina	ITRDB 2010
Quercus alba	0.54	0.228	North Carolina	ITRDB 2010
Quercus alba	0.51	0.202	North Carolina	ITRDB 2010
Quercus alba	0.50	0.211	Virginia	ITRDB 2010
Quercus alba	0.61	0.205	Virginia	ITRDB 2010
Quercus alba	0.58	0.197	Tennessee	ITRDB 2010
Quercus alba	0.54	0.175	Virginia	ITRDB 2010
Quercus montana	0.54	0.200	Southern Appalachians	Speer *et al.* 2009
Quercus montana	0.49	0.181	Virginia	ITRDB 2010
Quercus montana	0.57	0.186	Virginia	ITRDB 2010
Quercus montana	0.61	0.171	Tennessee	ITRDB 2010
Quercus montana	0.48	0.187	Tennessee	ITRDB 2010
Quercus montana	0.53	0.163	Virginia	ITRDB 2010
Quercus velutina	0.61	0.190	Southern Appalachians	Speer *et al.* 2009
Quercus velutina	0.59	0.174	Tennessee	ITRDB 2010
Quercus coccinea	0.58	0.180	Southern Appalachians	Speer *et al.* 2009
Quercus rubra	0.52	0.190	Southern Appalachians	Speer *et al.* 2009

more rigorous statistical evaluation. Because oaks rarely fail to form an annual ring (Baillie 1982), we elected to visually crossdate the cores using marker rings (Schweingruber *et al.* 1990) and the list method (Yamaguchi 1991). After measuring all tree rings to the nearest 0.001 mm using a Velmex measuring system, crossdating accuracy was ensured with the computer program COFECHA using 40-year segments lagged successively by 20 years (Holmes 1983; Grissino-Mayer 2001). Any measurement series that exhibited erratic ring patterns and could not be crossdated with confidence were excluded from further analyses, but these were few in number. We developed our three chronologies with the computer program ARSTAN and elected to detrend the series by applying a 30-year smoothing spline to ensure removal of effects from internal stand processes (Cook 1985).

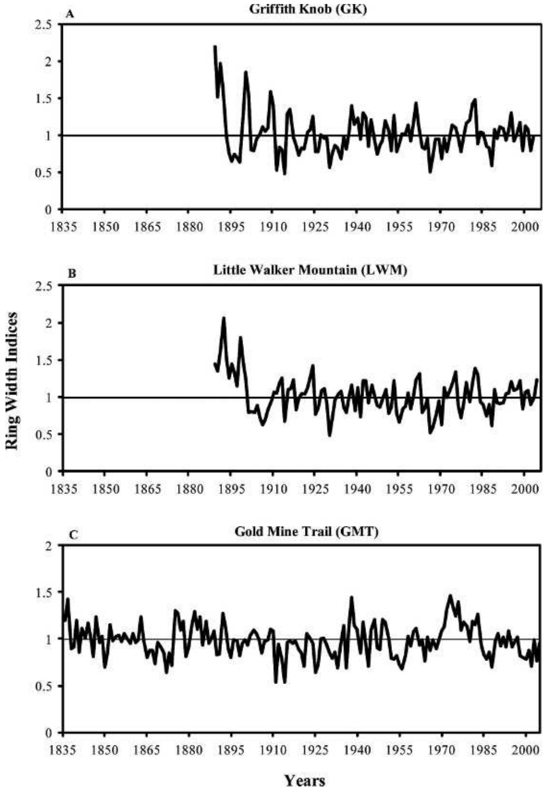

Figure 2. Master chronologies for Griffith Knob, Little Walker Mountain, and Gold Mine Trail.

Climate Analyses

We analyzed the relationships between oak tree growth and monthly climate data using precipitation, temperature, the Palmer Drought Severity Index (PDSI), and the Palmer Hydrological Drought Index (PHDI) obtained from the National Climatic Data Center (NCDC 2007). For the GK and LW sites, climate data came from the Southwestern Mountain climate division for Virginia. Climate data for the GMT site were obtained from the Eastern climate division of Tennessee. Each chronology was analyzed individually for its relationships with each climatic variable for the years 1930 to 2003 for GK and LWM and the years 1930 to 2005 for GMT. We calculated Pearson's product-moment correlation coefficients annual growth and current and previous years' climatic variables (Fritts 1976). Finally, we seasonalized the precipitation, temperature, PDSI, and PHDI variables to isolate longer seasonal periods of climatic sensitivity based on consecutive months with statistically significant or near-significant correlations with monthly climate.

RESULTS

We found similar levels of inter-series correlation and mean sensitivity among the three chronologies despite their differing species compositions (Table 2). Compared to other oak chronologies from the southern Appalachian Mountains found on the International Tree Ring Data Bank (ITRDB 2010) and those developed by Speer *et al.* (2009), the correlation and sensitivity levels of the GK, LWM, and GMT chronologies were among the highest reported from the region (Table 3). We found similar groupings of narrow rings among the three chronologies during the early 1910s, 1930s, and late 1980s, indicating a similar regional climate signal (Figure 2).

Oak trees at GMT (the lowest elevation and farthest south) responded to climatic variables during more months of both the current and previous growing seasons than oak trees from GK and LWM. Significant positive relationships were found between precipitation and growth during the current growing season at each site and extending into the late growing season of the

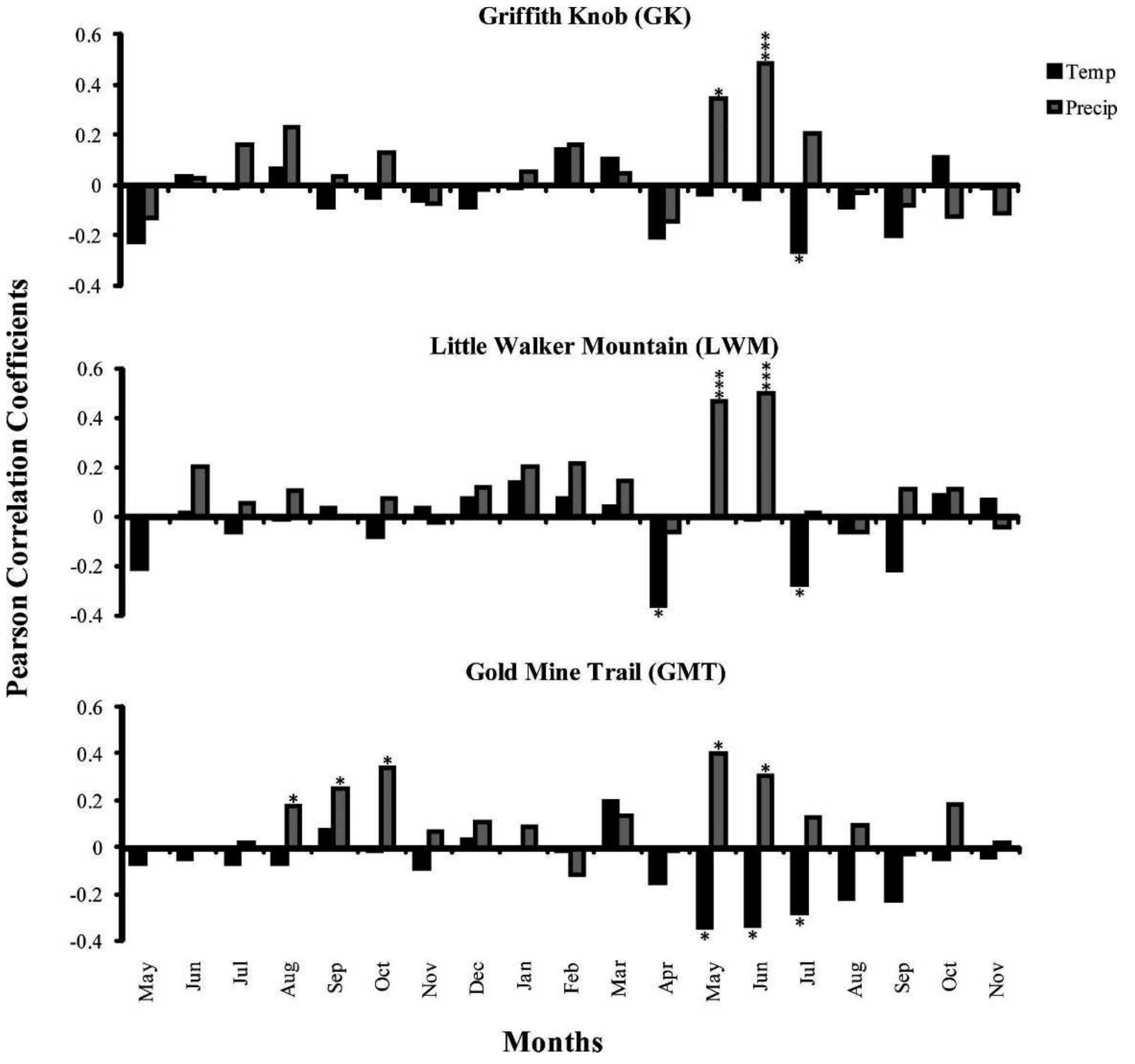

Figure 3. Monthly correlation coefficients between growth and temperature and precipitation at Griffith Knob, Little Walker Mountain, and Gold Mine Trail (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). May through Dec on left side of the "Months" axis labels refer to previous-year conditions.

previous year at GMT (Figure 3). Three months (August–October) of the previous season showed significant relationships ($p < 0.05$) with precipitation in addition to the current season's relationships at GMT, whereas GK and LWM were only significant in the current May and June. When precipitation was examined for a seasonal signal, the most significant correlations were identified at all sites from May to June or July (Table 4). We found significant negative relationships between growth and monthly growing season temperatures at each site, most consistently at GMT. A seasonalized negative temperature relationship was found at LWM and GMT only. At all sites, we found significant positive relationships between growth and both PDSI and PHDI; these relationships extended further into the preceding winter months and the previous year along a high to low elevational gradient from GK (fewer) to GMT (more) (Figure 4). PHDI-growth relationships were slightly later or more prolonged than PDSI at all of our sites. PDSI and PHDI exhibited the most significant monthly relationships with growth at our most southerly GMT study site.

Table 4. Results from the correlation analysis show the strongest relationships between tree growth and seasonal climate variables.

Climatic Variable	Period of Strongest Relationship	Correlation Coefficient
A. Griffith Knob (GK)		
Temperature	No Relationship	N/A
Precipitation	May–July	0.54 ***
PDSI	May–July	0.47 ***
PHDI	June–August	0.50 ***
B. Little Walker Mountain (LWM)		
Temperature	April–July	−0.25 *
Precipitation	May–June	0.61 ***
PDSI	May–July	0.57 ***
PHDI	May–September	0.58 ***
C. Gold Mine Trail (GMT)		
Temperature	April–July	−0.46 ***
Precipitation	May–June	0.49 ***
PDSI	May–August	0.53 ***
PHDI	June–November	0.50 ***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

DISCUSSION

The climatic variables tested were consistent with the climate response found in dendrochronological oak studies conducted in other areas in the eastern U.S., where greatest radial growth occurred during cool, moist summers (Cook and Jacoby 1977; Stahle and Hehr 1984; Bortolot *et al.* 2001; D'Arrigo *et al.* 2001; Speer *et al.* 2009). High correlations between tree growth and precipitation coupled with inverse relationships between temperature and growth at each site indicated moisture availability has the greatest influence on growth of southern Appalachian oak species. PDSI and PHDI correlated strongly at all three sites across more months than did precipitation and temperature variables, which shows the importance of long-term moisture availability. Notably, the oaks sampled at our three sites exhibited relatively high mean sensitivities despite being forest interior trees and not near their ecological limits, where more climatically sensitive trees are conventionally thought to be found (Stahle and Hehr 1984; Jacoby and D'Arrigo 1997; Hart *et al.* 2008).

We believe the temperature signal found at our sites contribute to water stress, as high temperatures increase evapotranspiration rates. The lower latitude, decreased elevation, and southern exposure of the GMT site contribute to this moisture stress signal. GMT is located 280 km southwest of the other two study sites and is subjected to a greater amount of sunlight on a daily and yearly basis, which creates a notably warmer climate. Temperatures from 1930–2006 averaged 22°C in July at Virginia's Southwestern Mountain climate division compared to 25°C at Tennessee's Eastern climate division (NCDC 2007). This warmer climate site is also affected by a southerly exposure and lower elevation. GMT is 595 and 330 m lower in elevation than GK and LWM, respectively. Conversely, GK, the highest of the three sites, had the least significant temperature relationship. The more dominant temperature signal may also account for the slightly lower mean sensitivity found at GMT because temperature and precipitation regulated tree growth here, whereas temperature did not strongly influence our northern sites. The drying effects associated with a southern exposure also likely increased moisture stress at GMT.

Moisture availability during the previous fall preconditions tree growth for the following year at GMT. At this site, fall moisture availability promotes the production and eventual storage of carbohydrates over the winter months, which promotes vigorous cell production when coupled with ample growing season moisture in the following growing season (Fritts 1976). In contrast, no moisture preconditioning effects were found at the northern sites, where a late growing season dry period is less pronounced than in the lower elevations of GMT. Site-specific soil regimes often play a role in limiting moisture availability in oak forests (*e.g.* well drained *vs.* poorly drained soils) (Estes 1970; Charton and Harmon 1973). However, we believe the effects of soil do not factor greatly in the variation among the site moisture regimes, as they are all shallow, well-drained upland soils.

We acknowledge that the multi-species composition of our chronologies may have influenced differences in the climatic signal among our sites.

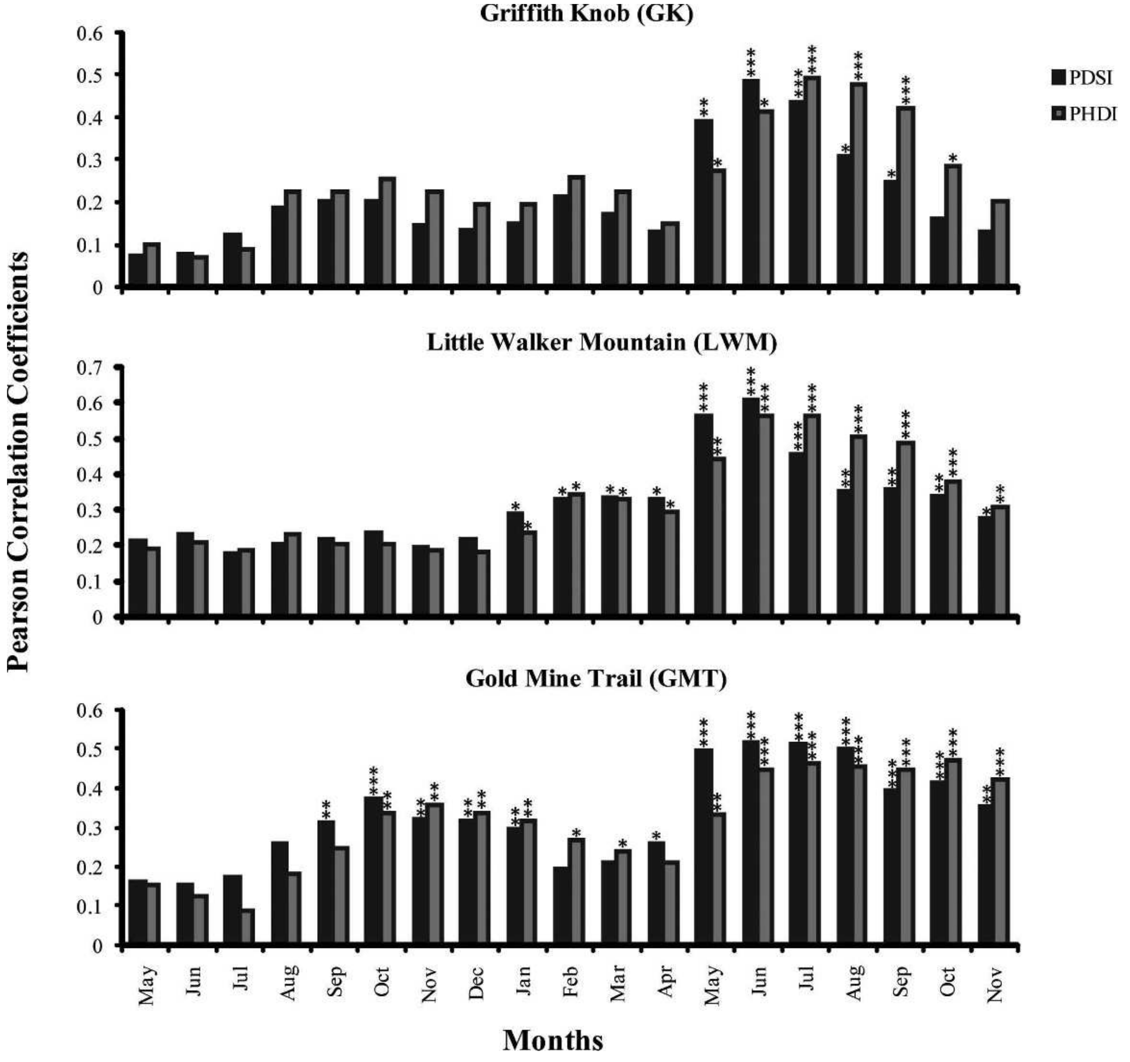

Figure 4. Monthly correlation coefficients between growth and PDSI and PHDI at Griffith Knob, Little Walker Mountain, and Gold Mine Trail (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). May through Dec on left side of the ''Months'' axis labels refer to previous-year conditions.

Because this study was part of a larger project reconstructing fire history at the study areas, we did not possess a sample depth statistically robust enough at all sites to develop species-specific oak chronologies. Consequently, we constructed genera-level chronologies. In particular, the GMT chronology was composed of a greater variety of oak species, which may contribute to the increased variability in the site's climate signal. However, other research conducted on oak in the southern Appalachian Mountains has demonstrated that the principal oak species used in this research (chestnut oak, white oak, black oak, scarlet oak, and northern red oak) respond quite similarly across species to temperature, precipitation, and drought (Speer *et al.* 2009). Therefore, we believe that our results are sound and uncompromised by the multi-species composition of these chronologies.

This research explored the climatic factors that limit growth in oak trees from three sites in the southern Appalachian Mountains. We found oak radial tree growth is highest during cool, moist summers. Fall moisture availability also proved to positively influence the growing season at GMT, our lowest elevation site. Our GMT chronology exhibited a more varied response to climatic variables, leading us to hypothesize that oak climate stress increases in variability with a decrease in elevation and latitude. A significant finding of this study was the presence of a relatively strong climate-growth relationship at sites not typically considered for dendroclimatic research involving oak. Our results accentuate the importance of the principle of site selection when using oaks for dendroclimatic research in the temperate southeastern United States.

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