

Radial growth responses of four oak species to climate in eastern and central North America

David C. LeBlanc and David W. Stahle

Abstract: This study characterized associations between climate variables and radial growth of four oak species at sites distributed across central and eastern North America. Tree-ring data were obtained from 24, 29, 33, and 55 sites for *Quercus prinus* L., *Quercus velutina* Lam., *Quercus macrocarpa* Michx., and *Quercus stellata* Wangenh., respectively. Pearson's correlation coefficients were computed between radial growth and monthly and seasonal temperature and precipitation. Growth was most strongly and consistently correlated with precipitation and temperature during the early growing season (May to July). Coincident positive correlations with precipitation and negative correlations with temperature indicate that this relationship is mediated by site water balance. The combination of this plausible cause–effect mechanism and extensive spatial replication of these correlations suggest that they reflect cause–effect relationships. Growth of *Q. stellata* was correlated with precipitation during the dormant season, suggesting that stored soil water is important for growth of this species in the southern Great Plains. Despite substantial spatial variation in temperature and growing-season initiation between sites in Texas and Manitoba, Canada, there was little variation in the phenology of growth–climate associations; growth–climate correlations were strongest during the same May–July period at all sites. Results of this study support the hypothesis that temperate zone ring-porous oak species have similar phenology of growth–climate correlations and can be treated as a biologically meaningful functional group in forest simulation models.

Key words: *Quercus macrocarpa*, *Quercus prinus*, *Quercus stellata*, *Quercus velutina*, dendroecologie.

Résumé : Cette étude caractérise les relations entre les variables climatiques et la croissance radiale de quatre espèces de chêne dans des stations réparties à travers le centre et l'est de l'Amérique du Nord. Des données dendrochronologiques ont été obtenues pour *Quercus prinus* L., *Q. velutina* Lam., *Q. macrocarpa* Michx. et *Q. stellata* Wangenh. dans respectivement 24, 29, 33 et 55 stations. Les coefficients de corrélation de Pearson ont été calculés entre la croissance radiale et les températures mensuelles et saisonnières ainsi que la précipitation. La croissance était le plus étroitement et constamment corrélée avec la précipitation et la température tôt (mai à juillet) durant la saison de croissance. Des corrélations positives avec la précipitation coïncidant avec des corrélations négatives avec la température indiquent que cette relation est conditionnée par le bilan hydrique de la station. Le fait que ce mécanisme de causalité soit plausible combiné à la réplication sur une vaste étendue de ces corrélations indique qu'elles reflètent des relations de causalité. La croissance de *Q. stellata* était corrélée avec la précipitation durant la saison de dormance, ce qui indique que l'eau emmagasinée dans le sol est importante pour la croissance de cette espèce dans le sud des Grandes Plaines. Malgré l'importante variation spatiale de la température et de l'amorce de la saison de croissance entre les stations du Texas et celles du Manitoba, au Canada, il y avait peu de variation dans la phénologie des relations entre le climat et la croissance; les corrélations entre la croissance et le climat étaient les plus fortes durant la même période, soit de mai à juillet, dans toutes les stations. Les résultats de cette étude supportent l'hypothèse que les espèces de chêne à zone poreuse des régions tempérées ont une phénologie similaire des corrélations entre la croissance et le climat et qu'elles peuvent être considérées comme un groupe fonctionnel biologiquement significatif dans les modèles de simulation. [Traduit par la Rédaction]

Mots-clés : *Quercus macrocarpa*, *Quercus prinus*, *Quercus stellata*, *Quercus velutina*, dendroécologie.

Introduction

Understanding how climate influences tree growth and mortality is important for predicting forest responses to climate change. There is substantial literature documenting how drought and high temperature events are directly or indirectly associated with widespread tree mortality and forest decline (Allen et al. 2010; Anderegg et al. 2012; Heres et al. 2014). Pederson et al. (2014) presented evidence for widespread overstory tree mortality associated with intense drought from 1772 to 1775 that altered forest ecosystems over a large part of eastern North America. These severe responses of trees and forests to past climate extremes provide cause for concern about the potential consequences of future climate change that may result in higher frequency and amplitude of extreme climate events (Easterling

et al. 2000; Seneviratne et al. 2012; Teskey et al. 2014). Better understanding of how climate influences tree growth and how much this varies among different taxonomic groups could increase the reliability of models used to project potential forest responses to future climate change.

McDowell et al. (2008) described three nonexclusive mechanisms by which drought and high temperature can directly or indirectly cause tree mortality. Understanding of these processes is not currently adequate for precise prediction of tree mortality and forest die-off events. However, two of these three mechanisms (disruption of hydraulic conductivity and carbon starvation) involve circumstances that would cause reduced photosynthesis and tree growth in general and reduced xylem production in particular. The latter is a consequence of the relatively low priority given to xylem pro-

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duction when photosynthate is in limited supply (Waring 1987). One direct study of these two mechanisms concluded that aspen mortality after a severe drought was mostly due to hydraulic failure and not carbon starvation (Anderegg et al. 2012). Another study of Scots pine mortality associated with drought implicated hydraulic failure caused by reduced carbon allocation to xylem production (Heres et al. 2014).

Dendroecological analyses of associations between annual tree-ring width and climate variables have long been used to evaluate the influence of environmental stresses on tree growth, vigor, and mortality (Fritts and Swetnam 1989). Recent dendroecological research has explored how climate change may influence growth, mortality, and distribution of various tree species (e.g., Granda et al. 2013; Pasho et al. 2012). Some have used results of dendroecological analyses to calibrate climate response functions in forest simulation models (Rickebusch et al. 2007). Associations between reduced radial growth and increased risk of tree decline and mortality are well documented (Pedersen 1998; Bigler et al. 2007). Bigler and Bugmann (2004) documented that empirical mortality functions based on the association between radial growth and mortality risk provide better predictions of tree mortality than theoretical functions widely used in forest simulation models.

Several researchers have proposed simplifying simulation models used to project forest responses to climate change by using “functional groups” of tree species with similar ecologies rather than trying to model every species independently (Graumlich 1993; Cook et al. 2001; LeBlanc and Terrell 2011). Cook et al. (2001) and Graumlich (1993) identified functional groups of tree species with similar growth–climate associations using a posteriori statistical methods. LeBlanc and Terrell (2011) proposed that functional groups might be identified a priori, based on similarities of tree species biology and ecology, and that these group designations could subsequently be tested as hypotheses.

This paper presents results of one such test of the hypothesis that temperate zone upland oak (*Quercus*) species with predetermined apical growth patterns and ring-porous wood anatomy form a functional group that should have similar growth–climate associations. Based on substantial literature that describes the growth biology and ecology of oak species, LeBlanc and Terrell (2011) predicted that radial growth of these species should be most strongly associated with soil water availability (as influenced by both precipitation and temperature) during the early months of the growing season. They also predicted that water availability in the late summer and early autumn of the year prior to growth may influence starch reserves that support production of early-wood xylem prior to leaf-out in the following year. The analyses presented here tested these hypotheses using data for four different oak species occurring at sites that span substantial temperature and precipitation gradients.

The objective of this study was to evaluate spatially replicated associations between climate variables and radial growth of four widely distributed oak species: *Quercus velutina* Lam. (Quve), *Quercus macrocarpa* Michx. (Quma), *Quercus prinus* L. (Qupr), and *Quercus stellata* Wangenh. (Qust). Sites where these oaks were sampled spanned eastern North America from Atlantic coastal states to the western Great Plains and from Gulf Coast states to southern Canada. The study reported here continues the analysis of oak growth–climate relationships in this region that began with analyses of *Quercus alba* L. (LeBlanc and Terrell 2009) and *Quercus rubra* L. (LeBlanc and Terrell 2011). The current study expands the regional analysis to include the Great Plains of the central United States, beyond the eastern deciduous forest and into drier prairie environments. This study also includes a larger number of sites at more southern latitudes than the preceding two studies, providing a stronger basis for evaluating effects of phenological differences on growth–climate associations.

Methods

Sources of tree-ring data

To study growth–climate relationships for multiple oak species over a subcontinental spatial scale required the use of data from a variety of sources. The objectives and procedures of the original studies varied and sampling sites were not randomly selected from the species range (Fig. 1). All of the Qust and Quma data were obtained for studies that use tree rings to reconstruct historical climate or hydrology (Sieg et al. 1996; St. George and Nielsen 2003; Stahle and Cleaveland 1988; Stahle and Hehr 1984; Stahle et al. 1985a, 1985b). Dendroclimatology studies focus sampling on the oldest trees on climate-sensitive sites. In contrast, most of the data for Qupr and Quve were obtained for studies of air pollution effects on tree and forest health (LeBlanc 1998; McLaughlin et al. 1986). These studies obtained data from trees and sites that were more representative of mature forests across larger regions. Results of these studies found no clear evidence of pollution effects that would obscure tree growth–climate associations (LeBlanc 1998). Furthermore, LeBlanc and Terrell (2009) provided evidence that differences in original study objectives and methods had little systematic influence on growth–climate correlations of *Q. alba*.

Although the spatial distribution of sampling locations is not representative of the species distributions (Fig. 1), and the site and tree selection criteria were not random, we believe that these data can still be useful for addressing the primary study objective. If tree species that share a determinate apical growth pattern and ring-porous wood anatomy have the same phenology of carbon allocation to radial growth, then the phenological pattern of growth–climate correlations should be similar to those previously documented for *Q. alba* (LeBlanc and Terrell 2009) and *Q. rubra* (LeBlanc and Terrell 2011). In this study, Qust and Quma were sampled almost exclusively in the western half of the species range and Qupr was sampled mostly at sites east of the Appalachian Mountains. Nonetheless, the diversity of site conditions and oak species included in the present study may provide for a more rigorous test of the hypothesis that all ring-porous oak species have similar phenology of growth–climate correlations, as proposed by LeBlanc and Terrell (2011). Finally, because the sampling locations are not representative of the entire species range, results from this study cannot be confidently extrapolated to general statements regarding growth responses of the four individual oak species to climate. However, a common pattern of climate correlations among different regions and species would provide evidence for generalizable patterns of growth–climate relationships for the genus *Quercus*.

Most of the tree-ring data used for this study were obtained from the International Tree-Ring Data Bank (ITRDB), IGBP PAGES/World Data Center for Paleoclimatology, NOAA National Climate Data Center, Boulder Colorado, USA; the remaining data were either developed by the authors or contributed by individuals for use in this analysis.

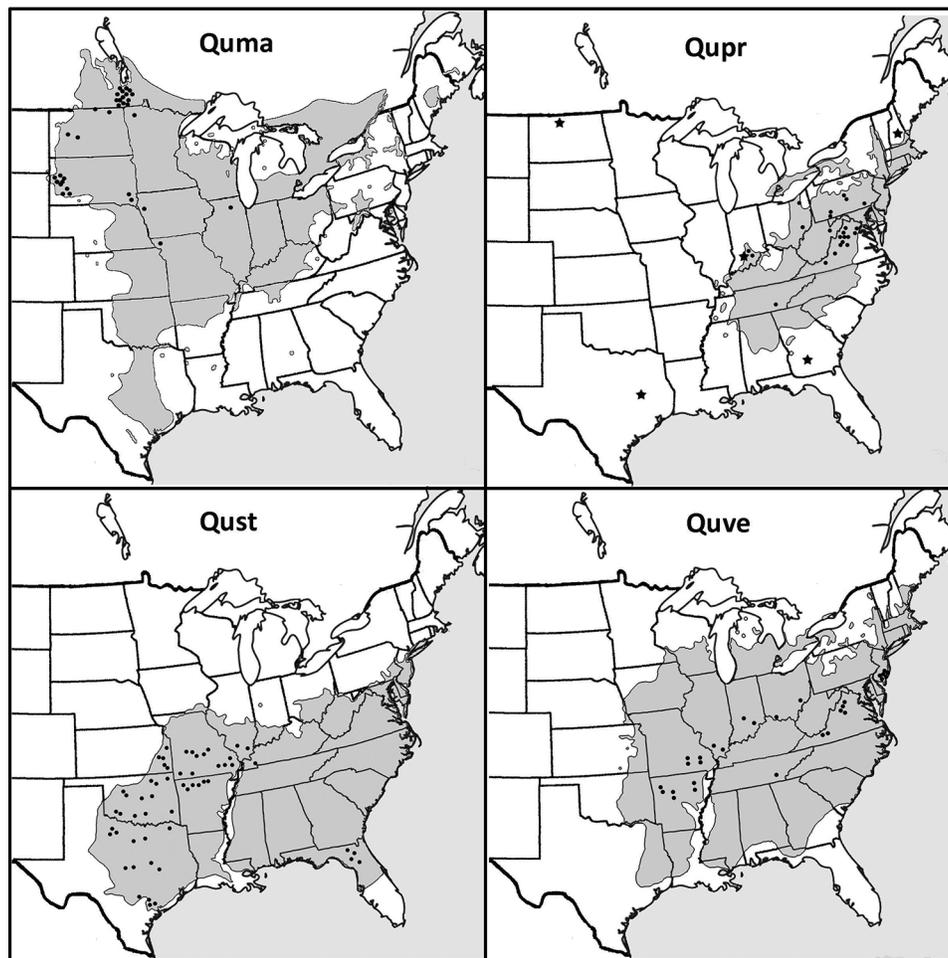
Quercus stellata data sources

Most Qust tree-ring data (47 of 55 sites) were collected for dendroclimatology research (Stahle and Cleaveland 1988; Stahle and Hehr 1984; Stahle et al. 1985a, 1985b). Collections from this source included from 14 to 73 increment cores per site. Other collections were from studies of climate, fire history, or air pollution effects on forests and included 42 to 60 increment cores per site.

Quercus macrocarpa data sources

Quma tree-ring data were collected for two dendroclimatology studies. Sieg et al. (1996) sampled Quma in North and South Dakota to evaluate the potential for dendroclimatic reconstruction of drought in the north central Great Plains states. Sampling focused on trees growing on drier slopes, and two cores were taken from opposite sides of each of 20 trees (Sieg et al. 1996). However,

Fig. 1. Black dots indicate approximate locations of study sites within species' ranges, indicated by the gray shaded areas. Stars in the Qupr panel show locations of weather reporting sites that provided daily temperature data used to compute cumulative degree days for comparisons across latitudinal climate gradients.



the data sets obtained from ITRDB varied from five trees and 10 cores per site to 23 trees and 32 cores per site.

St. George and Nielsen (2003) sampled Quma at the upper boundary of the riparian zone at 16 sites along the Red River and Assiniboine River near Winnipeg, Canada. These trees would have been inundated only during infrequent extreme flooding events. One core was taken from each of 10 to 38 trees per site.

Quercus velutina and *Q. prinus* data sources

Data for 13 Qupr sites and 33 Quve sites were obtained from the FORAST database (McLaughlin et al. 1986). The objective of this study was to identify air pollution effects on tree growth in the eastern United States. Sites were selected to be representative of mature forests throughout this region, but selection was not random. Sites close to air pollution point sources and major urban areas were excluded, as were sites with recent history of logging or fire. Trees were sampled on flat ridge tops or in valley bottoms. Two increment cores were taken from each of 15 dominant or co-dominant crown class trees per site that showed no signs of physical damage or competitive release during the period of 1930 to 1980.

Data for three Qupr and six Quve sites were developed during a dendropollution study in the Ohio River Valley from Illinois to Ohio (LeBlanc 1998). Sites were xeric, generally south-facing upper ridge slopes on acidic soils. Tree selection criteria were the same as in the FORAST study. Two increment cores were sampled from each of 30 trees for each species.

Given the highly variable and sometimes limited sample sizes of increment cores, only those sites with at least 10 increment cores and an expressed population signal (EPS) greater than 0.85 for the period of 1930 to 1980 were retained for the present study (Wigley et al. 1984).

Tree-ring chronology development

The processing of tree-ring data to develop site chronologies followed LeBlanc and Terrell (2009, 2011). All increment cores collected by the authors were visually cross-dated and measured to 0.01 mm precision, and dating was verified using COFECHA (Holmes 1983). Cross-dating was also verified for tree-ring data downloaded from the ITRDB. Data for cores that could not be cross-dated were dropped from analyses.

Ring width chronologies for individual cores were processed using ARSTAN (Cook 1985) to produce a mean tree-ring index chronology for each site–species combination. A 50-year smoothing spline was used to remove long-term trend, and temporal autocorrelation was removed from each individual core chronology. A robust biweight mean was used to average the resulting tree-ring indices by year to produce a residual tree-ring index chronology for each site and species combination.

Sources of climate data

Data for mean monthly temperature (T), mean monthly maximum temperature (MxT), and total monthly precipitation (P) were obtained from the same sources described in LeBlanc and Terrell

(2009, 2011). Data for T and P were obtained from the National Climate Data Center (NCDC 1994). Data values were averages for weather recording stations within state climate divisions (SCDs). Data for MxT were obtained from the United States Historical Climatology Network (Easterling et al. 1999). Individual reporting stations were aggregated into the SCDs based on their latitude and longitude, and data for multiple stations were averaged by year for each SCD. Climate data for sites located near Winnipeg, Canada, were obtained from Environment Canada (Adjusted and Homogenized Canadian Climate Data, <http://ec.gc.ca/dccha-ahccd>); data from the Winnipeg reporting station was used for all of these sites.

Analyses of radial growth–climate relationships

Pearson's correlation analysis was performed between the ARSTAN residual tree-ring chronology and monthly, seasonal, and annual T , MxT, and P variables for a common period of 1930 to 1980, using climate data for the local SCD for each site. Monthly climate variables spanned the period from June of the year prior to tree-ring formation (pJ) through October of the year that the ring was formed (O). Seasonal climate variables included prior summer (pSm: June–August), prior autumn (pAt: September–November), prior winter (pWn: December–February), spring (Spr: March–April), and early growing season (MJJ: May–July). Annual climate variables (Ann) averaged monthly values from prior-year June through current-year October.

Because the correlation analyses included a total of 69 climate variables for 141 different site–species combinations, a Bonferroni approach was used to reduce cumulative type I error rate. The 17 monthly climate variables for each of T , MxT, and P were considered to involve the same number of independent tests of significance, each with an acceptable type I error rate of 0.05. Seasonal and annual climate variables were not independent of the associated monthly variables and these were not included in the Bonferroni adjustment. For each climate variable, a correlation analysis was done for each site–species combination. To limit overall type I error rate for correlation analyses for each species, a cumulative binomial probability distribution was determined with N = number of sites and p = 0.05. Radial growth of an oak species was deemed to be significantly correlated with a particular monthly climate variable only if correlations with a p value of ≤ 0.05 were observed at a minimum number of sites (X) defined by a cumulative binomial probability of $1 - 0.05/17 = 0.997$. With the varying number of chronologies for each species, this critical minimum number of sites varied from five sites for Qupr and Quve to eight sites for Qust.

Correlations between oak radial growth and MxT variables were generally stronger and more spatially replicated than corresponding correlations with T variables. With 25 temperature variables (monthly, seasonal, annual) and four species, 100 comparisons could be made between T versus MxT correlations. Only 40 significant correlations were adequately spatially replicated, as defined above. Only three of 40 comparisons showed that correlations with T occurred at more sites than correlations with the corresponding MxT variable. Only four of 40 comparisons indicated that the correlation with T was stronger than the correlation with MxT. Finally, significant correlations with MxT and T variables occurred in the same months. Hence, only MxT correlations were presented in the Results and Discussion sections.

Three different versions of current growing season climate variables were compared to determine which had the strongest correlations with radial growth, May–July (MJJ), July–August (JJA), or May–August (MJJA). A block design ANOVA was used to compare mean correlations among these different seasonal variables, with site used as the blocking variable. Fisher's exact test was used to compare the proportion of sites where each of these three versions of current growing season variables was significantly correlated with growth for each oak species.

For both MxT and P variables and for all four oak species, the MJJ version of the current growing season variable had stronger correlations with growth than the JJA version of this seasonal variable (Fig. 2). Mean correlations with the MJJA version of the variables were intermediate between the MJJ and JJA versions. Significant differences in correlations between MJJ and JJA seasonal variables ranged from 0.03 to 0.14. For Quma and Qust, correlations with the MJJ seasonal variables were observed at a greater percentage of sites than the corresponding JJA variables ($p < 0.05$). A similar pattern was observed for Qupr and Quve, but these differences were not statistically significant. Analyses of correlations between radial growth and current growing season climate variables in the Results and Discussion sections will focus on the MJJ version of these seasonal variables.

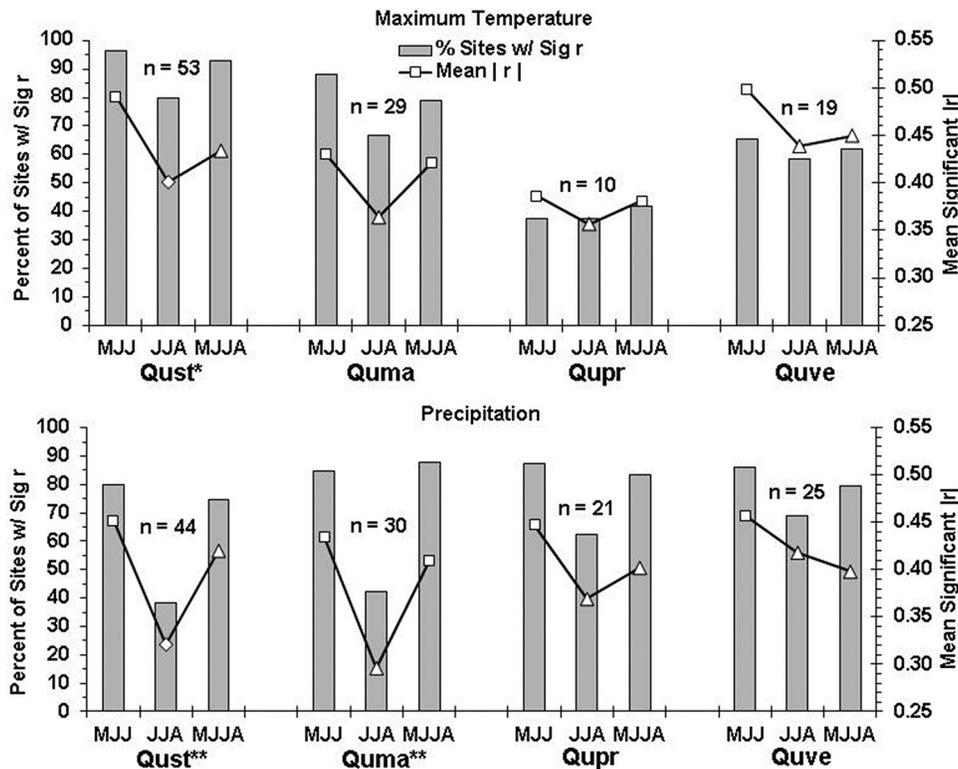
Paired t tests and Fisher's exact test were used to compare the strength and spatial replication of correlations between pairs of climate variables. To compare the strength of correlations, the difference between absolute values of correlation coefficients was calculated for each site, and a paired t test used to determine if the mean difference value differed from zero. To limit the multiplicity of tests and to provide sufficient power, this analysis was performed only for seasonal variables that were significantly correlated with radial growth for at least 15 sites. In all but one case, the difference values were normally distributed. When the normality assumption of the t test was violated, a sign test was used. To compare spatial replication of correlations between pairs of climate variables, Fisher's exact test was used to compare the proportion of sites where each of the two climate variables was significantly correlated with radial growth.

The sites where each of the four oak species were sampled spanned ranges of latitude and longitude that are associated with substantial variation in climate. To determine if growth–climate correlations varied across these climate gradients, sites for each species were divided into two regions. For Quve and Qupr, sites were divided into regions east of the Appalachian Mountains (New Jersey, Pennsylvania, Virginia, West Virginia) and west of the Appalachian Mountains (Ohio, Indiana, Tennessee, Illinois, Missouri, Arkansas). For Qust, sites were divided into eastern deciduous forest (Missouri, Arkansas, Illinois, Florida) and Great Plains (Kansas, Oklahoma, Texas) regions. These regions are located along a longitudinal precipitation gradient (Court 1974). The northernmost sites where Quma was sampled are near the species' northern range limit (Fig. 1), so the regional division was into north (Manitoba, Minnesota, North Dakota) and south (Iowa, Missouri, South Dakota). For each species, a Fisher's exact test was used to compare the number of sites where climate variables were significantly correlated with radial growth between two regions. Only those climate variables that met the spatial replication criterion described above were included in this analysis of regional variation. For each species separately, a Bonferroni adjustment based on the number of climate variables so identified was used to determine the critical p value ($= 0.05/N$ variables) for the Fisher's exact tests.

Results

Growth–climate correlations for the four oak species growing on sites spread across a wide range of latitude and longitude displayed unexpectedly strong patterns of similarity. For all species and most sites, radial growth was most strongly correlated with temperature and precipitation variables for the months of May through July during the growing season when the annual ring is formed. There is little to no evidence of a phenological shift in oak growth–climate correlations between sites in Texas at 30°N latitude and sites in southern Canada at 50°N. There was a general east to west pattern of increasing strength of correlations with current growing season precipitation. There was more spatial and interspecific variability in correlations that were weaker and less

Fig. 2. Comparison of growth–climate correlations among three versions of current summer seasonal variables (MJJ, May through July; JJA, June through August; MJJA, May through August) for four oak species (Qust, *Q. stellata*; Quma, *Q. macrocarpa*; Qupr, *Q. prinus*; Quve, *Q. velutina*). Asterisks after the abbreviated species names indicate the percentage of sites where the climate variable was significantly correlated with growth differed among the three seasonal variables (*, $p \leq 0.05$; **, $p \leq 0.01$, as determined by a χ^2 test). Different plot symbols indicate that mean significant correlation differed among the three seasonal variables ($p \leq 0.05$, as determined by block design ANOVA and Tukey's test, using site as the block variable). Sample sizes (n) listed are for the ANOVA and included only those sites where at least one of the three summer variables was significantly correlated with radial growth.



spatially replicated. These results are described in more detail below.

The phenology of significant correlations between MxT variables and radial growth of all four oak species is restricted mostly to the current growing season when the trees have foliage (Fig. 3). For all four species, significant negative correlations with MxT were strongest and most spatially replicated for current-year MJJ variables. Three of four species (Qust, Qupr, Quve) also had spatially replicated negative correlations with current September MxT. Radial growth for two of the four oak species (Qust and Quve) was negatively correlated with prior-year late growing season MxT variables. However, these correlations were not as spatially replicated as those for early growing season MxT. Spatially replicated significant correlations with MxT during the spring months of March and April were restricted to Qust at southern sites. There were no spatially replicated significant correlations with winter temperature (mean or maximum), even for Quma growing on sites at 50°N latitude, near its northern range limit. The only spatially replicated positive correlation with MxT was between Quma radial growth and prior-November MxT. Significant positive correlations were observed at six of 33 (18%) Quma sites, all in the northern region, with an average correlation of $r = 0.32$.

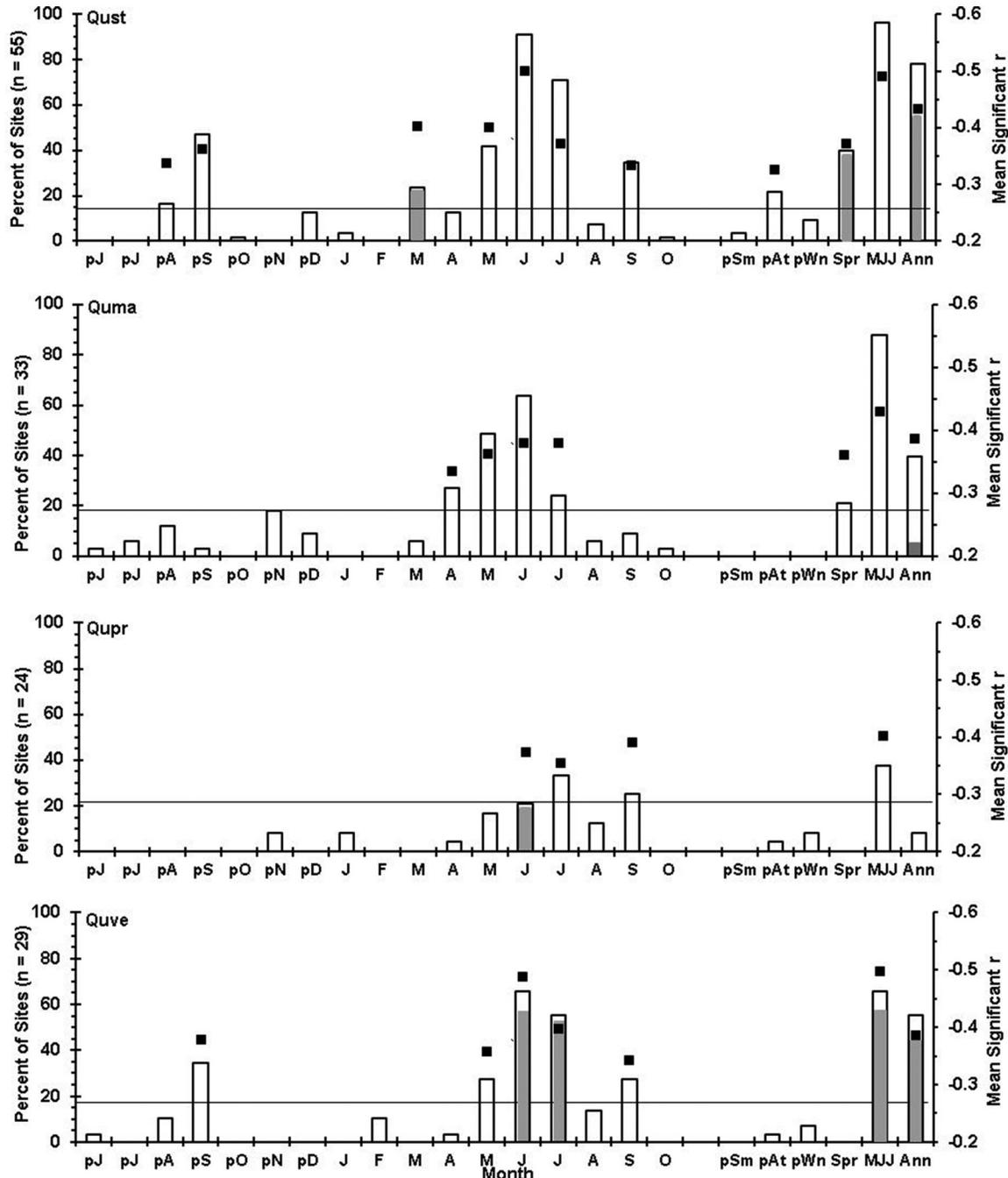
There was some evidence of spatial variation in growth–temperature correlations for all four oak species (Fig. 3; Fisher's exact test $p \leq 0.05$). Significant correlations between radial growth of Qust, Qupr, and Quve and several MxT variables were observed at a greater proportion of western sites than among eastern sites. Significant correlations between Quma radial growth and annual MxT were observed mostly at southern sites.

The phenology of significant correlations between precipitation (P) variables and radial growth was broadly similar among the four oak species, but Qust had more correlations with dormant-season P variables (Fig. 4). All four species had spatially replicated positive correlations with MJJ P during the current year. Current-June P was most strongly correlated with growth for all species except Quma on sites in the northern Great Plains, which was more strongly correlated with May P . Qust results differed from those of the other species in that growth was also correlated with monthly and seasonal P variables for prior autumn (pAt), prior winter (pWn), and current-year spring (Spr). This was particularly apparent for sites in Texas, where 11 of 14 sites had significant correlations with P in two or more months between prior-year November and April. Growth of other oak species at sites in more northern and eastern regions was much less commonly correlated with P during months prior to the growing season.

There was modest evidence of regional differences in spatial replication of correlations with P variables for two of the four oak species (Fig. 4; Fisher's exact test $p \leq 0.05$). For both Qust and Quve, significant correlations between radial growth and a number of P variables were observed more frequently among western sites than eastern sites.

Early growing season (MJJ) P was more strongly correlated with radial growth than early growing season MxT for Qupr, but MxT was more strongly correlated with growth of Qust (Table 1). The pattern of variation in spatial replication of significant correlations mirrored this pattern of mean differences in absolute correlation coefficients. There were no significant differences between correlations with P versus MxT for Quve or Quma. Data for *Q. alba* (LeBlanc and Terrell 2009) and *Q. rubra* (LeBlanc and Terrell 2011)

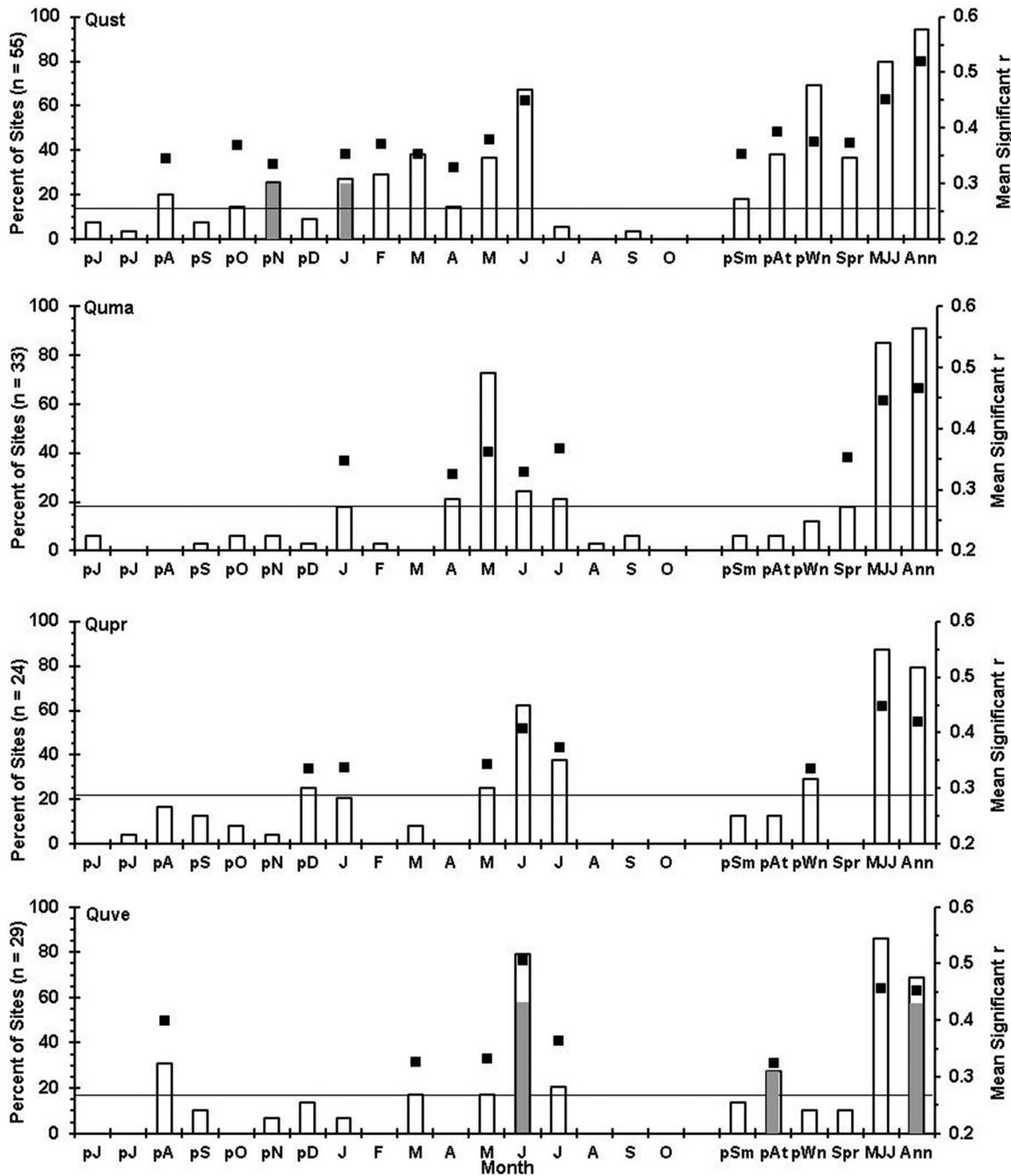
Fig. 3. Correlations between tree-ring chronologies and mean monthly maximum temperature (MxT) for four oak species (Qust, *Q. stellata*; Quma, *Q. macrocarpa*; Qupr, *Q. prinus*; Quve, *Q. velutina*). Histogram bars indicate the percentage of sites where a significant correlation ($r \geq 0.288$, $p \leq 0.05$) was observed. Solid square symbols indicate the mean of significant correlations for those climate variables that had sufficient spatial replication to limit overall type I error rate for monthly variables to $p \leq 0.05$ (indicated by the horizontal solid line), as described in the Methods. Note that all significant temperature correlations but one were negative and the scale on the right y axis is inverted. Monthly climate variables on the x axis begin with June of the year prior to annual ring formation (pJ) and end with October of the year that the annual ring was formed (O). Correlations with seasonal (pSum to MJJ) and annual (Ann) MxT variables are displayed on the right. Gray areas within some histogram bars indicate climate variables that had regional differences in the percentage of sites with significant correlations. Gray and white areas within bars indicate the proportion of sites in regions, as follows: Qust: gray = west (KS, OK, TX) and white = east (MO, AR, IL, FL); Quma: gray = north (MB, ND, MN) and white = south (SD, IA, IL, MO); Qupr and Quve: gray = west (OH, IN, TN, IL, MO, AR) and white = east (NJ, PA, VA, WV). Bars with no gray shading indicate no significant regional differences.



were similarly analyzed and these two species also displayed stronger, more spatially replicated correlations with MJJ P compared with MxT. Climate variables for the early growing season were the only seasonal variables that had significant correlations

at a sufficient number of sites to perform these analyses for all oak species. However, other seasonal climate variables were significantly correlated with Qust growth. For both prior-autumn and prior-winter seasons, Qust growth was much more strongly correlated

Fig. 4. Correlations between tree-ring chronologies and total monthly precipitation (P). Explanations are the same as for Fig. 3, except that precipitation correlations were all positive and the right y axis scale is not inverted.



with P than MxT, opposite to the pattern for the summer variables. There was no difference in strength of correlations between spring P and MxT, suggesting a period of transition from dormant-season P exerting stronger influence on subsequent growth to growing-season MxT becoming more influential.

Growth-climate correlations for MxT appear to be weaker and less spatially replicated for Qupr than for the other three species (Figs. 3). However, almost all of the Qupr sites were east of the Appalachian Mountains, whereas the other three species were sampled at many sites further west (Fig. 1). To evaluate if the weaker growth-climate correlations for Qupr were due to this difference in locations of study sites, 10 sites were identified where both Qupr and Quve were sampled; the other two oak species did

not occur at Qupr sites. Paired t tests were used to compare correlations for June and MJJ MxT between Qupr and Quve. These were the MxT variables that had the strongest and most spatially replicated correlations with growth of both species. Where these two species grew on the same site, correlations with MxT for Qupr were either similar to those of Quve or perhaps slightly stronger; no significant differences were identified. Hence, the pattern of weaker, less spatially replicated correlations for Qupr in Fig. 3 is likely an artifact of the more eastern locations where this species was sampled.

The Quma and Qust sites in the Great Plains spanned a substantial temperature gradient from 29°N to 50°N latitude and provided an opportunity to evaluate if this was associated with

Table 1. Comparison of correlations with seasonal precipitation (*P*) versus seasonal mean maximum temperature (MxT) based on the difference between absolute correlations (paired *t* test by site) and the difference in percentage of sites where significant correlations were observed (Fisher's exact test).

Species and season	No. of sites	$ r_P - r_{MxT} $	No. of sites	%Sig _{<i>P</i>}	%Sig _{MxT}
<i>Q. macrocarpa</i>					
MJJ	30	0.008	33	84.9	87.9
<i>Q. prinus</i>					
MJJ	21	0.188***	24	87.5	37.5***
<i>Q. stellata</i>					
Prior autumn ^a	24	0.123***	55	38.2	21.8
Prior winter	40	0.231***	55	69.1	9.1***
Spring	31	0.007	55	36.4	40.0
MJJ	53	-0.078***	55	80	96.4**
<i>Q. velutina</i>					
MJJ	25	-0.008	29	86.2	65.5
<i>Q. alba</i> ^b					
MJJ	128	0.067***	149	85.2	69.1**
<i>Q. rubra</i> ^c					
MJJ	65	0.081***	82	76.8	48.8***

Note: Only sites where at least one of the two climate variables (*P* or MxT) was significantly correlated with radial growth were included in paired *t* tests. %Sig_{*P*}, percentage of sites where *P* was significantly correlated with radial growth; %Sig_{MxT}, percentage of sites where MxT was significantly correlated with radial growth. Significance: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

^aSign test used in place of paired *t* test. Tabled value is the median difference.

^bData from LeBlanc and Terrell (2009).

^cData from LeBlanc and Terrell (2011).

differences in phenology or strength of growth–climate associations. The strongest, most spatially replicated correlations were with early growing season climate variables (MJJ MxT and MJJ *P* in Figs. 3 and 4) and annual variables (Ann MxT and Ann *P* in Figs. 3 and 4). Neither the percentage of sites where significant correlations were observed nor the average significant correlation with MJJ MxT, MJJ *P*, and Ann *P* differed between southern Qust and northern Quma. However, significant correlations with Ann MxT were observed at a greater percentage of Qust sites than Quma sites (78% versus 39%, $p < 0.001$). Average significant correlation with Ann MxT was only modestly higher for Qust sites ($p = 0.081$, two-sample *t* test). Southern Qust sites also had spatially replicated significant correlations with many more monthly *P* variables for autumn, winter, and spring prior to the growing season compared with northern Quma sites (Figs. 4). However, the phenology of the strongest correlations with early growing season monthly variables was surprisingly similar given the latitudinal gradient in temperature and associated difference in timing of leaf-out between south Texas and Manitoba, Canada. The higher percentage of Quma sites where significant correlations with May *P* were observed was opposite to expectations given the later timing of the growing season at these locations compared with more southern Qust sites.

For reasons that will be explained later, the negative correlations between radial growth and current-September MxT did not seem to have a biologically plausible mechanism. Hence, correlations with September MxT were evaluated for multicollinearity among climate variables using backward selection multiple regression analyses. Growth–climate regression models for each species–site combination started with September MxT and other climate variables that were significantly correlated with growth. Of the 46 species–site combinations that had significant growth–climate correlations with September MxT, only 13 retained this variable in the multiple regression model at the $p \leq 0.05$ level (no Quma sites, four or five sites for each of the other three species).

Of these 13 species–site combinations, 11 were spatially clumped into four clusters of sites with the same climate data or sites in adjacent state climate divisions. Hence, most of the significant correlations with September MxT could be due to multicollinearity with climate variables for earlier months. The spatial clustering of the remaining sites diminishes the spatial replication in support of an actual biological relationship between growth and September temperature.

Discussion

The spatial and interspecific consistency of growth–climate correlations observed among four oak species at sites spanning substantial climate gradients was unexpected but consistent with results of earlier studies showing that phylogeny better explained patterns of growth–climate correlations than site ecology (Cook et al. 2001; Graumlich 1993). This discussion will describe the spatial climate gradients, how they are related to spatial patterns of growth–climate correlations (or not), how the ecology of sites can explain spatial differences in the strength of significant growth–climate correlations, and how the biology of *Quercus* spp. radial growth might explain the similarities of growth–climate correlations across substantial climate gradients. In closing, we will make the case that deciduous *Quercus* species can be treated as a single functional group in forest simulation models.

A study of tree growth responses to climate at sites from 29°N to 50°N latitude must consider phenology. Radial growth of tree species will be most directly affected by environmental conditions when trees are physiologically active and growing (Fritts 1976). For temperate deciduous trees, this is when they have foliage and are photosynthesizing and transpiring and the cambium is producing xylem. For the most part, the results of this study support this premise.

There are limited data available for oak phenology, but timing of spring leaf-out may differ by as much as two months between the southern United States and southern Canada. Spring leaf-out of lilac (*Syringa* spp.) can begin in late February in southern Texas but not until mid-May in Saskatchewan (Schwartz and Caprio 2003; PlantWatch, <https://www.naturewatch.ca/plantwatch/>). Frost ring formation in *Q. alba* and Qust in the southern United States indicated that cambial activity can be initiated as early as March 1st (Stahle 1990). Cambial activity in oaks precedes leaf-out (Zimmerman and Brown 1971; Wang et al. 1992). Hence, oaks in Texas may begin leaf-out in mid- to late March. In contrast, *Q. alba* and Quve in Massachusetts leaf-out in mid-May (O'Keefe 2010).

Spring leaf-out of temperate deciduous trees is most strongly associated with accumulation of growing degree days (GDD) (Lechowicz 1984). An analysis of GDD sums for the years 2007 to 2013 (base temperature 4 °C, start date January 1st) using daily mean temperature data for five sites (Fig. 1) indicated that the site in North Dakota did not attain the average March 1st GDD value for the sites in Georgia and Texas until June 13th and attained the average April 1st GDD value for Georgia and Texas on July 8th. Results for the New Hampshire and Indiana stations were intermediate between the extreme northern and southern sites. This suggests that timing of leaf-out may differ by two months between the southernmost and northernmost sites included in this study. However, trees exposed to greater chilling during winter may require less warming to initiate bud burst (Polgar and Primack 2011). Lechowicz (1984) reported that Quma in northern Minnesota had initiated leaf expansion and Quma and Quve in northern Ohio and *Q. rubra* in southern Quebec had fully formed leaves by mid-May. Hence, leaf-out at these sites was one month earlier than expected based on a simple GDD analysis.

Given this analysis of phenological information, the similar phenology of growth–climate correlations among the four oak species was unexpected. For all four species growing on sites that span 21° latitude, the initiation of strong, spatially consistent cor-

relations with temperature was in May. There was little difference in the phenology of significant temperature correlations between Qust at sites in Texas and Quma at the sites in southern Canada. For all four oak species, MxT during the period from May through July was the seasonal temperature variable most strongly correlated with radial growth. The initiation of significant correlations with *P* began earlier at the southernmost Qust sites than at more northern sites. However, water can be stored in the soil for later use by trees and these correlations may be less tightly linked to tree leaf-out phenology.

Oak growth responses to temperature may be linked more to water balance than to direct temperature effects. For all four oak species included in the present study, the correlation with MxT was stronger than the correlation with mean *T*. Similar results were reported for *Q. alba* (LeBlanc and Terrell 2009) and *Q. rubra* (LeBlanc and Terrell 2011). This suggests that daytime temperature, when leaf stomatal conductance is greatest, has stronger influence than nighttime temperature, when stomatal conductance would be minimal (Voicu et al 2008). Well-replicated correlations with MxT occurred only during months when leaves were present on trees. In almost all cases, negative correlations with MxT variables were paired with positive correlations with *P* during the same months. Finally, for three of the four species, mean significant correlations with MJJ *P* were stronger than correlations with MJJ MxT. Taken together, these results indicate that the negative relationship between temperature and radial growth is likely mediated by water balance. This has been recognized by others who have studied oak growth–climate correlations (Fritts 1962; Estes 1970). This is also consistent with results of a band dendrometer study of oak radial growth showing that oak radial growth decreased when soil moisture decreased and depth to water table increased (Robertson 1992).

There is a steep gradient of decreasing precipitation from the eastern deciduous forest region east of the Mississippi River to the prairie region of the Great Plains (Court 1974). In addition, year-to-year variation in precipitation is greater in the Great Plains than in the eastern region of North America. Lower summer precipitation in this region is correlated with higher summer temperature (Zhao and Khalil 1993), which would drive higher evaporation rate. Finally, drought duration is generally greater in the interior region of North America than in locations closer to the coast (Karl 1983). This latitudinal variation in climate between central and eastern North America is a likely reason for regional variation in the percentage of sites where oak radial growth was significantly correlated with climate variables. Growth of Qust and Quve was negatively correlated with MxT and positively correlated with *P* at a higher percentage of sites in the western region than in the eastern region for both species. This spatial pattern of variation also indicates that these growth–climate correlations are mediated by site water balance.

The observation that radial growth of Qust growing on the southernmost sites in the Great Plains was more strongly correlated with MJJ MxT than with MJJ *P* suggests that high daytime temperature might act directly to reduce growth. These sites have the hottest and driest climate of any sites included in this analysis (Court 1974). High summer temperature and limited soil water for evaporative cooling have been shown to cause foliar damage and reduced photosynthetic capacity for extended periods of time (Hamerlynck and Knapp 1996; Teskey et al. 2014). Alternatively, extreme rainfall events at southern Texas sites associated with occasional hurricanes could have degraded the strength of correlations with precipitation. In either case, this observed difference in Qust correlations between MJJ MxT and *P* was relatively small.

In contrast to the consistency of correlations with temperature, there was greater interspecific and regional variation in the phenology of correlations with precipitation. Precipitation variables for months prior to the growing season were more strongly and consistently correlated with Qust radial growth at sites in the

southern Great Plains region than with other oak species and regions. LeBlanc and Terrell (2009) also found that *Q. alba* radial growth was positively correlated with precipitation during prior autumn, winter, and spring at more sites in the western part of the species range, especially Iowa, Illinois, and Missouri, than in the eastern part. This analysis of *Q. alba* included sites distributed across the same wide longitudinal climate gradient as the sites sampled for the present study. The fact that correlations for a single species exhibited a pattern of stronger correlations with dormant-season precipitation at western sites, similar to the pattern observed for Qust, suggests that the latter is not just an artifact of interspecific differences among the four oak species described in this paper.

Correlations between Qust growth and precipitation during the dormant season were not as spatially replicated as correlations with precipitation during the early growing season. This variability of correlations with dormant-season precipitation among spatially proximate sites suggests a role for site-related factors. Oak species in the eastern deciduous forest are more common on drier, well-drained soils typically found on upper ridge slopes (Burns and Honkala 1990). These sites often have shallower soils overlying bedrock. Soil water holding capacity on upper ridge slopes would be limited; with little storage capacity, tree growth depends mainly on precipitation during the growing season. Hence, few Quve and Qupr sites had correlations with precipitation prior to leaf-out in May–June. In the Great Plains and adjacent states, oaks are more common on sites with deeper soils, fractured bedrock, and locations near rivers, where soil water holding capacity is greater (Burns and Honkala 1990; Anderson and Bowles 1999). Soils in eastern Texas, Oklahoma, Kansas, Nebraska, and Iowa have greater available soil water capacity than most areas of the deciduous forest east of the Mississippi River (Miller and White 1998). Hence, many sites where Qust was sampled on the Great Plains likely had soils that could retain dormant-season precipitation for later use after leaf-out. However, observations during tree core sampling indicated that some Qust sites had shallow soils overlying bedrock where soil water capacity might be limited. This may explain why significant correlations with dormant-season precipitation variables were observed at fewer Qust sites compared with correlations with growing-season precipitation variables.

If stored soil water from dormant-season precipitation supports Qust radial growth after leaf-out, we might predict that correlations would be found with precipitation that fell in any dormant-season month, recharging the soil water reservoir. Among those sites where a correlation with dormant-season precipitation was observed, 26 of 39 sites had significant correlations with precipitation that fell in two or more months from prior November to April. However, there was no pattern regarding which dormant-season months had significant correlations, consistent with this prediction.

It should also be noted that positive correlations with dormant-season *P* did not match up with coincident negative correlations with MxT, as was the case with correlations during the growing season. Although water can be stored in the soil for later use after leaf-out, heat cannot. Leafless trees do not transpire during the dormant season and there is little direct evaporation of water from the soil reservoir. Hence, dormant-season temperature would have minimal direct influence on site water balance.

Radial growth of Quma on riparian sites in the northern Great Plains was correlated with May *P* at more sites than with June *P*. In contrast, June MxT was correlated with Quma growth at more sites than May MxT. This suggests that stored water from precipitation prior to leaf-out supports radial growth after leaf-out. Deep-rooted oaks near riparian zones might access stored water from the upstream watershed.

The spatially replicated correlations between oak radial growth and September MxT found in this study were not observed in

regional studies of growth–climate associations for *Q. alba* or *Q. rubra* (LeBlanc and Terrell 2009, 2011). The September MxT correlation was also not predicted based on biology of oak species and is not consistent with ecological explanations. The few band dendrometer studies that have been performed with oak species have all indicated that radial expansion is complete by mid-August (Day and Monk 1977; Jackson 1952; Robertson 1992). In both the current study (Figs. 3 and 4) and in LeBlanc and Terrell (2009, 2011), the strongest and most spatially replicated significant negative correlations between radial growth and MxT variables were paired with positive correlations with concurrent precipitation. Given the interplay of temperature, evaporative demand, water availability, transpiration, and CO₂ uptake, this pattern has a clear causal mechanism. However, correlations between radial growth and September MxT observed in this study were not matched with positive correlations with concurrent precipitation. If the correlations with September MxT reflect a real effect, it would have to be a direct effect that does not involve water balance. However, temperature in September is not as extreme (high or low) as temperatures in months before or after September. Also, significant correlations with September MxT were observed for Qust at southern sites and for Qupr at more northern latitudes, indicating that this is not a direct effect mediated by length of growing season. Hence, biological and ecological explanations for this correlation seem less plausible than the alternative that correlations with September temperature are a statistical artifact of multicollinearity among climate variables, as described earlier.

The growth–climate relationships identified in this study are broadly consistent with associations reported by others for individual sites or subregions. Similar analyses of the geographic variation in *Q. alba* growth–climate associations in eastern North America (Goldblum 2010; LeBlanc and Terrell 2009) arrived at virtually identical results as those described here. A multispecies regional dendroclimatic analysis of hardwood species in eastern North America also found very similar phenological patterns of growth–climate correlations with temperature and precipitation for four oak species (Martin-Benito and Pederson 2015). Speer et al. (2009) found that growth–climate correlations for five oak species in the southern Appalachian Mountains region were strongest during months of the current growing season, especially June. Their results also indicated that scarlet oak (*Quercus coccinea* Muenchh.) can be added to the list of oak species that have similar growth–climate associations. Speer et al. (2009) found significant correlations between radial growth and Palmer drought severity index (PDSI) for August through November, unlike our results that indicate few correlations after July. These correlations with late-season PDSI are likely the result of strong temporal autocorrelation in PDSI among successive months (LeBlanc and Terrell 2009) and not real relationships between growth and climate during these months. Because the analyses presented here focused on the monthly phenology of correlations, we chose to present correlations with precipitation and temperature variables rather than PDSI. Speer et al. (2009) also found significant correlations with current-September temperature. Six of 13 sites where we observed correlation with September MxT that could not be attributed to multicollinearity were located in the same southern Appalachian Mountain region that they studied. Hence, Speer et al. (2009) used the same state climate division weather data that we used in our study, so this similarity of results does not constitute an independent replication of these correlations.

Friedrichs et al. (2008) described patterns of growth–climate correlations for two species of oak in Germany. Similar to our results, correlations with precipitation were stronger and more spatially replicated than correlations with temperature. Some of the strongest correlations were with June and early growing season precipitation. Correlations for one of the two oak species studied were restricted to precipitation during the growing season, whereas growth of the other oak species was correlated with

precipitation in months prior to the growing season, similar to our results for Qust. Results from this study differed from ours in that there were very few significant correlations with temperature and those few correlations were positive. The sites included in the German study were located in a relatively small geographic region but included greater variation in elevation and site characteristics. Also, the climate regime in western Europe differs from that in eastern North America. These environmental differences likely explain why they did not find many negative correlations with temperature. Nonetheless, climate in the early growing season had the strongest influence on growth of oak species in both western Europe and eastern North America.

Anning et al. (2013) integrated dendroecological analysis with a geospatial model of topography and edaphic features to identify the influence of local site conditions on growth responses of *Q. alba* to climate in southern Ohio. Climate variables for current-year June were most strongly correlated with oak radial growth, consistent with results reported here. However, radial growth was greater and growth–climate correlations were weaker on mesic sites than on xeric sites. This small-scale study is consistent with the phenology of correlations in our results and provides a plausible explanation for the variation in strength of correlations among proximate sites located in the same state climate division.

The results of the study presented here are also broadly consistent with those from an earlier regional analysis of *Q. alba* and Quve growth–climate relationships by Estes (1970). This study only evaluated correlations with precipitation but also found that the strongest correlations were with precipitation during the months of June–July, similar to results presented in this analysis.

The results reported here and by LeBlanc and Terrell (2009, 2011) support the hypothesis presented by LeBlanc and Terrell (2011) that growth of temperate zone, deciduous, ring-porous hardwood species should be most strongly correlated with climate during the early growing season. Tree species with preformed apical growth produce most of the annual growth increment in the first half of the growing season (Zimmerman and Brown 1971). Once rapid apical growth has ceased, radial growth also slows to low levels. Photosynthate no longer being used to support apical and radial growth is shifted to other sinks, including bud formation, root growth, and storage. Temperate zone ring-porous tree species must produce large earlywood vessels prior to leaf-out to replace hydraulic conductivity lost due to freeze-induced cavitation of vessels (Wang et al. 1992). Production of earlywood vessels prior to leaf-out in spring is supported by stored carbon. However, the results presented here and by LeBlanc and Terrell (2009, 2011) do not support the hypothesis that climate during prior autumn has a strong influence on radial growth of oak during the following growing season. Correlations with prior late-summer and autumn climate variables were not spatially well replicated for any of the four oak species analyzed, or for *Q. alba* (LeBlanc and Terrell 2009) or *Q. rubra* (LeBlanc and Terrell 2011). This suggests that carbon storage to support essential production of earlywood vessels prior to leaf-out is not restricted to just a few months at the end of the prior growing season. Because more than 90% of water transport in temperate zone ring-porous tree species is through the large earlywood vessels produced each year (Ellmore and Ewers 1986), it would be extremely maladaptive to allow short-term fluctuations in climate conditions to strongly influence the carbon reserves needed to support production of these vessels.

Our results support the conclusion of Cook et al. (2001) and Graumlich (1993) that phylogenetic influences are more important determiners of growth–climate relationships than site environmental factors. However, these prior studies include a greater diversity of tree species, including conifers and hardwoods with diffuse-porous wood anatomy. The similarity of growth–climate relationships among the four oak species included in the present study and similarities with *Q. alba* and *Q. rubra* (LeBlanc and Terrell 2009, 2011), in spite of strong environmental gradients, is evi-



dence for a strong influence of phylogeny. All of these oak species are deciduous, with determinate apical growth pattern and ring-porous wood anatomy. These shared traits result in similar phenology of cambium initiation, leaf-out, and carbon allocation, as described by LeBlanc and Terrell (2011), which in turn is reflected in similar phenology of growth–climate associations. These results support the hypothesis described by LeBlanc and Terrell (2011) that deciduous trees with ring-porous wood anatomy constitute a “functional group” that should have similar growth–climate relationships. A more rigorous test of this hypothesis would be a study of growth–climate relationships for deciduous, ring-porous tree species that are not in the genus *Quercus* or the family *Fagaceae*. Such an analysis could evaluate the relative importance of function (anatomy and physiology) versus phylogenetic relationships.

Although the main conclusion of this study and those of LeBlanc and Terrell (2009, 2011) is that oak species have similar growth–climate responses, there is also evidence that environmental gradients exert influence. Growth–climate correlations of *Q. alba* were stronger and observed at more sites in the western part of the species range compared with eastern sites (LeBlanc and Terrell 2009). Similar regional differences were observed for Quist and Quve in the study presented here. Strong associations were found between Quist radial growth and precipitation prior to the growing season but not for the other three oak species. We have suggested here that many of these differences are linked to different dynamics of site water balance. A wetter climate with more regular precipitation east of the Appalachian Mountains would reduce strength of correlations with variables that act via site water balance. Deeper soils at sites in the Great Plains allow for water storage and result in correlations between radial growth and precipitation that falls months before the trees leaf-out. Warmer climates result in more rapid depletion of stored soil water after leaf-out and increase strength of correlations with growing-season precipitation. While phylogeny may be the primary determinant of which climate variables are correlated with tree growth, environmental conditions likely influence the strength and spatial consistency of these correlations across local gradients.

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