

Temporal aspects of *Quercus rubra* decline and relationship to climate in the Ozark and Ouachita Mountains, Arkansas

L.J. Haavik, D.W. Stahle, and F.M. Stephen

Abstract: Extreme climate events are frequently important factors associated with episodes of forest decline. A recent oak decline event and concurrent outbreak of a native wood-boring beetle, the red oak borer (*Enaphalodes rufulus* (Haldeman)), occurred throughout Arkansas Ozark and Ouachita Mountains. To investigate the role of drought and stand maturity on northern red oak (*Quercus rubra* L.) decline, we analyzed tree-ring growth patterns and their relationships to climate from 815 live and 161 recently dead *Q. rubra*. While younger *Q. rubra* exhibited faster growth rates and stronger climate relationships than older *Q. rubra*, some individuals within all stands that originated >60 years ago were susceptible to growth decline or mortality. A significant growth interaction occurred among the three age classes identified where currently healthy *Q. rubra* were initially growing at slower decadal rates than currently declining or recently dead *Q. rubra* and later transitioned to higher growth rates than the others. These differences appear to be related to carbon allocation patterns towards rapid aboveground and (or) belowground growth early in development that led to later decline and (or) mortality. Decline in growth and weakening tree growth – climate relationships appeared to be initiated by an unusually severe and sustained drought in the early 1950s.

Résumé : Les conditions climatiques extrêmes se retrouvent souvent parmi les principaux facteurs associés aux épisodes de dépérissement des forêts. Un épisode récent de dépérissement du chêne et une épidémie simultanée du grand longicorne du chêne rouge (*Enaphalodes rufulus* (Haldeman)), un cérambycidé indigène, sont survenus dans les monts Ozark et Ouachita en Arkansas. Pour étudier le rôle de la sécheresse et de la maturité des peuplements sur le dépérissement du chêne rouge (*Quercus rubra* L.), nous avons analysé les patrons de croissance des cernes annuels et leurs relations avec le climat chez 815 tiges vivantes et 161 tiges mortes récemment de *Q. rubra*. Alors que la croissance des jeunes *Q. rubra* était plus rapide et plus étroitement reliée au climat que celle des plus vieux *Q. rubra*, certains individus dans tous les peuplements qui avaient plus de 60 ans étaient sujets à une diminution de croissance ou à la mort. Parmi les trois classes d'âge identifiées, il y avait une interaction significative dans le cas de la croissance : les *Q. rubra* présentement en santé ont initialement eu un taux de croissance décennal plus faible que les *Q. rubra* actuellement dépérissants ou morts récemment et ont par la suite connu un taux de croissance plus élevé que les autres. Ces différences semblent être reliées aux patrons d'allocation du carbone vers les zones aériennes ou souterraines de croissance rapide tôt dans le développement, ce qui a plus tard entraîné le dépérissement ou à la mort. Le déclin de la croissance et l'affaiblissement des relations entre le climat et la croissance des arbres ont semblé être initiés par une sécheresse exceptionnellement sévère et prolongée au début des années 1950.

[Traduit par la Rédaction]

Introduction

Climate extremes have been linked to many forest decline events. Abnormally cold winters and storm damage were found in association with red spruce (*Picea rubens* Sarg.) decline (Johnson et al. 1988), while warm temperatures and low precipitation were found in relation to paper birch (*Betula papyrifera* Marsh.) decline (Jones et al. 1993). Drought has been implicated in several oak decline events throughout the eastern United States (Kessler 1992) as well as in the Ozarks (Jenkins and Pallardy 1995).

While slight to moderate drought may be favorable for carbon allocation to tree resistance against secondary invaders by reducing growth rates proportionately more than photosynthesis, sustained drought can seriously deplete carbohydrate reserves (Waring 1987). This may be a primary mechanism of mortality during oak decline events (Staley 1965). Age is also linked to this phenomenon in that decline is a natural process that becomes more likely as trees reach overmaturity (Mueller-Dombois 1987) and physiological resistance to biotic and abiotic environmental stress deteriorates (Kozłowski 1969).

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In the late 1990s and early 2000s, an oak decline event affected over one third of the 930 000 ha of timber land in Arkansas, Missouri, and Oklahoma (Starkey et al. 2004). Forest history was undoubtedly linked to this decline. Stands became crowded, even-aged, and overmature as a result of clearcutting in the early 1900s and fire suppression throughout the remainder of the century (Strausberg and Hough 1997). Summer drought in 1998–2001 was also identified as a probable factor in this widespread oak mortality event (Starkey et al. 2004), although no empirical evidence exists to support this theory. Apparently concurrent with this oak decline event was an eruptive outbreak of a unique secondary invader, the red oak borer (*Enaphalodes rufulus* (Haldeman)) (Stephen et al. 2001). This wood-boring beetle was not previously known as an eruptive species where large populations were evidenced by densities of fewer than 10 beetles per tree (Hay 1974) compared with hundreds found per tree during this recent outbreak (Fierke et al. 2005).

Temporal study of tree growth patterns and radial growth–climate relationships may provide insight into the role of drought in general, the importance of specific drought events and stand maturity in this recent oak decline event, and *E. rufulus* outbreak. Specific objectives of this study were to (i) determine the general timing of northern red oak (*Quercus rubra* L.) growth decline throughout the Ozark and Ouachita Mountains of Arkansas by examining tree-ring chronologies of currently healthy, currently declining, and recently dead trees, (ii) identify and describe any age-related differences in growth decline and growth relationships with climate, and (iii) determine whether *Q. rubra* growth relationships with climate change over time and, if so, whether these changing relationships differ between younger and older *Q. rubra*. We predict that older trees had slower growth rates and a diminished response to climate compared with younger trees, although variability in tree age was likely minimal as a result of forest history and the presence of even-aged stands. We predict that the timing of *Q. rubra* growth decline occurred before the 1998–2001 drought and corresponded to a weakening climate relationship and growing populations of *E. rufulus*.

Materials and methods

Study sites and climate

We searched for study sites with a Geographic Information System (GIS) developed within Environmental Systems Research Institute's (ESRI) ArcGIS 9.2 software using data layers downloaded from GeoStor, run by the Arkansas Geographic Information Office, the University of Arkansas' Center for Advanced Spatial Technology, and the USDA Forest Service Web sites. Potential sites were located using the following criteria: oak–hickory- or shortleaf pine–oak-dominant forest type according to the Southern Forest Inventory and Analysis (USDA Forest Service 2001), comparable topography (ridge tops and adjacent north and south facing slopes), and accessibility by road (within 400 m of nearest road). We selected sites that were as similar as possible in topography and dominant species composition in an attempt to hold these variables constant so that the importance of other variables could be more clearly observed. Generally, we avoided prescribed burn areas, although this was more

difficult in the Ouachita National Forest, as most oak-dominant stands were burned. We visited >100 potential sites located by the GIS and finally selected eight sites, somewhat evenly distributed throughout these National Forests, that exhibited a range of observable *Q. rubra* mortality. Four sites were located within the Ozark National Forest and four were located within the Ouachita National Forest (Table 1).

We collected tree-ring data from three stands at each study site: one on the ridge top and one each on the adjacent south- and north-facing slopes. At one site in the Ouachita National Forest, Fork Mountain, the north-facing slope consisted of ~100% dead *Q. rubra*, so we collected north-facing slope data from a nearby slope, Rattlesnake Mountain, which was ~3 km north of Fork Mountain. We collected increment cores from 35 *Q. rubra* at each stand, or from all live trees present, ~105 trees per study site, and cross sections from ~20 dead standing or fallen *Q. rubra* per site. Overall sample sizes were 815 live and 161 *Q. rubra* that died between 1990 and 2008 (Haavik and Stephen 2010a). We extracted one increment core per live tree on the west-facing side of the bole (parallel to the slope) at breast height. This direction was specified to avoid capture of any reaction wood and to maintain consistency of sampling among trees growing on various aspects and at various sites. We cut cross sections from fallen and standing dead trees at approximately breast height and brought them back to the laboratory for processing along with the increment cores.

Climate in the Ozark–Ouachita region is temperate with hot summers and mild winters. Mean January temperature is 4 °C, mean August temperature is 27 °C, and the annual mean is 16 °C. Most precipitation occurs during spring and fall, totaling 124 cm in the Ozark Mountains and 150 cm in the Ouachita Mountains (National Climatic Data Center 2009). Rock formations of limestone, sandstone, and shale comprise much of the Ozark Plateau, which is characterized by deep valleys, steep ledges, and cliffs with elevations up to 750 m with slopes facing all cardinal directions (Adamski et al. 1995). The Ouachita Mountains are oriented such that ridges run east to west with maximum elevations reaching 790 m where upper slopes are steep, gradually leveling off at lower elevations into U-shaped valleys (J.M. Guldin, unpublished observations). Soils in both forests are generally rocky, acidic, and clay-rich with low organic matter content (Adamski et al. 1995).

Chronology development

We mounted cores and sanded them along with dead tree cross sections with progressively finer sandpaper beginning with 36 grit and ending with 600 grit. We then cross-dated all cores and cross sections according to standard techniques (Douglass 1941) using *Q. rubra* master chronologies developed individually by skeleton plots for each of the eight study sites. We measured individual tree-ring width time series to the nearest 0.001 mm using a Velmex "TA" system (Velmex Inc. 2008) in conjunction with the "Measure J2X" software program (VoorTech Consulting 2007). We used the computer program COFECHA as a quality control tool to check for errors in measurements and cross-dating (Holmes 1983) and then the program ARSTAN (Cook and Holmes 1986) to standardize individual tree-ring series. Mean sensitivity and series intercorrelation are reported by site in Ta-

Table 1. Site name (defined by local geography), exact location, number of declining, healthy, and dead tree-ring series per site, mean sensitivity, and interseries correlation of chronologies by site.

Site name	UTM site coordinates*	Declining series n	Healthy series n	Dead series n	Mean sensitivity	Interseries correlation
Ozark National Forest						
Mule Farm	426427, 3960826	54	44	28	0.243	0.645
Red Star	453091, 3970897	69	28	17	0.227	0.635
Cowell	488167, 3967424	59	35	17	0.241	0.674
Stack Rock	507522, 3969035	44	53	19	0.232	0.653
Ouachita National Forest						
Dry Creek Mountain	421005, 3878915	48	54	12	0.284	0.662
Flatside	508658, 3857814	23	76	19	0.241	0.692
Fork Mountain	405103, 3812246	27	42	0	0.262	0.630
Talimena	367539, 3837775	58	42	19	0.265	0.644

*UTM Zone 15N.

ble 1. We selected a linear detrending in ARSTAN because it provided a better fit to the biological growth trends of these trees than the commonly used negative exponential curve. We separated live trees by decline status based on the sign of the linear detrending slope, i.e., positive slopes indicated healthy trees and negative slopes indicated declining trees. The direction of detrending slopes was primarily influenced by growth patterns within the late 1990s and early 2000s where healthy trees experienced a growth release during the recent *E. rufulus* outbreak and declining or recently dead trees experienced a period of suppressed growth during this time (Haavik and Stephen 2010a). In a previous study, we tested whether growth decline was consistent with host suitability for *E. rufulus* as measured by second-year larval survivorship. Second-year larval survivorship was significantly greater within recently dead *Q. rubra* (65%) than within *Q. rubra* designated as declining (50%) and least within those designated as healthy (35%) (Haavik and Stephen 2010a).

In the laboratory with the Velmex "TA" system, we used Duncan's (1989) method to estimate age of trees when cores did not include pith but were no more than 5 years off. If we missed pith by more than 5 years, we returned to field sites and recored trees for better accuracy. For some sampled trees (215), age determination was not possible due to heart rot, carpenter ant galleries, or scars at the pith. To address objectives concerning tree growth and climate relationships, we used residuals of standardized chronologies developed by ARSTAN because residuals remove persistence (Cook 1985). To examine tree growth patterns over time and delineate timing of decline, we used raw ring width chronologies, as our goals were to assess changes in actual tree growth and variables such as tree age that may affect such changes.

Data analyses

Growth models

We conducted tree growth analyses with the statistical package R (R Development Core Team 2008). We assigned each of the 672 tree-ring series into one of three age classes based on tree age in the year 2000. The age classes used were 60–80, 81–100, and >100 years. We developed these age classes based on the relation to the early 1900s logging event where trees included within the oldest age class were likely present at the time of cutting but too small to be eco-

nomically valuable. Those included within the middle age class likely established in the few years before or after cutting and those included within the youngest age class likely established a decade or two after the logging event. We calculated mean cumulative growth every decade from 1901 to 2000 for the oldest age class, from 1921 to 2000 for the middle age class, and from 1941 to 2000 for the youngest age class. We first compared mean decadal growth across all decades among age classes with a one-way ANOVA. We then used three two-way ANOVAs with cumulative growth as the response variable and decline status and decade as descriptor variables to test each tree age class separately. We transformed cumulative growth by the Box–Cox method (Box and Cox 1964) when it did not meet normality assumptions. Means reported were untransformed values, errors were standard errors, and the level of significance was set at $P < 0.05$.

To determine timing of growth decline, we used simple linear regressions of mean ring width chronologies for healthy, declining, and dead *Q. rubra* of two age classes with year as the independent variable. Sample sizes of tree-ring series in the oldest age class were low due to the low frequency of older trees at the study sites (series n ranged from 7 to 15), so we did not model this age class. We used healthy tree chronologies to represent trees not affected by decline in radial growth patterns for comparison with trees that were affected by decline (i.e., declining and recently dead chronologies). Timing of growth decline was designated as the year when healthy and declining or healthy and dead fitted models crossed, calculated separately for each age class. In other words, the time period after fitted models were equal identified the time frame of the general negative growth trend of trees affected by decline compared with that of trees not affected by decline. Parameter estimates and variance explained were not reported for these models, as observations were not independent, i.e., tree growth of the current year was correlated with growth of the previous year and thus violated model assumptions. Our goal was to determine when fitted models, i.e., best fit growth trends, were equal to one another, not to estimate parameters. For all linear models, diagnostics included residual plots, standardized residual plots, normal probability plots, plots of full and partial autocorrelation functions, and the Durbin–Watson test (Durbin

and Watson 1950) to examine influence points and violation of normality and constant variance assumptions.

Climate models

Traditional linear regression methods (Fritts 1976) coupled with Kalman filtering (Kalman 1960; Visser and Molenaar 1988) can help identify climate variables important for tree growth and whether such relationships change over time. The Kalman filter essentially facilitates time-dependent regression analysis and has been used previously to investigate forest declines (Visser and Molenaar 1992; LeBlanc 1993).

We used climate data from the National Oceanic and Atmospheric Administration averaged across Arkansas climate divisions 1, 2, 4, and 5 (Guttman and Quayle 1996). All of our study sites were located within one of these four National Oceanic and Atmospheric Administration divisions and some divisions overlapped both the Ozark and Ouachita Mountains. Divisional data capture region-wide variability in climate, eliminating microclimate issues associated with individual weather stations (Speer et al. 2009). We assessed the climate variables mean monthly temperatures, total monthly precipitation, and mean monthly Palmer drought severity indices (PDSI) (Palmer 1965) as potential explanatory variables in ordinary least squares regression models with residual chronologies as response variables. Residuals of standardized tree-ring chronologies do not contain significant autocorrelation and are thus ideal for ordinary least squares regression (Cook 1985). We tested models and used Akaike's information criterion (AIC) (Akaike 1974), R^2 , and mean square error to select the best model.

To determine time dependence of *Q. rubra* climate response, we applied the Kalman filter (Kalman 1960) separately to healthy, declining, and dead young age class and healthy and declining middle age class residual chronologies with mean July PDSI as the explanatory variable with the program KALMAN obtained from E. Cook, Lamont-Doherty Geological Observatory. We did not apply the Kalman filter to the middle age class dead chronology due to the small sample size (series $n = 11$). The Kalman filter is an iterative procedure that estimates regression coefficients for each time step, e.g., year, and has been adapted for use in dendrochronology (Visser 1986). The model is described in depth in Visser (1986) and Visser and Molenaar (1988). It is written in state-space form:

$$y_t = z_t' \alpha_t + \xi_t$$

$$\alpha_t = \alpha_{t-1} + \eta_t$$

where the time index t runs over 88 successive years (1920–2007) for the middle age class and 78 successive years (1930–2007) for the younger age class. The dependent variable y_t represents a residual tree-ring chronology at year t , standardized to have a zero mean and unit variance. Vector z_t contains the climate variable mean July PDSI, α_t represents the regression coefficients, ξ_t is random error, and η_t is the disturbance. Error ξ_t and disturbance η_t are both assumed to be independent and normally distributed, where ξ_t is assumed to have mean zero and variance σ^2 and η_t is assumed to have mean zero and variance $\sigma^2 Q$. The regression coefficients may vary over time according to a Markovian process, and the temporal variance of each coefficient are the diagonal ele-

ments of a covariance matrix Q . The Kalman filter first produces maximum likelihood estimates of these diagonal elements of Q , then iteratively estimates regression coefficients for the tree growth – climate relationship from the beginning of the time period to the end, year by year, and finally smoothes these year-by-year estimates for examination of temporal trends. To determine if time dependence was significant, we evaluated the time-dependent R^2 , compared it with the constant model R^2 , and compared the AIC statistics for both of these models. If the AIC statistic was smaller for the time-dependent model and the 95% confidence interval did not include zero, then we considered time dependence as significant.

Results

Growth models

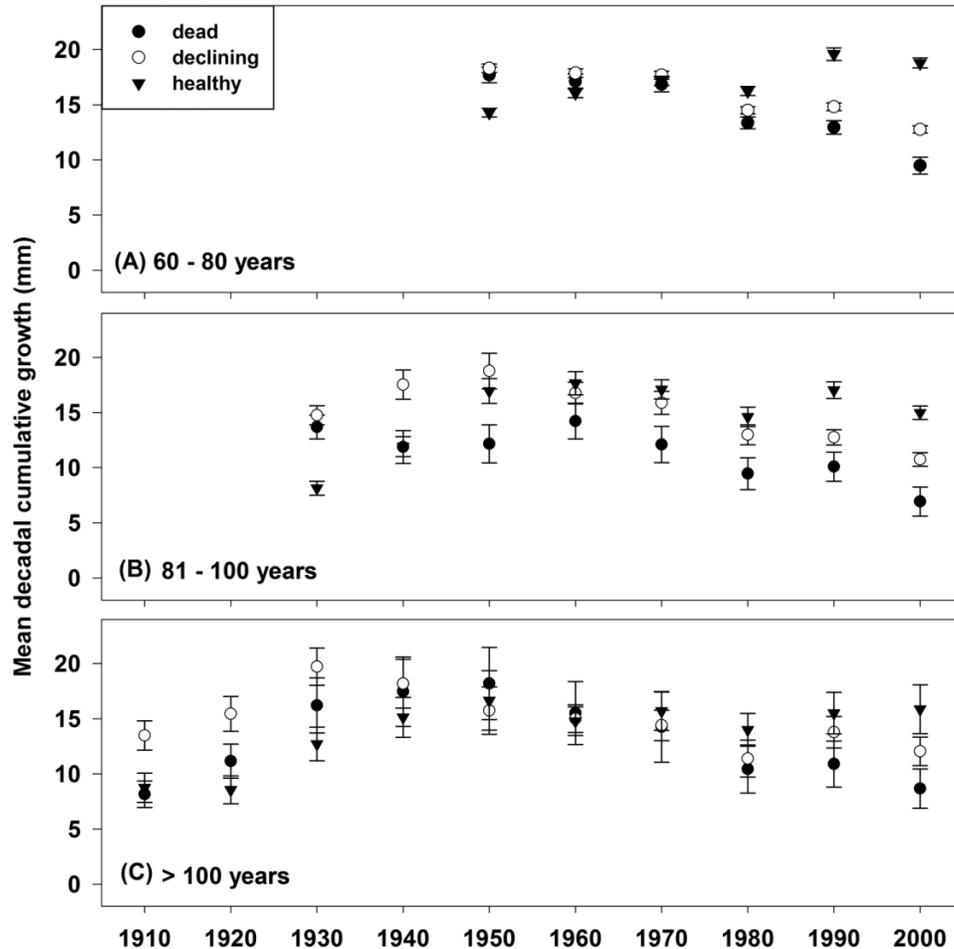
Age varied among *Q. rubra* sampled throughout the Ozark and Ouachita Mountains, although the majority of trees sampled, over 80%, belonged to the youngest age class. Mean decadal cumulative growth differed among the three age classes during the common period ($P < 0.0001$, 1941–2000) where the youngest age class (60–80 years in 2000) had greater mean decadal growth than both the middle age class (81–100 years in 2000) and older age class (>100 years in 2000), which were no different from one another. Mean decadal cumulative growth averaged across all decades was 15.86 ± 0.61 mm for the youngest age class and 13.55 ± 0.51 mm for the middle and older age classes combined. Mean decadal growth modeled separately for each age class revealed a significant interaction effect between decade and tree decline status for all three models where healthy trees had lower mean decadal growth in earlier decades and higher mean decadal growth in more recent decades compared with declining and recently dead trees ($P < 0.0001$) (Fig. 1).

To determine timing of growth decline separately for the youngest and middle age classes, we modeled long-term growth by least squares linear regression. We designated healthy trees as unaffected by growth decline and then fit linear models to healthy ring width chronologies and compared them with linear models of declining and recently dead ring width chronologies. We designated onset of decline as the year when the fitted models were equal and thereafter the declining or recently dead chronology fitted models were decreasing beneath the healthy chronology's growth trend. For the youngest age class, fitted models of the dead chronology and declining chronology equaled that of the healthy chronology in 1959 and 1967, respectively (Fig. 2A). For the middle age class, fitted models of the dead chronology and declining chronology equaled that of the healthy chronology in 1938 and 1961, respectively (Fig. 2B).

Climate models

For climate variable selection, we used Pearson correlations of residual chronologies with monthly mean temperature and total precipitation from March of the previous year ($t - 1$) through November of the current year (t). Total monthly precipitation was significantly correlated with all chronologies for May and June of the current year. Mean monthly temperatures in June, July, August, and September of the current year were also significantly correlated with all

Fig. 1. Mean cumulative decadal growth of dead, declining, and healthy *Quercus rubra* pooled across all sites that were (A) 60–80 years in 2000, (B) 81–100 years in 2000, and (C) >100 years in 2000. Each age class represents a separate ANOVA. Means are untransformed values and error bars represent 1 SE of the mean. Sample sizes: (A) 194 healthy, 250 declining, and 98 dead, (B) 41 healthy, 42 declining, and 12 dead, and (C) 13 healthy, 15 declining, and 7 dead.



chronologies. For modeling, we used mean monthly PDSI to integrate the importance of precipitation and temperature for June, July, and August of the current year. Mean July PDSI was the best explanatory variable of all residual chronologies where the fitted model was significant with the lowest AIC and mean square error and highest R^2 (Table 2). Variance explained by the time-independent regression model varied among chronologies where the younger age class had a stronger relationship with climate than the middle age class (Table 2). No time-independent models explained more than 36% of the variation within the chronologies.

There was significant time dependence in the climate relationship as indicated by Kalman filtering for four of the five chronologies (Fig. 3). Healthy trees in the middle age class did not exhibit a significant time-dependent climate response according to AIC scores for the constant versus the time-dependent model (Fig. 3D). This chronology also had a lower time-independent R^2 than all other chronologies examined (Table 2). For the remaining chronologies, variance explained by July PDSI improved by 3%–7% with the time-dependent model where the younger age class had a stronger time-dependent climate relationship than declining trees within the

middle age class (Table 2). Weakening climate responses occurred throughout a similar time period for these chronologies, between 1950 and 1980, with rapid weakening between 1960 and 1980 (Figs. 3A–3C and 3E). Soon after 1980, models were no longer significant, as confidence intervals included zero.

Discussion

Age, growth, and decline

Healthy trees in all three age classes grew at slower rates than declining and (or) recently dead trees during their first few decades and yet became the most vigorous throughout recent decades (Fig. 1). This growth interaction between time and healthy versus declining individuals was a common theme in other oak decline events (Tainter et al. 1990; Biocca et al. 1993; Jenkins and Pallardy 1995). Three possible explanations for this phenomenon have been discussed in the above literature: carbon allocation, tree age, and microsite conditions. Microsites may exist that favor or inhibit resource acquisition, and properties of these sites may change over time due to stand processes such as gap formation. Their in-

Fig. 2. Mean ring width chronologies of dead, declining, and healthy *Quercus rubra* pooled across all sites that were (A) 60–80 years in 2000, (B) 81–100 years in 2000, and (C) mean regional July PDSI from 1920 to 2007. Regression models were fitted separately for each chronology (fitted models not plotted) with year as the independent variable. Fitted models of declining chronologies were equal to healthy chronologies in (A) 1967 and (B) 1938. Sample sizes: (A) 236 healthy, 311 declining, and 107 dead and (B) 40 healthy, 40 declining, and 11 dead.

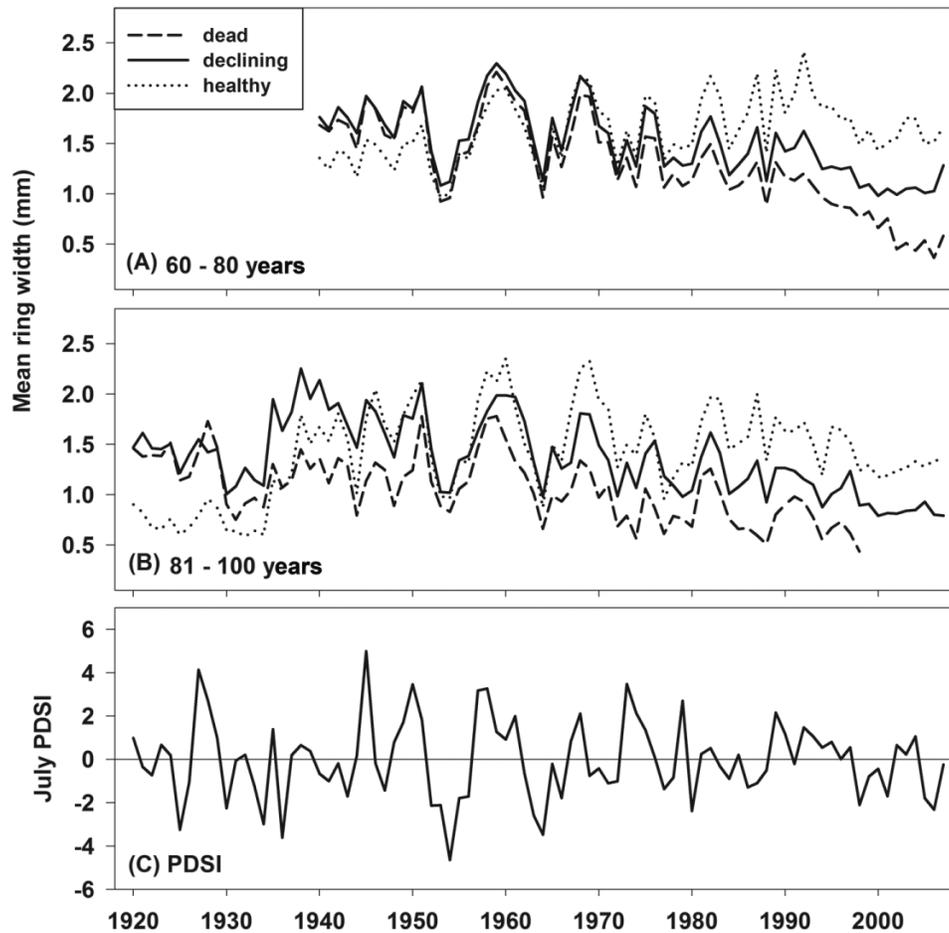


Table 2. Time-independent regression model parameter estimates and variance explained by both time-independent and time-dependent models of each chronology.

Chronology	Intercept	July PDSI \pm SE	<i>P</i>	Time-independent R^2	Time-dependent R^2
Healthy (60–80 years)	0.988	0.050 \pm 0.008	<0.0001	0.333	0.404
Declining (60–80 years)	0.985	0.050 \pm 0.008	<0.0001	0.358	0.410
Dead (60–80 years)	0.970	0.052 \pm 0.008	<0.0001	0.336	0.376
Healthy (81–100 years)	0.990	0.056 \pm 0.010	<0.0001	0.279	na
Declining (81–100 years)	0.988	0.050 \pm 0.008	<0.0001	0.308	0.330

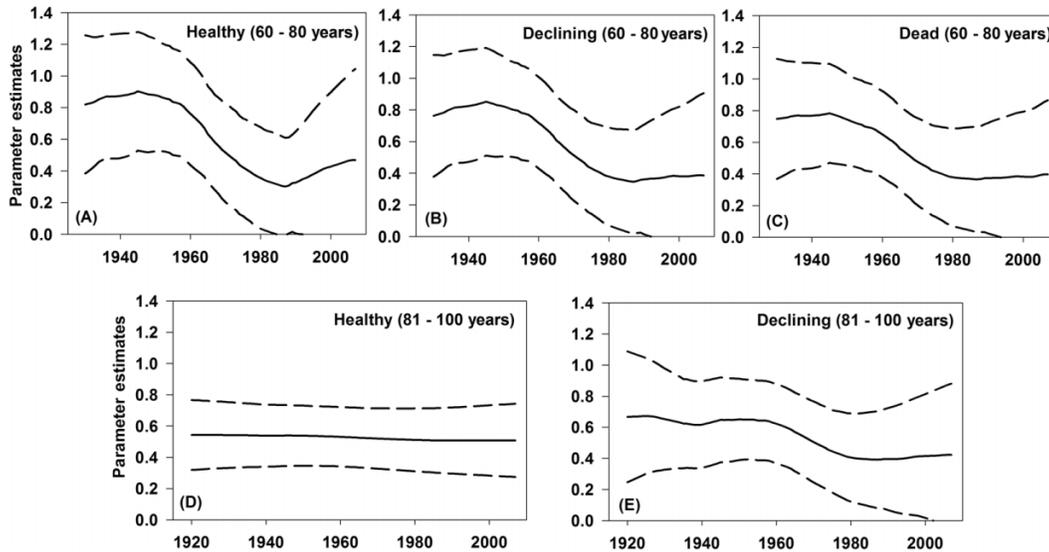
fluence would be difficult to decipher from the results of this study without further data collection and analysis within sites.

High radial growth rates in earlier years suggest that recently dead and declining trees were superior competitors early on. This competitive edge may have been due to proportionately greater amounts of carbon allocated to growth compared with currently healthy individuals. Carbon invested directly into radial growth, or indirectly through increased resource acquisition from energy investment in an expansive root system, likely resulted in fewer stored reserves for use during drought events and later for resistance to *E. rufulus*

attack in the late 1990s and early 2000s. Trees with large root systems may have been more susceptible to root rot fungi, *Armillaria* spp., (Tainter et al. 1990), a stressor that would have affected water relations and competitive status (Kozłowski 1969).

Advancing age is often associated with a plateau or decline in radial growth in most tree species (Kozłowski 1969), which may be related to changes in source–sink relationships or physiological decline in resource use efficiency (Ryan et al. 1997). Consistent with this, the youngest age class exhibited greater mean decadal growth rates averaged across all common decades than the middle and older age classes and

Fig. 3. Time-dependent parameter estimates (solid lines) after Kalman filtering and approximate 95% confidence intervals (broken lines) for the relationship between mean regional July PDSI and the younger age class of (A) healthy, (B) declining, and (C) dead and the middle age class of (D) healthy and (E) declining *Quercus rubra*. Sample sizes are the same as in Fig. 2. Note that models are no longer significant when confidence intervals include zero and that Fig. 3D is not significant at any time.



timing of growth decline was later for the youngest age class. July soil moisture was the best explanatory climate variable for both age classes, although the relationship was stronger within the younger compared with the middle age class (Table 2). Some individuals within each age class were apparently susceptible to decline during the recent mortality event (i.e., dead and declining *Q. rubra*), implying that a threshold age of susceptibility may have existed such that individuals within all three age classes had surpassed it when the oak mortality event occurred.

Biological age of the stand and of individual trees may have played a role in the timing of growth decline. Onset of growth decline varied in time by tree age class where the youngest trees experienced decline in later decades compared with older individuals (Fig. 2). The decadal growth interaction between recently dead and healthy trees over time occurred at a similar biological age for both age classes, at 20–40 years after pith formation, likely during the stem exclusion stage (Johnson et al. 2002). Canopy positions are established during that stage (Johnson et al. 2002), and as a result of either spatial location disadvantage, poor competitive ability, or both, trees that died in the 1990s and 2000s likely became inferior within the canopy at that time, leading to several decades of suppression prior to mortality.

Growth interaction between currently living, but declining trees and currently healthy trees occurred 6 years earlier for the middle age class than for the younger age class, in 1961 and 1967, respectively (Fig. 2). Biological age at timing of decline overlapped by 10 years between age classes (younger trees were 30–50 years and the others were 40–60 years) and was less likely related to stand structural development than was the healthy versus recently dead tree interaction. Stands may have transitioned to the understory reinitiation stage by this time where competition for resources relaxes due to high mortality throughout the preceding stem exclusion stage (Johnson et al. 2002).

Drought

Severe regional droughts occurred during 1952–1956 and 1963–1964 (Fig. 2C). The 1950s drought is well represented in the regional tree-ring record (Stahle et al. 2007) and has been noted as the worst drought on record for the Ozark–Ouachita region (Dwyer et al. 1995). Trees with low reserves may have become disproportionately weakened during the 1950s drought compared with those with more reserves. Alternatively, the unusually wet period (1957–1961, Fig. 2C) of the same duration as the prior drought may have elicited future drought susceptibility in these *Q. rubra*. The hydraulic framework hypothesis predicts that abnormally wet periods may be responsible for drought susceptibility in later years due to increased carbon investment in leaf area growth rather than root and sapwood growth (McDowell et al. 2008). Declining individuals then did not have the root and (or) sapwood area required to support a now greater leaf area throughout the next drought (1963–1964), at which point shoot dieback likely occurred and their radial growth trajectories fell below those of the currently healthy individuals.

Uncommonly severe drought events that occur within the lifetime of oaks have been proposed as initiators of decline events (Staley 1965). This unusually severe and sustained 1950s drought, a precursor to the onset of growth decline in both age classes (Fig. 2), weakening climate relationships in both age classes (Fig. 3), and increasing populations of *E. rufulus* (Haavik and Stephen 2010b), was likely the initiator of this oak decline event. Other droughts, 1962–1964 and 1998–2001, were also instrumental in further compromising the physiological status of trees already weakened from previous drought and stand competition.

After 1980, time-dependent climate relationships became extremely variable. *Enaphalodes rufulus* densities were increasing rapidly at these sites during this time (Haavik and Stephen 2010b), and the trees' response to this herbivory may have further weakened climate relationships of infested

trees. Borer infestation was also variable among individual trees and stands (Haavik and Stephen 2010a) and may have influenced the observed variable *Q. rubra* – climate relationship during this time.

Consistent with our results, other studies have found weakening tree–climate relationships over time (Visser and Moleenaar 1992; Rozas 2005). Whether the temporally weakening climate response was related to tree age in this study remains unclear. Another study found a weakened climate response of young and mature English oak (*Quercus robur* L.) over time, with no trend among old-growth *Q. robur* (Rozas 2005). The middle age class of currently healthy trees did not exhibit a significant temporal climate response (Fig. 3D), and sample sizes were too small to examine this age class of recently dead trees. Chronologies of declining *Q. rubra* in both age classes exhibited a significant time-dependent climate response during the same time period (Figs. 3B and 3E), suggesting that this phenomenon was independent of tree age.

Conclusions

While younger *Q. rubra* exhibited greater growth rates and stronger climate relationships than older *Q. rubra*, some individuals among each age class were affected by growth decline or mortality during the recent *E. rufulus* outbreak. All age classes (>60 years) appear to include *Q. rubra* of a susceptible age to decline. Differences in growth patterns between *Q. rubra* affected or not affected by decline were likely related to carbon allocation patterns towards rapid aboveground and (or) belowground growth early in development that led to later decline and (or) mortality. Competition during stand structural development may have also rendered some individuals more susceptible to mortality. Decline in growth and weakening tree growth – climate relationships were most likely initiated by an unusually severe and sustained drought in the early 1950s. The combination of stand-level factors involving maturity and competition as well as the stress of multiple drought events probably further weakened *Q. rubra*, which eventually died or experienced severe growth decline following the 1998–2001 drought.

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References

Adamski, J.C., Petersen, J.C., Freiwald, D.A., and Davis, J.V. 1995. Environmental and hydrologic setting of the Ozark plateaus study unit, Arkansas, Kansas, Missouri, and Oklahoma. US Geological Survey, Water-Resources Investigations Report 94-4022, Little Rock, Ark.

Akaike, H. 1974. A new look at the statistical model identification.

IEEE Trans. Automat. Contr. **19**(6): 716–723. doi:10.1109/TAC.1974.1100705.

Biocca, M., Tainter, F.H., Starkey, D.A., Oak, S.W., and Williams, J. G. 1993. The persistence of oak decline in the western North Carolina Nantahala Mountains. *Castanea*, **58**(3): 178–184.

Box, G.E., and Cox, D.R. 1964. An analysis of transformations (with discussion). *J. R. Stat. Soc. B*, **26**: 211–246.

Cook, E.R. 1985. A time series analysis approach to tree ring standardization. Ph.D. dissertation, Graduate College, University of Arizona, Tucson, Az.

Cook, E.R., and Holmes, R.L. 1986. Guide for computer program ARSTAN: chronology development, statistical analysis. Laboratory of TreeRing Research, University of Arizona, Tucson, Az.

Douglass, A.E. 1941. Crossdating in dendrochronology. *J. For.* **44**: 825–831.

Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrydium dacrydioides*). *N.Z. Nat. Sci.* **16**: 31–37.

Durbin, J., and Watson, G.S. 1950. Testing for serial correlation in least squares regression, I. *Biometrika*, **37**(3–4): 409–428. PMID: 14801065.

Dwyer, J.P., Cutter, B.E., and Wetteroff, J.J. 1995. A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. *For. Ecol. Manag.* **75**(1–3): 69–75. doi:10.1016/0378-1127(95)03537-K.

Fierke, M.K., Kinney, D.L., Salisbury, V.B., Crook, D.J., and Stephen, F.M. 2005. Development and comparison of intensive and extensive sampling methods and preliminary within-tree population estimates of red oak borer (Coleoptera: Cerambycidae) in the Ozark Mountains of Arkansas. *Environ. Entomol.* **34**(1): 184–192. doi:10.1603/0046-225X-34.1.184.

Fritts, H.C. 1976. *Tree rings and climate*. The Blackburn Press, Caldwell, N.J.

Guttman, N.B., and Quayle, R.G. 1996. A historical perspective of U. S. climate divisions. *Bull. Am. Meteorol. Soc.* **77**(2): 293–303. doi:10.1175/1520-0477(1996)077<0293:AHPOUC>2.0.CO;2.

Haavik, L.J., and Stephen, F.M. 2010a. Stand and individual tree characteristics associated with *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae) infestations within the Ozark and Ouachita National Forests. *For. Ecol. Manag.* **259**(10): 1938–1945. doi:10.1016/j.foreco.2010.02.005.

Haavik, L.J., and Stephen, F.M. 2010b. Historical dynamics of a native cerambycid, *Enaphalodes rufulus*, in relation to climate in the Ozark and Ouachita Mountains of Arkansas. *Ecol. Entomol.* **35** (6): 673–683. doi:10.1111/j.1365-2311.2010.01225.x.

Hay, C.J. 1974. Survival and mortality of red oak borer larvae on black, scarlet, and northern red oak in eastern Kentucky. *Ann. Entomol. Soc. Am.* **67**: 981–986.

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

Jenkins, M.A., and Pallardy, S.G. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Can. J. For. Res.* **25**(11): 1119–1127. doi:10.1139/x95-124.

Johnson, A.H., Cook, E.R., and Siccama, T.G. 1988. Climate and red spruce growth and decline in the northern Appalachians. *Proc. Natl. Acad. Sci. U.S.A.* **85**(15): 5369–5373. doi:10.1073/pnas.85.15.5369. PMID:16593962.

Johnson, P.S., Shifley, S.R., and Rogers, R. 2002. *The ecology and silviculture of oaks*. CABI Publishing, New York.

Jones, E.A., Reed, D.D., Mroz, G.D., Liechty, H.O., and Cattelino, P. J. 1993. Climate stress as a precursor to forest decline: paper birch in northern Michigan, 1985–1990. *Can. J. For. Res.* **23**(2): 229–233. doi:10.1139/x93-030.

- Kalman, R.E. 1960. A new approach to linear filtering and prediction problems. *Trans. ASME D*, **82**: 35–45.
- Kessler, K.J., Jr. 1992. Oak decline on public lands in the central forest region. U.S. For. Serv. Res. Note NC-362.
- Kozłowski, T.T. 1969. Tree physiology and forest pests. *J. For.* **67**(2): 118–123.
- LeBlanc, D.C. 1993. Temporal and spatial variation of oak growth – climate relationships along a pollution gradient in the midwestern United States. *Can. J. For. Res.* **23**(5): 772–782. doi:10.1139/x93-102.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., and Yezpe, E.A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* **178**(4): 719–739. doi:10.1111/j.1469-8137.2008.02436.x. PMID:18422905.
- Mueller-Dombois, D. 1987. Natural dieback in forests. *Bioscience*, **37** (8): 575–583. doi:10.2307/1310668.
- National Climatic Data Center. 2009. Climatology: eastern Oklahoma/northwest Arkansas. Available from <http://www.srh.noaa.gov/tsa/?n=climo> [accessed 8 December 2009].
- Palmer, W.C. 1965. Meteorological drought. US Weather Bur. Res. Pap. No. 45. US Weather Bureau, Washington, D.C.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rozas, V. 2005. Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. *Ann. For. Sci.* **62**(3): 209–218. doi:10.1051/forest:2005012.
- Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* **27**: 214–262.
- 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. *Can. J. For. Res.* **39**(3): 507–518. doi:10.1139/X08-194.
- Stahle, D.W., Fye, F.K., Cook, E.R., and Griffin, R.D. 2007. Tree-ring reconstructed megadroughts over North America since A.D. 1300. *Clim. Change*, **83**(1–2): 133–149. doi:10.1007/s10584-006-9171-x.
- Staley, J.M. 1965. Decline and mortality of red and scarlet oaks. *For. Sci.* **11**(1): 2–17.
- Starkey, D.A., Oliveria, F., Mangini, A., and Mielke, M. 2004. Oak decline and red oak borer in the interior highlands of Arkansas and Missouri: natural phenomena, severe occurrences. *In* Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. Edited by M.A. Spetich. U.S. For. Serv. Gen. Tech. Rep. SRS-73. pp. 217–222.
- Stephen, F.M., Salisbury, V.B., and Oliveria, F.L. 2001. Red oak borer, *Enaphalodes rufulus* (Coleoptera: Cerambycidae), in the Ozark Mountains of Arkansas, U.S.A.: an unexpected and remarkable forest disturbance. *Integrated Pest Manag. Rev.* **6**(3/4): 247–252. doi:10.1023/A:1025779520102.
- Strausberg, S., and Hough, W.A. 1997. The Ouachita and Ozark – St. Francis National Forests: a history of the lands and USDA Forest Service tenure. U.S. For. Serv. Gen. Tech. Rep. SO-121.
- 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. *Eur. J. For. Pathol.* **20**(2): 95–105. doi:10.1111/j.1439-0329.1990.tb01277.x.
- USDA Forest Service. 2001. Southern forest inventory and analysis: Southern Research Station field guide. USDA Forest Service, Southern Research Station, Asheville, N.C.
- Velmex Inc. 2008. The Velmex “TA” system for research and non-contact measurement analysis. Velmex, Inc., Bloomfield, N.Y.
- Visser, H. 1986. Analysis of tree-ring data using the kalman filter technique. *IAWA Bull.* **7**(4): 289–297.
- Visser, H., and Molenaar, J. 1988. Kalman filter analysis in dendroclimatology. *Biometrics*, **44**(4): 929–940. doi:10.2307/2531724.
- Visser, H., and Molenaar, J. 1992. Estimating trends and stochastic response functions in dendroecology with an application to fir decline. *For. Sci.* **38**(2): 221–234.
- VoorTech Consulting. 2007. MeasureJ2X. VoorTech Consulting, Holderness, N.H.
- Waring, R.H. 1987. Characteristics of trees predisposed to die. *Bioscience*, **37**(8): 569–574. doi:10.2307/1310667.