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Variation in radial growth responses to drought among species, site, and canopy strata

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Abstract Radial growth responses to drought were examined in the tree-ring records of six species growing within two locations of differing land-use history and soil moisture characteristics, and in overstory and understory canopy positions in northern Virginia. Tree species experienced differential ring-width reductions during or immediately following four severe drought periods occurring from 1930 to 1965 and were influenced by climatic variables including annual and summer temperatures, annual precipitation, and annual Palmer Drought Severity Index. Relative growth comparisons averaged across species before and after drought years indicated that understory trees on dry-mesic sites grew 11% faster after drought compared to pre-drought rates while mesic site trees in both canopy positions grew approximately 4% slower. Superposed epoch analysis indicated that *Liriodendron tulipifera* growing on mesic sites experienced greater ring-width reductions associated with drought than co-occurring, more drought-tolerant *Quercus alba* and *Q. velutina*. On dry-mesic sites, *L. tulipifera* also experienced greatly reduced growth as a result of drought but exhibited significant growth increases following individual drought events. *Quercus alba* was the only species that exhibited a consistent, significant ring-width decrease associated with all droughts on dry-mesic sites. In contrast, *Pinus virginiana* was least impacted by drought on dry-mesic sites but was much more impacted by drought on mesic sites, indicating a drought×site interaction for this species. Overstory *Carya glabra* and *Q. alba* experienced larger growth decreases during drought on dry-mesic versus mesic sites. Understory tree growth reductions did not differ between site types but were often significantly larger than overstory responses of the same species on mesic sites. Following drought, most trees exhibited growth reductions lasting 2–3 years, although several species experienced reductions lasting up to 6 years. The results of this study suggest that tree rings represent an important long-term proxy for leaf-level ecophysiological measurements of growth responses to drought periods.

Key words Drought · Dendroecology · Ecophysiology · Temperate oak forests · Superposed epoch analysis

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Introduction

Drought intensity and frequency are considered dominant influences on plant distribution and productivity around the world (Kramer 1983). Drought, defined in this paper as an absence of precipitation for a period of time resulting in a depletion of soil moisture (Kramer and Kozlowski 1979), can affect plant response across all biological levels, from molecular to landscape (Hinckley et al. 1979; Abrams 1990; Newton et al. 1991; Kubiske and Abrams 1994). Researchers over the last half-century have published extensively on the biochemical and physiological effects of drought on plants in agricultural and natural systems (Paleg and Aspinall 1981; Pallardy et al. 1983). However, little is known concerning the impacts of drought across sites with differing site moisture conditions in a region. In one of the few such studies of radial growth responses, Tardif and Bergeron (1997) reported that *Thuja occidentalis* L. (white cedar) growing on xeric sites were more affected by drought than trees from mesic sites. In contrast, a few ecophysiological studies have reported reported greater decreases in net photosynthesis (Kubiske and Abrams 1994) and predawn water potential (Zobel 1974) in mesic-site versus xeric-site species. Thus, species on xeric sites were better able to tolerate drought despite having lower soil moisture compared to mesic sites. There is also a scarcity of information and lack of agreement concerning drought responses of plants in differing light environments, such as individuals in high versus low light sites or in upper versus lower canopy positions. Some studies indicate that shade plants are more sensitive to drought than sun plants, whereas in other studies the reverse has been reported (Gauhl 1979; Abrams 1986; Abrams et al. 1992; Ellsworth and Reich 1992; Abrams and Mostoller 1995). Few studies have examined radial growth responses to drought in trees of differing canopy positions in closed-canopied forests (Liu and Muller 1993; Vose and Swank 1994) on more than one site.

Radial growth responses may be helpful in elucidating tree responses to past droughts because tree rings have long been recognized as indicators of annual climatic information such as precipitation and temperature. For example, early researchers observed drought impacts in many species by the presence of narrow rings produced during years of low moisture availability (Stewart 1913; Douglass 1914; Stickel 1933; Lyon 1936). Tree-ring patterns from arid sites such as the southwestern United States have been shown to be climatically sensitive, or more strongly limited by precipitation (Fritts 1976), whereas ring widths from high altitude trees have been correlated with temperature variables (LeMarche 1982). These examples underscore the principle that the trees most sensitive to climate are found at the climatic limits of their distributions. Variation in tree responsiveness to climatic variables has been reported among species within a site and by individuals of a species between sites (Fritts 1976; Jacobi and Tainter 1988; Graumlich 1993; Villalba et al. 1994; Jenkins and Pallardy 1995; Little et al. 1995).

In general, individual tree growth in closed-canopied temperate forests is limited more by disturbance and competition for light and other resources than by climate (Cleaveland 1980; Phipps 1982). However, trees growing under humid conditions typical of many forests of the eastern United States may still retain a strong climatic signal, especially during drought years when available soil moisture may be limiting to tree growth (Cook and Jacoby 1977; Graumlich 1993; Abrams and Orwig 1995; Parshall 1995). We believe the use of tree rings as ecophysiological proxy measures holds great promise in evaluating drought responses at the scale of individuals, stands, and landscapes. No studies have examined tree-ring records to simultaneously evaluate drought responses across contrasting species, sites, and light regimes. This type of approach will evaluate radial growth responses to drought periods in a manner that is analogous to measuring gas exchange and tissue water parameters during drought. An advantage of tree-ring records is that they may include several centuries of information, whereas field ecophysiological studies generally contain data from only 1 or 2 growing seasons. The radial growth record in each tree represents an ecophysiological record that can be related to past climate and ecological conditions (cf. Sass and Eckstein 1995). Therefore, this study was designed to (1) assess the impact of periodic droughts on radial growth of six temperate tree species growing in two different locations within the study region, (2) determine how drought affects radial growth of trees in different canopy classes, and (3) evaluate the relationship between tree-ring growth and climatic parameters in different species. We hypothesize that drought will have a less pronounced effect on radial growth of trees growing on dry-mesic versus mesic sites. We further predict that responsiveness to drought will be greater in overstory versus understory trees.

Materials and methods

Site characteristics

Fredericksburg and Spotsylvania National Military Park comprises four Civil War Battlefields on approximately 3200 ha of forested land. The area is located 81 km southwest of Washington, D.C., in Spotsylvania County, Virginia (38°12′ N. Lat. and 77°36′ W. Long.). The climate of the area is warm continental with relatively mild winters and hot, humid summers. Mean annual temperatures average 13 °C, while winter and summer daily mean temperatures are 2 °C and 23 °C, respectively (Elder 1985). Precipitation averages 102 cm annually and is typically distributed evenly throughout the growing season. The average frost-free period extends from April 23 to October 17, a total of 178 days (National Park Service 1986). The general topography is gently rolling (slopes $<15\%$) with elevations of 20–130 m above sea level (U. S. Geological Survey 1984). Bedrock of the area consists of a mixture of crystalline rocks, including granite, granite gneiss, and hornblende gneiss of the Paleozoic and Precambrian ages (Robinson et al. 1961).

Two battlefields located approximately 6 km apart and within the Piedmont Plateau physiographic province were examined in this dendroecological study. Soils within Chancellorsville Battlefield (CVB) are predominantly deep, well-drained sandy loams with moderate available water, while soils within Wilderness Battlefield (WB) are primarily moderately well-drained to well-drained loams with high available water (Carter et al. 1971; Elder 1985). *Quercus alba* L. (white oak) was the most abundant overstory species in local forests but was commonly associated with *Liriodendron tulipifera* L. (tulip poplar), *Quercus coccinea* Muenchh. (scarlet oak), *Pinus virginiana* Mill. (Virginia pine), and *Carya* (hickory) species (Orwig and Abrams 1994a).

Sites located in Chancellorsville Battlefield experienced repeated, massive cutting in the early to mid-1800s to fuel a nearby (within 1 km) iron furnace which resulted in coppice forests being described as stunted and scrubby during the late 1800s (Harrison 1990). Currently, these stands contain low basal areas (22–24 m^2/ha), high ericaceous shrub cover (30–55%), and are representative of dry-mesic sites in the region (Orwig and Abrams 1994a). In contrast, Wilderness Battlefield sites experienced less frequent cutting and clearing, contained high basal areas (28–35 m^2/ha) and low shrub cover (6–15%), and are representative of mesic site conditions in the area (Orwig and Abrams 1994a, 1995). Sites also differed in characteristic vegetation as CVB sites had an abundance of *Q. alba* and *Q. coccinea*, and the presence of *Quercus stellata* Wanghen. (post oak) and *Quercus marilandica* Muenchh. (blackjack oak), whereas WB sites contained a higher importance of *Quercus rubra* L. (northern red oak), *Cornus florida* L. (dogwood), and *Fagus grandifolia* Ehrh. (beech). Trees examined in this study were selected from stands that have not been disturbed by humans for at least 70 years since they were acquired by the National Park Service in the 1920s (National Park Service 1986). As a result, these stands have only experienced small-scale localized disturbances during the twentieth century (Orwig and Abrams 1994a, b).

Methods

Increment cores (one per tree) were obtained at breast height (1.4 m) from six species (*P. virginiana*, *L. tulipifera*, *Q. alba*, *Q. velutina* Lam. (black oak), *Carya glabra* (Mill.), Sweet (pignut hickory), and *Nyssa-sylvatica* Marsh. (blackgum) occurring at both WB and CVB sites and in understory (overtopped) and overstory (dominant and codominant)

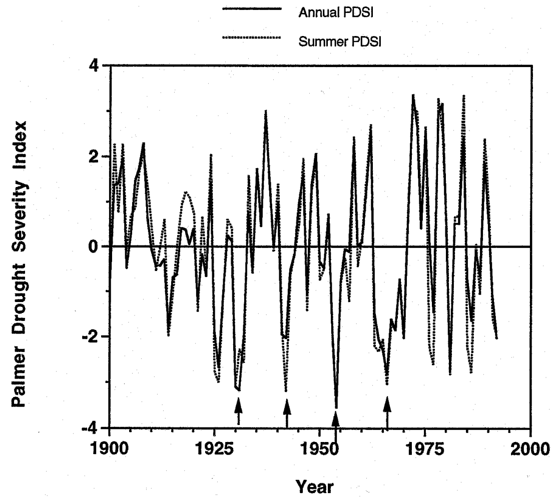


Fig. 1 Annual and summer (April–September) values of the Palmer Drought Severity Index (PDSI) for the time period 1900–1993 in Wilderness and Chancellorsville Battlefields. *Arrows* indicate the four severe drought periods examined in this study

canopy positions. Cores were obtained from two to four different sites within each battlefield for each species-canopy combination to minimize the non-climatic effects of site features not controlled for in this study such as tree size, canopy gaps, and competition from neighbors. Site selection within battlefields was determined by edaphic properties and stand attributes (described above). No understory *P. virginiana* cores of adequate age were obtained due to its extreme shade intolerance (Burns and Honkala 1990).

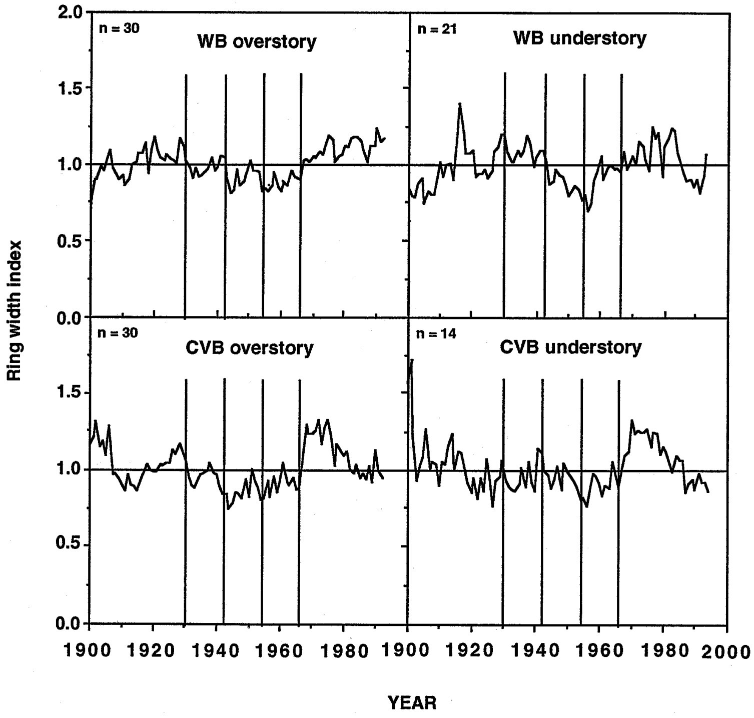
All cores were mounted, sanded, and measured for annual radial growth to the nearest 0.01 mm with a tree-ring scanning system and recorded using the MacDendro computer program (Regents Instruments, Quebec, Canada). Cores were crossdated using pointer years (Fritts 1976). Narrow rings in 1911, 1927, 1932, 1943, 1954, 1967, 1978 and 1988 and particularly wide rings during 1920, 1938, 1970, 1975 and 1990 aided in the crossdating process and indicated that there were no false rings. All cores were examined for release events using sequential 15- or 10- year ring-width means according to Lorimer and Frelich (1989), who defined major sustained releases as a ≥ 100% radial growth increase lasting for at least 15 years and moderate temporary releases as a 50–99% radial growth increase lasting for 10 years. These non-climatic signals could inhibit the detection of drought responses, and therefore cores exhibiting major releases during the period of 1925–1970 were removed from the analysis. Several cores exhibiting a single moderate release event were retained in the analysis due to the lower magnitude and duration of increase and to maintain an adequate sample size for analysis.

Four severe drought years during the twentieth century (1930, 1942, 1954, 1966) were identified using National Park Service (NPS) annual and summer (April - September) precipitation data for the years 1930–1993 and summer values of the Palmer Drought Severity Index (PDSI) for the years 1900–1993 (Palmer 1965; Fig. 1). This index, derived from NPS weather station records, integrates temperature, precipitation, and evapotranspiration into a measure of soil moisture availability that is representative of conditions in the study area. Values normally range from – 4 (extreme drought) to + 4 (extremely wet), while values near zero are considered normal conditions (Palmer 1965). Monthly index values indicate soil moisture availability based on antecedent and current weather data. The four drought periods were selected because they contained the lowest monthly PDSI values in the last 90 years (– 4.3 to – 5.6), and growing season (April - September) precipitation values ranged from 18–46% below the 60-year average of 55.7 cm.

To remove non-climatic, age-related growth trends, a ring-width index (RWI) was created for each core by standardization via linear least squares regression or negative exponential curve fitting and division of each measured width by the value of the fitted line (Fritts and Swetnam 1989). This process creates stationary time series for each tree with a mean of 1 and a homogenous variance. Ring-width chronologies were developed by averaging the annual standardized ring widths for each species-site-canopy combination to minimize competition effects (Phipps 1982).

Superposed epoch analysis (SEA) was used to test the significance of a mean tree growth response to drought events according to Lough and Fritts (1987). Departures from the mean RWI values of each core for the 5 years prior to each drought year (pre-drought), the drought

Fig. 2 Site ring-width index chronologies averaged across six species for each combination of site and canopy position in Wilderness (WB) and Chancellorsville (CVB) Battlefields. *Vertical bars* indicate the four severe drought periods examined in this study, *n* = sample sizes



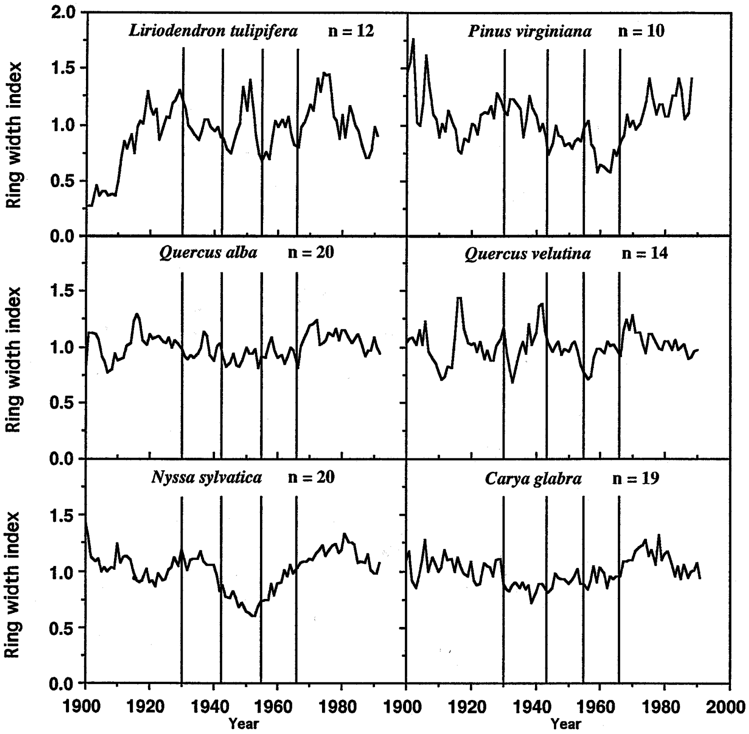


Fig. 3 Species ring-width index chronologies averaged across sites and canopy positions in Wilderness and Chancellorsville Battlefields. *Vertical bars* indicate the four severe drought periods examined in this study, *n* = sample sizes

year, and the 5 years immediately after each drought (post-drought) were averaged and plotted to determine if RWI for these years was significantly different from randomly selected sets of 11 other years. Resampling Stats (Bruce 1991) was used to randomly select 10 000 sets of 11 years from each species' data set and estimate confidence intervals ($P < 0.05$) for the plotted departures (cf. Hauritz and Brier 1981).

To determine if mean ring widths before and after drought differed among species and between site and canopy positions, analysis of variance tests were performed on species' relative growth values using the general linear models (GLM) procedure in SAS (SAS 1985). Relative growth rates were calculated for each core as the absolute change in raw ring width during drought years normalized to the 5-years prior and following the drought. In addition, absolute growth changes in the 5-years following droughts were normalized to the 5-year pre-drought rates. Multiple comparisons were accomplished using Tukey's mean separation procedure while site and canopy differences were assessed with Fisher's least significant difference (LSD) test. Spearman rank correlation was used to determine relationships between ring-width index and climatic data. Serial correlation of climatic data were relatively low (<0.35) and therefore, no procedure was performed to remove the autocorrelation.

Results

Site and species chronologies

Chronologies were constructed from trees of a relatively uniform mean age of 86 ± 4 years across species and sites, with the exception of a few overstory cores from *N. sylvatica*, *Q. alba*, and *C. glabra* cores that exceeded 150 years in age. Site chronologies displayed RWI patterns that varied with canopy position although several growth trends were common across site and canopy position (Fig. 2). Generally, RWI values declined during or immediately following the four drought periods examined in this study and most trees experienced above average growth beginning in the late 1960s following the severe drought of the mid-1960s. Relative growth comparisons indicated that understory trees on CVB sites grew an average of 11% faster after drought compared to pre-drought rates while WB site trees in both canopy positions grew roughly 4% slower after drought. These differences were greatest following the 1966 drought, when CVB understory stems grew 39% faster while WB understory stems grew at pre-drought rates.

Species displayed different long-term radial growth patterns across site and canopy position (Fig. 3). With the exception of a major release during 1900 in *L. tulipifera*, no growth increases in species chronologies were attributed to major or moderate release criteria. All species exhibited short-term RWI reductions during or immediately following the four drought periods, although there was less RWI variation observed in *Q. alba* and *C. glabra*. *Nyssa sylvatica* and *P. virginiana* exhibited a general growth decline throughout the entire four drought period followed by more favorable growth in the 1970s and 1980s.

Drought responses

Superposed epoch analysis (SEA) enabled us to examine the average growth trends of species pooled over the four drought events. Growth comparisons before and after droughts revealed that a majority of species at both sites grew more slowly following drought. Overstory trees in CVB exhibited different average growth responses to drought (Fig. 4). *Quercus alba* was the only species that experienced statistically significant growth reductions associated with drought years. Moreover, it was the only

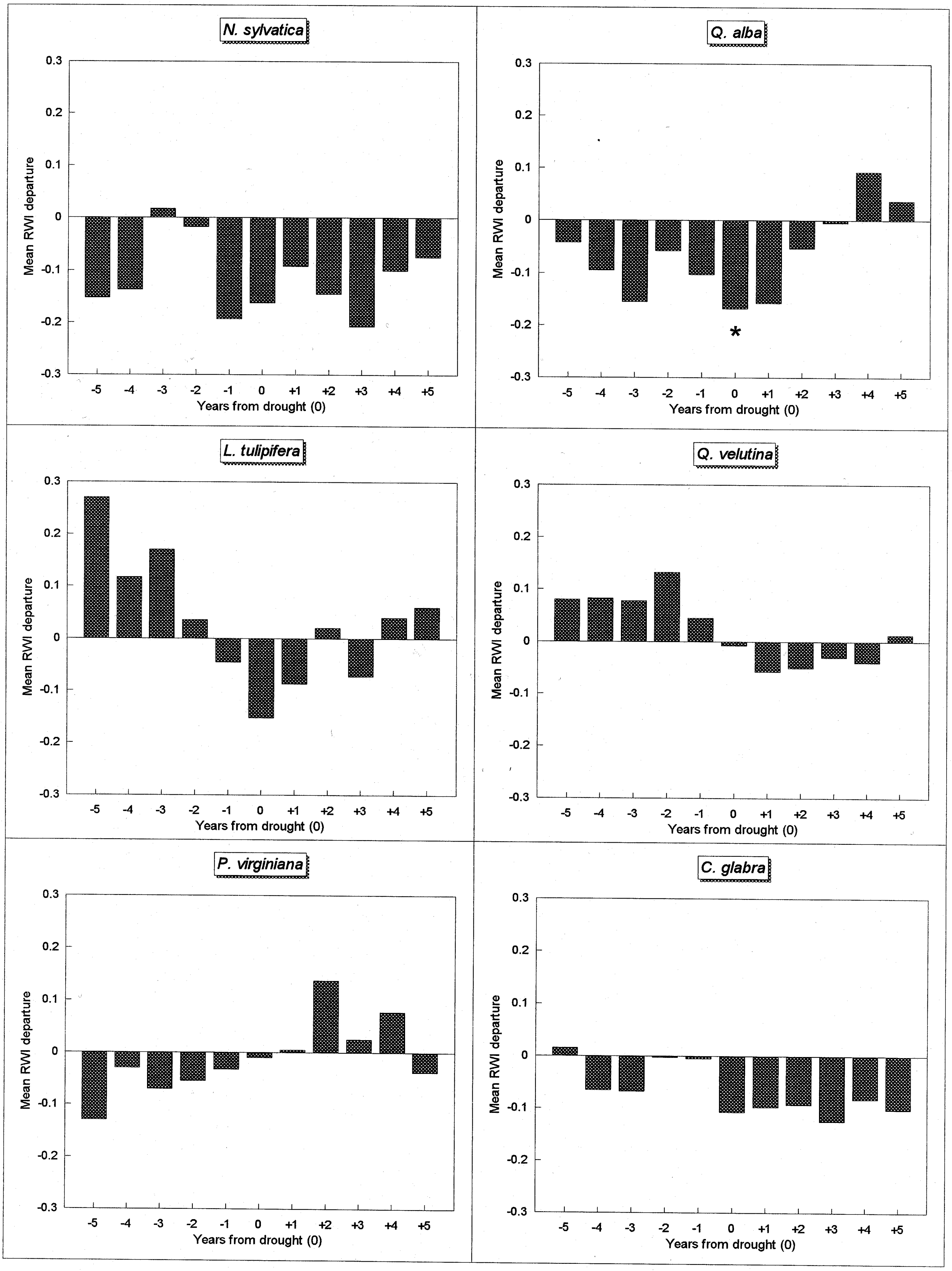

N. sylvatica
Q. alba
L. tulipifera
Q. velutina
P. virginiana
C. glabra
Mean RWI departure
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-5
-4
-3
-2
-1
0
+1
+2
+3
+4
+5
Years from drought (0)
*

Table 1 Relative (% ± SE) changes (Δ) in radial growth of 6 overstory tree species in Wilderness (*WB*) and Chancellorsville (*CVB*) Battlefields. Average differences are pooled from four drought periods during the years 1930–1993 in north-central Virginia and include 5 years prior to drought (*pre-*), the drought year, and the 5 years following drought (*post*). Sample size = 20 for each species. Means in a column followed by the same letter are not significantly different at $P < 0.05$

Site	Δ From pre- to drought		Δ From drought to post		Δ From pre- to post	
	WB	CVB	WB	CVB	WB	CVB
Carya glabra	–14 ± 3 ab	–24 ± 3 a	14 ± 5 a	6 ± 5 a	–3 ± 4 a	–20 ± 4 a
Liriodendron tulipifera	–27 ± 5 a	–30 ± 5 a	22 ± 12 a	45 ± 19 b	–12 ± 8 a	–9 ± 8 ab
Nyssa sylvatica	–17 ± 4 ab	–22 ± 6 a	18 ± 6 a	20 ± 9 ab	–4 ± 6 a	–2 ± 8 ab
Pinus virginiana	–21 ± 6 ab	–4 ± 9 b	19 ± 12 a	20 ± 10 ab	–8 ± 8 a	9 ± 9 b
Quercus alba	–6 ± 4 c	–18 ± 5 ab	9 ± 4 a	28 ± 10 ab	2 ± 5 a	–1 ± 6 ab
Quercus velutina	–12 ± 5 bc	–19 ± 5 ab	9 ± 6 a	15 ± 6 ab	1 ± 9 a	–7 ± 7 ab

Table 2 Relative (% ± SE) changes (Δ) in radial growth of 5 understory tree species in Wilderness (WB) and Chancellorsville (CVB) Battlefields. Average differences are pooled from four drought periods during the years 1930–1993 in north-central Virginia and include 5 years prior to drought (*pre-*), the drought year, and the 5 years following drought (*post*). Numbers in parentheses are sample sizes in Wilderness and Chancellorsville sites respectively. Means in a column followed by the same letter are not significantly different at $P < 0.05$

Site	Δ From pre- to drought		Δ From drought to post		Δ From pre- to post	
	WB	CVB	WB	CVB	WB	CVB
Carya glabra (19, 15)	–25 ± 5 a	–19 ± 4 a	19 ± 5 a	36 ± 9 a	–3 ± 10 a	11 ± 11 a
Liriodendron tulipifera (8, 0)	–20 ± 9 a	–	15 ± 20 a	–	–17 ± 7 a	–
Nyssa sylvatica (20, 20)	–22 ± 5 a	–17 ± 6 a	27 ± 9 a	39 ± 9 a	7 ± 10 a	18 ± 11 a
Quercus alba (20, 20)	–24 ± 5 a	–15 ± 8 a	20 ± 7 a	33 ± 13 a	–10 ± 7 a	9 ± 11 a
Quercus velutina (15, 0)	–15 ± 4 a	–	16 ± 9 a	–	–6 ± 8 a	–

species to exhibit growth reductions during drought that differed significantly between site types (Table 1). *Liriodendron tulipifera* showed a marked growth reduction during drought years, recovered to above average growth rates within 2 years and then fluctuated after that (Fig. 4). Recoveries were accentuated following the 1954 and 1966 droughts, when *L. tulipifera* grew an average of 85–95% faster. Thus, *L. tulipifera* on CVB sites experienced among the most suppressed growth during drought and some of the greatest releases following individual drought events (Table 1). In contrast, *P. virginiana* was least impacted by drought at CVB, experiencing very small reductions during drought and above average growth within 2 years of droughts.

At WB, all species continued to experience reduced average growth in the 5-year period examined following drought events (Fig. 5). *Liriodendron tulipifera* experienced significantly greater ring-width reductions associated with drought than co-occurring *Q. alba* and *Q. velutina* (Table 1), and average growth reductions that lasted up to 3 years following drought years. *Nyssa sylvatica* and *C. glabra* exhibited average reduced growth throughout the period examined in this study, with no period of recovery within 5 years following droughts.

Understory trees were more consistent in their growth response to drought events (SEA data not shown). Species growing in CVB exhibited only minor growth reductions in response to drought years and small increases following drought. At WB, average growth of *L. tulipifera* and *Q. alba* was more severely impacted during years 2 and 3 following drought than during the drought year itself. Following drought, understory *Q. alba* in WB experienced significantly larger relative growth reductions than overstory trees, while understory *C. glabra* in CVB grew significantly faster than overstory trees (Table 2).

Upon closer examination of individual cores, some trees were observed to exhibit extended periods of reduced growth for up to 5 years following drought (Fig. 6). Overstory *L. tulipifera* on both site types experienced reduced growth for 2–5 years following the 1930 and 1942 droughts, and an extended period seen as a U-shaped depression (cf. Lorimer and Frelich 1989) during the dry period of the mid- to late 1960s. During the 1966 drought, both *L. tulipifera* trees represented in Fig. 8 experienced moderate releases that were not seen in species chronologies due to the merging of many cores. These releases may be due to gaps created during winter storms in late January of that year which carried 97 km/h winds (NOAA 1966). Overall, the majority of individual tree ring-width patterns coincided well with the PDSI extremes (Fig. 1), which indicated short, severe droughts starting in 1930, 1942, and 1954, and an extended dry period during the mid- to late 1960s.

Carya glabra on different sites experienced short-term growth reductions associated with drought in 1930, disparate patterns after 1942, and 3–4 year declines after 1954 (Fig. 6). CVB site *C. glabra* experienced a moderate release in the mid-1930s and a 5 year growth depression associated

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Fig. 4 Superposed epoch analysis showing tree growth departures for the drought year and 5 years before and after the drought event in overstory trees in Chancellorsville Battlefield. Values are averaged over the four drought events. The *asterisk* denotes a departure that is greater than would have occurred by chance as determined from 10 000 random simulations ($P < 0.05$)

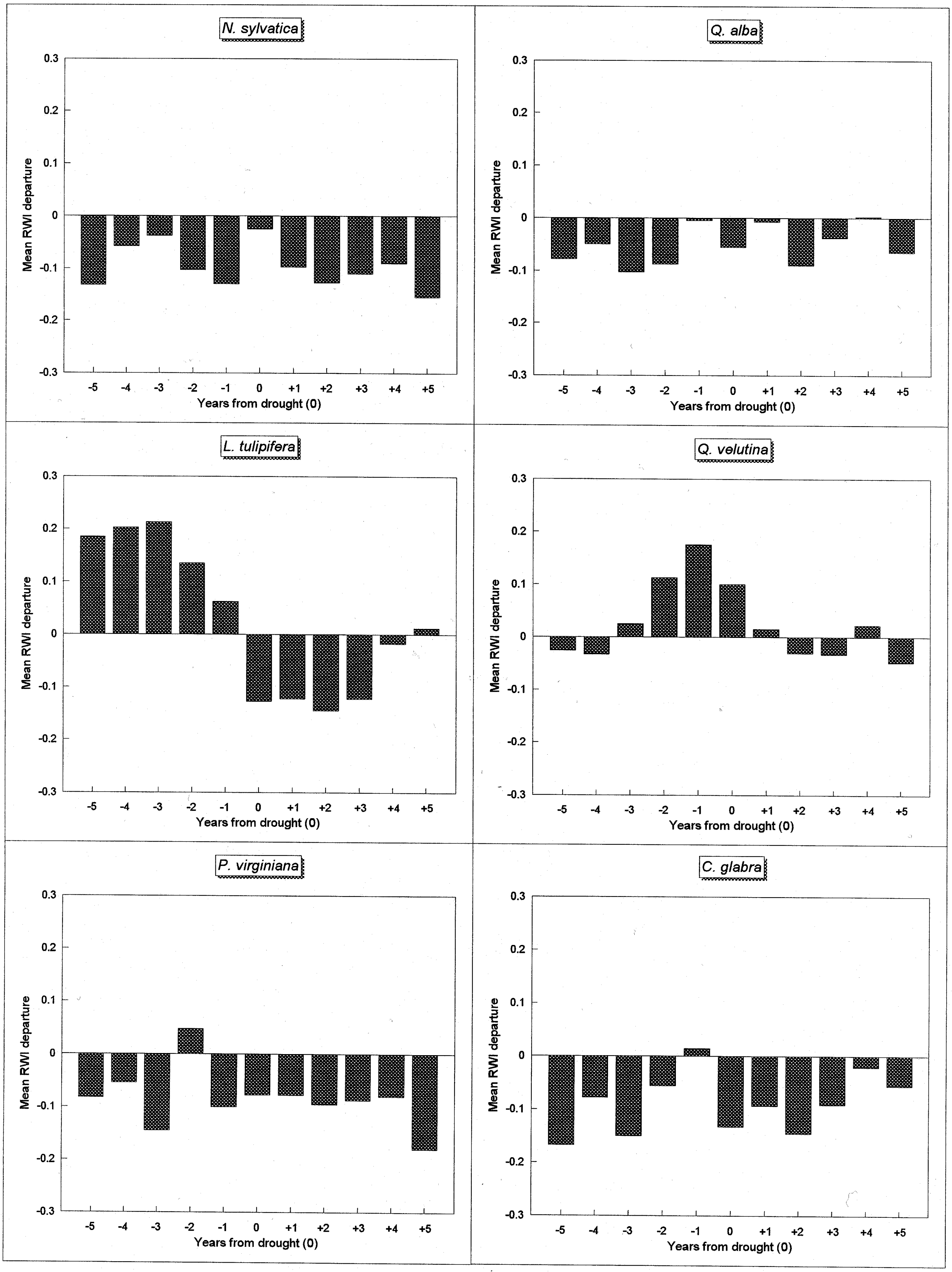
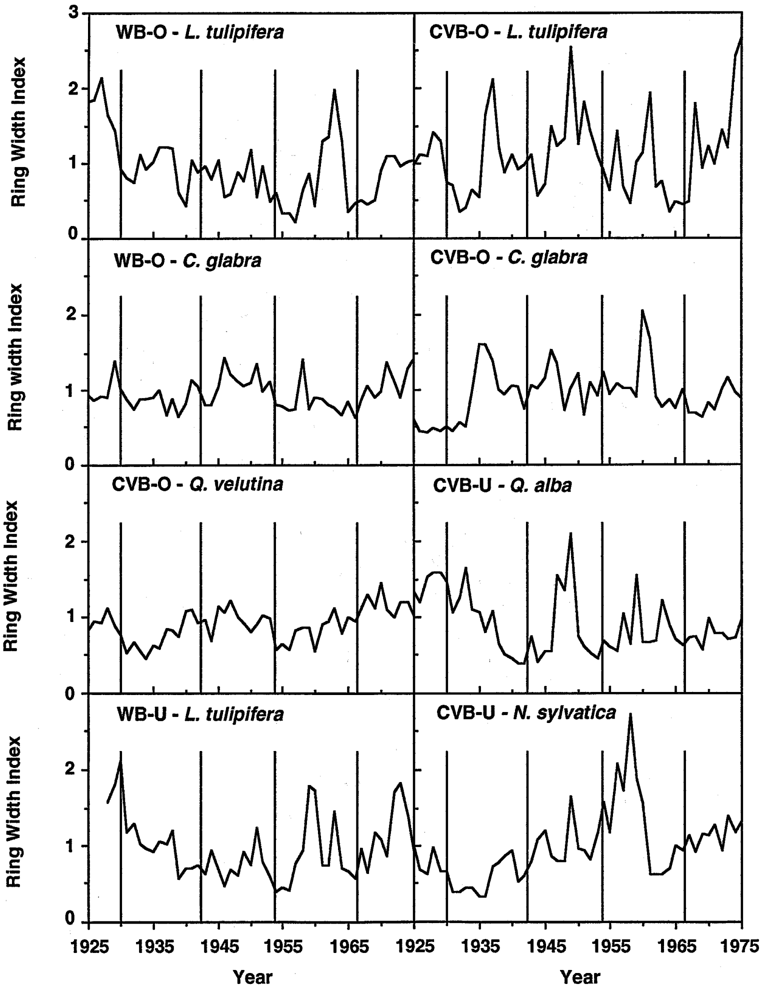

N. sylvatica
Q. alba
L. tulipifera
Q. velutina
P. virginiana
C. glabra
Mean RWI departure
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-5
-4
-3
-2
-1
0
+1
+2
+3
+4
+5
Years from drought (0)

Fig. 6 Representative ring-width index patterns of individual trees showing growth reductions associated with drought periods in Wilderness (WB) and Chancellorsville Battlefields (CVB). *Vertical bars* indicate the four severe drought periods examined in this study, *O* and *U* = overstory and understory canopy positions



with the 1966 drought which was not observed in the WB site trees. Overstory *Q. velutina* and understory *Q. alba* on CVB sites grew more slowly for 2–3 years following the 1930 and 1954 drought periods, and *Q. alba* maintained very low growth rates following the 1966 drought. Understory *L. tulipifera* and *N. sylvatica* growing on WB and CVB sites, respectively, experienced 5–6 years of reduced growth after the 1930 drought but only short-term reductions or slight increases in subsequent droughts. The peak in radial growth seen in both cores during the late 1950s was a result of moderate releases from localized disturbance in 1957 and 1952, respectively.

Ring-width climate relationships

Species differed in their relationship of ring-width index to various climatic variables. RWI values of overstory *L. tulipifera* on WB sites and *P. virginiana* on CVB sites were positively correlated with annual temperatures ($P < 0.01$, $r = 0.45$ and $r = 0.40$, respectively). Similarly, radial growth of understory *Q. alba* and *Q. velutina* on CVB sites was correlated with annual and summer temperature ($P < 0.05$, $r = 0.35$ and $r = 0.27$, respectively). Within CVB sites, overstory *C. glabra* and overstory *L. tulipifera* had RWI growth that was significantly related to annual PDSI ($r = 0.22$ and $r = 0.21$, respectively), while understory *C. glabra* was the lone species-site combination with a significant relationship to annual precipitation ($r = 0.33$).

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Fig. 5 Superposed epoch analysis showing tree growth departures for the drought year and 5 years before and after the drought year in overstory trees in Wilderness Battlefield. Values are averaged over the four drought events

Discussion

Observed differences in species response to drought may be affected by a combination of many factors including morphological, anatomical, and physiological differences among species, age and developmental history, and competitive interactions with neighbors (Fritts 1976). Despite these confounding factors, several trends among species and between sites became apparent in the ring-width response to droughts examined in this study. Larger drought-induced RWI decreases were observed in overstory *L. tulipifera* on WB sites compared to *Q. alba* and *Q. velutina*. Similarly, in the midwestern and southeastern U.S., *L. tulipifera* had higher growth rates than several

Quercus species in moist years, but had significantly reduced growth during drought, which was not observed in the *Quercus* species (Jacquart et al. 1992; Elliot and Swank 1994). These findings are consistent with the drought tolerance ability of these species (Burns and Honkala 1990). It is well established that a majority of *Quercus* species have a reputation for high drought tolerance (Abrams 1990), while *L. tulipifera* is considered highly sensitive to drought (Kolb et al. 1990). In addition, species that tend to grow on mesic sites may compete more intensively for light since moisture is less often limiting, and typically possess lower root to shoot ratios and fewer drought adaptations (Kaufmann 1981; Kramer 1983). This suggests that during periods of severe drought, competition for water may be more severe on mesic versus xeric sites.

On dry-mesic CVB sites, overstory *L. tulipifera* also exhibited greatly reduced growth as a result of drought and experienced some of the largest growth increases following individual droughts. In contrast, overstory *P. virginiana* experienced only slight growth reductions as a result of drought on CVB sites and was the only species to exhibit enhanced post-drought growth relative to pre-drought growth. However, *P. virginiana* growing in WB was much more impacted by drought, indicating an interaction of site and drought for this species. *Pinus virginiana* is well adapted to sandy, droughty sites and experiences a longer growing season than co-occurring deciduous species due to its evergreen foliage. However, it appears that these traits conferred less of an advantage to *P. virginiana* during drought years on mesic WB sites. RWI values from both *P. virginiana* and *L. tulipifera* were positively correlated with annual temperatures but not summer temperatures, suggesting that extended periods of radial growth in these species may have occurred due to warm early spring and/or autumn temperatures (Estes 1970).

Our results indicate that the radial growth of overstory *Q. alba* was reduced during drought to a greater degree on CVB sites than WB sites, implying that even though this species is considered well adapted to drought-prone sites (Abrams 1990), low soil moisture may be especially limiting to radial growth on CVB sites. This may also represent a trade off in allocation patterns from radial growth to root growth during drought to ensure survival (Kolb et al. 1990; Latham 1992). In contrast, a few ecophysiological studies have reported greater drought-induced decreases of net photosynthesis and predawn water potential in species on mesic versus dry-mesic sites (Zobel 1974; Kubiske and Abrams 1992, 1994).

It is believed that shade-tolerant species are more sensitive to climatic variation including drought than intolerant species (Phipps 1982). Of the species examined in this study, only *N. sylvatica* was characterized as shade tolerant (Burns and Honkala 1990), and it did not exhibit a significant drought response in either canopy position or site type. In addition, radial growth dynamics in this species was not significantly correlated with any of the climate variables. Individualistic radial growth patterns of *N. sylvatica* with no clear relationship to climate have been reported in other forests, suggesting that site and disturbance factors may have a greater influence on growth of this species than climate (McCaw and Eckenwalder 1987; Orwig and Abrams 1994b).

Interestingly, many overstory trees exhibited prolonged, post-drought growth reductions. It should be noted that the lack of statistically significant growth reductions in our SEA results does not render the observed trends meaningless. Rather, it indicates that species differed in their duration of reduced growth following individual drought events. Generally, radial growth reductions lasted 2–3 years and were more prevalent following 1930, which was the driest year examined in terms of growing season precipitation. However, our SEA results indicate that several species, including *L. tulipifera*, *C. glabra*, and *N. sylvatica*, experienced reductions lasting up to 6 years following individual droughts. Precipitation returned to above average levels within 1–2 years of each drought, and therefore, extended lag effects were not related to ambient climatic conditions. Prolonged post-drought growth reductions have been observed elsewhere in *Quercus* species and *L. tulipifera* (Jacobi and Tainter 1988; Jacquart et al. 1992; LeBlanc and Foster 1992; Jenkins and Pallardy 1995). In addition, Lorimer and Frelich (1989) reported that overstory trees in hemlock-hardwood forests experienced post-drought growth depressions that averaged 5 years. Possible reasons for prolonged growth decreases include reduced leaf photosynthetic capacity, twig, bud, and branch dieback, xylem cavitation, and changes in carbon allocation patterns from bole to roots as a result of drought stress (Fritts 1976; Hendrick and Pregitzer 1993; Waring and Pitman 1985; Tyree and Sperry 1989).

Relative growth reductions during drought in understory trees were not significantly different between site types but were often significantly larger than overstory responses of the same species. Larger growth reductions in understory versus overstory trees have been observed in *Pinus strobus* L. (white pine; Vose and Swank 1994) and *Picea abies* (L.) Karst. (Norway spruce; van den Brakel and Visser 1996) but not in a mixed-mesophytic forest, where growth of understory hardwood species was maintained at 97% of pre-drought growth during an extended drought (Liu and Muller 1993). Our results may differ from the latter because we examined a different group of species over four drought periods. Following drought, CVB understory trees had larger relative growth increases than overstory trees or WB understory trees. These data are similar to trends determined from ecophysiological measurements made in shaded plants of xeric species which were better able to tolerate drought than sun plants or mesic species (Abrams et al. 1992; Kubiske and Abrams 1994). The radial growth responsiveness of understory trees observed in this study was not anticipated because it is generally accepted that overstory trees are influenced less by crowding, treefall gaps, and overtopping of neighbors and therefore are more climatically sensitive than understory trees (Phipps 1982). However, drought effects may be felt sooner and more severely by understory rather than overstory individuals due to shallower root systems and lower stem capacitance (Jacquart et al. 1992). Similar results have been found in ecophysiological studies which have documented greater drought stress in understory versus open-grown saplings due to greater competition for soil moisture (Abrams 1986; Kloeppel et al. 1993; Abrams and Mostoller 1995). However, differences in microclimate and atmospheric drought may lead to greater water losses in upper canopy trees than understory trees (Thompson and Hinckley 1977; Liu and Muller 1993). The inconsistencies between this study and other studies indicate that broad generalizations about how drought affects radial growth within trees in different portions of the forest canopy should not be made, and emphasize the need for additional research on drought impacts among different vertical strata, and leaf level physiology versus radial growth responses.

The results of this study suggest that tree rings represent an important ecophysiological record of growth responses to periodic drought events. Our ring-width evidence indicates that tree species growing on different sites and in different canopy positions responded differentially during drought periods and were influenced by various climatic variables. SEA was a useful tool for examining tree growth responses to multiple drought events and appears well-suited for tree-ring analysis in areas where climate has a much stronger influence over radial growth than competition and canopy dynamics. The frequency of extreme drought events may increase in the future with the predicted rise of global temperatures, potentially leading to dramatic reductions in wood productivity and changes in species composition and structure (LeBlanc and Foster 1992; Graumlich 1993). The approach used in this study of examining long-term drought responses of sympatric species on contrasting sites would appear to be an important first step in understanding and anticipating overstory and understory responses to future climate change. In addition, this method shows promise for providing supporting evidence of data typically obtained in leaf-level physiological studies.

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