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Fire and gap dynamics over 300 years in an old-growth temperate forest

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Nomenclature
Jones (2005)

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Abstract

Questions: What are the long-term patterns of wildfire occurrence and gap dynamics in an old-growth deciduous forest? Are there temporal patterns in fire and gap dynamics over the last ca. 300 yrs? How is drought related to fire occurrence? Are there temporal interactions between gap dynamics and fire?

Location: Lilley Cornett Woods Appalachian Research Station, Southeastern Kentucky, USA. LCW; 37°05′ N, 83°00′ W.

Methods: We cross-dated and analysed annually-resolved tree-ring data from 35 tree cross-sections in an old-growth deciduous forest to reconstruct historical fire and canopy disturbance and explore connections among these processes. Canopy disturbance patterns as indicated by tree growth release within this collection [fire history collection: (FHC)] were compared to cores from 26 trees collected in 1983 for the purposes of climate reconstruction [climate collection: (CC)].

Results: Initiation dates in the FHC ranged from ca. 1670 to 1925. Thirty-three fire scars were identified from 1678 to 1956. The mean interval between fire events was 9.3 yrs, and there were many more fires after 1800 than before that date. Gap dynamics, as reconstructed through growth release detection, were relatively constant through the FHC record and were supported by a similar result in the CC. The mean number of years between detected release events was 5.2 yrs. Many individual trees, and the mean growth chronology for the FHC, indicate that many oak trees exhibit growth release after long periods of suppression and, after a final release, exhibit a step-change in growth rate suggesting canopy accession.

Conclusions: Fire and gap dynamics occurred through much of the last ca. 350 yrs in this old-growth forest. There was not evidence to support that these two processes were temporally linked – gap dynamics were ostensibly independent of fire occurrence. Even so, we posit that these two processes may have a synergistic effect on long-term dynamics, wherein fire ‘filters’ the seedling pool and gap openings provide canopy accession opportunities. We also note several instances where release events are associated with stand-wide growth increases suggesting large-scale canopy accession. These events could influence the overstorey composition of the forest for centuries.

Introduction

An early, but sophisticated, conception of the relationship between forest dynamics and historical disturbance was delivered by A.S. Watt (1947; pp 13–14) who noted that:

> … there are exceptional factors of rare or sporadic occurrence, such as storms, fire, drought, epidemics, which create…an age class of abnormal area…. In other words, the relative areas under the age classes…need bear no relation to current meteorological factors but be explicable in terms of some past event which happened, it may be, 200 or 300 years ago.

This idea has gained much support, and many studies have shown that forest structure and composition can be mediated by disturbance and successional processes that can unfold over centuries (e.g. White 1979; Sprugel 1991; Turner et al. 1998; Jackson et al. 2009; McEwan et al. 2011). For instance, variability in drought conditions and fire regimes can drive long-term patterns in tree recruitment, and those trees can then dominate stands for centuries (Swetnam & Betancourt 1998; Brown & Wu 2005; Brown 2006). Establishing historical baselines for disturbance processes is important for both theory and management, and is increasingly pressing in an era of 'compounded perturbations' (*sensu* Paine et al. 1998), including pulses of tree mortality due to exotic pests and pathogens, and climate change (Rizzo & Garbelotto 2003; van Mantgem et al. 2009; Knight et al. 2013).

The fire and oak hypothesis is an important disturbance ecology paradigm for the Eastern Deciduous Forest (EDF) in North America. Fire is postulated to have been a relatively constant disturbance process historically and has been associated with ignitions from Native Americans and Euro-American settlers (e.g. Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). Fire suppression (and other factors) have caused the virtual elimination of fire in the EDF, and this change is thought to have benefited 'mesophytic' species (especially maples: *Acer rubrum, Acer saccharum*) and hindered oak regeneration (Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). The oak-to-maple dynamic has important ecological and economic ramifications, and impeding 'oak loss' is an important consideration in oak forest management (Nodvin & Waldrop 1991; Yaussy 2000; Albrecht & McCarthy 2006; Chiang et al. 2008; Alexander & Arthur 2010; Hutchinson et al. 2012). There are well-replicated and verified fire scar data from forests of the western margin of the EDF that support the idea that fire was an important and dynamic factor over the last 400 yrs (e.g. Cutter & Guyette 1994; Guyette et al. 2002; Guyette & Spetich 2003). In other regions of the EDF, there are plentiful fire scar data from the last ca. 100 yrs (e.g. McEwan et al. 2007; Hutchinson et al. 2008); however, tree-ring data that could provide a pre-European baseline for fire are relatively scarce (Aldrich et al. 2010; Hessl et al. 2011).

The quasi-random process of individual tree death and canopy gap formation is another important deciduous forest disturbance paradigm. Long-term forest development is thought to proceed through a directional, multi-phased process culminating in old-growth forests in which gap dynamics are prevalent (e.g. Braun 1950; Bormann & Likens 1979; Runkle 1982; Oliver & Larson 1996). As trees die due to age, pathogens, wind or other factors, a gap is created in the forest canopy (Franklin et al. 1987). The gap is captured by individuals 'recruiting' into the canopy from the mid-storey or sapling layer, and by lateral branch extension from trees adjacent to the gap. Canopy gaps effectively 'release' suppressed understorey individuals by providing a high light patch in an otherwise densely shaded environment. Gap dynamics are an essential part of most forest development models and a distinguishing feature of mature deciduous forests (Bormann & Likens 1979; Runkle & Yetter 1987; Sprugel 1991; Oliver & Larson 1996; Rentch et al. 2003; Buchanan & Hart 2012).

We used dendroecology to reconstruct ca. 330 yrs of fire and gap dynamics in an old-growth temperate deciduous forest in the central Appalachians of North America. This system offered a unique opportunity due to (1) the depth of the available chronology; (2) the fact that the system is deciduous (instead of pine-dominated); and (3) the species compliment in the site is representative of forests across much of the EDF. Our overall goal was to describe tree establishment and growth, and the activity of fire and gap dynamics over the course of the available chronology. We hypothesized that (H_1) both fire and gap dynamics would be relatively constant through time except for the last several decades where fire suppression should eliminate fire while gap dynamics continue unabated. Fire is often associated with the occurrence of drought, and we hypothesized that (H_2) fire scars would coincide with periods of drought, as indicated in the chronology. This study relied on analysis of tree cross-sections from upper slopes in the watershed; however, we also had access to data from increment cores collected in an adjacent old-growth area as part of an earlier climatological study. We compared tree-ring measurements in this climate collection (CC) with cross-section data from the fire history collection (FHC) to confirm the occurrence and timing of gap dynamics, and also to test for differences between the collection types.

Methods

Study area description

This study was conducted in Big Everidge Hollow (BEH), a 52-ha watershed within the Lilley Cornett Woods Appalachian Research Station (LCW; 37°05′ N, 83°00′ W) on the Cumberland Plateau in southeastern Kentucky, USA (Martin 1975). The climate at the study site was temperate humid continental with warm summers, cool winters and no distinct dry season (Trewartha 1968). Mean annual precipitation and temperature were 113 cm and 13 °C, respectively (Hill 1976). Elevation in the study site ranged from 320 to 600 m a.s.l. with a mean slope of 55% (Muller 1982). There was no evidence of commercial timber cutting or significant damage from ice glaze or severe winds in BEH (R. Watts, pers. obs.).

This project represents an extension of a long-term ecological analysis of the site (e.g. Muller 1982; McEwan & Muller 2011; Chapman & McEwan 2012). Decadal woody species inventories have been ongoing since 1975 (Martin 1975; Muller 1982), and coarse woody debris, vegetation–site relationships of woody species and patterns of overstorey dynamics have been previously described (e.g. Muller 2003; McEwan et al. 2005; McEwan & Muller 2006).

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Upper slopes, and mid-slopes on south-facing aspects, have been shown to be sites of oak dominance, where species such as *Quercus alba*, *Quercus montana* and *Quercus velutina* intermingle with hickories (e.g. *Carya ovata, Carya tomentosa*) and a mix of other species (McEwan & Muller 2006). Mid-slopes are dominated by 'mixed mesophytic' vegetation (Braun 1950) while lower slopes are dominated by *Tsuga canadensis* and *Fagus grandifolia* (McEwan & Muller 2006). On the oak-dominated upper slopes, maples (*A. rubrum* and *A. saccharum*) have been shown to have substantially higher densities than oaks in sub-canopy strata (Chapman & McEwan 2012). Invasive species were present at exceedingly low densities at the time of this sampling and had not impacted dynamics in the system (Chapman et al. 2012). Taxonomic nomenclature follows Jones (2005).

Sample collection, lab methods and sample dating procedure

During the summer of 2009, samples of large downed trees were opportunistically collected within BEH on oak-dominated upper slopes. Live tree sampling was not allowed due to the quality and uniqueness of the old-growth forest. Fire history samples were collected from 41 trees through ca. 25 ha across the upper slopes of the watershed including north-, south- and east- facing slopes in elevations ranging from ca. 450 to 600 m a.s.l. The most frequent species in the sample collection were *Q. montana* (n = 12) and *Q. alba* (n = 10), and an additional six samples were sound enough for data collection but could not be classified below the white oak subgroup Leucobalanus (n = 6). Samples were also collected from *Q. velutina* (n = 3), and two stems were classified into the red oak subgroup Erythrobalanus without being identified to species (n = 2). Additional samples were collected from two hickory (*Carya* sp.; n = 2) stems not identified to species. In total, six stems were collected but were unusable for data collection (e.g. too extensively decayed for data collection; n = 6) and were discarded, leaving a total of 35 stems in the fire history analysis. One *Q. velutina* and one *Q. montana* sample were datable and were used in the fire history analysis, but ring measurements were not made because of distortions and decay, leaving 33 samples for disturbance analyses. In general, because we collected cross-sections near the tree base, and we did not collect samples that were badly decayed; the inner ring dates presented in this paper are from actual pith dates.

All samples were processed following typical dendrochronology methods (Stokes & Smiley 1968). Each ring was dated using the 'list' method (Yamaguchi 1991). Annual increments were then measured to the nearest 0.001 mm using a VELMEX unislide stage (VELMEX Inc., Bloomfield, NY, USA) with at least two radii measured within each cross-section when possible. Occasionally four radii were measured. Increasing the number of radii sampled per tree can improve reconstructions of disturbance history (Copenheaver et al. 2009). The accuracy of assigned dates was then verified, first by comparing radii within each tree, and then within each species using the program COFECHA (Holmes 1983). Flagged segments were examined under the microscope to ensure dating accuracy. Finally, dating was checked vs existing tree-ring data for Lilley Cornett Woods (see below) and in-house data including series of old-growth *Q. alba* and *Q. montana* from nearby Blanton Forest (Pederson et al. 2012). Inter-series correlation of the 67 measured series within the fire history collection was 0.505 (P < 0.001). Inter-series correlations ranged from 0.427 for the combined series from the *Quercus* subgroup Erythrobalanus to 0.511 for the unidentifiable trees falling into the *Quercus* subgroup Leucobalanus. Composite master series of each group (*Q. alba*, *Q. montana*, *Quercus* subgroup Erythrobalanus, *Quercus* subgroup Leucobalanus and *Carya* sp.) were correlated against pre-existing species-appropriate residual chronologies in or near LCW. All series presented here are significantly correlated with one another and prior collections from old-growth forests, except for the *Carya* sp. collection (of two trees) vs the two Blanton Forest (Kentucky) chronologies (Table S1). Dating in each group prior ca. 1700 was constrained by the heavy suppression experienced by sampled trees from that era and low replication.

Determination of fire history

All wound events were dated and seasonality of wounding was noted. Wound data were entered into the fire scar analysis software FHX2 (Grissino-Mayer 2001); a fire history diagram was generated and summary statistics were calculated. The mean number of years between fires is presented excluding the years after 1954 due to fact that recent decades are during the fire suppression era.

Reconstruction of canopy disturbance history

Tree-ring methods were used for canopy disturbance reconstruction (Lorimer 1980, 1985; Lorimer & Frelich 1989). In particular, we used ring-width intervals of 15 yrs and thresholds of growth increases of at least 50% to infer canopy disturbance events (McEwan & McCarthy 2008). These thresholds, which are generally more conservative than the method developed by Lorimer & Frelich (1989), were used to reduce the number of potential false-positive growth release detections. The threshold for a 'minor release' was a growth release of 50–99.99% over a 15-yr period vs the prior 15-yr period. The major release thresh-

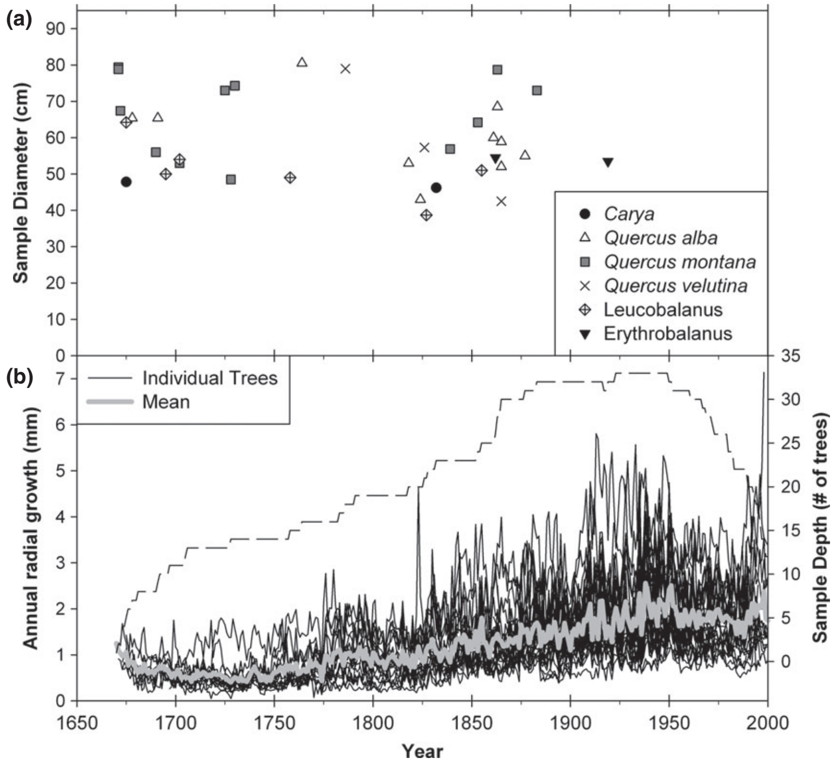

Fig. 1. Diameter and initiation dates **(a)** and annual growth **(b)** of tree cross-sections collected in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

old, likely to be canopy accession events (Lorimer & Frelich 1989), was set at ≥100%. Following Fraver & White (2005), mathematically determined releases at low radial growth, intervals when radial increment was <0.5 $mm \cdot yr^{-1}$, were not counted as a release to reduce the risk of potential false-positive growth release events. Detected events are presented at the annual time step as all series were cross-dated and the lag between disturbance and growth response is often 2 yrs or less (Rentch et al. 2002). To verify patterns of canopy disturbance in BEH, a collection of *Q. alba* ring widths from 26 trees in Lilley Cornett Woods was downloaded from the International Tree-ring Databank (ITRDB; Cook 1982). Similar to the fire history collection, this collection targeted large, downed trees from old-growth forest. The main differences between the two collections are that the tree samples collected by E. Cook and P. Sheppard in 1983 were cored for characteristics of great age in another part of Lilley Cornett Woods for an investigation of regional drought (hereafter CC for 'Climate Collection').

Test for drought association

We assessed the relationship between drought, as estimated by a reconstruction of the Palmer Drought Severity Index (PDSI; Palmer 1965), and both fire and canopy release. Data were extracted from a 0.5°× 0.5 version (2a) of the North American Drought Atlas (Cook et al. 1999, 2004; Cook 2008). For this study, 16 grid points within a 2° square box (36.00°–38.00° N, 81.50°–83.50° W) were averaged to create a single time series of reconstructed drought for the LCW region. The relationship between fire and drought was assessed using Superposed Epoch Analysis comparing fire years and reconstructed drought (see below).

Results

The earliest tree-ring date for the FHC was 1669, and 16 of the samples initiated before 1800 (Fig. 1a). The median inner ring date in this collection was 1782. Only three of the samples initiated after 1870, and the most recent inner ring date is 1918 (Fig. 1a). Sample diameters ranged from ca. 40–80 cm. There was no statistically discernible relationship between sample diameter (tree size) and initiation date (tree age) in these samples (Fig. 1a; line not shown: $P = 0.17$, $r^2 = 0.054$). Considering all stems, and all years, tree-ring width ranged from ca. <1 to 5 mm, and mean tree growth for all samples ranged generally between 1 to 2 mm (Fig. 1b). There was some indication that ring

Applied Vegetation Science
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widths increased consistently over the life span of the trees sampled here (grey line, Fig. 1b). Individual series exhibited long-term growth patterns characterized by suppression and growth pulses. For example, the oldest tree in the FHC was a *Quercus montana* (top panel, Fig. 2) that exhibited ca. 100 yrs of suppression followed by a growth release that resulted in a step change increase in growth rate. The overall pattern, as evidenced by individual series (Fig. 2) and the mean for all samples (Fig. 1b), suggests that maximum growth rates for these trees were being achieved near the end of the chronology, after the trees were ca. 200 yrs old.

A total of 33 fire scars representing 29 fire years were identified from 21 samples (60%) while 14 samples did not contain fire scars (top panel, Fig. 3). Years with fire scars on more than one tree were 1948 (n = 2), 1880 (n = 3) and 1820 (n = 2). Across all dates, the mean number of years between a detected fire was 9.3 (SD of the mean: 10.9). The composite fire record suggests that the study site experienced relatively infrequent fires in the pre-settlement period followed by an increase in burn frequency ca. 1870–1950 (Fig. 3). Only four fires were detected in the ca. 100 yrs from the beginning of the chronology to 1775 (Fig. 3).

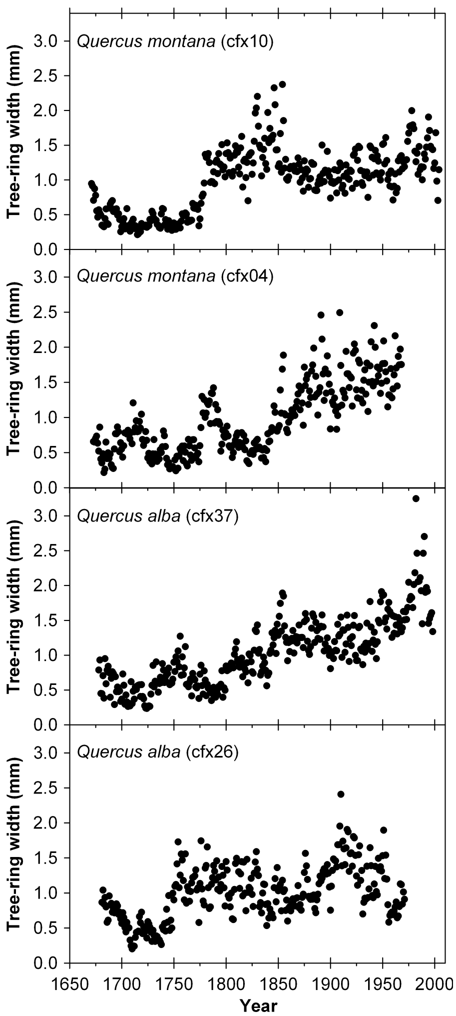

Fig. 2. Long-term growth patterns of the four oldest trees sampled as part of a fire history collection made in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

In the FHC, a total of 70 growth releases were found in 58 different years, and 31 of the 33 trees (94%) exhibited at least one growth release (bottom panel, Fig. 3). The mean number of years between detected release events was 5.2 yrs (SD: 4.7 yrs). Median release per tree was two with a maximum of five growth releases in a single tree. Growth releases were relatively evenly distributed throughout the chronology (bottom panel, Fig. 3). One important feature of the FHC release event record is that over the last 100 yrs of the chronology, the number of detected releases in the oldest trees is far fewer than those in younger trees (bottom panel, Fig. 3). Of the 19 releases during the 1900s, 14 come from trees <200 yrs and only five are found in the trees >200 yrs (Fig. 3).

In the CC, a total of 42 growth releases were found in 37 different years, and 20 of the 21 trees (95%) exhibited at least one growth release. Similar to the fire collection, median release per tree was two with a maximum of four growth releases in a single tree. The earliest first date of major growth release was similar in both collections (1718 in the fire collection vs 1719 in the dendroclimatic collection). The collections were similar in years between the inner ring and (1) the first major growth release; (2) the last major growth release; and (3) last growth release (Table S2).

Evidence of a temporal link between fire and growth release was circumstantial and weak. We found growth releases in the late 1700s and early 1800s during long periods where we did not detect fires, and also growth releases after 1954 when there were no fires (Fig. 3). To compare these two disturbance processes more specifically we trimmed both chronologies to exclude the 15 yrs prior to 1686, during which time it would be mathematically impossible to detect release due to our methodology, and after 1954, as this time period is during the era of fire suppression. During the intervening 271 yrs, there were 28 yrs in which a fire was detected and 51 yrs during which a growth release was detected, yielding 75 total 'event years'. During this time period, there were only 4 yrs (5.3%) when there was both a fire and release event detected. To examine the possibility that fire could create a release after a time lag, we sought instances of release in the 3 yrs following each fire. We detected 17 (out of 51 possible) release years in the 3 yrs following a fire, suggesting that only 33% of releases in our record have some possibility of a temporal link with fire occurrence.

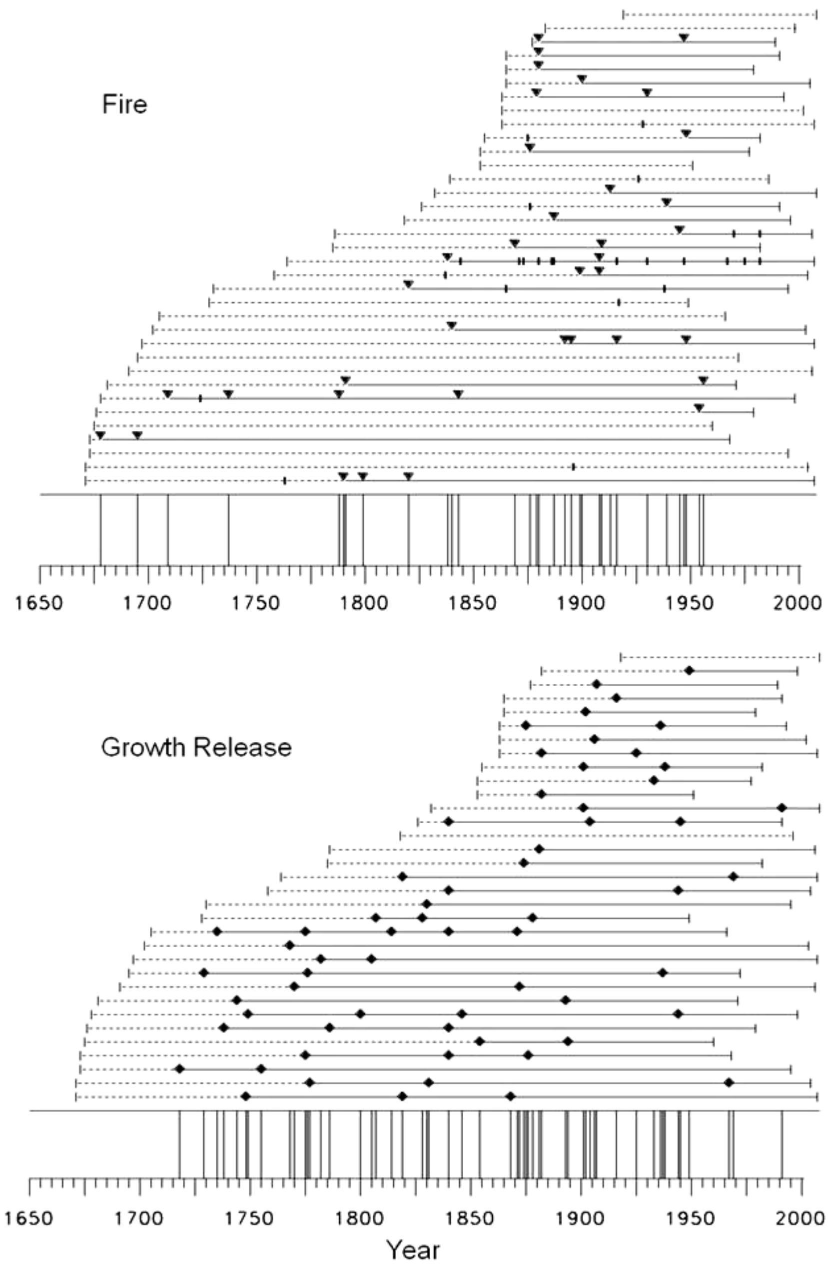

Fig. 3. Fire history and growth release from trees in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Horizontal lines represent the individual tree chronologies. In top panel, triangles indicate fire scars and dashes represent non-fire wound events. In bottom panel, diamonds represent release events (both major and minor releases). Lines are dotted prior to the occurrence of an event and solid afterward. A horizontal line below the individual tree lines represents a composite for the site and lines connecting these to the chronology (at the bottom of the panel) indicate the year of an event (either fire or release).

We did not find an overall statistically significant relationship linking fire and drought (Fig. 4). The long-term mean (±SE) reconstructed PDSI value for years without fire (-0.014 ± 0.07) was not statistically different from that of fire years (-0.13 ± 0.25). Superposed Epoch Analysis did not reveal a significant association between fire and drought the year of the fire ($P = 0.76$), the prior year ($P = 0.11$) or any of the preceding 10 yrs ($P > 0.1$ for all years). There were instances of apparent association between fire and drought. In particular, the years 1820 and 1880, which were years of multiple scars, were also 1 yr after a major drought (Fig. 4).

Applied Vegetation Science
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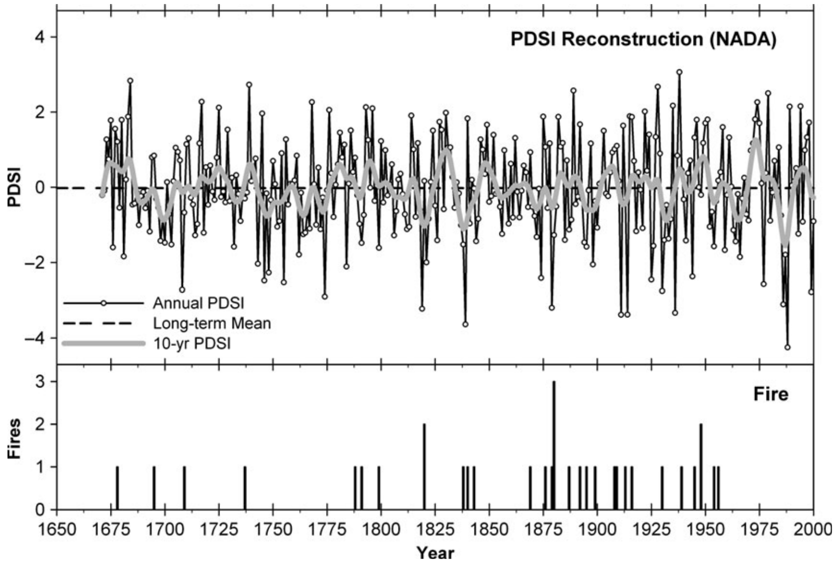

Fig. 4. Climate and fire in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Palmer Drought Severity Index (PDSI) indicates moisture levels on the landscape where negative values are dry years. Fire histograms (bottom panel) represent the number of trees recording a fire event.

Discussion

Development of temporally deep fire histories for deciduous forests in eastern North America provides an important context for management and a baseline for understanding long-term vegetation dynamics. Long and extensive fire histories have been developed in the Ozark and Ouachita Mountains and along the broader prairie–forest boundary in central North America (e.g. Cutter & Guyette 1994; Guyette et al. 2002; Guyette & Spetich 2003). In the central Appalachian region, some dendroecological work has connected fire and forest dynamics, especially in pine stands (Mann et al. 1994; Aldrich et al. 2010), and post-settlement fire history is well-developed in some areas (Lafon et al. 2005; McEwan et al. 2007; Hessl et al. 2011). Temporally deep fire history has been derived from charcoal in pollen and soil cores that clearly demonstrates fire was present in these systems for thousands of years (Davis 1969; Clark & Royall 1996; Parshall & Foster 2003; Hart et al. 2008; Fesenmyer & Christensen 2010). Despite this progress, annually resolved fire histories from deciduous forests in the centuries just prior to Euro-American settlement are relatively rare.

In our old-growth study site, fire was detected over most of the 350-yr chronology. This finding supports the idea of fire as an important disturbance process in Appalachian oak forests (e.g. Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). We hypothesized (H_1) that fire would be a relatively constant factor in this forest except for recent decades where fire suppression was in force. The disappearance of fire near the end of our timeline (1950–Present) was obvious and has been generally detected in forests of eastern North America (McEwan et al. 2007). We detected many fewer fires in the 1700s and early 1800s than in the period from 1875 to 1950. Studies conducted in deciduous forests that have access to fire scars from prior to 1850 largely support these findings. For instance, working in southern Indiana, Guyette et al. (2003) found an absence of fire in the landscape from ca. 1675 to 1800, which was followed by a period of frequent fires, particularly from 1880 to 1930. Working in the Boston Mountains of Arkansas, Guyette et al. (2006) found a longer return interval (34.7 yrs) from ca. 1605 to 1810, followed by a much shorter return interval (around 2 yrs) from 1810 up through 1920. Hessl et al. (2011) studied fire scars from three species in West Virginia with trees dating to ca. 1780 and reported an absence of fire on the landscape until 1868. An increase in the frequency of fire as a landscape process has been attributed to settlement activities by Euro-Americans (Guyette et al. 2002). Drought and fire occurrence (H_2) were not statistically linked in our data set. This lack of coherence between fire and drought was also found by McEwan et al. (2007) who posited that the fire regime post-1850 is related to settlement and land development activity, such that ignition pressures overwhelm the climatic pattern.

There are at least two important, and countervailing, caveats associated with our data set. The first is that trees are imperfect recorders of fire history. McEwan et al. (2007) found that oak trees were excellent recorders of fire if there were several years between fires, but noted a 'blind spot' relative to fires that occur in concurrent years. All dendrochronological records suffer from the 'fading record' phenomenon, in which the record becomes increasingly less reliable from the present into the past. For instance, older fires may not have been recorded because (1) not all trees are scarred by any given fire; and (2) fires may have passed through the stand scarring trees that have since fallen and decayed and are, thus, unavailable for sampling. In fact, the fading record phenomenon could help explain why relatively few fires were detected early in our chronology. For these reasons, the fire history presented here could be considered a baseline minimum of fire occurrence.

The second caveat in our fire history reconstruction is that, for oak trees, wounds that are caused by fire scars are difficult to distinguish from wounds caused by other sources of injury (falling branches, animal activity, etc.; McEwan et al. 2007). In this study, we only include wounds that have the characteristics of fire scars as indicated in McEwan et al. (2007); however, because fire-related wounds on oak trees are most often caused by heating of the cambium, but not combustion of the bark, these wounds did not include charcoal and are technically impossible to differentiate from other kinds of wounds. In fact, McEwan et al. (2007) suggest that fire history reconstruction from scars that do not contain charcoal should require a minimum of two wounds in a given year to identify a fire year. If we had applied the two scar per year 'filtering' to our data set we would have only identified three fires in the stand over the nearly 350 yrs represented in our chronology – with fire absent from the forest until Euro-Americans were already involved in settlement activity in the region (1820). For these reasons, the fire history presented here could be considered a vast overestimation of the actual occurrence of fire in the stand. This uncertainty is an unavoidable feature of this kind of reconstruction. The more conservative approach of requiring two scars/year has not been generally adopted in the field, thus we defaulted to standard data presentation and interpretation.

Release events occurred throughout the chronology, consistent with gap-phase-dominated forests, and some instances of stand-wide changes in growth were associated with release events. One important pattern we found in the release chronology was an apparent decrease in release detection in older trees. The FHC collection included a range of tree ages, and we note that, particularly over the last 100 yrs, the releases detected in our chronology were generally in younger trees (Fig. 3). Canopy trees, by definition, have achieved a full-light condition for at least a substantial portion of their leaf mass and are less sensitive to reductions in competition; thus these trees are less likely to respond to, and record, a disturbance (Nowacki & Abrams 1997; Rentch et al. 2002). This is an important finding for studies that focus on canopy disturbance using targeted tree collections like those from the International Tree-ring Data Bank. Due to the lack of sensitivity in disturbance detection in canopy trees, using targeted collections of samples from trees that have long-since attained canopy status could be subject to false-negative bias.

Individual tree mortality and the subsequent formation of canopy gaps are thought to be fundamental to the ecology of old-growth forests (Romme & Martin 1982; Runkle 1982; Runkle & Yetter 1987; Wright et al. 2003; Buchanan & Hart 2012). Our data suggest that gap creation and capture were relatively even throughout the 300+ yr time span of this study. We also found instances of synchronicity in gap occurrence. For instance, four of the five times when average ring width abruptly increases across the landscape, ca. 1730s–early 1740s, late 1770s, late 1820s, 1840s and ca. 1910, we also detected release events. Interestingly, we found that many individual trees, and also the population as a whole, exhibit patterns wherein tree growth increases markedly and then remains elevated for centuries (examples shown in Fig. 2). The 1770s event, most notably, is a period of intense canopy disturbance and inferred canopy accession which matches findings from other regional forests (Lorimer 1980).

In this study we have simultaneously assessed gap dynamics and fire over a long period (ca. 350 yrs) using annually resolved data in a deciduous forest. Although impossible for us to experimentally verify, it is highly probable that these processes interact, and synergies between the two may be a key feature of long-term forest dynamics. Fires in oak forests are generally low intensity with very little mortality of overstorey trees associated with any particular fire and little change to the understorey light environment (Chiang et al. 2008). Even so, fires could play a critical role in selectively filtering understorey seedlings, which then access the forest canopy via the patches of high light levels associated with canopy gaps generated by natural disturbance (e.g. windthrow, disease, insects, etc.). Experimental work of Hutchinson et al. (2012) demonstrates this kind of interaction. They show that multiple prescribed fires result in an altered tree regeneration layer, where oaks (*Quercus* spp.), hickories (*Carya* spp.) and sassafras (*Sassafras albidum* L.) are promoted and are then able to respond to canopy gaps caused by tree mortality (Hutchinson et al. 2012). This interaction of disturbance processes provides an opportunity for management application and is likely a key component of the long-term ecology of deciduous forests. A long-term fire regime, such as is suggested by our data, coupled with gap formation and capture, could synergistically drive long-term dominance in oak forests. One important advance suggested by our data is the idea of temporal clustering of gaps, and simultaneous canopy accession, occurring in our site over a time frame that matches findings in other forests (Lorimer 1980). We propose that historical interactions between gap formation and fire occurrence could drive landscape-scale canopy accession of fire-tolerant species which then maintain dominance for centuries (McEwan et al. 2011) – a process that would support Watt's formulation (1947) and could provide new opportunities for understanding long-term dynamics in deciduous forests.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Correlation matrix of residual chronologies from new fire collections by species or subgenus versus residual chronologies from local and nearby old-growth forest chronologies.

Table S2. Comparison of growth-release structure between fire (n = 33) and dendroclimatological (n = 21) collections at LCW.