



Fire history and its relations with land use and climate over three centuries in the central Appalachian Mountains, USA

Serena R. Aldrich^{1†}, Charles W. Lafon^{1*}, Henri D. Grissino-Mayer² and Georgina G. DeWeese³

¹Department of Geography, Texas A&M University, College Station, TX 77843, USA,

²Department of Geography, University of Tennessee, Knoxville, TN 37996, USA,

³Department of Geosciences, University of West Georgia, Carrollton, GA 30118, USA

ABSTRACT

Aim Our aims were to: (1) reconstruct the fire history of pine–oak forests in the central Appalachian Mountains, USA, with an annual resolution over as long a time period as possible using dendroecological techniques; (2) estimate the frequency of fire in the study area before the fire-suppression era; and (3) investigate how variations in land use and climate have affected the occurrence of fire in the study area.

Location Temperate forests at three study sites within the central Appalachian Mountains, Virginia, USA.

Methods Cross-sections were taken (sawn) from fire-scarred pine (*Pinus* L.) trees growing in pine-dominated patches within a hardwood forest matrix. Dendroecological techniques were used to date the scars, which were used to calculate fire intervals. A variety of analyses were carried out: Pearson correlation analysis, to investigate whether fire activity varied over time (under changing land uses); Kruskal–Wallis analysis, to examine whether fire frequency varied spatially (among study sites); chi-square analysis, to test whether scar seasonality changed temporally; and superposed epoch analysis, to explore whether fire activity was associated with interannual climatic variations in moisture, as characterized by the Palmer drought severity index (PDSI).

Results Fire scars dated back to the 17th or early 18th century (depending on site). The filtered composite fire interval, considered to be a particularly reliable estimate of fire interval, averaged between 6 and 8 years. Fire frequency remained fairly constant from the beginning of the record until effective fire suppression began in the early 20th century, after which burning virtually ceased. Fire occurred more frequently at the easternmost site, which was located in the Blue Ridge province of the Appalachian Mountains, than at the other two sites, in the Ridge and Valley province. Scar seasonality showed no discernible trend over time. Fire was associated with low PDSI (i.e. dry years) at two of the study sites.

Main conclusions Fire occurred frequently at these central Appalachian study sites during the period of aboriginal depopulation that preceded European colonization, and throughout the periods of European settlement and industrialization (with mining, logging and railroads) that followed. Our results match those from other fire-history sites in the central and southern Appalachian Mountains, and suggest that fire was an important factor influencing vegetation development in the temperate forests covering this region.

Keywords

Appalachian Mountains, disturbance, fire ecology, fire geography, fire history, fire interval, spatial patterns, temperate forest, tree ring, vegetation dynamics.

*Correspondence: Charles Lafon, Department of Geography, 3147 TAMU, College Station, TX 77843, USA.
E-mail: clafon@geog.tamu.edu

†Present address: Geography Faculty, Division of Social Science, Blinn College, Bryan, TX 77805, USA

INTRODUCTION

The vegetation in the Earth's temperate regions has developed largely without fire since the early to mid-20th century because of fire suppression combined with the low ignition frequency inherent to land uses such as sedentary agriculture and modern timber management (Williams, 1989; Niklasson *et al.*, 2010). Fire suppression has been based on the understanding that fire historically played a limited role in vegetation development (e.g. Clements, 1936; Raup, 1937) and that vegetation requires protection from fire (Brown & Davis, 1973). This view has been challenged widely (e.g. Stewart, 1956; Komarek, 1962). Today, fire is considered to be essential to a number of mid-latitude ecosystems, from dry forests and woodlands to grasslands and mediterranean shrublands (Grissino-Mayer *et al.*, 2004; Bond & Keeley, 2005). Until quite recently, the role of fire in the temperate forests occupying humid regions such as eastern North America has received relatively little attention (Runkle, 1990). However, in the last two decades it has become increasingly apparent that fire has shaped these forests too (e.g. Lorimer *et al.*, 1994; Abrams *et al.*, 1999).

In the absence of fire, important temperate tree species are declining in abundance and failing to regenerate. Pine (*Pinus* L.) and oak (*Quercus* L.) species, for example, are being replaced by fire-intolerant mesophytic species such as maple (*Acer* L.) and beech (*Fagus* L.), throughout eastern North America, Europe and eastern Asia (Lorimer *et al.*, 1994; Abrams *et al.*, 1999; Niklasson *et al.*, 2010). Humid climates generally promote forests with a continuous canopy and strong vertical light attenuation (Smith & Huston, 1989). Low understorey light availability impedes the establishment and growth of pines and oaks (Lorimer *et al.*, 1994), and the abundance of pine and oak trees in older age classes of many temperate forests suggests that the stands burned regularly in the past (e.g. Abrams *et al.*, 1999; Niklasson *et al.*, 2010). According to the fire-oak hypothesis (Lorimer *et al.*, 1994; Nowacki & Abrams, 2008), periodic surface fires maintained open canopy and understorey conditions that enabled oaks to establish. The relatively thick bark, large roots and strong sprouting capacity of oaks appear to favour them over competing fire-intolerant hardwoods under conditions with frequent burning of low to moderate severity. Likewise, several temperate pines have traits, including serotinous cones and thick bark (e.g. Williams, 1998), that promote post-fire regeneration and protect them from lethal temperatures.

A key question regarding temperate forest development is how often the forests burned under past land uses, before fire suppression (Niklasson *et al.*, 2010; McEwan *et al.*, 2011). Several authors have suggested that fire was common. Pyne (1982), for example, argued that extensive land use, such as agricultural expansion, promoted widespread burning of European forests, and that switching to sedentary agriculture and commercial forestry reduced fire frequency. Such land-use changes have occurred more rapidly, and more recently, in North America than in the Old World (Pyne,

1982), and therefore more evidence exists regarding the fire history of North America. For the present study, we investigated how often fires have burned pine-oak forests in the Appalachian Mountains, in Virginia, USA. These mountains, which lie within the heart of eastern North America's temperate forest region, are covered primarily by oak-dominated forests, with pine and other stands interspersed.

The region's aboriginal inhabitants used fire for various reasons, such as maintaining clearings and driving game (Williams, 1989). Early European travellers reported open forests and scattered prairies, conditions apparently maintained by fire, and some travellers witnessed aboriginal burning (Williams, 1989; Denevan, 1992). However, such anecdotes do not allow quantitative estimates of fire intervals, and do not indicate whether fires were widespread (e.g. Denevan, 1992) or only locally common near Indian villages (e.g. Russell, 1983). Witness tree records from original land surveys imply that fire-associated species such as oak and pine were extensive before European settlement began (e.g. Cowell, 1995), although, like travel accounts, these records are inadequate for quantifying fire intervals. Also, because native populations collapsed well before European settlement in many places (Denevan, 1992; Egloff & Woodward, 2006), some researchers have questioned the role of fire in shaping the vegetation that existed at the time of settlement (McEwan *et al.*, 2011).

Fire frequency after European settlement also remains uncertain. Fire may have occurred rarely at first, as pockets of settlement emerged on depopulated landscapes, and then increased gradually under expanding human land use (Williams, 1998). Alternatively, mild surface fires may have occurred regularly throughout both aboriginal and white occupancy (Pyne, 1982). What seems clear is that frequent, severe burning erupted in the late 19th-early 20th centuries (McEwan *et al.*, 2011), when extensive industrial logging produced slash that fed devastating wildfires (Pyne, 1982). These fires threatened forest recovery and prompted the subsequent fire-suppression efforts (Pyne, 1982; Williams, 1989). Without reliable, multi-century estimates of fire frequency, however, the fire regimes of the logging period and the fire-exclusion era cannot be placed within a historical context.

For this study, we sought direct evidence of past fires using fire-scarred trees. Dendroecological analyses of fire scars permit fire-frequency estimates, including temporal variations in frequency as climate or land use changed. Such work supports our understanding of vegetation history and plant distributions while guiding ecosystem restoration, including controlled burning to reintroduce fire with intervals and variability similar to those of the past. Eastern USA provides fewer opportunities for fire-history research than western USA because past forest clearance and rapid wood decay have destroyed old trees that may have contained fire scars that preserved a long record of burning. Most fire-history reconstructions developed for eastern forests reach back only to the mid- or late 1800s (e.g. McEwan *et al.*, 2007; Hessl *et al.*, 2011). They portray frequent burning, with

intervals of a few years between fires, around the turn of the 20th century, when industrial logging climaxed. For a few locations scattered across the eastern forest region (e.g. Shumway *et al.*, 2001; Guyette *et al.*, 2002; Brose *et al.*, 2013; Flatley *et al.*, 2013; McEwan *et al.*, 2014), older fire-scarred trees have revealed two or more centuries of frequent burning before the 20th-century decline in fire frequency. If uncertainties over the role of fire in vegetation development are to be clarified, it is essential that fire-scar records are obtained covering the period of aboriginal depopulation and early European settlement (McEwan *et al.*, 2011).

For the study presented here, we identified sites in the central Appalachian Mountains that contained numerous old, fire-scarred pine trees that enabled us to address three objectives. (1) To reconstruct an annually resolved record of fire from tree-ring records over as long a period as possible using dendroecological techniques: this research extends our previous work at Mill Mountain in western Virginia (Aldrich *et al.*, 2010), where we compiled a fire-scar record that extends back to 1704 and therefore pre-dates European settlement. Here we add two additional study sites, providing an even longer history of fire. (2) To estimate historical fire intervals for these two sites. (3) To investigate how variations in land use and climate affected fire occurrence at these two sites and at Mill Mountain. Did fire occurrence increase as human land use expanded? Did it peak under industrial exploitation in the mid-1800s–early 1900s? Were interannual climatic cycles of wetness and drought associated with variations in fire activity?

MATERIALS AND METHODS

The central Appalachian study area

The three study sites, Mill Mountain, Reddish Knob and Kelley Mountain, lie within the George Washington National Forest (GWNF), which straddles portions of the Ridge and Valley and the Blue Ridge physiographical provinces of the Appalachian Mountains in Virginia, USA (Fig. 1). The area lies within a humid temperate ecoregion (Bailey, 1998). January temperatures average -3.4 – 0.2 °C at weather stations across the study area, while July temperatures average 18.9 – 23.8 °C (NCDC, 2002). Moderate precipitation falls every month. Mean annual precipitation is 850–1150 mm for the Ridge and Valley, and 1000–1400 mm for the Blue Ridge (NCDC, 2002).

The primary vegetation feature on major ridges within GWNF is a montane oak–pine complex that comprises alternating patches of oak-dominated and pine-dominated forest (Simon, 2011). This vegetation was our focus. Oak-dominated stands containing several oak and other hardwood species occupy a broad range of submesic to subxeric sites across the dissected mountain slopes (Simon, 2011). Within this hardwood forest matrix, patches of yellow pine cloak west-facing aspects (Fig. 2) and create a pine–hardwood mosaic that is repeated throughout the GWNF and the larger

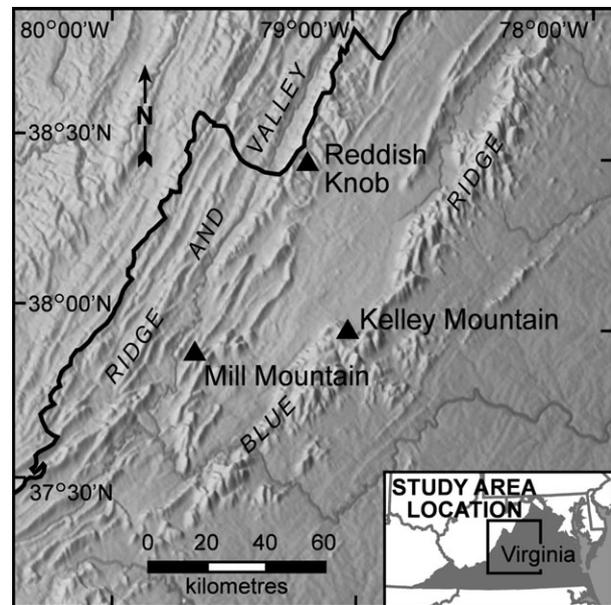


Figure 1 The study area within the central Appalachian Mountains, Virginia, USA. Triangles mark the location of the three fire-history study sites. The shaded relief image is from T. Patterson of the US National Park Service, Harpers Ferry, WV, USA.

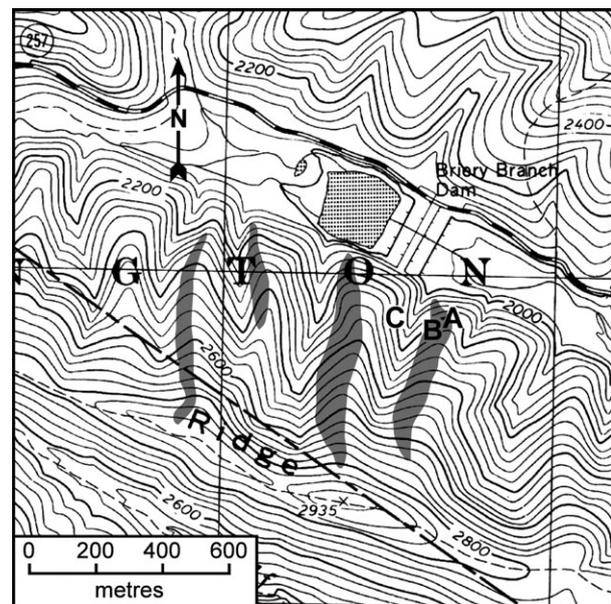


Figure 2 The Reddish Knob study site, which exemplifies the dissected slopes typical of the central Appalachian Mountains, Virginia, USA. The shaded strips along the west-facing facets of the spurs indicate the approximate location of the four pine stands from which we collected fire scars. The letters A, B and C along the easternmost pine stand correspond with the points in the photograph in Fig. 3. The underlying topographical map is a portion of the Reddish Knob 7.5' × 7.5' quadrangle of the US Geological Survey (<http://nationalmap.gov/ustopo/>; accessed June 2014), with a contour interval of 40 ft (12 m).

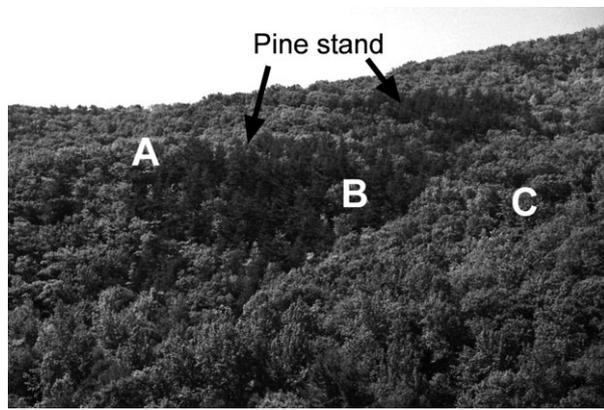


Figure 3 Photograph of a portion of the Reddish Knob study site from the central Appalachian Mountains, Virginia, USA. The photograph was taken from the Briery Branch Dam (see Fig. 2), with a southwards view towards the easternmost of the four pine stands we sampled. The pine stand is visible as a patch of darker trees surrounded by lighter hardwood forest. The letters A, B and C correspond with the points marked on the topographical map (Fig. 2), where A is positioned at the crest of a spur, B is on the west-facing facet of the spur, and C is on the east-facing facet of the adjacent spur.

region. These pine-dominated stands, the source of our fire-scarred trees, contain Table Mountain pine (*Pinus pungens* Lamb.), pitch pine (*Pinus rigida* Mill.), Virginia pine (*P. virginiana* Mill.) and a few hardwoods. The pine stands cover about 10% of GWNF, and the associated oak-dominated forests account for about 64% (Simon, 2011). Therefore, oak- and pine-dominated forests similar to the study sites occupy about 74% of GWNF, and 63% of a larger region encompassing GWNF and other public and private lands (Simon, 2011). Our study therefore represented most of the landscape in and around the GWNF. The remainder of the landscape is covered with various ecosystems (Simon, 2011), from xerophytic pine–oak woodlands on shale outcrops to mesophytic hardwood–eastern hemlock [*Tsuga canadensis* (L.) Carr.] forests in ravines and coves.

People have inhabited the region for thousands of years (Egloff & Woodward, 2006). By the late Woodland Period (AD 900–1600), Indians had established villages along major streams, practising agriculture combined with hunting and gathering. They may have maintained grassland areas through regular burning (Mitchell, 1977). Their settlements were abandoned before the 1700s, possibly reflecting depopulation associated with intertribal conflicts and/or European diseases (Mitchell, 1977; Egloff & Woodward, 2006). Native American trading, hunting and warring parties continued to use the area, however. Europeans began settling the area during the mid-1700s (Morton, 1917; Mitchell, 1977), although the study sites we identified were located in mountainous terrain that was settled after the river valleys. The three study sites resembled oak- and pine-forested mountain slopes throughout the central Appalachian Mountains but probably did not represent conditions near aboriginal or European villages.

The study sites

Our field reconnaissance showed that pines with ‘catfaces’ bearing fire scars (Arno & Sneek, 1977) were widespread across GWNF. We narrowed our study to three sites containing abundant fire-scarred trees that would yield large sample sizes and reliably portray fire history (Van Horne & Fule, 2006). Fire-scarred wood was collected at each study site from four pine stands, each about 2–11 ha in area and separated from neighbouring stands by oak-dominated forests on alternating slope facets (Figs 2 & 3). The dissected slopes were drained by ephemeral streams that ordinarily would not impede fire spread between stands.

The Mill Mountain site encompassed four pine stands within about 1 km² on the north-west side of the mountain (37°53′N, 79°38′W; elevation 690–900 m), within a large, forested Ridge and Valley landscape. Closely spaced ridges around Mill Mountain form a rugged landscape with limited agricultural opportunities. The area was isolated from large aboriginal populations (Geier & Boyer, 1982) and remained sparsely populated after European settlement, which began 6–7 km to the south-west along the Cowpasture River, a James River tributary, around 1745 (Morton, 1917). According to GWNF land records (on file at the Forest Supervisor’s Office in Roanoke, VA, USA), original land grants on Mill Mountain itself were issued mostly during 1795–1825, possibly indicating settlement along the narrow valleys near the study site at that time. The greatest human influence resulted from iron furnaces, which probably spread wildfires onto Mill Mountain while operating along the valley to its south-east during 1827–1925 (Russ *et al.*, 1995). Other human influences included a railroad constructed in 1857 (Morton, 1917), logging of the lower slopes of Mill Mountain in 1927–1928, and US Forest Service (USFS) acquisition in 1937 (GWNF land records). The middle and upper slopes of Mill Mountain, including the stands we sampled, were apparently not logged (Aldrich *et al.*, 2010).

The Reddish Knob site included four pine stands within about 0.5 km² on Wolf Ridge (38°26′N, 79°09′W; elevation 630–900 m), a spur of Reddish Knob within a series of rugged, forested ridges on the east slope of Shenandoah Mountain within the Ridge and Valley. The study site was about 35 km north-west of the Shenandoah River. Aboriginal villages along the river may have been too distant to affect the fire regime at the site, but small seasonal camps have been found only 3 km away (Nash, 1991). Pockets of European settlement appeared in the Shenandoah Valley as early as c. 1730 (Mitchell, 1977) but the issuance of land grants (recorded in GWNF land records) around the study site suggests that settlement and/or other land uses emerged about 1796 and expanded gradually throughout the 19th century. The USFS purchased the area in 1916. Timberland descriptions at that time indicate a landscape affected by repeated burning, cattle grazing, insect outbreaks and timbering, but little agriculture.

The Kelley Mountain site included four pine stands that occupied steep middle and upper slopes (37°55' N, 79°02' W; elevation 930–1010 m) within about 1 km² of the Blue Ridge Mountains south-east of the Shenandoah Valley. Archaeological evidence has revealed several aboriginal camps and quarries near the study site, as near as 1 km (Tolley, 1983). The mountainous terrain probably precluded substantial European settlement. Land grants issued in 1796–1797 may indicate limited settlement but the major human activities in the vicinity were iron and manganese mining, which had begun by the mid-1800s (Watson *et al.*, 1907), and logging, which occurred around 1900 (GWNF land records). Logging, burning, insect outbreaks and ice storms had eliminated most of the merchantable timber before USFS acquisition in 1923–1924.

Data collection and analysis

During 2003–2005, we sawed full or partial fire-scarred cross-sections from living and dead Table Mountain pine and pitch pine trees, and cored additional living pines with increment borers to aid chronology development. Cores and cross-sections were surfaced with a belt sander (Orvis & Grissino-Mayer, 2002). The tree rings were cross-dated visually and assigned a calendar year using skeleton plots and lists of narrow rings (Stokes & Smiley, 1968; Yamaguchi, 1991). We measured tree rings to the nearest 0.001 mm using a Velmex measuring stage (Velmex, Bloomfield, New York, NY) and j2x measurement software (ProjectJ2X; Voor-tech Consulting, Holderness, NH, USA), and entered the measurements into the software program COFECHA (Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, USA) to verify and refine dating (Holmes, 1983).

We dated fire scars to the year of formation in order to reconstruct fire history (objective 1). We designated scar seasonality based on the position within the ring (Grissino-Mayer, 2001): (1) dormant, positioned between rings and assigned the date of the following ring; (2) earlywood; (3) latewood; and (4) undetermined. Scar information was input into the FHX2 program (Grissino-Mayer, 2001) for graphing, summarizing scar seasonality and analysing fire-return intervals. To characterize the central tendency in fire intervals (objective 2), we fitted a Weibull distribution (Weibull, 1951) in FHX2 and calculated the mean fire interval (MFI) and Weibull median interval (WMI). We also delineated the range of historical variability within the Weibull-modelled distribution by calculating lower and upper exceedance intervals (LEI and UEI, respectively), within which 75% of all fire intervals would be expected to fall.

A fire-scarred tree yields an imperfect record of the fires that burnt it (Van Horne & Fule, 2006). Therefore, to improve the reliability of fire-interval estimates we grouped the fire-scarred trees from each study site in five different ways to obtain the following estimates of MFI, WMI, LEI and UEI (Aldrich *et al.*, 2010). (1) The point fire interval estimated fire frequency at any point in the landscape using

fire intervals from individual trees. For each tree it included only the intervals covered by 'recorder' years (Grissino-Mayer, 2001). Recorder years began with the initial scar, which increased susceptibility to subsequent scarring, and continued through later intervals until the tree had healed over the wound. If subsequent decay or burning obscured part of the cross-section, that segment was considered as non-recording. Limiting the fire-interval analysis to recording intervals is standard practice (Grissino-Mayer *et al.*, 2004) to ensure that calculations are based only on periods covered by fire-scar data (Aldrich *et al.*, 2010). Unfortunately, trees may not record all the fires that burn them, even during recording periods, and therefore the point fire interval probably overestimates fire-interval length. (2) The stand-level composite fire interval was calculated by combining the fires recorded by all trees in a stand, to diminish the probability of missing a fire and overestimating the fire interval. FHX2 does not exclude non-recording intervals in this case, because non-recording intervals of one tree are often covered by recording intervals in others. (3) The combined-stand composite fire interval was calculated by combining the fires recorded by all trees in all four stands at the study site. This analysis is widely used because it minimizes the probability of missing a fire. It provides the most comprehensive fire record and is useful for exploring temporal variations in fire activity (Aldrich *et al.*, 2010). However, it can overcompensate for the imperfect recorder problem if many of the fires did not burn the entire study site, in which case fire-interval length would be underestimated. (4) The filtered combined-stand composite fire interval addressed this potential overcompensation by considering only 'major' fires, defined here as those scarring $\geq 25\%$ of all recorder trees and a minimum of two trees. Filtering appears to provide a reliable estimate of the typical fire interval (Van Horne & Fule, 2006). (5) The area-wide fire interval was calculated from the most widespread fires, those found in all recording stands at a study site, unless only one stand was recording. The first published designation of 'area-wide' fires (Fisher *et al.*, 1987) referred to fires that spread throughout a 5.5-km² study area to encompass all clusters of fire-scarred trees and the vegetation between them. The designation pertains equally to our smaller sites, hence our usage of the term. An area-wide fire evidently burned through the intervening hardwood forests to reach multiple pine stands at a study site (Aldrich *et al.*, 2010).

Having characterized the fire record at Reddish Knob and Kelley Mountain, we analysed temporal trends in burning for all three study sites (objective 3), including the Mill Mountain site for which we had already created a fire chronology (Aldrich *et al.*, 2010). For each site, we first calculated the mean number of fire scars per recording tree per decade, a fire-frequency characterization that permits comparison across decades with different sample sizes of recording trees (Flatley *et al.*, 2013). We then used Pearson correlation (Zar, 1999) to determine whether this measure of fire frequency changed over time as human land use expanded. We also

tested whether it varied among the three study sites, using a Kruskal–Wallis analysis and Dunn’s post-hoc pairwise comparisons (Zar, 1999). To explore whether scar seasonality varied temporally, as, for example, might occur if the proportion of human versus lightning ignitions changed (Grissino-Mayer *et al.*, 2004), we used chi-square analysis (Zar, 1999) and tested whether the number of growing-season scars was related to time period (defined here as before 1750, 1750–1850, and after 1850). In this case, growing-season scars included both earlywood and latewood scars.

We used superposed epoch analysis (SEA) to ascertain whether fires were associated with anomalous climatic conditions during the year of fire or preceding years (Grissino-Mayer, 2001). The climate variable used here was the dendroclimatically reconstructed summer Palmer drought severity index (PDSI) for grid 247 in western Virginia (Cook *et al.*, 1999). The fire data we used were the ‘major’ fires described above. We also conducted SEA for region-wide fire years, defined as years with a fire recorded at all three study sites.

RESULTS

Fire history of Reddish Knob and Kelley Mountain

The fire-history reconstructions were based on 76 fire-scarred trees from Reddish Knob and 92 fire-scarred trees from Kelley Mountain. Fires occurred regularly from the beginning of each chronology until the early 1900s (Fig. 4). The Reddish Knob trees bore 418 scars that corresponded to 55 fire years during 1671–1913. One tree also contained four scars formed between 1963 and 1980. The trees from Kelley Mountain had 495 scars corresponding to 62 fire years during 1638–1921. For scarred trees that we could age, i.e. they had an intact pith, the mean age at the time of initial scarring was 12.8 years at Reddish Knob (range 4–33 years, $n = 37$) and 12.6 years at Kelley Mountain (range 5–33 years, $n = 40$). The mean stem diameter of the trees at the time of initial scarring was 5.2 cm at Reddish Knob (range 4.5–33.0 cm, $n = 31$) and 5.1 cm at Kelley Mountain (range 1.6–10.8 cm, $n = 33$).

We could determine the seasonality of 124, or 29.7%, of the Reddish Knob scars; 56.5% of them were dormant, 37.1% were earlywood, and 6.4% were latewood. For Kelley Mountain, we determined the seasonality of 223, or 52.3%, of the fire scars; 86.1% of them were dormant and 13.9% were earlywood.

Fire intervals at Reddish Knob and Kelley Mountain

The intervals between fires ranged from 1 to 34 years (Table 1). The Reddish Knob fire interval calculations excluded four recent intervals resulting from a tree with scars formed after the last major fire in 1913. These intervals were excluded because of our interest in the pre-suppression fire regime, as in other studies (e.g. Grissino-Mayer *et al.*, 2004)

where one or more trees bear a few suppression-era scars. For the period of reliability (Grissino-Mayer *et al.*, 2004), which began with the first year with two or more scarred trees and ended with the last major fire, the various analyses yielded MFI and WMI estimates of 4.6–12.5 years for Reddish Knob and 3.7–7.8 years for Kelley Mountain (Table 1). The fire-interval estimates for Mill Mountain were reported by Aldrich *et al.* (2010).

Variations in fire occurrence at Mill Mountain, Reddish Knob and Kelley Mountain

The mean number of fire scars per recording tree per decade (Fig. 5) did not vary temporally during the centuries preceding fire exclusion (correlation analysis for Mill Mountain, $r = 0.06$, $P = 0.77$; for Reddish Knob, $r = -0.05$, $P = 0.81$; for Kelley Mountain, $r = 0.03$, $P = 0.88$). It varied among the study sites, however (Kruskal–Wallis test, $\chi^2 = 10.07$, d.f. = 2, $P = 0.01$), with Kelley Mountain showing a higher fire frequency than Mill Mountain or Reddish Knob (Dunn’s tests, $P < 0.05$).

Scar seasonality varied temporally at Reddish Knob. The period 1750–1850 had an unexpectedly low frequency of growing-season scars compared with the earlier (pre-1750) and later (post-1850) periods (chi-square test, $\chi^2 = 9.01$, d.f. = 2, $P = 0.01$). No such relationship existed for Mill Mountain ($\chi^2 = 3.01$, d.f. = 2, $P = 0.22$) or Kelley Mountain ($\chi^2 = 2.21$, d.f. = 2, $P = 0.33$).

Interannual variations in moisture were related to fire occurrence at Mill Mountain (Fig. 6a) and Reddish Knob (Fig. 6b), where fires were associated with drought (negative PDSI) during the year of fire. Kelley Mountain did not display such a relationship (Fig. 6c). The region-wide fire years exhibited a pattern similar to Mill Mountain and Reddish Knob, albeit not statistically significant (Fig. 6d).

DISCUSSION

The history and frequency of fire at Reddish Knob and Kelley Mountain

The record of frequent burning going back to the 17th century, before European settlement, agrees with suggestions that fire was common in pine- and oak-dominated forests. Frequent fire would have subdued heavy fuel accumulations (Harrod *et al.*, 2000) and thereby favoured burns of modest severity that scarred even small pines without killing them. Our findings are consistent with the general expectation (Pyne, 1982) that fire was common under extensive land uses, such as hunting and agricultural expansion. These land uses probably encouraged the growth of large fires, as fire suppression and modern landscape fragmentation were lacking. Spatially extensive fires could help account for short fire intervals, especially during periods with sparse human ignitions, because a regime of expansive fires would have conveyed fire regularly through many stands without requiring

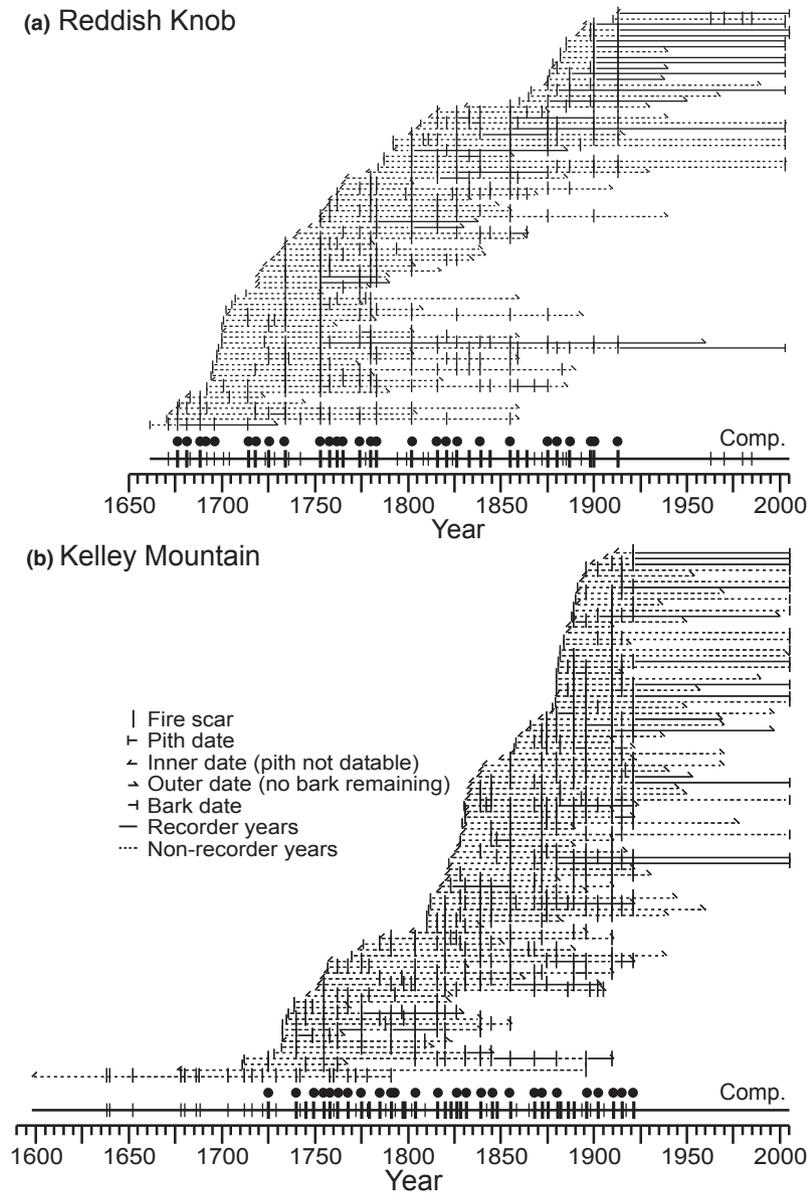


Figure 4 Fire charts for sites from the central Appalachian Mountains, Virginia, USA: (a) Reddish Knob and (b) Kelley Mountain. Horizontal lines represent the time spanned by the trees sampled, and short vertical lines indicate dated fire scars. On the composite fire axis (Comp.), extending along the bottom of each chart, the longer and heavier vertical bars indicate major fires recorded by 25% or more trees. The shorter, thinner bars portray the remaining fires that scarred fewer trees. The closed circles over the composite axis indicate the area-wide fires.

frequent ignitions in every stand (Pyne, 1982; Ward *et al.*, 2001).

The area-wide fires we documented are consistent with the spread of fires across multiple stands within oak–pine vegetation covering a mountain slope. The short intervals between area-wide fires suggest that fires regularly extended beyond individual pine stands to encompass the intervening oak-dominated stands, which would have promoted fire spread because of the relatively combustible oak litter (Nowacki & Abrams, 2008) and flammable grass–shrub understorey that apparently developed through frequent burning (Harrod *et al.*, 2000). Although some area-wide fires conceivably

originated from multiple synchronous ignitions across all the pine stands at a study site, rather than by fire spreading between stands, fires could not have been ignited concurrently at that density on a regular basis. To ignite four pine stands synchronously within a 1-km² area (roughly the size of the study sites) would require about 4000 times the current annual lightning ignition density (0.00101 ignition km⁻² year⁻¹) in the central Appalachian region (Lafon *et al.*, 2005), or almost 900 times the current anthropogenic ignition density (0.00448 ignition km⁻² year⁻¹). Such elevated ignition densities are a less likely explanation of the frequent, synchronous burning of multiple pine stands than the

Table 1 Fire-interval calculations for Reddish Knob and Kelley Mountain (central Appalachian Mountains, Virginia, USA).

	MFI	WMI	SD	LEI	UEI	Range	Number of intervals	Years covered
Reddish Knob								
Point fire interval (<i>n</i> = 76)	12.5	11.3	6.5	4.9	19.8	2–34	70	1676–1913
Stand-level composite fire interval								
Stand A (<i>n</i> = 13)	9.5	9.1	5	4.3	15	4–20	25	1676–1913
Stand B (<i>n</i> = 32)	6.5	5.8	4.7	2	11.7	2–19	30	1718–1913
Stand C (<i>n</i> = 7)	9.6	8.6	6.3	3.2	16.8	2–19	14	1725–1913
Stand D (<i>n</i> = 21)	7.1	6.2	5.5	2	13.1	2–23	28	1714–1913
Combined-stand composite fire interval	4.8	4.6	2.6	2	8	2–13	49	1676–1913
Filtered composite fire interval	8.2	7.4	5.6	2.7	14.4	2–26	29	1676–1913
Area-wide fire interval	8.8	8	5.7	3	15	2–20	27	1676–1913
Kelley Mountain								
Point fire interval (<i>n</i> = 92)	7.1	7	3.1	3.6	10.9	3–16	84	1725–1921
Stand-level composite fire interval								
Stand A (<i>n</i> = 27)	5.5	5.3	2.3	2.8	8.2	3–12	25	1785–1921
Stand B (<i>n</i> = 37)	6.3	5.5	5.2	1.8	11.6	1–29	28	1745–1921
Stand C (<i>n</i> = 17)	5.7	5.3	3.3	2.2	9.5	2–13	32	1740–1921
Stand D (<i>n</i> = 10)	6.7	6.2	4.3	2.4	12	2–16	27	1740–1921
Combined-stand composite fire interval	3.9	3.7	1.9	1.8	6.2	2–11	50	1725–1921
Filtered composite fire interval	5.8	5.5	3.1	2.5	9.4	2–15	34	1725–1921
Area-wide fire interval	7.8	7	3.6	3.8	12.1	2–16	25	1725–1921

MFI, mean fire interval (years); WMI, Weibull median interval (years); SD, standard deviation (years); LEI, lower exceedance level (years); UEI, upper exceedance level (years).

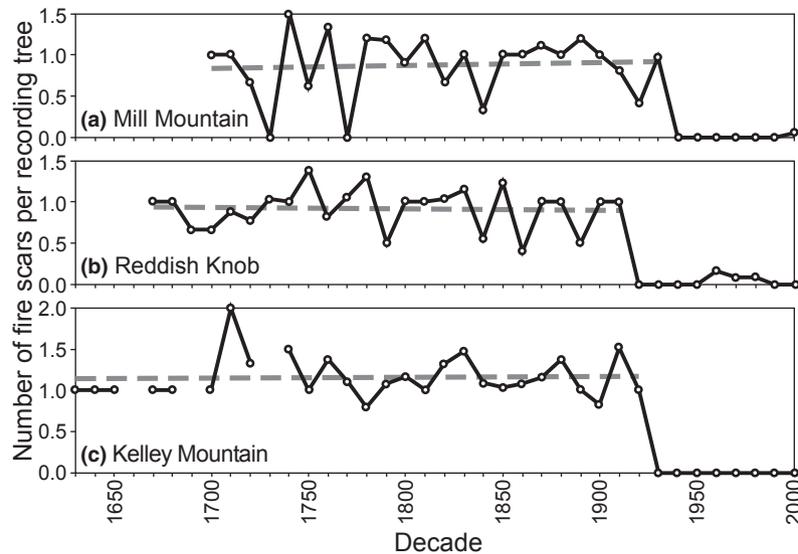


Figure 5 Temporal trends in fire activity from sites in the central Appalachian Mountains, Virginia, USA, depicted as the number of fire scars per recording tree per decade. Gaps in the data line indicate decades without recording trees. The dashed lines are the trend lines fitted to the pre-suppression points.

expansion of individual fires to cover areas well beyond their ignition points, especially considering the sparse human populations of the 1600s–1700s.

We contend, therefore, that our fire histories apply not only to pine stands, but to the entire oak–pine mosaic covering Appalachian slopes. These oak- and pine-dominated stands developed under frequent burning. Unfortunately, the ability of pines and xerophytic hardwoods to occupy droughty ridgetops and rocky outcrops has, in some cases, given

the erroneous impression that fire-history results obtained from montane pine stands, such as those studied here, apply only to narrow ridgetop communities and not to the broader forested landscape (Hart & Buchanan, 2012). Based on such an interpretation, Matlack (2013) argued that, within eastern North America’s temperate forest region, frequent burning was probably confined to isolated ridgetops and other xeric microsites, and to the immediate vicinity of aboriginal villages. The extensive forests between these sites would have

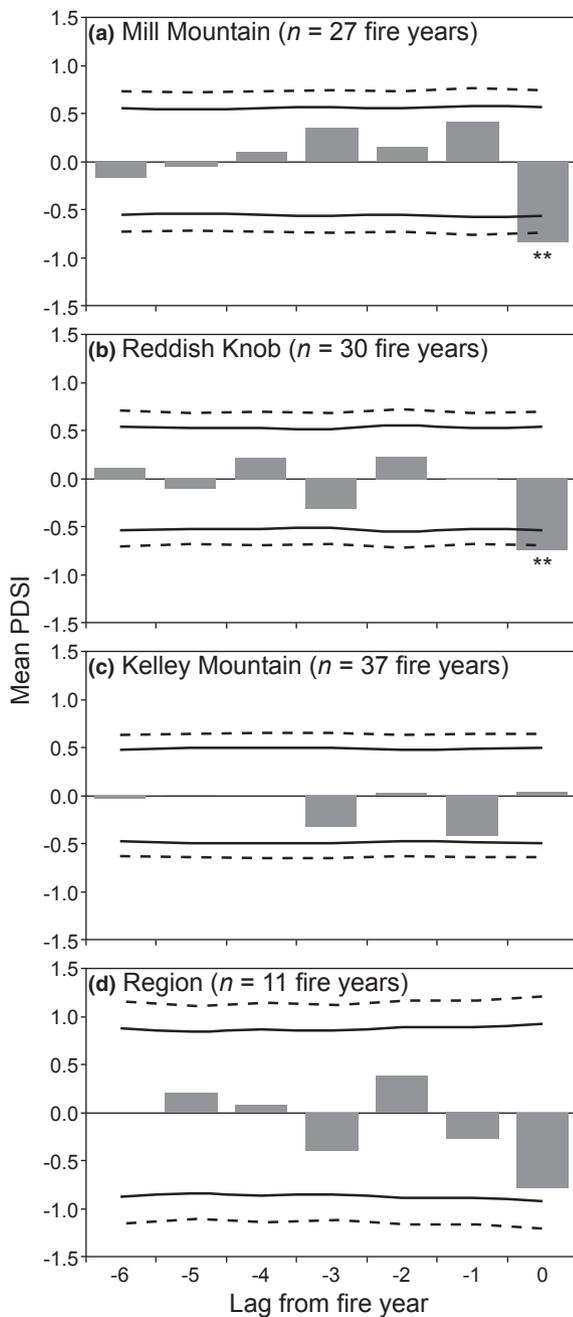


Figure 6 Results of the superposed epoch analysis for sites from the central Appalachian Mountains, Virginia, USA: (a–c) the major fire years at each site and (d) the region-wide fire years. The 95% and 99% confidence intervals are indicated by the solid and dashed lines, respectively. Asterisks mark the statistically significant Palmer drought severity index (PDSI) anomalies.

burned infrequently. Note, however, that the pine stands we sampled, like most central Appalachian pine stands, occupied west-facing facets of mountain slopes, not merely ridgetops, and were interspersed among hardwood-dominated forests. The area-wide burns indicated that fires commonly passed through various forest stands. These results agree with charcoal evidence of fires spanning a southern Appalachian

topographical gradient with pine and oak stands and even mesophytic hardwood forests (Fesenmyer & Christensen, 2010). Indeed, wildfires sometimes elude control today and envelop broad swathes of terrain (Flatley *et al.*, 2011). Such fires appear to have been common historically across the oak- and pine-forested slopes at our study sites, which were outside the local vicinity of aboriginal and early European villages.

Variations in fire occurrence at Mill Mountain, Reddish Knob and Kelley Mountain

Our findings highlight temporal variations in burning at two scales. First, and most striking, is the switch from consistent, frequent burning to fire exclusion. Before the 20th century, burning continued despite dramatic changes in land use and human population. Fires burned as commonly under aboriginal depopulation and nascent European settlement as under subsequent land uses, probably through large fires spreading from sparse lightning and/or human ignitions. Whether lightning or humans ignited most fires cannot be ascertained through fire scars, but scar seasonality suggests no major temporal shifts in ignition source. The prevailing dormant and earlywood scars match the bimodal spring–autumn peaks observed today for human ignitions (Lafon *et al.*, 2005), suggesting that anthropogenic fires dominated historically, although the current lightning fire season overlaps the spring anthropogenic fire season, and therefore lightning cannot be ruled out as an ignition source for historical dormant-season fires.

The failure to discern a rise in fire frequency during the industrial exploitation period matches some other fire-history records (e.g. Shumway *et al.*, 2001; Flatley *et al.*, 2013) and suggests that fires were not abnormally common during that time. It is the fire-suppression era that contrasts with all previous land-use episodes. Without fire, the vegetation developing since the early 20th century has emerged within a starkly different environment than existed for 250 years or more prior to fire suppression.

The second temporal pattern of burning emerges at an annual time scale, between wetter and drier years. Dry conditions at Mill Mountain and Reddish Knob favoured burning, and this finding agrees with fire–climate relationships observed today in the Appalachian Mountains and other humid regions (Lafon *et al.*, 2005). It contrasts, however, with the pattern found at Kelley Mountain and other Appalachian fire-history sites (McEwan *et al.*, 2007; Brose *et al.*, 2013; Flatley *et al.*, 2013), where statistically significant fire–climate relationships fail to emerge. Those weak relationships may indicate that people overwhelmed climatic influences by igniting fires within favourable burning windows during normal or even wet years (McEwan *et al.*, 2007), and/or that the seasonal mismatch between reconstructed PDSI (summer) and fire scars (mostly dormant season) obscures fire–climate relationships. Why the relationships for Mill Mountain and Reddish Knob differ from Kelley Mountain and other

locations is not readily apparent, but they may reflect a lower level of human influence.

The differences in climatic sensitivity between Mill Mountain/Reddish Knob and Kelley Mountain might also indicate a more favourable overall burning environment at Kelley Mountain: fire ignition and spread would not require anomalous dry years if widespread burning was favoured during normal years at Kelley Mountain. The Blue Ridge, which includes Kelley Mountain, favours greater fire activity than the Ridge and Valley and the Appalachian Plateau to the west, apparently because of its greater intra-annual precipitation variability (Lafon & Quiring, 2012). High intra-annual variability emerges along the Blue Ridge because heavy precipitation events alternate with stretches of multiple consecutive dry days. The dry spells permit fuels to dry and fires to spread. These spatial differences in historical fire frequency mirror the broader geography of recent burning (last 25–40 years) across the eastern US temperate forest region, where fire activity rises along a gradient of intra-annual precipitation variability between the north-eastern USA and Gulf Coastal Plain (Lafon & Quiring, 2012). If such climatic differences consistently moulded the geography of burning for centuries, as suggested by our fire histories, they could have indirectly shaped the biogeographical distributions of fire-associated plants.

Today, in the general absence of fire, such plants as oak and pine are being replaced by shade-tolerant, fire-sensitive trees across broad sections of eastern North America, and also in the temperate forests of Europe and eastern Asia. These ongoing changes have raised concerns about the long-term viability of oak- and pine-dominated vegetation, and have contributed to a growing understanding that fire is an important process in temperate forests. Central to this understanding is the hypothesis that fires occurred regularly in the past. The fire-scarred trees in our study reveal a steady level of frequent fire before the suppression era. This finding is consistent with the fire-oak hypothesis and with previous empirical studies, for example of fire scars and witness trees, suggesting that oak- and pine-dominated forests developed historically under frequent burning.

ACKNOWLEDGEMENTS

This research was funded by the National Interagency Fire Center's Joint Fire Science Program through cooperative agreements with the George Washington and Jefferson National Forests. We appreciate the cooperation of Steve Croy, Elaine Kennedy Sutherland and other US Forest Service personnel, including George Annis, Beth Atchley, Beth Buchanan, Carol Hardy Croy, Jason Hattersley, Kenneth Hickman, Herbie Huffman, Mitch Kerr, Jesse Overcash, Zach Pennington, Butch Shaw, Steve Smestad and Danny Wright. We thank Keith Egloff and Laura Galke for access to archaeological reports. We also thank John Aldrich, Jessica Brogden, Gabe Burns, James Dalton, Alexis Green, Jennifer Hoss, Adam Krustchinsky, Nelson Lafon, Lisa LaForest, Evan Larson, Daniel Lewis, David Mann, Alison Miller, Stockton

Maxwell, Michelle Pfeffer, Paul Rindfleisch, Lauren Spencer, Kirk Stueve, Chris Underwood and Saskia van de Gevel for assistance with fieldwork and sample preparation/analysis. We thank three anonymous referees for suggestions that improved the manuscript.

REFERENCES

- Abrams, M.D., Copenheaver, C.A., Terazawa, K., Umeki, K., Takiya, M. & Akashi, N. (1999) A 370-year dendroecological history of an old-growth *Abies-Acer-Quercus* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research*, **29**, 1891–1899.
- Aldrich, S.R., Lafon, C.W., Grissino-Mayer, H.D., DeWeese, G.G. & Hoss, J.A. (2010) Three centuries of fire in montane pine-oak stands on a temperate forest landscape. *Applied Vegetation Science*, **13**, 36–46.
- Arno, S.F. & Sneek, K.M. (1977) *A method for determining fire history in coniferous forests of the Mountain West*. General Technical Report INT-42. USDA Forest Service, Ogden, UT.
- Bailey, R.G. (1998) *Ecoregions: the ecosystem geography of the oceans and continents*. Springer, New York, NY.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–394.
- Brose, P.H., Dey, D.C., Guyette, R.P., Marschall, J.M. & Stambaugh, M.C. (2013) The influences of drought and humans on the fire regimes of northern Pennsylvania, USA. *Canadian Journal of Forest Research*, **43**, 757–767.
- Brown, A.A. & Davis, K.P. (1973) *Forest fire: control and use*, 2nd edn. McGraw-Hill Book Company, New York, NY.
- Clements, F.E. (1936) Nature and structure of the climax. *Journal of Ecology*, **24**, 252–284.
- Cook, E.R., Meko, D.M., Stahle, D.W. & Cleaveland, M.K. (1999) Drought reconstructions for the continental United States. *Journal of Climate*, **12**, 1145–1162.
- Cowell, C.M. (1995) Presettlement piedmont forests: patterns of composition and disturbance in central Georgia. *Annals of the Association of American Geographers*, **85**, 65–83.
- Denevan, W.M. (1992) The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers*, **82**, 369–385.
- Egloff, K. & Woodward, D. (2006) *First people: the early Indians of Virginia*, 2nd edn. University of Virginia Press, Charlottesville, VA.
- Fesenmyer, K.A. & Christensen, N.L. (2010) Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. *Ecology*, **91**, 662–670.
- Fisher, R.F., Jenkins, M.J. & Fisher, W.F. (1987) Fire and the prairie-forest mosaic of Devils Tower national monument. *American Midland Naturalist*, **117**, 250–257.
- Flatley, W.T., Lafon, C.W. & Grissino-Mayer, H.D. (2011) Climatic and topographic controls on patterns of fire in the southern and central Appalachian Mountains, USA. *Landscape Ecology*, **26**, 195–209.

- Flatley, W.T., Lafon, C.W., Grissino-Mayer, H.D. & LaForest, L.B. (2013) Fire history, related to climate and land use in three southern Appalachian landscapes in the eastern United States. *Ecological Applications*, **23**, 1250–1266.
- Geier, C.R. & Boyer, W.P., Jr (1982) *The Gathright Dam–Lake Moomaw cultural resource investigations: a synthesis of the prehistoric data*. Occasional Papers in Anthropology No. 15. James Madison University, Harrisonburg, VA.
- Grissino-Mayer, H.D. (2001) FH2: software for analyzing temporal and spatial patterns in fire regimes from tree rings. *Tree-Ring Research*, **57**, 115–124.
- Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L. & Hanna, D.D. (2004) Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology*, **85**, 1708–1724.
- Guyette, R.P., Muzika, R.M. & Dey, D.C. (2002) Dynamics of an anthropogenic fire regime. *Ecosystems*, **5**, 472–486.
- Harrod, J.C., Harmon, M.E. & White, P.S. (2000) Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. *Journal of Vegetation Science*, **11**, 465–472.
- Hart, J.L. & Buchanan, M.L. (2012) History of fire in eastern oak forests and implications for restoration. *Proceedings of the 4th Fire in Eastern Oak Forests Conference* (ed. by D.C. Dey, M.C. Stambaugh, S.L. Clark and C.J. Schweitzer), pp. 34–51. General Technical Report NRS-P-102. USDA Forest Service, Newtown Square, PA.
- Hessl, A.E., Saladyga, T., Schuler, T., Clark, P. & Wixom, J. (2011) Fire history from three species on a central Appalachian ridgetop. *Canadian Journal of Forest Research*, **41**, 2031–2039.
- Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–78.
- Komarek, E.V., Sr (1962) Fire ecology. *Proceedings of the 1st Annual Tall Timbers Fire Ecology Conference* (ed. by E.V. Komarek Sr), pp. 95–107. Tall Timbers Research Station, Tallahassee, FL.
- Lafon, C.W. & Quiring, S.M. (2012) Relationships of fire and precipitation regimes in temperate forests of the eastern United States. *Earth Interactions*, **16**, 1–15.
- Lafon, C.W., Hoss, J.A. & Grissino-Mayer, H.D. (2005) The contemporary fire regime of the central Appalachian Mountains and its relation to climate. *Physical Geography*, **26**, 126–146.
- Lorimer, C.G., Chapman, J.W. & Lambert, W.D. (1994) Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology*, **82**, 227–237.
- Matlack, G.R. (2013) Reassessment of the use of fire as a management tool in deciduous forests of eastern North America. *Conservation Biology*, **27**, 916–926.
- McEwan, R.W., Hutchinson, T.F., Long, R.P., Ford, D.R. & McCarthy, B.C. (2007) Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America. *Journal of Vegetation Science*, **18**, 655–664.
- McEwan, R.W., Dyer, J.M. & Pederson, N. (2011) Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, **34**, 244–256.
- McEwan, R.W., Pederson, N., Cooper, A., Taylor, J., Watts, R. & Hruska, A. (2014) Fire and gap dynamics over 300 years in an old-growth temperate forest. *Applied Vegetation Science*, **17**, 312–322.
- Mitchell, R.D. (1977) *Commercialism and frontier: perspectives on the early Shenandoah Valley*. University Press of Virginia, Charlottesville, VA.
- Morton, O.F. (1917) *Annals of Bath County, Virginia*. The McClure Co., Inc., Staunton, VA.
- Nash, C.L. (1991) *Archaeological survey of the proposed Gaitor Bait timber sale*. North River watershed, George Washington National Forest, Harrisonburg, VA.
- NCDC (2002) *Climatology of the United States, No. 81*. National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC.
- Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., Jedrzejska, B., Gutowski, J.M. & Brzeziecki, B. (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for central European lowland fire history. *Journal of Ecology*, **98**, 1319–1329.
- Nowacki, G.J. & Abrams, M.D. (2008) The demise of fire and ‘mesophication’ of forests in the eastern United States. *BioScience*, **58**, 123–138.
- Orvis, K.H. & Grissino-Mayer, H.D. (2002) Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Research*, **58**, 47–50.
- Pyne, S.J. (1982) *Fire in America: a cultural history of wildland and rural fire*. Princeton University Press, Princeton, NJ.
- Raup, H.M. (1937) Recent changes of climate and vegetation in southern New England and adjacent New York. *Journal of the Arnold Arboretum*, **18**, 79–117.
- Runkle, J.R. (1990) Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. *Canadian Journal of Forest Research*, **20**, 632–641.
- Russ, K.C., McDaniel, J.M. & Wood, K.T. (1995) *The archaeology of nineteenth-century iron manufacturing in southwestern Virginia: an example from the Longdale Iron Mining Complex*. Paper on file at Anthropology Laboratory, Washington and Lee University, Lexington, VA.
- Russell, E.W.B. (1983) Indian-set fires in the forests of the northeastern United States. *Ecology*, **64**, 78–88.
- Shumway, D.L., Abrams, M.D. & Ruffner, C.M. (2001) A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA. *Canadian Journal of Forest Research*, **31**, 1437–1443.
- Simon, S.A. (2011) *Ecological zones on the George Washington National Forest: first approximation mapping*. Unpublished

- report. The Nature Conservancy, Virginia Field Office, Gloucester, VA.
- Smith, T. & Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, **83**, 49–69.
- Stewart, O.C. (1956) Fire as the first great force employed by man. *Man's role in changing the face of the Earth* (ed. by W.L. Thomas Jr), pp. 115–133. The University of Chicago Press, Chicago, IL.
- Stokes, M.A. & Smiley, T.L. (1968) *An introduction to tree-ring dating*. University of Chicago Press, Chicago, IL.
- Tolley, G. (1983) Blue Ridge prehistory: perspective from the George Washington National Forest. *Upland archaeology in the East: a symposium* (ed. by C.R. Geier, M.B. Barber and G.A. Tolley), pp. 104–115. USDA Forest Service, Southern Region, Atlanta, GA.
- Van Horne, M.L. & Fule, P.Z. (2006) Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Canadian Journal of Forest Research*, **36**, 855–867.
- Ward, P.C., Tithcott, A.G. & Wotton, B.M. (2001) Reply: a re-examination of the effects of fire suppression in the boreal forest. *Canadian Journal of Forest Research*, **31**, 1467–1480.
- Watson, T.L., Bassler, R.S., Heinrich, R. & Holden, R.J. (1907) *Mineral resources of Virginia*. P. Bell Company, Lynchburg, VA.
- Weibull, W. (1951) A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, **18**, 293–297.
- Williams, M. (1989) *Americans and their forests: a historical geography*. Cambridge University Press, Cambridge, UK.
- Williams, C.E. (1998) History and status of Table Mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). *Natural Areas Journal*, **18**, 81–90.
- Yamaguchi, D.K. (1991) A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research*, **21**, 414–416.
- Zar, J.H. (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ.

BIOSKETCH

The members of this research team are physical geographers interested in vegetation dynamics and dendroecology. The research reported here was conducted as part of S.R.A.'s PhD dissertation.

Author contributions: C.W.L. and H.D.G.M. conceived the project; S.R.A., C.W.L., H.D.G.M. and G.G.D. planned the project and collected the data; S.R.A. prepared and dated the fire-scarred specimens; S.R.A. and C.W.L. analysed the data; S.R.A. and C.W.L. led the writing.

Editor: Jack Williams