Fire history from three species on a central Appalachian ridgetop

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Abstract: The impact of settlement era fires on Appalachian forests was substantial, but whether these fires affected the extent of fire-adapted ridgetop plant communities is poorly understood. Here we present fire history and stand structure of an Appalachian ridgetop (Pike Knob, West Virginia) based on fire scars from three species (*Pinus pungens* Lamb., *Pinus resinosa* Soland., and *Quercus rubra* L.) and stand structure from two species (*P. pungens* and *P. resinosa*). Our research objectives are to determine (*i*) the degree to which the fire frequency on Pike Knob was affected by European American settlement (~1780–1900) and (*ii*) how the history of fire on Pike Knob shaped the current age structure of *P. resinosa* and *P. pungens*. All three species documented fire activity beginning in the mid- to late 1800s and continuing into the middle of the 20th century, when pasture lands were most active. The majority of *P. pungens* and *P. resinosa* established during or shortly after the ~85-year period of fires (1868–1953), suggesting a strong influence of past land use on current forest composition. Ridgetop pine communities have been resilient to both the absence of fire and frequent fire, indicating that pine communities will also be resilient to modern fire management, whether fire is excluded or re-introduced.

Résumé : L'impact des feux à l'époque de la colonisation sur les forêts appalachiennes a été important mais on ne sait pas si ces feux ont influencé l'étendue des communautés végétales adaptées au feu sur le sommet des montagnes. Nous présentons ici l'historique actuel des feux et la structure du peuplement situé sur un sommet des Appalaches (Pike Knob en Virginie-Occidentale) en se basant sur les cicatrices de feu présentes sur trois espèces (*Pinus pungens* Lamb., *Pinus resinosa* Soland. et *Quercus rubra* L.) et sur deux espèces (*P. pungens* et *P. resinosa*) dans le cas de la structure du peuplement. Nos objectifs consistaient à déterminer (*i*) dans quelle mesure la fréquence des feux à Pike Knob a été influencée par la colonisation de l'Amérique par les européens (~1780–1900) et (*ii*) comment l'historique du feu à Pike Knob a modelé la structure d'âge actuelle de *P. resinosa* et *P. pungens*). Les trois espèces témoignaient de l'activité du feu à partir du milieu à la fin des années 1800 jusqu'au milieu du 20e siècle, lorsqu'il y avait le plus de pâturages. La majorité des *P. pungens* et *P. resinosa* se sont établis durant ou peu de temps après la période des feux qui a duré 85 ans (1868–1953), ce qui indique que l'utilisation passée des terres a fortement influencé la composition actuelle de la forêt. Les communautés de pin situées sur les sommets ont résisté tant à l'absence du feu qu'au passage fréquent du feu, ce qui indique que les communautés de pin résisteront aussi à la gestion moderne du feu, que le feu soit exclu ou réintroduit.

[Traduit par la Rédaction]

Introduction

In Appalachian forests of North America, lightning-caused fires are currently infrequent (<1%) (Lynch and Hessl 2010; Malamud et al. 2005), but human-ignited fires may have had a substantial impact on ecosystems prior to, during, and after Euro-American settlement. Paleoecological evidence indicates that Native American use of fire may have been important for millennia, particularly near native settlements during the Woodland period (3000 years before present) (Delcourt and Delcourt 1997, 1998; Fesenmyer and Christensen 2010). The few fire history studies based on fire-scarred trees that extend prior to Euro-American settlement also document a history of frequent fire (fire return intervals of ~5–8 years) in eastern forests, despite major cultural and population changes resulting from contact between Europeans and Native Americans (Shumway et al. 2001; Aldrich et al. 2010).

During the settlement period, fire activity increased in many locations, likely the result of increased population densities, logging, railroads, and other activities (Harmon 1982; Guyette and Spetich 2003; Maxwell and Hicks 2010). However, whether these changes in land use, ignitions, and fire frequency affected the extent of fire-adapted plant communities is poorly understood.

It is well known that Appalachian ridgetop pine forests are fire-adapted (Whittaker 1956; Harmon 1982; Williams 1998). These xeric forests are dominated by shade-intolerant pines (*Pinus pungens*, *Pinus rigida*), with thick fire-resistant bark, serotinous cones, and other adaptations to disturbance such as epicormic and root sprouting (Zobel 1969). In some locations, hardwood species have outcompeted the pines following fire exclusion (Harrod et al. 2000), suggesting that fire may be required to maintain these systems (Lafon and Kutak 2003). Others have argued that Appalachian pine stands
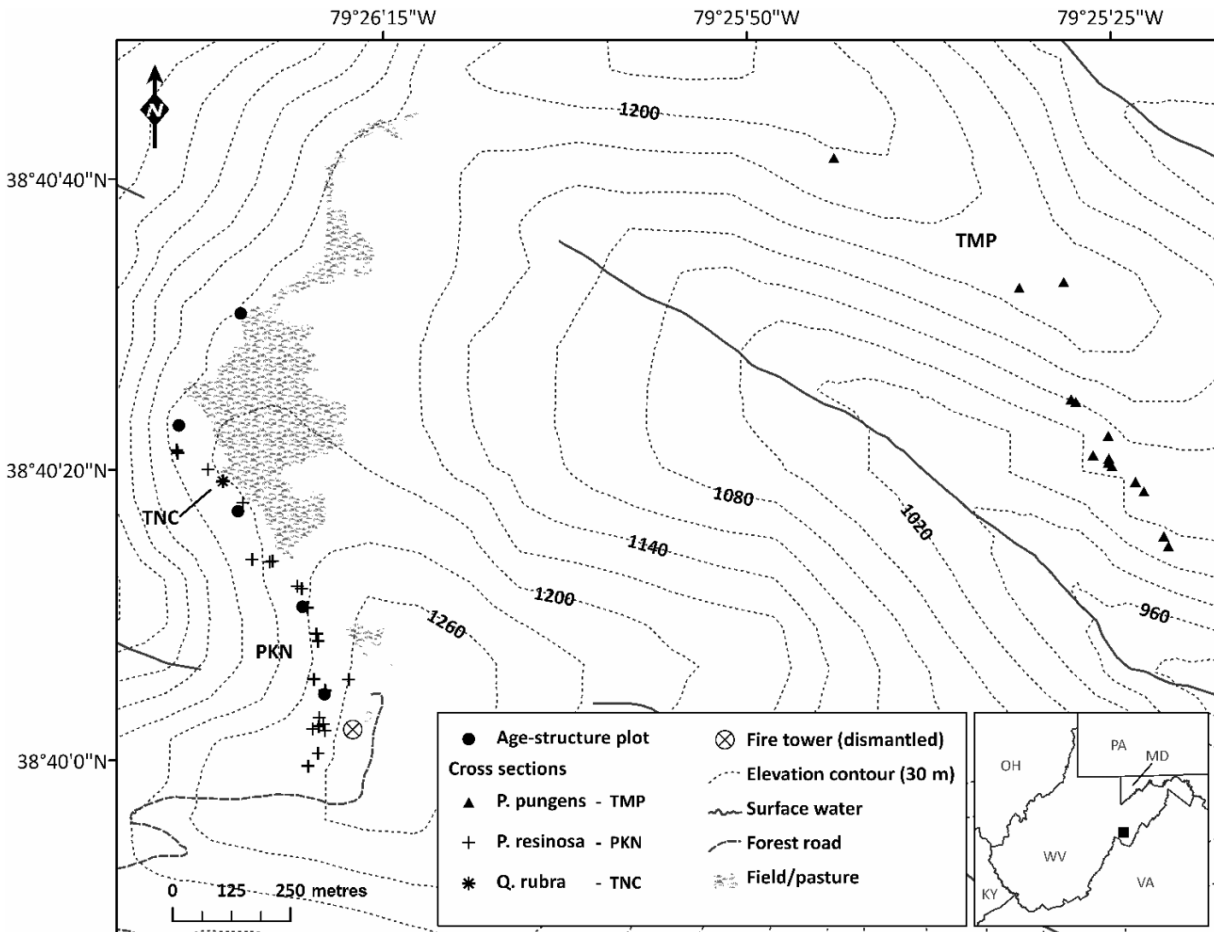
Fig. 1. Study area map showing the location of Pike Knob Preserve, fire scar sample locations for *Pinus resinosa* (+), *Quercus rubra* (*), and *P. pungens* (▲) and age structure plots (*P. resinosa*) and transects (*P. pungens*) (●). The single symbol for the *Q. rubra* sample location represents a small plot at which 16 cross sections were collected (Schuler and McClain 2003).

might be sustained in the absence of fire, especially on infertile sites with little soil development (Zobel 1969; Barden 1977; Brose and Waldrop 2006). It is unclear whether frequent fire and other land use activities during Euro-American settlement caused pine communities to extend their local range (Barden and Woods 1976; Harmon 1982) or whether frequent fire has been a component of these ecosystems for centuries (Aldrich et al. 2010). Appalachian ridgetop pine forests, though limited in spatial extent, contain many rare species and are a high priority for conservation in eastern North America (Zobel 1969; Brose and Waldrop 2006). Questions about the role of fire in these systems are critical to managers interested in maintaining resilience in natural ecosystems (Bengtsson et al. 2003) as the limited extent of these ridgetop pine forests makes them vulnerable to exotic plant invasions, climate change, disease, disturbance, and other stochastic events.

Two species of special concern in the pine communities of the central Appalachian Mountains are Table Mountain pine (*Pinus pungens* Lamb.), endemic to the Appalachian Mountains, and red pine (*Pinus resinosa* Soland.), a glacial relict where it occurs in the central Appalachian Mountains (Stephenson et al. 1986) (Fig. 1). In West Virginia, both species occur naturally in small populations that have been further isolated and fragmented by human disturbance and settle-

ment. Both species benefit from fire, but each maintains a different suite of adaptations to fire. *Pinus pungens* is a small scrub pine that occurs on high-elevation, xeric ridgetops throughout the Appalachian Mountains. Its adaptations to fire are consistent with low, moderate, and high severity fire regimes, including thick bark, deep rooting habit, self-pruning limbs, precocious reproduction, and serotinous cones (McIntyre 1929; Barden 1977; McCune 1988; Keeley and Zedler 1998). The absence of fire since the mid-20th century has lead to a decline in regeneration of *P. pungens* in portions of its range (Barden 1977; Waldrop and Brose 1999; Lafon and Kutak 2003; Brose and Waldrop 2006).

Pinus resinosa is common throughout northeastern North America where its range extends from Newfoundland south to West Virginia (Fig. 1). In West Virginia, it occurs in only two small populations thought to be relicts of the last glacial period (Stephenson et al. 1986). *Pinus resinosa*'s adaptations to fire are consistent with low, moderate, and possibly high severity fire. It has thick bark, an elevated crown, and is self-pruning (Keeley and Zedler 1998; Jackson et al. 1999). *Pinus resinosa* has restrictive seedbed requirements, including exposed mineral soil, and may benefit from the open environments created by fire (Ahlgren 1976). Historical fires in red pine stands within its typical range were of low to moderate intensity, with fire return intervals ranging from about

15 to 30 years, but occasionally high severity fires with intervals of 50 years or more occurred (Bergeron and Brisson 1990; Roberts and Mallik 1994). Other researchers have observed shorter fire intervals corresponding to the period of local Euro-American settlement (Drobyshev et al. 2008). Though the fire history and disturbance response of red pine is fairly well understood within its typical range, less is known about the fire history of smaller relict stands and adjacent oak–pine communities (Schuler and McClain 2003).

Like much of the eastern deciduous forest, forests of West Virginia experienced major changes during Euro-American settlement. These changes may have been direct via land clearing (Clarkson 1964; Jurgelski 2008), as well as indirect through changes in Native American land use resulting from the introduction of disease, migrations, and warfare. Following settlement, Euro-American impacts on fire regimes likely continued, as traditional agricultural methods brought from Europe included fire as a management tool, particularly for improving pastures for grazing animals (Jurgelski 2008). From the 1930s to the 1950s, much of West Virginia's agricultural land was abandoned, allowing forests to regrow and fuel contiguity to increase, likely altering the fire regime once again. During the same time period, fire suppression became more effective (Jurgelski 2008). Some of these social and cultural changes may be reflected in both the fire history and current stand structure of central Appalachian pine forests.

Here we present fire history and stand structure data for an Appalachian ridgetop (Pike Knob, West Virginia) based on fire scars from three species (*P. pungens*, *P. resinosa*, and *Quercus rubra* L.) and stand structure from two species (*P. pungens* and *P. resinosa*). Our research objectives are to determine (*i*) the degree to which the fire frequency on Pike Knob was affected by European American settlement (~1780–1900) and (*ii*) how the history of fire on Pike Knob shaped the current age structure of both *P. pungens* and *P. resinosa*.

Study area

Pike Knob Preserve, managed by The Nature Conservancy (TNC), is a 650 ha preserve within the mixed hardwood region of the central Appalachian Mountains. The preserve contains a small (~2 ha) isolated stand of *P. resinosa*, as well as several cliff-edge pine communities (*P. pungens*, *P. virginiana*, *P. rigida*). Pike Knob is located in the ridge and valley physiographic province in Pendleton County, West Virginia (38°40′3″N and 79°26′18″W). Elevations within the preserve range from 1250 to 1310 m. The cliff and ridgetop communities of *P. resinosa* and *P. pungens* are underlain by resistant sandstones, quartzites, and conglomerates. Outcrops are Tuscarora sandstone. Soils are primarily of Tuscarora sandstone parent material and are acidic, stony, and characterized by low nutrient levels (Stephenson et al. 1986).

The region lies in the rain shadow of the high ridge of the western Allegheny Mountains, with average annual precipitation of 90 cm/year (NOAA-NCDC, West Virginia Division 6). The average monthly temperatures for January and July are 0 °C and 23 °C, respectively (NOAA-NCDC, West Virginia Division 6). Vegetation along this portion of North

Fork Mountain includes a mixture of oak–pine forest, northern hardwood forest, grass balds, and the southernmost stand of red pine. Ridgetops, however, are populated by herbaceous and grass species such as silvery nailwort (*Paronychia argyrocoma* (Michx.) Nutt.), three-toothed cinquefoil (*Sibbaldiopsis tridentate* (Aiton) Rydb.), rusty woodsia (*Woodsia ilvensis* (L.) R. Br.), Canada mountain-ricegrass (*Piptatherum canadense* (Poir.) Dorn), and poverty oatgrass (*Danthonia spicata* (L.) P. Beauv. Ex Roem. & Schult.). Several exotic invasive species are also present, including cheat grass (*Bromus tectorum* L.), spotted knapweed (*Centaurea maculosa* Lam.), and vipers bugloss (*Echium vulgare* L.).

Once thought to be largely uninhabited prior to Euro-American settlement, the uplands of West Virginia were extensively used by prehistoric people, though use was likely concentrated along primary stream floodplains and river valleys (Lesser 1993). Ridgetops and other high areas contain evidence of a diverse array of short-term sites, particularly in areas conducive to travel (gaps or saddles), but long-term settlement was more common in the valleys and floodplains (Lesser 1993). Like the natives before them, European settlers initially favored river valleys for agriculture and settlement. European settlement of Pendleton County began ca. 1747 when farmers cleared valleys for agriculture and pasture, often with the use of fire (Brooks 1911). However, settlement did not extend into the high-elevation mountain regions until ca. 1850 (Morton 1910).

We used data from three locations within the Pike Knob Preserve: (*i*) a nearly monospecific stand of *P. resinosa* on the west-facing upper slope of the mountain; (*ii*) a *Q. rubra* dominated stand adjacent to the *P. resinosa* stand, sampled as part of a previous study (Schuler and McClain 2003); and (*iii*) a cliff pine stand dominated by *P. pungens*, *P. rigida*, and *P. virginiana* located along the south-facing edge of an east–west trending outcrop of Tuscarora sandstone (Fig. 1).

Methods

Fire history

Due to the sensitive nature of the *P. resinosa* stand, we did not collect cross sections from living trees. Instead, we searched the entire stand for remnant snags, stumps, and logs. We cut complete cross sections with a chainsaw from all snags, downed logs, and stumps regardless of whether we were able to identify the presence of any fire scars in the field. Fieldworkers took samples at approximately 10 to 15 cm above the ground, unless a fire scar was visible, in which case we collected samples to maximize the number of fire scars. Complete cross sections were collected from a small oak stand just north of the *P. resinosa* stand as part of previous study (Schuler and McClain 2003). Seventeen basal cross sections were collected from *Q. rubra* in a 0.06 ha area that had been illegally cut during the spring of 2002. Samples were collected from cuts stumps at about 10 to 15 cm above the ground.

To develop a long history of fire from the *P. pungens* stand, we searched along a cliff edge for fire-scarred *P. pungens*. Due to concerns about the conservation of this species, we sampled partial cross sections from 10 live fire-scarred trees, targeting the oldest trees with the largest number of

Table 1. Number of trees, scars, and injuries for each species, fire season (D, dormant; E, early earlywood; MLA, middle earlywood – late earlywood – latewood), length of the fire history records for each species, and WMFI (Weibull median fire interval) and MFRI (median fire interval) (10% and two trees scarred).

Species	No. of trees	No. of scars/injuries	Fire season (D/E/MLA)	Earliest ring	Latest ring	Earliest fire/injury	Latest fire	WMFI/MFRI	No. of intervals
P. resinosa	25	64/11	16/56/28	1801	2008	1868/1827	1974	6.3*/7.1	12
Q. rubra	16	11/7	89/11/0	1850	2001	1885/1868	1962	NA	2
P. pungens	11	20/1	12/53/35	1770	2010	1887/1828	1953	7.9/9.4*	7
Total	51	92/16	23/51/26	1770	2010	1868/1828	1974	8.6/10.6	

Note: An asterisk (*) indicates the appropriate fire return interval model based on Kolmogorov–Smirnoff distribution test (Grissino-Mayer 2001). NA, there were not enough intervals (two) to calculate WMFI or MFRI for *Q. rubra*.

fire scars. We also sampled all stumps, snags, and logs encountered with visible fire scars present.

Age structure

We delineated and digitized the extent of the *P. resinosa* stand in a GIS from a 2007 aerial photograph (USDA Forest Service 2008). We then randomly located five sample points throughout the stand using the Hawth's Tools extension developed for ESRI's ArcMap (www.SpatialEcology.com), where we recorded slope, aspect, and elevation at each point. We also recorded the distance and compass bearing to the ~10 nearest living *P. resinosa* trees. For each tree, we recorded species and diameter at breast height (DBH) and collected two increment cores from the base of each tree to obtain approximate recruitment dates (*n* = 63 trees). Because the *P. pungens* stand is linear in shape, we collected increment cores for age structure along four 40 m transects beginning at a baseline running along the top of the cliff edge and continuing uphill into the stand. Along each transect, we collected two increment cores from the base of the nearest tree at 4 m intervals (*n* = 40 trees). We included all cross sections with the pith present in the age structure as well (*P. pungens*, *n* = 16; *P. resinosa*, *n* = 5).

Laboratory methods

All tree cores and cross sections were allowed to air dry. We mounted increment cores and sanded all tree ring specimens according to standard dendrochronological methods (Stokes and Smiley 1968; Speer 2010). We used progressively finer grades of sandpaper (40–1000 grit) to create a flat surface and polish each core or cross section until individual cells were visible under a stereomicroscope. Using skeleton plots, we visually cross-dated cores and cross sections against a master chronology derived from the cores of living trees, as well as the record from the North American Drought Atlas (point 247) (Cook and Krusic 2004). We identified fire scars in cross sections based on the presence of cambial injury and subsequent curl of woundwood in *P. resinosa* and *P. pungens* and based on cambial injury and compartmentalization in *Q. rubra* (Smith and Sutherland 1999). Because cambial injuries can arise from many sources, particularly in oak (McBride 1983; McEwan et al. 2007*a*), we used conservative methods to define fire scars. If identification of an injury as a fire scar was at all suspect and no other trees of the same species had a clear fire scar in the same year, we recorded it as an injury. We dated all fire scars and injuries to the season (early earlywood (E), middle earlywood (M), late earlywood (L), latewood (A), dormant (D), or unknown (U)) based on the position of the scar within the annual ring. We assigned dormant-season fires to the year prior to the scar unless scars occurred in other trees during the earlywood season of the following year, in which case we assigned events to the subsequent year. West Virginia has two fire seasons, spring and fall, but larger burned areas typically occur in fall (Lynch and Hessl 2010).

We developed age estimates for each tree derived from cross-dated increment cores (two from each tree) collected as close to the base of each tree as possible (<10 cm). If the pith was missed by more than two rings (*P. resinosa* = 45%, *P. pungens* = 74%), we made corrections according to the curvature of the innermost visible rings (Arno and Sneck 1977). Due to the inherent error in age estimation, we collapsed ages into 10-year bins.
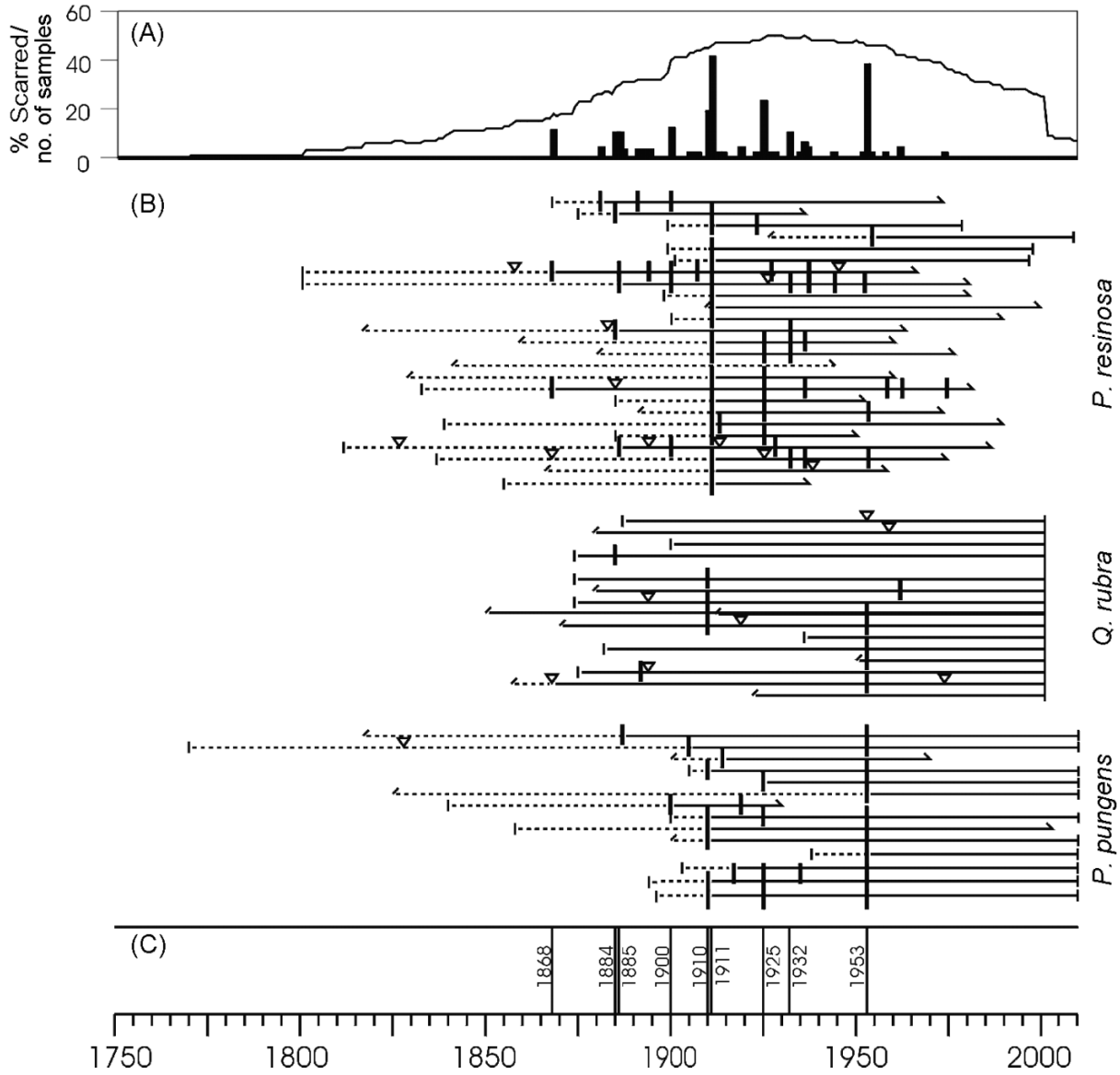
Results

Fire scars

The three species recorded unique but complementary records of past fire (Table 1; Fig. 2). Fire scars in *P. resinosa* were most common, averaging 2.5 scars/tree compared with 1.8 scars/tree for *P. pungens* and 1.5 scars/tree for *Q. rubra*. Mean fire return intervals reflect these differences among the three species. For example, the mean estimated fire return interval (MFRI) for fires affecting ≥10% of samples and at least two trees is shortest for *P. resinosa* (MFRI = 7.3 years) and slightly longer for *P. pungens* (MFRI = 7.9). Though we only identified two intervals affecting ≥10% of samples and at least two trees for *Q. rubra* (25 years and 43 years), the MFRI appears substantially longer than for the pines. All three records documented fire activity beginning in the mid- to late 1800s and continuing into approximately the middle of the 20th century. Though the time period covered by the *Q. rubra* cross sections is considerably shorter than that of the pines, the period of frequent fires is approximately the same (Fig. 2). Both pine species have injuries prior to the first fire scar in 1868; however, these injuries are infrequent and do not coincide with other injuries or fire scars, so we did not include them as fires here.

Fire season is less consistent across the three species. Fire season was difficult to determine in the *Q. rubra* cross sections as scars most commonly occurred between rings during the dormant season (89%) (Table 1). For *P. resinosa* and *P. pungens*, scars occurred predominantly in the dormant or earlywood portions of annual rings (72% and 65%, respectively), suggesting a spring fire season. Both *P. resinosa* and *P. pungens* cross sections also recorded fires (28% and 35%,

Fig. 2. Fire history for 52 trees, stumps, and logs from Pike Knob Preserve, West Virginia. (A) Number of samples (line) and percentage scarred (bars), (B) fire chart, and (C) fire years that represent more than 10% and two or more of all recorder trees scarred. Horizontal lines in (B) represent individual trees or remnants, broken lines represent the years prior to the first fire scar, vertical lines indicate fire scars, and inverted triangles indicate injuries. Inner ring dates are denoted by a forward slash, outer ring dates are denoted by a backward slash, pith dates and bark dates are denoted by a short vertical line.

respectively) in M, L, or A positions indicative of mid-summer or fall fires. These results are consistent with the two fire seasons documented by historical observations (Lynch and Hessl 2010).

Nine fire years were recorded by at least two species, and one fire year was recorded by all three species (1953; Table 2). The *P. resinosa* stand and the *Q. rubra* stand, which are immediately adjacent, recorded the most fire years in common (five), though the *Q. rubra* and the *P. pungens* stands have three synchronous fire years. Though 1911 was a major fire in *P. resinosa* (20 of 44 recorder trees scarred), no *Q. rubra* or *P. pungens* trees were scarred by this fire. A fire in 1910 affected both *Q. rubra* and *P. pungens* but was not recorded by *P. resinosa*. It is unlikely that this pattern

represents a dating error as other large fire years before and after this event are common to trees across sites. It is also unlikely that this pattern developed from seasonal assignment as several *P. resinosa* have latewood scars in 1910. Rather it appears that 1910 and 1911 were large fire events that burned different portions of the study area.

Age structure

Peaks in establishment, especially for *P. resinosa*, co-incided with periods of frequent fires (Fig. 3). Though two living individuals predate this period, the majority of *P. resinosa* and *P. pungens* currently on the landscape established during or shortly after the ~85-year period of fires (1868–1953) on Pike Knob. A second pulse of establishment ap-

Table 2. Fire years observed in common across more than one species (although note that 1911 is not included because it affected only *P. resinosa*).

Fire year	Scars/injuries		
	P. resinosa	*Q. rubra*	*P. pungens*
1868	1/1	1/0	0/0
1885	1/1	2/0	0/0
1894	1/0	0/2	0/0
1900	4/0	0/0	1/0
1910	0/0	3/0	4/0
1919	0/0	0/1	2/0
1925	7/1	0/0	2/0
1953	2/0	5/1	8/0
1962	1/0	1/0	0/0

Note: Included here are both fire scars and injuries.

pears after fire cessation in 1953 (though note that one tree recorded a fire in 1972). This secondary peak in regeneration may be due to the absence of recent fires thinning postfire regeneration. The absence of regeneration in the last 20 years is likely real in both species as we searched for seedlings (trees less than 1.37 m in height) in our plots and transects and found none. The spatial arrangement of *P. pungens* tree ages reflects the fire history at the site. The oldest trees are located on the cliff edge where fires would be less likely to spread due to the absence of continuous fuel. One *P. pungens* established in 1739 on a protected cliff edge is the oldest known individual of that species (Eastern OLDLIST, http://www.ldeo.columbia.edu/~adk/oldlisteast/).

Discussion and conclusions

Though the three sites were located within less than 2 km of each other, the annual record of fire across the three sites and three species was less consistent than expected. Synchroneity (or lack thereof) of fire years across sites may be a function of proximity, the fuel structure under each forest type, and the tendency of each species to record fires (Hare 1965; McBride 1983). The most recent fires (e.g., 1925 and 1953) were recorded by more trees and species than older events (e.g., 1868, 1911). This could be a function of better preservation of fire scars during recent decades rather than a true measure of the spatial extent of previous fires. Regardless, the two major 20th century fires were relatively extensive and may have even spanned a hardwood-dominated drainage between the stand of red pine and Table Mountain pine (Fig. 1).

Though the records for *P. resinosa* and *Q. rubra* were most similar and the stands were immediately adjacent, differences in fire history across species may be a function of morphological characteristics of the species. Oaks are not consistent recorders of fire (Guyette and Stambaugh 2004) and may contain wounds from other causes that are indistinguishable from fire scars (McEwan et al. 2007*b*). Fires might have burned through both pine and oak but were only recorded by the pines, especially if fires burned through the oak litter at temperatures too low to create fire scars (Smith and Sutherland 1999). Two injuries in *Q. rubra* in 1894 coincide with a single fire scar in *P. resinosa*, suggesting that a

low-intensity fire may have occurred in the *Q. rubra* and *P. resinosa* in that year. When oaks do record fires, they continue to decay following injury and many wounds completely close, leaving no obvious scar (Smith and Sutherland 2001), so fire history records from oaks may be conservative records of past fire. Here, we used complete cross sections of *Q. rubra*; nevertheless, fires in the oak stand were either not as common as in the pine stands or did not burn at sufficient temperatures to produce scars in the oak. Even though fewer fires were recorded in the oak, the fire frequency may be higher than in similar oak stands in the region due to the stand's proximity to *P. resinosa*.

Pinus resinosa recorded the most fires but also may be the most reliable recorder. Pines, in general, produce fire scars more readily than other genera due to the higher resin content of the bark. The presence of resin exuded around fire scars may thus enhance the likelihood of subsequent scarring (McBride 1983) and may improve the preservation of the wood after scarring has occurred (Verrall 1938). *Pinus resinosa* needles are among the most flammable of all pines in the United States (Morgan Varner, personal communication, 2011), making *P. resinosa* stands highly susceptible to frequent fire given sufficient ignition sources.

Despite differences in susceptibility to scarring, all three species record the earliest fires within a range of 19 years (1868–1887). Seven samples were present on the landscape between 1825 and 1850 but were not scarred during this period. Clearly, this was a period of reduced fire activity. All three species record a similar period of frequent fires (late 19th to mid-20th century) and a steep reduction of fires after 1953. Clarkson (1964) describes a period of frequent and intense fires occurring between 1863 and 1908 in Pendleton, Randolph, Grant, and Tucker counties of West Virginia, beginning with an escaped campfire from Confederate Army scouts and ending in logging-related fires in 1908. The fires that we document here might have been associated with these previously described historical events. However, the near absence of fire prior to 1868 is inconsistent with the results of Aldrich and others (Aldrich et al. 2010), who observed fires occurring every ~5 years from 1705 to 1930 in a similar ridgetop pine community approximately 200 km south of Pike Knob. The land use history of Pike Knob, though not unique, indicates that activities following early settlement may have been important drivers of ecological change, particularly in eastern forests where lightning ignitions are limited.

In the early 19th century, the south branch of the Potomac was a major cattle-raising section of the mid-Atlantic region, supplying cattle to Philadelphia, Baltimore, and other cities. By 1822, most people of moderate means were engaged in cattle raising in glades (Rice 1970). Clearing land for pasture was one of the major uses of fire during settlement in the Appalachian Mountains (Jurgelski 2008). The increase in fire activity beginning in the mid- to late 1800s may have resulted from a shift from subsistence agriculture to market-based livestock production. The population density of Pendleton County reached its maximum during this period as well, reaching a peak of ~6 humans/km^2 in 1940, declining rapidly thereafter to approximately 3.8 humans/km^2 in 1970 (www.census.gov; Morton 1910). Guyette and Spetich (2003), working in Arkansas, observed that human population density was associated with changes in fire regimes

Fig. 3. (A) Percentage scarred over time when ≥ two trees record fire and (B) age structure of *Pinus resinosa* and *Pinus pungens*. Solid bars are pith or estimated pith dates from plots or transects; open bars are pith dates from cross sections from fire scarred trees, snags, or stumps.
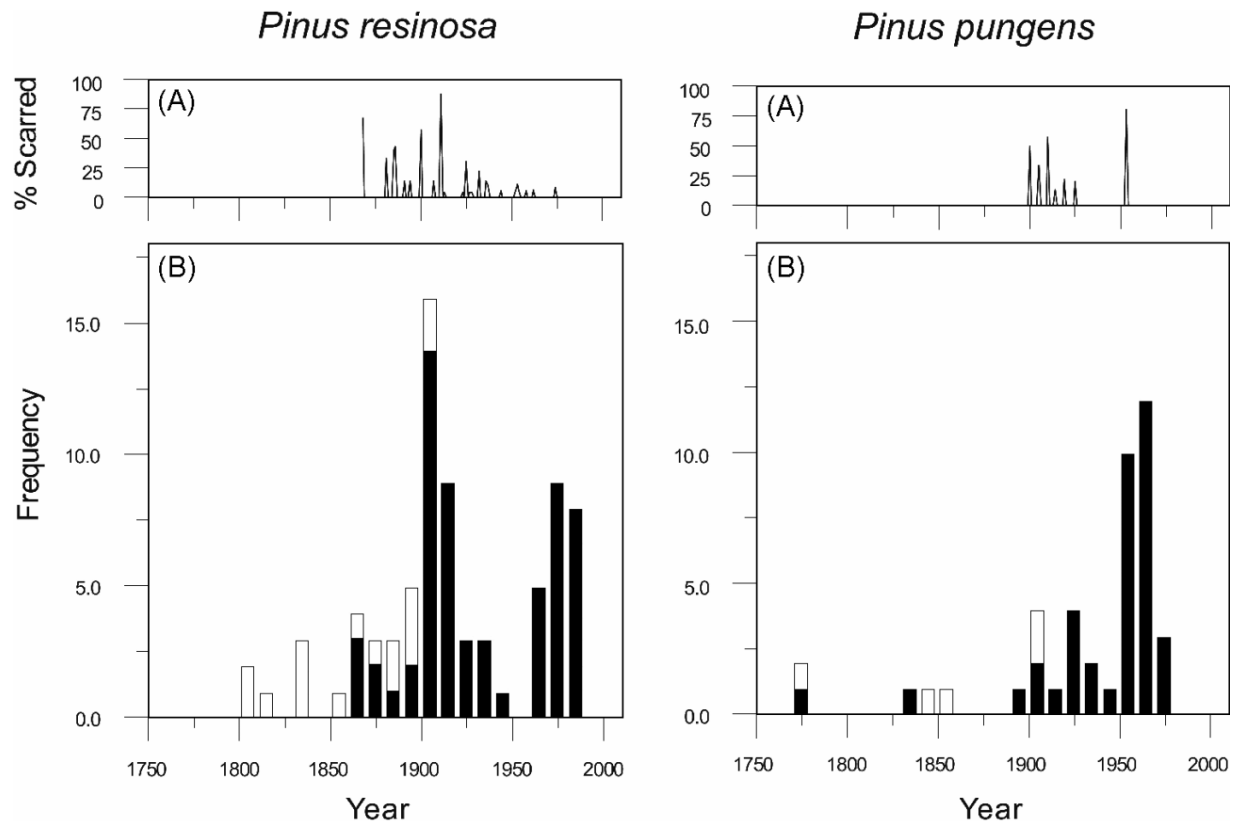
such that moderate populations positively correlated with fire activity, whereas low and high population densities were negatively correlated. They observed a peak in fire frequency when human populations were approximately 5 humans/km², a value on par with the highest densities observed here (~6 humans/ km²). Though human population density in Pendleton County was highest during the period with the highest fire activity, this period also corresponds to a change in land use with known connections to ignitions (grazing), so changes in the fire regime may reflect both human population density and a change in land use.

Prior to the late 1800s, we have little evidence of fire on the landscape and either little regeneration of pines or few surviving trees. The low fire activity prior to the mid- to late 1800s may be a result of a diminishing record of fire history with time or the absence of human ignitions. Like all paleoecological records, fire histories derived from fire scars suffer from the "fading record problem" or reduced replication with time. Fire-scarred stumps, snags, and other remnant material decompose relatively rapidly in the humid climate of the eastern United States. In addition, subsequent fires can burn off earlier fire scars. Additional data from fire scars or soil charcoal could confirm whether a major change in the fire regime occurred following settlement (~1868), as we observe here.

Though the absence of fire prior to 1868 requires further investigation, the ecological effects of the fires between 1868 and 1953 left a legacy visible today. Nearly all of the *P. resinosa* and *P. pungens* trees that we sampled established dur-

ing or immediately after those fires. The absence of fire after 1953 opened a window during which substantial establishment of both species occurred, particularly *P. pungens*. Without subsequent fires, these *P. pungens* seedlings survived in great numbers, creating a thicket of *P. pungens* extending uphill from the cliff edge under which no regeneration is currently occurring. We observed that many *P. resinosa* have recently established in the abandoned field adjacent to the sampled stand (Fig. 1), and some regeneration has occurred in the understory of *Q. rubra* dominated stands, indicating that for *P. resinosa*, fire is not a prerequisite for establishment.

The history of fire and stand age presented here indicate that ridgetop pine species are resilient to both the absence of fire (1800–1868, 1953–present) and frequent fire (1868–1953). Although models suggest that fire would expand the populations of pine species on Appalachian ridgetops (Lafon et al. 2007), *P. pungens* have successfully regenerated in the absence of fire for a century or more (Barden 2000). Here, long-lived *P. pungens* on the cliff edge (two trees are older than 260 years) were protected from high severity fires by an open canopy and little fuel accumulation and may have served as a seed source for regeneration after fire (Zobel 1969). Establishment of *P. resinosa* in small openings and under the closed canopy of *Q. rubra* may sustain this relict stand in the absence of fire. Though the pines may be resilient to substantial changes in the fire regime, other species, particularly native grasses and forbs, may be more susceptible to such changes. Invasive species commonly occur on

central Appalachian ridgetops, and some of these species have expanded their range following fire (D'Antonio and Vitousek 1992). Pike Knob has populations of several exotic species highly sensitive to fire, including *B. tectorum*, complicating fire management.

Managers throughout central Appalachian Mountains are currently prioritizing dry ridgetop pine and oak communities to implement burn treatments (USDA Forest Service 2006; Thomas-Van Gundy et al. 2007). At Pike Knob and in other similar ridgetop pine communities where stand densities are high, low severity prescribed fires meant to encourage pine regeneration might result in high severity burns with less predictable consequences. The 1953 fire, and the absence of disturbance since, led to extensive pine (*P. pungens* and *P. resinosa*) regeneration. However, it is unclear whether modern prescribed fire would produce the same results because of current high fuel loads and dense forest structure. A stand-replacing fire could have major impacts on stand structure, associated vegetation, and soils. If fire continues to be excluded in the *P. resinosa* stand, recruitment will likely continue in adjacent old fields and other openings. Continued fire exclusion in the *P. pungens* stand would likely reduce the overall extent of the stand, but the existence of old individuals on the rocky outcrops strongly suggests that edaphic conditions will maintain a small population capable of establishing in adjacent disturbed areas. Modern management of fire in similar Appalachian ridgetops, whether fire is excluded or re-introduced, will have effects on stand structure, invasive species, and other understory plants, but it is unlikely to result in local extirpations of either pine species.

Acknowledgements

References

Ahlgren, C.E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. J. For. **74**: 135–140.

Aldrich, S.R., Lafon, C.W., Grissino-Mayer, H.D., DeWeese, G.G., and Hoss, J.A. 2010. Three centuries of fire in montane pine–oak stands on a temperate forest landscape. Appl. Veg. Sci. **13**(1): 36–46. doi:10.1111/j.1654-109X.2009.01047.x.

Arno, S.F., and Sneck, K.M. 1977. A method for determining fire history in coniferous forests of the Mountain West. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, Gen. Tech. Rep. INT-GTR-42.

Barden, L.S. 1977. Self-maintaining populations of *Pinus pungens* Lam. in the southern Appalachian Mountains. Castanea, **42**(4): 316–323.

Barden, L.S. 2000. Population maintenance of *Pinus pungens* Lam. (Table Mountain pine) after a century without fire. Nat. Areas J. **20**: 227–233.

Barden, L.S., and Woods, F.W. 1976. Effects of fire on pine and pine–hardwood forests in the southern Appalachians. For. Sci. **22**(4): 399–403.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., and Nystrom, M. 2003. Reserves, resilience and dynamic landscapes. AMBIO, **32**(6): 389–396. PMID:14627367.

Bergeron, Y., and Brisson, J. 1990. Fire regime in red pine stands at the northern limit of the species' range. Ecology, **71**(4): 1352–1364. doi:10.2307/1938272.

Brooks, A.B. 1911. Forestry and wood industries. West Virginia Geological Survey, **5**: 247–249.

Brose, P.H., and Waldrop, T.A. 2006. Fire and the origin of Table Mountain pine – pitch pine communities in the southern Appalachian Mountains, USA. Can. J. For. Res. **36**(3): 710–718. doi:10.1139/x05-281.

Clarkson, R.B. 1964. Tumult on the mountains. McClain Printing Company, Parsons, West Virginia.

Cook, E.R., and Krusic, P.J. 2004. North American Drought Atlas. Available from http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html [accessed November 2010].

D'Antonio, C.M., and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Systematics, **23**: 63–87.

Delcourt, H.R., and Delcourt, P.A. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conserv. Biol. **11**(4): 1010–1014. doi:10.1046/j.1523-1739.1997.96338.x.

Delcourt, P.A., and Delcourt, H.R. 1998. The influence of prehistoric human-set fires on oak–chestnut forests in the southern Appalachians. Castanea, **63**(3): 337–345.

Drobyshev, I., Goebel, P.C., Hix, D.M., Corace, R.G., and Semko-Duncan, M.E. 2008. Pre- and post-European settlement fire history of red pine dominated forest ecosystems of Seney National Wildlife Refuge, Upper Michigan. Can. J. For. Res. **38**(9): 2497–2514. doi:10.1139/X08-082.

Fesenmyer, K.A., and Christensen, N.L., Jr. 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. Ecology, **91**(3): 662–670. doi:10.1890/09-0230.1. PMID:20426326.

Grissino-Mayer, H.D. 2001. FHX2 — software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Res. **57**: 115–124.

Guyette, R.P., and Spetich, M.A. 2003. Fire history of oak–pine forests in the Lower Boston Mountains, Arkansas, USA. For. Ecol. Manage. **180**(1–3): 463–474. doi:10.1016/S0378-1127(02)00613-8.

Guyette, R.P., and Stambaugh, M.C. 2004. Post-oak fire scars as a function of diameter, growth, and tree age. For. Ecol. Manage. **198**(1–3): 183–192. doi:10.1016/j.foreco.2004.04.016.

Hare, R.C. 1965. Bark surface and cambium temperatures in simulated forest fires. J. For. **63**: 437–440.

Harmon, M. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. Bull. Torrey Bot. Club, **109**(1): 74–79. doi:10.2307/2484470.

Harrod, J., Harmon, M., and White, P. 2000. Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. J. Veg. Sci. **11**(4): 465–472. doi:10.2307/3246576.

Jackson, J.F., Adams, D.C., and Jackson, U.B. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. Am. Nat. **153**(6): 614–632. doi:10.1086/303201.

Jurgelski, W.M. 2008. Burning seasons, burning bans: fire in the southern Appalachian Mountains, 1750–2000. Appalach. J. **35**: 170–217.

Keeley, J.E., and Zedler, P.H. 1998. Evolution of life histories in *Pinus*. The Press Syndicate of the University of Cambridge, Cambridge, UK.

Lafon, C.W., and Kutac, M.J. 2003. Effects of ice storms, southern

pine beetle infestation, and fire on Table Mountain pine forests of southwestern Virginia. Physical Geography, **24**(6): 502–519. doi:10.2747/0272-3646.24.6.502.

Lafon, C.W., Waldron, J.D., Cairns, D.M., Tchakerian, M.D., Coulson, R.N., and Klepzig, K.D. 2007. Modeling the effects of fire on the long-term dynamics and restoration of yellow pine and oak forests in the southern Appalachian Mountains. Restor. Ecol. **15**(3): 400–411. doi:10.1111/j.1526-100X.2007.00236.x.

Lesser, W.H. 1993. Prehistoric human settlement in upland forest region. McClain Printing Co., Parsons, West Virginia.

Lynch, C., and Hessl, A.E. 2010. Climatic controls on historical wildfires in West Virginia, 1939–2008. Physical Geography, **31**(3): 254–269. doi:10.2747/0272-3646.31.3.254.

Malamud, B.D., Millington, J.D.A., and Perry, G.L.W. 2005. Characterizing wildfire regimes in the United States. Proc. Natl. Acad. Sci. U.S.A. **102**(13): 4694–4699. doi:10.1073/pnas.0500880102. PMID:15781868.

Maxwell, R.S., and Hicks, R.R., Jr.. 2010. Fire history of a rimrock pine forest at New River Gorge National River, West Virginia. Nat. Areas J. **30**(3): 305–311. doi:10.3375/043.030.0311.

McBride, J.R. 1983. Analysis of tree rings and fire scars to establish fire history. Tree-Ring Bull. **43**: 51–67.

McCune, B. 1988. Ecological diversity in North American pines. Am. J. Bot. **75**(3): 353–368. doi:10.2307/2443983.

McEwan, R.W., Hutchinson, T.F., Ford, R.D., and McCarthy, B.C. 2007a. An experimental evaluation of fire history reconstruction using dendrochronology in white oak (*Quercus alba*). Can. J. For. Res. **37**(4): 806–816. doi:10.1139/X06-294.

McEwan, R.W., Hutchinson, T.F., Long, R.P., Ford, D.R., and McCarthy, C.B. 2007b. Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America. J. Veg. Sci. **18**(5): 655–664. doi:10.1111/j.1654-1103.2007.tb02579.x.

McIntyre, A.C. 1929. A cone and seed study of the Mountain Pine (*Pinus pungens* Lambert). Am. J. Bot. **16**(6): 402–406. doi:10.2307/2435887.

Morton, O.F. 1910. A history of Pendleton County, West Virginia. Orin F. Morton, Franklin, West Virginia.

Rice, O.K. 1970. The Allegheny frontier: West Virginia beginnings, 1730–1830. 1st ed. University Press of Kentucky, Lexington, Kentucky.

Roberts, B.A., and Mallik, A.U. 1994. Responses of *Pinus resinosa* in Newfoundland to wildfire. J. Veg. Sci. **5**(2): 187–196. doi:10.2307/3236151.

Schuler, T.M., and McClain, W.R. 2003. Fire history of a ridge valley

oak forest. USDA Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, Res. Pap. NE-724.

Shumway, D.L., Abrams, M.D., and Ruffner, C.M. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. Can. J. For. Res. **31**(8): 1437–1443. doi:10.1139/x01-079.

Smith, K.T., and Sutherland, E.K. 1999. Fire-scar formation and compartmentalization in oak. Can. J. For. Res. **29**(2): 166–171. doi:10.1139/x98-194.

Smith, B., and Sutherland, E.K. 2001. Terminology and biology of fire scars in selected central hardwoods. Tree-Ring Res. **57**(2): 141–147.

Speer, J.H. 2010. Fundamentals of tree ring research. The University of Arizona Press, Tucson, Arizona.

Stephenson, S.L., Adams, H.S., and Lipford, M.L. 1986. Ecological composition of indigenous stands of red pine (*Pinus resinosa*) in West Virginia. Castanea, **51**(1): 31–41.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. The University of Arizona Press, Tucson, Arizona.

Thomas-Van Gundy, M.A., Nowacki, G.J., and Schuler, T.M. 2007. Rule-based mapping of fire-adapted vegetation and fire regimes for the Monongahela National Forest. USDA Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, Gen. Tech. Rep. NRS-12.

USDA Forest Service. 2006. Monongahela National Forest Land and Resource Management Plan. USDA Forest Service, Eastern Region, Elkins, West Virginia.

USDA Forest Service. 2008. NAIP (National Agriculture Imagery Program) Digital Ortho Photo Image. USDA Forest Service, Aerial Photography Field Office, Salt Lake City, Utah.

Verrall, A.F. 1938. The probable mechanism of the protective action of resin in fire wounds on red pine. J. For. **36**: 1231–1233.

Waldrop, T.A., and Brose, P.H. 1999. A comparison of fire intensity levels for stand replacement of Table Mountain pine (*Pinus pungens* Lamb.). For. Ecol. Manage. **113**(2–3): 155–166. doi:10.1016/S0378-1127(98)00422-8.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. **26**(1): 1–80. doi:10.2307/1943577.

Williams, C.E. 1998. History and status of Table Mountain pine – pitch pine forests of the southern Appalachian Mountains (USA). Nat. Areas J. **18**: 81–90.

Zobel, D.B. 1969. Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. Ecol. Monogr. **39**(3): 303–333. doi:10.2307/1948548.