FIRE REGIMES OF THE SOUTHERN APPALACHIAN MOUNTAINS: TEMPORAL AND SPATIAL VARIABILITY AND IMPLICATIONS FOR VEGETATION DYNAMICS

A Dissertation

by

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ABSTRACT

Ecologists continue to debate the role of fire in forests of the southern Appalachian Mountains. How does climate influence fire in these humid, temperate forests? Did fire regimes change during the transition from Native American settlement to Euro-American settlement? Are fire regime changes resulting in broad vegetation changes in the forests of eastern North America? I used several approaches to address these questions.

First, I used digitized fire perimeter maps from Great Smoky Mountains National Park and Shenandoah National Park for 1930-2009 to characterize spatial and temporal patterns of wildfire by aspect, elevation, and landform. Results demonstrate that fuel moisture is a primary control, with fire occurring most frequently during dry years, in dry regions, and at dry topographic positions. Climate also modifies topographic control, with weaker topographic patterns under drier conditions.

Second, I used dendroecological methods to reconstruct historical fire frequency in yellow pine (*Pinus*, subgenus Diploxylon Koehne) stands at three field sites in the southern Appalachian Mountains. The fire history reconstructions extend from 1700 to 2009, with composite fire return intervals ranging from 2-4 years prior to the fire protection period. The two longest reconstructions record frequent fire during periods of Native American land use. Except for the recent fire protection period, temporal changes in land use did not have a significant impact on fire frequency and there was little discernible influence of climate on past fire occurrence.

Third, I sampled vegetation composition in four different stand types along a topographic moisture gradient, including mesic cove, sub-mesic white pine (*Pinus strobus* L.)-hardwood, sub-xeric oak (*Quercus* L.), and xeric pine forests in an unlogged watershed with a reconstructed fire history. Stand age structures demonstrate changes in establishment following fire exclusion in xeric pine stands, sub-xeric oak stands, and sub-mesic white pine-hardwood stands. Fire-tolerant yellow pines and oaks are being replaced by shade-tolerant, fire sensitive species such as red maple (*Acer rubrum* L.) and hemlock (*Tsuga canadensis* L. Carr.). Classification analysis and ordination of species composition in different age classes suggest a trend of successional convergence in the absence of fire with a shift from four to two forest communities.

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NOMENCLATURE

AF	All Fires
AWF	Area Wide Fire
AWI	Area Wide Fire Interval
CART	Classification and Regression Tree
CFI	Composite Fire Interval
DBH	Diameter at Breast Height
DEM	Digital Elevation Model
EP	Exclusion Period
FFI	Filtered Fire Interval
FP	Fire Period
GSMNP	Great Smoky Mountains National Park
ISA	Indicator Species Anlaysis
LEI	Lower Exceedance Interval
MCFI	Mean Composite Fire Interval
MF	Major Fire
MFI	Mean Fire Interval

MRPP	Multi-Response Permutation Procedure
NCDC	National Climatic Data Center
NMS	Non-metric Multidimensional Scaling
OS	Origin to Scar
PDSI	Palmer Drought Severity Index
PFI	Point Fire Interval
PP	Post-fire Period
RF	Regional Fire
RFI	Regional Fire Interval
SD	Standard Deviation
SEA	Superposed Epoch Analysis
SNP	Shenandoah National Park
UEI	Upper Exceedance Interval
WFI	Weibull Median Fire Interval

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CHAPTER I

INTRODUCTION*

Disturbance history is a key factor explaining contemporary vegetation properties and is often an essential consideration for ecosystem restoration (Baker 1994, Foster et al. 1996, Fulé et al. 1997, Foster 2000). Fire is a particularly important source of disturbance that controls the global distribution of fire-dependent ecosystems (Bond and Keeley 2005), the landscape-scale spatial arrangement of community types, and individual species establishment or persistence (Barton 1993). Extensive fire research has been carried out in coniferous forests of western North America, boreal forests, grasslands, and savannas (Anderson and Brown 1983, Frelich and Reich 1995, Uys et al. 2004, Sibold et al. 2006). However, the role of fire disturbance in temperate deciduous and mixed forests remains unclear (Morgan et al. 2001).

Fire regimes in many temperate regions were drastically altered in recent centuries. Anthropogenic activities such as agricultural clearance, logging, and fire protection disrupted patterns of ignition and the spread of fire in the forest of eastern North America, northern and central Europe, and northeastern China (Brose et al. 2001, Lorimer 2001, Drobyshev et al. 2004, Chang et al. 2007, Bowman et al. 2009). In most of these temperate regions fire has been almost entirely excluded from the landscape for the past century (Niklasson et al. 2002, Lindbladh et al. 2003, McEwan et al. 2007b, Aldrich et al. 2010, Niklasson et al. 2010). As a result, minimal information is available on the nature of temperate fire regimes preceding their disruption by recent human activities. The historical frequency, extent, and spatial controls of wildfire in temperate

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forests are largely unknown. Consequently, a potentially significant contributor to the development of contemporary forest vegetation in these regions is missing from our understanding.

In particular, questions remain about the importance of fire in the development of oak (*Quercus* L.)-chestnut (*Castanea dentate* (Marsh.) Borkh.) forests that dominated eastern North America for the last 4,000 years. A number of the principal tree species in eastern forests require fire or are thought to be fire-associated (Abrams 1992, Lorimer 2001). Mature oak trees, particularly those in the white oak subgenus (*Leucobalanus*), are relatively fire-resistant because of their thick bark and ability to compartmentalize rot (Brose and Van Lear 1999, Smith and Sutherland 1999). Oak seedlings thrive in the aftermath of fire because of their strong sprouting ability and the open understory conditions that result from burning (Abrams 1992, Lorimer et al. 1994, Brose and Van Lear 1998). In the absence of fire, stand density increases and oaks are replaced by more shade-tolerant, fire-sensitive hardwoods, a phenomenon observed widely today after decades of fire exclusion (Lorimer et al. 1994, Harrod et al. 1998, Harrod et al. 2000, Reid et al. 2008). Additionally, some pine (*Pinus* L.) species found in eastern forests are even more closely associated with fire than oaks. For example, Table Mountain pine (*P. pungens* Lamb.), a species that is endemic to the Appalachian Mountains, has serotinous cones and shade-intolerant seedlings that regenerate most successfully immediately following fire disturbance (Zobel 1969, Williams 1998, Jenkins et al. 2011).

Historical records also suggest that fire played an important role in the pre-settlement forests of eastern North America. Vegetation reconstructions using pre-settlement land surveys indicate that oak and pine species have declined in contemporary forests throughout the region (Abrams and Ruffner 1995, Foster et al. 1998b, Dyer 2001). Written accounts from early travelers and naturalists describe oak forests as open and park-like, with widely spaced trees and a variety of grasses, forbs, and shrubs (Whitney 1994, Lorimer 2001). Historical accounts also depict Native American use of fire for a multitude of purposes, including promotion of mast-producing species, improvement of game habitat, and facilitation of hunting (Cronon 1983, Whitney 1994, Abrams and Nowacki 2008).

Despite these lines of evidence, the historic role of fire in eastern forests has been the subject of considerable debate (Russell 1983, Clark and Royall 1996, Abrams and Seischab 1997). One notion is that fires ignited by humans and possibly lightning were common across eastern North America prior to Euro-American settlement (e.g. Abrams 1992, Frost 1998 , Brose et al. 2001) and that aboriginal burning practices were adopted and continued by settlers (Prunty 1965, Pyne 1982). A frequent burning regime may have maintained open stands with contiguous fine fuels that promoted fire spread (Harrod et al. 2000) and favored tree species such as oak and pine. Forests in this region have remained largely unburned for decades, though, because of fire protection efforts initiated in the early twentieth century. In the absence of fire, oak and pine species are failing to regenerate and are declining in abundance throughout eastern North America (Lorimer 1984, Nowacki and Abrams 1992, Harrod et al. 2000, McEwan and Muller 2006, Fei et al. 2011). Species composition has shifted toward mesophytic trees like maple (*Acer* L.), birch (*Betula* L.) and hemlock (*Tsuga* Carrière). Nowacki and Abrams (2008) termed this change “mesophication.” They argued that the rather incombustible litter of mesophytic plants will diminish burning further and hasten the loss of pyrogenic vegetation. The demise of fire-associated habitats may lead to declines in vegetation diversity(Rogers et al. 2008), loss of wildlife habitat and food resources (Rodewald and Abrams 2002), and changes in ecosystem function (Alexander and Arthur 2010).

Nevertheless, many academics continue to question the importance of fire in the development of eastern forests. There is general acceptance that fires burned frequently during the industrial period in the late 19th and early 20th century, promoting the establishment of oak and pine species (Harmon 1982a, Abrams and Nowacki 1992, Brose et al. 2001, McEwan et al. 2007b). However, critics of the fire-oak hypothesis view high fire frequency during the industrial period as an unprecedented shift in the disturbance regime outside of the historical range of variation (Williams 1998, Hessl et al. 2011). According to this view fires were not an important driver of vegetation pattern in eastern forests prior to the late 19th century. Consequently, the decline of oak and pine during recent decades is viewed as a natural process of recovery from a historically atypical disturbance period. Recent literature has also suggested that changes in moisture regimes, wildlife populations, and land use – not fire exclusion – are the primary drivers of oak decline (McEwan et al. 2011). If so, the restoration of fire in eastern forests is unnecessary: pine and oak communities will persist on dry, exposed sites in the absence of fire (Maxwell and Hicks 2010, Hessl et al. 2011).

In light of this ongoing debate, it is important to characterize historical and contemporary patterns of fire and vegetation response in southern Appalachian forests. The knowledge produced in this dissertation will add to our understanding of the underlying processes that drive vegetation pattern in the region. The results will also provide specific restoration targets for land managers in terms of fire frequency, species assemblage, and landscape pattern. Hopefully, this research will also provide a step towards resolution of the debate over fire's role in eastern forests prior to Euro-American settlement.

Purpose of the Study

In this study I use dendroecological techniques and GIS to characterize historical and contemporary fire disturbance in the Southern Appalachian Mountains. I also assess the roles that fire disturbance and fire exclusion have played in the development of forest composition in the region. The study is organized around three objectives: (1) Characterization of landscape-scale controls on contemporary patterns of fire disturbance; (2) Development of long-term fire history reconstructions at three sites that predate the period of fire exclusion, industrial disturbance, and Euro-American settlement and (3) Characterization of forest composition and tree establishment patterns in an unlogged watershed prior to and following the implementation of fire protection.

Contemporary Landscape Patterns of Fire

Fire regime characteristics such as fire frequency, size, and intensity are spatially and temporally variable (Parisien et al. 2006, Lafon and Grissino-Mayer 2007). Variability of fire regime characteristics often contributes to landscape heterogeneity in fire prone ecosystems (Minnich and Chou 1997, Taylor 2000b). Therefore, it is important to assess the underlying controls on patterns of fire, which in turn influence vegetation patterns. However, in the absence of prohibitively large numbers of fire-scarred samples, it can be extremely difficult to discern landscape patterns of historical fire disturbance from the dendroecological record (Hessl et al. 2007a, Kellogg et al. 2008). Therefore contemporary fire records can be a valuable supplement to dendroecological reconstructions of historical fire regimes, providing information about landscape controls on fire occurrence (Rollins et al. 2002, Shapiro-Miller et al. 2007, Farris et al. 2010).

Climate and topography have been demonstrated as key drivers of fire disturbance patterns (Swetnam and Betancourt 1998, Taylor and Skinner 1998). Climate contributes to fire regimes in two primary ways, by influencing vegetation productivity and fuel accumulation and by controlling the frequency of weather conducive to fire initiation and spread (Baker 2003). Regional climate acts as a broad scale control on fire, influencing fire regimes at broad spatial scales (Heyerdahl et al. 2001, Cyr et al. 2007). Regional climatic gradients have been linked to spatial variations in fire frequency, size, shape, and intensity (Parisien et al. 2006). Temporal fluctuations in climate also have been related to shifts in fire frequency and area burned, but the climatic conditions that promote fire vary by region and forest type (e.g. Swetnam and Betancourt 1998, Lafon et al. 2005, Sibold and Veblen 2006, Drever et al. 2008).

Topography acts as a local-scale control on many types of disturbance (e.g. Zhang et al. 1999, Boose et al. 2004, Stueve et al. 2007). Topographic variation (e.g. aspect, slope position, and elevation) influences precipitation, runoff, temperature, wind, and solar radiation, which in turn affect flammability through fuel production and moisture (Daly et al. 1994, Dubayah and Rich 1995). Spatial patterns of fire have been linked to topographic features in portions of the western U.S. (Taylor and Skinner 1998, Rollins et al. 2002, Howe and Baker 2003). However, topography appears to play a limited role in other locations (Kafka et al. 2001, Bigler et al. 2005, Schulte et al. 2005). One potential explanation for these seemingly contradictory findings is that climate modulates topographic influences on fire. For example, large, high-intensity wildfires occurring during drought conditions have been shown to exhibit weaker topographic control than small disturbances of lower intensity (Parker and Bendix 1996, Moritz 2003, Mermoz et al. 2005). A landscape in a generally more fire-prone climatic setting, therefore, might have weaker topographic patterns of fire than a landscape in a less fire-prone environment. Topographic patterns of fire also might vary temporally as climates shift over time and render a landscape more or less prone to disturbances.

In the interest of addressing these questions, I analyze mapped fire perimeters during the 20th century from Shenandoah National Park (SNP) in the central Appalachian Mountains and Great Smoky Mountains National Park (GSMNP) in the southern Appalachian Mountains. My objective is to assess how climate and topography influence spatial patterns of fire, and whether region-scale spatial variations in climate influence the interaction between fire and topography at a finer scale. The research questions that I will address are the following:

1. Does climate impose regional-scale pattern on the occurrence of fire? Therefore, does the relatively dry SNP have a higher density of fires, larger fires, and a shorter fire cycle than GSMNP? Likewise, is fire activity related to temporal variations in climate, with more burning in dry years than wet years in both locations?

2. Does topography impose local-scale pattern on the occurrence of fire? Is fire most common in both study sites on dry south-facing slopes, ridgetops, and at low elevations?

3. Do regional climate and local topography interact such that topographic patterns of fire are more pronounced in a less fire-prone landscape than a more

fire-prone landscape? Are fires more strongly confined to dry topographic settings in the relatively wet GSMNP than in the drier SNP?

4. Is the fire-topography association also influenced by temporal climatic variability? Does topography exert a stronger influence on fire occurrence during wet years than dry years in both national parks? Additionally, are lightning-ignited fires more strongly confined to dry topographic settings because of the moist conditions that accompany lightning, compared to anthropogenic fires, which often are ignited during dry, windy weather?

Fire History

Paleoecological data from fire-scarred trees (e.g. Taylor 2000b, Grissino-Mayer et al. 2004, Hessl et al. 2004) provide an opportunity to document the occurrence of fire during preceding centuries. A limited number of long fire chronologies have been developed for temperate forests in eastern North America (Harmon 1982a, Mann et al. 1994, Sutherland et al. 1995, Shumway et al. 2001, Guyette and Spetich 2003, Schuler and McClain 2003, McEwan et al. 2007b, Hoss et al. 2008, Aldrich et al. 2010), with the exception of the Ozark Plateau near the western margin of the temperate forest which has been sampled extensively (Guyette et al. 2002). This knowledge gap is primarily the result of agricultural clearance and industrial logging, which have obliterated many of the fire-scarred trees in eastern North America and temperate forests globally. Two fire history reconstructions in the central Appalachians of western Virginia document frequent burning in remote, upland pine and oak stands throughout the 18th and 19th century (Hoss et al. 2008, Aldrich et al. 2010). Other chronologies that have been developed for eastern North America (e.g. Harmon 1982a, Schuler and McClain 2003, McEwan et al. 2007b) are primarily restricted to the mid- or late-nineteenth through twentieth century. These studies document widespread burning, with the establishment of pine and oak stands in concert with fires at approximately 2-17 year intervals during the late 1800s and early 1900s. However these temporally short studies cannot inform our understanding of the role of fire prior to industrial logging disturbances approximately a century ago.

Fire regimes prior to Euro-American settlement are of particular interest because they frequently are used as restoration targets. Several studies have demonstrated that Native Americans exerted a strong influence, primarily through the use of fire, on forests in close proximity to their villages (Dorney and Dorney 1989, Black and Abrams 2001, Foster et al. 2004, Black et al. 2006). However, there is vigorous debate about the extent of their impact on vegetation across the broader landscape (Russell 1983, Delcourt 1987, Denevan 1992, Whitney 1994, Delcourt and Delcourt 1997, Delcourt et al. 1998, Vale 1998). One important aspect of the southern Appalachian region is that substantial Cherokee populations remained through the early 1800s. My fire chronologies, therefore, offer a glimpse of aboriginal influences on fire that cannot be obtained from many other parts of the eastern U.S., such as the central Appalachian Mountains, where native depopulation occurred a century or more ahead of European settlement (Aldrich et al. 2010, McEwan et al. 2011). The burning practices of Cherokee populations may have significantly affected southern Appalachian forests, as they did following relocation to the Ozark Mountains in the late 19th century (Guyette et al. 2006).

Fire history researchers of the western U.S. have sought to understand how climatic variability influenced the occurrence of fire. Many studies reveal a strong role of climate. In the dry forests of the Southwest, for example, fires often occurred in dry years following wet years that promoted abundant production of fine fuel (Baisan and Swetnam 1990, Donnegan et al. 2001). The humid environments of the East permit copious fuel production every year, but the fuel often remains too moist to burn. Drought may have been particularly important under such conditions, but most eastern fire history studies do not report climatic analyses. Schuler and McClain (2003) and McEwan et al. (2007b) found little influence of climate on fire occurrence; however, their fire chronologies were limited to the late 1800s and early 1900s, when anthropogenic burning was so widespread that it may have obscured the role of climate.

Discovering how land use history and climatic variability affected fire occurrence in the southern Appalachian region is important for managing forests within its extensive public lands and, more generally, for understanding the historic role of fire on temperate forest landscapes. Therefore, it is important to establish whether there is a long history of fire in southern Appalachian forests. It is also important to assess the historical drivers of fire disturbance. For example, did fire regime characteristics change in concert with shifts in climate and land use? Finally, fire history reconstructions will also provide a historic range of variation in fire disturbance and quantitative restoration targets for land managers. Consequently, I have used dendroecological methods to address the following research questions:

1. How frequently did fires occur on southern Appalachian Mountain slopes during the last three centuries?

2. Did temporal changes in land use alter fire frequency?

3. How did interannual climatic variability influence the occurrence of fire?

Vegetation Dynamics

If fire disturbance was common in eastern forest in the past, then it is important that we incorporate this disturbance process into our understanding of contemporary vegetation patterns. Research demonstrates that in the absence of fire, successional changes are occurring in xeric forest communities (Harrod et al. 1998, Harrod et al. 2000, Hoss et al. 2008, Aldrich et al. 2010). However, the mesophication hypothesis posits successional change across a much broader landscape than just xeric topographic positions (Nowacki and Abrams 2008). Fire associated oak, chestnut and pine species were found across a wide range of topographic positions in pre-settlement forests (Abrams and McCay 1996, Dyer 2001, McEwan et al. 2005). Indeed, fire must have been widespread if it played an important role in the development of oak-chestnut forests that dominated much of the pre-settlement landscape in eastern North America (Delcourt et al. 1998, Foster et al. 2002). Yet, the impact of contemporary fire exclusion outside of the most xeric forest communities is largely unknown.

If fire disturbance was frequent on xeric ridge-tops, then it is likely that fires also burned into more mesic positions, although fires may have occurred with less frequency and at lower intensities at these mesic positions. Soil charcoal provides some evidence that fires burned in mesic forest communities in the southern Appalachian region during the last several millennia (Hart et al. 2008, Fesenmyer and Christensen 2010). Yet studies of disturbance regimes in mesic forest types have largely ignored the potential role of fire in species establishment and persistence (Lorimer 1980, Busing 1998, Buchanan and Hart 2012). A lack of fire history reconstructions from old growth, mesic forest communities has been a major impediment. Hardwoods do not reliably preserve fire scars in this region (McEwan et al. 2007a). However, the presence of yellow pine stands with abundant fire scarred material adjacent to unlogged mesic forest communities in the Licklog watershed provides an opportunity to address this knowledge gap. The combination of a fire history reconstruction along with dendroecological data on tree establishment from surrounding forest communities enables me to examine whether successional change is occurring in multiple communities in response to changes in the fire regime. If fire disturbance was a driver of vegetation dynamics across the broader landscape, then changes in species establishment should be discernible not only in xeric communities, but along the entire topographic moisture gradient.

The synthesis of disturbance history and compositional change also provides an opportunity to assess the role of fire in the maintenance of community differentiation or beta diversity. Typically, topographic moisture has been proposed as the primary control on the spatial arrangement of species in southern Appalachian forests (Whittaker 1956, Golden 1981). However, topographic moisture and fire disturbance are generally parallel gradients in this region (e.g. higher fire frequency/severity at drier topographic positions)(Harmon et al. 1984, Wimberly and Reilly 2007). Fire disturbance in the past may have magnified differences in site conditions between mesic cove positions and xeric ridge positions not only by causing fire related mortality but also by altering vegetation structure. For example, frequently burned upper ridges may have supported lower tree densities, an herbaceous understory, and increased solar insolation at the ground surface (Harrod et al. 2000). In the absence of fire, the topographic zonation in vegetation might have developed less strongly. If fire disturbance did accentuate differences in site conditions, then fire exclusion should result in a decline in community differentiation along the topographic moisture gradient.

Fire exclusion provides a “natural experiment”, in which I can use dendroecology to investigate temporal shifts in tree establishment across an unlogged watershed following the cessation of fires. My research aims to test competing conceptual models of forest development along a topographic moisture gradient which includes xeric pine stands, sub-xeric oak stands, sub-mesic white pine-hardwood stands, and mesic cove stands. I will address the following research questions:

1. Do variations in species composition between different age classes relate to fire suppression in mesic as well as xeric forest communities?
2. Do changes in successional trajectory due to fire suppression suggest a decrease in community differentiation or beta diversity across the entire site?

CHAPTER II

LITERATURE REVIEW

Fire Regimes in the Southern Appalachian Mountains

Fire is an important source of disturbance in forested ecosystems (White et al. 1999, Frelich 2002b, Bond and Keeley 2005). Recent ecological research has demonstrated the diversity of fire regimes which influenced the development of North American forests (Abrams 1992, Fulé et al. 1997, Parshall and Foster 2002, Schulte and Mladenoff 2005). However, natural disturbance regimes are particularly difficult to quantify in eastern North America because of the enormous changes North American forests have undergone during the centuries since Euro-American settlement (Cronon 1983, Whitney 1994, Russell 1997, Foster et al. 1998b, Burgi et al. 2000, Hall et al. 2002). Consequently, a lack of information exists on the frequency and severity of prescribed fire that is necessary to maintain and restore xerophytic pine and oak stands in the southern Appalachian Mountains (Welch et al. 2000, Van Lear and Brose 2002, Waldrop et al. 2002, Schuler and McClain 2003).

Xerophytic forests in the Appalachian Mountain region are dominated by tree species such as Table Mountain pine, pitch pine (*P. rigida* Mill.), and white oak (*Q. alba* L.), which have adaptations to high intensity, stand replacing fires (e.g. serotinous cones or vigorous sprouting) and low intensity, surface burns (e.g. thick bark). Much research has indicated that stand replacing fires are necessary for the regeneration of these pine-oak stands (Zobel 1969, Groeschl et al. 1993, Elliott et al. 1999, Randles et al. 2002). However, research has also supported the conclusion that these stands will regenerate most successfully under frequent, low severity fires (Abrams and Nowacki 1992, Waldrop et al. 2000, Shumway et al. 2001). Therefore it is important to identify historical fire regimes in order to better understand the disturbance regimes that produced current forest ecosystems.

Models of Fire and Vegetation Development in Eastern Forest

The fire-oak hypothesis (e.g. Abrams 1992, Lorimer et al. 1994, Abrams 2003) contends that oak forests throughout eastern North America developed over centuries of periodic surface burning that impeded the establishment of fire-intolerant mesophytic competitors. Brose et al. (2001) argued that in Appalachian oak forests low-intensity surface fires occurred periodically, perhaps about once per decade, from before European settlement until the logging boom of the 1890s to 1920s. Frost (1998) proposed that montane pine stands were maintained on presettlement landscapes under "polycyclic" fire regimes characterized by a short cycle (about 5–7 years) of understory fires combined with a long cycle (about 75 years) of stand-replacing fires. Supporters of the "frequent fire" perspective argue that fire protection during the 20th century has represented an unprecedented shift in the disturbance regime for much of eastern North America (Nowacki and Abrams 2008). Consequently, fire tolerant, shade intolerant pine and oak species are being replaced by fire sensitive, shade tolerant species. Shifts in species composition and community structure have been noted in forests throughout eastern North America (Abrams and Nowacki 1992, Harrod et al. 2000, Heinlein et al. 2005, Hutchinson et al. 2008, Rogers et al. 2008).

However, alternative models of fire disturbance and vegetation development have also been proposed. William's (1998) model of Table Mountain pine-pitch pine history proposes that fire regimes and pine extent varied with land use history on Appalachian Mountain landscapes. Specifically, the model suggests fire was infrequent before European settlement and that pines were largely restricted to self-replacing stands on extreme sites, e.g., rock outcrops, too dry for hardwoods. After settlement fire frequency increased gradually. Pines expanded to less extreme sites, particularly during the logging boom, before declining in the twentieth century. Under this scenario many existing stands may be artifacts of industrial disturbances. Similar hypotheses have been proposed about the expansion of oaks due to logging, agricultural clearance, and increased fire activity during the period of Euro-American settlement and industrialization (Abrams and Nowacki 1992, McEwan et al. 2007b, McEwan et al. 2011).

Pre-Euro-American Settlement Fire Regimes

Historical records and archaeological evidence demonstrate that Native Americans used fire for multiple purposes in eastern North America (Chapman 1982, Cronon 1983, Denevan 1992, Whitney 1994, Delcourt and Delcourt 1997). Accounts from early European visitors are one of the primary sources of information about aboriginal use of fire. Written records note that Native Americans used fire in order to clear land, drive game during hunts, increase early successional habitats, control pests, and reduce underbrush for ease of travel (Whitney 1994, Abrams and Nowacki 2008). Yet debate continues regarding whether aboriginal use of fire influenced broad vegetation patterns in eastern North America (Russell 1983, Clark 1997, Vale 1998, McEwan et al. 2011).

Paleoecological studies of pollen cores and soil charcoal support the view that Native Americans actively burned and altered vegetation in the southern Appalachian region. Delcourt and Delcourt (1998) recorded increases in the pollen of chestnut, oak, and pine species in concert with increases in charcoal from sediment cores at three sites in the southern Appalachians. They hypothesized that early successional, fire tolerant species increased in abundance due to shifts in Native America land use at the start of the Woodland Period (ca. 700 BC). Similar increases in soil charcoal coinciding with forest conversions to oak and pine in relation to Native American land use have been noted at other sites in the southern and central Applachians (Chapman 1982, Delcourt et al. 1986, Delcourt and Delcourt 1997, Delcourt and Delcourt 1998, Delcourt et al. 1998, Springer et al. 2010) and in the upper Midwest (Clark and Royall 1995). Additional soil charcoal studies in the region have demonstrated a long history of fire occurrence in both xeric and mesic forests without linking the fires to changes in anthropogenic activities (Welch 1999, Hart et al. 2008, Fesenmyer and Christensen 2010).

Foster and Cohen (2007) found increases in soil charcoal during the 18th century in sediment cores from the piedmont of Georgia. They concluded that the increase in soil charcoal was a product of increased Native American burning in the southern Appalachians due to the deer skin trade. They argued that both Creeks and Cherokees burned wide swaths of the landscape in order to harvest increasing numbers of deer pelts for trade with European markets. However, there has been disagreement in the literature over the interpretation of these results (Piker 2010). Bolstad and Gragson (2008) analyzed Cherokee patterns of settlement during this same period and concluded that Cherokees would have had to exploit their entire region of control in the Appalachian

Mountains from northern Georgia to southern Virginia in order to satisfy rates of deer harvest.

Pre-settlement land surveys also provide evidence that Native American burning altered vegetation in eastern forests. Black and Abrams (2001) used witness trees in southeastern Pennsylvania to demonstrate a higher abundance of favored mast producing species such as black walnut (*Juglans nigra* L.) and hickories (*Carya sp.* Nutt) in watersheds with known Native American villages compared to those without villages. Black et al. (2006) found similar patterns of increasing frequency of oak, hickory and chestnut in regions with greater Native American activity. In east-central Alabama the frequency of hickories increased and pines decreased with increasing proximity to Native American villages (Foster et al. 2004).

Despite these lines of evidence, several ecologists have questioned the impact of Native American burning on eastern vegetation. Russel (1983) argued that aboriginal burning had little influence on vegetation beyond the area immediately surrounding their villages, suggesting that historical accounts are inconclusive and unreliable. Clark and Royall (1996) found minimal evidence of cultural burning aside from locations adjacent to Native American villages. They concluded that fire frequencies may be overstated in prior sediment studies and that fire may not be necessary for the maintenance of pine-oak forests. Finally, McEwan et al. (2011) noted the scarcity of fire history data across much of eastern North America prior to 1800. They argue that further work is needed to characterize fire regimes during the transition from Native American to Euro-American land use.

Tree-ring reconstructions of fire history are one approach to answering the eastern fire debate. Dendroecology can provide annually resolved records of fire disturbance at a site. Unfortunately, agricultural clearance, logging and rapid rates of decay have severely limited the quantity of old, fire-scarred material available for reconstructions. Currently, there are no published fire history reconstructions from the southern Appalachians that predate Euro-American settlement. There have been only a handful of studies published on the broader eastern forest region of North America that predate Euro-Americans. Aldrich et al. (2010) reported frequent surface fires at approximately 5 year intervals dating back to the early 1700s at an isolated site in the mountains of western Virginia. Hoss et al. (2008) reported even shorter fire intervals of 2.2 years, but the record only stretched back to the earliest period of Euro-American settlement at the beginning of the 1800s. Both fire history reconstructions recorded pine and oak establishment during the period of frequent fire. Shumway et al. (2001) reported fire intervals of 7.6 years from 1615 to 1958, in an oak forests in western Maryland. None of these fire history reconstructions demonstrated a significant change in fire frequency during the transition from Native American to Euro-American settlement. Buell et al. (1954) calculated a mean fire interval of 14 years from 1641 to 1711 at a site in New Jersey, but the reconstruction was based on a single tree. Mann et al. (1994) documented 100 to 200 year intervals of increased fire activity in a pine-hemlock stand in Vermont during the pre-settlement era. A number of studies have documented frequent fire during the pre-settlement period on the edge of the eastern deciduous forest in longleaf pine (*P. palustris* Mill.) forests of Louisiana (Stambaugh et al. 2011), oak forests in the Ozarks Mountains (Guyette et al. 2002, Guyette and Spetich 2003, Stambaugh and Guyette 2006), the prairie boundary in Oklahoma (Allen and Palmer 2011), and in post-oak (*Q. stellata* Wangenh.) woodlands of southern Indiana (Guyette et al. 2003) and southern Illinois (McClain et al. 2010). However, a paucity of early fire history studies exist in eastern deciduous forests (McEwan et al. 2011).

Post Euro-American Settlement Fire Regimes

Evidence of the use of fire by early Euro-American settlers is much more prevalent. Several tree-ring reconstructions of fire have been developed that span the 19th and 20th century in the southern and central Appalachian region. Schuler and McClain (2003) estimated fire return intervals of 14.8 to 19.5 years for an oak forest in the Ridge and Valley of West Virginia. Harmon (1982a) documented frequent fire, 12.8 year individual-tree fire intervals, for the western portion of Great Smoky Mountains National Park from 1856-1940. Several other studies have documented frequent fires during the late 19th century coinciding with the establishment of oaks and pines in eastern forests (Sutherland et al. 1995, McEwan et al. 2007b, Hutchinson et al. 2008, Maxwell and Hicks 2010, Hessl et al. 2011). The absence of older samples in these fire history reconstructions has occasionally been interpreted as evidence of the absence of fire from previous land use periods (Hessl et al. 2011).

Several historians have hypothesized that Euro-American settlers appropriated aboriginal burning practices and there was no disruption of fire regimes during the transition from Native American to Euro-American land use and settlement (Prunty 1965, Pyne 1982, Brose et al. 2001). Others have argued that there was a lull in fire frequency for a century or more following Native American depopulation and preceding the arrival of large numbers of Euro-American settlers (Denevan 1992, Williams 2002, Fowler and Konopik 2007, McEwan et al. 2011). There is evidence in the tree-ring record from some regions that there was a decline in fire frequency during this transition period (Guyette et al. 2002, Guyette et al. 2003, McEwan and McCarthy 2008). However, in other areas there seems to be no disruption of fire regimes during the transition from Native American to Euro-American land use (Mann et al. 1994, Shumway et al. 2001, Hoss et al. 2008, Aldrich et al. 2010).

It is generally accepted that fire frequency increased with changes in land use during the 19th century (Pyne 1982, Brose et al. 2001). Population increased across most of the eastern United States and the operation of small iron furnaces may have driven heavier cutting in forests and contributed to ignitions on the landscape (Whitney 1994, Whitney and DeCant 2003). The initiation of large scale, industrial logging in the forests of the Lake States and the Appalachian Mountain region resulted in widespread, high intensity fires at the turn of the century (Lambert 1961, Pyle 1988). It was concern over erosion resulting from logging activities that spurred the initial conservation movement and eventually led to the establishment of the national forests in the eastern U.S. Concern over wood supply and soil conservation led to the implementation of a federal policy of fire prevention and suppression on all federal lands early in the 20th century (Mastran et al. 1983, Steen 2004). This policy became increasingly effective as fire suppression techniques improved during the mid-century. Consequently, fire has been largely excluded from most forests in the eastern U.S. during the past 90 years (Schuler and McClain 2003, McEwan et al. 2007b, Hutchinson et al. 2008, Aldrich et al. 2010).

Fire Atlases

Characterizing Fire Regimes

Fire atlases are useful in characterizing several aspects of fire regimes. They are most useful in the calculation of area derived measurements of fire occurrence. Records of area burned across a region are important in assessing climatic factors that induce severe fire years (Larsen and Macdonald 1995, McKelvey and Busse 1996, Turetsky et al. 2004). Records of area burned are also necessary for the accurate calculation of the fire rotation, which is defined as the length of time required to burn an area equal to the landscape of interest (Frelich 2002b). Paleo-records can be used to identify the occurrence of fire at some time in the past, however it is difficult (fire scars) or impossible (pollen records) to re-create an accurate fire perimeter. Therefore fire atlases provide an important record of the area affected by fire over time. Additional terms which relate to the area burned are fire return interval (the expected return time per stand), annual percent burned (proportion of the landscape that burns per year), and the fire frequency (the probability of a point burning per unit time) (Johnson and Gutsell 1994). Fire atlases will often contain details in addition to a map of the area that burned in the fire. This data can be used to assess the severity of a fire, which refers to that amount of mortality that occurs in a stand as a result of the fire (Frelich 2002b). This information is important in differentiating between low severity surface fires that do not cause significant mortality among canopy trees and high severity, stand replacing fires. Fire atlases also enable the location of re-burn areas that are subject to multiple fires in short succession, creating unique ecosystem structures and responses (McKelvey and Busse 1996, Holden et al. 2006).

Assessing Modern Changes in Fire Regimes

One of the primary values of historical records in the study of ecosystems is that they allow us to observe and quantify shifts in pattern and process over time. The advent of fire atlases as a technique in fire suppression has meant that there is a detailed record of changes in fire regimes over the past decades of fire suppression. Several studies have attempted to assess the impact of the widespread policy of fire suppression in North America during this century (Forman and Boerner 1981, Minnich 1983, McKelvey and Busse 1996, Minnich and Chou 1997, Keeley et al. 1999, Cleland et al. 2004, Grenier et al. 2005, Parisien et al. 2006).

In one of the earliest studies that utilized fire atlases, Forman and Boerner (1981) demonstrated that the number of fires in the New Jersey Pine Barrens has remained relatively constant during the last century. However the average annual area burned has decreased from 22,000 ha during 1906-1939 to 8,000 ha during 1940-1980 following the advent of fire suppression. This has led to an increase in the fire interval from 20 years to 65 years. The results suggest that the current conditions will favor the succession of fire intolerant species and the replacement of Atlantic white cedar (*Chamaecyparis thyoides* L. Britton, Sterns & Poggenb.) swamps with hardwood swamps.

Keeley et al. (1999) addressed the perception that wildfires have become increasingly destructive due to suppression efforts during the last century in California shrublands. In contrast to this hypothesis, they found that area burned, fire frequency, and fire size have not changed significantly. They did correlate fire occurrence with population density and concluded that fire suppression plays a major role in offsetting the large increase in anthropogenic ignitions.

Several studies have examined the dynamics of lightning versus human ignitions during recent decades (Minnich et al. 1993, McKelvey and Busse 1996, Ruffner and Abrams 1998, Lafon et al. 2005). Minnich et al. (1993) found a high rate of lightning strikes in northern Baja California and Mexico resulting in wildfires. Widespread lightning ignitions meant that wildfire occurrence was little affected by human ignitions. Ruffner and Abrams (1998) compared archival records of lightning strikes and resultant fires from 1912-1917 and 1960-1997 in Pennsylvania forests. Their study found evidence of lightning fires during both periods and suggests that lightning could have been a significant source of fire on the pre-European landscape in concert with Native American ignitions. These studies demonstrate the variable role that ignition source can play in shaping local fire regimes, particularly when fires are actively suppressed.

Several studies have analyzed the effect of fire suppression on landscape patterns of wildfire (Forman and Boerner 1981, Erman and Jones 1996, Minnich and Chou 1997, Rollins et al. 2001). The field of landscape ecology has developed techniques in the evaluation of spatial metrics which have been applied to wildfire patch dynamics (Turner 2005). Erman and Jones (1996) found mixed results in relation to the perception that fire suppression in forests of the Sierra Nevada Mountains in California has led to larger fires during the second half of this century. The Eldorado National Forest exhibited a trend of larger fires, however the majority of national forests in the region did not experience larger fires. Recent fires that have been perceived as extreme were actually within the historical range of variation. Forman and Boerner (1981) and

Minnich and Chou (1997) both found that fire suppression has affected the patch structure of fire disturbance in forests. They found that the spatial pattern of fire disturbance has historically included a fine grained network of small frequent fires within a larger network of coarse grained, less frequent large fires. However Forman and Boerner (1981) found that suppression eliminates the coarse grained pattern of larger fires in the New Jersey Pine Barrens. In contrast, Minnich and Chou (1997) found that in the chaparral of Southern California, where fires are driven by fuel accumulation, fire suppression has led to increases in fire size and the elimination of the finer grained structure created by frequent, smaller fires. Rollins et al. (2001) also found divergent results in the southern Rockies of New Mexico and the northern Rockies of Idaho and Montana. The fire rotation was shorter during the era of suppression in the southern Rockies, while the fire rotation increased in the northern Rockies during the same period. The results show a diversity of responses to fire suppression in different ecosystems. The complexity of fire cycles does not lend itself to application of results between ecosystems. This supports the conclusion that techniques applied in certain regions might produce unique and valuable results in a different region.

Identification of Controls on Fire Regimes

Recent research has attempted to characterize the variety of driving factors that influence fire regimes in different forest ecosystems. The development of GIS has facilitated studies on the influence of topography on fire dynamics. Heyerdahl et al. (2001) distinguished between bottom up, landscape level factors (i.e. aspect, elevation, and vegetation) and top down, regional factors (i.e. climate). They compared fire scars within and among four watersheds in the Blue Mountains of Oregon and Washington.

Several studies have utilized fire atlases to infer similar relationships between landscape controls and climatic influences (Romme and Knight 1981, Barton 1994, Morgan et al. 2001, Rollins et al. 2001, Rollins et al. 2002, Turetsky et al. 2004). Barton (1994) recorded soil water, litter depth, organic carbon, canopy cover, forest floor light, soil temperature, pH, and percentage bare soil across an elevation gradient of historical burns. The occurrence of fire increased with elevation and was most strongly correlated with soil moisture availability. Rollins (2002) used fire perimeters collected in the Gila/Aldo Leopold Wilderness Complex (GALWC) in New Mexico and the Selway-Bitterroot Wilderness Complex (SBWC) in Idaho and Montana from 1880 to 1996. Their results demonstrate the unique nature of fire responses in different ecoystems. Fire frequencies were highest on north facing slopes in the GALWC where the arid climate was less of a factor in limiting the continuity of fine fuels. However, fire frequencies were highest on south facing slopes in the SBWC where the drying of large woody fuels is necessary for the spread of fires.

Climate is one of the primary factors that influence variation in fire occurrence between years. Extreme fire events are highly correlated with severe droughts (Swetnam et al. 1999, Grissino-Mayer and Swetnam 2000). Several studies have correlated annual area burned in regions with records of warmer, drier weather (Larsen and Macdonald 1995, McKelvey and Busse 1996, Rollins et al. 2001, Rollins et al. 2002, Turetsky et al. 2004). Large fire years are also often correlated with high moisture and above average vegetation growth in preceding years.

Combining Fire Atlases with Other Techniques

Perhaps the most promising applications of fire atlases have been their combination with other techniques in characterizing fire regimes. Satellite imagery, aerial photographs, dendroecological techniques, and historical surveys have all been supplemented with data from fire atlases (Baisan and Swetnam 1990, Larsen and Macdonald 1995, Minnich and Chou 1997, Fulé et al. 2003, Stephens et al. 2003, Cleland et al. 2004, Grenier et al. 2005, Holden et al. 2005). Each of these techniques has limitations which can be addressed with the information provided in fire atlases.

Fire atlases have been an important source of calibration for fire scar analysis. Baisan and Swetnam (1990) used modern fire records to assess seasonality, fire size, and fuel type in combination with historic fire return intervals obtained through fire scar analysis. A major debate within the field of dendroecology has been the accuracy of fire return intervals developed from fire scars (Baker and Ehle 2001, Baker 2006, Fulé et al. 2006). Baker and Ehle (2001) questioned the sampling techniques in fire scar studies, suggesting that small, localized fires were being interpreted as large fires that burned across the entire landscape. Fule et al. (2003) used fire atlases to assess the accuracy of fire return intervals constructed from fire scar data in the Grand Canyon. They found that sampling methods and analysis of fire scars was accurate in identifying all of the fires that had been recorded on the study site and that the results did not underestimate fire return intervals.

Aerial photographs and satellite imagery have been used to construct modern fire atlases and to supplement information recorded in these records (Minnich and Chou 1997, Minnich et al. 2000a, Stephens et al. 2003, Holden et al. 2005). Holden et al.

(2005) used fire atlases to calibrate techniques for mapping of fires using Landsat Thematic Mapper derived images. Comparison of fire perimeters constructed from satellite images with fire perimeters measure on the ground allowed for the development of successful techniques and underlined the importance of the timing of image acquisition.

Cleland et al. (2004) compared records from the Public Land Survey with modern fire perimeter records in northern-lower Michigan. Historical fire rotations were interpolated from pre-settlement land surveys and compared to current fire rotations calculated from fire record during 1980-2000. The results showed that fire rotations have increased from 250 years in the past to 3,000 years in the present.

Issues of Bias within Fire Atlas Data

There are inherent limitations and sources of bias that must be considered when using historical fire records. Fire atlases are imperfect records of occurrence of fire on a landscape. Changes in technology, resources, and public awareness have influenced the accuracy and completeness of the fire record through time. The increase in industrial and recreational use of forests has also improved the accuracy of fire records (Murphy et al. 2000). However, fire records, particularly those extending into the earlier part of the century are biased towards the largest fires on a landscape (Strauss et al. 1989, Murphy et al. 2000, Reed and McKelvey 2002, Rollins et al. 2002). Larger fires require suppression methods and cause greater damage, while many smaller fires may go unnoticed, particularly in remote regions (McKelvey and Busse 1996) However, it is generally accepted that the few largest fires account for the vast majority of area burned in all forested ecosystems(Strauss et al. 1989, McKelvey and Busse 1996, Rollins et al.

2001, Rollins et al. 2002). Strauss et al. (1989) applied statistical analysis to fire size distributions in the western United States, concluding that the largest one percent of fires accounted for 80% - 96% of the area burned. Evaluation of Canada's fire statistics found that only 2-3% of fires were larger than 200 hectares and these fires accounted for 97-98% of the area burned (Stocks 1991). These studies have established that fire atlases, although biased towards large fires, are generally a good indicator of area burned. However it should be noted that fire atlases are a poor indicator of total number of fires. This bias is uneven over time, most likely increasing as one moves further back in the record (Murphy et al. 2000). Therefore, the use of fire atlases is probably not appropriate for examination of trends in the number of fires through time. Fire atlases might also be misleading in the comparison of anthropogenic versus lightning ignitions, since anthropogenic ignitions are generally closer to human populations and more likely to be recorded (Murphy et al. 2000).

Another important limitation in the use of fire atlases is their relatively short temporal extent. At the most, mapped fire records in North America will span a century (McKelvey and Busse 1996, Keeley et al. 1999, Rollins et al. 2002). Most studies are limited to several decades (Minnich 1983, Cleland et al. 2004, Parisien et al. 2006). The use of a temporally limited data set can lead to the overestimation of fire rotation (Li 2002). This problem is magnified in areas such as the boreal forest that are characterized by infrequent, stand replacing fires. Boreal fire return intervals can range from 5 - 500 years depending on topography and climate (Wein 1993). A century of data may be insufficient to characterize this long disturbance interval. As a result, many studies in the higher latitudes have used spatially extensive records covering an entire region or country in order to gain a representative sample of area burned on an annual or decadal time scale (Stocks 1991, Parisien et al. 2006). However, fluctuations in climate on a decadal or multi-decadal scale can bias results using spatially extensive records that only span a few decades. Recent paleo-fire records have demonstrated that multi-decadal fluctuations in climate can drive the occurrence of fire, particularly in regions where large fire years account for the majority of area burned (Grissino-Mayer and Swetnam 2000, Heyerdahl et al. 2001). Climatic fluctuations, combined with the shifting patterns of human land use and suppression efforts must be considered in any analysis of fire records (Veblen et al. 2000, Grenier et al. 2005). Rollins et al. (2002) attempted to minimize the effects of fire suppression by examining fire records from wilderness areas where suppression efforts are restricted. It is important to recognize the potential influence of humans during a period of record. Climatic shifts should also be recognized, particularly in cases where a researcher is attempting to extrapolate conclusions beyond the period of record.

Fire atlases are an imperfect record of the occurrence of fire on a landscape. Issues with size bias, incomplete recording, and limited temporal availability have been identified as sources of inaccuracy. However, fire atlases can provide spatially explicit information on wildfire that is not available through other sources of fire history. They provide perimeters and area burned for individual fires, which cannot be explicitly reconstructed from paleo-techniques such as fire scars and pollen records (Hessl et al. 2007b). This information is important in characterizing fire rotations and assessing the influence of topographic variability on fire regimes (Morgan et al. 2001).

Fire History Reconstructions

Methods for Using Fire Scars to Characterize Fire Regimes

Fire scars have been the primary source of information on historical surface fire regimes and their interaction with climate, landform, vegetation, and human influence (Goldblum and Veblen 1992, Heyerdahl et al. 2001, Grissino-Mayer et al. 2004, Guyette et al. 2006). When a fire burns through a forest, high temperatures can kill a portion of the cambium at the base of the tree leaving a scar. Fire scars are most likely to form on the leeward side of trees burned in head fires (Fahnestock and Hare 1964, Gill 1974, Gutsell and Johnson 1996). The presence of a previous open wound or high fuel loads near the base of a tree may increase the likelihood of scar formation (Lachmund 1923). Older and larger trees are more resistant to scarring due to greater bark thickness (Vines 1968). Tree-rings can be used to date the formation of these fire scars and consequently they provide a record of the occurrence of fire at a single point on the landscape. Multiple dated scars on a single sample or many samples from across the landscape have been used to infer the fire regime for a given point to an entire landscape.

Several parameters are used to characterize fire regimes in the literature. Johnson and Gutsell (1994) argue that fire rotation calculated from time since fire maps is the only statistically valid method of reconstructing fire events because it accounts for spatial and temporal variability. However historical surface fire perimeters are nearly impossible to ascertain because the fires may cause little or no mortality within the forest canopy and therefore they do not produce the even-aged cohorts associated with stand replacing fire regimes (Mast et al. 1999). Instead, surface fire regimes must be characterized using fire scar data compiled from points within a study area. The period of time between recorded fires, or the fire return interval, is the most commonly reported parameter (Baker and Ehle 2001). The range of return intervals are often reported along with a mean fire return interval that is calculated for all of the intervals between fire scars. The mean fire interval is interpreted as an estimate of the average frequency of fire within a particular stand. It has been determined that fire intervals are not normally distributed at many locations and therefore the Weibull distribution is a preferable measure of central tendency (Grissino-Mayer 1999). Therefore, the Weibull median interval is often reported along with the standard mean fire interval.

Individual-Tree Fire Interval

The mean individual-tree fire interval is generally viewed as an upper estimate of the population fire interval since it makes no correction for unrecorded fires (Baker and Ehle 2001). Individual-tree fire intervals are intervals between scars that are contained on a single specimen. It is a sampling of fire interval at the scale of individual trees. Therefore it avoids the uncertainty of the small fire question discussed below. However, the inconsistency of an individual-tree scarring in any one fire means that the mean individual-tree fire interval may greatly overestimate the population mean fire interval (Dieterich and Swetnam 1984). Van Horne and Fulé (2006) found that the mean individual fire interval was a good estimate of the maximum fire interval at the scale of individual trees. However, the mean individual-tree fire interval was sensitive to the quality (number of fires recorded) of specimens. Therefore it can be influenced by targeted sampling. The authors suggest that a random sample of fire scarred remnants should be used to quantify the mean individual-tree fire interval.

The Mean Composite Fire Interval

The mean fire return interval can be calculated for intervals recorded on individual trees, or more commonly in the recent literature as a mean composite fire return interval (Kipfmueller and Baker 2000b, Taylor 2000a, Baker and Ehle 2001, Gonzalez et al. 2005, Martin and Fahey 2006). The mean composite fire return interval was developed to address the problem of unrecorded fires. A single fire will often only scar a small portion of the trees on a landscape. This may be due to the lack of previous scars on a tree, unburned areas within a fire perimeter, resistance to scarring of individual trees, inconsistent heating loads, or only a small portion of the study area burning in a fire (Lindenmuth 1962, Wooldridge and Weaver 1965, Eberhart and Woodard 1987). The mean composite fire interval attributes unrecorded fires to any of the first four reasons but largely ignores the latter explanation which has led to much of the criticism of this method (Baker and Ehle 2001). The MCFI combines the fire dates from all of the samples within the study area to create a composite fire record (Dieterich and Swetnam 1984). Therefore intervals between fires recorded at separate points on the landscape are used to calculate the mean composite fire interval. As a result, if the study site is characterized by many small fires, i.e. (Minnich et al. 2000b) then the MFI may be very different from the fire rotation. The MCFI will underestimate the population mean fire interval, leading to an underestimation of the fire rotation (Kou and Baker 2006, McKenzie et al. 2006). Baker (2006) uses data collected by Fulé et al. (2002, 2003) to perform his own calibration in which the CFI significantly underestimates the length of the population mean fire interval and fire rotation. Actual population mean fire interval may be 10 times as long. Baker and Ehle (2001) suggest that the MCFI be used as a minimum population mean fire interval bracket, since it is the lowest estimate of the fire interval and only accurate if each recorded fire burns across the entire study area and if every fire is recorded by scars.

Baker and Ehle (2001) also criticize the equivocal nature of MCFI interpretation. The MCFI can be misinterpreted by managers as indicating that an entire stand burned at this interval (Baker et al. 2007). It can only be said that a MCFI demonstrates that fire occurred somewhere in the stand at this interval(Arno and Peterson 1983, USDA) (Barrett 1988, Goldblum and Veblen 1992). They argue that the MCFI has not been differentiated from fire rotation in the literature. The use of a MCFI also makes comparison of fire intervals difficult because it varies with the spatial scale of the sample area. Baker and Ehle (2001) argue that as the sample area increases more small fires will be recorded and the MCFI will decrease until it reaches a minimum one year fire interval. They contend that this equivocal interpretation of composite fire interval means that it is not suitable as an estimator of population mean fire interval for a study area. They argue that small fires were common in historic ponderosa pine (*P. ponderosa* Lawson & C. Lawson) forests and that much of the reported frequent fire intervals are based on fires that only scarred one tree (Baker and Ehle 2001, Baker 2006). The patchy nature of wildfires in terms of area burned and intensity of burn within the fire perimeters should also be noted (Eberhart and Woodard 1987). The record of multiple fire scars across a stand in a single year should not be interpreted as an indication that fire burned through the entire stand without unburned areas or shifting intensity.

The use of a restricted mean composite fire interval (i.e. the exclusion of fires that are recorded by less than a certain percentage of trees) has been used as correction for this uncertainty (Fisher et al. 1987, Brown and Sieg 1996, Veblen et al. 2000, Heinlein et al. 2005). The application of a restriction aims to remove small fires from the calculation of mean fire interval by only including fires that were recorded by multiple trees across a landscape. MFIs with a 25% filter have been shown to be consistent regardless of sample size or area sampled (Van Horne and Fulé 2006). Without the filter, smaller fires continued to be identified as the sampled area increased. This suggests that concern over undue weight being given to small fires can be avoided by using a 25% filter. However, Baker and Ehle (2001) criticize this technique as arbitrary, since little empirical research has been carried out on the process of scar formation. It is also possible that a small fire could be recorded by a cluster of samples within a limited area and still exceed the restriction requirement.

Origin-to-Scar Interval

Baker and Ehle (2001) also criticize surface fire history studies for the exclusion of the origin-to-scar (OS) interval in the calculation of mean fire return intervals. They argue that the interval between establishment and the first fire scar on each sample represents a real interval between fire occurrences and should be included in calculations of mean fire interval. When the origin-to-scar interval was included, the mean individual-tree fire interval increased by an average of 1.6 times.

The authors place particular importance on the origin-to-scar interval because they interpret this interval as the necessary amount of time required for successful regeneration. They use data from several studies to calculate that a fire free interval of at least 50 years is required to have successful ponderosa pine regeneration (Baker and Ehle 2001). This does not mean that the study area as a whole must have a mean fire interval of 50 years. Successful regeneration requires that some point within the study area experience this longer interval between fires. The shifting nature of unburned patches might only leave a few points within a large landscape unburned for this longer interval and these would be the points of successful regeneration.

Age structure data and historical photos demonstrate the open nature of historical ponderosa pine stands (Fule et al. 2002). This stand structure suggests that successful regeneration and recruitment into the canopy was infrequent. Therefore these windows of extended fire free intervals must have been infrequent, representing a relatively small portion of the total landscape. In terms of regeneration the maximum fire interval (highest value within bracketed range) is most important and the mean fire interval is less important. This maximum fire interval does not reach 50 years in many studies, particularly in New Mexico and Arizona (Baker and Ehle 2001). However, for many studies the MCFI and mean individual-tree fire interval would provide a range large enough for regeneration. It is also important to recognize that the introduction of prescribed fire to a stand does not mean that the entire area will be burned consistently. Fires are generally patchy, leaving unburned locations within the fire perimeter available for regeneration even with the application of fire at regular intervals.

However, there are several problems with the inclusion of the OS interval in calculation of the mean fire interval. OS often cannot be measured because fires are not recorded, older fire scars can be burned out or even the pith can be burned out (Stephens et al. 2003). In addition, it has been argued that the OS interval is not an interval between fire, because it is not bounded by two scars. A tree might have grown to a resistant size during a fire free interval, then experienced mild fires without scarring, and then finally scarred during an intense fire, resulting in an OS interval of a century or more. Also, ponderosa pine regeneration is not always initiated by fire (Savage et al. 1996). It is also a problem to sample at ground level and therefore obtain an accurate date of sprouting (Dieterich and Swetnam 1984). Van Horne and Fulé (2006) address the OS interval issue in their census of an entire population of fire scars. They mapped all of the collected samples with piths that were datable in order to determine whether the OS intervals recorded on these samples were actually fire free. They found multiple trees that recorded scars were within 1 meter of trees that had not recorded an original scar. These results suggest that it is possible for seedlings to be exposed to fire and not scar. I believe that the origin-to-scar interval provides important information about a study sites fire regime, particularly in relation to the time required for successful regeneration.

However, I do not think that it is correct to use the OS interval in the calculation of fire intervals for the reasons listed above by Van Horne and Fulé (2006). The points of regeneration represent the longest intervals between fire on the landscape and as a result they are also the points where trees have established and the only points where samples are available. For each point where the fire interval is infrequent enough for regeneration, there are many more points where the fire interval is too frequent for regeneration and as a result there are no established trees to sample. I believe that inclusion of the OS interval in the calculation of mean fire interval places undue emphasis on these atypically long fire intervals that allow for successful regeneration. I think that the OS interval is a valuable parameter on its own, providing managers with necessary information on the length of fire intervals necessary for successful regeneration of the target species. There certainly would have been portions of the landscape which experienced fire at longer intervals than the reported range of mean fire intervals, however it would be incorrect to present these exceptionally long intervals as a "mean" fire return interval. The concept of mean range of variation when applied to ecological systems incorporates the possibility of longer intervals and recognizes that across an extensive landscape these longer intervals will be present. I think that reporting average OS interval is an important step, and valuable fire parameter. But it is incorrect to include the OS interval in calculation of the mean fire interval because of the uncertainty of its representation of a true fire interval and the overrepresentation of these points because the fire scar method depends solely on the collection of samples from trees that were established during these exceptionally long fire intervals. Essentially, the inclusion of the OS interval requires that the researcher include a sample of the longest fire intervals on the landscape without including a sample of the shortest fire intervals on the landscape because these short intervals result in seedling mortality. In my opinion this technique would bias the results towards much longer mean fire intervals than the population truly experienced.

Sample Size

Given limited resources and time, an important consideration for researchers is how many fire scarred trees must be collected in order to identify the majority of fires. Baker and Ehle (2001) argue that sampling intensity (area, number of trees) accounts for a significant portion of the variation in fire regimes of different regions of the west. Baker calculates from the literature that 10 or more contiguous fire scarred trees are needed to identify the majority of fires in a ponderosa pine stand. However, he states that, "Even after sampling at-least ten trees, on average 70% or more of fires in the composite are recorded by only one or two trees, suggesting they could be small (Baker and Ehle 2001, p. 1217)." The collection of ten specimens is sufficient for establishing that fire was present on a landscape, which was the primary goal of certain early studies (Harmon 1982a). However, ten specimens are insufficient today, given the specific management implications of fire history studies and the uncertainty of scarring rates and variability of fire occurrence across the landscape. A threshold of 50 samples has been suggested at which little additional information is gained by continued sampling (Stephens et al. 2003, Van Horne and Fulé 2006).

Targeted Sampling

Dendrochonology fire history reconstructions often use targeted sampling during the collection of fire-scarred specimens. Researchers search a particular stand or landscape for specimens that exhibit the most scars. This technique is often necessary in order to provide a reasonably complete and long record of fire at a particular site. Although, the targeted sampling method has been criticized because it is not a random sample from a well-defined population; therefore introducing issues of accuracy and precision (Johnson and Gutsell 1994). Baker and Ehle (2001) argue that targeted sampling of multiple scarred samples and clusters of scarred samples biases results towards a lower mean fire interval. Criteria for sampling that are listed in the literature include: old trees, high scar densities, trees with multiple fire scars, tress with open wounds, and relict, un-harvested stands. There are several potential problems with targeting dense clusters of fire scarred samples. The most fundamental problem is that this focused sampling does not adequately represent the landscape or even the study area as a whole. Focusing on areas with high densities of fire scarred samples means that research is focusing on the areas that are most likely to produce remnant or living trees with multiple scars. These are the areas on the landscape that are most likely to experience repeated surface fires that reach a level of intensity high enough to scar adult pines but not intense enough to cause mortality. The question is whether these sites that produce multiple valuable samples are really indicative of the fire regime of entire study site or the landscape. The majority of the landscape that is not sampled may be subject to much less frequent fire or stand replacing fires (Baker and Ehle 2001). Sherriff and Veblen (2007) related spatial variation in fire frequency to topography and vegetation in ponderosa pine forests of Northern Colorado. Their results suggested that less than 20% of the landscape was subject to frequent fires and that the majority of the landscape was characterized by a much less frequent or more variable fire regime. These areas of lower fire incidence should be considered in the management of a landscape since they allow fire sensitive species to persist and provide seed sources (Greenberg and Simons 1999, Signell and Abrams 2006). The necessity of sampling within un-harvested stands where older samples can broaden the temporal extent of the study introduces additional bias in that un-harvested stands tend to be in isolated, steep, or rugged areas that made harvesting untenable (Arno 1995, USDA). These areas may be more or less prone to fire than surrounding areas.

Kipfmueler and Baker(2000a) found that in sub-alpine forests the targeting of multiple scarred samples led to a decrease in the mean individual-tree FI of as much as 2.6 times, when only samples with at least four scars are used. However they did not test whether restricting sampling to recorder trees affected results. In contrast, Van Horne and Fulé (2006) found that targeted sampling does not affect estimates of fire frequency.

They sampled all 1,479 scarred trees within a 1 km^2 study site and found that any 50 specimens yielded an accurate estimate of fire frequency. They conclude that targeting requires the smallest sample size, yields the same results, and probably produces longer, more reliable records of fire.

The potential biases of targeted sampling are generally amplified as the temporal extent of the study is extended further back in time. Fewer ancient samples are still present on the landscape; however this is often the period of most interest when it predates Euro-American settlement. It is important to display not only the sample size over time, but also the spatial extent and potential spatial bias of the sample over time (Veblen et al. 2000). If all of the ancient samples collected are from one clustered area on landscape the calculated fire interval during this period may only be applicable to a small sub-section of the study area. This restricted sampling could result in a change in the fire regime that is only an artifact of sampling within a particular landform. Since mean composite fire interval is affected by sample size, the spatial extent of the older samples should set the spatial extent of the rest of the samples if comparisons are to be made.

Vegetation Dynamics

Community vs. Individualistic Concepts of Vegetation Association

Clements (1936) established the concept of climax communities which were stable, classifiable, vegetation communities whose composition and geographic location were the result of climate. The Clementsian view of vegetation stressed stability as the universal tendency, with disturbance as the exception that set climax vegetation back into an earlier stage of preclimax which was not in equilibrium with climate. The Clementsian view of vegetation was part of a larger paradigm within the earth sciences that used evolutionary or life stages in order to classify transient earth systems. This series of life stages generally included an immature developmental stage which evolved into a mature, climax stage which was in equilibrium with its environment. The modern climaxes evolved from preceding climaxes, with vegetation units migrating as a whole according to climatic shifts.

Gleason (Gleason 1926) developed the individualistic concept of plant association. This concept characterized vegetation communities as a "fluctuating phenomenon". Vegetation at any one point is controlled by interactions between individual species and the environment. Species migrate as individuals and current vegetation assemblages are merely a single point on a continuum of vegetation transition. This view of vegetation associations stresses the variability of conditions over space and time. This variation is along a continuous axis, along which no two communities are exactly alike and therefore the precise classification of the Clementsian system is impossible.

Vegetation Disturbance

Contemporary North American ecologists have gravitated towards the Gleasonian view of plant communities. There has been recognition that change is the norm in natural systems. Natural systems rarely reach a state of equilibrium or stability, but are constantly adjusting to changes in environmental conditions. These changes can be long term shifts in the physical environment or short term events known as disturbances. Pickett and White (1985) define vegetation disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment (p. 7)." Examples of terrestrial disturbances are fire, wind, flooding, ice storms, pathogens, avalanches, landslides, and volcanic eruptions. Disturbance dynamics is the study of vegetation's response to these disturbances. Recent research has recognized that the composition of a vegetative community may be more a function of disturbance than current environmental conditions (Foster et al. 1998a, Richter et al. 2000, Taylor 2000b, Bellemare et al. 2002, Gragson and Bolstad 2006).

Characterizations of Disturbance

In order to assess the role of disturbance in ecosystem function and development, ecologists have attempted to classify or group disturbances into disturbance regimes. A disturbance regime is a characterization of the types of disturbances that effect a particular vegetation association. Disturbance regimes can be a description of the type, cause, frequency, predictability, spatial extent, magnitude of impact, synergism with other disturbances, and seasonal timing (MacDonald 2003). Ecologists will also describe the stability of a particular disturbance regime. The stability of a disturbance regime at any one location depends on the spatial and temporal scale that one is considering (Frelich 2002a). Viewed on an epochal time scale, very few if any disturbance regimes are stable. However, viewed within a decadal time scale certain disturbance regimes such as a fire return interval may be considered relatively stable. Individual disturbances can also be characterized by intensity and severity. Disturbance intensity refers to the energy released by particular disturbance, while severity refers to the amount of vegetative mortality resulting from a particular disturbance (Frelich 2002a).

Disturbances may occur at random intervals (i.e. hurricanes) or they may occur at regular intervals (i.e. insect outbreaks). Assuming that a particular disturbance regime is stable and occurs at random intervals, the concept of rotation and disturbance interval may be applied and projected towards future disturbance/vegetation interactions. The rotation period is the period of time required for a disturbance to impact an area equal to the entire study area (Frelich 2002a).

Disturbance as regressive succession

Disturbance affects the successional stage of development of a vegetation association. The effect of a single disturbance on the successional sequence is determined by the severity of the disturbance at any one point and the severity of the disturbance within the space surrounding this point. In its most basic form, a disturbance returns the successional development of a vegetation association to an earlier sere. The greater the severity of the disturbance the further back the location will be set in the successional series. A sufficiently severe disturbance can remove all of the vegetation or all of the woody vegetation at a location, returning the site to the initial stages of succession. Such disturbances are often referred to as stand replacing disturbances. An example of a stand replacing disturbance would be an intense crown fire (Parker and Parker 1994, Buechling and Baker 2004), a stand flattening wind event (Everham and Brokaw 1996, Schulte and Mladenoff 2005), or a volcanic eruption (Halpern et al. 1990).

Disturbance mediated accelerated succession

The effect of disturbance on vegetation is not limited to a return to an earlier sere in the successional sequence. Abrams and Scott (1989) recognized that disturbance may selectively impact earlier successional, shade intolerant species. If conversion to the next successional sere is initiated by mortality of the currently dominant early successional species, the removal of the early successional species may accelerate the development of vegetation towards dominance by later successional/shade tolerant species. This type of disturbance has been named disturbance mediated accelerated succession. Examples of this disturbance effect include logging conversion of northern white cedar (*Thuja occidentials*) and jack pine (*P. banksiana*) to later successional hardwoods; wind disturbance converting aspen (*Populus tremuloides*) and oak stands to later successional hardwoods, and ice storms removing pitch pine from oak-hickory and maple stands (Abrams and Scott 1989, Dyer and Baird 1997, Lafon 2006).

Disturbance as a fundamental alteration in the successional sequence

It is possible for an even more intense disturbance to impact the edaphic characteristics and even the physical environment of a location in addition to removing vegetation associations. A disturbance that results in a major alteration of the physical environment of a location can change the successional trajectory of the location. The successional stages of vegetation development might be shifted resulting in new vegetation associations. Examples of disturbances that can alter the soil characteristics resulting in a change in the successional sequence at a location are landslides, extreme flooding, and human agricultural disturbance. Dune migration is an example of a disturbance that would alter the topography and soils at a location. Flooding is an example of a disturbance that might completely remove the soil at a location. This site would be set back to the vegetation colonization stage of succession and would have to proceed through primary succession. The primary succession might occur along a pathway similar to the vegetation development prior to the disturbance or it might develop in a completely different sequence according to altered characteristics of the physical environment.

Disturbance and Vegetation Diversity

The non-equilibrium model does not view vegetation associations as the result of stable interactions between vegetation and environmental conditions. Instead, the vegetation associations that we observe are primarily the result of instability in environmental conditions (disturbance). Connel (1978b) summarizes this concept in stating, "communities of species are not highly organized by co-evolution into systems in which optimal strategies produce highly efficient associations whose species composition stabilizes." The non-equilibrium model theorizes that under conditions of stability, which are rarely if ever realized in nature, the process of competitive elimination would reduce diversity to a small number of species with optimal competitive strategies. This leads to the intermediate disturbance hypothesis (Connell 1979) which attributes vegetation community composition to the ratio of disturbance effects and the rate of compositional recovery. This theory hypothesizes that under intermediate levels of disturbance diversity will be greatest, because disturbance is not intense enough to limit the establishment of a variety of species. However, disturbance is at a level of intensity which prevents the completion of competitive elimination which would prevail under conditions of stability. This ratio of disturbance and recovery is a driving characteristic in the development of vegetation communities as much as other environmental variables such as climate or soils. A characteristic level of disturbance may have been associated with a vegetation community through evolutionary time (Connell 1979).

Huston (1979) further develops the concept of non-equilibrium by placing emphasis on the rate of competitive displacement in determining diversity. His theory applies the concept of maximum diversity at intermediate levels in the rate of both disturbance and the rate of competitive displacement. The diversity and community composition are directly related to the ratio of disturbance and competitive displacement.

CHAPTER III

METHODS*

Study Area

Topography and Soils

This study pertains to the southern and central Appalachian Mountains in eastern North America, USA. Contemporary landscape patterns of fire were examined for Shenandoah National Park (SNP) in the central Appalachian Mountains of Virginia and Great Smoky Mountains National Park (GSMNP) in Tennessee and North Carolina. The field based portions of the study (i.e. fire history reconstructions and vegetation dynamics) were carried out in the southern Appalachian Mountains of Tennessee and North Carolina (Figure 3.1).

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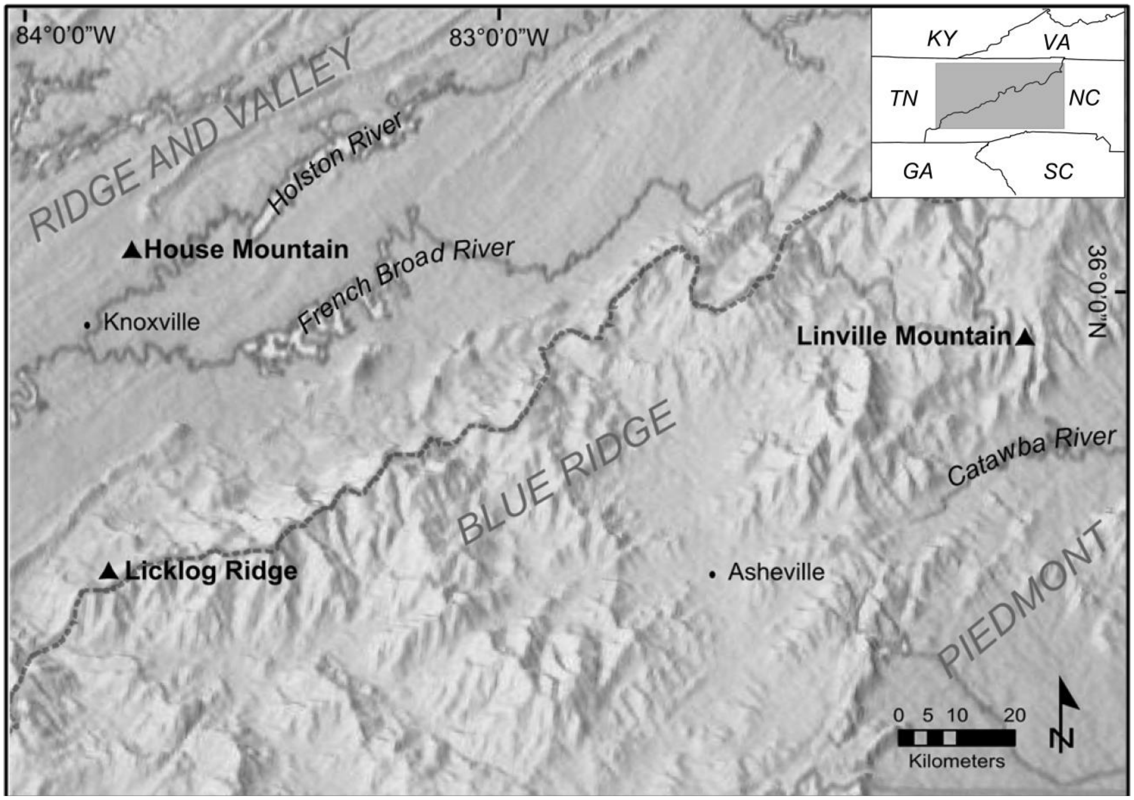

Figure 3.1 Location of field sample sites in Tennessee and North Carolina, USA. Fire history reconstructions were carried out at House Mountain, Licklog Ridge, and Linville Mountain. Vegetation sampling was also carried out at Licklog Ridge.

In the context of this study, the Appalachian Mountains include both the Ridge and Valley physiographic province and the Blue Ridge physiographic province. The Ridge and Valley is located east of the Appalachian Plateau physiographic province and west of the Blue Ridge, extending from central Alabama to southeastern New York (Fenneman 1938). The landscape comprises parallel northeast to southwest trending valleys and ridges, composed of tightly folded and intensely faulted shale, siltstone, sandstone, chert, and carbonates (McNab and Avers 1994). Ridges are composed of sandstone, chert, and resistant carbonates. Valleys are formed from less resistant carbonates and shale. Elevations within the province range from 100 to 1435 m. Soils are primarily Ulfisols, Alfisols, and Inceptisols with a mesic temperature regime and primarily udic moisture regime (McNab and Avers 1994).

The Blue Ridge physiographic province is located east of the Ridge and Valley and west of the Piedmont physiographic province in the southern and central Appalachian Mountains, stretching from northern Georgia to Pennsylvania (Fenneman 1938). The province consists of a relatively narrow strip of highly metamorphosed parallel mountain ranges (McNab and Avers 1994). The southern half of the province extends from northern Georgia to southern Virginia. It is broader and higher than the northern half of the Blue Ridge, which extends from central Virginia to southern Pennsylvania. The southern Blue Ridge includes Mt. Mitchell (2025m) which is the highest point in eastern North America. Elevations within the province range from 300 to 2025 m. Bedrock is composed of quartzite, schist, gneiss, granite, rhyolite, basalt, and gabbro. Soils are primarily Ochrepts and Udults with a mesic temperature regime (below 1400m) and a udic moisture regime (McNab and Avers 1994).

Climate

Topographic complexity in the central and southern Appalachian Mountain regions results in considerable climatic heterogeneity (Konrad 1994). This climatic heterogeneity influences fine scale spatial patterns of fire in the central Appalachian Mountains of Virginia and West Virginia (Lafon and Grissino-Mayer 2007) and likely also influences spatial patterns of fire in the southern Appalachian Mountains of Tennessee and North Carolina. The entire southern and central Appalachian region is classified as a humid continental climate with cold winters and warm summers (Bailey

1978). The Ridge and Valley province is drier with a mean annual precipitation range of 760 to 1140 mm, while the Blue Ridge province receives a mean annual precipitation of 1020 to 1270 mm. The Virginia portion of the Blue Ridge and the Ridge and Valley receives less precipitation due to the Allegheny Mountains of West Virginia which block precipitation from the west. While in the southern Appalachians, the Cumberland Plateau is much lower west of the Ridge and Valley and Blue Ridge which results in the southern portions of these physiographic provinces receiving higher precipitation. The southern Appalachians also receive moisture from the Atlantic and Gulf of Mexico to the east and south (Konrad 1994). Underlying these regional trends in precipitation are finer landscape-scale topographic controls on precipitation, with rainfall generally increasing as elevation increases (Shanks 1954). The regions also exhibit spatial variation in seasonality of rainfall. The central Appalachians exhibit a summer precipitation peak and are within the "Ohio Transition" precipitation regime (Robinson and Henderson-Sellers 1999). The southern Appalachians do not exhibit this summer peak and are within the "Sub-Tropical Interior" rainfall regime. These climatic gradients provide the opportunity to test the influence of regional climate on the variation of fire regime characteristics such as seasonality, frequency, and the importance of human versus lightning ignited fires.

Vegetation

Southern Appalachian forests were originally classified as oak-chestnut (Braun 1950). American chestnut was a dominant species in the region (MacKenzie and White 1998). However, the introduction of the chestnut blight fungus (*Endothia parasitica*) resulted in the near complete removal of American chestnut from the landscape by the late 1930s (Woods and Shanks 1959, McCormick and Platt 1980). As a result, forests in the region are now classified as oak-hickory (Stephens et al. 1993).

Forest community types generally vary according to topographic landform within the region (Whittaker 1956, Golden 1981). Oak dominated forests, composed of chestnut oak (*Q. montana* L.) white oak, black oak (*Q. velutina* Lam.), and hickories, cover the broad submesic to subxeric portions of the landscape (Stephenson et al. 1993). Yellow pines (*Pinus*, subgenus *Diploxylon* Koehne), including shortleaf pine (*P. echinata* Mill.), pitch pine, Virginia pine (*P. virginiana* Mill.), and Table Mountain pine occupy dry ridgetops and south-facing slopes. Shortleaf pine dominates pine stands at lower elevations (below 750 m), while Table Mountain pine is found at mid-elevations (Whittaker 1956). Table Mountain pine is an Appalachian endemic, with several adaptations to fire disturbance, including thick bark, serotinous cones, and increased germination on bare mineral soil (Zobel 1969). Pitch pine is most abundant at mid-elevations, but is found in both mid- and low-elevation stands. Virginia pine is most common at lower elevations and is generally associated with anthropogenic disturbance, particularly old fields. Since the implementation of fire protection in the 1930s, red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and black gum (*Nyssa sylvatica* Marsh.) have become an increasingly important component of xeric pine and subxeric oak stands in the region (Harrod et al. 1998, Harrod and White 1999, Harrod et al. 2000, Aldrich et al. 2010).

Mesic lower slopes, valleys, and ravines are covered by cove forests which are dominated by eastern hemlock (*Tsuga canadensis* L. Carr.) and yellow poplar (*Liriodendron tulipifera* L.), but also include sugar maple (*A. saccharum* Marsh.), birch (*betula spp.* L.), and a number of other mesophytic hardwood species (Lorimer 1980, Clebsch and Busing 1989). Mesic mid- to high-elevations sites (above 1000 m) are typified by eastern hemlock and a northern hardwoods type which includes American beech (*Fagus grandifolia* L.), yellow birch (*Betula alleghaniensis* Britton), sugar maple, American basswood, (*Tilia Americana* Vent.), yellow buckeye (*Aesculus octandra* Marsh.). Xeric mid- to high-elevation sites are dominated by northern red oak (*Q. rubra* L.). The highest peaks (generally above 1500 m) are covered by red spruce (*Picea rubens* Sarg.)-fraser fir (*Abies fraseri* Pursh Poir.) forests (Whittaker 1956, Cogbill and White 1991).

Land Use History

Native American

The archaeological record demonstrates a long history of human habitation in the southern Appalachian Mountain region. Current archaeological evidence indicates that humans arrived in the southeastern United States at least as early as 12,000 years ago (Steponaitis 1986). People likely arrived in the uplands of the southern Appalachians not long after this and have inhabited the area and exploited its resources since (Purrington 1983). Archaeologists divide the prehistory of the southeastern United States into four general periods. The Paleo-Indian (ca. 12,000 B.P.–10,000 B.P.), Archaic (8000 B.C.-700 B.C.) Woodland (700 B.C.- A.D. 1000), and Mississippi (A.D. 1000 – Contact) periods each correspond with major technological, economic, and political changes (Steponaitis 1986).

The Paleo-Indian period (ca. 12,000 B.P. -10,000 B.P.) in the southern Appalachians was characterized by a hunting and gathering culture. During this period glacial conditions were coming to an end and spruce-fir and northern jack pine forests were being replaced by mixed oak-hickory forests (Delcourt and Delcourt 1981, Delcourt 1985). Stone projectile points found in the upland regions of the southern Appalachians Mountains indicate that the earliest people were probably hunting large grazers in tundra and forest habitats (Guilday 1982, Purrington 1983). They likely formed low density bands, probably no more than 50 individuals, and established temporary settlements that shifted with the availability of food resources (Steponaitis 1986). However, the use of local stone for tools indicates that they were permanent residents within the upland region (Purrington 1983). By the end of the Paleo Era (ca 8000 B.C.) the climate had begun to warm, resulting in a shift in subsistence strategy to a wider resource base. Temperate deciduous forests had migrated into the area and the Pleistocene megafauna had largely been replaced by modern species assemblages (Guilday 1982, Delcourt 1985). Hunting focused on smaller game such as white tailed deer, turkey, rabbit, squirrel, fish, turtle, and other small animals (Steponaitis 1986). The presence of hickory and walnut remains indicate that plant resources had also become an important supplement to the diet.

The Archaic Period (8000 B.C.-700 B.C.) is characterized by continued environmental change, regional specialization of stone tools, and a further widening of the food resource base culminating in the earliest stages of plant domestication. In the early Archaic, groups remained small, setting up base camps in lowland areas where they increasingly exploited floodplain and riverrine resources, including fish and freshwater mussels (Chapman 1985, Davis and Daniel 1990). Archaeological sites in GSMNP and the Pisgah National Forest contain tools made from stone from the Ridge and Valley, suggesting that groups used the high mountains only as hunting territory and not for permanent settlement (Bass 1977, Purrington 1983). Archaeological sites in lowland areas contain large midden sites, substantial structures, food storage pits, less portable pottery, stone containers, evidence of long distance trade, and the earliest appearance of textiles and basketry (Chapman and Adovasio 1977, Chapman 1985). Toward the end of the Archaic Period groups increased in size, density and stability. These changes may have been related to the first stages of plant domestication which began from 2500 to 1000 BC in the upper south and west of the Appalachians (Chapman 1982, 1985, Yarnell 1998). Early domesticated plants included gourds, squash, sunflowers, goosefoot, marshelder, and maygrass.

The Woodland Period (700 B.C.- A.D. 1000) was characterized by further increases in the size and permanence of settlements in the southern Appalachians along with increasing social complexity. These changes were likely a result of a shift in subsistence strategy from dependence on wild food plants to intensified agriculture (Fritz 1990, Smith et al. 2006). The adoption of agriculture in the Southern Appalachian region occurred during the Middle Woodland Period, several centuries later than the regions directly south and west (Purrington 1983, Chapman 1985, Chapman and Crites 1987). The later adoption of agriculture was likely a product of lower population densities and shorter growing seasons. Communities were small, year round settlements established along floodplains with one to six houses covering less than a hectare. However, settlements were not inhabited for more than a few years when surrounding food resources became stressed (Steponaitis 1986). The adoption of agriculture likely resulted in increased forest clearance along floodplains and the charcoal records from this period indicate an increase in disturbance associated species (Chapman 1982, Delcourt et al. 1986).Technological innovations included the spread of the bow and arrow and the arrival of agricultural crops from Mexico, including maize, beans, pumpkins, cushaw, amaranth, and tobacco (Purrington 1983, Smith et al. 2006).

The Mississippian Period (A.D. 1000 – 1540) saw the rise of south Appalachian Mississippian culture in the southern portion of the Appalachian Mountains. After 800 A.D., maize became an important crop in the region with the development of new varieties that could be grown in shorter growing seasons at higher altitudes (Chapman and Crites 1987, Smith et al. 2006). The cultivation of beans began in the eastern US around 1000 A.D. (Yarnell 1976a). The adoption of intensive agriculture, particularly maize cultivation, enabled the production of food surpluses and the development of permanent political hierarchies (Steponaitis 1986, Yarnell 1998). Palisaded settlements were established in valleys with fertile soils, and near shoals for fishing. Larger civic structures were also built, including earth banked buildings, public plazas, and platform mounds. In the Little Tennessee River Valley clearance for agriculture spread out from the floodplain to lower stream terraces as populations became increasingly dependent on intensive maize agriculture (Delcourt et al. 1986). Wild plants and animals were still important food resources, however hunting pressure on animal populations declined from its peak in the Late Woodland (Dickens 1976, Yarnell 1976b).

During the late Mississipian Period, both the Lamar and Qualla cultures developed large chiefdoms within the southern Appalachian region. The Lamar culture was centered in the Ridge and Valley of eastern Tennessee. Towns were 1 to 6 hectares with fields stretching along the valleys from one town to the next (Elvas 1993, Hally 1994). Ridges and lands outside of cultivated valleys were forested (Priestley 2010). Political units varied in size from a few small towns to large regional chiefdoms (Widmer 1994). The largest Lamar chiefdom was Coosa, which stretched from northern Alabama to northeastern Tennessee (Steponaitis 1986, Hudson 1994). The Qualla culture was originally located in north-western North Carolina, but they migrated southwest during the late 1500s into the Little Tennessee, Hiwassee, Chatahoochee, Chatooga, and Keowee river valleys (Dickens 1978). The Qualla peoples apparently replaced the Lamar culture in this region and are the likely ancestors of the Cherokees. The French Broad River valley and areas to the northeast in the North Carolina summit regions were devoid of permanent settlements during this period (Purrington 1983). However there is evidence that these areas were visited by mobile hunting, raiding, and trading parties.

The Historic Period in the southern Appalachians begins with the Spanish conquistador Hernando DeSoto's exploration of the interior Southeastern United States. DeSoto's expedition crossed the southern Appalachians Mountains, encountering both the Lamar and Qualla cultures (Elvas 1993, Hudson 1994). The early Spanish expeditions of DeSoto, Juan Pardo, and Tristan de Luna provide a glimpse of Native American societies immediately prior to their decimation by waves of disease. Following European contact, death rates among Native Americans due to malaria, smallpox, and cholera may have been as high as 95% (Crosby 1976, Whitney 1994).

The results of these disease die offs were political and social decentralization and a shift from palisaded towns to loosely grouped households along rivers (Purrington 1983).

By the late 17^{th} century, the Cherokee people were the only intact culture in the southern Appalachians and they controlled most of the region as a hunting ground (Smith 1989, Hatley 1995). Cherokee towns were concentrated along the southern end of the Appalachians in Tennessee, North Carolina, South Carolina and Georgia (Gragson and Bolstad 2007). The Cherokee towns are generally divide into four groups: Overhill towns, Middle towns, Valley towns, and Lower towns. The Overhill towns were located along the lower Little Tennessee and lower Hiawassee Rivers west of the Blue Ridge in the Ridge and Valley of Tennessee. The Middle towns were located along the upper Little Tennessee River in the Blue Ridge of North Carolina. The Valley towns were located along the upper Hiawassee River in the Blue Ridge of North Carolina. Finally, the Lower towns were located along the headwaters of the Tugaloo and Kiowee Rivers on the northwestern edge of the South Carolina piedmont. While their towns were concentrated in the southern end of the Blue Ridge, the Cherokees territorial claims stretched from the Ohio River in the North to western Tennessee, Northern Alabama, Northern Georgia, western South Carolina, and the mountainous regions of North Carolina and southwestern Virginia.

As early as the late 16^{th} century, European trade goods were becoming a source of change in the southern Appalachians. European traders began to enter the southern Appalachian Mountains in the early 1700s, however the Cherokee traded with Spanish settlements on the coast much earlier (Briceland 1991). The deerskin and bison hide trade had begun in the 1560s and became an increasingly important component of

Native American economies during the 17th and 18th centuries (Waselkov 1989). Bolstad and Gragson's (2008) analysis of resource constraints on Cherokee settlements (ca 1721) identified white tailed deer as their primary limiting resource. Driven by European markets for deer skins, the Cherokee may have harvested deer across much of their vast territory (Bolstad and Gragson 2008). Records indicate that fire was used to drive deer during hunts and fires may also have been intentionally lit to improve deer habitat across the Cherokee territory (Hatley 1995). Palynological records from the coastal plain of Georgia and Alabama indicate that forest fires increased significantly during the height of the deer skin trade from 1715-1770 (Foster and Cohen 2007). The Cherokees were also influenced by European agricultural practices. In addition to traditional crops of maize and beans, the Cherokee incorporated cowpeas, watermelon, and sweet potatoes in their fields. They also began to raise hogs and fowl after 1750 (Hatley 1995).

Cherokee land claims slowly shrunk through a series of treaties at the end of the 18th century. From 1759-1784, several wars were fought between colonists and the Cherokees, culminating in the Treaty of Henry's Station (1785) (Rothrock 1946). The treaty opened up lands in the Holston and Tennessee River Valleys to an influx of Euro-American settlers. However, the Cherokee retained control of the area around the Middle towns in the mountainous interior up until 1837. Finally, the Indian Removal Act of 1837 forcibly moved the remaining Cherokee out of the Appalachians to a reservation in Oklahoma.

Early Euro-American Settlement

Euro-American settlement in the Appalachian Mountains generally occurred from the northeast to the southwest, with people moving down the Great Valley of

Virginia and Tennessee (Yarnell 1998). The southern end of the Blue Ridge in Tennessee and North Carolina was the last portion of the Appalachian Mountains to be permanently settled by Euro-Americans, due to the presence of the Cherokee Nation and their hostility to white settlement (Govan and Livingood 1952). Settlement occurred first in the Ridge and Valley of Tennessee and the Blue Ridge of Northwestern North Carolina along the outskirts of Cherokee territorial claims.

The earliest settlers chose land along floodplains and in upland valleys and coves with productive limestone soils (Yarnell 1998). Many of these preferable locations had been abandoned by Native Americans relatively recently and still exhibited early successional habitats such as canebreaks and recently abandoned fields (Hatley 1995). Euro-Americans practiced mixed farming of grains and livestock. Their farming practices were similar to Native Americans, in that they planted crops on newly cleared land for several years until productivity declined (Otto 1987). Then they let the land fallow or grazed livestock on it, while moving on to clear new patches of forest. Fallow fields could then be re-cleared after a decade or two of forest growth. Livestock were allowed to graze freely on mast in hardwood forests and in lowland canebrakes (Blethen and Wood 1991). In the years from settlement to the Civil War, the Appalachian Mountains were a major exporter of livestock. Hogs, cattle, and mules were raised in the uplands and then driven to plantation markets on the coastal plain. Eastern Tennessee, Knoxville in particular, was a major center for animal distribution. Migrating herds also created markets for corn and fodder throughout the Mountains. Grains, dairy products, potatoes, wool, orchard products and honey were also produced commercially (Inscoe 1989).

Industrial activity was limited in the region during the early Euro-American settlement period. Early logging was primarily carried out for local use, with the exception of landowners along rivers who floated poplar and walnuts to markets along the Mississippi and Ohio Rivers (Yarnell 1998). Small charcoal fire iron furnaces were an essential source of iron tools and had spread throughout the mountain region by the 1850s (Smith 1982, Inscoe 1989, Moore 1991). Furnaces required large amounts of wood fuel, resulting in the cutting of forests in surrounding areas (Moore 1991). The operation of furnaces also likely contributed ignitions in the landscape that could have increased fire frequency. Salt, copper, gold, lead, and zinc were also mined by small operations in eastern Tennessee and western North Carolina (Inscoe 1989).

Period of Extractive Industry

The logging era in the Appalachian Mountains occurred during the late 19th and early 20th century. Timber shortages in the Northeast and Lake States and the spread of railroad networks increased the profitability of commercial logging during this period (Eller 1982). Economic prosperity at the close of the century led to a boom of mining and logging after 1900. From 1900-1920 heavy cutting was carried out across the entire region. Narrow gauge railroads, overhead cables, and yarding machines increased the accessibility of rough terrain and the rate of cutting (Lambert 1961). Spruce-fir forests on the upper peaks were clear-cut along with lower elevation hardwoods. The forest clearance caused high rates of soil erosion and flooding. Slash left on the sites dried out and often caught fire, resulting in high intensity fires that burned across much of the cutover landscape (Lambert 1961, Pyle 1988). Logging had already begun to decline by 1909 and most timber companies had moved on by the 1920s. Some coal mining was carried out in the Ridge and Valley of Tennessee, but most of the coal mining activity was centered in Kentucky, West Virginia and southwestern Virginia.

Era of Fire Protection and Suppression

Concerns over the environmental impacts of logging and other industrial activities led to the growth of a national conservation movement in the early 20th century. The Division of Forestry was created within the U.S. Department of Agriculture in 1881 and the first forestry bill passed in 1891 enabled the president to proclaim forest reserves on public lands (Steen 2004). In 1911 the Weeks Act authorized the purchase of private lands by the federal government and led to the establishment of national forests in the eastern United States. During 1911-1916, the Forest Service purchased most of the land that would become the Pisgah, Nantahala, Chattahoochee, Cherokee, and Jefferson National Forests. By 1936, the national forests were approximately the size that they are today (Mastran et al. 1983). The Organic Act was passed in 1916 creating the National Park Service and in 1926 Congress passed a bill authorizing the creation of SNP and GSMNP. The final dedications of the parks occurred for SNP in 1936 and for GSMNP in 1940 (Lambert 1989, Campbell 1993).

Federal ownership of forest land in the southern Appalachians led to important changes in land use. Traditional forest uses of livestock grazing, hunting, and wood cutting continued on forest service land but were not permitted within the national parks. Fire control was prioritized in both national forests and national parks due to concerns about the damage it caused to timber. Yet, arson cases did not greatly decline until the onset of World War II, because timber was seen as important to the war effort and burning was seen as an act of treason (Hays 1993, Sarvis 1993).

Chestnut blight (*Cryphonectria parasitica*), an exotic fungus from Asia that infected American chestnuts, had a major impact on forests in the southern Appalachian region. Chestnut blight was initially reported in New York in the first decade of the 20th century. The blight spread quickly, infecting the southern Blue Ridge of Tennessee and North Carolina during the 1920s (Keever 1953, Woods and Shanks 1959). In GSMNP, growth releases in co-occurring tree species indicate that chestnut mortality commenced in 1925 (Woods and Shanks 1959). Chestnut blight killed all mature chestnuts in eastern forests. Prior to the blight, chestnut had been a dominant tree species throughout the southern Appalachians, constituting up to 70% of the overstory in certain stands in GSMNP (Whittaker 1956, MacKenzie and White 1998).

Landscape Patters of Fire

Study Areas

Great Smoky Mountains National Park

GSMNP contains 209,000 ha in the southern portion of the Appalachian Mountains (35°37′N, 83°31′ W, Figure. 3.2).

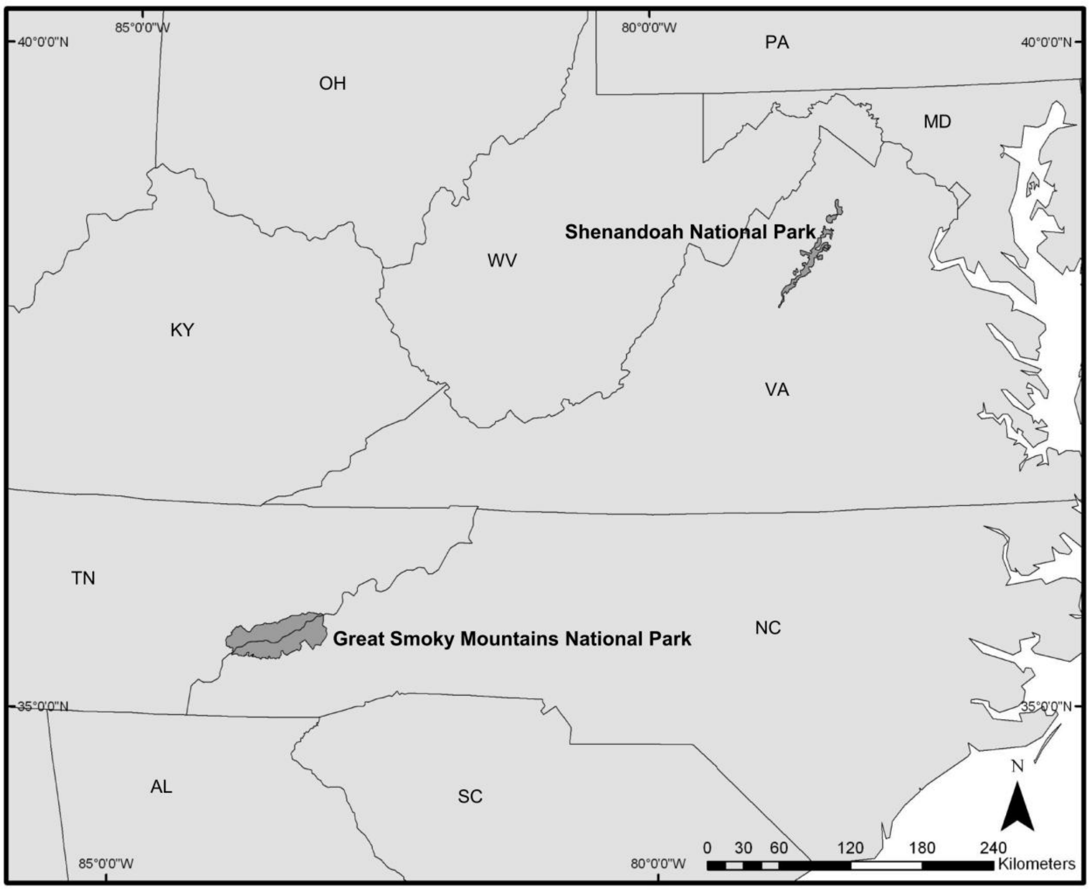

Figure 3.2. Locations of Great Smoky Mountains National Park and Shenandoah National Park in the southern and central Appalachian Mountains, USA.

Located on the border between Tennessee and North Carolina, the park lies in the Southern Section of the Blue Ridge Physiographic Province, and ranges in elevation from 256 to 2025 m (Fenneman 1938). The southern Appalachian Region has a hot continental climate with cold winters and warm summers (Bailey 1978). The greatest amount of precipitation occurs in the summer months (Figure 3.3).

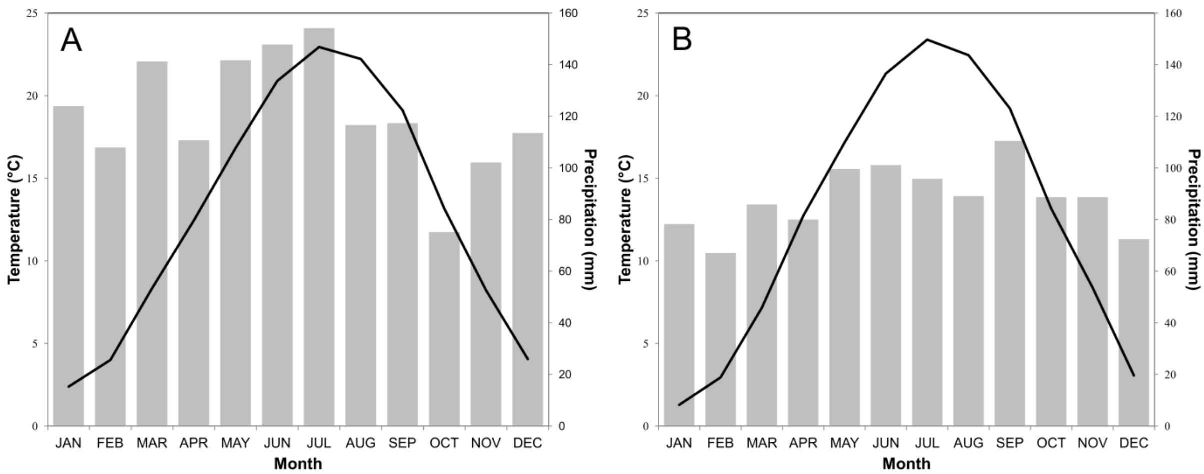

Figure 3.3 Mean monthly climate average for each park NCDC (2002), based on data (1971–2000) from local climate stations, (A) Gatlinburg, Tennessee (elevation 443 m, adjacent to GSMNP), and (B) Luray, Virginia (elevation 427 m, adjacent to SNP). Bars are precipitation and lines are temperature.

However climate varies significantly within the boundaries of GSMNP, as precipitation increases and temperature decreases with elevation (Shanks 1954). The vegetation is classified as Appalachian oak (Stephens et al. 1993). Oak-dominated forests cover the broad submesic to subxeric portions of the landscape. Pines occupy dry ridgetops and south-facing slopes, while mesophytic conifers and hardwoods inhabit the lower slopes, valleys, ravines, and high elevations.

Shenandoah National Park

SNP encompasses 80,000 ha in the central Appalachian Mountains (38°32′N 78°21′ W; Figure 3.2). The park lies within the Northern Section of the Blue Ridge Physiographic Province in Virginia and ranges in elevation from 150 to 1234 m. SNP is also a hot continental climate but receives less precipitation than GSMNP. The vegetation in SNP is also classified as Appalachian oak (Stephens et al. 1993).

Spatial Data

Fire Perimeter Maps

Digital maps of fire perimeters were used to assess landscape patterns of wildfire at a regional scale. Following the implementation of fire suppression in the early 20th century, the spatial extent of wildfires was mapped within the boundaries of both GSMNP and SNP. I obtained digitized fire perimeters for 1930–2003 from each national park. GSMNP records included 744 fires that burned 10,497 ha, and SNP recorded 573 fires that burned 31,610 ha. In GSMNP, anthropogenic ignitions accounted for 643 fires that burned 9,978 ha, and lightning ignited 101 fires that burned 519 ha. SNP maps did not record fire cause consistently. Resource management burns intentionally ignited by park management were excluded from analysis. The fire records did not include perimeters for small fires (< 1 ha); instead ignition points were recorded for these. Therefore, I included ignition points in calculations of the number of fires and area burned, but not in the analyses of topographic patterns of fire. Their exclusion should have little influence on the results of the spatial analyses because the small fires accounted for less than 0.5% of the total area burned in both parks. A number of the fires that occurred in SNP were not mapped, but the size of the burned area was estimated. These fires could not be used for topographic analysis, but were included in all other calculations.

For the examination of topographic patterns of fire, I limited my analysis within GSMNP to areas below 1400m because few fires burned above this elevation (portions of 19 fires, with a total area of 74.5 ha, < 0.5% of total area burned). The exclusion of upper elevations in GSMNP also made the two study areas more similar in terms of elevation range. Finally, the digital fire maps included some fires that burned across park boundaries and some fires that occurred entirely outside of the park boundaries. Therefore, I used the digitized park boundaries obtained from the National Park Service to clip the fire maps, removing any areas that burned outside the park. Digital maps of individual fires were then combined to create a map of cumulative fire occurrence since 1930 (Figure 3.4).

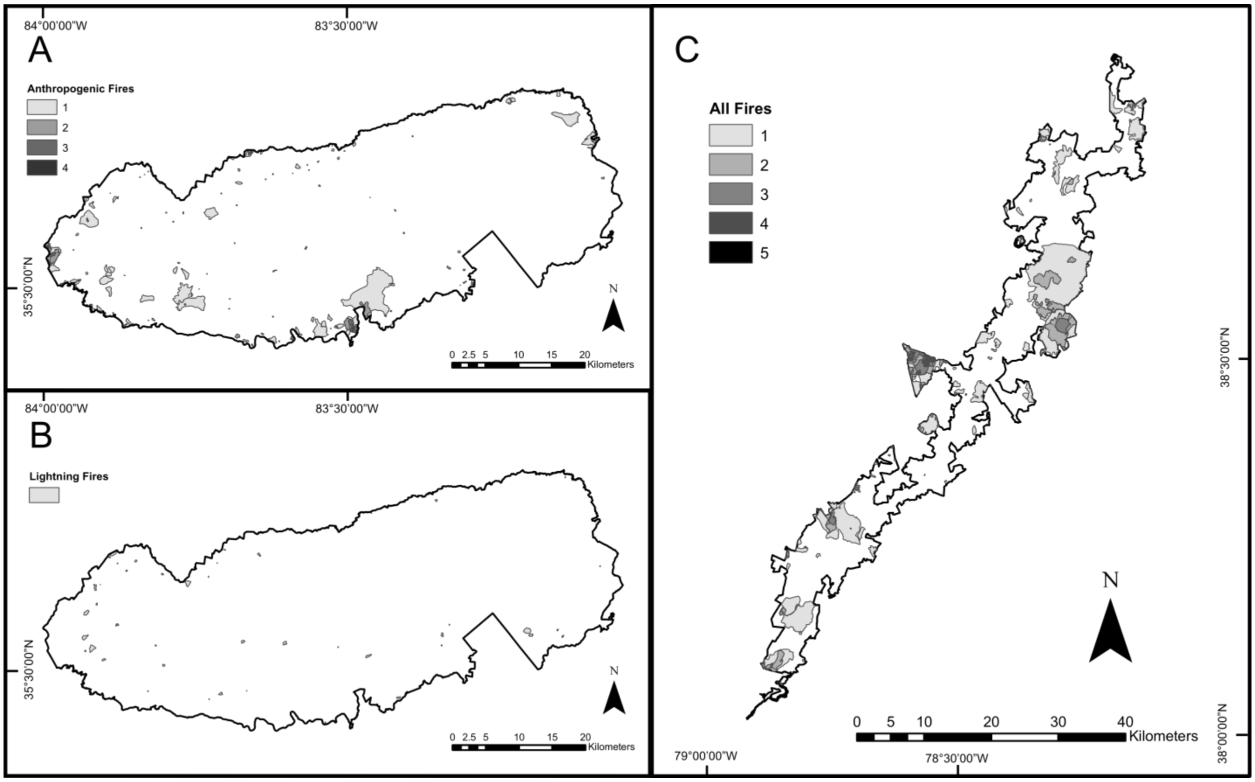

Figure 3.4. Mapped fire perimeters from 1930–2003 for (A) anthropogenic fires and (B) lightning fires in Great Smoky Mountains National Park and (C) all fires in Shenandoah National Park. Darker grey indicates areas that burned multiple times.

Inherent limitations and sources of bias exist that must be considered when using historical fire perimeter records. Issues with size bias, incomplete recording, limited temporal availability, and mapping inaccuracy have been identified as potential sources of error (Morgan et al. 2001, Shapiro-Miller et al. 2007). The fire records in both parks were recorded during an era of active fire suppression, which affected the extent and spatial pattern of the fires. However, the records provide valuable information on spatial patterns of fire in this region that are not available from other sources. Previous work reveals that climatic and topographic influences on fire can be discerned even on fire-suppressed landscapes (Rollins et al. 2002, Mitchener and Parker 2005, Lafon and Grissino-Mayer 2007).

Climate Data

As a record of temporal variations in climate, monthly Palmer Drought Severity Index (PDSI) values were used for the period of mapped fires, obtained from the National Oceanic and Atmospheric Administration National Climatic Data Center (NCDC 2002). PDSI is a soil moisture/water balance index that accounts for moisture conditions during antecedent months. It is derived from a time series of daily temperature and precipitation, and available soil water content (Palmer 1965). PDSI commonly ranges from four to negative four, with positive values indicating high moisture conditions, negative values indicating drought, and zero indicating average moisture conditions. PDSI values from Virginia Climate Division 4 were used as a record of drought in SNP, and PDSI values from Tennessee Climate Division 1 and North Carolina Climate Division 1 were averaged to provide a record of drought in GSMNP.

Topographic Data

I obtained Digital Elevation Models (DEMs) at 10 m resolution for each park, including a 1 km buffer around the park boundary. I used the DEMs to derive slope aspect using the ArcGrid command “slope” (ESRI 2006). Aspect values (1–360°) were combined into eight aspect classes. Slope position classes were derived using the GIS application LANDFORM (Klingseisen et al. 2008), which classified the landscape into four categories in increasing order of topographic wetness: ridge, upper slope, lower slope, and bottom. Finally, the DEMs were used to partition the landscape into 200 m elevation classes. Each of the derived topographic layers was then clipped using the park boundaries and the upper elevation limit in GSMNP.

Data Analysis

Unclipped fire perimeters were used to calculate mean fire size for GSMNP and SNP. In order to facilitate comparison between the two parks, fire perimeters were then clipped along the park boundaries and used to calculate the mean annual fire density, mean annual area burned, and fire cycle for the area within each park boundary. Mean annual fire density and mean annual area burned were corrected for park size and expressed as area burned/km^2. Fire cycle is the time required to burn an area equivalent to the area of the entire park, and is calculated as period of record × total area of park / total area burned during the period of record (Heinselman 1973). Mann-Whitney U tests were used to assess differences in mean annual fire density, mean annual area burned, and mean fire size (Zar 1999). Relationships between fire and temporal variations in climate were examined by correlating the annual number of fires and area burned (log-transformed) in each park with the average PDSI for each year (calculated from monthly PDSI values). The correlations also were calculated for each of the previous four years to test for lagged influences of previous wet or dry years. Fire-climate correlations at a finer temporal scale (monthly area burned correlated to monthly PDSI) were not possible because many of the records provided only the year, but not the month, in which the fire burned. Monthly data likely would have yielded stronger correlations, given the bimodal (spring-fall) fire season of the Appalachian region (Lafon et al. 2005). Nonetheless, annual-level correlations should be adequate for revealing the major fire-climate relationships because wildfires in the Appalachian Highlands generally require longer periods of drought compared to adjacent regions such as the southeastern Coastal Plain (Mitchener and Parker 2005).

It is possible that different levels of anthropogenic ignition and fire spread could occur between SNP and GSMNP because of variations in population density or land use surrounding the parks, or simply because of differences in the shape of the parks. Such differences might obscure the influence of climate. In particular, if SNP has more fires ignited near the park borders than does GSMNP, I might incorrectly attribute the fire activity at SNP to its drier climate. To estimate whether such a factor may influence the analyses, I tallied the ignitions that occurred within 500 m zones parallel to the park boundaries to compare whether the proportion of fires occurring near the boundary differed between the parks

To examine my second hypothesis that topography is a control on patterns of fire, maps of fire occurrence were used to calculate the area burned in each elevation, aspect, and slope position class. Log-likelihood tests for goodness of fit (G-tests) were performed to investigate the topographic patterns of fire with respect to elevation, aspect, and slope position (Rollins et al. 2002). The expected frequency was based on the number of cells in each topographic class within the park boundaries (Sokal and Rohlf 2003). Cramer's V coefficient was used as a measure to compare the strength of association for log-likelihood values (Zar 1999), with a value ≥ 0.1 indicating a relationship and a value ≥ 0.3 indicating a strong relationship.

I tested my third and fourth hypotheses concerning the interaction of climate and topography by comparing the strength of topographic trends in area burned between different regional climates (i.e., GSMNP vs. SNP) and different temporal climatic conditions. For the latter (temporal) comparison, I produced maps of fires that occurred during significant drought years and significant wet years. The 18 dry years that fell within the lowest quartile of annual PDSI values were identified for each park. All mapped fires that occurred during these years were combined into a fire map for drought years (GSMNP, n = 152 fires; SNP, n = 61 fires), and the topographic patterns were analyzed using G-tests and Cramer's V. The same procedure was used to analyze topographic patterns for wet (high-PDSI) years (GSMNP, n = 54 fires; SNP, n = 32 fires). I also used the same tests to compare topographic patterns of lightning-ignited versus anthropogenic fires in GSMNP (n = 60 lightning fires; n = 499 anthropogenic fires).

I further examined the relationship of burning patterns with climate and topography through a GIS based classification and regression tree (CART) model that incorporated the topographic patterns of fire and the climatic conditions under which they occurred. A CART model is a non-parametric statistical modeling technique that provides a collection of rules displayed in the form of a binary tree (Breiman et al. 1984, Venables and Ripley 1999). The advantage of CART models is that they are straightforward to interpret with a mix of numeric and categorical data and are capable of representing non-additive behavior (Bourg et al. 2005). Moderate PDSI condition fire maps were created for each park using fires that occurred during years with PDSI values in the second and third quartile. These maps, along with the high PDSI and low PDSI maps created for the previous analysis produced a total of six burn maps (one for each PDSI condition in each park). Stratified random sampling was used to select 100 points from the burns and 100 points from the unburned sections of each of these six burn maps (total of 600 sample points per park). Values from each of the topographic layers (elevation, slope position, and aspect) were also recorded for each of the sample points.

For the CART analysis, topographic variables were treated as ordinal integers, ranked according to the presumed moisture conditions, from dry to wet. Elevation categories were (1) 0-200 m, (2) 200-400 m, (3) 400-600 m, (4) 600-800 m, (5) 800-1000 m, (6) 1000-1200 m, (7) 1200-1400 m. Slope categories were (1) ridge, (2) upper slope, (3) lower slope, (4) bottom. Treating the aspect variable as an ordinal integer required me to reassign the cells as follows: (1) south- and southeast- facing slopes that burned most frequently were assigned the value of one, (2)southwest and east aspects, (3) northeast and west, (4) north and northwest. Climate categories were (1) points sampled from the low PDSI burn map, (2) moderate PDSI burn map, (3) high PDSI burn map. The S-PLUS 6.0 statistical package was used to perform classification tree analysis, producing a tree for each park that predicted an outcome of burned (1) or unburned (0) (Insightful Corporation 2001). A second training sample of 1200 points was collected in the same manner as above in order to assess misclassification error and guide the pruning of the trees. Optimal recursive shrinking was performed using the training sample in order to prevent over fitting of the model. The model was pruned for parsimony in terms of the number of descriptors while maintaining a high level of accuracy.

Fire History

Study Sites

Historical fire occurrence was reconstructed at three sites in the southern Appalachian Mountains of Tennessee and North Carolina. Sites were chosen that exhibited minimal human disturbance (i.e., logging and agricultural clearance) in order to obtain the longest record of fire possible. Sites were also chosen to represent a range of climatic and human influences within the region.

House Mountain

House Mountain (36° 6'N, 83°46'W) is located within the House Mountain State Natural Area, TN in the Ridge and Valley Physiographic Province. House Mountain is a disjunct extension of Clinch Mountain, 5 km north of the Holston River and 21 km northeast of Knoxville, TN. The summit ridge stretches approximately 2.4 km northeast to southwest, with a peak elevation of 640 m. Annual precipitation is 1170 mm at an elevation of 338 m in Jefferson City, TN, 26 km east of House Mountain (NCDC 2002). September and October are the driest months, with monthly precipitation means of 66.5 mm and 54.6 mm respectively. Mean January temperature is 1.5°C and mean July temperature is 24.6°C. Forests types at the site were mixed yellow pine and oak-hickory. Pine stands were dominated by Virginia pine and Table Mountain pine and contained a lesser component of chestnut oak and pignut hickory (*Carya glabra* Mill.). Large individual pitch pines and shortleaf pine were also scattered along the mid-slope below the ridge crest. Oak-hickory stands were composed of chestnut oak, black oak, yellow poplar, pignut hickory and northern red oak.

Throughout most of the 18th century the upper Tennessee river valley watershed was controlled by the Cherokee. However, the main concentration of Cherokee settlement in the Overhill towns was further south along the Hiawassee and Little Tennessee Rivers (Gragson and Bolstad 2007). The first Euro-American settlers established farms along the Holston River in 1785 (Rothrock 1946). Today, House Mountain State Natural Area contains 202 ha managed by the Knox County Department of Parks and Recreation. The surrounding landscape is a mix of cleared fields and forests.

Fire history was sampled from three separate pine stands located along the ridge top and upper slope of the southwestern portion of House Mountain (Figure 3.5). The sampled stands ranged in elevation from 520 to 610 m, comprising 3 ha within an 8 ha landscape.

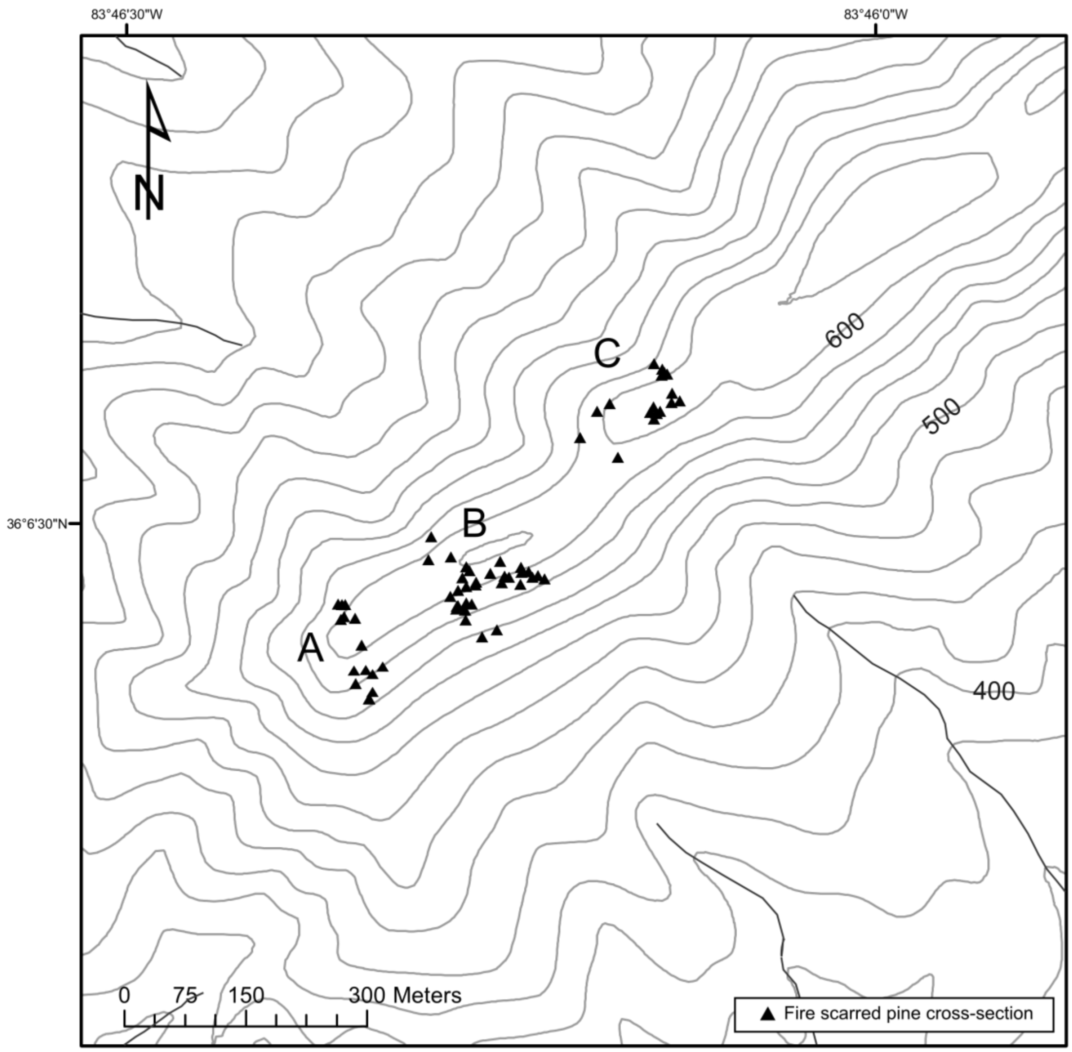

Figure 3.5 House Mountain fire history reconstruction site, Knox County, Tennessee. Triangles depict locations where fire scarred pine cross-sections were sampled (n = 82). Letters (A, B, C) indentify individual pine stands used in area-wide fire analysis.

Licklog Ridge

Licklog Ridge (35°33'N, 83°50’W) is located in GSMNP, Tennessee within the Blue Ridge Physiographic Province. Average annual precipitation is 1480 mm at an elevation of 443 m in Gatlinburg, Tennessee, 29 km northeast of Licklog Ridge (NCDC

2002). October and November are the driest months, with monthly precipitation means of 75.2 mm and 102.1 mm respectively. Mean January temperature is 2.4°C and mean July temperature is 22.9°C. Forest vegetation at the site varies along the topographic moisture gradient from xeric to mesic landform positions. Xeric yellow-pine stands occupy upper ridges and southeast to southwest-facing upper to lower slopes. Table Mountain pine dominates these stands along with a mix of scarlet oak (*Q. coccinea* Muenchh.), pitch pine, black gum, sourwood (*Oxydendrum arboreum* L. DC.) and red maple. Submesic mixed-oak stands occupy west and east-facing slopes. Oak stands are dominated by chestnut oak with a mix of red maple, white pine, sourwood, and scarlet oak. Submesic white pine-hardwood stands are located on south facing toe slopes. These stands are dominated by white pine and also contain red maple, scarlet oak, hemlock, chestnut oak, and sourwood. Mesic cove forests occupy the protected cove positions. Cove forests are dominated by eastern hemlock and a mix of hardwoods including sweet birch (*Betula lenta* L.), yellow poplar, red maple, white basswood (*Tilia heterophylla* Vent.), sugar maple, northern red oak, sourwood, white pine, chestnut oak, pignut hickory, and black gum.

One ridge south of the site (c. 0.5km) is the Ekaneetlee Gap Trail, a Native American trail that was used for travel across the Appalachian crest (Burns 1957). Licklog ridge is 3 km south of Cades Cove, which the Cherokee may have farmed and likely burned to maintain an open landscape (Shields 1977, Bratton et al. 1980). Euro-Americans began to settle in the cove in the 1820s and maintained farms up until the federal government began to purchase land for the park in 1928. A single iron forge, Cades Cove Bloomery Forge, operated in the cove from 1827-1847 (Dunn 1988). It was located on Forge Creek, 3 km north of Licklog Ridge on the southwestern edge of Cades Cove. Licklog watershed was not subject to large scale logging disturbance or agricultural clearance (Pyle 1988).

Fire history was sampled from four pine stands located on separate south-east facing spurs of Licklog Ridge (Figure 3.6). The sampled stands were 700 to 900 m in elevation and totaled 28 ha within a 64 ha forested landscape.

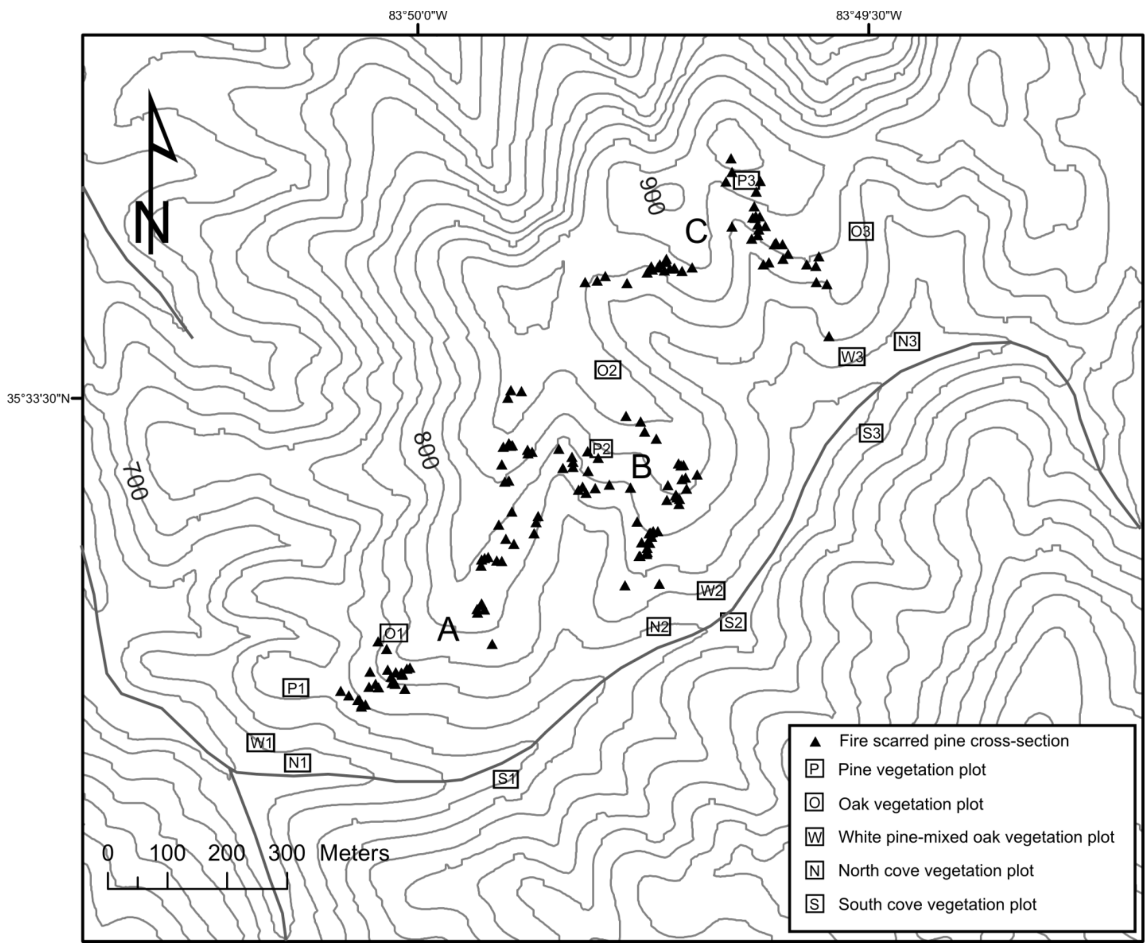

Figure 3.6 Licklog Ridge fire history reconstruction site, Blount County, Tennessee. Triangles depict locations where fire scarred pine cross-sections were sampled (n = 104). Letters (A, B, C) indentify individual pine stands used in area-wide fire analysis. Squares identify vegetation sampling plots.

Linville Mountain

Linville Mountain (35°55'N, 81°55'W) is in the Grandfather Ranger District, Pisgah National Forest, McDowell County, North Carolina, on the western edge of the Blue Ridge Physiographic Province. Average annual precipitation is 1494 mm at an elevation of 817 m in Celo, North Carolina, 26 km west of Linville Mountain (NCDC 2002). October and December are the driest months, with monthly precipitation means of 106.2 mm and 106.4 mm respectively. Mean January temperature is 1.1°C and mean July temperature is 21.4°C. Sampled forests contained Table Mountain pine, pitch pine, shortleaf pine and Virginia pine. The surrounding forests are Appalachian oak-hickory, hemlock, and cove hardwood.

At the beginning of the 18th century, the Linville Mountain region was a hunting ground used by both the Cherokee and Catawba people (Phifer 1979). There were neither Native American nor Euro-American settlements in the region. The Old Cherokee Path to Virginia, a Native American trail, was several miles west of Linville Mountain running between Newland and Morganton, NC (Myer 1928). Euro-American settlement in Burke County began in 1763; however the initial land grant on Linville Mountain was not issued until 1831 (Grandfather Ranger District Office). The lower and mid-slopes of Linville Mountain were logged in the early 20th century, as indicated by old logging roads and parcel ownership by the Linville Lumber Company. However, many old pines on the upper slopes of the mountain indicate that the pine stands were not logged. Ownership of the tract was transferred to the Pisgah National Forest in 1939.

Fire history samples were collected from two pine stands located on separate south-west facing spurs of Linville Mountain (Figure 3.7). The sampled stands were 970 to 1115 m in elevation and totaled 6 ha within a 22 ha forested landscape.

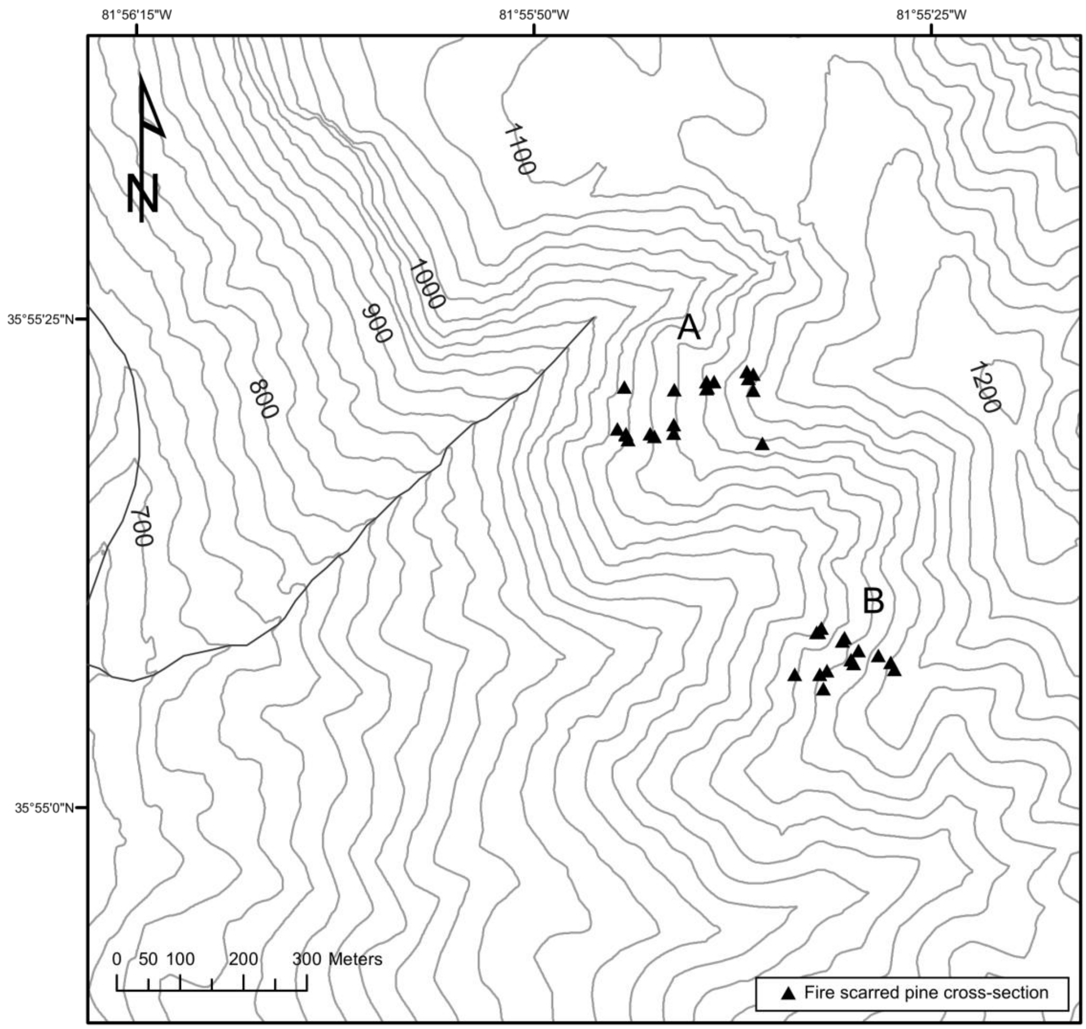

Figure 3.7 Linville Mountain fire history reconstruction site, Burke County, North Carolina. Triangles depict locations where fire scarred pine cross-sections were sampled (n = 45). Letters (A, B) indentify individual pine stands used in area-wide fire analysis.

Field Methods

Prior to field sampling, potential fire history reconstruction sites were scouted in order to determine whether old, fire-scarred material was present at the site in sufficient quantities to enable a long-term fire history reconstruction. Leaf-off infrared aerial photographs, digital stand inventory data, and conversations with managers from the National Park Service and U.S. Forest Service were used to identify unlogged pine and mixed hardwood-pine stands on south to southwest facing ridges. Potential sites were then intensively surveyed for living pine trees or remnant wood (i.e. snags, stumps, and logs) with multiple fire scars. Fire scarred material was flagged and marked with a GPS for efficient sampling upon return. Among the sites visited (ca. 20 locations), House Mountain, Licklog Ridge, and Linville Mountain were chosen because they contained abundant, old fire-scarred material and exhibited minimal evidence of logging or agricultural clearance. During 2008-2009, chainsaws were used to collect partial cross sections from living and dead yellow pine trees with basal fire scars at each of the three fire history reconstruction sites (Arno and Sneck 1977).

Laboratory Methods

Cross-sections were brought back to the laboratory and dried. Fragile cross-sections were mounted on plywood to provide stabilization. Some of the larger cross-sections were re-sectioned using a hand saw in order to reveal additional scars. Cross-sections were then surfaced and sanded with a belt sander using increasingly finer sandpaper (ANSI 40-grit [500–595 µm] to 400-grit [20.6–23.6 µm]) until the cellular structure of the wood was visible under standard magnification (Orvis and Grissino-Mayer 2002).

For living cross-sections, annual rings were visually crossdated and assigned a calendar year using established methods to compare patterns of wide and narrow annual ring growth patterns between samples (Fritts 1976, Stokes and Smiley 1996). Ring widths were then measured to 0.001 mm with a Velmex measuring stage and the J2X software program. Measured ring widths were entered into the COFECHA software package in order to statistically verify cross-dating and measurement accuracy (Holmes 1986, Grissino-Mayer 2001a). Correlation analysis was performed on each tree-ring series using overlapping 40 year segments lagged by 20 years. Segments that fell below a critical correlation threshold of 0.37, representing the 99% confidence interval, were flagged by the program and manually re-examined for dating or measurement errors. A master chronology was then compiled using the oldest living samples with high inter-series correlations (Dieterich and Swetnam 1984). "Floating" cross-sections, pieces for which the bark date was unknown, were then cross-dated against the master chronology in COFECHA (Stokes 1981). For cross-sections that did not intersect the pith, establishment dates were estimated according to the width and curvature of the earliest rings (Applequist 1958).

Fire scars on the cross-sections were dated to the year of formation and assigned seasonality according to the position of the scar within the annual ring (Dieterich and Swetnam 1984, Baisan and Swetnam 1990). Fire scar seasonality was designated as (1) dormant, positioned on the ring boundary between the latewood of one years growth and the early wood of the next years growth; (2) earlywood, positioned within the first third of the early wood; (3) mid-earlywood, positioned in the second two thirds of the earlywood; (4) latewood positioned in the latewood: (5) undetermined, seasonality of the scar could not be determined (Hoss et al. 2008, Aldrich et al. 2010). Dormant-season scars were assigned the date of the ring following the scar. Each interval of annual rings between scars on an individual sample was identified as either a recording or non-recording interval. Recording intervals were periods of growth between two scars in which the outer growth curl was not decayed and therefore it could be determined that no additional scarring occurred during the recording interval. A non-recording interval was an interval in which the healing rings between the two scars were decayed and it was not possible to determine if additional scarring occurred during the interval. The interval between the pith date and the first scar was not included as a recording interval because (1) trees are more resistant to scarring prior to their initial scarring and may have experienced several fires before recording a scar and (2) the interval between the pith and first scar does not represent an interval between fires, since the pith is not a fire scar (Grissino-Mayer 2001b, Van Horne and Fulé 2006). For each cross-section, fire history information (fire years, fire seasonality, recording/non-recording intervals, outer/bark dates, and inner/pith dates) was entered into the FHX2 software package (Grissino-Mayer 2001b).

Data Analysis

Fire Frequency

The FHX2 software package was used to archive, graph, and analyze fire intervals (Grissino-Mayer 2001a). Fire interval calculations were carried out on intervals following the start of the reliable record (i.e. intervals following the first fire that was recorded by at least two samples at a site)(Grissino-Mayer et al. 2004). The period after 1940 was not included in fire interval calculations because I was interested in fire regime characteristics prior to the era of fire protection. The U.S. Forest Service and National Park Service were not very successful in excluding fire from public forest land until the 1940s (Hays 1993, Sarvis 1993). For each of the different fire interval types, I calculated a mean fire interval (MFI), Weibull median fire interval (WFI), standard deviation (SD), lower exceedance interval (LEI), and upper exceedance interval (UEI) (Grissino-Mayer et al. 2004). 75% of the intervals are expected to fall between the lower and upper exceedance interval.

Fire scars are imperfect recorders of fire occurrence in forests (e.g. fires are not recorded on all trees and all fires do not necessarily burn across the entire study area)(Baker and Ehle 2001, Van Horne and Fulé 2006). Therefore, I used a range of fire regime metrics to characterize historical fire frequency at each individual fire history sample site. (1) Point fire intervals (PFI) were generated using only the intervals recorded on individual samples and did not include non-recording intervals (i.e. years preceding the first scar year)(Grissino-Mayer 2001b). The use of recording years is a necessary practice in order to ensure that the MFI is based only on actual fire free intervals (Grissino-Mayer et al. 2004). Otherwise fire free intervals might include years in which fires occurred but the tree was not susceptible to scarring or intervals which contained scars that were removed from the tree through subsequent burning or rotting of the scar surface. The PFI provides a conservative estimate of fire frequency, since a single fire often does not scar all trees in a stand (Dieterich and Swetnam 1984, Van Horne and Fulé 2006). However, calculation of mean fire interval at a single point ensures that the area sampled does not influence the length of fire intervals and facilitates comparison between different studies. (2) Composite fire intervals (CFI) were generated by combining fire years from all of the fire scarred samples at a site into a single record of fire. The CFI included both recording and non-recording intervals, since non-recording intervals on one sample are likely to be covered by recording intervals on other samples from the site. (3) 25% filter composite fire intervals (FFI) were generated using a composite record of all fires at a site that were recorded on at least two samples and ≥ 25% of the samples that were recording during that particular fire year. The use of a percent scarred filter ensures that only larger fires that scarred multiple trees are used in the analysis. Recording and non-recording intervals were included in the calculation of the FFI. (4) Area-wide fire intervals (AWI) were generated using only fires that burned across each of the individual stands at a site and included non-recording years since the intervals were a composite of fire years at the site. Each study site included multiple distinct pine stands that were separated by minor drainages or intervening oak forest (House Mountain, n = 3; LickLog Ridge, n = 4; Linville Mountain, n = 2). An area-wide fire year was a year in which a fire was recorded in each of the stands that had a recording tree during the particular year at the study site (Fisher et al. 1987, Aldrich et al. 2010). If a fire occurred during a year in which only one stand was recording, then the fire year was not considered an area-wide fire year. (5) Regional fire intervals (RFI) were generated using fire years in which a fire was recorded at all three study sites. The RFI also included non-recording years since the fire record was a composite of multiple sites (Aldrich et al. 2010).

Temporal Variations in Fire Activity

To assess the influence of changing land use, I divided the fire history record into four land-use periods: (1) The Cherokee period included the earliest portion of the record at each site prior to Euro-American settlement, except at House Mountain, where the dendroecological record did not extend back far enough to provide a distinct Cherokee period. (2) The Euro-American settlement period began in 1790 at House Mountain, 1820 for Licklog Ridge, and 1770 for Linville Mountain. (3) The industrialization period was the same at all sites, 1880-1940, when large scale industrial logging and mining were carried out in the region. (4) The fire protection period (FP) at all of the sites was from 1940 to 2009. In order to compare fire frequency during the different land-use periods I calculated the number of fire scars per recording tree by decade at each of the sites (Hoss et al. 2008). The number of fire scars per recording tree provides a fire frequency index that can be used to compare across decades with different sample sizes of recording trees. A nonparametric Kruskal-Wallis *H*-test was used to test for differences in the mean decadal fire frequency index values for the different land-use periods (Sokal and Rohlf 2003). I then performed post-hoc pairwise comparisons between the land use periods (Dunn 1964, Zar 1999).

Fire-climate Relationships

The influence of annual drought on the occurrence of fire was assessed using superposed epoch analysis (SEA), which is available in the FHX software package (Grissino-Mayer 2001b). SEA compares climate conditions (e.g. precipitation, temperature, teleconnection indices) in the year of the fire and in preceding years to climate conditions during non-fire years (Swetnam and Baisan 1996). Comparisons are carried out by identifying all fire years as year zero (t = 0) and then calculating average climate conditions prior to (t-6, t-5, etc.) and during the individual fire years (t = 0) (Grissino-Mayer 1995, Grissino-Mayer 2001b). Monte Carlo techniques are then used to construct confidence intervals for significant departures from mean climate conditions throughout the record (Veblen 2003). SEA was used to test for significant departures in moisture conditions prior to (t-6) and during fire years (t = 0) in order to examine whether moisture conditions influenced fire occurrence in the southern Appalachians. As a proxy for drought conditions at each of the three fire history sites, I used a tree-ring reconstruction of summer (June-August) Palmer Drought Severity Index (PDSI), grid point 238, from western North Carolina (Cook et al. 1999, Cook et al. 2004). Grid point 238 is part of a gridded network for North America, with 286 points covering 2.5° x 2.5° (Cook et al. 2004). The temporal coverage of grid point 238 is 1612 years (367-1979) and 28 tree-ring chronologies were used in the reconstruction from 1700-1930 (Cook et al. 2004). Reconstructed PDSI values are available for download from the National Climatic Data Center website (NCDC 2002).

I performed SEA on three different fire event data sets per site: (1) all fires (AF) recorded by all trees at a single site; (2) major fires (MF) recorded by at least two trees and ≥ 25% of the recorder trees at a single site; (3) and area wide fires (AWF) recorded by a tree in each of the stands that were recording during the fire year at a single site. Regional fires (RF) recorded at each of the three fire history sites across the southern Appalachian region were also analyzed. I further divided the four fire event data sets by seasonality. SEA was carried out separately on all fires, dormant season fires, and growing season fires for all four fire event types. Growing season fires included earlywood, mid-earlywood, and latewood fires.

Vegetation Dynamics

Study Site

Vegetation data was collected on the south facing slope of Licklog Ridge and in the adjacent cove in GSMNP (Fig 3.3). The site was chosen for three reasons: (1) a long term dendroecological record of frequent fire; (2) no history of agricultural clearance or logging; (3) the presence of multiple forest community types typical of vegetation in the southern Appalachian region.

Field Methods

To characterize age structure and species composition, vegetation plots were sampled during 2008-2010 at Licklog Ridge. Three 50 m X 20 m plots were sampled in each of the four forest vegetation types located on or adjacent to the south facing slope of Licklog Ridge where fire history material had previously been collected. The forest types sampled were yellow pine, oak, mixed white pine-hardwood, and cove (referred to as north cove stands for remainder of the study). An additional three 50 m X 20 m plots were sampled in cove stands on the south side of Licklog Branch (referred to as south cove stands for remainder of the study). The south cove stands were opposite the slope with abundant evidence of past fires and at the base of a north-facing slope covered with mesophytic forest. These cove plots were sampled with the goal of assessing whether species composition and establishment dates differed from the other cove plots due to the branch acting as a fire break. Each of the vegetation plots was randomly located within the stand types by starting at the edge of the stand and selecting two random numbers for distance and direction to the initial plot corner. The 50 m plot line was then laid out perpendicular to the hillslope.

In each of the 15 vegetation plots, two cores were extracted from opposite sides at the base of living trees with a stem diameter at breast height (DBH measured at 1.37m) ≥ 5 cm, and the species and DBH were recorded. Dead tree stems were identified as yellow pine, white pine, hemlock or hardwood and the DBH was recorded. Saplings (< 5 cm DBH, ≥ 50 cm height) were recorded by species but were not cored. However, pine sapling ages were estimated by counting nodes on the stems (Pfeffer 2005). Multiple saplings sprouting from a single root base (i.e. living trees, snags, stumps, or independent saplings with multiple stems) were recorded as a single sapling with an additional count for the number of separate stems sprouts. Multiple connected sprouts were not counted as separate saplings; since it is unlikely that more than one individual from a single root base will survive into the tree stage. Seedlings (> 50 cm height) were recorded by species within five 2 m belt transects evenly spaced at 10 m intervals within the plot. The same method described above was used to differentiate seedling sprouts. Duff depth was measured using a trowel at 12 evenly spaced points along the outer edge of the plot. Each of the plot corners were marked with a GPS and aspect and slope of plot location were recorded.

Laboratory Methods

Increment cores were brought back to the laboratory, dried and mounted on wooden core mounts. Increment cores were then surfaced and sanded with a belt sander using increasingly finer sandpaper (ANSI 40-grit [500–595 µm] to 400-grit [20.6–23.6 µm]) until the cellular structure of the wood was visible under standard magnification (Orvis and Grissino-Mayer 2002).

Increment cores were ring counted from the cambium to the pith in order to determine the year of establishment. The earlier of the pith dates determined from the two cores collected for each tree was used as the establishment date. For cores that did not intersect the pith, the date of establishment was estimated according to the width and curvature of the earliest rings (Applequist 1958). Broken cores and rotten cores, for which a pith date could not be estimated, were marked as incomplete and the date of the earliest ring was recorded.

Data Analysis

Tree data were used to calculate relative basal area, relative density, and relative importance values for each tree species in the different stand types at Licklog Ridge. Relative sapling and seedling density were also calculated for each species in each stand type.

Tree establishment in different species groups was graphed by decade for each of the community types to identify temporal patterns of species recruitment. Tree species groups were determined according to subgenus affiliation and species moisture requirements. The tree groups were: (1) Yellow Pines (Table Mountain pine, pitch pine), (2) White Oaks (white oak, chestnut oak), (3) Red Oaks (scarlet oak, northern red oak, black oak), (4) Eastern White Pine (eastern white pine), (5) Maples (red maple, sugar maple, striped maple (*A. pensylvanicum* L.)), (6) Mesophytic Hardwoods (yellow buckeye, sweet birch, white ash (*Fraxinus americana* L.), Carolina silverbell (*Halesia carolina* L.), yellow poplar, white basswood, American holly (*Ilex opaca* Ait.), fraser magnolia (*Magnolia fraseri* Walt.)), (7) Xerophytic hardwoods (pignut hickory, shagbark hickory (*C. ovata* Mill. K. Koch), mockernut hickory (*C. tomentosa* Poir.

Nutt.), black gum, common serviceberry (*Amelanchier arborea* Michx. F. Fernald), sourwood, and sassafras (*Sassifras albidum* Nutt. Nees)) and (8) Eastern Hemlock (eastern hemlock).

Several shorter-lived understory species were primarily represented in younger age classes. These species could have been present on the landscape prior to fire suppression but individuals did not persist long enough to be represented in the older age classes. Therefore, I removed the following species from the remainder of the analysis so that their absence from the early record would not bias the results of successional change: striped maple, common serviceberry, American holly, Fraser magnolia, sourwood, and sassafras.

Classification analysis and ordination were carried out on tree and sapling establishment data from the vegetation plots. The objective was to quantitatively assess changes in species establishment that have coincided with changes in the disturbance regime. Shifts in the composition of species establishment should be a good indication of ongoing successional change and future stand composition. To test for shifts in the composition of species establishment, each of the plots was divided into three samples according to the establishment dates of the trees. The first sample, the fire period (F), consisted of all trees that established prior to 1910, since the last major fire occurred in 1916 and establishment patterns shifted immediately after this fire. The second sample, the post-fire period (P), consisted of all trees that established from 1910-1950. This sample represents trees that established in the environment immediately following the end of the frequent fire regime. On the xeric sites and perhaps the more mesic sites, forest canopies may have been fairly open, with high light availability in the understory.

However, unlike the trees established prior to 1910, trees from the post-fire sample were not subject to frequent fire disturbance during their establishment. The third sample, the exclusion period (E), includes all trees that established after 1950 and all saplings. By 1950, forest establishment should no longer be responding to the last fire, with the canopy having closed and the resulting light and moisture levels approximating stand conditions today.

The division of the data set resulted in 45 samples (15 vegetation plots X 3 disturbance periods). Species counts were then standardized according to plot totals to make sample units equitable in species abundance and enhance the detection of compositional similarities among samples. I then performed hierarchical agglomerative cluster analysis to identify groupings based on similarity of species composition in samples. Sorensen distance was used as a dissimilarity measure and the furthest neighbor method was used to link groups (McCune and Grace 2002). The appropriate number of clusters was determined according to dendrogram structure; with the dual goals of retaining a high level of information and the production of ecologically meaningful groupings. Multi-response permutation procedure (MRPP) was then performed to test for significant differences in the composition of groupings identified by the cluster analysis. Indicator species analysis (ISA) was also carried out to identify species that were significant indicators for each group.

Next, I performed non-metric multidimensional scaling (NMS) ordination on the vegetation samples to assess the structure of variance within the dataset. All classification and ordination procedures were carried out in PC-ORD version 4.14. Sorensen distance was used as the dissimilarity measure with a random starting configuration. The stability criterion was 0.0001 and the maximum number of iterations was 200. In order to reduce the likelihood of local minima, I performed multiple runs of NMS (n = 40) and performed a Monte Carlo test (n = 40). The Monte Carlo test indicated the minimum number of dimensions to produce the lowest stress.

The influence of disturbance regime on beta diversity within the watershed was assessed using two approaches. First, species richness was calculated for each of the disturbance period samples in each of the plots. Beta diversity was then calculated for each of the disturbance period samples in each of the plots using Whittaker's β_W ($\beta_{W} = \lambda / \bar{\alpha}$) (Whittaker 1960). Gamma diversity (λ) is the total number of species establishing across all fifteen plots during a single disturbance period. Mean alpha diversity ($\bar{\alpha}$) was the mean plot species richness for trees establishing during each disturbance period. The same diversity calculations were carried out on compositional data from the plots divided according to trees, seedlings, and saplings. This analysis provided another assessment of diversity changes across forest strata rather than species establishment over time.

My second approach in assessing changes in beta diversity was to use multivariate dispersion of the three groups of tree establishment data as an assessment of beta diversity (Anderson et al. 2006). The computer program PERMDISP (Anderson 2004) was used to calculate distance from observations to their centroids according to the Sorensen dissimilarity measure. Then the averages of these distances among groups were compared using ANOVA. Pair-wise a posteriori tests were then performed in order to assess which group means differed significantly.

CHAPTER IV

RESULTS*

Contemporary Landscape Patterns of Fire

Fire-climate Relationship

Research Question: Does climate impose regional-scale pattern on the occurrence of fire, with the relatively dry SNP exhibiting a higher density of fires, larger fires, and a shorter fire cycle than GSMNP. Additionally is fire activity related to temporal variations in climate, with more burning in dry years than wet years in both locations?

SNP had a greater mean annual fire density (Mann-Whitney test, $U = 1136$, $n_1 = n_2 = 72$, $p < 0.05$), mean annual area burned (Mann-Whitney test, $U = 2038$, $n_1 = n_2 = 72$, $p < 0.05$), and shorter fire cycle than GSMNP (Table 4.1).

*Part of this chapter is reprinted with permission from "Climatic and topographic controls on patterns of fire in the southern and central Appalachian Mountains, USA." by Flatley, W.T., Lafon, C.W., Grissino-Mayer, H.D. *Landscape Ecology* 26(2): 195-209. Copyright 2011 by Springer Science+Business Media B.V.

Table 4.1 Mean (standard deviation) annual ignition density, mean annual area burned, mean fire size, and fire cycle for fire records from 1930-2003 in GSMNP and SNP for all fires, and for anthropogenic and lightning fires in GSMNP. Values followed by a letter differ significantly from values followed by the same letter (Mann-Whitney test, $p < .05$).

	Fire density (N/1000 km^2/yr)	Area burned (ha/1000 km^2/yr)	Mean fire size (ha)	Fire cycle (yrs)
SNP All Fires	13.5 (8.3) [a]	488. 2 (1692.3) [c]	42.7 (309.7)	204
GSMNP All Fires	6.3 (5.2) [a]	83.5 (422.2) [c]	25.6 (186.2)	1197
GSMNP Anthropogenic Fires	5.5 (4.9) [b]	79.6 (418.8) [d]	28.3 (199.9)	1257
GSMNP Lightning Fires	0.9 (1.0) [b]	3.9 (16.2) [d]	8.2 (19.3)	25397

These differences in fire activity do not appear to result from a greater level of human ignitions along the border at SNP compared to GSMNP. The evaluation of ignition distances from park boundaries revealed that a higher percentage of ignitions in GSMNP occurred within the first 500 m of the park boundary and there was a more rapid decrease in ignitions within the first 2000 m of the park boundary. The pattern suggests that increased fire activity in SNP is not the product of exterior ignitions, but a product of lower moisture conditions in the region. GSMNP had a greater concentration of burning along the border (Figure 4.1); consequently for fire activity at SNP to exceed that at GSMNP it had to overcome the effect of greater human influence near the GSMNP boundary.

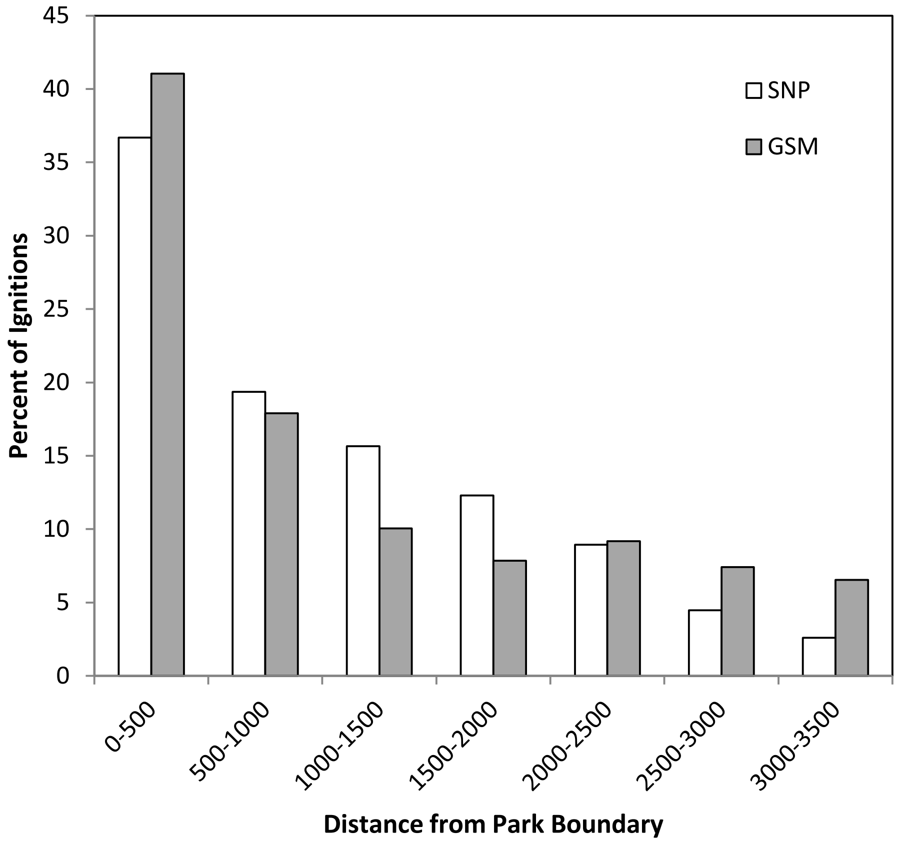

Figure 4.1 Percent of ignitions occurring at different distances from the park boundaries.

In both parks, small fires were numerous, but the few largest fires (> 1000 ha) accounted for the majority of area burned (GSMNP = 39%, SNP = 55%) (Figure 4.2).

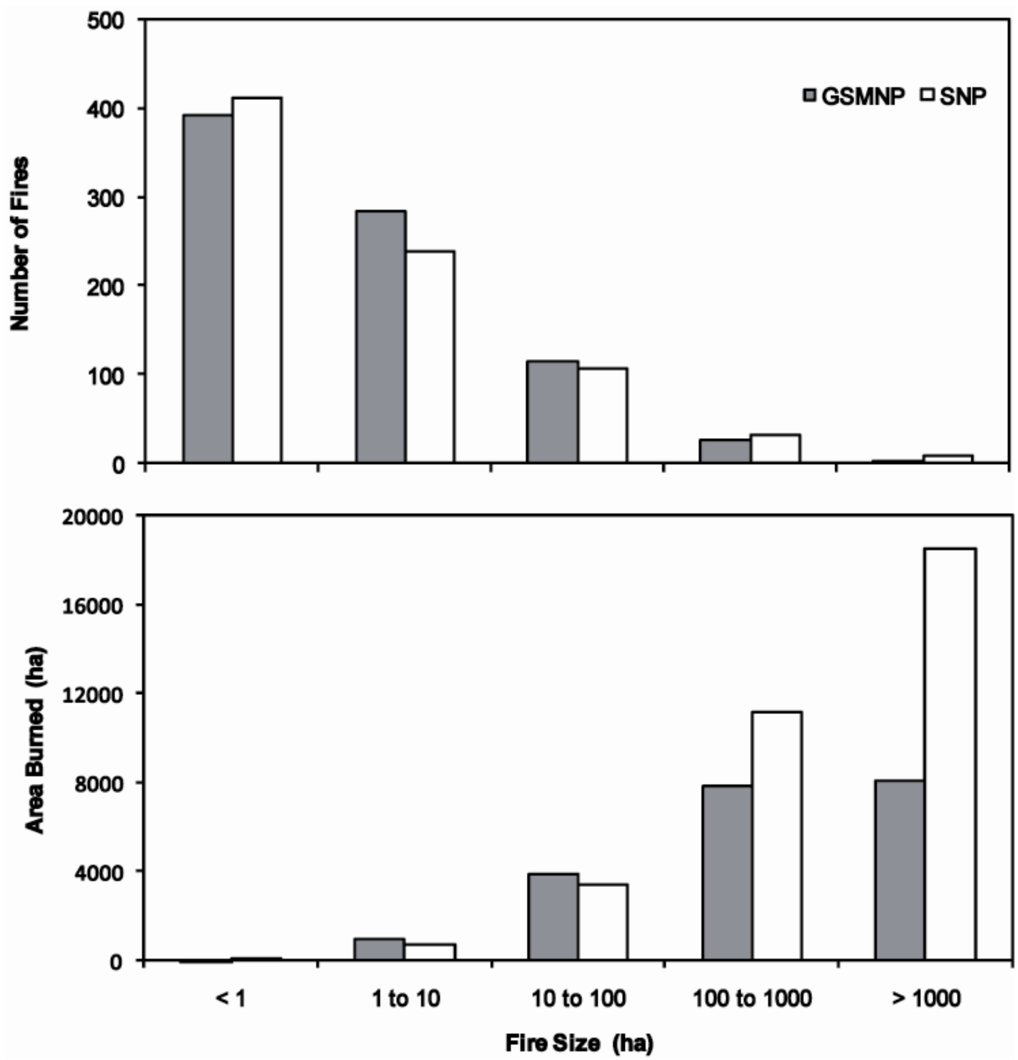

Figure 4.2 Distribution of number of fires and area burned for different fire size categories in each national park.

More extensive burning occurred in dry years than wet years, as shown by the negative correlation between annual area burned and PDSI in the year of the fire (Figure 4.3). Positive correlations also existed between annual area burned and PDSI of preceding years.

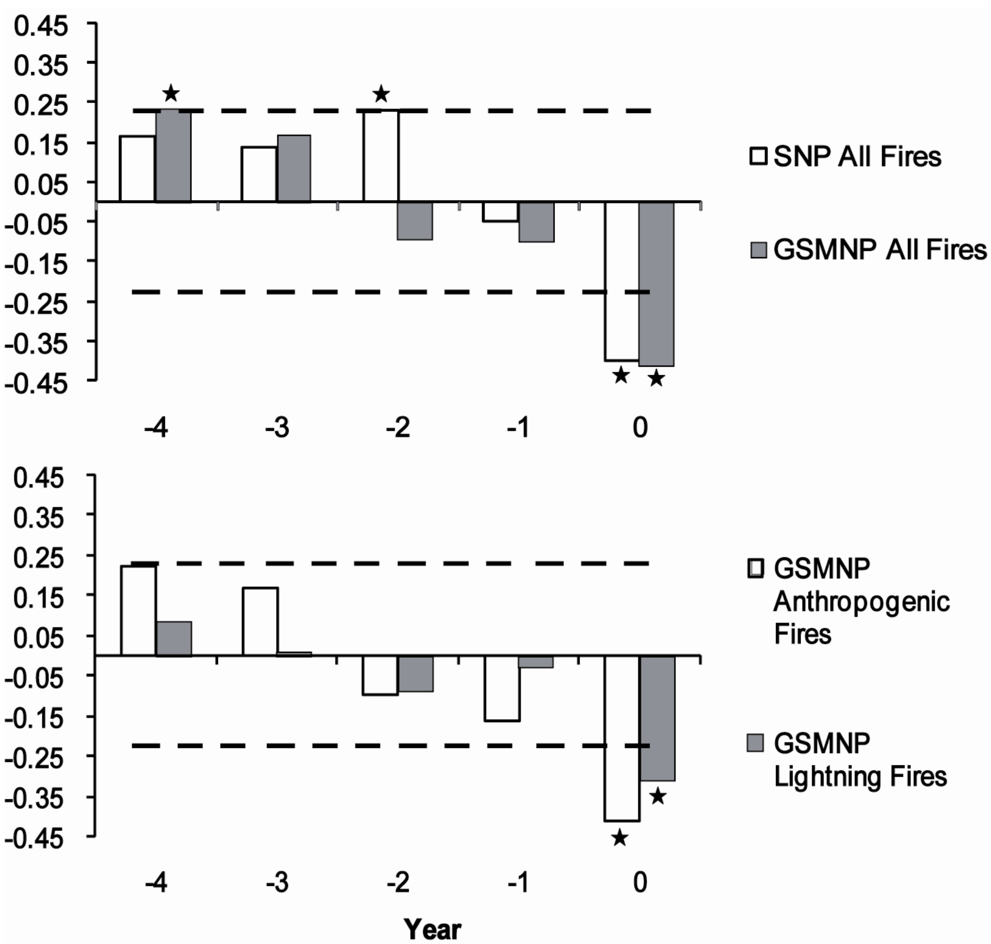

Figure 4.3 Correlation of log annual area burned with average annual Palmer Drought Severity Index for actual year and previous four years. The dashed lines are confidence intervals ($p < 0.05$) and stars indicate years with a significant correlation.

Fire-topography Relationships

Research Question: Does topography impose local-scale pattern on the occurrence of fire, with fire occurring most frequently in both study sites on dry south-facing slopes, ridgetops, and at low elevations?

The expected pattern emerged for all fires at GSMNP (Figures 4.4-4.6), with fire occurring most frequently on south-facing slopes, ridgetops, and at low elevations. However, the patter was strong only for elevation (Table 4.2, top row). At SNP, elevation showed a modest relationship with fire (Figure 4.6) while aspect showed a weak tendency for burning to occur on north-facing slopes (Figure 4.4). All three topographic variables were more strongly related to fire occurrence in GSMNP than SNP (Table 4.2).

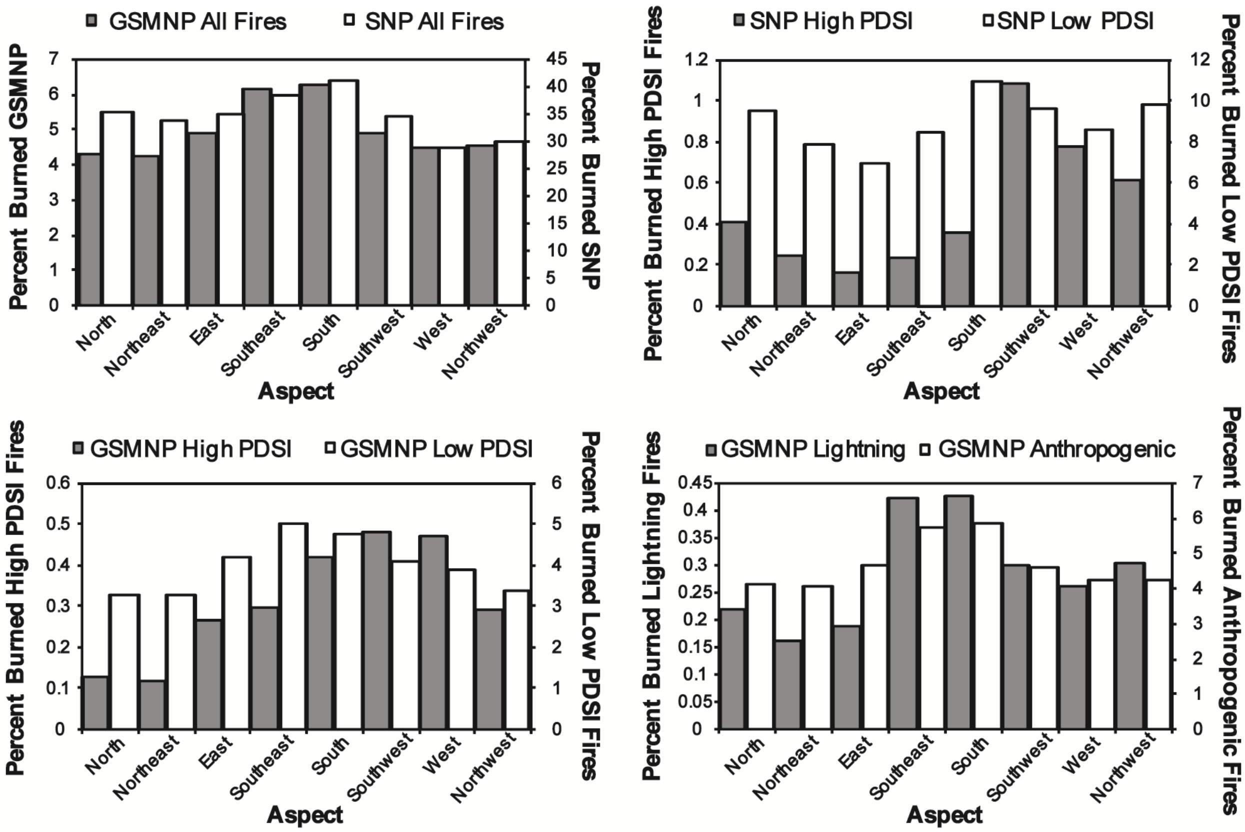

Figure 4.4 Percent of total area in aspect categories that burned. Note that two y-axes with separate scales were used for each graph.

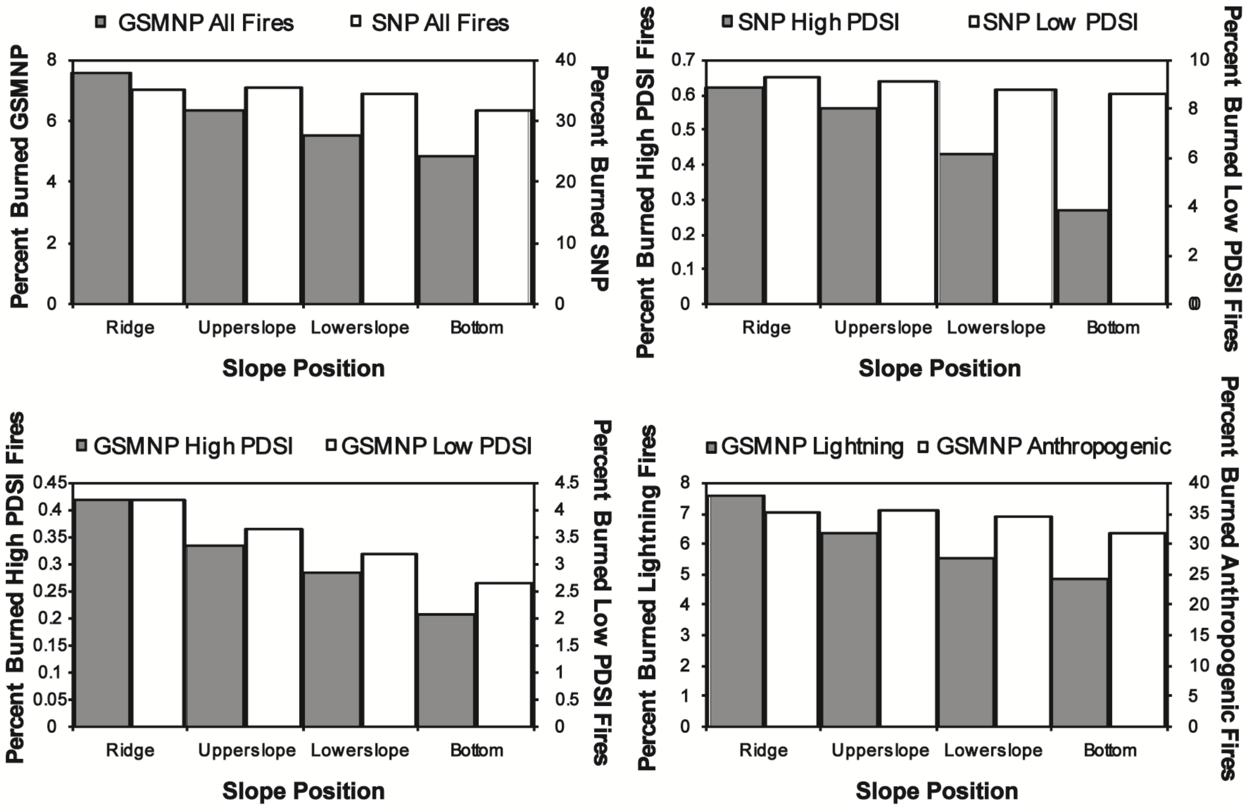

Figure 4.5 Percent of total area in slope position categories that burned. Note that two y-axes with separate scales were used for each graph.

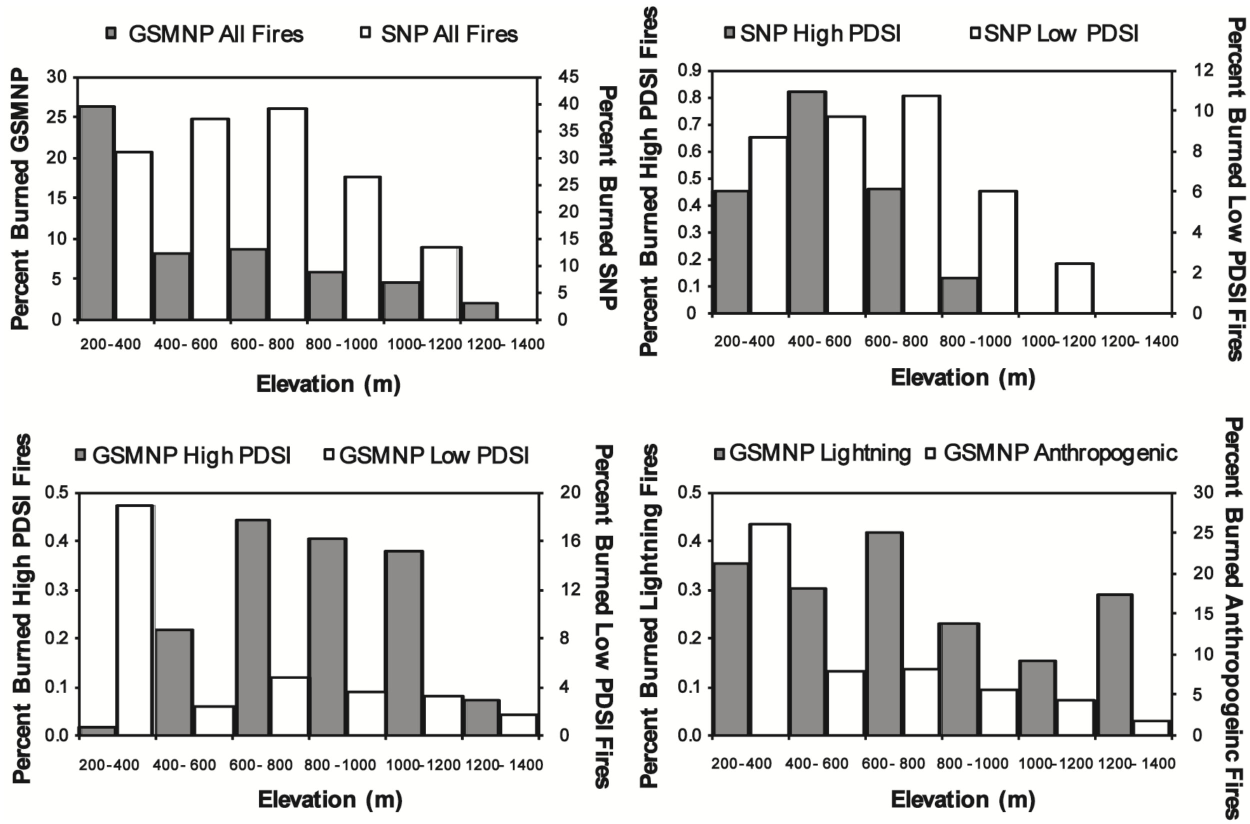

Figure 4.6 Percent of total area in elevation categories that burned. Note that two y-axes with separate scales were used for each graph.

Table 4.2 Cramer's V coefficients from log-likelihood tests on distribution of area burned across different topographic classes for different fire types. Values greater ≥ 0.3 (indicating strong trend) are shown in bold.

	Aspect	Slope Position	Elevation
GSMNP All Fires	0.15	0.15	**0.57**
SNP All Fires	0.11	0.04	0.19
GSMNP High PDSI Fires	**0.42**	0.22	**0.47**
GSMNP Low PDSI Fires	0.16	0.15	**0.62**
SNP High PDSI Fires	**0.60**	0.26	**0.54**
SNP Low PDSI Fires	0.13	0.03	0.24
GSMNP Lightning Fires	**0.32**	**0.44**	**0.33**
GSMNP Anthropogenic Fires	0.14	0.14	**0.59**

Climate-topography Interaction

Research Questions: First, do regional climate and local topography interact such that topographic patterns of fire are more pronounced in a less fire-prone landscape than a more fire-prone landscape? Therefore, are fires more strongly confined to dry topographic settings in the relatively wet GSMNP than in the drier SNP? Second, is the fire-topography association also influenced by temporal climatic variability? Does topography exert a stronger influence on fire occurrence during wet years than dry years in both national parks? Additionally, are lightning-ignited fires more strongly confined to dry topographic settings than anthropogenic fires, which often are ignited during dry, windy weather?

Fire was more strongly related to all three topographic variables during high-PDSI (wet) years than low-PDSI (dry) years except in the case of elevation at GSMNP (Table 4.2; Figures 4.4-4.6). Generally, wet-year fires showed a more pronounced preference for south- or west-facing slopes, ridgetops and upper slopes, and moderate and low elevations. In dry years, burning extended more broadly over the terrain and into zones (e.g., high elevations) where fire was uncommon during wet years. Also, lightning-ignited fires at GSMNP had stronger aspect and slope position patterns, but not elevational patterns, than anthropogenic fires (Table 4.2; Figures 4.4-4.6). Lightning fires accounted for smaller mean annual fire density (Mann-Whitney test, $U = 605.5$, $n_1 = n_2 = 72$, $p < 0.05$), and mean annual area burned in the park (Mann-Whitney test, $U = 961$, $n_1 = n_2 = 72$, $p < 0.05$), and exhibited a much longer fire cycle (Table 4.1). Both anthropogenic and lightning fires were significantly correlated with PDSI in the year of the fire, but lightning fires were less strongly correlated (Figure 4.3).

The CART model identified elevation, slope position, and aspect as determinant variables (burn ~ elevation + slope position + pdsi + aspect). Optimal recursive shrinking identified trees with 15 nodes and an acceptable level of misclassification error for both parks (GSMNP = 0.35, SNP = 0.36; Figure 4.7). Elevation was the primary determinant of fire, with areas below 800 m (the boundary between elevation categories 4 and 5) burning in SNP. In GSMNP, areas below 1200 m (boundary between elevation categories 6 and 7) were the most fire prone. Above 1200 m in GSMNP fires were confined to ridges (slope position 1) during dry years. Slope position and PDSI were determining variables at lower elevation within both parks, with dry slope positions and dry aspects burning most frequently. Aspect was the least important topographic variable within the models.

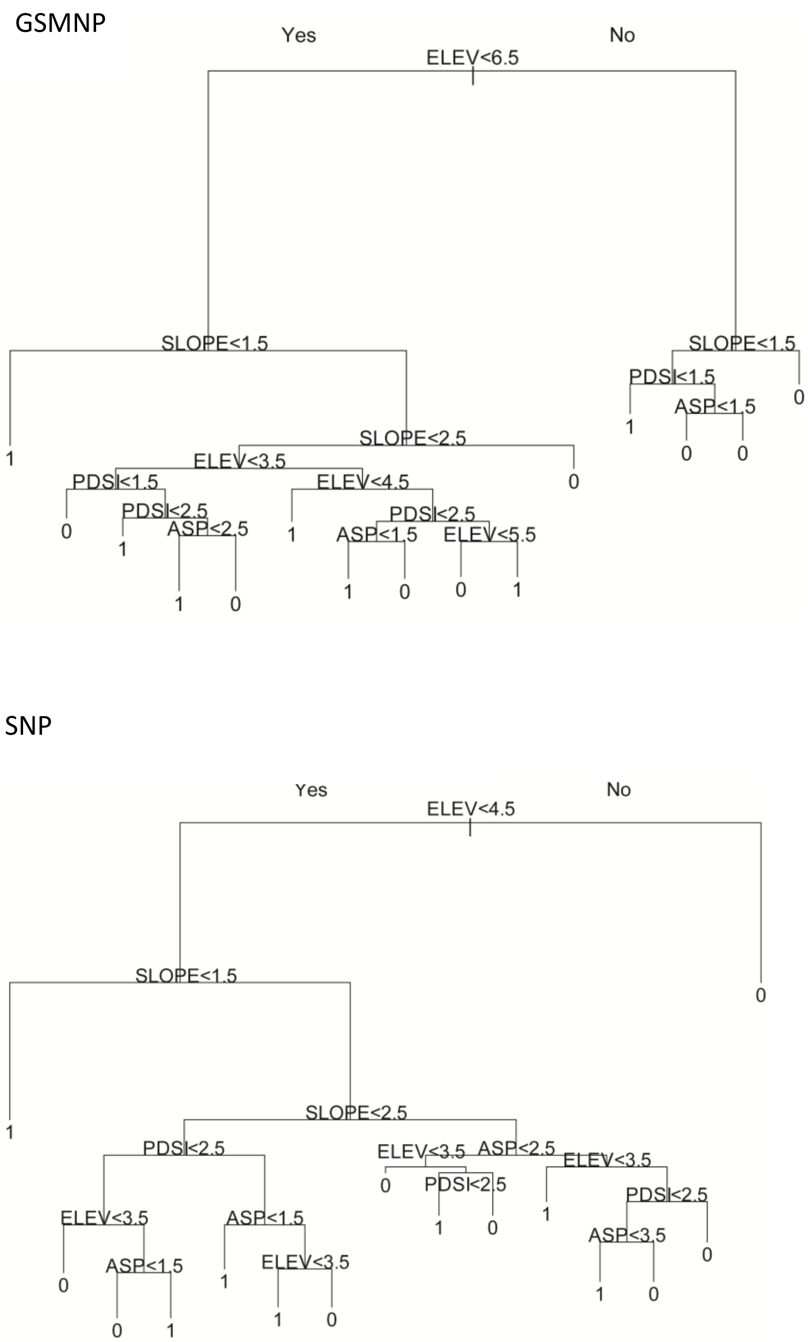

Figure 4.7 Pruned classification tree model (CART) predicting fire occurence as a product of elevation, slope position, aspect, and palmer drought severity index. The classifications are burn (1) and no burn (0).

Fire History

Fire history reconstructions for this study were developed from cross-sections and remnant wood from 244 individual trees at three separate sites. I was able to date 1078 scars, recording a total of 158 fire years. The length of the chronologies ranged from 265 to 308 years (Table 4.3).

Table 4.3 Summary of data for fire history reconstruction sites.

Site	Length of Chronology (years)	Number of Specimens	Number of Scars	Number of Fire Dates	Inner Ring	Outer Ring	First Fire Scar	Last Fire Scar
House Mountain	265	82	273	81	1742	2007	1763	1968
Licklog Ridge	285	104	543	78	1723	2008	1729	1935
Linville Mountain	308	45	167	50	1701	2009	1725	1950
Total		244	1078	158				

Fire Frequency

Research Question: How frequently did fires occur on southern Appalachian Mountain slopes during the last three centuries?

Fire charts at each site demonstrate a regime of frequent fire from the beginning of the chronology until the onset of fire suppression during the early- to mid- 20th century, depending on the site (Figures 4.8-4.13). Many of these fires scarred multiple trees and a number of widespread fires scarred trees in each of the stands at a site (Figure 4.14). During twelve regional fire years, scars were recorded at all three sites (Figure 4.15). Point mean fire intervals at the individual sites ranged from 9.1-14.3 years, mean composite fire intervals were 2.2-4.0 years, , and area-wide mean fire intervals were 6.2-9.8 years (Tables 4.4-4.6). The mean fire return interval for regional fires was 12.4 years (Table 4.7).

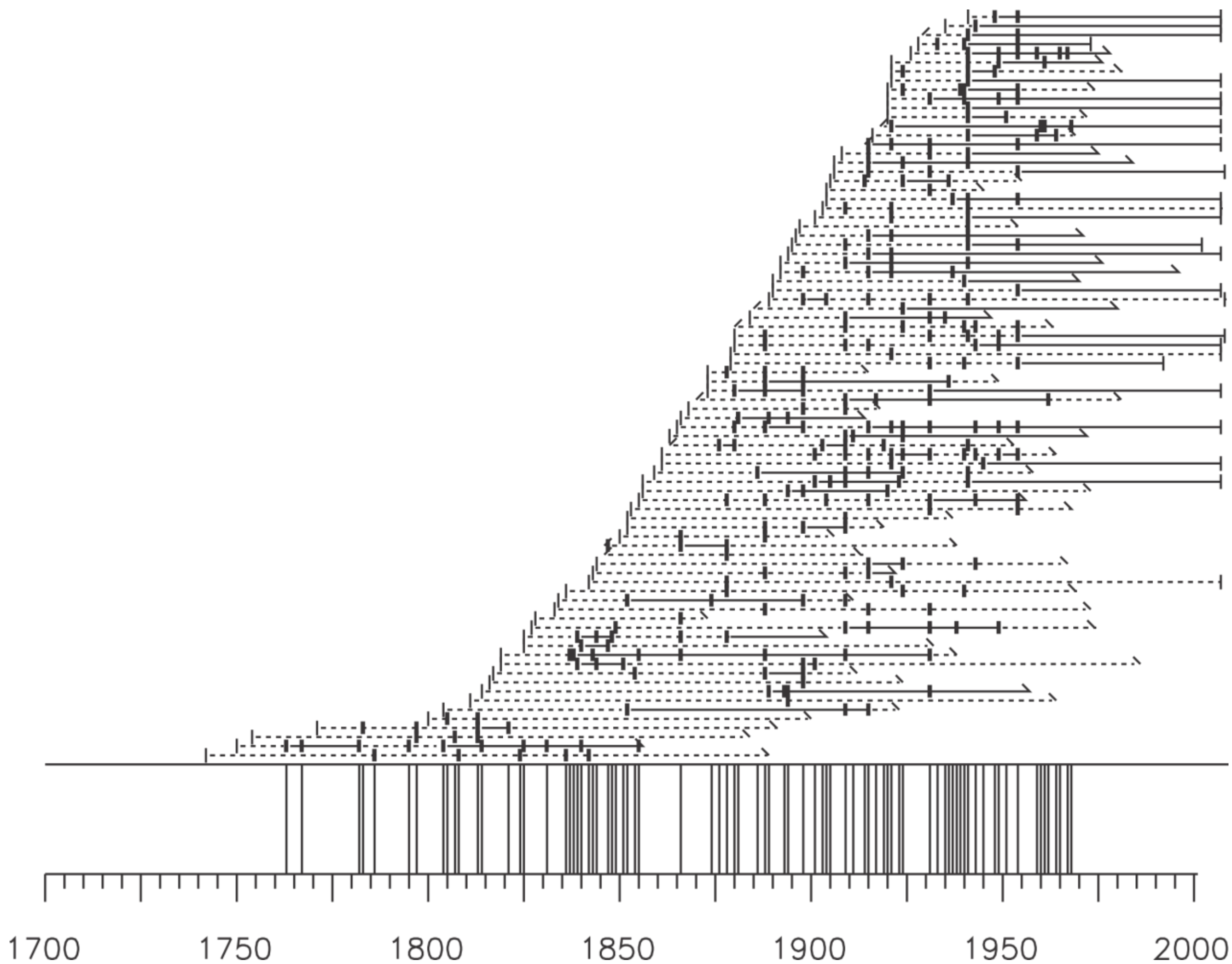

Figure 4.8 Unfiltered fire chronology for House Mountain, TN showing the dated fire scars for each tree specimen, 1742-2007. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all specimens combined.

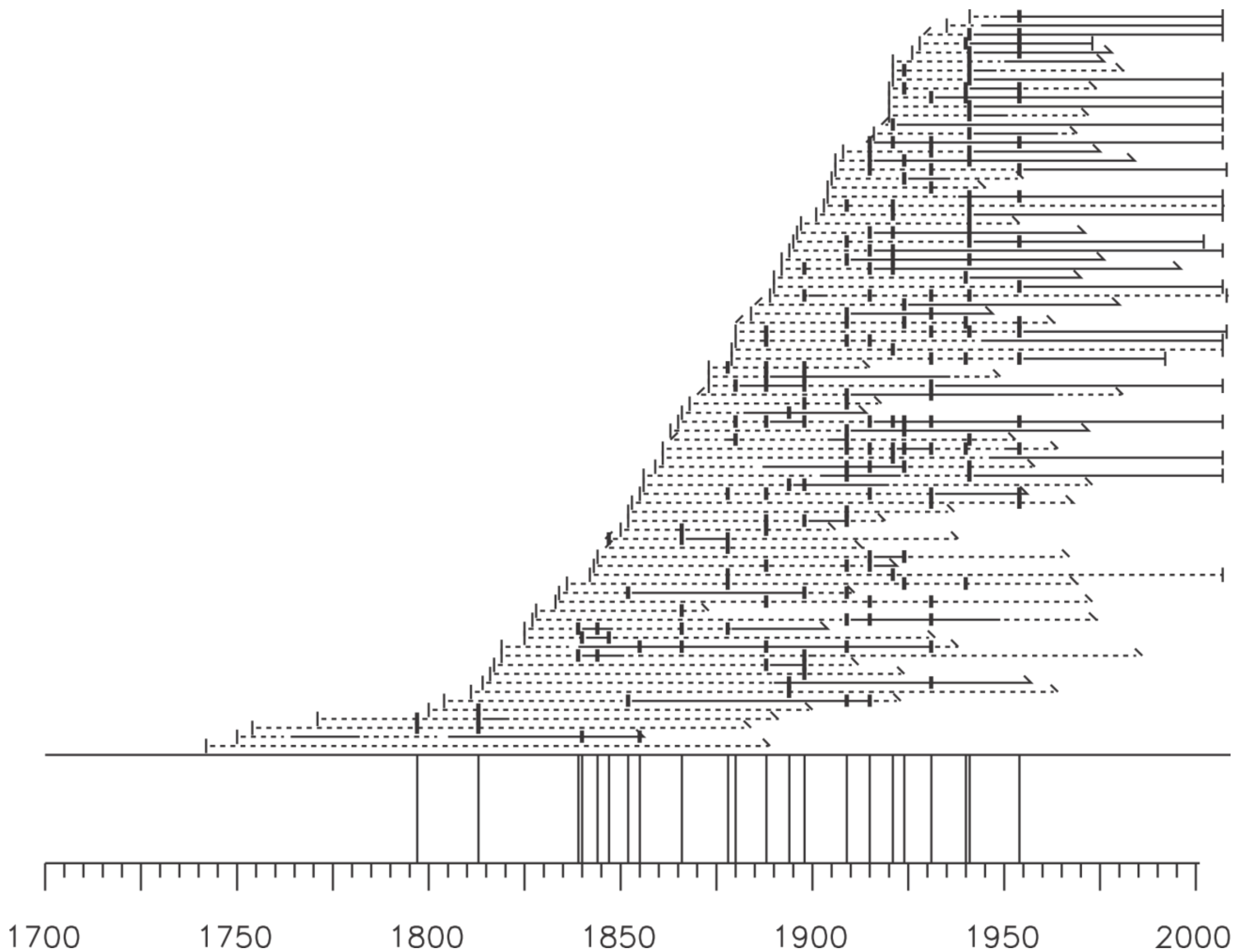

Figure 4.9 Filtered fire chronology for House Mountain, TN, 1742-2007. Filtered fire chronology includes only "major" fires which were recorded by at least 2 specimens and on ≥ 25% of specimens recording during fire year. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all specimens combined.

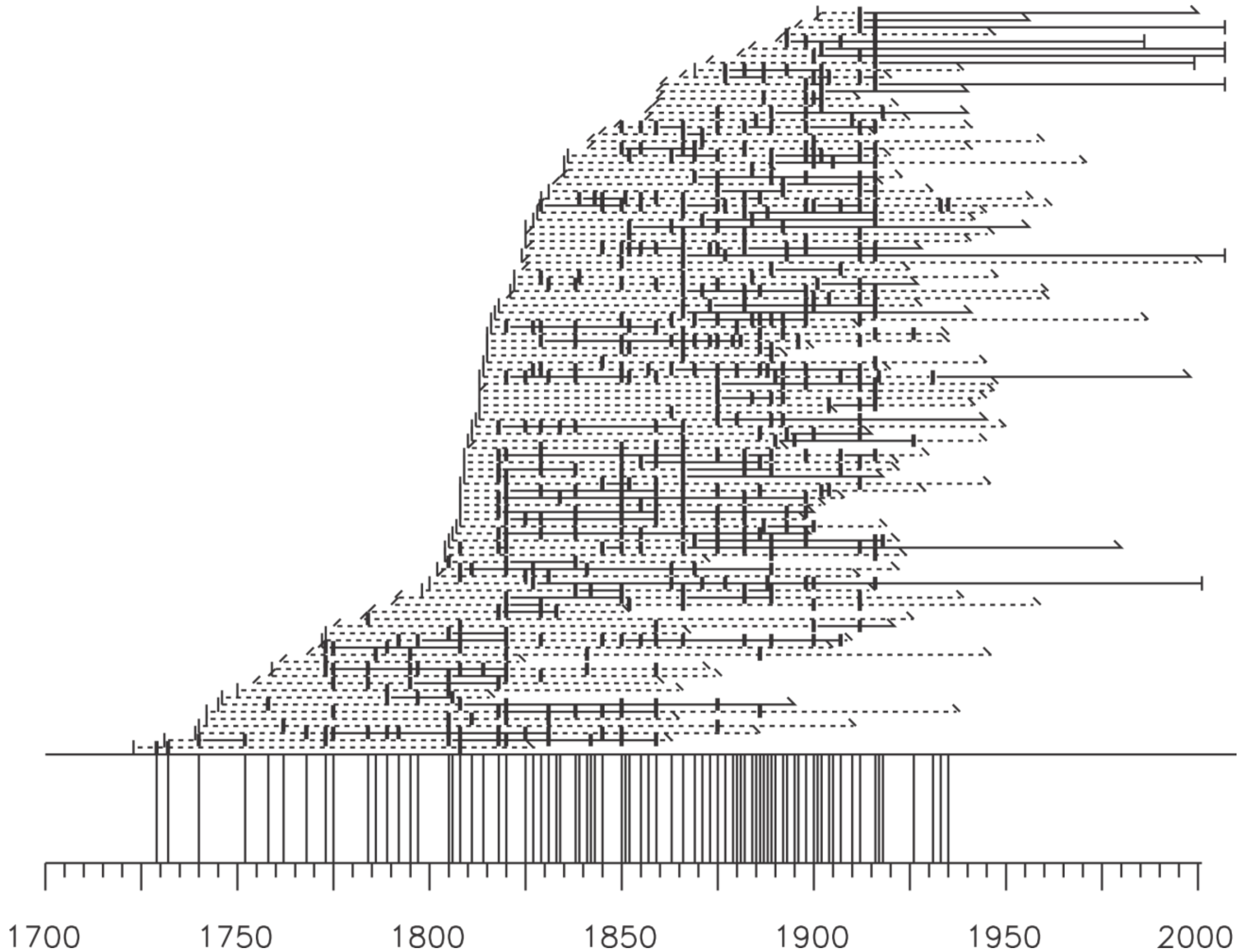

Figure 4.10 Unfiltered fire chronology chart for Licklog Ridge, TN showing the dated fire scars for each tree specimen, 1723-2008. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all speciments combined.

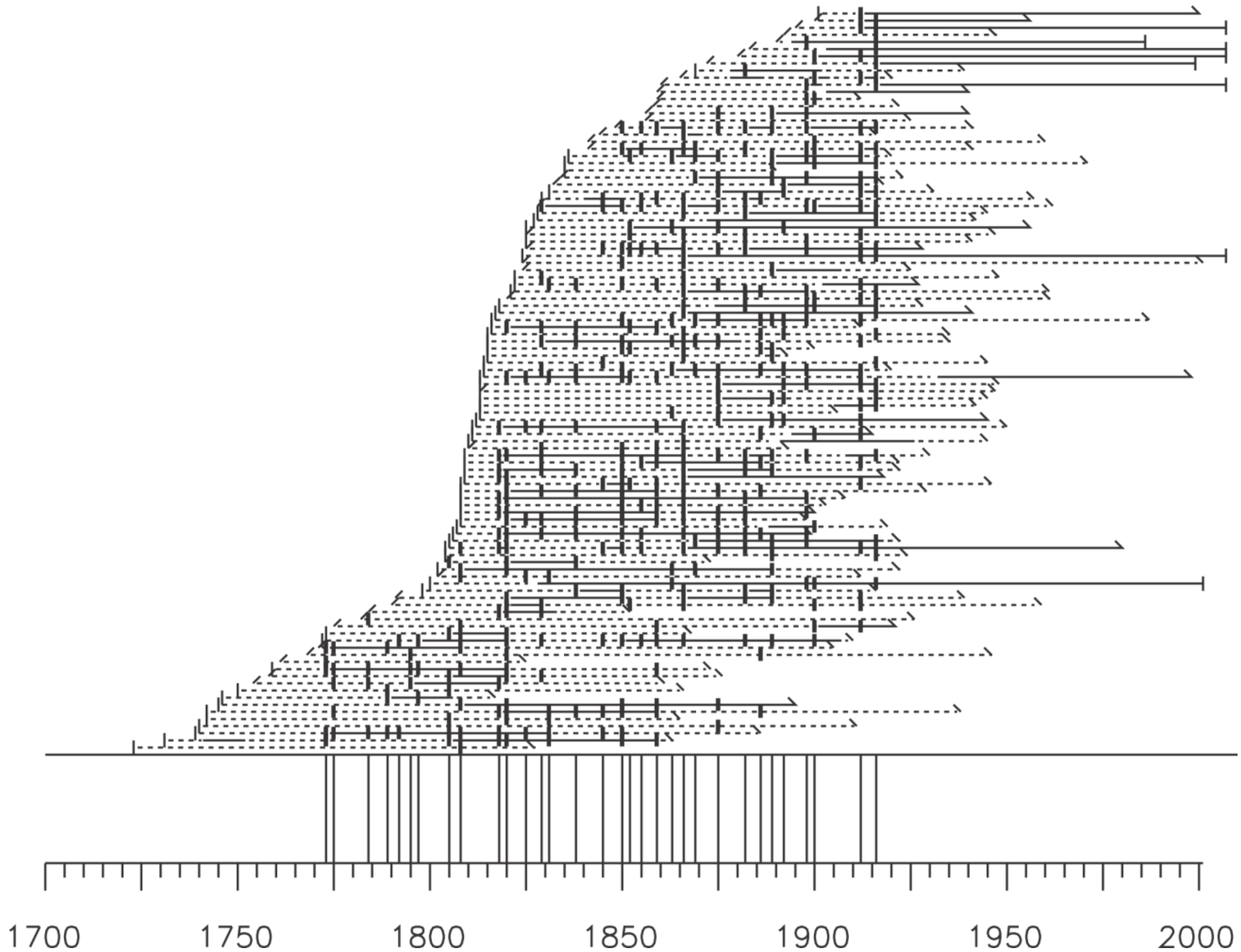

Figure 4.11 Filtered fire chronology for Licklog Ridge, TN, 1723-2008. Filtered fire chronology includes only “major” fires which were recorded by at least 2 specimens and on ≥ 25% of specimens recording during fire year. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all samples combined.

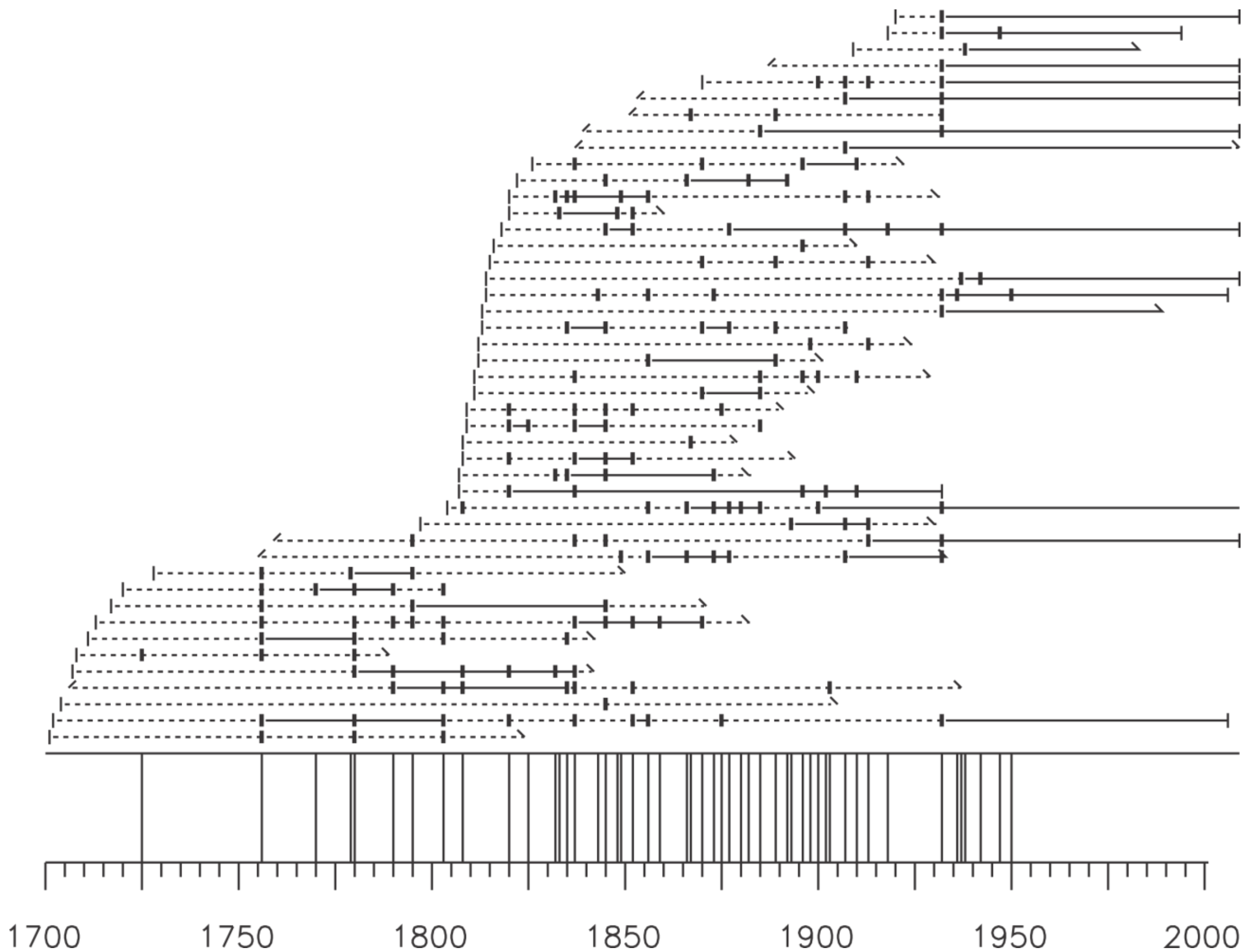

Figure 4.12 Unfiltered fire chronology chart for Linville Mountain, NC showing the dated fire scars for each tree specimen, 1701-2009. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all specimens combined.

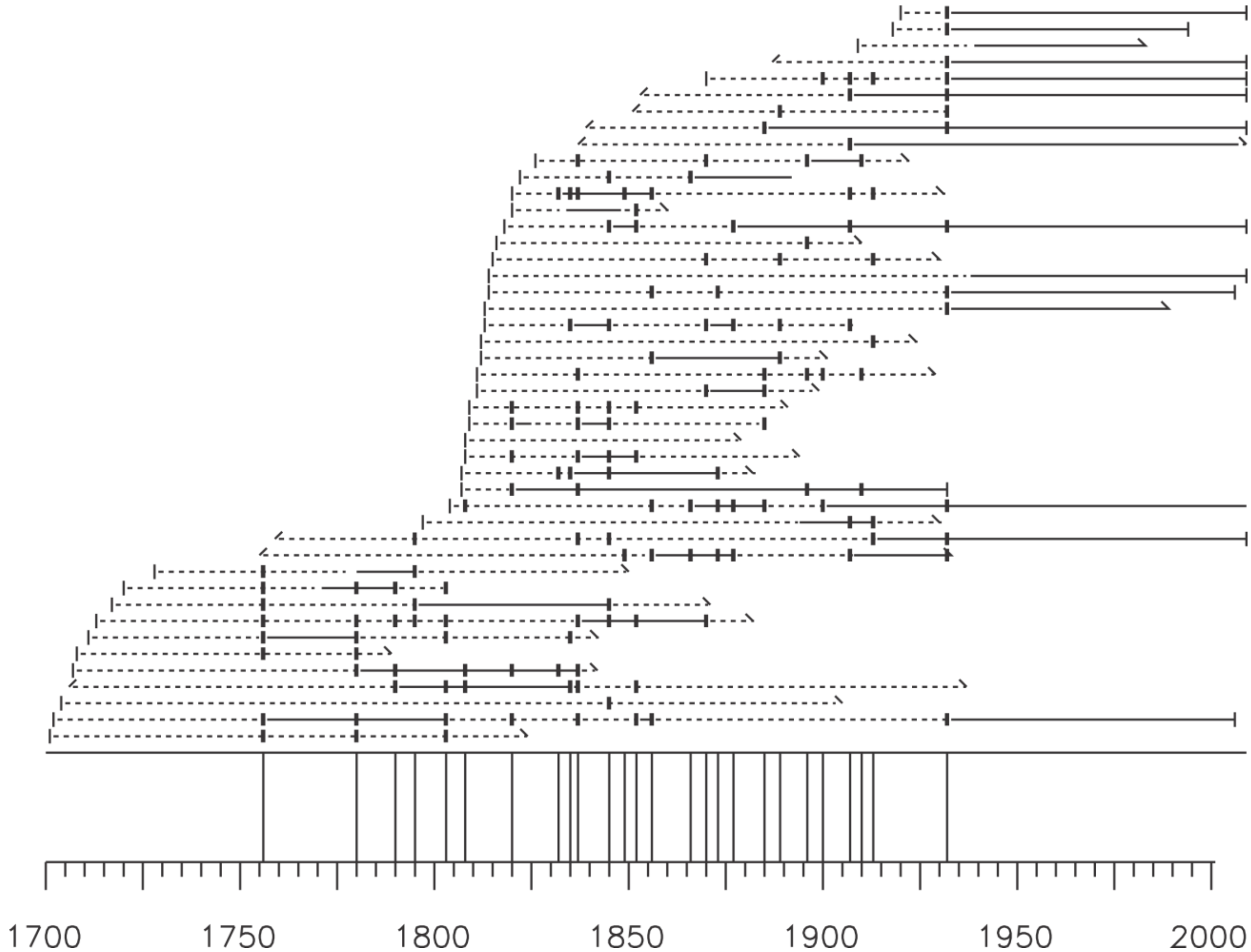

Figure 4.13 Filtered fire chronology for Linville Mountain, NC, 1701-2009. Filtered fire chronology includes only “major” fires which were recorded by at least 2 specimens and on ≥ 25% of specimens recording during fire year. Horizontal lines indicate the time spanned by each tree specimen with dotted lines indicating non-recording intervals and solid lines indicating recording intervals. Short vertical bars represent dated fire scars. Long vertical bars at the bottom of the chart depict fire years from all specimens combined.

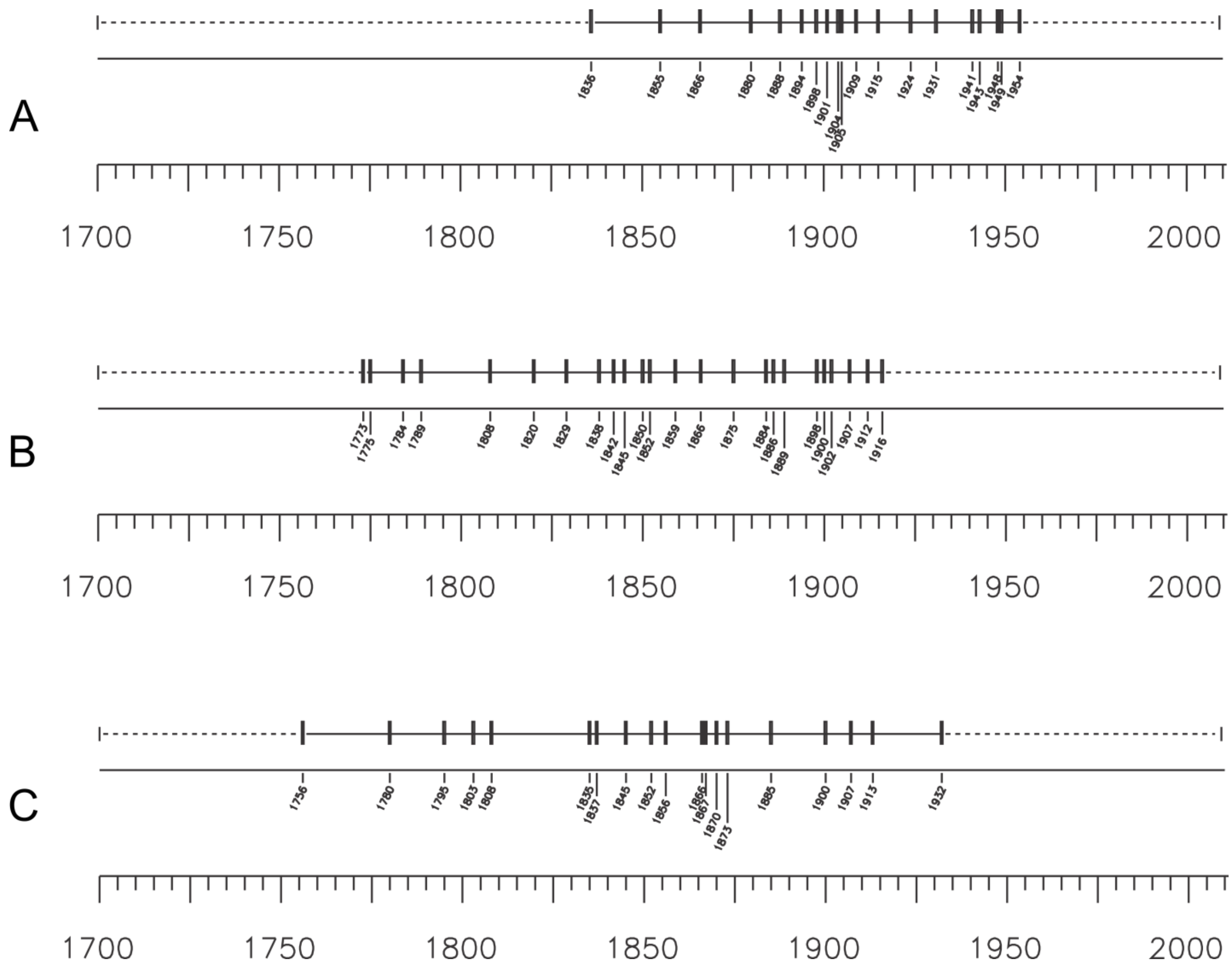

Figure 4.14 Area-wide fire records for (A) House Mountain, TN; (B) Licklog Ridge, TN; and (C) Linville Mountain, NC. Area-wide fires were recorded in all stands at a single site, if the year of the fire was a recorded year in all stands. If fire year was a recorder year in only two or three stands, an area-wide fire was one that scarred trees in all of those stands.

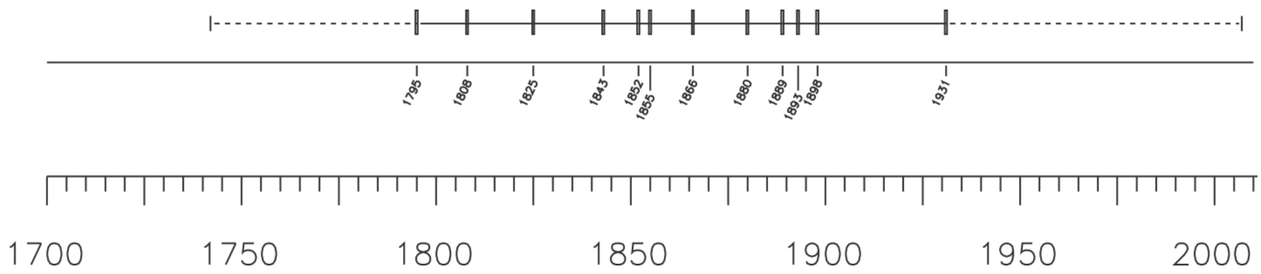

Figure 4.15 Regional fire record depicting years in which fires were recorded at all three fire history sites, 1742-2007.

Table 4.4 Fire interval calculations for House Mountain, TN. Abreviations: MFI = mean fire interval, WMI = weibull median interval, SD = standard deviation, LEI = lower exceedance interval, UEI = upper exceedance interval.

House Mountain (n = 82)	MFI	WMI	SD	LEI	UEI	Range	Number of intervals	Years covered
Point fire interval	9.7	8.1	8.8	2.4	18.6	1-57	53	1763-1920
Composite fire interval	2.6	2.1	2.2	0.6	4.9	1-11	48	1797-1920
Filtered composite fire interval	7.9	6.5	6.6	1.9	14.9	1-26	15	1797-1920
Area-wide fire interval	7.2	6.2	5.5	2.0	13.2	1-19	11	1836-1920

Table 4.5 Fire interval calculations for Licklog Ridge, TN. Abreviations: MFI = mean fire interval, WMI = weibull median interval, SD = standard deviation, LEI = lower exceedance interval, UEI = upper exceedance interval.

Licklog Ridge (n = 104)	MFI	WMI	SD	LEI	UEI	Range	Number of intervals	Years covered
Point fire interval	9.1	8.1	6.3	2.8	16.2	2-50	275	1729-1920
Composite fire interval	2.2	2.0	1.5	0.7	3.9	1-9	66	1773-1920
Filtered composite fire interval	4.6	4.4	2.6	1.9	7.6	2-12	31	1773-1920
Area-wide fire interval	6.2	5.6	4.1	2.1	10.9	2-19	23	1773-1920

Table 4.6 Fire interval calculations for Linville Mountain, NC. Abreviations: MFI = mean fire interval, WMI = weibull median interval, SD = standard deviation, LEI = lower exceedance interval, UEI = upper exceedance interval.

Linville Mountain (n = 45)	MFI	WMI	SD	LEI	UEI	Range	Number of intervals	Years covered
Point fire interval	13.1	11.1	11.1	3.3	24.7	2-59	53	1725-1920
Composite fire interval	4.0	3.4	3.0	1.1	7.3	1-14	41	1756-1920
Filtered composite fire interval	6.5	5.8	4.8	2.1	11.7	2-24	24	1756-1920
Area-wide fire interval	9.2	7.7	7.4	2.3	17.4	1-27	17	1756-1920

Table 4.7 Fire interval calculations for regional fires recorded at all three sites. Abreviations: MFI = mean fire interval, WMI = weibull median interval, SD = standard deviation, LEI = lower exceedance interval, UEI = upper exceedance interval.

	MFI	WMI	SD	LEI	UEI	Range	Number of intervals	Years covered
Regional fire interval	10.3	9.9	5.3	4.7	16.2	3-18	10	1795-1920

Pith dates from the fire scarred cross-sections indicated that yellow pines were present at each of the sites at least as early as the mid- 1700's (Figure 4.16). Yellow pine establishment was relatively continuous throughout the record at House Mountain. Pulses of yellow pine establishment occurred at Licklog Ridge from 1800-1820 and at Linville Mountain from 1800-1810. Linville Mountain may also have experienced a pulse of yellow pine establishment during the earliest portion of the record from 1700-1730.

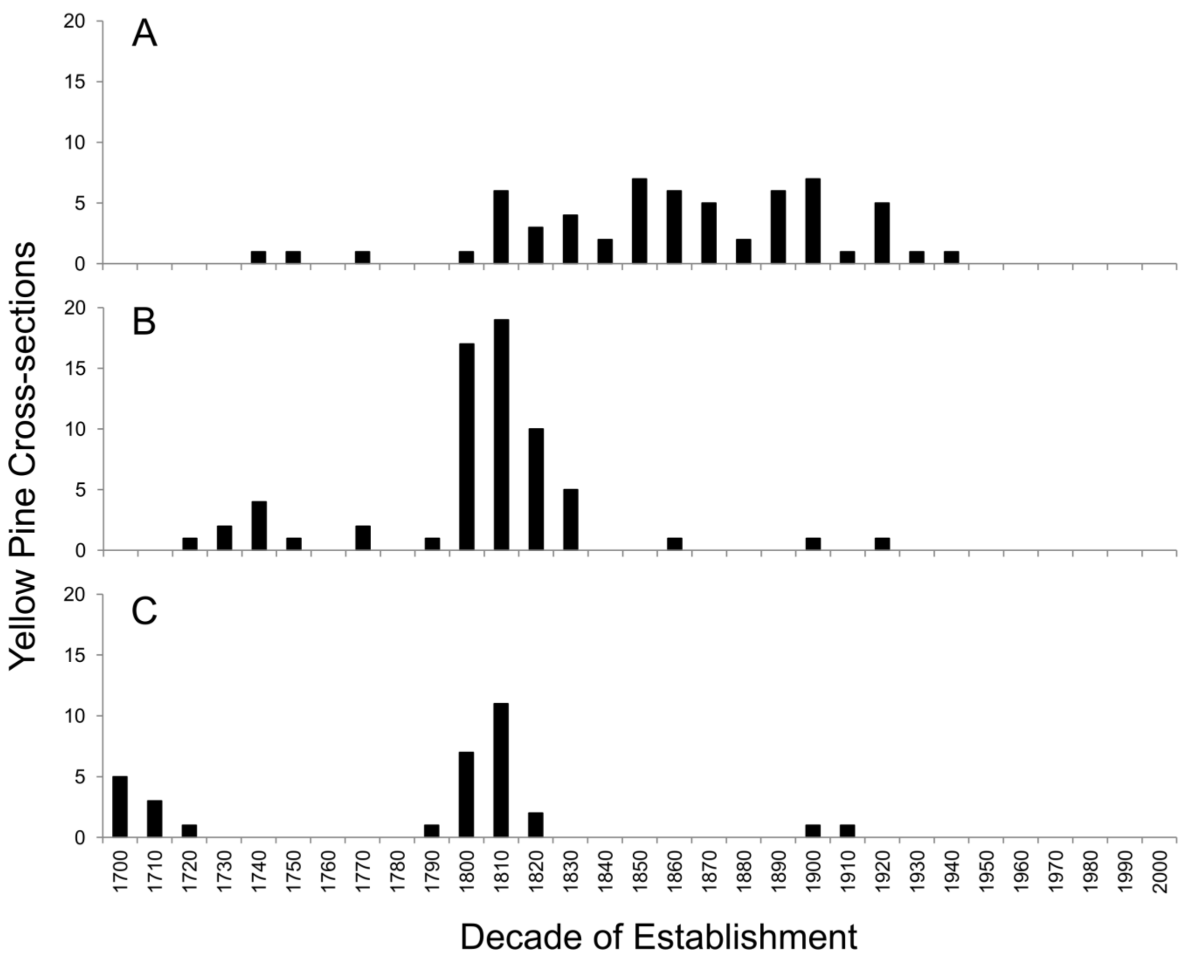

Figure 4.16 Decade of establishment for fire-scarred yellow pine cross-sections at (A) House Mountain, (B) Licklog Ridge, and (C) Linville Mountain.

Seasonality was determined for 75.7% of fire scars from all three sites. Fire scars for which seasonality could be determined were primarily dormant season (83.8%), indicating that the fires could have burned during the late fall, winter, or early spring. The remainder of scars occurred during the early growing season (13.8%) or mid- to late-growing season (2.3%).

Table 4.8 Seasonality of fire scars at each fire history site. Seasonal designations include: (1) dormant, occurring between the latewood of one ring and the earlywood of the next (2) early, occurring within the first third of the earlywood, (3) middle, occurring within the second or last third of the earlywood, (4) late, occurring in the latewood band and (5) undetermined, seasonality of scar cannot be determined.

Site	% With Seasonality	% Seasonality Undetermined	% Dormant Season	% Early Season	% Late Season
House Mountain	78.5	21.5	59.1	18.6	0.7
Licklog Ridge	74.7	25.3	67.6	6.7	0.3
Linville Mountain	74.6	25.4	56.1	18.5	0

Temporal Variations in Fire Activity

Research Question: Did cultural changes or land use intensification alter fire frequency?

Fires burned regularly at all three sites during each of the land use periods, except the most recent fire protection period (Figure 4.17). Kruskal-Wallis *H*-tests indicated that the mean number of fire scars per recording tree per decade differed between land use periods at each of the three sites (House Mountain $H = 7.63$, $p = 0.02$; Licklog Ridge $H = 16.90$, $p = 0.001$; Linville Mountain $H = 8.96$, $p = 0.03$). Post-hoc comparisons indicated that the significantly different periods depended on the site (Table 4.9).

Table 4.9 Mean fire scars per recording tree per decade for each of the land use periods. For each site, values with same letter were not significantly different from each other according to post hoc comparisons ($\alpha < 0.05$).

Site	Native American Period	Euro-American Settlement Period	Industrial Period	Fire Protection Period
House Mountain	--	1.00^{a}	0.91^{ab}	0.43^{b}
Licklog Ridge	1.05^{a}	1.10^{a}	1.05^{a}	0.03^{b}
Linville Mountain	0.67^{ab}	0.82^{a}	0.82^{ab}	0.14^{b}

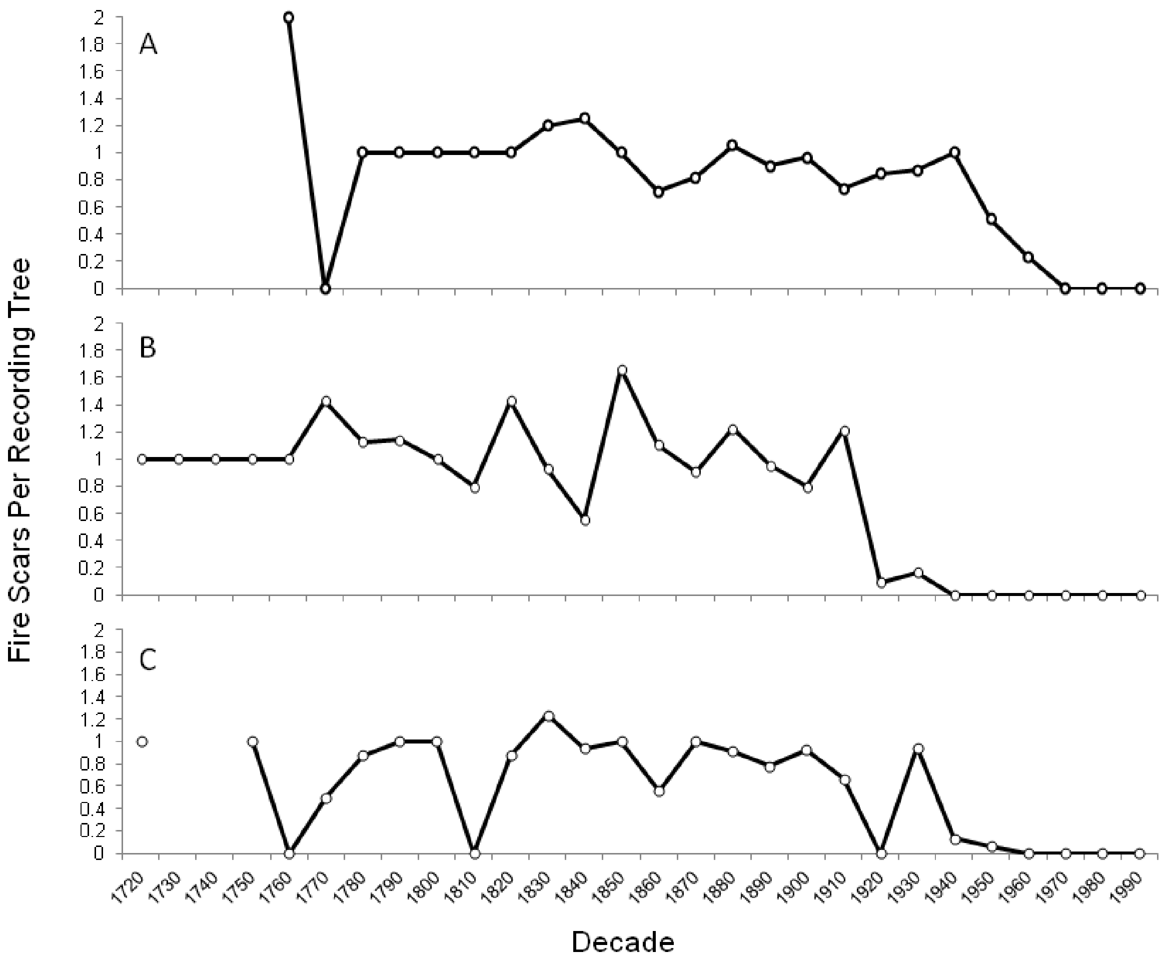

Figure 4.17 Temporal trend in fire activity, as indicated by number of scars per recording tree by decade for each of the fire history sites; (A) House Mountain, (B) Licklog Ridge, (C) Linville Mountain. Missing values indicate an absence of recording trees during corresponding decades.

Fire-climate Relationships

Research Question: How did interannual climatic variability influence the occurrence of fire?

No consistent relationships were found between fire and drought at any of the three sites or during regional fire years (Figure 4.18 - 4.21). The only significant relationship was negative PDSI values during the year of the fire (t=0) in the analysis of major fire years burning during the dormant season at House Mountain. SEA revealed no other significant relationships between fire years and moisture conditions for any of the fire type or seasons across the three sites or during regional fire years. There also were no significant lag effects from moisture conditions in years preceding fire years.

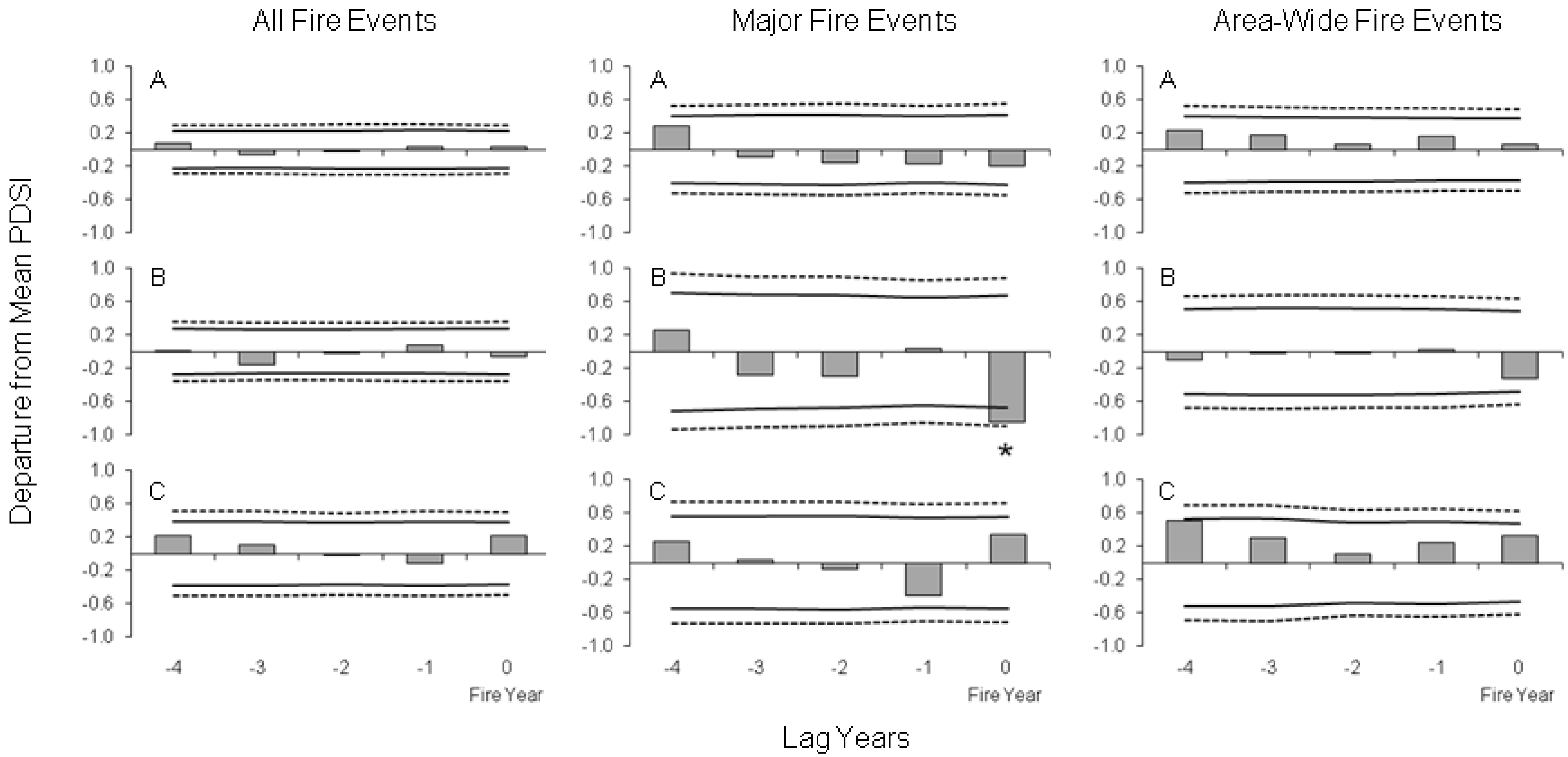

Figure 4.18 Superposed epoch analysis for House Mountain fire record comparing PDSI during fire years to average PDSI conditions throughout the record. Analysis was carried out on all fire events, major fire events, and area-wide fire events. Fire event types are further subdivided by seasonality: (A) all seasons, (B) dormant season and (C) growing season. Asterisk indicates a significant relationship ($p < 0.05$). Solid lines represent significance at the $p < 0.05$ threshold and dashed lines represents significance at the $p < 0.01$ threshold.

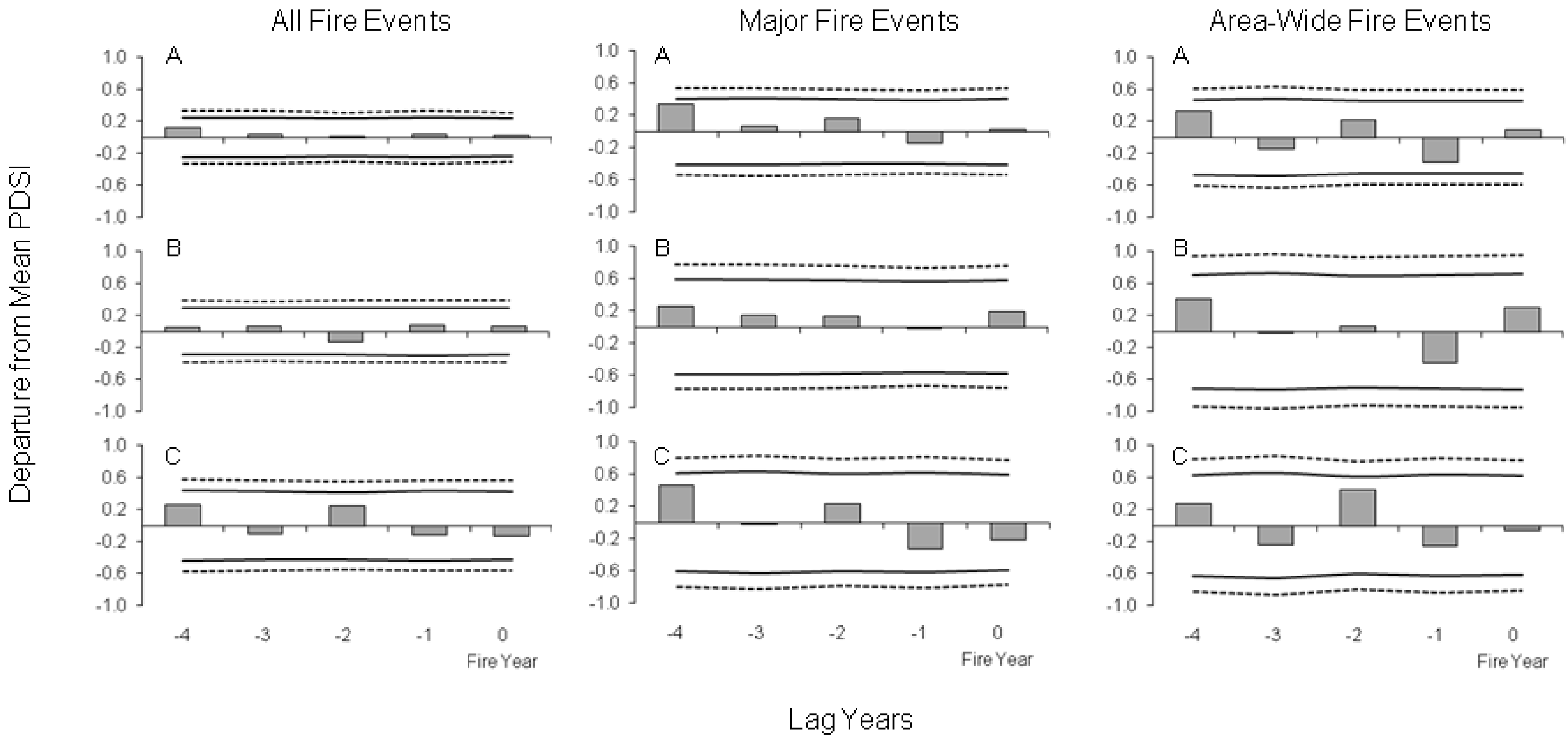

Figure 4.19 Superposed epoch analysis for Licklog Ridge fire record comparing PDSI during fire years to average PDSI conditions throughout the record for all fire events, major fire events, and area-wide fire events. Fire event types are further subdivided by seasonality: (A) all seasons, (B) dormant season and (C) growing season. Asterisk indicates a significant relationship ($p < 0.05$). Solid lines represent significance at the $p < 0.05$ threshold and dashed lines represents significance at the $p < 0.01$ threshold.

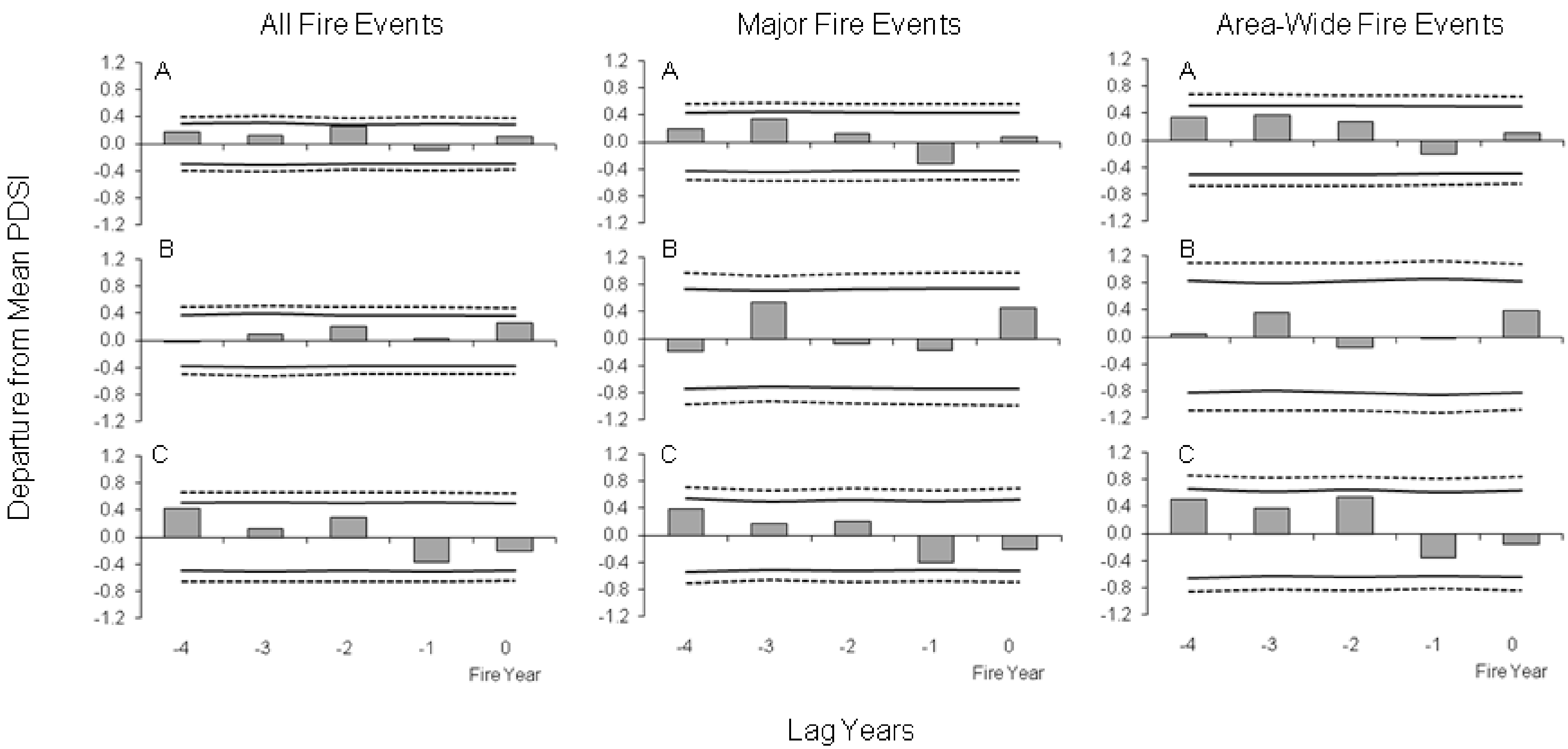

Figure 4.20 Superposed epoch analysis for Linville Mountain fire record comparing PDSI during fire years to average PDSI conditions throughout the record for all fire events, major fire events, and area-wide fire events. Fire event types are further subdivided by seasonality: (A) all seasons, (B) dormant season and (C) growing season. Asterisk indicates a significant relationship ($p < 0.05$). Solid lines represent significance at the $p < 0.05$ threshold and dashed lines represents significance at the $p < 0.01$ threshold.

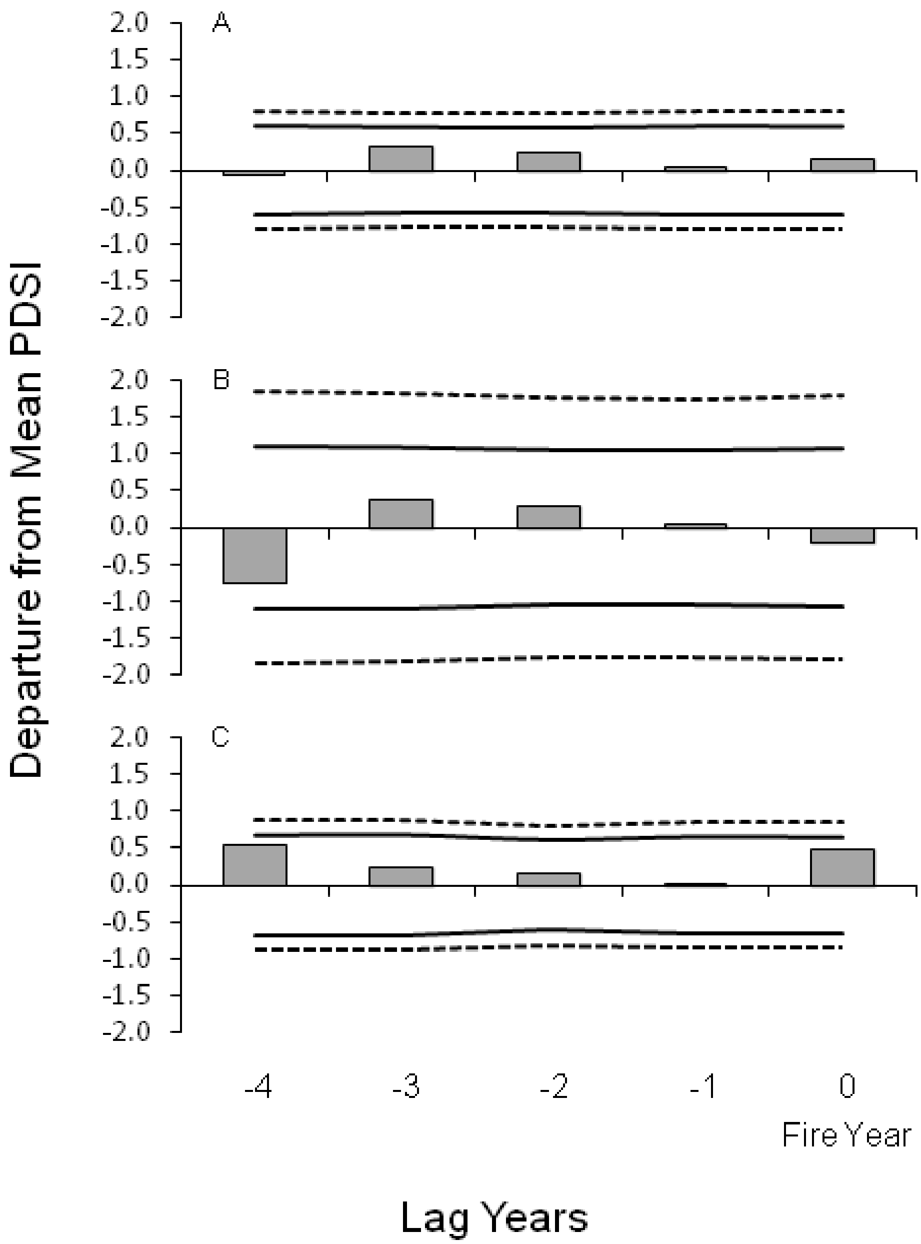

Figure 4.21 Superposed epoch analysis for regional fire record comparing PDSI during fire years to average PDSI conditions throughout the record. Regional fire years are subdivided by seasonality: (A) all seasons, (B) dormant season and (C) growing season. Asterisk indicates a significant relationship ($p < 0.05$). Solid lines represent significance at the $p < 0.05$ threshold and dashed lines represents significance at the $p < 0.01$ threshold.

Vegetation Dynamics

Research Question: Do variations in species composition between different age classes relate to fire suppression in mesic as well as xeric forest communities?

Pine Stands

The pine stands were heavily dominated by Table Mountain pine with additional components of scarlet oak, pitch pine and black gum (Table 4.10). Pine stands had the lowest total basal area and highest tree density among the five stand types (Table 4.11). Total sapling and seedling density were also much higher in the pine stands than the other stand types (Table 4.12). Sourwood and red maple dominated the seedling and sapling layer. Table Mountain pine and pitch pine were poorly represented in the understory.

Few trees in the pine stands predated the last major fire. Nearly all of the yellow pines in the stand established during 1920-1950 (Figure 4.22). Only three of the pines, for which I was able to assign a pith date, established prior to this period. However, I was unable to assign pith dates to three additional large pines (dbh > 40 cm) due to rotten cores. Each of these large pines exhibited solid rings preceding the rotten section that predated 1920. Very few pines have established in the stands since 1950. Red oaks, maples and xeric hardwoods began establishing a decade earlier than the yellow pines from 1910-1920. Red oaks and xeric hardwoods peaked in establishment during the 1920s, while maples have established at a fairly constant rate since 1910. Hemlock establishment has increased during the latter part of the record.

Oak Stands

The oak stands were dominated by red maple and chestnut oak, with minor components of black gum, sourwood and white pine. Oak stands contained a high density of red maple stems. The sapling layer was dominated by black gum, red maple, hemlock, and sassafrass. Seedlings were heavily dominated by chestnut oak, however there was limited recruitment of oaks into the sapling layer.

The majority of older trees in the oak stands were chestnut oak (Figure 4.23). Several chestnut oak individuals established in the early 1700s and were some of the oldest trees on the site. Chestnut oak stems also established during 1810-1870 and during 1890-1940. I was unable to assign pith dates to eight additional large chestnut oak stems (dbh>40 cm), but each of them exhibited rings that predated the cessation of fires. Red maples dominated establishment from 1910-1940, following the last fire. Xeric hardwoods also peaked in establishment following the last fire from 1910-1950. A small number of red oaks and yellow pines established following the last fire. A similar pattern to the pine stands is apparent in which the yellow pines established a decade later than the hardwoods following the last fire. Establishment during recent decades has primarily consisted of white pine and hemlock. There has been no oak tree establishment since the 1940s.

White Pine-Hardwood Stands

White pine-hardwood stands were dominated by white pine, hemlock, and red maple. Basal area and tree density were the second highest of the different stand types. Hemlock had the highest sapling density and red maple was most frequent in the seedling layer.

The trees that established prior to fire suppression in the white pine-hardwood stands were a diverse mix of yellow pine, white oaks, red oaks and xeric hardwoods (Figure 4.24). A single large (dbh > 40 cm) red maple, white pine, and chestnut oak were too rotten to assign a pith date. The red maple and chestnut oak had rings that predated fire cessation. The rotten white pine did not have rings that predated fire cessation and likely established after fire suppression since all of the other white pines cored in this plot established after fire suppression. A pulse of maples and xeric hardwoods established in the stand following the last fires from 1910-1950. There was a sharp pulse of white pine establishment that occurred in the 1930s. Hemlock peaked in establishment from 1940-1970. A limited number of mesic hardwoods have begun to establish since 1930.

North Cove Stands

The north cove stands were strongly dominated by hemlock, with a secondary component of red maple and a minor component of sweet birch and sourwood. North cove stands exhibited the highest total basal area and the second lowest tree density. Sapling density was low, while seedling density was high. The most abundant sapling species were striped maple, hemlock, American holly, and yellow poplar. The seedling layer was heavily dominated by red maples and to a much lesser extent yellow poplar.

The north cove stands were primarily composed of hemlock individuals that established in a pulse that peaked in the 1930s (Figure 4.25). A mix of white oak, red oak, maples, xeric hardwoods, mesic hardwoods, and eastern hemlock predated fire suppression. Two red maples and a single yellow poplar, sourwood, white pine, and a northern red oak were large in diameter (dbh > 40 cm) but too rotten to assign a pith date. There has been very little recruitment of trees in these stands since 1970.

South Cove Stands

The south cove stands were also heavily dominated by hemlock, with a secondary component of sweet birch, and a minor component of yellow poplar, white basswood, and sugar maple. The south cove stands exhibited the lowest total tree density and the lowest total sapling density of the five stand types. The most abundant saplings were yellow buckeye, hemlock, and sugar maple. The vast majority of seedlings were red maple.

The south cove stands contained the highest proportion of trees that established prior to fire protection (Figure 4.26). Mesic hardwoods established in the 1700s and 1800s and hemlocks established sporadically during the 1800s. Two sugar maples and a single red maple, white basswood, and hemlock were large in diameter (dbh > 40 cm) but too rotten to assign a pith date. Both mesic hardwoods and hemlocks increased in establishment during the last century, and hemlock exhibited a pulse of establishment from 1930-1950. However, the number of stems established during this pulse in the south cove stands was much lower than the number established during the corresponding peak in the north cove stands (36 versus 132 trees respectively).

Table 4.10. Relative importance values of tree species in each stand type at Licklog Ridge, GSMNP, TN.

	Pine Stands	Oak Stands	White Pine-Hardwood Stands	North Cove Stands	South Cove Stands
	Relative Importance				
Acer pensylvanicum			0.2		
Acer rubrum	7.4	35.7	19.1	16.9	3.2
Acer saccharum					7.1
Aesculus octandra				0.3	0.9
Amelanchier Arborea	0.4	0.3	0.3		
Betula lenta			0.9	6.6	15.3
Carya glabra			0.4	3.2	
Carya ovate					2.2
Carya tomentosa					0.4
Fraxinus americana				0.2	
Halesia Carolina					1.2
Ilex opaca	0.1		0.1		2.2
Liriodendron tulipifera			0.5	4.2	8.3
Magnolia fraseri	0.9		0.8	0.6	1.0
Nyssa sylvatica	8.4	6.1	1.7	1.8	0.5
Oxydendrum arboreum	5.1	6.7	7.0	6.0	1.3
Pinus pungens	45.4				
Pinus rigida	9.5	1.9	0.8		
Pinus strobus	3.3	6.2	29.9	1.7	3.2
Quercus alba				0.3	0.7
Quercus coccinea	11.9	3.8	9.1	0.5	
Quercus montana	0.3	32.3	4.9	3.3	
Quercus rubra		0.8		4.7	0.4
Quercus velutina	0.3				1.6
Sassafras albidum	2.3	1.0	0.3		
Tilia heterophylla				8.3	
Tsuga canadensis		4.7	5.3	23.8	49.4

Table 4.11. Basal area and tree density for tree species in each stand type at Licklog Ridge, GSMNP, TN.

	Pine Stands		Oak Stands		White Pine-Hardwood Stands		North Cove Stands		South Cove Stands	
	Basal Area (m^2/ha)	Tree density (stems/ha)	Basal Area (m^2/ha)	Tree density (stems/ha)	Basal Area (m^2/ha)	Tree density (stems/ha)	Basal Area (m^2/ha)	Tree density (stems/ha)	Basal Area (m^2/ha)	Tree density (stems/ha)
Acer pensylvanicum						3.3				
Acer rubrum	1.3	146.5	6.0	569.4	5.9	296.4	9.0	109.9	2.1	3.3
Acer saccharum									3.2	26.6
Aesculus octandra							0.1	3.3	0.2	6.7
Amelanchier Arborea		10.0	0.1	3.3		6.7	0.0			
Betula lenta					0.3	13.3	3.1	53.3	4.9	83.3
Carya glabra					0.2	3.3	1.9	16.7		
Carya ovate									0.6	13.3
Carya tomentosa									0.1	3.3
Fraxinus Americana								3.3		
Halesia Carolina									0.3	6.7
Ilex opaca		3.3				3.3			0.4	16.7
Liriodendron tulipifera					0.3	3.3	3.1	6.7	4.6	20.0
Magnolia fraseri	0.3	13.3			0.1	16.7	0.4	3.3	0.2	6.7
Nyssa sylvatica	1.6	159.8	0.7	109.9	0.7	20.0	1.1	10.0	0.1	3.3
Oxydendrum arboretum	1.4	76.6	1.8	83.3	2.1	109.9	2.5	53.3	0.5	6.7
Pinus pungens	14.6	576.1								
Pinus rigida	2.9	126.5	0.7	16.7	0.5	3.3				
Pinus strobus	1.2	33.3	2.1	59.9	16.5	229.8	0.9	10.0	2.1	3.3
Quercus alba					0.1	3.3	0.3	6.7		
Quercus coccinea	4.4	126.5	1.7	23.3	5.4	59.9	0.3	3.3		
Quercus montana	0.1	3.3	17.0	113.2	3.0	26.6	1.9	16.7		3.3
Quercus rubra			0.2	10.0			2.9	20.0	0.9	3.3
Quercus velutina	0.1	3.3								
Sassafras albidum	0.2	53.3	0.1	20.0	0.1	3.3				
Tilia heterophylla									3.5	33.3
Tsuga Canadensis	1.2	73.3	0.9	83.3	4.0	479.5	12.9	632.7	13.1	243.1
Total	**29.3**	**1405.3**	**31.3**	**1092.2**	**39.3**	**1282.1**	**40.3**	**949.1**	**36.6**	**482.9**

Table 4.12. Sapling density and seedling density for tree species in each stand type at Licklog Ridge, GSMNP, T

	Pine Stands		Oak Stands		White Pine Stands		North Cove Stand		South Cove Stand	
	Sapling Density (saplings/ha)	Seedling Density (seedlings/ha)	Sapling Density (saplings/ha)	Seedling Density (seedlings/ha)	Sapling Density (saplings/ha)	Seedling Density (seedlings/ha)	Sapling Density (saplings/ha)	Seedling Density (seedlings/ha)	Sapling Density (saplings/ha)	Seedling Density (seedlings/ha)
Acer pensylvanicum	6.7	20.0	3.3	23.3	10.0	20.0	86.6	103.2	6.66	6.66
Acer rubrum	969.0	1182.2	346.3	96.6	109.9	666.0	10.0	2314.4	3.33	2234.43
Acer saccharum							10.0	13.3	26.64	133.2
Aesculus octandra									46.62	29.97
Amelanchier Arborea	26.6	43.3	3.3		3.3	10.0	6.7	20.0		
Betula lenta										159.84
Carya glabra			3.3				10.0			
Carya ovate									3.33	9.99
Castanea dentata			186.5	16.7	13.3					
Fraxinus Americana							23.3	123.2	6.66	26.64
Halesia Carolina									9.99	6.66
Ilex opaca	20.0	3.3	3.3	3.3	53.3	13.3	53.3	36.6	6.66	23.31
Liriodendron tulipifera							53.3	233.1	9.99	362.97
Magnolia fraseri	156.5	59.9	23.3	20.0	79.9	13.3	10.0	6.7	6.66	53.28
Nyssa sylvatica	189.8	156.5	359.6	96.6	20.0	13.3	20.0	176.5	3.33	43.29
Oxydendrum arboreum	279.7	50.0	103.2		93.2		3.3	26.6	3.33	3.33
Pinus pungens	36.6	6.7	3.3							
Pinus rigida	33.3	13.3								
Pinus strobus	233.1	116.6	50.0	6.7	20.0	6.7				
Prunus serotina								13.3		
Quercus alba	3.3	33.3								
Quercus coccinea	176.5	572.8	66.6	103.2	10.0	169.8		66.6		3.33
Quercus Montana	13.3	13.3	16.7	1132.2		40.0		119.9	3.33	3.33
Quercus rubra	6.7	59.9	16.7	56.6		13.3	36.6	96.6		136.53
Quercus velutina	20.0	33.3	6.7	3.3				3.3		
Robinia pseudoacacia			6.7					3.3		
Sassafras albidum	1228.8	2174.5	233.1	196.5	13.3	10.0	3.3	30.0	23.31	13.32
Tilia heterophylla									16.65	
Tsuga Canadensis	83.3	16.7	273.1	26.6	482.9	23.3	86.6	10.0	36.63	3.33
Total	**3483.2**	**4555.4**	**1705.0**	**1781.6**	**909.1**	**999.0**	**412.9**	**3396.6**	**213.1**	**3253.4**

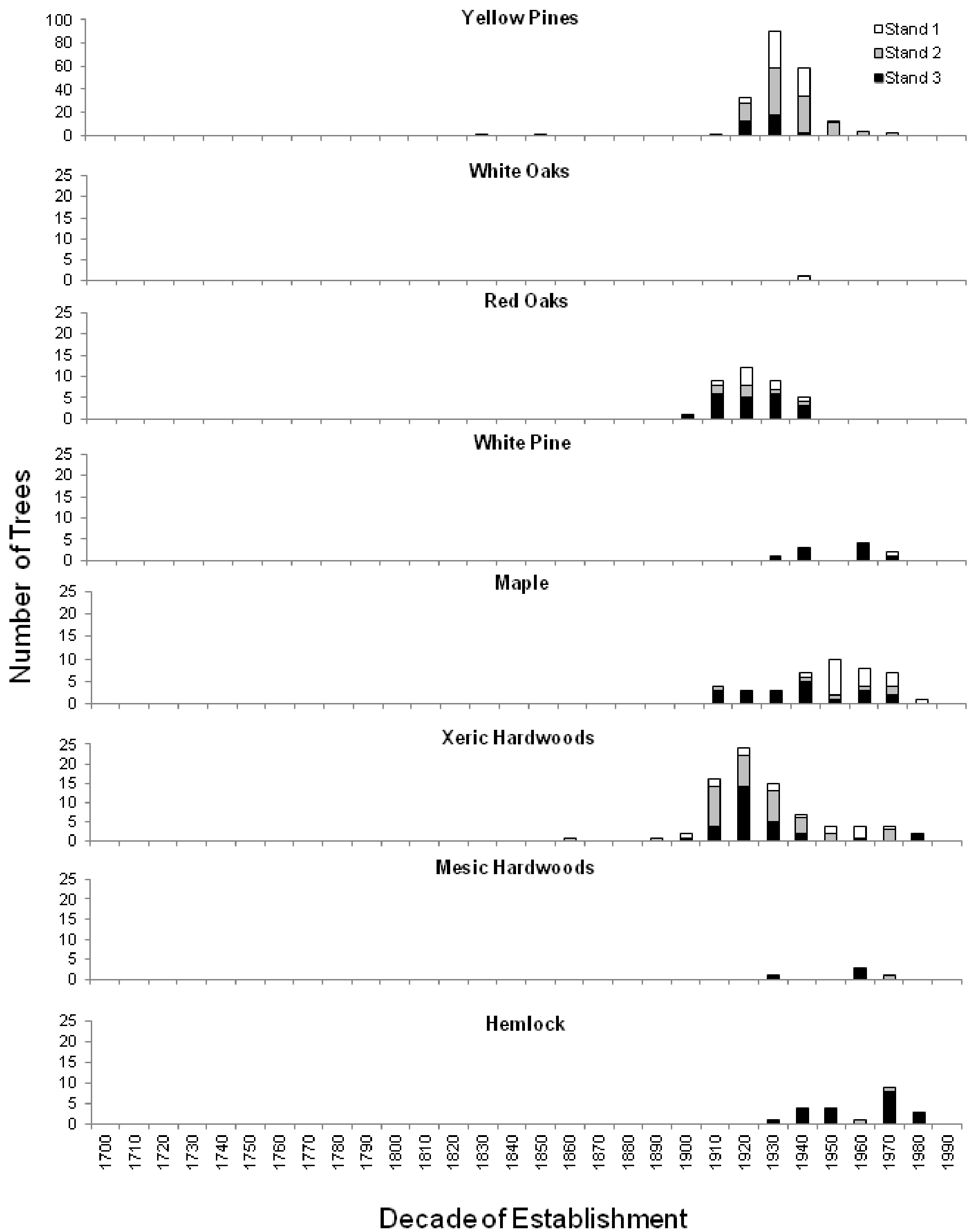

Figure 4.22 Decade of establishment of trees cored in three pine plots at Licklog Ridge, GSMNP. Species groups are: Yellow Pines (Table Mountain pine, pitch pine), White Oaks (white oak, chestnut oak), Red Oaks (scarlet oak, northern red oak, black oak), Eastern White Pine (eastern white pine), Maples (red maple, sugar maple), Mesic Hardwoods (yellow buckeye, sweet birch, white ash, Carolina silverbell, yellow poplar, white basswood), Xeric hardwoods (pignut hickory, shagbark hickory, mockernut hickory, black gum) and Eastern Hemlock (eastern hemlock). Note the different y-axis scale for yellow pine group.

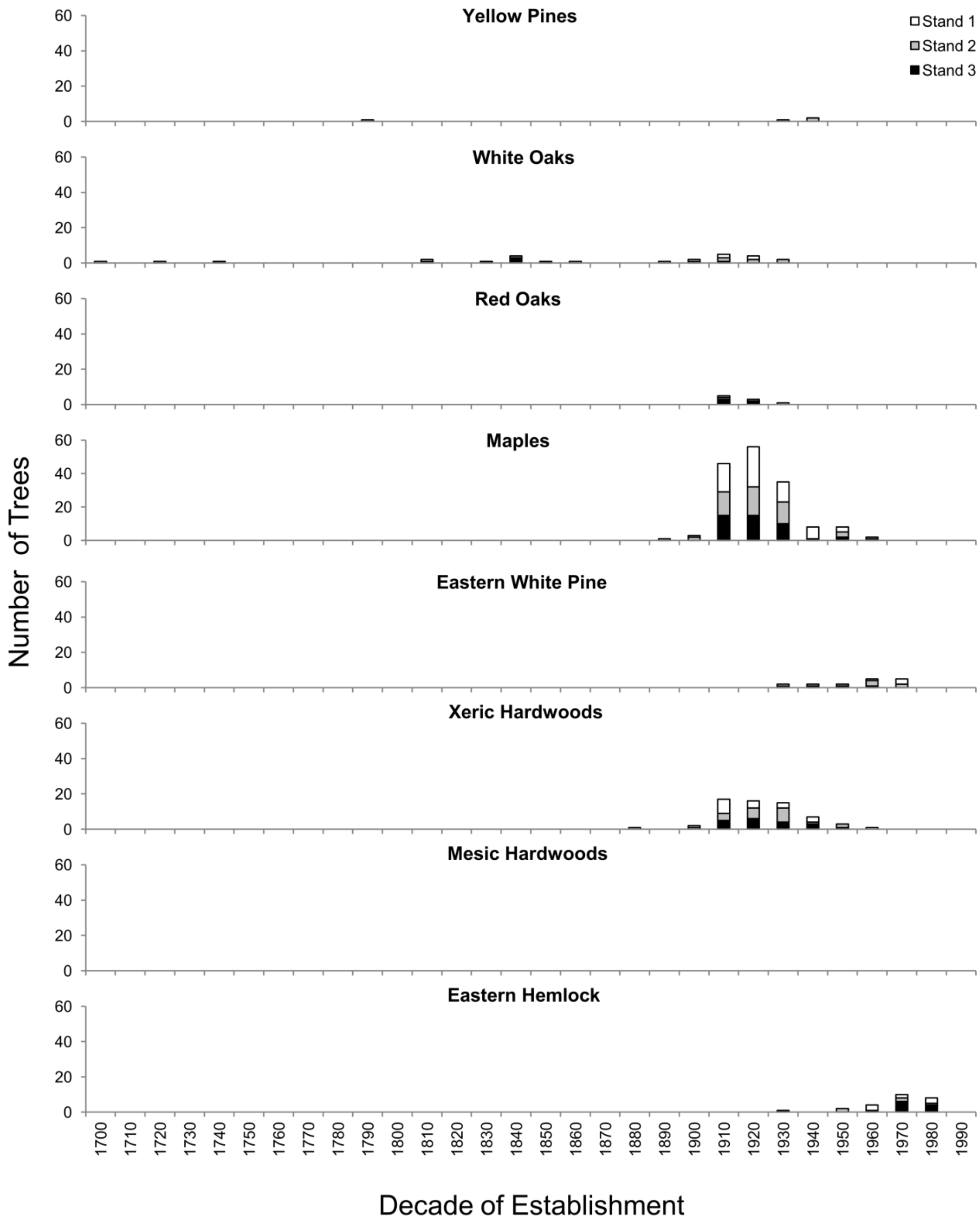

Figure 4.23 Decade of establishment of trees cored in three oak plots at Licklog Ridge, GSMNP. Species groups are: Yellow Pines (Table Mountain pine, pitch pine), White Oaks (white oak, chestnut oak), Red Oaks (scarlet oak, northern red oak, black oak), Eastern White Pine (eastern white pine), Maples (red maple, sugar maple), Mesic Hardwoods (yellow buckeye, sweet birch, white ash, Carolina silverbell, yellow poplar, white basswood), Xeric hardwoods (pignut hickory, shagbark hickory, mockernut hickory, black gum) and Eastern Hemlock (eastern hemlock).

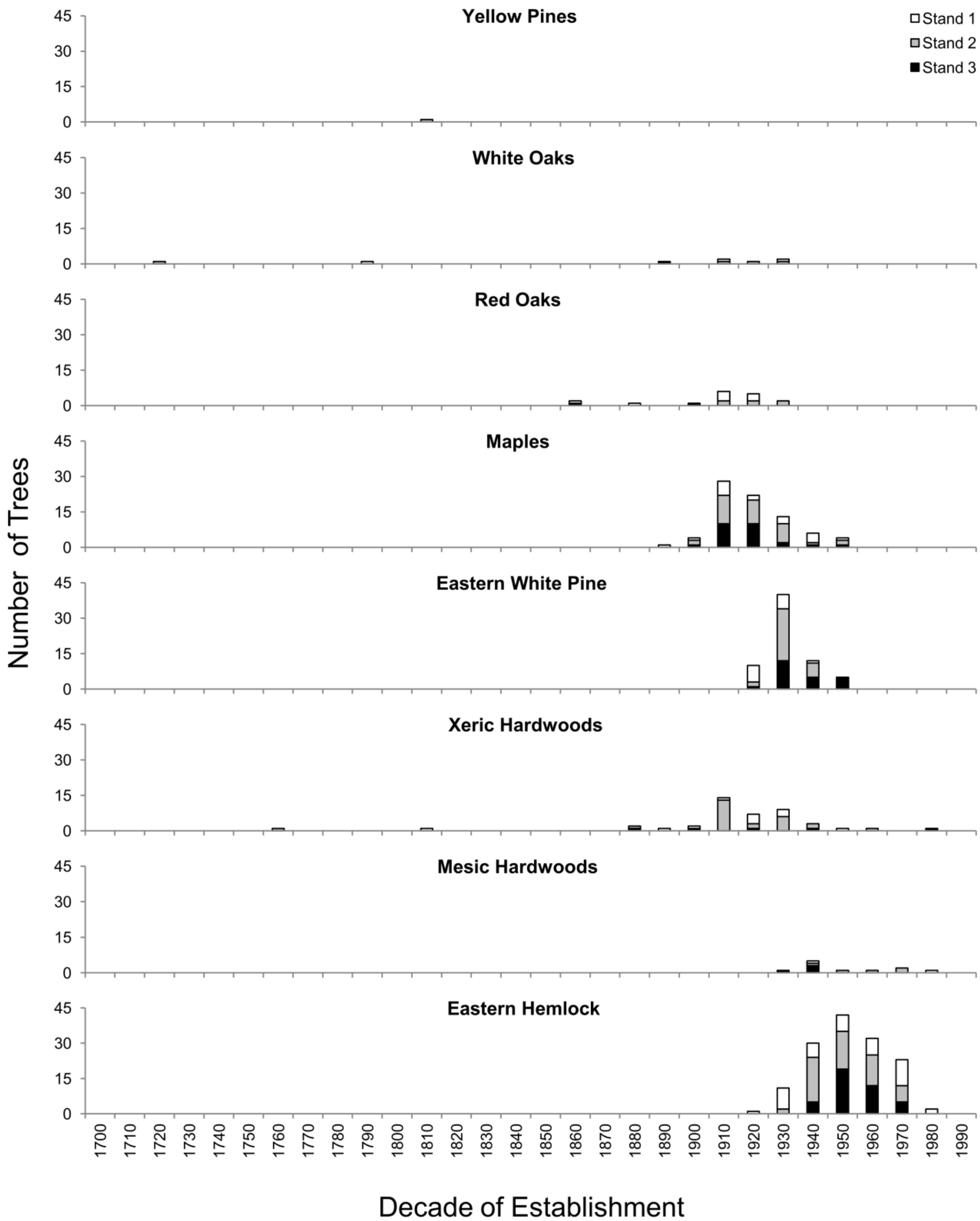

Figure 4.24 Decade of establishment of trees cored in three white pine-hardwood plots at Licklog Ridge, GSMNP. Species groups are: Yellow Pines (Table Mountain pine, pitch pine), White Oaks (white oak, chestnut oak), Red Oaks (scarlet oak, northern red oak, black oak), Eastern White Pine (eastern white pine), Maples (red maple, sugar maple), Mesic Hardwoods (yellow buckeye, sweet birch, white ash, Carolina silverbell, yellow poplar, white basswood), Xeric hardwoods (pignut hickory, shagbark hickory, mockernut hickory, black gum) and Eastern Hemlock (eastern hemlock).

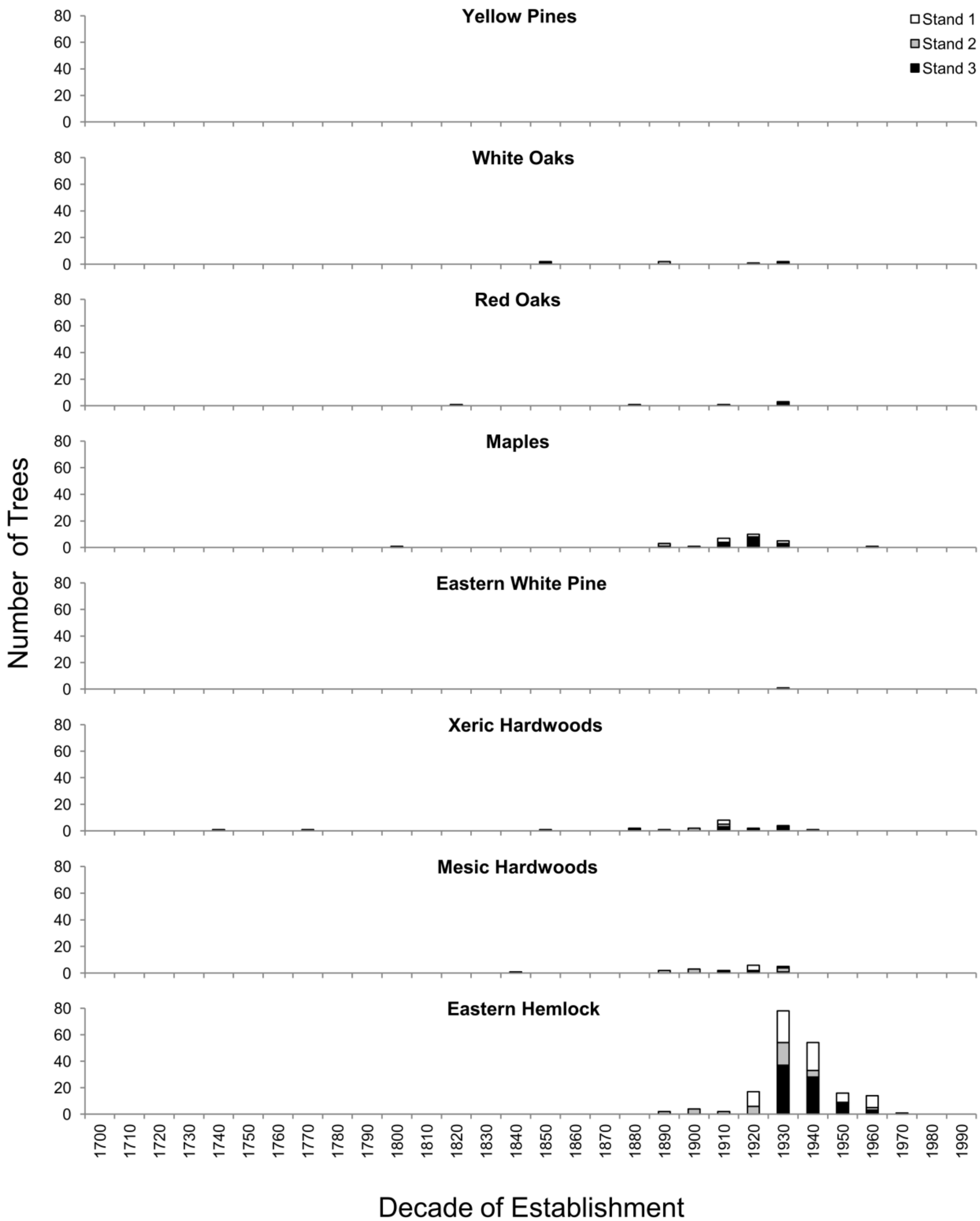

Figure 4.25 Decade of establishment of trees cored in three north cove plots at Licklog Ridge, GSMNP. Species groups are: Yellow Pines (Table Mountain pine, pitch pine), White Oaks (white oak, chestnut oak), Red Oaks (scarlet oak, northern red oak, black oak), Eastern White Pine (eastern white pine), Maples (red maple, sugar maple), Mesic Hardwoods (yellow buckeye, sweet birch, white ash, Carolina silverbell, yellow poplar, white basswood), Xeric hardwoods (pignut hickory, shagbark hickory, mockernut hickory, black gum) and Eastern Hemlock (eastern hemlock).

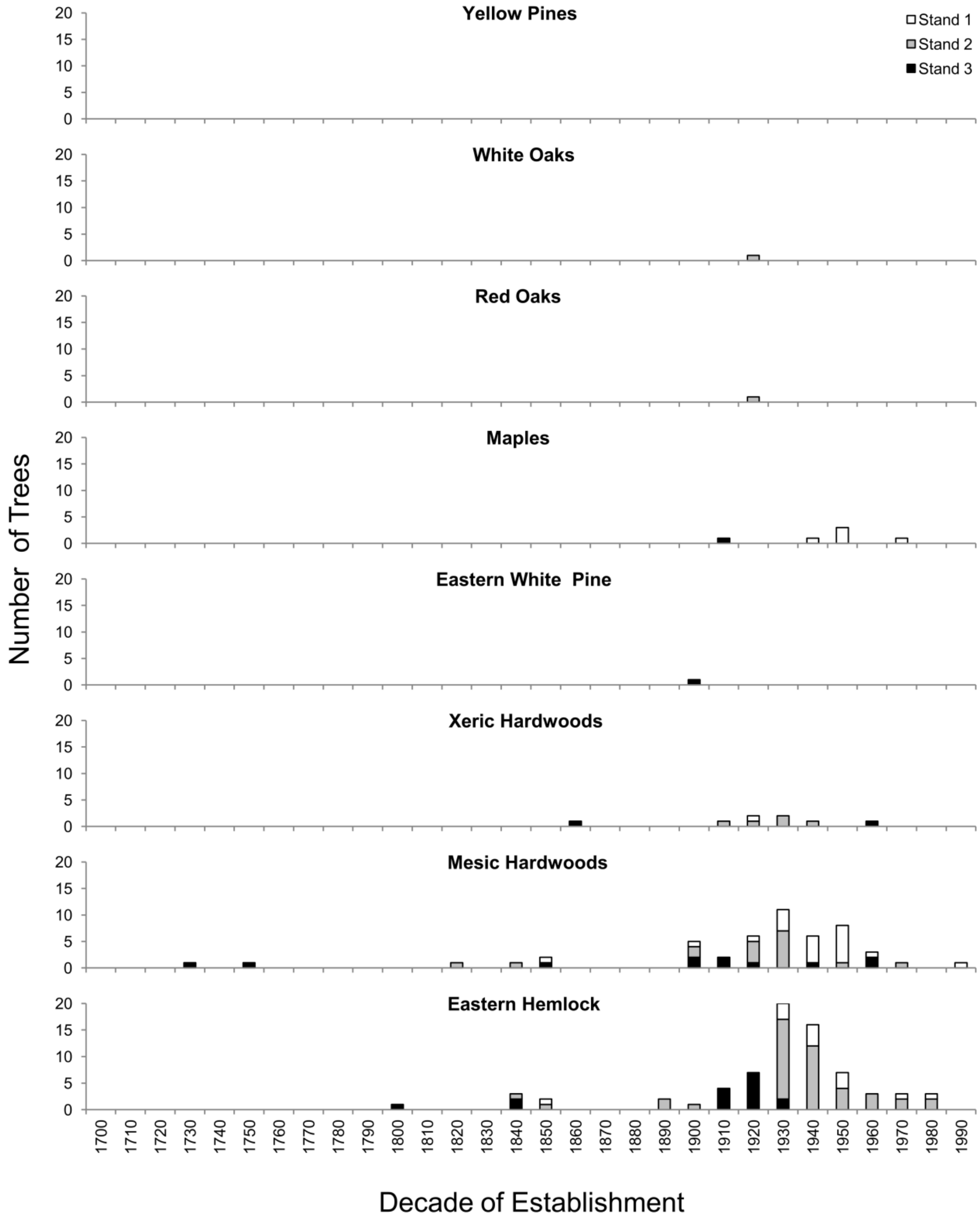

Figure 4.26 Decade of establishment of trees cored in three south cove plots at Licklog Ridge, GSMNP. Species groups are: Yellow Pines (Table Mountain pine, pitch pine), White Oaks (white oak, chestnut oak), Red Oaks (scarlet oak, northern red oak, black oak), Eastern White Pine (eastern white pine), Maples (red maple, sugar maple), Mesic Hardwoods (yellow buckeye, sweet birch, white ash, Carolina silverbell, yellow poplar, white basswood), Xeric hardwoods (pignut hickory, shagbark hickory, mockernut hickory, black gum) and Eastern Hemlock (eastern hemlock).

Classification of Forest Communities

Cluster analysis of the community composition data produced a dendrogram with discernible communities that were ecologically meaningful (Figure 4.27). Visual examination of the dendrogram structure identified a pruning level which retained maximum information and did not produce any groupings composed of a single plot. Pruning of the dendrogram produced four groups (Table 4.13). MRPP demonstrated significant differences in species composition between the groupings ($T = -19.5$, $A = 0.33$, $p < 0.0001$). Pairwise comparisons were also significant for all grouping comparisons ($p < 0.01$). ISA identified eight significant indicator species across the four communities. The four communities matched the four stand types that were identified during sampling (i.e. pine/group A, oak/group B, white pine-hardwood/group C, and cove/group D). The fire period samples were each classified into the expected communities. The post-fire period samples included only three of the communities, with the oak stands moving into group C. The fire-exclusion period samples included two communities, with the pine stands moving into group C and the white pine-hardwood stands moving into group D.

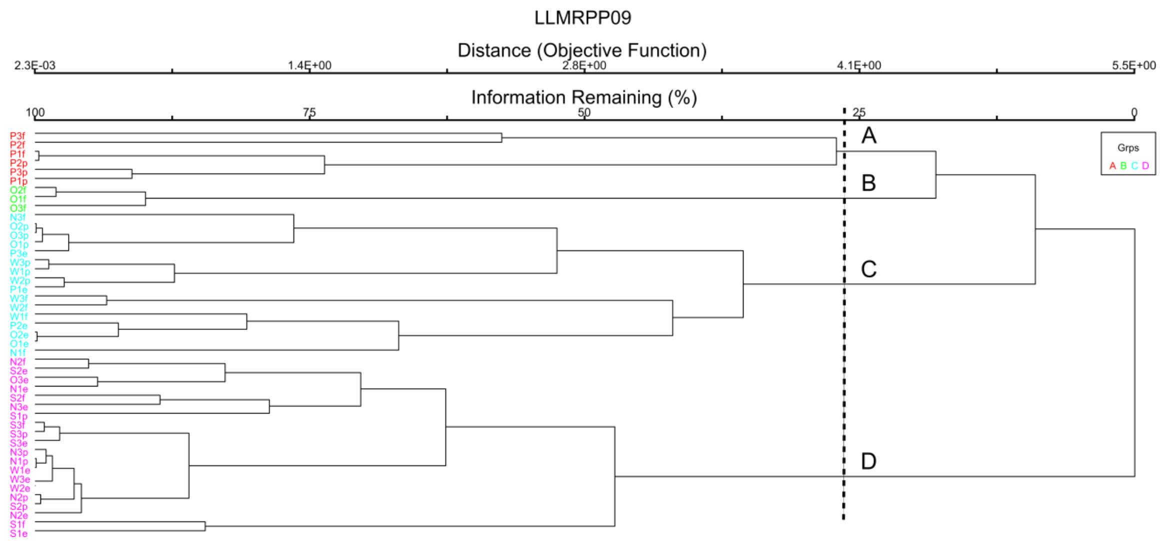

Figure 4.27. Dendrogram produced from cluster analysis on tree species establishment in plots prior to and following fire exclusion at Licklog Ridge, GSMNP, TN. Dotted line indicates where dendrogram was pruned. Letters (A-D) designate compositional groups identified through cluster analysis.

Table 4.13 Compositional groupings based on cluster analysis of tree establishment in vegetation plots under differing disturbance regimes (fire, post-fire, exclusion). Indicator species are significant at p<0.05.

Compositional Group	Vegetation plot; disturbance regime (Ordination plot code)	Significant Indicator Species (Observed Indicator Value)
Group A	Pine stand 1; fire (P1f) Pine stand 2; fire (P2f) Pine stand 3; fire (P3f) Pine stand 1; post-fire (P1p) Pine stand 2; post-fire (P2p) Pine stand 3; post-fire (P3p)	*Pinus pungens* (65) *Nyssa sylvatica* (61.1) *Pinus rigida* (49.6)
Group B	Oak stand 1; fire (O1f) Oak stand 2; fire (O2f) Oak stand 3; fire (O3f)	*Quercus montana* (89.8)
Group C	White pine-hardwood stand 1; fire (W1f) White pine-hardwood stand 2; fire (W2f) White pine-hardwood stand 3; fire (W3f) North cove stand 1; fire (N1f) North cove stand 3; fire (N3f) Oak stand 1; post-fire (O1p) Oak stand 2; post-fire (O2p) Oak stand 3; post fire (O3p) White pine-hardwood stand 1; post-fire (W1p) White pine-hardwood stand 2; post-fire (W2p) White pine-hardwood stand 3; post-fire (W3p) Pine stand 1; exclusion (P1e) Pine stand 2; exclusion (P2e) Pine stand 3; exclusion (P3e) Oak stand 1; exclusion (O1e) Oak stand 2; exclusion (O2e)	*Acer rubrum* (63.6) *Pinus strobus* (53)
Group D	North cove stand 2; fire (N2f) South cove stand 1; fire (S1f) South cove stand 2; fire (S2f) South cove stand 3; fire (S3f) South cove stand 1; post-fire (S1p) South cove stand 2; post-fire (S2p) South cove stand 3; post-fire (S3p) North cove stand 1; post-fire (N1p) North cove stand 2; post-fire (N2p) North cove stand 3; post-fire (N3p)	*Tsuga Canadensis* (87.8) *Betula lenta* (51.9)

Oak stand 3; exclusion (O3e)
White pine-hardwood stand 1; exclusion (W1e)
White pine-hardwood stand 2; exclusion (W2e)
White pine stand-hardwood 3; exclusion (W3e)
North cove stand 1; exclusion (N1e)
North cove stand 2; exclusion (N2e)
North cove stand 3; exclusion (N3e)
South cove stand 1; exclusion (S1e)
South cove stand 2, exclusion (S2e)
South cove stand 3; exclusion (S3e)

Successional Change and Community Diversity

Research Question: Do changes in successional trajectory due to fire suppression suggest a decrease in community differentiation or beta diversity across the entire site?

NMS ordination indicated a two dimensional solution for the species establishment (Figure 4.28). The two dimensional solution produced a final stress of 17.3 (22.9, $p = 0.024$). The values in parenthesis are the mean stress and significance produced by Monte Carlo tests. The ordination illustrates the changes in tree establishment within the stands during the three disturbance periods (Figure 4.29). The samples from the fire disturbance period are spread across the ordination space, representing the four distinct communities. During the final fire exclusion phase, the samples have contracted towards the lower right quarter of the ordination space which was originally occupied by the sub-mesic white pine-hardwood stands and the mesic cove stands. Results from the permutational test of multivariate dispersion indicated that the mean distance from the centroid differed significantly for the different time periods (Figure 4.29, $F = 5.41$, $p = 0.008$). Pair-wise a posteriori comparisons indicated that mean distance differed significantly only between the fire period and the exclusion period ($t = 3.15$, $p = 0.004$). Diversity calculations for the different time periods and different forest strata indicated a trend of decreasing beta diversity within the watershed (Table 4.14-4.15). Species richness increased in each of the plots following fire suppression, with the largest increases occurring in the xeric pine and sub-xeric oak stands. However, beta diversity declined due to more shared species between the different stand types.

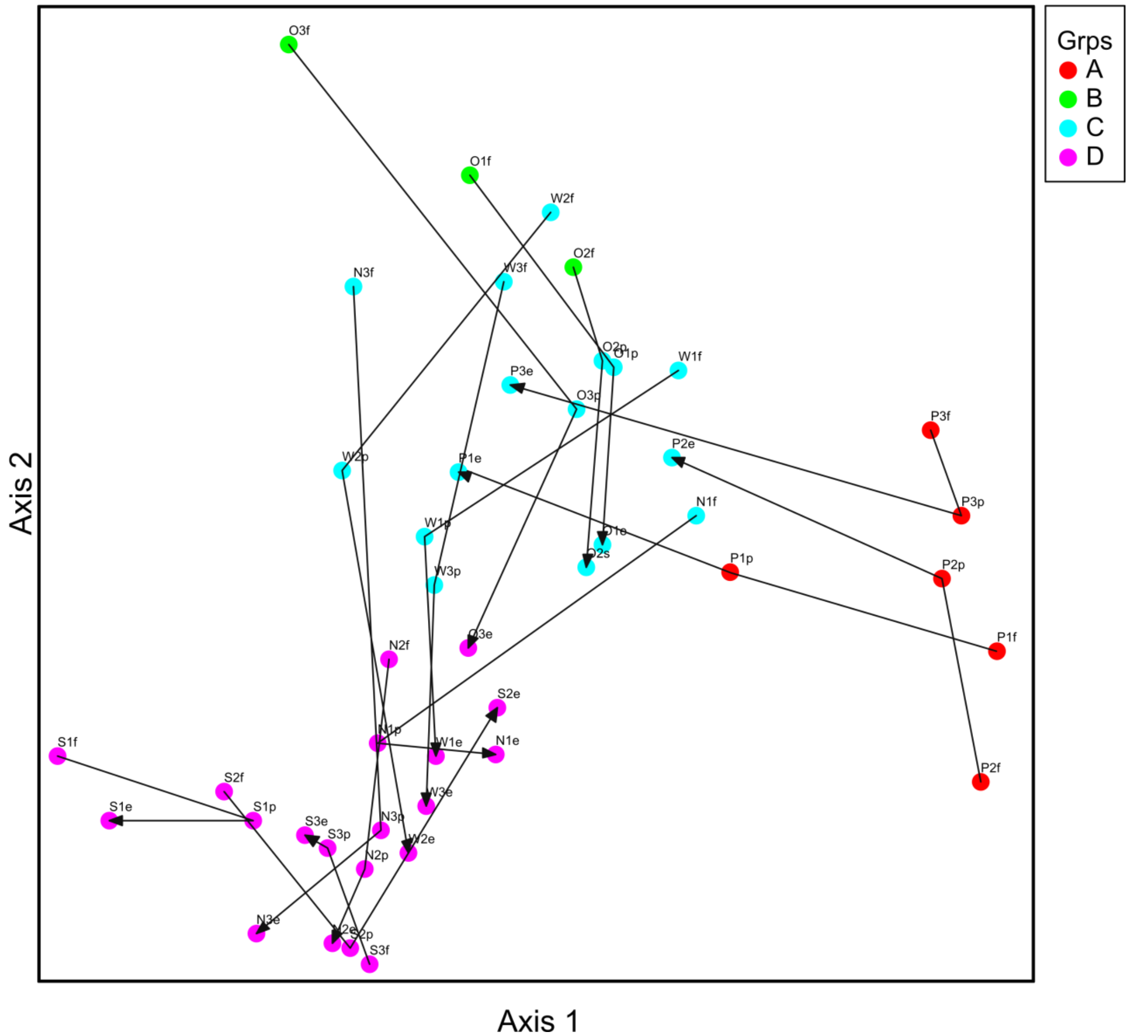

Figure 4.28 Non-metric multidimensional scaling ordination for composition of species establishment in each of the vegetation plots during the three different disturbance periods at Licklog Ridge, GSMNP, TN. See table 4.13 for plot codes.

Table 4.14 Mean species richness of tree establishment under differing disturbance periods for each stand type at Licklog watershed, GSMNP, TN.

Disturbance Regime	Pine	Oak	White Pine-Hardwood	North Cove	South Cove
Fire	2.0	2.3	3.7	5.3	4.0
Post-fire	6.3	6.0	6.3	5.3	5.0
Exclusion	9.0	8.0	5.0	5.7	6.3

Table 4.15 Landscape scale diversity calculations for species establishment under differing disturbance regimes and for different forest strata in vegetation plots at Licklog watershed, GSMNP, TN.

	Gamma Diversity	Mean Plot Level Alpha Diversity	Beta Diversity
Disturbance Regime			
Fire	20	4.1	3.9
Post-fire	25	7.3	2.4
Exclusion	26	9.9	1.6
Forest strata			
Trees	27	9.3	1.9
Saplings	25	9.4	1.7
Seedlings	24	10.1	1.4

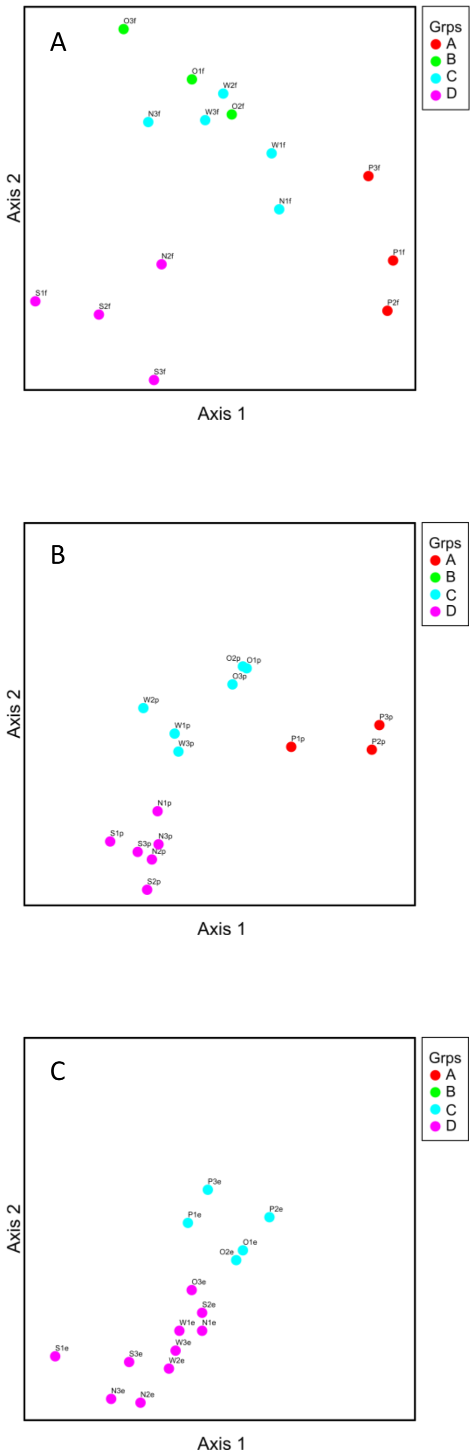

Figure 4.29 Non metric multidimensional scaling ordination of vegetation plots, separated according to sequential disturbance periods: (A) fire, (B) post-fire, and (C) exclusion. See table 4.13 for plot codes.

CHAPTER V

DISCUSSION*

Contemporary Landscape Patterns of Fire

Climatic Controls on Spatial Patterns of Fire

As hypothesized, the drier SNP burned more frequently than GSMNP. The drier climatic conditions likely contributed to lower fuel moisture and consequently to greater flammability. Fuel moisture is the primary limitation on fire in the humid southeastern United States (Beckage et al. 2003, Lafon et al. 2005, Mitchener and Parker 2005). Reduced fuel moisture results in a higher susceptibility to combustion (higher fire density) and increased fire spread (larger mean fire size). Additionally, the seasonality of precipitation may amplify the effects of differences in total annual precipitation on fire. The five driest months in SNP are December to April, preceding or occurring in the early months of the fire season. Fuels from the previous year have had several months to cure and trees have not leafed out. Fall is the driest season in GSMNP, which follows the precipitation peak in May, June, and July. Fuels produced during the summer growing season in GSMNP have less time to dry preceding fall droughts.

Gradients in fire activity have previously been identified from west to east within the central Appalachian physiographic provinces (Lafon and Grissino-Mayer 2007). The easternmost Blue Ridge province burns more frequently than the Ridge and Valley and the Appalachian Plateau provinces to the west, apparently because of differences in seasonality and extent of dry periods. My results suggest that a gradient of increasing fire activity also exists from south to north along the Blue Ridge province itself. This pattern

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corresponds with a gradient of decreasing precipitation and varying precipitation seasonality.

Climatic Controls on Temporal Patterns of Fire

Patterns of fire activity were also influenced by temporal patterns of drought. Significant negative correlations between annual PDSI and area burned indicated that large fire years are associated with droughts. The slightly stronger correlations in GSMNP matched my expectation that burning a wetter landscape would require longer and more intense droughts. The significant positive correlations with lagged PDSI were not expected for these parks with humid climatic conditions. They may suggest that moisture in preceding years promotes fire by increasing fuel production as demonstrated in the drier forests of the southwestern U.S. (Veblen et al. 2000, Grissino-Mayer et al. 2004). In the Southwest the relationship emerges because of the dry climate, where wet years enhance the production of fine fuels that promote fire spread during subsequent dry years. Scatterplots of the lagged PDSI-area burned correlations (not shown) identified some potential outliers but did not produce an interpretable pattern. Without a longer time series of data, I can simply say that there may be an influence of prior moisture, but if so it is quite weak and does not assume the importance that it does in drier climates like the western US.

Topographic Controls on Spatial Patterns of Fire

Consistent with my second hypothesis, moisture appears to influence topographic patterns of fire, with drier elevations, slope positions and aspects burning most frequently. The patterns of area burned are particularly strong in GSMNP, where the high incidence of burning on south-facing slopes, ridges, and low elevations matches patterns found in mesic environments in the northwestern U.S. and elsewhere (Zhang et al. 1999, Rollins et al. 2002, Howe and Baker 2003). In SNP, however, these topographic patterns emerged strongly only during wet years. Apparently the relatively low precipitation in SNP results in sufficiently dry fuels across a wide range of elevations and slope positions. During the driest years in SNP, few topographic features may have high enough fuel moisture to impede the spread of fire.

The CART models enabled me to integrate the influences of climate and multiple topographic variables on the likelihood of a particular location burning. The effect of different topographic categories on model predictions was consistent between the model and the previously examined trends in area burned, with drier topographic features being most prone to fire. However, the classification tree was helpful in determining interactions between the variables. For example, the model predicted that fires would occur above 1200 m in GSMNP only on dry ridge and upper slopes during low PDSI years. The major difference between the CART model and the results from the G-tests of area burned was the reduced influence of aspect. This was likely a consequence of the variability in aspect patterns for burns in the different parks and under differing PDSI conditions. South and southeast aspects burned most in both parks, especially under low PDSI conditions. However, southwest and west aspects burned most frequently during high PDSI conditions. These differences in the susceptibility of certain aspects to fire under differing moisture conditions probably blurred the influence of the aspect variable and reduced its importance in the classification trees. Slope position and elevation, in contrast, maintained a consistent order of burn frequency under differing PDSI conditions in both parks. As a result, the G-tests complemented the CART model in terms of identifying the presence of aspect patterns that likely would have been lost in the modeling assessment.

The differences in topographic patterning between GSMNP and SNP, and between wet and dry years, are consistent with my third and fourth hypotheses— broad climatic conditions interact with the topography such that topography exerts less influence under dry, fire-prone conditions than under wet conditions. Regional or temporal climatic variations that reduce fuel moisture across a range of topographic positions render much of the landscape susceptible to the spread of fire. My findings match and expand upon previous work concerning individual disturbance events, where large or high-intensity disturbances have been shown to have less topographic control than small or low-intensity disturbances (Parker and Bendix 1996, Moritz 2003, Mermoz et al. 2005, Stueve et al. 2007). The same principle appears to apply to the entire disturbance regime, i.e., disturbance-prone landscapes have weaker topographic patterns of disturbance than do less disturbance-prone landscapes.

Differences in fire disturbance patterns between the two parks likely generate different landscape patterns for fire-associated yellow pine and oak communities. My results suggest that broader topographic patterns of fire in SNP may expand the range of fire-associated species down the moisture gradient to wetter slope positions, slope aspects, and elevations. A further understanding of this interaction between precipitation regimes, fire disturbance and vegetation is particularly important in light of possible future climate change. Predicted precipitation patterns for the southeastern U.S. are uncertain (Chen et al. 2003). However, my results suggest potential changes in fire disturbance patterns and the resulting vegetation patterns in response to precipitation increases or decreases.

The differences in climatic conditions and topographic patterns of lightning fires compared to anthropogenic fires suggest that the two fire types may impart different disturbance patterns on a landscape. My results indicate that lightning fires, occurring during wetter conditions, are more constricted to the driest aspects and slope positions. Anthropogenic fires, meanwhile, occur during drier conditions and burn across a much wider range of topographic positions. This distinction may be particularly important given the debate over the role of Native American ignitions and lightning ignitions in shaping pre-European settlement disturbance regimes in eastern North America (Petersen and Drewa 2006, Abrams and Nowacki 2008). Landscape patterns that result from a lightning fire regime probably differ substantially from the patterns caused by an anthropogenic fire regime. It is possible that patterns of contemporary anthropogenic ignitions may differ from Native American ignitions in terms of seasonality and location. However, the addition of human ignition sources, regardless of the season or location, represents an increase in the range of conditions under which fires are ignited.

Patterns of burning during dry and wet years have important implications for fire management. Prescribed fires generally are implemented during relatively moist conditions that facilitate their control. In the past, however, most burning likely occurred under drought conditions when topography imposed less control on patterns of fire. Where possible, fire managers should not consider only the typical frequency of fire and area burned in a particular landscape. They also may need to consider the typical climatic conditions and fire types (wetter vs. dry; anthropogenic vs. lightning) in order to reproduce landscape patterns that reflect historical disturbance regimes.

Fire History

Fire Frequency

Records of fire in old growth forests of the eastern US are rare, due to the extent of forest clearance that occurred in this region following Euro-American settlement. My fire history reconstructions extend the annually resolved fire record beyond the period of logging and industrial disturbance, to include early Euro-American settlement and a period of Native American land use. One of the critiques of the fire-oak hypothesis has been the suggestion that the current abundance of fire tolerant oaks and pines in the overstory of eastern forests is the product of land clearance, logging and resulting atypical fires during the industrial period at the end of the 19th century (Williams 1998, Hessl et al. 2011, McEwan et al. 2011). According to this reasoning, the invasion and eventual replacement of pine-oak forests with fire intolerant, mesophytic hardwoods is a natural process of recovery to conditions that preceded the period of atypical fire disturbance associated with logging and industrialization. However, my reconstructions demonstrate that fires burned frequently in upland forests of the southern Appalachian Mountains for at least two centuries prior to the logging boom.

Composite fire intervals indicate that fires occurred somewhere on the sites at an average of every 2-4 years during the 18th and 19th century. Forest models project that similarly short fire intervals produce open pine and oak woodlands in eastern forests (Lafon et al. 2007, Bean and Sanderson 2008).Composite fire intervals likely included some smaller fires that did not burn across the entire site, but the limited collection areas (8-64 ha) should reduce the influence of smaller fires on the fire intervals. Point fire return intervals, a more conservative estimate of fire frequency, indicate that fires burned at any single point at decadal intervals. However, point fire intervals may underestimate fire frequency, since all fires are not recorded on all trees (Smith and Sutherland 1999). The point fire interval provides an upper boundary fire interval for each site.

Point fire intervals from my sites match those reported by Harmon et al. (1982a) (12.7 years) but extend the record of frequent fire back to the period preceding Euro-American settlement. The pre-settlement fire regime at my sites matches previous fire history records from adjacent regions of the Appalachian Mountains in southwestern Virginia and Maryland (mean composite fire interval 1-3 years, point fire interval 8-15 years) (Shumway et al. 2001, Hoss et al. 2008, Aldrich et al. 2010).

The large number of cross sections collected for this study should decrease the level of uncertainty associated with previous fire reconstructions in eastern forests (Harmon 1982a, Schuler and McClain 2003, Maxwell and Hicks 2010, Hessl et al. 2011). Studies based on a limited number of fire scarred tree samples are less likely to include older samples that predate the industrial period. However, the absence of older samples from a particular location does not preclude fire disturbance prior to the industrial period, which has sometimes been the conclusion in previous studies (Hessl et al. 2011). When possible, the collection of large numbers of cross-sections may be a way to increase the likelihood of producing a fire reconstruction that includes earlier time periods. The number of cross-sections may be particularly important in humid eastern forests where wood decay is a serious limitation to long term fire reconstructions.

The frequency of area-wide fires that scarred multiple, non-adjacent pine stands indicates that many of the fires were large in extent and necessarily burned across the intervening mixed oak-chestnut forests. The large proportion of fires that scarred $\geq$ 25% of the recording trees also suggests that many fires were large in extent and likely burned broad portions of the landscape. The identification of trees with multiple scars, up to 13 on a single living individual, indicates that these fires were low severity, surface fires. There is some evidence of high severity fires at Linville Mountain, since there are two clear pulses of establishment (1700-1720 and 1800-1820) among the fire scarred tree samples at this site. However, this conclusion must be cautious since the cross sections were targeted for collection due to visible fire scars, rather than according to a systematic sampling design. Linville Mountain may have experienced a mixed severity fire regime, with frequent low severity fires that were occasionally punctuated by spatially limited high severity fires. A high severity lightning fire burned portions of Linville Mountain outside of my sample area during the growing season in 2001.

The fires at my study sites could have been the result of human activities or lightning ignitions. However, the high percentage of dormant season scars suggests that many of the fires were anthropogenic in origin. Today, lightning fires in the region can occur throughout the year; but they are most common and burn the most area during the late spring and summer when convection produces thunderstorms and associated lighting (Barden and Woods 1974, Cohen et al. 2007). If lightning was the primary source of ignitions in the past, one would expect to have more growing season scars in the record. Additionally, the contemporary annual rate of one lightning ignition per 100,000 hectares seems insufficient to have accounted for the 2 to 4 year MCFI at the three fire history sites (Flatley et al. 2011).

Native Americans used fire in the forests of eastern North America for multiple purposes including the promotion of mast trees, maintenance of game populations, and clearance of vegetation (Cronon 1983, Whitney 1994, Abrams and Nowacki 2008). Historic land surveys have demonstrated the impact of Native American populations on forest composition prior to Euro-American settlement, particularly in close proximity to known archaeological sites (Black and Abrams 2001, Black et al. 2006). Accounts from the 18th century describe Cherokee in the Southern Appalachian region using fire in order to drive deer during hunts in the fall and winter months (Corkran 1962). Recent analysis has suggested that in response to European markets for deerskins, Native Americans in the southern Appalachian region harvested deer across a broad landscape, well beyond the areas adjacent to villages (Foster and Cohen 2007, Bolstad and Gragson 2008).

Temporal Changes in Fire Activity

The replacement of Native American peoples by Euro-American settlers did not significantly change fire frequency or seasonality at any of the sites. The absence of change in fire regime characteristics during this cultural transition lends empirical support to the notion that Euro-American settlers appropriated Native American burning practices in eastern forests (Prunty 1965, Pyne 1982). The lack of change in fire frequency at my sites also suggests that that fire frequency in these forests was not closely tied to population levels. Fires continued to burn with similarly high frequency during the late 18th and early 19th century when Euro-Americans were first settling in the region and population was likely the lowest during my record. It is possible that vegetation patterns allowed for large fires to burn across broad portions of the landscape. Open, woodland forest structure developed under frequent burning would have supported herbaceous fuels in the understory, capable of carrying fire across the landscape (Harrod et al. 2000). Woodland forest structure would also have facilitated the drying of understory fuels, providing more frequent opportunities for burning, even during wetter years. The frequency of area-wide fires, lends further support to the idea that many of the fires burned large areas. As a result, relatively fewer ignitions would have been required to burn large portions of the landscape at short intervals.

I expected to see an increase in fire frequency during the industrial period. However, the fire index did not change during the industrial period at any of the sites. This was surprising since it has generally been assumed that fire frequency reached a peak during this period (Brose et al. 2001). A number of additional studies have produced similar results, countering the notion that fire regimes during the industrial period fires were a departure from previous land use periods (Shumway et al. 2001, Hoss et al. 2008, Aldrich et al. 2010). There certainly were large slash fires in areas that were logged during the early 20th century (Pyle 1988). Yet, the stands that I sampled were not logged and may have been fairly resilient to the spread of high intensity fires. Woodland forest structure and a lack of fuel build-up could have reduced the severity of fires when they did spread into these stands. The forests that I sampled continued to experience frequent surface fires that were not a significant departure from the fire regime that had characterized the sites during the previous centuries.

In stark contrast to the early portion of the record, fires were infrequent during the fire protection era. The drastic reduction in fire frequency at these sites underscores the effectiveness of federal fire protection campaigns in the temperate forests of the eastern US. The impact of fire protection at these sites matches with other fire reconstructions in eastern forest (Harmon 1982a, Shumway et al. 2001, Schuler and McClain 2003, Hoss et al. 2008, Aldrich et al. 2010) Fires did continue to burn at House Mountain up until the 1970s. Perhaps this was due to the preserve's limited size and the agricultural landscape that surrounds it.

The majority of fires that were recorded during the fire protection period occurred at the beginning of the fire protection era. There was a near complete absence of fire during the most recent decades. This trend probably reflects improving fire suppression techniques and increasingly effective public service campaigns. The complete absence of fire during recent decades might also be an indication of the forest state change that Nowacki and Abrams (2008) termed mesophication. As time passed without fire, forest canopies would have progressively closed, mesophytic species would have invaded, and forest fuels would have become less flammable. As a result, ignitions and fire spread would have been much less likely to occur in these landscapes.

Fire-climate Relations

The lack of a significant relationship between fire years and reconstructed annual drought suggests that fire-climate relationships typical of conifer forests in the western U.S. do not apply to past fire regimes in the mesic southern Appalachian Mountain region. Reconstructions from other portions of the eastern forest have found a similar lack of association between historical fire and drought (Guyette et al. 2003, Schuler and McClain 2003, McEwan et al. 2007b, Allen and Palmer 2011, Stambaugh et al. 2011). One potential explanation for the lack of a fire-drought association is the joint seasonality of dormant season scars. For example, a fire occurring during a fall drought, followed by a wet growing season would be represented in the record as a dormant season fire from a wet year. Dormant season scars that represent a mix of fall and spring fires would likely weaken fire-climate associations.

Another possible explanation for the weak fire-drought association is that fire regimes driven by purposeful human ignitions are less closely linked to annual precipitation patterns than natural fire regimes. Native Americans and Euro-American settlers could have avoided purposeful burning during drought years in order to avoid high severity fires. Preventing ignitions during droughts or the ignition of fires during short periods of preferred weather, in particular vegetation types or for particular management goals, would likely weaken fire-climate associations. Similarly weak fire-climate associations have been noted in studies of past fire regimes that were driven by human ignitions in Europe (Lindbladh et al. 2003, Drobyshev et al. 2004, Niklasson et al. 2010). The lack of a strong correlation between climate and fire has been suggested as a measure of human impacts on natural fire regimes (Drobyshev et al. 2004).

Vegetation Dynamics

Post-fire Succession

Forest composition and tree establishment patterns at Licklog Ridge indicate that fire disturbance played an important role in the development of multiple forest communities at the site. The shift from a frequent fire regime (mean fire interval of 2-6 years) to complete fire exclusion during the last eight decades appears to have influenced tree establishment in xeric pine, sub-xeric oak, sub-mesic white pine-hardwood communities and possibly mesic cove communities. In the xeric, sub-xeric, and sub-mesic stand types, large pulses of tree establishment initiated following the last major fire in 1916. There were no comparable periods of tree establishment either preceding or following the decades immediately after the cessation of fires.

Compositional changes matched my expectations, with fire tolerant oaks and yellow pines being replaced by fire sensitive hardwoods, hemlocks and white pines. Similar patterns of post-fire succession have been noted in xeric pine and oak stands in both the southern and central Appalachian region (Harrod et al. 2000, DeWeese 2007, Hoss et al. 2008, Aldrich et al. 2010). However, successional changes in more mesic forest types have not previously been combined with direct evidence of change in the fire regime. Pulses of establishment in the submesic white pine-hardwood stands indicate that these stands also responded to fire suppression, with the establishment of hardwoods and hemlocks immediately following the cessation of fires.

Fire tolerant yellow pines or oaks established along the entire moisture gradient during the period of frequent fire disturbance. Today, oaks and pines are nearly absent from the younger age classes. The patterns of species establishment are consistent with the fire-oak hypothesis that frequent low intensity fires maintained pine and oak species in the presettlement forests of eastern North America (Lorimer 1984, Abrams 1992, Nowacki and Abrams 2008).

Alternative Drivers

McEwan et al. (2011) argue that the fire-oak hypothesis is an over simplification of the processes driving oak decline. They note that multiple interacting ecosystem drivers, including changes in climate, land use, keystone species and wildlife populations have occurred in concert with oak decline and should be evaluated as drivers of the oak to maple transition. Annually resolved tree establishment dates and fire occurrence data from my site provide an opportunity to assess the relative timing of vegetation changes, fire cessation, and variations in other known drivers of forest dynamics.

Several insects and pathogens have affected forests in GSMNP during the last century, removing portions of the canopy and creating opportunities for tree establishment and compositional change. From 1925-1930, chestnut blight resulted in the mortality of all mature American chestnuts (Woods and Shanks 1959). The removal of this canopy dominant apparently initiated tree establishment in the white pine-hardwood and cove stands at my site (the details of which will be discussed below). However, establishment related to chestnut blight occurred nearly two decades after the changes initiated by fire exclusion. Southern pine beetle outbreaks were recorded in 1954-1958, 1967-1977, and 1999-2002 (Kuykendall 1978, Jenkins et al. 2011). Presumably, pine beetle outbreaks also occurred earlier at the site. Hemlock wooly adelgid infestations have caused widespread mortality of eastern hemlock during the last decade. Yet, the hemlock wooly adelgid and the recorded pine beetle outbreaks do not align with the major pulses of establishment that occurred at the site from 1910-1930. These insect infestations are also limited to particular species (hemlock) or genus (*Pinus*). Therefore it is unlikely that they would initiate establishment across multiple stand types.

Changes in land use and climate have both been demonstrated as important drivers of forest change. However, unlike the vast majority of eastern forests in North America, Licklog Ridge was not subject to agricultural clearance or logging. The establishment of GSMNP and the removal of livestock, humans, and hunting pressure may have influenced tree establishment. But once again, these changes occurred in the 1930s, after the cessation of fire at the site (Pyle 1988, Campbell 1993). Climate driven changes in mature forest vegetation are likely to require many decades, if not centuries (Loehle and LeBlanc 1996). Therefore, it is unlikely that precipitation changes would have resulted in such a rapid change in species establishment patterns. Additionally, the earliest cohorts of tree establishment include both drought tolerant pines and oaks and less drought tolerant mesic hardwoods.

Viewed at broad spatial or temporal scales, it is difficult to discern the influence of fire suppression from other potential drivers of ecosystem change. Fire regimes and the dates of fire cessation vary by site. As a result, when successional change is examined across multiple sites the cessation of fires may vary by decades. Consequently it is difficult to separate the influence of fire regime changes from other drivers of forest change. Similarly, comparisons of pre-settlement forest composition with contemporary forest composition provide only two snapshots of forest conditions. However, when forest dynamics are viewed at finer scales (e.g. annually resolved data from individual stands) it is feasible to begin separating the influence of these different drivers. In this study, the combination of stand level fire history and dendroecological data on tree establishment provide strong evidence that fire exclusion has been the primary driver of forest change at Licklog Ridge.

Forest Structure

The mesophication hypothesis posits not only changes in forest species composition, but increases in forest density and canopy closure. Forest models applied to the southern Appalachian region project that frequent burning would produce open, woodland forest structure (Lafon et al. 2007). Indeed, Whittaker's (1956) description of vegetation in Great Smoky Mountains National Park ca. 1950 provides evidence that frequent burning maintained open canopy stands of pine and oak. Whittaker characterized forest vegetation on mid-elevation upper slopes as oak-chestnut heath and pine heath with widely scattered trees and a dense undergrowth of *Kalmia* L. shrubs. He estimated that total tree coverage in oak-chestnut heaths may have been below 40 to 50% prior to chestnut blight. Pine heaths were estimated at 70% tree coverage.

I cannot reconstruct past forest structure since tree mortality has occurred and dead logs decompose rapidly in the humid climate (Harmon 1982b). However, my data provide evidence that forest structure was open in the past. First, the low number of trees that predate the post-fire cohort, particularly in the xeric pine and sub-xeric oak stands, suggests that these forests exhibited low density. Second, the large number of trees establishing immediately after the last major fire, including shade intolerant yellow pines, indicates that the canopy was fairly open when this cohort established. The lack of older trees and primarily even aged structure cannot be attributed to logging or agricultural clearance in this unlogged watershed. It is possible that the last fire or series of fires were high intensity, canopy replacing events facilitating the establishment of a major cohort of pines, oaks, and xeric hardwoods. Another possibility is that frequent fire maintained open pine and oak woodlands on the drier upper slopes. Harrod et al. (2000) estimated that during the early 20th century most xeric sites in GSMNP were occupied by early successional communities with open canopies and sapling layers. There may have been gradients from woodland to closed canopy forest along the moisture gradient, with canopy cover increasing from xeric ridges to mesic cove positions. Similar gradients in forest structure have been hypothesized in pre-settlement forests along moisture gradients and gradients of anthropogenic fire (Nuzzo 1986, Dorney and Dorney 1989, Anderson 1998). The use of radial growth measurements to detect growth releases in older pine and oak cores could aid in determining whether stands were continuously open in the past.

In contrast to the open, woodland structure that may have existed in the past; forests at the site today exhibit closed canopies and high tree density. Stand density is highest at the xeric end of the moisture gradient. Since Whittaker carried out his study, pine and oak-chestnut heaths have succeeded to closed canopy forests. The resulting changes in light levels in the understory have important implications for tree establishment and shrub and herbaceous communities. Increases in forest density related to fire suppression in ponderosa pine, shortleaf pine, and longleaf pine communities have resulted in declines in diversity of understory communities (Covington and Moore 1994, Sparks et al. 1998). Similar changes in the understory of northern hardwood forests have also been noted (Rooney et al. 2004). Understory plant diversity plays an important role in ecosystem function, providing food resources, nutrient cycling, and regulating overstory regeneration (Hart and Chen 2006, Gilliam 2007).

Differences in Cove Forests

Differences in the composition and structure of the north and south cove forests suggest that fire may have influenced the north cove stands, which are adjacent to the frequently burned south facing slope. Neither the north nor south cove plots exhibited pulses of establishment that clearly coincided with fire exclusion. The pulse of establishment in the north cove plots aligns most closely with the arrival of chestnut blight. North cove stands one and three are primarily even aged hemlock stands that established in the 1930s. They exhibited high stem density and sapling density, suggestive of a stand recovering from major canopy disturbance. Initially, I thought that this stand might be a product of a fire that burned down into the cove position and caused heavy mortality among fire sensitive cove species. However, there were no widespread fires at the site during this period. Additionally, both of these stands contained older oaks, maples, and xeric hardwoods that predated the hemlock pulses. Therefore it is more likely that hemlock establishment was a response to chestnut blight. The extent of establishment in these stands in the 1930s suggests that chestnut was a major component of the north cove stands prior to the blight.

Chestnut has generally been viewed as a former dominant in xeric upper ridge and sub-xeric mid-slope forest communities in GSMNP (Whittaker 1956). However, several studies have noted a high frequency of chestnut in mesic stands preceding the blight (Woods and Shanks 1959, Vandermast and Van Lear 2002). In their broad assessment of chestnut replacement in GSMNP, Woods and Shanks (1959) were surprised by the mesic nature of chestnut which was commonly associated with hemlock, yellow poplar, fraser magnolia, sweet birch, and a number of other mesophytic species. Their data led them to the conclusion that chestnut should be identified as a member of the Appalachian rich cove forest type. Vandermast and Van Lear (2002) noted a high frequency of chestnut stumps in contemporary riparian forests of the southern Appalachians. It is possible that chestnut distribution extended further into mesic cove positions in locations that were subject to fire disturbance (e.g. the north cove stands adjacent to the frequently burned south slope of Licklog Ridge). Historically, chestnut has been shown to increase in frequency in landscapes that are burned (Delcourt and Delcourt 1998, Foster et al. 2002).

In contrast, the three south cove stands more closely approximated the structure and composition of typical old growth mesic forests described in the literature (Whittaker 1956, Lorimer 1980, Clebsch and Busing 1989). The stands exhibited an uneven age distribution, high basal area, low stem density, and low seedling density. Trees that established in the south cove stand prior to fire suppression were primarily fire intolerant species such as, yellow poplar, hemlock, sweet birch, Carolina silverbell, and white basswood. The oldest trees in the north cove stands were hickories, chestnut oaks, northern red oaks, red maples, black gums, and a single sweet birch. The north cove stands contained no hemlock or yellow poplar stems that predated 1895. There is a pulse of establishment in south cove stand two that aligns with chestnut blight disturbance, but the number of stems successfully establishing is much lower than in the north cove stands. The difference in species composition of the north and south cove stands can also be seen in the classification and ordination. During the fire phase, two of the three north cove plots were classified in the mixed oak-hardwood group. Following fire cessation, the north cove stands migrated into the cove forest group along with the south cove stands.

The differences in composition and structure between the north and the south cove stands suggests that fires occasionally burned into the north cove stands adjacent to the frequently burned south slope of Licklog Ridge. I don't think that fires were nearly as frequent in the cove positions as they were on the south slopes. Perhaps fires only burned into the cove positions during extreme droughts. Occasional fires would explain the lack of older hemlocks and yellow poplars in the north cove stands. In contrast, the south cove stands were protected from fire disturbance by their position on the opposite side of Licklog creek. Harmon (1982a) estimated that north facing lower slopes were the least frequently burned landform position prior to fire suppression in GSMNP. Research in other regions has demonstrated the influence of fire prone landforms and fire breaks on pre-settlement forest composition (Leitner et al. 1991).

Post-fire Successional Processes

Temporal changes in tree establishment at the site reflect three different successional environments. These distinct successional environments were the basis for dividing the ordination samples into three successional phases: fire, fire exclusion, and mesophication. During each of these phases tree establishment was affected by differing levels of fire disturbance, light availability, and moisture availability. Changes in these controls on tree establishment are responsible for the pulses of establishment and the consequent movement of the plots within ordination space. The magnitude of the change in successional environment from one period to the next differed along the moisture gradient. For example, the change in fire disturbance impacts between the fire phase and the fire exclusion phase was probably greatest in the xeric pine stands and least in the cove stands. Similarly, changes in light levels and moisture during the transition from the fire exclusion phase to the mesophication phase were probably greatest in the xeric pine stands.

Establishment during the initial fire period was limited by fire disturbance and moisture availability. Fire disturbance preferentially selected for fast growing, fire resistant species. Fire also produced an open canopy, high light environment that enabled the establishment of shade intolerant species. Moisture limitations may have been amplified due to increased solar radiation at the ground surface. Yellow pine proliferated on the xeric sites and chestnut oak, likely along with chestnut, dominated sub-xeric and sub-mesic stands. Both of these species thrive in high light environments (Abrams 1992, Mikan et al. 1994, Brose and Van Lear 1998, Jenkins et al. 2011) and have thick bark that enables them to survive low intensity fires (Harmon 1984). Yellow pines and chestnut oak dominated slopes in Virginia that were frequently burned in the past (Hoss et al. 2008, Aldrich et al. 2010). Topography appears to control the balance between pines and oaks, with yellow pines dominating upper ridges and south facing slopes, while chestnut oak and chestnut dominated the remaining aspects. Topographic moisture seems to be the driver. However this process may be due to direct moisture limitation of vegetation or through moisture influences on fire characteristics (frequency/severity) and subsequent mortality. Ultimately, the result of the successional environments present on the landscape during the fire phase is four distinct communities: yellow pine, chestnut oak, mixed oak-hardwood, and cove.

The fire exclusion phase is a transitional stage. Fire disturbance is no longer limiting establishment. However, due to the open canopy, light levels remain high and moisture availability varies by aspect and topographic position. The result is intense competition within the post-fire cohort in a race to the canopy. Early successional, fast growing species are successful during this period. Topographic position influences the outcome of interspecific competition, with different species dominating this stage in the different stands. Pines successfully regenerate on the driest sites along with red oaks, xeric hardwoods and red maples to a lesser extent. Consequently, compositional change is limited in the pine stands during this stage. In contrast, the canopy dominant chestnut oaks failed to regenerate in the sub-xeric and sub-mesic stands. Red maples dominate establishment in the oak stands during the post-fire period, initiating more rapid compositional change in these stands.

Eventually, the canopy closes and the stands move into the mesophication phase. This third phase is characterized by continued absence of fire, low light conditions, and increased moisture availability. The conditions promote later successional, shade tolerant species. Red maple continues to establish in the drier pine and oak stands. White pine and hemlock, absent from the initial post-fire cohort, begin to establish in the pine, oak, and white pine-hardwood stands. Hemlock establishment is most notable in the sub-mesic stands. Hemlock establishment in the xeric and sub-xeric stands has initiated only recently and has been less pronounced. Hemlock seedlings are generally shallow rooted and susceptible to drought and high temperature (Burns and Honkala 1990, Mladenoff and Stearns 1993). It has been suggested that the transition from oak and pine to mesic hardwoods will increase moisture levels in the forest understory due to changes in light levels and litter composition (Nowacki and Abrams 2008). Therefore it is likely that, were hemlock wooly adelgid not present, hemlock establishment would increase in the xeric and sub-xeric stands as the mesophication process advances and moisture availability increases.

Successional change will likely continue in the stands as the remnant trees from both the fire and fire exclusion period are eventually replaced by the mesophytic, shade tolerant species that currently dominate the understory. The length of time before complete successional conversion depends on the longevity of the overstory species. Chestnut oaks are long lived and may persist in the overstory of the oak and white pine-hardwood stands for centuries. The presence of chestnut oak in the overstory ensures a long term seed source for restoration. Yellow pines are shorter lived, particularly in dense contemporary stands where they are susceptible to pine beetle infestation (Schowalter et al. 1981, Showalter and Turchin 1993, Knebel and Wentworth 2007). An intense outbreak of pine beetle occurred at the site from 1998-2001, removing the majority of mature pines at the site. Consequently there is a concern about adequate seed sources for restoration of yellow pine stands in the region.

One interesting difference between the Licklog site and post-fire suppression pine and oak stands sampled in Virginia is a lack of dense *kalmia* in the understory. *Kalmia* was clearly present when Whittaker sampled the area. Perhaps my sites are further along in the successional sequence responding to both fire suppression and chestnut blight. The southern Appalchians are warmer and wetter than the central Appalchians. Therefore forests at my site should be more productive and likely would progress through the successional sequence more quickly. It would have important implications if the lack of a dense ericaceous understory is due to a more advanced stage of succession in my stands. Currently there is great concern about the effects of ericaceous shrubs on regeneration in former pine and oak stands (Swift et al. 1993, Dobbs and Parker 2004). In other regions it has been hypothesized that a dense ericaceous layer will impede tree establishment and eventually convert forests into shrublands (Mallik 1995). However, the lack of a dense shrub layer at my sites suggests that ericaceous coverage is not necessarily impeding tree establishment.

Impact of Chestnut Blight

American chestnut was a species of great importance in forests of the southern Appalachian region, composing up to 70% of the canopy in particular stand types in GSMNP (Whittaker 1956, MacKenzie and White 1998). Therefore, it was not surprising to find pulses of establishment at Licklog during the 1930s, following the arrival of chestnut blight. However, I did not expect to find these post blight cohorts primarily in the submesic and mesic forests types. The absence of chestnut sprouts in the contemporary understory seems to indicate that chestnut was not a major component in submesic and mesic stands. However, previous examinations of chestnut sprouts persisting in the understory of contemporary forests have noted that chestnut sprouts are currently absent from stands where chestnut was formerly abundant and that environmental conditions at the time of chestnut blight arrival may have strongly influenced the persistence of chestnut sprouts (Paillet 1988, 2002). Ultimately, the establishment of large cohorts immediately following the arrival of the blight provides strong evidence that chestnut was widely distributed in the sub-mesic and mesic stands. However, I cannot definitively determine their presence. A future assessment of radial growth releases in the different stand types might further clarify the role of chestnut blight in the formation of these cohorts.

The large white pines that dominate the overstory of the sub-mesic stands established during the post-blight cohort. I am aware of no previous studies that note white pine as a replacement species for chestnut. This is interesting considering the strength of the trend in the stands shown here and the fact that white pine is a species that readily seeds into disturbed areas and exploits canopy gaps (Hibbs 1982, Burns and Honkala 1990). Generally, oaks, hickories, and maples are recognized as the species that benefited from chestnut removal (Keever 1953, Nelson 1955, Woods and Shanks 1959, McCormick and Platt 1980). Perhaps the early cessation of fires at this site enabled white pine establishment following chestnut blight. Forests that continued to experience fires through the era of chestnut decline may have been more likely to succeed into oak or hickory. White pine abundance declined in forests that were both logged and burned in Pennsylvania (Abrams and Nowacki 1992, Nowacki and Abrams 1992).

The north and south cove stands both exhibit pulses of hemlock establishment that coincide with the impacts of chestnut blight in GSMNP and the initiation of establishment in the white-pine hardwood stands in the 1930s. If these cohorts are related to chestnut blight, then the larger establishment cohorts in the north cove stands compared to the south cove stands indicate that chestnut was a larger component on the north side of Licklog Creek. This interpretation would also indicate that hemlock was a replacement species for chestnut on mesic cove sites.

The lack of post-chestnut blight regeneration in the pine and oak stands is probably a result of post-fire successional processes. Chestnut was a significant component of pine and oak stands prior to the blight (Whittaker 1956, Woods and Shanks 1959, MacKenzie and White 1998). Chestnut sprouts are still common in the understory of the oak stands today. However, at the time of chestnut decline, a dense understory of *kalmia* and tree saplings had probably established in the open light environment following the cessation of fires. This dense understory likely prevented the establishment of large post chestnut blight cohorts in the xeric and sub-xeric stands. In contrast, the post-fire cohorts were less pronounced in the sub-mesic stands due to a less open canopy at the time of fire cessation. The removal of chestnut from this closed canopy would have provided more opportunity for regeneration during the 1940s and 1950s.

Individual Species Responses

Pines

Yellow pine reproduction was clearly linked to fire disturbance and the high light conditions produced by fire. Pre-fire suppression pine stands were dominated by Table mountain pine along with pitch pine and black gum. There were a limited number of yellow pines that predated fire suppression in my plots, but this was likely a reflection of low stand density and my limited plot size (as discussed above). Yellow pine cross-sections collected for the fire history reconstruction demonstrate that pines were established widely across the site at least as early as the mid-18th century. Table mountain pine and pitch pine are both adapted to fire disturbance and capable of surviving frequent low intensity surface burns.

Current pine stands are dominated by individuals that established immediately following the last fire. Both yellow pines have shade intolerant seedlings that regenerate most successfully immediately following a fire disturbance (Zobel 1969, Williams 1998, Jenkins et al. 2011). Under the preceding frequent fire regime most of these new seedlings would have been killed by subsequent fires, with occasional seedlings surviving due to rapid growth or heterogeneity in spatial or temporal patterns of fire. Following the last fire on the site, this pulse of pine regeneration was not thinned and the result has been a primarily even aged pine overstory. This pattern has been noted in yellow pine stands across the southern Appalachian region (Harrod and White 1999, DeWeese 2007, Hoss et al. 2008, Aldrich et al. 2010, Hessl et al. 2011). The presence of even aged cohorts has been interpreted as evidence of high intensity fires occurring immediately prior to fire suppression (Williams 1998, Hessl et al. 2011) or ongoing successful regeneration in the absence of fire (Whittaker 1956). However, these cohorts are more likely the product of the open canopy in pine forests immediately following the last fire.

Pines regeneration stopped after the initial pulse, likely due to canopy closure. There was some regeneration following the recent pine beetle outbreak. High stand density likely contributed to the severity of the pine beetle outbreak, which also caused white pine mortality at the site. However, regeneration appears patchy and will likely include a significant hardwood component. Yellow pine will be an increasingly smaller component of the overstory due to mortality and hardwood replacement. Consequently, with fewer yellow pines in the overstory, future pine beetle outbreaks will create smaller openings in the canopy and less opportunities for yellow pine regeneration. Therefore, pine beetle outbreaks are unlikely to perpetuate yellow pines at the site in the absence of fire or other major canopy disturbances.

Oaks

Chestnut oak was a dominant species, probably along with American chestnut, in the sub-xeric and sub-mesic forests prior to fire suppression. Chestnut oak has thick bark and is recognized as one of the more fire resistant oak species (Abrams 2003). Chestnut oak has been noted as a dominant in other frequently burned stands in the central Appalachian Mountains of Virginia (Hoss et al. 2008, Aldrich et al. 2010). There has been no recruitment of chestnut oaks into the tree strata since 1940. Chestnut oak is well represented in the seedling layer, but nearly absent from the sapling layer. It appears that chestnut oak seedlings are unable to compete in the dense, low light understory (Lorimer et al. 1994). The decline of chestnut oak represents a drastic compositional change, since chestnut oaks were a major component of both the oak and white pine-hardwood stands prior to fire suppression. Chestnut oaks are probably outcompeted on these sites by other hardwoods, in particular maples. In contrast to yellow pines, chestnut oaks did not regenerate in the post-fire cohort. This pattern was different from the results found by Aldrich et al. (2010) and Hoss et al.(2008) .

Scarlet oak did regenerate successfully in the post-fire cohort, particularly in the pine stands. It is a frequent component of current xeric ridge communities. Scarlet oak is less fire tolerant than chestnut oak and has increased in prominence in other stand where fire frequency has declined (Hoss et al. 2008). Some have hypothesized that oaks will invade and successfully persist by replacing pines on the driest site (Williams and Johnson 1990, Williams 1998, McEwan and Muller 2006). If oaks are viewed as a whole then early stand response might indicate that oaks are successfully regenerating on the most xeric sites. However, the maintenance of oaks on xeric sites is largely a function of increases in scarlet oak, which was not a major component of forests at the site prior to fire suppression. Additionally, scarlet oaks have not recruited into the tree strata during recent decades despite being fairly abundant in the sapling and seedling layer. It is unclear if scarlet oak will continue to recruit into the canopy on these xeric sites.

Red Maples

Red maple is the species that has benefited most from fire exclusion. Outside of the cove forests, there were few red maples on the landscape that predated fire suppression. However, red maple was a major component of tree establishment following fire suppression in the pine, oak, and white pine-hardwood stands. It appears that red maple competes most successfully in the middle of the moisture gradient. Today, the species exhibits the highest relative importance in oak stands and the second highest relative importance in white pine-hardwood stands. The species is likely to maintain or increase its dominance in these stands due to strong representation in both the sapling and seedling layers. The success of red maple in the understory of pine and oak forests is a trend that has been noted throughout eastern North America (Lorimer 1984, Abrams 1998, Harrod and White 1999, Hutchinson et al. 2008).

In the pine stands, red maple was a smaller proportion of the post-fire establishment pulse. However, they continued to establish in these stands after the early successional pines and oaks stopped establishing. The trend seems to indicate that maples are less competitive on the driest sites during this initial stage of succession. However, they appear to compete well on the xeric sites later in the successional series once the canopy has closed. Perhaps the sites are too droughty in the early stages of post fire succession. This trend could also be due to red maples prolific sprouting. It is possible that the rapid establishment of red maples in the oak and white pine-hardwood stands is due to advanced regeneration from individuals that were top killed by fires. Higher fire frequency or fire intensity in the pine stands may have prevented establishment or continued re-sprouting of red maples prior to the last fire, resulting in a delayed establishment through seed. Regardless of the cause of the delay, red maple appears to be gaining importance in pine stands and it is well represented in seedling and sapling layers.

Hemlock

Hemlock is recognized as a mesic cove species at lower elevations in the southern Appalachians (Whittaker 1956, Callaway et al. 1987). Yet the species has begun to invade xeric sites at Licklog during recent decades. Prior to fire suppression, hemlocks were even more restricted than red maples, with older individuals occurring only in the south cove plots. Hemlock seedlings are shallow rooted and particularly susceptible to drought (Mladenoff and Stearns 1993). Hemlocks were only able to establish outside of the cove stands during recent decades as canopies closed following the initial stage of post fire succession. Canopy closure would have reduced sunlight at the forest floor and increased moisture availability. Changes in leaf litter composition may have also impacted moisture availability and increased suitability for hemlock establishment (Nowacki and Abrams 2008). Hemlocks have become a particularly important component of the white pine-hardwood stands and are now the most common species in the sapling layer. It appears that hemlock can successfully compete at mid-slope positions under a closed canopy in the absence of major canopy disturbances.

Community Diversity

Regarding my second research question, tree establishment patterns suggest that ongoing successional change following fire suppression will eventually result in forest homogenization and a decline in beta diversity at Licklog Ridge. Conclusions regarding changes in diversity at the site are not definitive, since contemporary dendroecological sampling cannot fully determine past species composition. Contemporary sampling will necessarily miss some trees that were present in the plots during earlier periods but have not persisted until today. Yet, the long life span of the tree species sampled indicates that my data set provides a good assessment of past species composition. None of the species included in the ordination assessment exhibit life spans shorter than 100 years, which would explain their absence from earlier age classes. Dendroecological studies commonly use tree ages to determine successional trends in sampled forests (Frelich and Reich 1995, Abrams and Copenheaver 1999, Taylor 2000b). While the quantification of diversity within the different age classes is not an ideal assessment of past diversity; I think that the analysis provides valuable information on the potential outcome of successional trajectories at the site.

Vegetation disturbance has been recognized as an underlying control on species diversity (Grime 1973, Connell 1978a, Huston 1979). Plot level species richness increased dramatically in the pine and oak communities following the cessation of fires. These xeric and sub-xeric sites were invaded by more competitive species such as red maple, sourwood, scarlet oak, white pine, and hemlock. Increases in species richness were not as great in the more mesic white pine-hardwood and cove plots. The changes in species richness are consistent with Huston's dynamic equilibrium model which predicts species richness as a balance between disturbance and rates of competitive displacement. Low rates of competitive displacement on the drier, less productive sites result in higher species richness following a decline in disturbance frequency. Species richness has increased as competitive species invade sites that were formerly inhabited by disturbance tolerators. However, it remains to be seen whether rates of competitive displacement are sufficiently low to maintain both the competitive species (e.g. maple and hemlock) and the disturbance tolerators (e.g. pines and oaks). Younger age classes, saplings, and seedlings seem to indicate that the disturbance tolerators will eventually be displaced and species richness will decline in the xeric and sub-xeric stands.

Calculations of beta diversity indicate a trend of increasing compositional similarity between the different stand types. Red maple and hemlock establishment are the drivers of forest homogenization on the xeric and mesic ends of the moisture gradient, respectively. Red maple's ability to compete successfully under closed canopies in the absence of fire has driven homogenization at the xeric, sub-xeric and sub-mesic positions. Hemlocks have established across the entire moisture gradient, but have been particularly dominant in the submesic and mesic positions. Similar declines in landscape diversity have been noted in pine-oak-hemlock forests in the forests of Wisconsin (Rogers et al. 2008, Amatangelo et al. 2011). The loss of chestnut from the record probably did not impact the beta diversity results significantly, since it was likely distributed across the entire moisture gradient.

Cluster analysis and ordination provided an additional assessment of beta diversity that accounted for species abundance rather than species presence or absence. Cluster analysis performed on tree establishment phases identified the following four distinct community types: yellow pine, oak, white pine-hardwood, and cove forest. These four communities match Whittaker's (1956) characterization of forest associations along the topographic moisture gradient in GSMNP. The lack of chestnut in my sample has resulted in a modification of Whittaker's chestnut oak-chestnut heath and the chestnut oak-chestnut forest. Whittaker's sub-xeric chestnut oak-chestnut heath type matches my oak stands dominated by chestnut oak in the absence of chestnut. Whittaker's sub-mesic chestnut oak-chestnut forest has been replaced by a mixed hardwood stand (today's white pine-hardwood stands following the loss of the chestnut). All four of these groupings were represented on the site during the fire successional phase. Fire disturbance, light availability, and moisture availability varied with topographic position, promoting a range of different species assemblages including pine stands, chestnut oak-chestnut stands, mixed hardwood-chestnut stands, and cove forest stands.

The removal of fire has resulted in changes in the composition of tree establishment and a reduction in the number of communities establishing at the site. Younger age classes now fall into two groups, the mixed hardwood and cove forest types. The oak and pine stands have moved into the mixed hardwood group. The mixed hardwood and north cove stands have shifted into the cove group. Consistent with the mesophication hypothesis, each of these stand types has succeeded toward more mesic species assemblages. The south cove stands were the only communities that remained relatively stable throughout each of the three successional phases. The south cove stands probably did not experience fire disturbance prior to fire protection, therefore compositional change associated with fire exclusion should be minimal in these stands. South cove stand two did move towards the middle of the ordination space during the most recent successional phase. This was due to recent sapling responses to canopy openings resulting from the hemlock wooly adelgid. The final phase lacks variation in fire disturbance and light levels enabling certain competitive, late successional species to dominate along a wide swath of the moisture gradient, particularly red maple and hemlock. Post-fire succession has resulted in a contraction of the plots within ordination space, indicating that there has been a decline in compositional variance. This decline in compositional variance is primarily due to the decline in population reduction from fire disturbance. However, the length of the moisture gradient has probably also declined with the closure of the canopy on the driest sites. These two factors appear to be driving the decline of compositional variance (i.e. beta diversity) at the site.

Continued successional change is likely to reduce future landscape level species richness (gamma diversity). In the absence of fire disturbance yellow pines are unlikely to remain in the landscape. The understory, sapling, and seedling layers in yellow pine stands are dominated by shade tolerant red maples and other hardwoods. The recent pine beetle outbreak has spurred some yellow pine regeneration. Yet even if these pines are able to reach the canopy they will be scattered within a matrix of mesic hardwoods. Therefore, future pine beetle outbreaks will produce single tree gaps in the canopy which are unlikely to provide enough light for another generation of yellow pine establishment. My results do not suggest that the driest sites will provide refuge for either pines or oaks. At the landscape scale there are few rocky outcrops that are unlikely to be invaded by hardwoods. Complete forest conversion is not unprecedented, with similar successional change occurring in the temperate forests of Northern and Central Europe as a result of fire suppression at the end of the 18th century (Niklasson et al. 2002, Lindbladh et al. 2003, Niklasson et al. 2010). This transition is likely to accelerate due to pine beetle disturbance in the yellow pine and white pine-hardwood stands. The hemlock wooly adelgid will also impact future forest composition. Declines in hemlock regeneration in northern forests have been shown to benefit red maple (Rooney et al. 2004). The replacement of hemlock with red maple could result in further homogenization of forest communities.

Management should be guided by the goal of promoting diversity at multiple scales, including community diversity, species diversity and genetic diversity. Prescribed fire not only benefits individual species, but also promotes beta diversity. Increased beta diversity means a wider range of habitats available for a host of other ecosystem components. Diversity at multiple scales also increases the resilience of natural systems, which may be particularly important in the face of projected climate changes. The restoration of fire-associated habitat types provides an opportunity to increase species and community diversity on public lands in the eastern United States. Active restoration burning in these communities would likely benefit threatened species and provide additional habitat diversity in southern Appalachian forests.

CHAPTER VI

CONCLUSION AND RECOMMENDATIONS

"About as soon as the blackberries were gone, the blueberries were ripening on the piney south slopes of the surrounding ridges. The slopes were burned regularly, if not by lightning fires, then someone seeing to it that the berry crop would be good. If the slopes were not burned every three to five years, the process of succession would gradually eliminate the berry shrubs and later the pines. Pruning by burning encouraged the young growth of the blueberries, which produced the most fruit. I can still remember my delight as a child in seeing the beautiful fire patterns on the ridges at night when the undergrowth on the slopes was being burned."

-Arthur Randolph Shields, The Cades Cove Story, p. 20.

This dissertation provides a characterization of fire disturbance in the southern Appalachian Mountains and its contribution to vegetation pattern. In one sense, each of the dissertation pieces is an individual case study. Contingent events, many of which were anthropogenic in origin (e.g. fire suppression, fire ignitions, introduction of the chestnut blight) have influenced the processes I examined in each of the research sections. However, the research approach was designed with the intention of characterizing environmental processes that apply beyond these individual landscapes. My results include both basic and applied scientific knowledge. The following is a list of conclusions drawn from my research:

Contemporary Landscape Patterns of Fire

- Landscape patterns of fire disturbance in the region reflect the underlying control of moisture, which results in increased fire activity during dry years, in dry regions, and on dry topographic positions (i.e. upper slopes, south-facing aspects, and lower elevations).
- Dry conditions, both temporally (dry years) and spatially (dry regions), weaken topographic patterns of fire disturbance.

Fire History

- Prior to 1920, fires were frequent at all three fire history reconstruction sites, with mean composite fire intervals of 2.2-4 years.
- The two longer records (Licklog Ridge and Linville Mountain) demonstrated frequent fire prior to Euro-American settlement.
- Excluding the fire protection era, there were no significant changes in fire frequency during past land use periods (Native American, Euro-American, Industrial).
- There was little discernible influence of climate on past fire occurrence, with fires recorded during both dry and wet years.
- Fires occurred primarily during the dormant season

Vegetation Dynamics

- Tree ages reflect changes in establishment patterns due to fire exclusion in four different community types located at xeric, sub-xeric, sub-mesic, and mesic topographic positions.

- Fire tolerant, disturbance associated species (e.g. pine and oak) are being replaced by mesophytic species (particularly red maple and hemlock).
- Changes in community composition due to fire suppression are driving a decline in beta diversity, primarily through the loss of xeric pine and oak communities.

Scientific Contribution

Fire Disturbance

The findings in this dissertation contribute to the fields of vegetation disturbance and vegetation dynamics. The examination of historical and contemporary fire disturbance adds to the growing literature characterizing fire in the Appalachian Mountain region (Barden and Woods 1974, Harmon 1982a, Lafon et al. 2005, Lafon and Grissino-Mayer 2007, Wimberly and Reilly 2007, Hoss et al. 2008, Aldrich et al. 2010, Lynch and Hessl 2010). The influence of climate and landform on patterns of fire contributes to the broader field of fire science. The recognition that topographic patterns of fire are weaker during more extreme conditions (i.e. drought) may have important implications for fire disturbance patterns globally, particularly in temperate regions.

The dendroecological reconstructions of fire provide evidence that historically, fire was an important process in southern Appalachian forests. The fire history record indicates that fires burned frequently, at least in portions of the southern Appalachian landscape for centuries prior to the advent of fire protection. Consequently, it is important that fire be considered in the suite of disturbance processes that historically shaped forests in the region. Future research should expand the network of fire history reconstructions in the southern Appalachians. Fire records from sites with varying land use history, climate, and landforms could provide insight into the variability of past fire regimes in the region. Fire history sampling across a broader landscape, perhaps several adjacent ridges, could also provide important information on the size and spread of fires.

The differing climate responses between past and contemporary fires raises new questions about the role of humans in temperate fire regimes, particularly during past land use episodes. While I cannot definitively conclude the source of ignitions for historical fires, it seems likely that a significant portion of the fires were human in origin. The lack of strong fire-climate relationships found in this study, combined with other reconstructions from forests in eastern North America (Guyette et al. 2003, Schuler and McClain 2003, McEwan et al. 2007b, Allen and Palmer 2011, Stambaugh et al. 2011), and Europe (Lindbladh et al. 2003, Drobyshev et al. 2004, Niklasson et al. 2010), suggest that climate may play a less central role in human driven fire regimes. Consequently, the search for interaction between broad climate forcing mechanisms (e.g. El Nino Southern Oscillation or North Atlantic Oscillation) and past fire occurrence may not be as important in the historically more densely populated eastern landscapes compared to the less densely populated landscapes of the Rocky Mountains. Our understanding of fire-climate relationships would benefit from continued research in temperate forests globally that experienced a range of human impacts.

Forest Dynamics

The section on vegetation dynamics contributes to the body of literature addressing old growth forest dynamics in the southern Appalachian Mountains (Whittaker 1956, Lorimer 1980, Busing 1998, Harrod et al. 1998). This study is the first to incorporate fire disturbance into a conceptual model of xeric to mesic forest dynamics in the region. My results provide further evidence of post-fire compositional change in xeric oak and pine stands (Harrod et al. 1998, Harrod and White 1999, Harrod et al. 2000) and the first direct evidence of post-fire successional change in mesic forest types. Previous work noted evidence of fire in mesic southern Appalachian forests, but the authors were unable or chose not to incorporate fire into their explanation of the underlying drivers of vegetation pattern (Whittaker 1956, Lorimer 1980). In this dissertation, the integration of a long term, annually resolved fire record along with vegetation data from an unlogged watershed allowed me to draw more direct conclusions about the impacts of fire exclusion on vegetation arrangement in this landscape. Additional research on fire patterns in mesic forests types and vegetation response is greatly needed. This information could be obtained from multiple data sources including early settlement surveys, historical records, pre-logging timber assessments, and early surveys of vegetation in GSMNP. Another potential approach would be a re-examination of data collected in old growth studies in the region (e.g. Whittaker 1956, Lorimer 1980) with an eye for the influence of fire regime changes.

The decline in community diversity at Licklog has important implications for our understanding of the role that disturbance plays in maintaining diversity. Previous work in the southern Appalachian region has hypothesized that fire disturbance contributed to habitat diversity in the past (Harmon 1982a, Delcourt and Delcourt 1998) and my work provides evidence that supports this view. I cannot definitively state whether a similar process of forest succession and decline in community diversity has occurred in the wider southern Appalachian landscape. However, examination of previous scientific research, historical literature, and current vegetation distribution seems to indicate that fire adapted communities were distributed widely in the region (Whittaker 1956, Zobel 1969, Delcourt and Delcourt 1998). The loss of fire-adapted communities is likely to result in a decline of community diversity across much of the forested landscape in the southern Appalachian Mountains.

Management Recommendations

In the past, fire disturbance and fire-associated vegetation were an important component of the landscape at each of the three sites sampled in this dissertation. Fire maintained habitats were likely common throughout the southern Appalachian region. In contrast, fire maintained habitats are essentially non-existent in the region today. The work from this dissertation, along with a number of other dendroecological reconstructions from the Appalachian Mountains (DeWeese 2007, Hoss et al. 2008, Aldrich et al. 2010) have built a strong case for the reintroduction of fire in upland pine and oak stands. Clearly, the current forest communities at the sites will not persist under the policy of fire protection. The pre-settlement origin of the forest overstory, the high level of diversity, and the magnitude of recent changes in vegetation should make these sites, particularly Licklog Ridge, a conservation priority.

Critics have questioned the wisdom of re-introducing fire to public forests on the grounds that fire disturbance often promotes exotic species and edge species that are already abundant in agricultural and urban landscapes (Noss 1983, Hessl et al. 2011, Mandle et al. 2011). However, fire maintained upland pine-oak woodlands are fundamentally different from agricultural and urban landscapes, providing habitat that does not currently exist anywhere in the region. As a result, many species associated with fire disturbed ecosystems are currently threatened or declining in the Appalachian

Mountains, e.g. Peters Mountain mallow (Iliamna corei Sherff), mountain goldenheather (Hudsonia montana Nutt.), eastern turkeybeard (Xerophyllum asphodeloides (L.) Nutt). and red-cockaded woodpeckers (Picoides borealis) (Dimmick et al. 1980, Gross et al. 1998, Bourg et al. 2005).

The restoration of pine and oak communities may be challenging due to the extent of hardwood succession within these stands (Abrams 2005). Recent studies of prescribed burns have shown that a single fire will not necessarily promote pine and oak regeneration (Waldrop and Brose 1999, Welch et al. 2000, Elliott and Vose 2005, Albrecht and McCarthy 2006). In contrast, a single prescribed fire can actually increase the density of undesirable hardwoods due to aggressive post-fire sprouting. Successful regeneration of pine and oak may require multiple burns over several years to eliminate competing hardwood sprouts, reduce duff and litter layers, and open the canopy (Elliott et al. 1999, Welch et al. 2000). Additionally, many of the mesophytic hardwoods have reached a size that will allow them to survive low intensity fires (Harmon 1984). Therefore, during initial stages of restoration it may be necessary to carry out mechanical thinning in concert with prescribed burns to remove undesirable species and reduce forest density (Brose and Van Lear 1998, Iverson et al. 2008).

Declining seed sources are another potential limitation to restoration of these communities. Yellow pine seed sources are severely limited due to the recent pine beetle infestations and the trees shorter life span. Chestnut oak seed sources are likely to remain on the landscape for longer due to the trees longer lifespan. Restoration of American chestnut is obviously untenable currently, but chestnut oak might fill certain aspects of

American chestnut's former niche. Additionally, blight resistant American chestnuts may be available for restoration in the future.

Due to the current uncertainty of restoration outcomes and the likely expense of forest restoration, a targeted approach would be most prudent. Managers could focus on a limited number of demonstration areas. Licklog Ridge would be a particularly appealing site for restoration since it is within a heavily visited park, fire history exists for the site, and it is in close proximity to Cades Cove which has a long history of management as an anthropogenically shaped landscape. The restoration of a fire maintained habitat would provide visitors with another ecosystem type that is quite rare today, but traditionally covered large portions of the landscape.

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APPENDIX A

STANDARD TREE-RING CHRONOLOGY TABLES

A1. Standard tree-ring chronology for House Mountain, TN. These values are the tree-ring indices for each year in the chronology. The indices are displayed without the decimal points, but the actual value can be obtained by dividing the numbers by 100. The mean value for all indices is 1.0. Each line represents one decade of indices and the decades are shown in the left hand column. The numbers across the top of the table are the last numbers of the decade year for each decade. This is called the“Tucson format” and is the internationally accepted format of the World Data Center for Paleoclimatology.

Year	0	1	2	3	4	5	6	7	8	9
1754					697	1332	1313	1002	862	1069
1760	1080	1076	1005	577	822	881	819	807	883	829
1770	754	830	770	874	1068	1480	1159	1166	1036	995
1780	867	1014	841	1133	928	683	1000	1189	1432	1641
1790	1693	1138	924	1130	851	790	999	907	1187	994
1800	1080	1071	1058	872	497	646	739	568	839	879
1810	998	832	987	1000	998	881	981	1472	1396	1457
1820	1130	1130	1091	963	784	949	992	1089	1308	1115
1830	930	1251	1022	936	1130	927	1187	1062	937	740
1840	1074	760	1217	1150	1193	1012	903	1079	921	1341
1850	967	968	1072	1152	888	1038	698	753	1046	1398
1860	1108	1435	1054	1093	856	689	926	856	1072	856
1870	1334	939	838	894	837	1158	1137	1084	1177	725
1880	1134	774	1459	1004	1264	1240	1255	896	1468	1384
1890	1163	916	1005	875	571	565	702	887	782	541
1900	656	933	575	930	926	1330	1043	1073	953	1124
1910	1300	716	1156	692	819	1155	1301	957	846	1001
1920	1272	1005	1080	1056	829	620	1239	1196	1249	1224
1930	753	887	1038	1489	1045	1091	630	1191	1403	849
1940	1025	790	968	989	992	1656	1204	1013	1366	1171
1950	1206	812	749	1018	767	890	1277	1086	943	772
1960	896	978	606	868	706	837	674	1190	1237	1527
1970	1109	885	726	1021	1194	1075	1067	1037	897	855
1980	587	906	1084	708	980	655	573	646	610	891
1990	1089	1137	931	882	1185	887	1349	1130	1040	1250
2000	1169	833	774	1157	1185	1074	977	927	691	946

A2. Standard tree-ring chronology for Licklog Ridge, TN. These values are the tree-ring indices for each year in the chronology. The indices are displayed without the decimal points, but the actual value can be obtained by dividing the numbers by 100. The mean value for all indices is 1.0. Each line represents one decade of indices and the decades are shown in the left hand column. The numbers across the top of the table are the last numbers of the decade year for each decade. This is called the“Tucson format” and is the internationally accepted format of the World Data Center for Paleoclimatology.

Year	0	1	2	3	4	5	6	7	8	9
1725						1096	1110	1207	1063	1041
1730	1005	1296	1875	759	1129	1344	1750	1646	1834	1952
1740	2516	1459	1366	1331	736	957	972	947	734	931
1750	958	752	654	772	543	850	895	882	1111	1128
1760	918	1018	836	998	677	865	1146	1248	1346	1479
1770	1224	1110	702	949	705	652	529	343	493	765
1780	727	796	777	739	476	652	642	973	1001	1072
1790	1189	1104	795	920	1040	650	860	928	686	555
1800	626	847	1101	953	1259	751	959	1313	1222	1101
1810	1138	1486	1318	1341	1324	1508	1170	1281	843	862
1820	462	713	1148	1041	1016	1207	1137	1420	1116	958
1830	995	966	1295	1048	1074	1115	980	965	728	553
1840	601	718	681	622	839	953	1217	1148	1154	1102
1850	949	872	887	1064	1114	955	846	1181	1203	926
1860	739	864	663	554	649	916	825	1275	1062	967
1870	1053	1412	1116	954	1021	1008	904	891	1691	933
1880	1149	783	1325	999	1234	709	733	854	1119	1194
1890	1140	928	1039	1282	965	787	892	1004	957	996
1900	903	1049	1017	1231	1051	983	1062	1110	1018	1033
1910	911	947	1113	800	761	823	1017	744	784	814
1920	1069	895	1070	1173	1017	723	963	996	1124	1216
1930	649	816	748	1261	832	1077	841	1163	1502	1011
1940	874	764	908	993	872	1383	1394	1326	1403	1183
1950	1077	919	691	802	739	829	901	1054	1074	812
1960	827	974	681	782	791	899	950	976	684	669
1970	733	982	1289	1482	1509	1267	1089	901	840	843
1980	1018	1036	991	1184	1101	891	961	1007	872	1198
1990	1463	1434	1086	1147	873	811	1164	1198	1017	760
2000	875	830	821	1203	963	854	804	817		

A3. Standard tree-ring chronology for Linville Mountain, NC. These values are the tree-ring indices for each year in the chronology. The indices are displayed without the decimal points, but the actual value can be obtained by dividing the numbers by 100. The mean value for all indices is 1.0. Each line represents one decade of indices and the decades are shown in the left hand column. The numbers across the top of the table are the last numbers of the decade year for each decade. This is called the“Tucson format” and is the internationally accepted format of the World Data Center for Paleoclimatology.

Year	0	1	2	3	4	5	6	7	8	9
1701		614	685	309	376	292	487	299	865	853
1710	985	848	960	1030	1248	880	1237	1001	663	908
1720	1028	920	745	1048	1133	1007	1001	1271	942	1044
1730	1221	1259	1410	1468	1351	996	1374	1195	1072	1196
1740	871	1159	993	1069	966	1349	804	824	571	979
1750	954	968	1001	1171	1004	527	848	633	513	810
1760	939	1067	1047	1329	1408	1192	1058	1232	1354	1316
1770	1288	1228	696	782	893	953	964	1074	1502	1266
1780	1075	1698	1059	1419	1038	989	1053	1112	1271	1159
1790	809	776	684	919	829	526	754	889	572	645
1800	762	866	1413	484	650	932	677	842	614	938
1810	1006	1095	1146	1255	1264	1455	1242	1400	831	1099
1820	864	735	1108	1115	1035	1133	1186	1272	1364	1155
1830	1140	1209	986	989	1206	1093	1071	691	840	921
1840	1139	1016	1118	1030	1003	645	801	787	890	1005
1850	1216	1462	1108	1081	1322	1154	1072	1199	1247	977
1860	1154	1325	1045	733	697	896	662	785	754	712
1870	614	523	801	905	1068	996	1115	886	1353	1108
1880	1059	777	1426	767	1033	763	959	902	992	1244
1890	1126	693	729	855	1083	939	873	1233	1408	1043
1900	865	963	761	934	1009	1034	1497	1447	1627	1215
1910	1184	988	902	689	823	985	1498	909	1314	953
1920	906	984	1066	1118	1148	792	911	1107	999	1342
1930	719	1079	512	617	542	1111	562	728	871	689
1940	1065	1063	1344	1446	1006	1051	1161	1155	1538	1458
1950	1105	1040	832	1063	1029	1124	1228	1546	1121	867
1960	707	748	860	975	817	1052	791	1075	1281	1074
1970	1009	894	961	1009	1198	823	886	904	804	854
1980	934	1206	1171	756	1039	980	610	722	769	1226
1990	1268	1308	806	909	780	821	1037	1350	849	1188
2000	1416	1172	1004	1014	1264	1229	935	751	639	

APPENDIX B

STATISTICAL DESCRIPTION TABLES

B1. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at House Mountain, TN.

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
1	KHM501B	1858	1950	93	0.722	0.44
2	KHM502	1897	1954	58	0.797	0.332
3	KHM503	1826	1904	79	0.648	0.338
4	KHM504	1905	2006	102	0.481	0.306
5	KHM505	1877	1918	42	0.647	0.233
6	KHM506	1942	2006	65	0.67	0.362
7	KHM507	1874	1915	42	0.581	0.489
8	KHM508	1892	2006	115	0.705	0.344
9	KHM509	1885	1997	113	0.65	0.485
10	KHM510	1873	1936	64	0.611	0.217
11	KHM5112	1885	1947	63	0.635	0.364
12	KHM512	1854	1938	85	0.601	0.296
13	KHM513	1855	1919	65	0.713	0.324
14	KHM515	1851	1906	56	0.515	0.267
15	KHM516	1849	1950	102	0.453	0.38
16	KHM518	1846	1913	68	0.671	0.329
17	KHM519	1936	2006	71	0.521	0.369
18	KHM520	1818	1924	107	0.575	0.321
19	KHM521B	1879	1958	80	0.588	0.41
20	KHM522	1857	2007	151	0.514	0.394
21	KHM523C	1754	1845	92	0.163	0.319
22	KHM524	1905	1960	56	0.594	0.407
23	KHM525A	1768	1860	93	0.288	0.221
24	KHM526	1921	2006	86	0.573	0.345
25	KHM527	1929	1968	40	0.493	0.322
26	KHM528	1896	1992	97	0.479	0.361
27	KHM529	1843	1922	80	0.596	0.273
28	KHM530	1843	1969	127	0.615	0.313
29	KHM531B	1921	1982	62	0.636	0.341
30	KHM532	1864	1972	109	0.591	0.365
31	KHM533	1885	1964	80	0.618	0.339
32	KHM534	1929	1970	42	0.494	0.355
33	KHM536	1922	1981	60	0.493	0.32
34	KHM537B	1880	1920	41	0.53	0.373

B1. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at House Mountain, TN (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
35	KHM538	1922	2006	85	0.414	0.305
36	KHM539	1902	1950	49	0.361	0.305
37	KHM540	1896	2006	111	0.71	0.33
38	KHM541	1909	1940	32	0.674	0.34
39	KHM542	1918	2006	89	0.65	0.317
40	KHM543	1915	2006	92	0.62	0.289
41	KHM544	1829	1873	45	0.533	0.263
42	KHM545	1906	2006	101	0.534	0.345
43	KHM546	1909	1960	52	0.512	0.336
44	KHM547	1932	1969	38	0.651	0.372
45	KHM548	1898	1970	73	0.601	0.293
46	KHM549	1899	1996	98	0.699	0.332
47	KHM550	1892	1959	68	0.503	0.408
48	KHM551	1921	1970	50	0.307	0.417
49	KHM552	1901	2002	102	0.597	0.319
50	KHM553	1880	2004	125	0.428	0.427
51	KHM554B	1856	1945	90	0.372	0.364
52	KHM556	1855	1967	113	0.683	0.314
53	KHM557	1925	1972	48	0.638	0.351
54	KHM600	1825	1938	114	0.606	0.337
55	KHM601	1885	1949	65	0.712	0.31
56	KHM602	1840	1912	73	0.587	0.318
57	KHM603	1835	1907	73	0.583	0.337
58	KHM606	1910	1975	66	0.632	0.336
59	KHM607B	1927	1974	48	0.447	0.284
60	KHM608	1867	1914	48	0.407	0.294
61	KHM609	1819	1923	105	0.721	0.267
62	KHM610	1922	1976	55	0.687	0.342
63	KHM611	1828	1986	159	0.698	0.322
64	KHM612A	1820	1900	81	0.563	0.44
65	KHM613	1826	1860	35	0.467	0.326
66	KHM614	1815	1957	143	0.486	0.29
67	KHM615	1863	1953	91	0.67	0.355
68	KHM616	1865	1968	104	0.702	0.387
69	KHM618B	1870	1961	92	0.714	0.389
70	KHM619	1801	1900	100	0.419	0.339
71	KHM620	1905	1945	41	0.766	0.389
72	KHM621	1778	1891	114	0.384	0.317

B1. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at House Mountain, TN (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
73	KHM623	1885	1944	60	0.785	0.288
74	KHM624	1873	1972	100	0.636	0.285
75	KHM625	1891	2008	118	0.609	0.382
76	KHM626	1909	2009	101	0.526	0.402
77	KHM627	1790	1884	95	0.44	0.312
78	KHM629	1880	1963	84	0.176	0.388
79	KHM631	1950	2008	59	0.437	0.327
Total or Mean		**1754**	**2009**	**6371**	**0.568**	**0.341**

B2. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Licklog Ridge, TN.

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
1	LLA037B	1950	2007	58	0.459	0.256
2	LLA068A	1938	2007	70	0.576	0.221
3	LLA004B	1943	2007	65	0.593	0.223
4	LLA096B	1940	2007	68	0.346	0.236
5	LLA016A	1970	2007	38	0.581	0.293
6	LLA011A	1949	2007	59	0.547	0.23
7	LLA097A	1950	2007	58	0.417	0.267
8	LLA044A	1937	2007	71	0.588	0.346
9	LLB117B	1976	2007	32	0.645	0.287
10	LLB071A	1937	2007	71	0.353	0.28
11	LLB113B	1941	2007	67	0.358	0.357
12	LLB015A	1925	2001	77	0.349	0.31
13	LLB092B	1940	2007	68	0.466	0.222
14	LLB087B	1933	2007	75	0.495	0.235
15	LLB102A	1936	2007	72	0.514	0.409
16	LLB027B	1953	2007	55	0.519	0.237
17	LLB021B	1937	2007	71	0.428	0.364
18	LLA069B	1945	2007	63	0.509	0.267
19	LLA009A	1949	2007	59	0.522	0.254
20	LLA085B	1940	2007	68	0.541	0.237
21	LLA120A	1940	2007	68	0.472	0.292
22	LLA047A	1936	2007	72	0.579	0.217
23	LLA095A	1952	2007	56	0.44	0.231
24	LLA100B	1957	2007	51	0.574	0.218
25	LLA105A	1945	2007	63	0.532	0.229
26	LLA091B	1955	2007	53	0.618	0.175
27	LLA035B	1952	2007	56	0.444	0.302
28	LLA011A	1949	2007	59	0.547	0.23
29	LLA061B	1928	2007	80	0.634	0.406
30	LLX001	1827	1922	96	0.553	0.268
31	LLX2	1823	1946	124	0.521	0.295
32	LLX003	1820	1908	89	0.53	0.402
33	LLX216A	1816	1939	124	0.447	0.334
34	LLX218	1865	1920	56	0.598	0.261
35	LLX219	1822	1905	84	0.439	0.351
36	LLX220B	1830	1962	133	0.455	0.278
37	LLX221	1841	1960	120	0.562	0.313
38	LLX223	1900	1969	70	0.436	0.349

B2. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Licklog Ridge, TN (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
39	LLX226	1880	2006	127	0.479	0.283
40	LLX227B	1774	1809	36	0.349	0.424
41	LLX229	1844	1916	73	0.582	0.289
42	LLX235A	1850	1961	112	0.474	0.282
43	LLX236II	1859	1912	54	0.593	0.322
44	LLX237B	1841	1940	100	0.37	0.383
45	LLX239	1833	1916	84	0.368	0.291
46	LLX240	1850	1942	93	0.58	0.313
47	LLX242I	1830	1889	60	0.348	0.363
48	LLX250I	1780	1860	81	0.612	0.397
49	LLX251	1790	1959	170	0.561	0.307
50	LLX254B	1769	1865	97	0.494	0.273
51	LLX257	1924	1999	76	0.404	0.259
52	LLX259	1890	1969	80	0.577	0.319
53	LLX272	1813	1950	138	0.571	0.351
54	LLX275	1852	1941	90	0.592	0.296
55	LLX276I	1764	1938	175	0.543	0.259
56	LLX277	1813	1947	135	0.59	0.288
57	LLX279	1870	2001	132	0.583	0.207
58	LLX282	1791	1915	125	0.471	0.239
59	LLX284A	1831	1980	150	0.5	0.242
60	LLX285B	1825	1936	112	0.489	0.26
61	LLX287	1835	1928	94	0.712	0.24
62	LLX289	1831	1921	91	0.534	0.312
63	LLX291	1809	1918	110	0.625	0.311
64	LLX292	1809	1900	92	0.614	0.268
65	LLX295	1809	1939	131	0.564	0.337
66	LLX297	1890	1984	95	0.494	0.294
67	LLX299	1812	1906	95	0.569	0.286
68	LLX309	1813	1942	130	0.56	0.247
69	LLX310	1910	1979	70	0.434	0.296
70	LLX312	1780	1866	87	0.379	0.31
71	LLX313	1806	1873	68	0.451	0.236
72	LLX315A	1750	1875	126	0.438	0.332
73	LLX316	1732	1858	127	0.487	0.306
74	LLX318	1787	1870	84	0.496	0.317
75	LLX403	1725	1810	86	0.376	0.433
76	LLX405	1813	1950	138	0.367	0.39

B2. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Licklog Ridge, TN (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
77	LLX408	1900	1969	70	0.453	0.261
78	LLX410	1894	1947	54	0.492	0.297
79	LLX412A	1820	1946	127	0.59	0.335
80	LLX414C	1751	1883	133	0.674	0.329
81	LLX415	1850	1920	71	0.462	0.41
82	LLX416	1840	1961	122	0.432	0.343
83	LLX419	1870	1918	49	0.403	0.345
84	LLX421	1775	1921	147	0.521	0.34
85	LLX423II	1780	1946	167	0.545	0.321
86	LLX424	1824	1948	125	0.593	0.251
87	LLX426	1851	1945	95	0.543	0.28
88	LLX428	1822	1906	85	0.603	0.285
89	LLX430	1825	1956	132	0.575	0.293
90	LLX437I	1817	1912	96	0.436	0.419
91	LLX438	1821	1987	167	0.389	0.317
92	LLX440B	1815	1935	121	0.549	0.364
93	LLX443I	1870	1925	56	0.559	0.438
94	LLX444	1766	1860	95	0.442	0.31
95	LLX445	1856	1939	84	0.566	0.308
96	LLX446	1860	1941	82	0.515	0.321
97	LLX447I	1825	1920	96	0.498	0.266
98	LLX452	1859	1910	52	0.396	0.281
99	LLX460	1840	1941	102	0.493	0.322
100	LLX461	1790	1850	61	0.468	0.292
101	LLX462	1824	2007	184	0.391	0.238
102	LLX464	1900	2007	108	0.463	0.339
103	LLX465	1840	1883	44	0.608	0.238
104	LLX466	1810	1893	84	0.559	0.228
105	LLX467	1870	1920	51	0.299	0.284
106	LLX468	1824	1903	80	0.516	0.264
107	LLX469II	1825	1947	123	0.606	0.283
108	LLX470B	1824	1913	90	0.389	0.311
109	LLX472II	1900	1956	57	0.692	0.281
110	LLX473	1830	1910	81	0.505	0.295
111	LLX474	1809	1918	110	0.553	0.324
112	LLX475	1816	1945	130	0.572	0.256
113	LLX477	1840	1969	130	0.564	0.275
114	LLX479	1837	1900	64	0.643	0.422

B2. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Licklog Ridge, TN (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
115	LLX480	1754	1861	108	0.46	0.332
116	LLX481	1814	1898	85	0.633	0.265
117	LLX483	1814	1897	84	0.485	0.289
118	LLX484	1810	1909	100	0.502	0.329
119	LLX485A	1784	1852	69	0.421	0.286
120	LLX503	1819	1916	98	0.404	0.277
121	LLX504	1810	1922	113	0.552	0.372
122	LLX505	1870	1919	50	0.34	0.332
123	LLX611	1870	1922	53	0.616	0.291
124	LLX612I	1741	1800	60	0.443	0.319
125	LLX612II	1830	1911	82	0.436	0.306
126	LLX613	1834	1923	90	0.637	0.357
127	LLX614A	1851	1920	70	0.482	0.298
128	LLX615	1824	1909	86	0.447	0.272
129	LLX616	1820	1916	97	0.624	0.216
130	LLX618	1780	1817	38	0.528	0.248
131	LLX619	1922	2001	80	0.538	0.285
132	LLX624	1770	1810	41	0.315	0.364
133	LLX625	1803	1922	120	0.441	0.297
134	LLX628	1840	1893	54	0.568	0.377
135	LLX652	1830	1915	86	0.464	0.318
136	LLX653	1802	1912	111	0.535	0.295
Total or Mean		**1725**	**2007**	**12143**	**0.509**	**0.300**

B3. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Linville Mountain, NC.

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
1	LMA201	1812	1924	113	0.526	0.337
2	LMA202A	1814	1916	103	0.498	0.339
3	LMA203	1730	1789	60	0.579	0.262
4	LMA206B	1725	1802	78	0.469	0.273
5	LMA207	1809	1879	71	0.528	0.309
6	LMA208A	1827	1922	96	0.52	0.291
7	LMA209	1820	1860	41	0.463	0.292
8	LMA211	1830	1989	160	0.561	0.315
9	LMA213	1821	1895	75	0.597	0.229
10	LMA214	1728	1940	213	0.534	0.252
11	LMA215	1889	1940	52	0.468	0.409
12	LMA216	1921	1980	60	0.512	0.398
13	LMA217	1819	2006	188	0.482	0.345
14	LMA218	1900	2008	109	0.376	0.319
15	LMA221	1853	2008	156	0.566	0.293
16	LMA223	1830	1891	62	0.336	0.279
17	LMA300	1820	1931	112	0.5	0.288
18	LMA301	1831	2008	178	0.633	0.237
19	LMA302	1798	1930	133	0.668	0.256
20	LMA303	1701	1824	124	0.437	0.278
21	LMA305A	1808	1904	97	0.652	0.242
22	LMA307	1808	1872	65	0.339	0.29
23	LMA310	1810	1891	82	0.241	0.255
24	LMA311A	1735	1884	150	0.548	0.246
25	LMA314	1811	1899	89	0.445	0.306
26	LMA501	1738	1882	145	0.547	0.339
27	LMA503	1921	1994	74	0.41	0.433
28	LMA506A	1708	1831	124	0.301	0.405
29	LMA508	1809	1894	86	0.644	0.299
30	LMA512	1809	1883	75	0.298	0.328
31	LMD201	1816	1901	86	0.645	0.278
32	LMD202	1807	1950	144	0.466	0.421
33	LMD300	1914	1960	47	0.335	0.284
34	LMD302A	1719	1850	132	0.511	0.3
35	LMD303	1704	1850	147	0.434	0.324
36	LMD304	1780	2008	229	0.466	0.41
37	LMD305	1732	1850	119	0.592	0.299
38	LMD306	1816	1930	115	0.621	0.334

B3. Statistical description of each ring-width series from yellow pine cross-sections collected for fire history reconstruction at Linville Mountain, NC (continued).

	Series	Interval		No. of Years	Correlation with Master	Mean Sensitivity
39	LMD307I	1840	2008	169	0.517	0.364
40	LMD308	1839	2000	162	0.622	0.294
41	LMD309	1851	1930	80	0.533	0.267
42	LMD310	1887	2008	122	0.38	0.375
43	LMD502	1717	1842	126	0.506	0.286
44	LMD503	1830	1906	77	0.353	0.338
45	LMD504C	1755	1933	179	0.546	0.348
Total or Mean		**1701**	**2008**	**5105**	**0.505**	**0.315**