DISTURBANCE HISTORY AND ECOLOGICAL CHANGE IN A SOUTHERN APPALACHIAN LANDSCAPE:
WESTERN GREAT SMOKY MOUNTAINS NATIONAL PARK, 1936-1996

by

Jonathan C. Harrod

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Approved by:

Peter S White

Advisor: Professor Peter S. White

Reader: Professor Robert K. Peet

Seth R. Reice

Reader: Professor Seth R. Reice

Stephen J. Walsh

Reader: Professor Stephen J. Walsh

Bruce Winterhalder

Reader: Professor Bruce Winterhalder

ABSTRACT

JONATHAN C. HARROD: Disturbance history and ecological change in a southern
Appalachian landscape: western Great Smoky Mountains National Park, 1936-1996
(Under the direction of Peter S. White).

In western Great Smoky Mountains National Park (GSMNP), Tennessee, as in much of eastern North America, logging, agricultural clearing, and anthropogenic burning peaked in the mid 19th through early 20th centuries. I examined the effects of changes in disturbance regime on stand and landscape-level vegetation patterns using plot data from 1936-37, 1977-79, and 1995-96. Specifically, I asked: 1) have the site variables most strongly associated with landscape-level vegetation patterns remained constant through time, 2) what changes in vegetation composition and structure have occurred within groups of sites sharing similar environments and disturbance histories, and 3) have distributions of species along major environmental gradients changed through time?

Indirect gradient analyses using non-metric multidimensional scaling (NMDS) indicate that compositional variation during each time period was strongly correlated with elevation and topographic moisture. Comparisons of 1930s and 1970s plot data indicate that significant increases in canopy density, richness, basal area and biomass occurred on all site types. Castanea dentata disappeared from the forest canopy, and the relative abundance of shade-tolerant species increased. Several species largely restricted to mesic sites in the 1930s spread onto more xeric sites by the 1970s. Between the 1970s and 1990s, basal area, biomass, and density of canopy trees remained relatively constant. Relative abundance of shade-tolerant species continued to increase on all site types, and gradient distributions of several species contracted.

More detailed examination of xeric sites indicates that 1) age structure and radial growth patterns are highly consistent with conclusions based on historical plot data; 2) herbaceous richness and cover are higher during the first decade after fire than on environmentally similar sites that have not burned in > 40 years; and 3) decreases in fire frequency have led to the decline of several species historically important on xeric sites.

Changes in vegetation composition and structure in western GSMNP appear to reflect forest development and recovery following disturbance in the late 19th and early 20th centuries and ongoing disturbance by introduced pathogens. Future disturbances and environmental changes will interact with legacies of past land-use to produce ongoing changes in stand and landscape-level vegetation patterns.

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This project would not have been possible without the vision of the researchers who established the long-term data sets used in this study. I owe a special debt of gratitude to Frank Miller and the teams of Civilian Conservation Corps compassmen who conducted the initial vegetation survey of Great Smoky Mountains National Park in the 1930s. Their monumental sampling effort, representing more than 1300 plots, remains one the largest surveys of southern Appalachian vegetation. Equally impressive were their meticulous transcription, mapping, and tabulation of data, all done in an era before computers.

I am also grateful to Professors Peter White and Mark Harmon, who, in the 1970s, established the permanent plots that I resampled in the course of my field work. Peter's efforts computerizing and mapping of the 1930s plots also helped lay the groundwork for my study. As my graduate advisor, Peter provided unflagging support and contributed many stimulating ideas. Mark's studies of fire history and effects provided much of the impetus for my work, and he generously shared unpublished data and provided insightful comments on early drafts. It has been a pleasure to work with both of them.

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Dellinger also assisted with plant identification, and Rickie White helped count and measure tree rings. Several of the GIS coverages used in this study were provided by staff of Great Smoky Mountains National Park; others were developed by Stephanie Wilds.

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PREFACE

Understanding the ecological consequences of land-use activities and species introductions represents a central challenge for ecologists and for the human species as a whole. In contrast to many parts of the world, where land-use is occurring at unprecedented intensities, protected areas of the southern Appalachian mountains of North Carolina and Tennessee present an opportunity to study landscapes in the process of recovery from a period of peak human disturbance. The five chapters that comprise this dissertation represent my attempt to document the effects of human activity on a southern Appalachian landscape. They also present and test an approach to the analysis of long-term vegetation data that I hope will prove valuable to others interested in ecological change in environmentally heterogeneous landscapes.

Chapters one through four are written as a free-standing articles, each with its own abstract, introduction, study area description, methods, results, and discussion. While this organization has produced some repetition, it has facilitated the submission of the work for publication and sped its presentation to a broader audience. Chapter one, which was published in the September 1998 issue of *Castanea* (Harrod et al. 1998), examines changes in the canopy of xeric pine-oak forests using plot data from the 1930s, 1970s, and 1990s. Chapter two, currently in press in the *Journal of the Torrey Botanical Society* (Harrod and White 1999), presents dendrochronological data that agree closely with the plot-based results presented in chapter one and justify the broader use of my analytical approach. In chapter three, I combine data from permanent plots that burned in the 1970s with data on historic stand structure and fire regime to examine the effects of fire and fire suppression on herbs, shrubs, and tree regeneration on xeric sites. Chapter four expands my focus from xeric sites to the western GSMNP landscape as a whole. I examine structural and compositional changes on mesic, intermediate, and xeric sites and changes in species' distributions along the topographic moisture gradient, the dominant environmental gradient in the study area. Chapter five summarizes the results of chapters one through three and other studies on the fire ecology of southern Appalachian xeric communities.

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Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995

ABSTRACT

Yellow pines (*Pinus rigida, P. virginiana, P. echinata*, and *P. pungens*)* and oaks (*Quercus* spp.) dominate xeric slopes and ridges in western Great Smoky Mountains National Park (GSMNP). In the late nineteenth and early twentieth centuries, these sites burned frequently. Since about 1940, the Park Service has suppressed fire, prompting concerns over possible changes in forest composition and structure. This study documents changes in xeric forests using non-permanent plots sampled in 1936-37, permanent plots established in 1977-79, and a subset of those permanent plots resampled in 1995. Some permanent plots burned just prior to sampling in the 1970s, while others have not burned since before 1940.

Between the 1930s and 1970s, canopy density, basal area, and canopy richness increased dramatically on fire-suppressed sites. While high-intensity fires reduced canopy density and basal area to low levels, low-intensity fires did not significantly reduce canopy density or basal area relative to fire-suppressed sites. Between the 1970s and 1995, canopy density on fire-suppressed and low-intensity fire sites remained relatively stable, while that on sites of high-intensity fires increased rapidly. During this period, abundant regeneration of yellow pines occurred on some burned sites. On fire-suppressed sites, densities of *Acer*

rubrum, Nyssa sylvatica, Pinus strobus and *Tsuga canadensis* have increased. Changes in the canopies of xeric forests since the onset of fire suppression may alter response to future fire events and complicate the restoration of historical composition and structure in these communities.

Nomenclature: Kartesz (1994).

INTRODUCTION

In the southern Appalachians, xeric slopes and ridges below 1000 m elevation support forests dominated by yellow pines (*Pinus rigida, P. virginiana, P. echinata*, and *P. pungens*) and oaks (especially *Quercus coccinea* and *Q. prinus*) (Whittaker 1956). In the late nineteenth and early twentieth centuries, these sites burned frequently; ignition sources included both lightning and human activities (Harmon 1982, Barden and Woods 1973). Since the establishment of Great Smoky Mountains National Park (GSMNP) in 1934 and the onset of effective fire suppression about 1940, fire frequency has dropped dramatically, prompting concerns over possible changes in forest composition, structure, and dynamics (Harmon 1982, 1984; Harmon et al. 1983).

Fire appears to have played an important role in the creation and maintenance of xeric yellow pine and oak forests. Yellow pines are shade-intolerant species with thick, insulative bark (Harmon 1984, Burns and Honkala 1990). Fires promote yellow pine regeneration by opening the canopy and reducing leaf litter (Barden and Woods 1976, Harmon 1980, Williams et al. 1990). Fire also stimulates seed release in *P. pungens*, a partially serotinous species (Barden 1979). While some early researchers concluded that yellow pine populations could persist indefinitely in the absence of fire (Whittaker 1956, Racine 1966, Zobel 1969), more recent studies suggest that fire or other disturbance is necessary for yellow pine regeneration on all sites except extremely droughty rock outcrops (Barden 1976, 1977, 1988; Barden and Woods 1976; Harmon 1980; Williams and Johnson 1990).

Outbreaks of the southern pine beetle (*Dendroctonus frontalis*), a native insect, occur periodically in southern Appalachian yellow pine stands. Pine beetle outbreaks increase woody fuel levels and thus the likelihood of fires that could lead to pine regeneration (Harmon 1980, Nicholas and White 1984). However, in the absence of fire, pine beetle activity may lead to the rapid loss of yellow pines from the canopy (Kuykendall 1978).

Oaks also possess thick, insulative bark; in addition, they can resprout vigorously if above-ground parts are killed by fire. Short- and medium-term responses to fire suppression may include an increase in oak dominance (Williams and Johnson 1990). However, fire may be necessary for the longer-term maintenance of oak populations, promoting oak regeneration by reducing competition with more shade-tolerant species in the canopy and understory (Abrams 1992, Lorimer et al. 1994, SAMAB 1996).

The historical regime of frequent fires appears to have promoted yellow pine and oak dominance by killing small stems of more shade-tolerant and fire-sensitive species such as *Acer rubrum, Nyssa sylvatica, Pinus strobus,* and *Tsuga canadensis.* For most tree species, the probability of survival following low-intensity surface fire increases with tree diameter (Harmon 1980, 1984). Fire suppression has allowed fire-sensitive species to grow to resistant size. As a consequence, restoration of the pre-park fire regime may not immediately restore historical forest composition and structure (Harmon 1984).

While previous studies have predicted changes in low-elevation xeric forests and quantified short-term responses to fire and pine beetle outbreaks, none has documented long-term changes on these sites. This study of western GSMNP presents data on canopy structure and composition from non-permanent plots measured in 1936-37, permanently marked plots established in 1977-79, and a subset of those permanent plots re-measured in 1995. I use these data to address the following questions: 1) What changes have occurred in xeric forests since park establishment and the onset of fire suppression? 2) In what ways do forests that have not burned since park establishment differ from forests that have burned more recently?

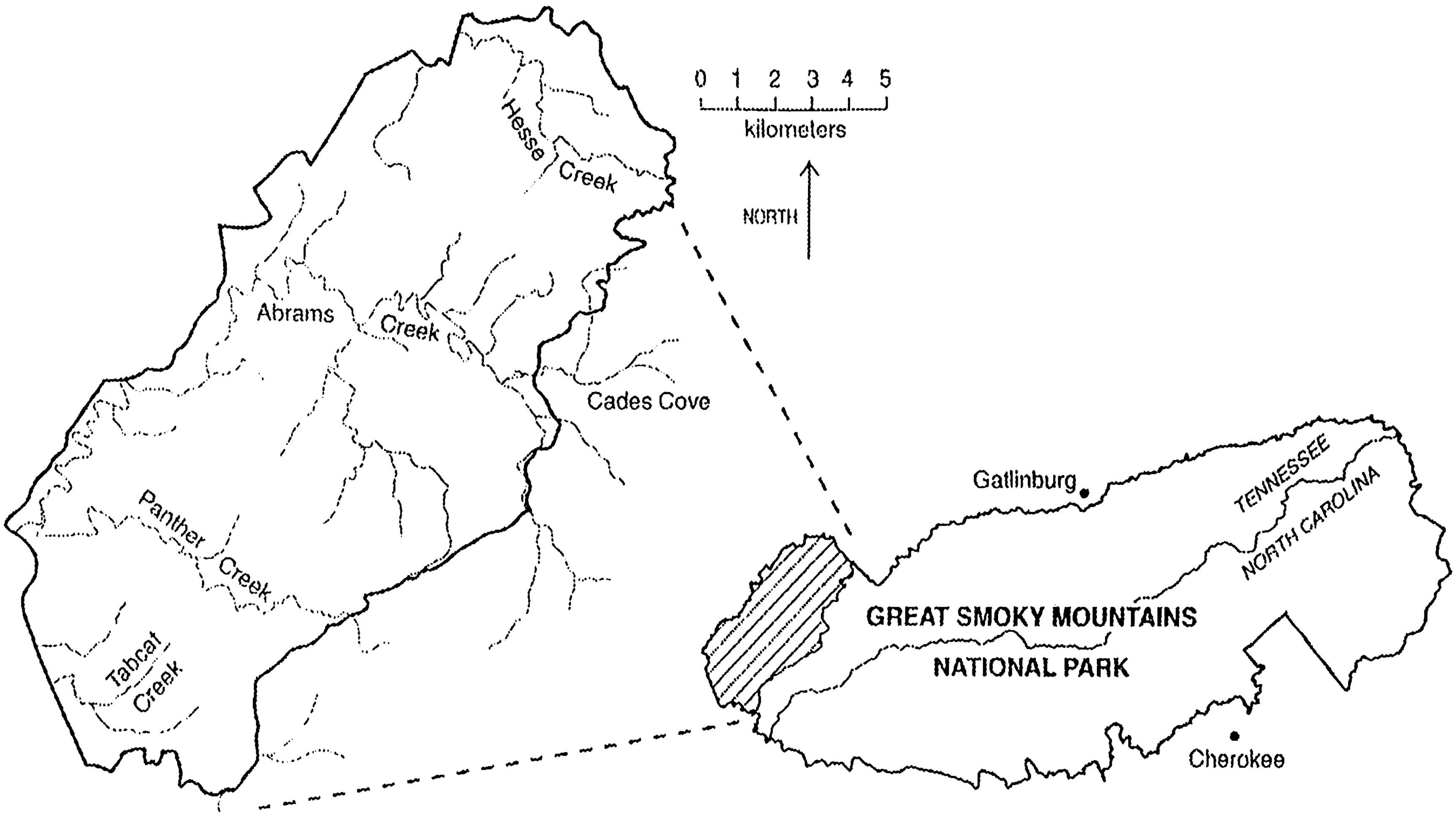
STUDY AREA

The westernmost portion of GSMNP forms a transition zone between the high peaks of the central Smokies and the Great Valley of eastern Tennessee. A series of southwest-northeast trending ridges dominate the steep and highly dissected topography. Elevations range from 260 to 942 m. The study area boundaries are the same as those used by Harmon (1980, 1982; Figure 1.1).

Bedrock is primarily Precambrian sandstone, siltstone, and shale (King et. al. 1968). Soils, mostly ultisols and inceptisols (Elder 1959), are relatively acidic and infertile. The mean annual temperature in Gatlinburg, approximately 40 km northeast of the study area and at 442 m elevation, is 12.9 °C; mean annual precipitation is 1425 cm (Weather America 1996).

Vegetation patterns in the study area vary with slope position and incident solar radiation (Harmon 1980). Canopy cover types include eastern hemlock (*Tsuga canadensis*) and cove hardwood forests on mesic sites, chestnut oak-scarlet oak, mixed oak and mixed hardwood forests on intermediate sites, and yellow pine and pine-oak forests on the most

Figure 1.1. Location of study area in western Great Smoky Mountains National Park, Tennessee.



xeric sites. Xeric yellow pine forests are more abundant in the study area than in GSMNP as a whole (Harmon 1982, MacKenzie 1993).

Native Americans have been present in western GSMNP since at least 8000 years before present (Bass 1977). Bog sediments from the Cherokee Nation which adjoins southeastern GSMNP show an increase in charcoal corresponding to the arrival of the Cherokee between 1450 and 1600 AD (Lynch and Clark 1996). Early historical accounts also suggest widespread use of fire by Native American populations. European-American settlement began in the late eighteenth century (Shields 1977) and continued until lands were incorporated into GSMNP between 1930 and 1940. European-American influences included agricultural clearing, grazing, and small-scale timber extraction (Pyle 1988). The community of Cades Cove adjoined the study area on the east, and isolated agricultural fields and home sites were also scattered throughout, mostly in coves and valley bottoms and along lower slopes. While mechanized logging operations affected much of central and eastern GSMNP, their impact on the study area was relatively small and restricted primarily to lower slope positions (Pyle 1988, Lambert 1958). Settlers were a major source of ignitions, setting fires to clear land, increase livestock forage and berry crops, and facilitate the gathering of chestnuts. For the period 1856 to 1940, the mean fire-return interval in xeric pine forests in western GSMNP was 12.7 years (Harmon 1982). Park establishment and fire suppression have reduced fire frequency dramatically; for the period 1940-1989, the mean fire-return interval on xeric sites was > 500 years (Harmon 1982, J. Harrod, unpublished data).

METHODS

Miller plots

Between 1935 and 1937, field crews under the supervision of GSMNP Assistant Forester F. H. Miller sampled approximately 1375, 20 × 40 m plots throughout GSMNP. Ninety-four of these plots were sampled in the western GSMNP study area in 1936 and 1937. Some plot locations were chosen randomly or spaced regularly along grids or transects; in other cases, plots were established non-randomly on ecotonal sites (MacKenzie 1993). Crews recorded plot locations on early topographic maps. I transcribed approximate plot locations to modern 1:24,000 USGS topographic quadrangles. Shape and location of some topographic features differed between the old and new maps; where discrepancies occurred, I attempted to transcribe plots to locations which matched original elevation, slope, aspect, and topographic position.

Within plots, crews tallied live and dead trees of each species using the following diameter at breast height (dbh) classes: 10 to < 30 cm, 30 to < 60 cm, 60 to < 91 cm, and ≥ 91 cm. Crews also recorded evidence of fire and logging, reporting, in some cases, the date of the most recent fire. MacKenzie (1993, this volume) provides additional information on this data set.

Uplands plots

Between 1977 and 1985, staff of the National Park Service (NPS) Uplands Field Research Laboratory sampled and permanently marked 410, 20 × 50 m plots in GSMNP. Of these, 110 were established in the western GSMNP study area between 1977 and 1979. Plot locations were chosen subjectively with the goal of capturing a range of site conditions and disturbance histories; plots include mature forests, former agricultural fields, and areas that had burned in 1976-77 prior to sampling. Plot locations do not correspond with those of the 1930s Miller plots. The 20 × 50 m plots were subdivided into five, 10 × 20 m subplots. Within each subplot, field crews recorded species and dbh to the nearest centimeter for all live woody stems ≥ 1 cm dbh and for all standing dead trees ≥ 10 cm dbh. On recently burned plots, trees which appeared to have died prior to the fire were distinguished from those which appeared to have been killed by the fire, allowing approximate reconstruction of the pre-fire stand. Crews also recorded evidence of fire and logging. Years of past fires were determined, where possible, by sectioning fire scars. Plot locations were marked on 1:24,000 topographic maps, and plot corners were monumented with tagged witness trees and iron bars. Harmon (1980) and White and Busing (1993) provide additional information on sampling methods. In 1995, I located and sampled 72 of these plots following original methods.

Analyses

I processed the 1970s and 1995 data sets to allow comparisons of density, basal area, and species richness with the 1930s data. The 20 × 50 m plots were truncated to 20 × 40 m by the deletion of the last 10 × 20 m subplot. Stems < 10 cm dbh were excluded from the analysis, and stems ≥ 10 cm were grouped into the size classes listed above. Because results presented in this paper represent only stems ≥ 10 cm dbh, I use the terms "canopy density" and "canopy richness" to describe stand attributes. Basal area estimates for all plots were generated following MacKenzie (1993), who based his calculations on the geometric mean of the upper and lower limits of each diameter class and set the upper limit for the ≥ 91 cm size class at 122 cm.

The locations of the 1930s, 1970s, and 1995 plots that fell within the study area were digitized using the ARC/INFO geographic information system (ESRI 1996). The NPS Twin Creeks Natural Resource Center provided the following digital coverages: elevation, slope, and aspect (all 30 m resolution) and historical settlements and post-1930 fires (both 90 m resolution). Additional terrain variables were derived from the digital elevation model. Curvature (CURV), a measure of local convexity or concavity, was generated using the ARC/INFO GRID module (ESRI 1996). Relative slope position (RSP; Skidmore 1990), which expresses downslope distance to the nearest cove or valley as a percentage of the total distance between valley and ridge, was calculated in GRID using algorithms developed by Wilds (1996); values range from 0 for valley bottoms to 100 for ridges and summits. Potential incident solar radiation (SOLRAD) for spring equinox (March 20) was estimated using the SOLARFLUX program (Rich et al. 1995). SOLARFLUX calculates insolation over the course of a day, taking into account shading effects of distant landforms as well as local slope and aspect. A topographic moisture index (TMI) combining slope position, solar radiation, and curvature was calculated following Newell (1997). Values of SOLRAD, RSP, and CURV were re-scaled with SOLRAD on a 30-point scale, RSP on a 20-point scale, and CURV on a 10-point scale. In each case, low values represent xeric conditions (high solar radiation, ridgetop, convex topography) and high values represent mesic conditions (low solar radiation, valley bottom, concave topography). TMI is then calculated as the sum of the three rescaled variables. Possible values range between 0 and 60; I identified xeric sites as those with TMI $\leq$ 15. Xeric sites selected using these criteria include ridges and east, south, and west-facing upper slopes; curvature on these sites ranges from slightly concave to highly convex.

The Uplands plots were then grouped on the basis of post-1940 fire history. Plots which burned in 1976-77 were placed in one of two severity categories. "Hot" fires removed more than 25% of basal area, while "cool" fires removed 25% or less. Plots which had not burned since before 1940 were considered "fire-suppressed." Three Uplands plots which burned in the 1950s and three Miller plots and two Uplands plots which were old agricultural fields or home sites were eliminated from the analysis. Multiple analysis of variance (MANOVA; SAS Institute 1994) revealed no significant differences in elevation, slope, cosine-transformed aspect, solar radiation, relative slope position, curvature, or topographic moisture index between these groups of xeric plots based on time of sampling or recent fire history (Wilks' $\lambda = 0.71$; $p = 0.50$). Groups of plots were also similar in their early fire history. Evidence of past fire was recorded in 26 of 28 Miller plots and in all 29 Uplands plots. The year of last fire, if known, ranged from 1916 to 1933 for the Miller plots, from 1910 to 1931 for the fire-suppressed Uplands plots, and from 1933 to 1942 for cool-fire and hot-fire Uplands plots.

Changes between the 1930s and 1970s were documented by comparing Miller plots with hot-fire, cool-fire, and fire-suppressed Uplands plots. One-way analysis of variance (ANOVA; SAS Institute 1994) was used to test for significant differences in total canopy density, basal area, and species richness. I also tested for differences in canopy densities of three categories of trees: yellow pines (*P. echinata*, *P. pungens*, *P. rigida*, and *P. virginiana*), oaks (all *Quercus* species), and others (including angiosperms such as *Nyssa sylvatica* and *Acer rubrum* and gymnosperms such as *Tsuga* and *Pinus strobus*). When ANOVA revealed significant effects, I used Tukey's HSD test for post-hoc comparisons. Changes between the 1970s and 1995 were documented using the subset of recently burned and fire-suppressed Uplands plots sampled in 1995. Factorial ANOVA (with one between-groups factor and one repeated measures factor) was used to test for significant main effects of fire and time period and for a fire × time period interaction for total canopy density, basal area, and canopy richness and for densities of yellow pines, oaks, and others. When factorial ANOVA revealed significant main effects or a significant interaction, one-way ANOVAs were performed to test for changes within fire categories over time and differences between fire groups within each time period. All canopy density and basal area values were log-transformed prior to analysis to reduce differences in variance. The rejection level for all statistical tests was set *a priori* at $\alpha = 0.05$.

RESULTS

Xeric forests in the 1930s

Mean canopy density and basal area of 1930s plots were significantly lower than those of fire-suppressed plots from later periods (Table 1.1). Yellow pines, mostly *P. rigida* and *P. virginiana*, comprised 55% of canopy trees (Table 1.2). Oaks made up 32% of the canopy; of these, *Q. alba*, *Q. coccinea*, and *Q. prinus* were the most abundant. Other species, including *Pinus strobus*, *Acer rubrum*, and *Castanea dentata*, occurred at low densities, together making up about 13% of the canopy. Canopy species richness at the 0.08 ha scale was also significantly lower than that of later fire-suppressed plots, reflecting both the heavy dominance of yellow pines and oaks and the low total density of canopy trees. The majority of standing dead trees were chestnuts *(Castanea dentata;* Table 1.3).

The use of average values obscures, to some extent, the considerable variation in composition and structure evident in the Miller data. Canopy densities for 1930s plots range

Table 1.1: Means ± standard deviations of canopy density, basal area, and canopy richness for 1930s plots and hot-fire, cool-fire, and fire-suppressed plots from the 1970s. p-values are for one-way ANOVA with one between-groups factor. Superscripts indicate significance of post-hoc multiple comparisons; means of groups sharing the same letter do not differ significantly (Tukey's HSD test, $\alpha = 0.05$). Numbers in parentheses are estimated pre-fire values.

			1970s		
	1930s	Hot-fire	Cool-fire	Fire-suppressed	p
Canopy density (stems/ha)	273 ± 126^{a}	73 ± 38^{b}	677 ± 329^{c} (423 ± 242)	743 ± 249^{c} (739 ± 324)	0.0001
Yellow pines	150 ± 133	50 ± 27	420 ± 470 (255 ± 209)	402 ± 349 (452 ± 483)	0.33(n.s.)
Oaks	87 ± 73^{a}	21 ± 22^{b}	205 ± 205^{a,c} (142 ± 133)	201 ± 113^{c} (220 ± 206)	0.0005
Others	35 ± 49^{a}	2 ± 5^{b}	52 ± 42^{a,c} (27 ± 33)	141 ± 91^{c} (64 ± 37)	0.0001
Basal area (m^2/ha)	14.59 ± 7.50^{a}	2.43 ± 1.28^{b}	23.26 ± 4.99^{c} (12.52 ± 8.00)	28.57 ± 5.81^{c} (24.92 ± 6.62)	0.0001
Canopy richness (species/0.08 ha)	4.50 ± 1.43^{a,b}	3.33 ± 1.37^{a}	6.00 ± 1.15^{b} (6.17 ± 2.14)	8.50 ± 2.06^{c} (6.86 ± 1.77)	0.0001
n	28	6	7	16	

Table 1.2: Average canopy densities (stems/ha) of species in 1930s plots and hot-fire, cool-fire, and fire-suppressed plots from the 1970s. "+" indicates species present at densities less than 1 stem/ha. Due to rounding errors, columns may not sum to totals.

		1970s		
	1930s	Hot-fire	Cool-fire	Fire-suppressed
Acer rubrum	7		14	33
Carya glabra	+		4	9
Carya alba	4			5
Castanea dentata	4			
Cornus florida				1
Halesia carolina				1
Liriodendron tulipifera				1
Nyssa sylvatica	3	2	18	24
Oxydendrum arboreum	2		13	27
Pinus echinata	2		5	8
Pinus pungens	1	8	80	51
Pinus rigida	75	21	155	193
Pinus strobus	13			36
Pinus virginiana	72	21	179	150
Quercus alba	25	2		4
Quercus coccinea	25	15	88	73
Quercus marilandica	1	4	5	9
Quercus prinus	19		73	80
Quercus rubra	7			10
Quercus velutina	10		39	26
Robinia pseudoacacia	2		4	2
Sassafras albidum				2
Tsuga canadensis				2
Total	273	73	677	743

Table 1.3: (a) Average canopy densities (stems/ha) of standing dead trees in 1930s plots and hot-fire, cool-fire, and fire-suppressed plots from the 1970s. For plots which burned in the 1970s, we also estimated pre-fire snag densities. + indicates presence at densities less than 1 stem /ha. (b) Average canopy densities (stems/ha) of standing dead trees in permanent plots initially sampled in the 1970s and resampled in 1995.

(a)		1970s				
		Hot-fire		Cool-fire		
	1930s	Pre	Post	Pre	Post	Fire-suppressed
Canopy density (stems/ha)	13	42	392	31	93	26
Yellow pines	+	42	246	27	63	15
Oaks	---	---	121	2	16	7
Castanea dentata	13	---	---	---	---	2
Others	---	---	25	2	14	2
Basal area (m^2/ha)	1.39	1.94	12.03	1.33	2.99	1.06

(b)	Hot-fire		Cool-fire		Fire-suppressed	
	1970s	1995	1970s	1995	1970s	1995
Canopy density (stems/ha)	472	16	204	42	29	14
Yellow pines	281	3	133	29	11	9
Oaks	156	13	38	13	11	4
Castanea dentata	---	---	---	---	4	---
Others	34	---	33	---	4	2
Basal area (m^2/ha)	15.37	0.65	6.69	0.95	1.08	0.54

from 84 to 602 stems/ha, basal areas from 3.39 to 33.92 m^2/ha, and canopy richness from 1 to 7 species/0.08 ha. Relative densities of yellow pines range from 0 to 100%, oaks 0 to 94%, and other species 0 to 69%.

Fire-suppressed sites

Fire-suppressed plots sampled in the 1970s had significantly higher canopy density, basal area, and richness than did 1930s plots. On these plots, yellow pines made up about 54% of the canopy, oaks 27%, and others, including *Pinus strobus, Acer rubrum, Oxydendrum, Nyssa*, and *Carya* spp., 18%. Absolute densities of oaks and of other species increased significantly relative to the 1930s. Mean density of standing dead trees was somewhat higher than in the 1930s; most of these snags were yellow pines and oaks.

In addition to increases in mean canopy density, basal area, and richness, the 1970s data suggest the disappearance of open-canopy, low-basal area habitats from fire-suppressed sites. Canopy density on individual plots ranged from 463 to 1388 stems/ha, basal area from 18.64 to 38.15 m^2/ha, and canopy richness from 6 to 13 species/0.08 ha. Species composition remained highly variable; relative densities of yellow pines ranged from 0 to 90%; oaks 1 to 60%, and other species 2 to 62%.

Canopy density, basal area, and richness on the resampled Uplands plots remained almost constant between the 1970s and 1995 (Table 1.4). On these plots, yellow pines (mostly *P. rigida* and *P. virginiana*) made up 33% of canopy trees in the 1970s and 30% in 1995 (Table 1.5). Oaks made up 40% of the canopy in the 1970s but only 27% in 1995; absolute densities of four of six oak species declined. While factorial ANOVA revealed no statistically significant changes in total oak density, decreases (ranging from 8 to 70%)

Table 1.4: Means ± standard deviations for canopy density, basal area, and canopy richness on permanent plots initially sampled in the 1970s and resampled in 1995. p-values are for factorial ANOVA with one between-groups factor and one repeated measures factor. Superscripts indicate significance of post-hoc multiple comparisons between groups within a time period; means of groups sharing the same letter do not differ significantly (Tukey's HSD test; $\alpha = 0.05$). Underlined numbers indicate statistically significant within-group changes over time (one-way ANOVA with repeated measures; $\alpha = 0.05$). For example, in the 1970s, total canopy density on hot-fire plots was significantly lower than on either cool-fire or fire-suppressed plots; means of the latter two groups did not differ significantly. Hot-fire plots showed a significant increase in density, while cool-fire and fire-suppressed plots did not. In 1995, canopy density did not differ significantly between groups.

	Hot-fire		Cool-fire		Fire-suppressed		
	1970s	1995	1970s	1995	1970s	1995	Significant effects
Canopy density (stems/ha)	59 ± 39^{a}	615 ± 128	533 ± 131^{b}	623 ± 188	618 ± 128^{b}	626 ± 115	GROUP (p = 0.0001) TIME (p = 0.005) GROUP x TIME (p = 0.0001)
Yellow pines	38 ± 14	420 ± 279	283 ± 202	363 ± 371	205 ± 195	186 ± 208	GROUP x TIME(p = 0.009)
Oaks	22 ± 28	97 ± 146	225 ± 253	197 ± 222	246 ± 98	170 ± 81	---
Others	0 ± 0^{a}	98 ± 148^{a}	25 ± 25^{b}	63 ± 45^{a,b}	166 ± 107^{b}	269 ± 103^{b}	GROUP (p = 0.0008) TIME (p = 0.008)
Basal area (m^2/ha)	2.1 ± 1.5^{a}	15.0 ± 3.6^{a}	23.1 ± 3.6^{b}	24.2 ± 6.3^{b}	25.9 ± 7.0^{b}	25.9 ± 5.4^{b}	GROUP (p = 0.0006) TIME (p = 0.005) GROUP x TIME (p = 0.0002)
Canopy richness (species/0.08 ha)	2.8 ± 1.26^{a}	6.3 ± 3.7	6.3 ± 1.5^{b}	6.3 ± 2.1	9.0 ± 2.0^{b}	8.7 ± 2.06	GROUP (p = 0.01) GROUP x TIME (p = 0.03)
n	4		3		7		

Table 1.5: Average canopy densities (stems/ha) of species in permanent plots initially sampled in the 1970s and resampled in 1995. Due to rounding errors, columns may not sum to totals.

	Hot-fire		Cool-fire		Fire-suppressed	
	1970s	1995	1970s	1995	1970s	1995
Acer rubrum		16	4	4	46	77
Carya glabra					9	4
Carya alba		3			11	2
Cornus florida					2	
Liriodendron tulipifera		41			2	2
Nyssa sylvatica		3	21	50	18	48
Oxydendrum arboreum		3		4	18	16
Pinus echinata			13	8	5	2
Pinus pungens	3	13	4		2	2
Pinus rigida	22	53	133	108	73	61
Pinus strobus				4	57	91
Pinus virginiana	13	353	133	246	125	121
Quercus alba	3	25		4	7	9
Quercus coccinea	16	25	175	171	54	45
Quercus marilandica	3	3	13	4	20	
Quercus prinus		3	21	4	116	102
Quercus rubra					2	2
Quercus velutina		41	17	13	48	13
Robinia pseudoacacia		31				
Sassafras albidum					2	2
Tsuga canadensis					2	27
Total	59	615	533	623	618	626

occurred in all seven fire-suppressed plots. Relative density of other species increased from 27 to 43%, and absolute density of these species increased significantly. Species showing strong gains include *Acer rubrum* (8 to 12%), *Nyssa* (3 to 8%), *Pinus strobus* (9 to 15%), and *Tsuga* (< 1 to 4%). By 1995, density of standing dead trees had dropped to a level comparable to that of the 1930s.

Cool-fire sites

Pre-fire canopy density and basal area of sites which experienced cool fires in 1976-77 were similar to those of fire-suppressed sites (Table 1.1). Prior to fire, yellow pines made up 61% of the canopy, oaks made up 30%, and other species, particularly *Nyssa, Acer rubrum,* and *Oxydendrum arboreum,* made up the remaining 9%. Pre-fire density of standing snags was similar to that on fire-suppressed sites.

Fire effects varied considerably between plots; canopy mortality ranged from 0 to 40%. On average, cool fires caused relatively minor changes, reducing canopy density by 8%, basal area by 5%, and canopy richness by 9%. Post-fire canopy density, basal area, and richness following cool fires remained significantly higher than those of 1930s plots but did not differ significantly from those of fire-suppressed plots. Cool fires also had little effect on canopy composition; following fire, yellow pines made up 62% of canopy trees, oaks 30%, and others, 8%. Fire mortality led to a moderate increase in the density of standing dead trees.

Cool-fire Uplands plots resampled in 1995 show small and non-significant increases in mean canopy density, basal area, and richness. Yellow pines, which made up 53% of the canopy of the resampled plots in the 1970s, increased to 58% in 1995. The absolute density of *P. rigida* decreased slightly, while that of *P. virginiana* nearly doubled. The increase in mean *P. virginiana* density was due largely to abundant regeneration on one plot. As a group, oaks made up 42% of the canopy in the 1970s and 32% in 1995; four of the five oak species present showed declines in absolute density. Other species (primarily *Nyssa*) made up 4% of canopy trees in the 1970s, increasing to 10% in 1995. By 1995, snag densities had fallen considerably.

Hot-fire sites

Mean pre-fire canopy density and basal area on plots that experienced hot fires in 1976-77 were considerably lower than those on cool-fire or fire-suppressed sites. Prior to fire, yellow pines made up 60% of the canopy, oaks 33%, and other species, primarily *Acer rubrum, Nyssa,* and *Pinus strobus,* 6%. Pre-fire snag density was higher than on cool-fire or fire-suppressed sites; all recorded snags were yellow pines.

Canopy mortality following hot fires ranged from 61 to 93%. On average, hot fires reduced canopy density by 79%, basal area by 75%, and richness by 46%. Post-fire canopy density and basal area were significantly lower than those of any other group; canopy richness was significantly lower than that of any group except the 1930s plots. Following hot fires, plots were dominated by *Pinus rigida, P. virginiana,* and *P. pungens*, which together made up 68% of the sparse canopy. Twenty-nine percent of canopy trees were oaks. The only other species present in the canopy was *Nyssa* (3%). Snag densities following hot fires were on the order of 400 stems/ha.

Hot-fire plots resampled in 1995 show large increases in mean canopy density, basal area, and richness. While canopy density and richness on hot-fire sites increased to levels similar to those on fire-suppressed and cool-fire sites, basal area on hot-fire sites remained significantly lower. In the 1970s, canopies of resampled plots which had recently experienced hot fires were made up entirely of yellow pines (63%) and oaks (37%). In 1995, relative density of yellow pines had increased to 68%, and absolute densities of yellow pine species had increased dramatically (*P. pungens* by 400%, *P. rigida* by 240%, *P. virginiana* by 2800%). While absolute densities of most oak species increased, total relative density fell to 16%. Other species, absent from the canopy shortly after hot fires in the 1970s, accounted for 16% of canopy trees in 1995. Important species in this group include *Acer rubrum*, *Liriodendron tulipifera*, and *Robinia pseudoacacia*. By 1995, snag densities in hot-fire plots had dropped to low levels.

DISCUSSION

I documented changes between the 1930s and 1970s by comparing plot data collected in two independent sampling efforts. In order to attribute observed differences to changes in disturbance regime (particularly the onset of effective fire suppression about 1940), I needed to establish that xeric plots in the Miller and Uplands data sets occupied similar sites. Previous studies in GSMNP have identified elevation and meso-scale topography (expressed in terms of solar radiation, slope position, exposure, or some combined index) as the most important environmental factors determining vegetation patterns (Whittaker 1956, Harmon 1980, Golden 1981, Callaway et al. 1987). In addition, detrended correspondence analysis (DCA; ter Braak 1987) ordinations performed separately on each of the data sets used in the present study identified a first axis strongly correlated with both relative slope position and topographic moisture index (which includes solar radiation, slope position, and curvature) and a second axis more weakly associated with elevation (J. Harrod, unpublished data). I found no significant environmental differences between any of the groups I compared. However, I limited my comparisons to topographic variables that could be derived from digital coverages and thus could be obtained for both the Miller and Uplands plots. Both Golden (1981) and Callaway et al. (1987) and studies elsewhere in the southern Appalachians (e.g., Newell 1997) have concluded that soil texture and chemistry also influence vegetation patterns. I acknowledge that some of the observed differences between the Miller and Uplands plots may reflect differences in soil conditions. I also acknowledge that some errors in the measurement of digital environmental variables may have arisen from inaccurate mapping of plots.

More recent changes were documented using the subset of Uplands plots resampled in 1995. This approach avoids questions of environmental similarity; because the same sites were measured repeatedly, changes can be confidently attributed to disturbance and succession. However, my inability to locate all the original Uplands plots may have subtly biased my results. Mean values of structural and compositional variables for the subset of Uplands plots that I resampled differ from those of the full data set. For example, yellow pines represent 54% of canopy trees in fire-suppressed xeric plots sampled in the 1970s, but only 33% of the canopy of resampled plots during that time period. These differences may reflect sampling errors arising from reduced sample size, or they may reflect systematic differences between the resampled plots and other fire-suppressed sites. Although I found little recent change in yellow pine densities on the fire-suppressed plots I resampled, at least two plots I searched for but could not locate were in areas of heavy pine beetle infestation. It thus seems likely that I have underestimated losses of yellow pines from the canopy.

To make the Uplands and Miller data sets compatible, I grouped tree diameters for the Uplands plots into the same classes used by Miller. This approach made direct comparisons of canopy density, basal area, and richness possible but precluded detailed size structure analyses and allowed only crude calculations of basal area. In addition, the lack of density data for stems < 10 cm dbh limited my analyses of regeneration dynamics. There is an inevitable lag between the establishment of a species in the understory and its growth to canopy size; thus, species that first appeared in the canopy in the 1970s may have already been present as seedlings and saplings in the 1930s. Similarly, regeneration failure may not be reflected in canopy changes for several decades. In fire-suppressed plots, densities of oaks and yellow pines less than 10 cm dbh decreased by more than 80% and more than 50% respectively between the 1970s and 1995, proportional losses much larger than those observed for canopy trees (J. Harrod, unpublished data).

In spite of these limitations and potential biases, my data show clear compositional and structural changes over the past six decades. In the 1930s, xeric sites in western GSMNP supported a mosaic of open, early-successional areas and closed-canopy forests. Mean canopy density, basal area, and richness were low relative to later fire-suppressed sites. Yellow pines and oaks made up the large majority of canopy trees, and other species occurred at low densities.

Descriptions of the western Smokies by Ayres and Ashe (1905, pp. 176-178) support the view that fires in the late nineteenth and early twentieth centuries maintained stands in an open condition and promoted yellow pine dominance. Of the Abrams Creek district, which includes much of the study area, Ayres and Ashe write, “Fires are very frequent. Many trees have been injured or killed, but no large areas are entirely deadened.” Of the Cades Cove district, just to the east, they write, "Fires are set whenever they will run, and the forest shows the effect of this practice. The brush is subdued; the timber is frequently scorched at the butt, often killed." And of Chilhowee Mountain, just northwest of the study area, they write, "Many seedlings start up, but they are usually killed by fire and grazing. Under these conditions pine reproduces better than other species."

Disturbances other than fire may have also contributed to the low canopy densities and basal areas observed in xeric stands in the 1930s. The chestnut blight (*Endothia parasitica*), a fungus of Asian origin, appeared in GSMNP about 1925. Between 1930 and 1940, the blight killed most canopy chestnuts in the park (Woods and Shanks 1959). Infected chestnuts died standing, and chestnut snags often remained standing for several decades after their death. The sum of living and dead chestnuts recorded in the Miller data thus represents a reasonable estimate of pre-blight abundance. In the 1930s, live chestnuts and chestnut snags were present in the canopy of xeric forests at densities of four and 13 stems/ha respectively. Prior to the blight, chestnut appears to have been among the most important canopy species on xeric sites, comparable in density and basal area to *Quercus alba*, *Q. coccinea*, and *Q. prinus* but considerably below *Pinus rigida* and *P. virginiana*. However, the death of chestnut alone is insufficient to explain differences in canopy density of > 300 stems/ha and in basal area of > 12 m^2/ha relative to fire-suppressed plots at later times. The very low abundance of yellow pine snags in the 1930s data (< 1 stem/ha) suggests limited southern pine beetle activity. Impacts of livestock grazing and small-scale timber and fuel wood extraction on xeric sites also appear to have been quite limited (Lambert 1958, Pyle 1988). Evidence of past logging is reported on only three of 28 Miller plots and three of 16 fire-suppressed Uplands plots used in the present study.

A severe regional drought in 1925 caused considerable oak mortality on xeric sites (Hursh and Haasis 1931). The 1925 drought also contributed to unusually large and severe fires throughout the southern Appalachians (Barden and Woods 1973). In general, fires in the early twentieth century appear to have been more frequent during years with below-average precipitation (Harmon 1980). Levels of pine beetle infestation and storm damage have also varied considerably (Kuykendall 1978, Lorimer 1980). Composition and structure of xeric forests in the late nineteenth and early twentieth centuries were probably highly dynamic, and the Miller data capture only a portion of this variation.

During the first few decades of fire suppression, canopy density and basal area increased rapidly. Open conditions during this period allowed successful regeneration of yellow pines, oaks, and other species. Canopy richness increased as increasingly dense canopies were invaded by species formerly excluded by fire. Some of these "other" species (e.g. *Nyssa, Acer rubrum)* resprout vigorously when fires kill above-ground parts (Harmon 1980). Before fire suppression, these species may have persisted in the understory of xeric forests as small individuals that were killed back before they could reach canopy size. Other species (e.g. *Tsuga)* are not capable of resprouting and may have become widespread on xeric sites only after the onset of fire suppression.

Following rapid initial increases, overall canopy density, basal area, and richness on fire-suppressed sites remained nearly constant between the 1970s and 1995. During this period, the relative density of "other" species increased from 27 to 43%. Prominent among these were *Acer rubrum, Pinus strobus*, and *Tsuga,* relatively shade-tolerant, fire-sensitive species (Harmon 1984, Burns and Honkala 1990) usually associated with more mesic sites (Whittaker 1956).

Increases in densities of these species appear to have occurred largely at the expense of oaks, which decreased from 40% to 27% of canopy trees. Declines in oak populations have been observed throughout the southern Appalachians (SAMAB 1996). Recent increases in oak mortality have been attributed, in part, to the aging of a cohort of oaks which reached the canopy following the chestnut blight. In low-elevation xeric forests in GSMNP, the onset of fire suppression, which roughly coincided with the arrival of chestnut blight, may have contributed to this pulse of oak regeneration. As these trees age, they become increasingly susceptible to herbivorous insects and root diseases, particularly when stressed by drought. A regional drought in the mid-1980s also contributed to high levels of canopy oak mortality (Clinton et al. 1993).

Regeneration failure appears to be another factor in declining oak densities. My data and other studies (SAMAB 1996) indicate that oaks, while still important in the canopy, are poorly represented in smaller size classes. One cause of low juvenile oak survivorship may be competition from more shade tolerant species such as *Nyssa* and *Acer rubrum* in the understory (Lorimer et al. 1994). Increases in *Nyssa* and *Acer rubrum* have been linked with declines in oak populations elsewhere in the southern Appalachians (SAMAB 1996).

Some researchers have raised concerns that fire suppression might lead to the rapid loss of yellow pine dominance (White 1987, SAMAB 1996). In the fire-suppressed plots I sampled, canopy densities of yellow pines have decreased only slightly over the past two decades. However, it seems likely that for reasons discussed above, I have underestimated the rate of yellow pine loss. Yellow pine regeneration is currently scarce in the understories of fire-suppressed plots, and size and age distributions appear increasingly skewed toward larger, older individuals (J. Harrod, unpublished data). In the absence of fire, this senescing yellow pine cohort will most likely be replaced by species such as *Pinus strobus*, *Acer rubrum*, *Nyssa*, and *Tsuga* which are abundant in the understory. Periods of elevated pine beetle activity such as those which occurred 1954-1958 and 1967-1977 (Kuykendall 1978) could accelerate losses of yellow pines from the canopy.

Data from burned plots indicate a range of fire effects. Comparison of sites experiencing cool and hot fires involves some circularity, since the initial criteria used to separate them (percent basal area removed) is likely to be inversely correlated with density, basal area, and species richness of surviving trees. On the other hand, pooling cool and hot-fire plots obscures important differences in stand composition and dynamics; examples include the nearly complete dominance of yellow pines and oaks following hot fires and the high levels of yellow pine regeneration on hot-fire sites. Distinguishing hot and cool fires also helped to control for the fact that hot fires are rare in the southern Appalachians (Barden and Woods 1973, 1976) and are over-represented in the Uplands data set.

Pre-fire canopies of cool-fire plots were very similar to those of fire-suppressed sites, and cool fires caused minimal changes in canopy structure and composition. Increases in survival probability with increasing tree diameter appear to underlie this lack of change. While small stems of species such as *Acer rubrum* are more sensitive to fire than those of oaks or yellow pines, trees ≥ 10 cm dbh have a high chance of surviving cool fires regardless of species (Harmon 1980, 1984). More recent changes on cool fire sites include decreases in oak densities and increases in densities of other species. Although an earlier study (Barden and Woods 1976) found that low-intensity surface fires result in little or no yellow pine regeneration, I found considerable recruitment of *P. virginiana* on one cool-fire plot. The plot with high *P. virginiana* recruitment lost 25% of its basal area in the fire, placing it at the upper limit of the cool-fire class. On that plot, fire killed more than 90% of stems < 10 cm dbh, compared with less than 50% on other cool-fire plots.

Pre-fire basal area and density of hot-fire plots were considerably lower than those of fire-suppressed and cool-fire plots. Most hot fires occurred in areas where southern pine beetle activity had led to high densities of pine snags and large accumulations of woody fuels (Harmon 1980). Hot fires caused dramatic reductions in canopy density, basal area, and richness. While species such as *Acer rubrum* and *Pinus strobus* occurred in the pre-fire canopies of most of these plots, post-fire canopies were composed almost entirely of yellow pines and oaks, with a few scattered *Nyssa*. Between the 1970s and 1995, canopy density increased to a level comparable to that of fire-suppressed and cool-fire plots. Species such as *Acer rubrum* re-appeared in the canopy. On some sites, hot fires have led to dense regeneration of yellow pines.

In the century prior to park creation and the onset of fire suppression, xeric forests in western GSMNP experienced frequent fires of variable intensity. Low-intensity surface fires, though causing little canopy mortality, may have thinned the understory and culled small stems of sensitive species. Low-intensity fires may thus have limited recruitment into the canopy and promoted the dominance of yellow pines and oaks. Variation in intervals between fires would have occasionally permitted fire-sensitive species to grow to fire-resistant size (Harmon 1982, 1984). The presence in the 1930s data of stands with very low canopy densities and basal areas suggests occasional hot fires that killed most or all canopy trees. Stands with high densities of yellow pines and few or no other canopy species also suggest the occurrence of high-intensity, stand-initiating fires.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The majority of xeric forests in western GSMNP have not burned since before 1940. As a result, the open yellow pine and oak stands that occupied xeric sites in the 1930s have been replaced by denser forests containing high densities of fire-sensitive, shade-tolerant species usually associated with more mesic sites. Although the structure and composition of xeric forests at the time of GSMNP establishment appear to have been maintained largely by human-set fires, the disappearance of open yellow pine and oak dominated habitats may threaten the persistence of some plant and animal species. Breeding colonies of the endangered red-cockaded woodpecker *(Picoides borealis)*, which requires open pine forest, occurred historically in western GSMNP but have not been observed since the early 1980s (B. Dellinger, pers. comm.). Fire also appears necessary for the maintenance of most populations of *Pinus pungens*, a southern Appalachian endemic. Declines in oak populations may reduce the availability of acorns, an important food for black bears (*Ursus americanus*), and changes in canopy structure may also affect shrub and herb populations.

At least until the role that historical fire played in the maintenance of biological diversity in low-elevation xeric forests is better understood, I support the use of prescribed fire to restore and maintain patches of open forest dominated by yellow pines and oaks. However, my results suggest that a single low-intensity fire after several decades of fire suppression may not be sufficient to restore the forest structure and composition typical of xeric forests at the time of park creation. The total density of trees large enough to survive low intensity fire has increased dramatically, as has the proportion of those trees which are shade-tolerant species once rare on xeric sites. Restoration of open yellow pine-oak stands may require thinning treatments, high fire intensities, and multiple fire events. Rapid increases in canopy density and basal area observed on hot-fire plots suggest that maintenance of open stands requires short disturbance return intervals (< 20 years) similar to those of the pre-park era.

Chapter 2:

Age structure and radial growth in xeric pine-oak forests in western Great Smoky Mountains National Park

ABSTRACT

In the 19th and early 20th centuries, xeric upper slopes and ridges in western Great Smoky Mountains National Park burned frequently, largely as a result of anthropogenic ignitions. Fire frequency dropped dramatically following the removal of human settlements in the 1920s and 1930s and the implementation of effective fire control measures circa 1940. To evaluate the effects of this change in fire regime on forest composition and structure, I measured tree ages, diameters, and radial growth rates in four xeric *Pinus-Quercus* stands. Most trees in the present canopy (stems $\geq$ 10 cm dbh) established between 1920 and 1959. Although canopy individuals of fire resistant, light-demanding *Pinus* and *Quercus* species established throughout the 19th and early 20th centuries, few have established since 1945. In addition, shade-intolerant *Pinus* species are absent from the sapling stratum (stems $\geq$ 1.37 m high, < 10 cm dbh), and *Quercus* species are poorly represented. The oldest extant individuals of *Pinus strobus, Acer rubrum,* and *Oxydendrum arboreum* established circa 1920. The abundance of fire-sensitive species in the canopy has increased steadily over the past 50 years, and these species are currently well-represented as saplings. Recent patterns of recruitment and decreases in rates of radial growth are consistent with the hypothesis that

changes in fire regime have caused xeric sites to develop from open-canopy woodlands dominated by fire-resistant, light-demanding *Pinus* and *Quercus* species to closed-canopy forests increasingly dominated by more fire-sensitive, shade-tolerant taxa.

INTRODUCTION

Lightning and human-caused fires have shaped ecosystems throughout North America, creating a diversity of stand structures and landscape patterns and facilitating the persistence of disturbance-dependent species (Kilgore and Taylor 1979, Romme and Knight 1981, Pyne 1982, Abrams 1992, Ware et al. 1993, Covington and Moore 1994). For much of the 20th century, wildland managers have suppressed most natural and anthropogenic fires. In recent decades, increasing awareness of the historical role of fire has prompted concern that changes in fire regime may lead to the disappearance of fire-dependent species and ecosystems.

The fire regime in western Great Smoky Mountains National Park (GSMNP) changed considerably following removal of human settlements in the 1920s and 1930s and implementation of effective fire control measures circa 1940. In the late 19th and early 20th centuries, xeric slopes and ridges in GSMNP experienced frequent, predominantly human-set fires (Barden and Woods 1973, Harmon 1982). Fire scars and written records indicate a fire rotation prior to 1940 of less than 20 years (Harmon 1982). Most fires during this period were low-intensity surface fires, though intense, stand-initiating fires did occasionally occur (Barden and Woods 1973, Chapter 1 this volume). After 1940, the apparent mean fire rotation on xeric sites increased to > 500 years (Harmon 1982). In 1996, the National Park Service began a program of prescribed burns on a few xeric sites in western GSMNP; in addition, lightning fires have been allowed to burn unimpeded in some areas.

In a previous study, I examined plot data from the 1930s, 1970s, and 1990s to assess the effects of changing fire regime on canopy composition and structure in xeric forests in western GSMNP (Chapter 1 this volume). Results of that study suggest that in the 1930s, xeric sites supported a mosaic of open woodlands and closed-canopy forests dominated by *Pinus* subgenus *Pinus* species *(P. echinata, P. pungens, P. rigida,* and *P. virginiana*)[1] and, to a lesser extent, *Quercus* species *(*mostly *Q. alba, Q. coccinea, Q. prinus, Q. rubra,* and *Q. velutina).* Between the 1930s and 1970s, mean canopy density and basal area on fire-suppressed sites approximately doubled. During that period, low-basal area woodlands, major components of the historical vegetation mosaic, were largely replaced by denser closed-canopy forests. Widespread recruitment in the 1930s and 1940s allowed *Pinus* subg. *Pinus* and *Quercus* to remain dominant canopy taxa through the 1970s. Since that time, canopy basal area and density have remained relatively constant, but composition has shifted. *Pinus* subg. *Pinus* and *Quercus* have declined, while more shade-tolerant species such as *Acer rubrum, Nyssa sylvatica, Pinus strobus,* and *Tsuga canadensis* have increased.

In this study, I examine data on tree ages and radial growth rates from four xeric stands. I ask whether dendrochronological data are consistent with my previous findings based on historical plot data, specifically 1) a large increase in stand density beginning circa 1940, and 2) a shift in canopy composition, with *Pinus* subg. *Pinus* and *Quercus* heavily dominant in the late 19th and early 20th centuries, and other species such as *Acer rubrum, Nyssa sylvatica,* and *Pinus strobus* increasing markedly after 1940.

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[1] I distinguish *Pinus* subg. *Pinus*, the relatively shade-intolerant, fire-resistant two and three-needled "yellow" pines, from the more shade-tolerant, fire-sensitive *Pinus strobus* (Little and Critchfield 1969, Harmon 1984, Burns and Honkala 1990). Botanical nomenclature follows Kartesz (1994).

METHODS

The westernmost portion of Great Smoky Mountains National Park is a region of relatively low (262-940 m above sea level) but steep and highly dissected topography between the high peaks of the central Smokies and the Great Valley of eastern Tennessee. Vegetation patterns vary along a topographic moisture gradient, with *Pinus* subg. *Pinus* and *Quercus* historically dominating xeric upper slopes and ridges (Whittaker 1956, Harmon 1980, Chapter 1 this volume). Fire-scar chronologies indicate that most xeric stands last burned between 1920 and 1949 (Harmon 1982). Additional information on vegetation, climate, geology, and disturbance history of the region can be found in Harmon (1980, 1982), Harmon et al. (1983), Pyle (1988), and Chapter 1(this volume).

I selected study locations using the GSMNP geographic information database. Xeric sites were identified using a topographic moisture index (TMI) derived from a 30 m resolution digital elevation model. TMI combines measures of incident solar radiation, slope position, and local convexity or concavity; for details see Chapter 1(this volume). Xeric sites were identified as those with TMI values of ≤ 15 out of a possible 60 and include ridges and east, west, and south facing upper slopes. This definition of a xeric site is identical to that used in Chapter 1(this volume). I established additional site selection criteria for the present study: 1. Because I were interested in the effects of reduced fire frequency, I excluded xeric sites that had burned since 1940. 2. To allow evaluation of earlier findings, I excluded sites within 100 m of plots used in previous studies. 3. To allow for 100 m point-quarter transects (see below), I excluded patches less than 120 m in length. 4. To ensure that each study site represented an independent sample of the landscape, I selected sites that were at least 500 m from each other and in separate patches of xeric habitat. To avoid bias in site location, I selected sites prior to initiating field work. The four study sites selected were two south to southeast-facing upper slopes and two south to southwest-facing ridges, all between 430 and 560 m elevation.

My field methods resemble those used by Abrams and Downs (1990) to examine successional changes in Pennsylvania oak forests. In April 1998, I established a 100 m transect at each study site. At 20 m intervals along the transect, I conducted point-quarter sampling (Cottam and Curtis 1956). The four transects, each with six sampling points, yielded a total of 24 sampling points for the study. I recorded species, diameter at 1.37 m (dbh), and distance to the sampling point for the nearest canopy tree (≥ 10 cm dbh) and sapling (≥ 1.37 m high, < 10 cm dbh) in each of four quadrants. I also cored and measured the nearest canopy tree in each quadrant at 1.37 m above ground, obtaining a total of 96 cores. Cores were mounted and sanded, and annual growth rings were counted and measured to the nearest 0.1 mm. For cores that did not intersect the central pith, I estimated the number of missing rings by dividing the radius of the innermost visible ring (estimated from its curvature) by the mean width of the 10 innermost counted rings. I used a similar procedure for hollow trees, except that I estimated the radius of the missing portion as the difference between the length of the sound portion of the core and radius of the tree minus bark. Bark thickness was estimated using species-specific equations in Harmon (1984). No age estimates were made for two heavily decayed *Quercus* or one hollow *Nyssa* missing > 30% of its radius.

I employed two methods to estimate the year in which an individual tree reached canopy size (i.e. 10 cm dbh): 1) Starting with the central pith or the innermost visible ring, measured annual increments were added until the resulting diameter, plus estimated bark thickness, equaled or exceeded 10 cm; 2) Starting with the most recent annual ring, measured annual increments were subtracted until the resulting diameter plus bark fell below 10 cm. For most trees, the two methods produced nearly identical results; in a few cases, asymmetries in tree growth caused the estimates to differ by several years. Data presented below are the mean of the two estimates.

To assess overall trends in radial growth, I calculated mean annual increments by decade. I defined a growth release as a decade in which mean growth was more than double that of the previous decade and a growth suppression as a decade in which mean growth was less than half that of the previous decade. Numbers of trees showing suppression and release were then tallied by decade. Statistical significance of differences in frequencies of growth suppressions and releases before and after 1960 was examined using χ^2 tests; actual numbers of suppressions and releases observed during each period were compared with numbers expected based on the total number of decadal growth measurements under the null hypothesis of no change in frequency. 1960 was chosen *a priori* as the cut-off date for the test based on the observations that effective fire suppression began circa 1940 (Harmon 1982) and that canopy closure typically occurs within 20 years after fire on xeric sites (Chapter 1 this volume).

RESULTS

Stand structure and composition

Densities of canopy trees in the four transects ranged from 463 to 865 stems/ha, with a mean of 663 stems/ha (Table 2.1). The most abundant canopy tree was *Pinus strobus,* with a mean density of 146 stems/ha. Mean densities of *Acer rubrum, Pinus echinata,* and *P.*

Table 2.1: Densities of canopy trees (stems $\geq$ 10 cm dbh) and saplings (stems $\geq$ 1.37 m tall, < 10 cm dbh) and basal areas for xeric forests in western GSMNP. Values are means based on four point-quarter transects. Due to rounding, columns may not sum to totals.

Species	Tree density (stems/ha)	Sapling density (stems/ha)	Basal area (m^2/ha)
Acer rubrum	97	216	2.41
Amelanchier spp.		26	0.04
Carya spp.	37	159	0.96
Cornus florida		80	0.12
Ilex opaca		16	0.03
Nyssa sylvatica	15	113	1.38
Oxydendrum arboreum	43	40	0.71
Pinus echinata	58		8.55
Pinus rigida	29		3.46
Pinus strobus	146	825	6.74
Pinus virginiana	127		7.39
Quercus alba	21		0.83
Quercus coccinea	6	13	0.46
Quercus prinus	41	26	3.30
Quercus rubra	29		3.00
Quercus velutina	9		0.67
Sassafras albidum	5	47	0.22
Tsuga canadensis		40	0.07
Total	663	1603	40.32

virginiana also exceeded 50 stems/ha. Total basal areas ranged from 33 to 49 m^2/ha with a mean of 40 m^2/ha. *Pinus echinata, P. strobus,* and *P. virginiana* were the basal area dominants, each contributing > 6 m^2/ha. Mean basal areas of *Acer rubrum, Pinus rigida, Quercus prinus,* and *Q. rubra* also exceeded 2 m^2/ha.

Total densities of saplings ranged from 1147 to 2525 stems/ha with a mean of 1603 stems/ha. More than 50% of saplings were *Pinus strobus.* Other species abundant as saplings included *Acer rubrum, Carya* spp., *Cornus florida,* and *Nyssa sylvatica.* While *Pinus* subg. *Pinus* species made up 32% of canopy stems, they did not occur in the sapling stratum. *Quercus* species, which comprised 16% of canopy trees, made up 2% of saplings.

Size structure of trees along transects varied considerably among species (Figure 2.1). *Pinus echinata* and *P. rigida* were represented entirely by large individuals (32 to 54 cm dbh for *P. echinata,* 19 to 51 cm dbh for *P. rigida*). With the exception of one 60 cm tree, all *Pinus virginiana* were between 11 and 36 cm dbh. *Pinus strobus* was represented by a few large trees and by a much greater number of individuals 0 to 25 cm dbh. *Quercus* ranged from 5 to 56 cm dbh, with most trees between 10 and 40 cm dbh. Recorded individuals of *Acer rubrum* ranged from 1 to 28 cm dbh. With the exception of one 44 cm *Nyssa,* no trees of other species exceeded 22 cm dbh.

Patterns of establishment and recruitment

Of the 93 canopy trees successfully aged, 23% established before 1920, 67% established between 1920 and 1959, and 11% established after 1959. Establishment of *Pinus* subg. *Pinus* species occurred from the late 18th through mid 20th centuries (Figure 2.1). The oldest trees in each transect were *Pinus echinata* that established before 1850. Establishment

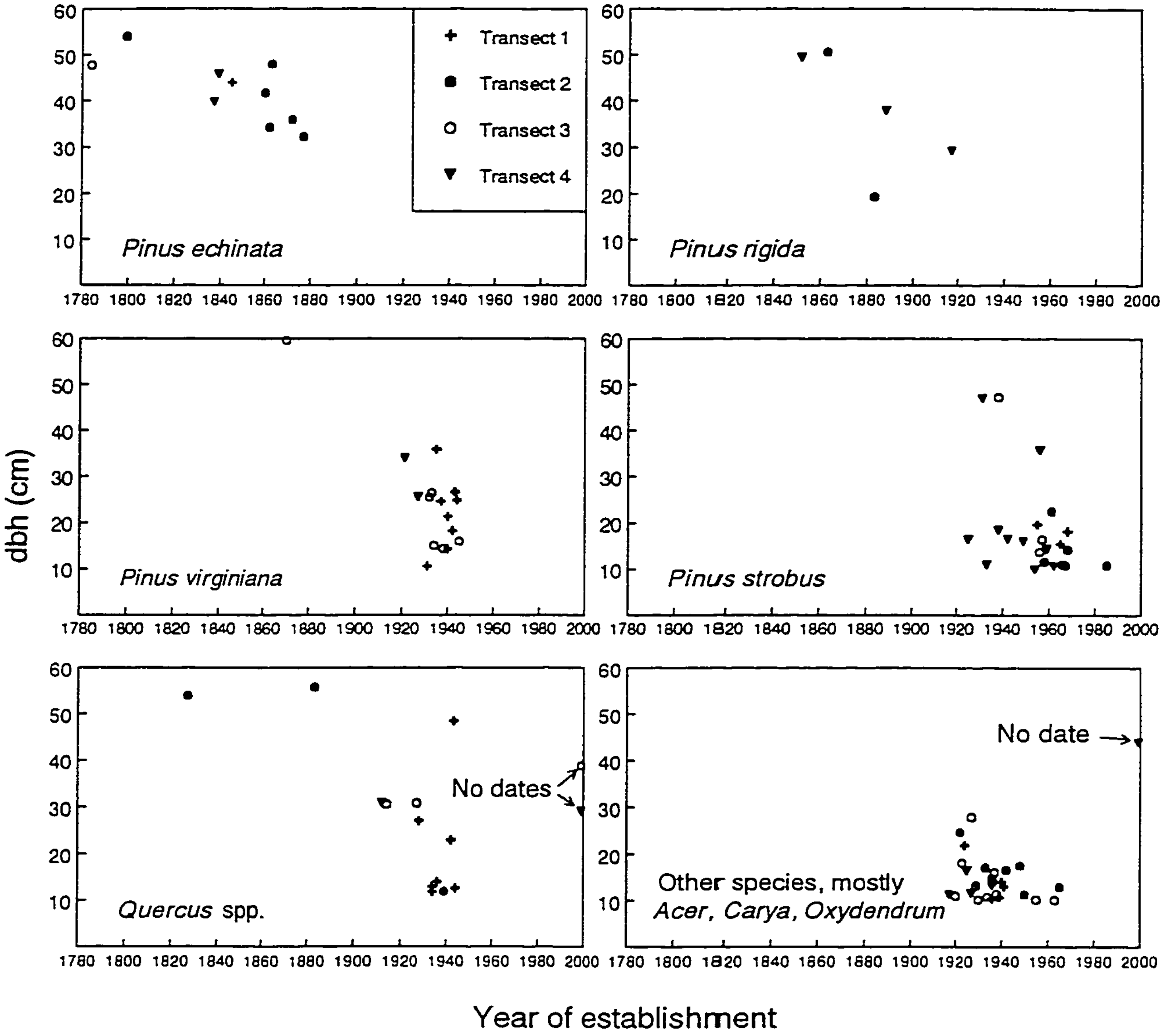

Figure 2.1 Date of tree establishment vs. diameter at breast height (dbh) for canopy trees (stems $\geq$ 10 cm dbh).

of *P. echinata* continued through the mid 19th century; the youngest observed *P. echinata* established in 1877. Five *P. rigida* established between 1852 and 1917; no younger *P. rigida* were observed. While a few *P. virginiana* established before 1930, the majority of extant *P. virginiana* established between 1930 and 1945, and none has established since then. A few individuals of *P. strobus* established between the 1920s and 1940s, but most of the *P. strobus* in the current canopy established in the 1950s and 1960s.

The oldest *Quercus* cores successfully aged were from a *Q. prinus* that established in 1827 and a *Q. rubra* that established in 1883, though two large, heavily rotted trees that could not be aged may have established earlier. *Quercus* establishment continued through the first half of the 20th century; the last *Quercus* to enter the canopy established in 1944.

The oldest extant *Acer rubrum* established in 1920; the youngest *A. rubrum* to reach canopy size established in 1963. The oldest sound cores of other species were from individuals of *Oxydendrum arboreum* and *Carya* spp. that established in the late 1910s and 1920s; the hollow, 44 cm dbh *Nyssa sylvatica* may have been considerably older. The youngest canopy tree that was not a *Pinus strobus* was an *Oxydendrum arboreum* that established in 1965.

I observed considerable variation in establishment patterns between transects. Transects 2 and 4 were dominated by large *Pinus echinata, P. rigida,* and *Quercus* that established in the 19th and early 20th centuries, while transects 1 and 3 contained fewer trees that established before 1920. In the 1920s, 1930s and 1940s, several *Pinus virginiana* established in transects 1 and 3, but only two established in transect 4 and none in transect 2. Other important canopy trees establishing after 1920 included *Carya* spp. and *Quercus* spp. in transect 1, *Acer rubrum* and *Oxydendrum arboreum* in transect 2, and *A. rubrum* in transect

3. In transect 4, most of the canopy trees establishing from the late 1920s onward were *Pinus strobus*; in transects 1 and 2, *P. strobus* did not appear until the mid 1950s.

Lags between establishment (defined here as growth to 1.37 m) and recruitment into the canopy (growth to 10 cm dbh) varied considerably, both within and among taxa. The fastest-growing individuals of *Pinus* subg. *Pinus, P. strobus,* and *Quercus* reached 10 cm dbh in about 10 years, and most individuals of these taxa reached canopy size in less than 30 years. The fastest-growing individuals of other species *(Acer rubrum, Carya* spp., *Nyssa sylvatica, Oxydendrum arboreum,* and *Sassafras albidum)* took more than 20 years to reach 10 cm dbh, and the median lag for each of these species was > 35 years.

Less than 23% of extant canopy trees entered the canopy before 1940. Most of the trees present in the pre-1940 canopy were *Pinus* subg. *Pinus;* a few *Quercus* were also present. While recruitment into the canopy occurred at high and relatively constant levels from the late 1940s through the 1990s, species composition of the recruits has changed. Between 1940 and 1969, large numbers of *Pinus virginiana* grew to canopy size, along with smaller numbers of *Acer rubrum, Carya* spp., *Oxydendrum arboreum, P. strobus,* and *Quercus.* Only one of 31 *Pinus* subg. *Pinus* attained canopy size after 1970. While limited recruitment of *Quercus* spp. into the canopy has occurred since 1970, the majority of trees that entered the canopy during this period were *Acer rubrum, Carya* spp., *Oxydendrum arboreum,* or *Pinus strobus.*

Patterns of radial growth

I observed 15 growth releases and 26 growth suppressions between the 1850s and 1980s (Table 2.2). Frequency of growth release (numbers of releases relative to number of

Table 2.2. Numbers of canopy trees (stems $\geq$ 10 cm dbh) showing growth releases (Rel.) and growth suppressions (Supp.), and total number of individuals examined for growth suppression and release (Tot.), by decade.

	Pinus subg. *Pinus*			*Quercus* spp.			*Pinus strobus*			Other			Total		
Decade	Rel.	Supp.	Tot.	Rel.	Supp.	Tot.	Rel.	Supp.	Tot.	Rel.	Supp.	Tot.	Rel.	Supp.	Tot.
1810			1												1
1820			1												1
1830			2												2
1840			2												2
1850	1		3										1		3
1860			5			1									6
1870			5			1									6
1880			10			1									11
1890		1	10			1								1	11
1900		1	11			2								1	13
1910	1	1	13			2							1	1	15
1920	1	1	15			2							1	1	17
1930			16			4						1			21
1940		1	17	2		6			1			8	2	1	32
1950	1		23		1	8			3			17	1	1	51
1960	1	5	31			12	1		7	3	1	24	5	6	74
1970	1	1	31		3	13		3	10	2		25	3	7	79
1980		1	31			13		1	20	1	5	27	1	7	91

trees extant in each decade) did not differ before and after 1960 (χ^2 test; $p > 0.5$). All releases prior to 1960 were of *Pinus* subg. *Pinus* and *Quercus;* most releases since 1960 were of *Acer rubrum* or *Oxydendrum arboreum*. While I observed no more than one suppression in any decade prior to 1960, I observed six suppressions in the 1960s and seven each in the 1970s and 1980s. Frequency of growth suppression after 1960 was significantly higher than in the preceding 11 decades (χ^2 test; $p < 0.05$). While most suppressions prior to 1970 involved *Pinus* subg. *Pinus*, suppressions in the 1970s and 1980s were mostly of *P. strobus, Quercus,* and *Oxydendrum.*

DISCUSSION

Changes in forest structure and composition on xeric sites in western GSMNP appear to reflect a dramatic reduction in fire frequency relative to the early 20th century. The 19th and early 20th century fire rotation of 10-15 years (Harmon 1982) apparently limited canopy recruitment by culling small individuals of fire-sensitive species. This fire regime favored *Pinus* subg. *Pinus* and *Quercus*, whose faster rates of sapling diameter growth and bark production enabled them to reach fire-resistant size rapidly (Harmon 1984).

Reductions in fire frequency associated with GSMNP establishment allowed the survival of a large cohort of trees that established between 1920 and 1959. Until the mid 1940s, a relatively open canopy and limited litter accumulation apparently provided conditions favorable for establishment and rapid growth of *Pinus* subg. *Pinus* and *Quercus* (Barden and Woods 1976, Williams et al. 1990). Since that time, canopy composition has shifted toward species such as *Pinus strobus* and *Acer rubrum* that are capable of establishment and growth under denser canopies. These species, sensitive to fire when small (Harmon 1984), were historically rare on xeric sites (Chapter 1 this volume).

Other anthropogenic disturbances may have contributed to observed patterns of canopy recruitment. Between 1926 and 1940, the chestnut blight (*Endothia parasitica)*, an introduced fungus, caused the death of most canopy *Castanea dentata* in GSMNP (Woods and Shanks 1959). Prior to the blight, *Castanea dentata* made up about 10% of canopy trees and 15% of basal area on xeric sites in western GSMNP (J. Harrod, unpublished data), and its demise may have contributed to the high rates of establishment and recruitment observed during the period 1920-1959. While logging profoundly affected many southern Appalachian landscapes, its impact on xeric sites in western GSMNP was relatively small (Pyle 1988, Chapter 1 this volume); no evidence of past logging was found on the four sites used in the current study. Ayres and Ashe (1905) mention livestock grazing along with fire as a factor inhibiting forest growth. Selective grazing in the late 19th and early 20th centuries may have promoted the dominance of *Pinus* subg. *Pinus* at the expense of more palatable angiosperm species (Pyle 1988).

The xeric sites examined in the present study are typical of exposed upper slopes and ridges in western GSMNP and adjacent portions of Nantahala and Cherokee National Forests. Some early researchers concluded that *Pinus* subg. *Pinus* populations could persist on such sites indefinitely in the absence of fire, citing as evidence bimodal size class distributions (Whittaker 1956) and wide ranges of tree ages observed within single stands (Racine 1966). My results and those of other age-structure studies on xeric sites in the southern Appalachian Mountains (e.g. Barden 1976, Ross et al. 1982, Williams and Johnson 1990, Bratton and Meier 1998) indicate that most populations of *Pinus* subg. *Pinus* are not reproducing successfully. My data suggest that the bimodal size distributions observed by Whittaker (1956) in the 1940s may have been the result of a large cohort of *Pinus virginiana* that established in the 1920s and 1930s. While establishment of *Pinus* subg. *Pinus* occurred fairly continuously throughout the 19th and early 20th centuries, little or none has occurred since the middle of the 20th century (Barden 1976, Ross et al. 1982, Williams and Johnson 1990, Bratton and Meier 1998). In the absence of fire, it seems likely that species of *Pinus* subg. *Pinus* will disappear from many of the sites they now occupy and become increasingly restricted to ultra-xeric rock outcrops and extremely steep, rocky ridges where encroachment by other species is slow and regeneration can occur without fire (Zobel 1969, Barden 1977, Williams 1998). The characteristics, distribution and abundance of sites on which *Pinus* subg. *Pinus* populations can persist in the absence of fire deserve further study.

My data indicate dominance of xeric sites by *Pinus* subg. *Pinus* since the beginning of European settlement in the first half of the 19th century and provide evidence of *P. echinata* establishment in the late 18th century, when western GSMNP was largely controlled by the Cherokee (Dunn 1988). Both Cherokee and Europeans used fire to facilitate travel and food gathering and to improve game habitat and berry yields (Harmon 1982, Delcourt and Delcourt 1997). Fossil pollen and charcoal suggest deliberate burning of xeric southern Appalachian sites by prehistoric populations for at least the past 4000 years (Delcourt and Delcourt 1997). Most post-1940 fires in the southern Appalachians were of human origin (Barden and Woods 1973, 1976; Harmon 1982, Bratton and Meier 1998), and the same appears to be true of fires during the periods of Native American and European settlement (Ayres and Ashe 1905, Delcourt and Delcourt 1997). Few recent lightning fires have been intense enough to produce regeneration of *Pinus* subg. *Pinus* (Barden and Woods 1973, 1976).

Prior to the onset of widespread anthropogenic burning, *Pinus* subg. *Pinus* species may have been largely restricted to the rocky, ultra-xeric sites described above. In this scenario, anthropogenic fires and other land-use activities allowed *Pinus* subg. *Pinus* to spread onto less xeric sites (Williams 1998), and declines in these species observed since the 1930s may represent succession towards conditions that would have existed in the absence of human influence. It is also possible that severe regional droughts and pine beetle (*Dendroctonus frontalis*) outbreaks occurring at intervals of several decades may have occasionally led to large, intense lightning fires that allowed episodic establishment of *Pinus* subg. *Pinus* on typical xeric sites (White 1987).

Several researchers have suggested that the exclusion of fire leads to an increase in *Quercus* dominance in xeric southern Appalachian forests (Harmon 1980, White 1987, Williams and Johnson 1990, Williams 1998). In my study area, little *Quercus* regeneration has occurred since the mid 20th century. Densities of *Quercus* saplings have declined sharply in the past two decades (Chapter 1 this volume), and *Quercus* are now poorly represented in sapling size classes. My data suggest that reduced fire frequency and concomitant increases in stand density are factors in declines of both *Pinus* subg. *Pinus* and *Quercus* on xeric southern Appalachian sites.

Chapter 3

Fire regimes, post-fire succession, and twentieth century vegetation change on xeric southern Appalachian sites

ABSTRACT

his study seeks to document post-fire succession on xeric sites in the southern Appalachian Mountains, USA, and to assess the effects of 20th century reductions in fire frequency on vegetation structure and composition. I observed the first 18 years of succession on permanently marked xeric plots that burned in 1976 or 1977. Post-fire response varied with site conditions, fuel load, fire severity, and season. In the first three years after fire, sprouts of angiosperm species dominated tree regeneration. On sites where fires reduced litter depth below 10 mm, densities of shade-intolerant *Pinus* seedlings increased steadily over this period. Four to eight years after fire, large numbers of seedlings and sprouts that established following fire had grown to 1-10 cm dbh. By year 18, growth of these saplings led to canopy closure on most sites. Herbaceous cover and richness peaked in the first decade after fire, then declined.

I compared vegetation on burned xeric plots with that on plots occupying topographically similar sites that had not burned in more than 50 years. Regeneration of shade-intolerant *Pinus* spp. and mean cover and richness of herbs on these later-successional sites were sharply lower than those observed on recently burned plots.

I used data from non-permanent plots sampled in the 1930s to reconstruct early 20th century fire regime and vegetation. The estimated fire rotation of 10-14 years, based on time-since-fire dates for the 1930s plots, agrees with previous fire-scar chronologies. The 1930s vegetation data, while not revealing clear successional trends, suggest that the early 20th century landscape was a mosaic of open patches and young aggrading stands. Reconstructions of early 20th century landscape conditions based on recent post-fire succession also support this conclusion, and suggest that reductions in fire frequency circa 1940 led to substantial decreases in cover and richness of herbaceous species.

INTRODUCTION

Fires started by lightning and humans have shaped ecosystems throughout North America. In many areas, the historical regime of frequent surface fires maintained open-canopy woodlands dominated by fire-resistant trees (Kilgore and Taylor 1979, Abrams 1992, Ware et al. 1993, Covington and Moore 1994). Understories in these communities typically included a vigorous grass component and often possessed high species richness, particularly at fine spatial scales (Peet et al. 1983). For much of the twentieth century, wildland managers have suppressed both natural and anthropogenic fires, prompting concern over possible changes in vegetation composition, structure, and dynamics.

In systems where the historic disturbance regime included frequent surface fires, effects of decreased fire frequency may include increases in tree basal area and density, poor regeneration by fire-resistant but light-demanding tree species, invasion of the canopy by fire-sensitive but shade-tolerant species, and declines in understory richness and productivity (e.g. Ware et al. 1993, Covington and Moore 1994). In some cases, increases in canopy density and decreases in grass cover have contributed to a shift in disturbance regime from low-intensity surface fires to infrequent but catastrophic crown fires (e.g. Myers 1985, Covington and Moore 1994). In other cases, fires of all types have become less likely as open-canopy woodlands have been replaced by less pyrogenic mesic forests (e.g. Ware et al. 1993).

In western Great Smoky Mountains National Park (GSMNP), changes in fire regime have led to considerable changes in canopy composition and structure. In the late 19th and early 20th centuries, xeric slopes and ridges burned frequently; ignition sources included both lightning and human activities (Barden and Woods 1973). For the period 1856 to 1940, the mean fire return interval in xeric pine forests in western GSMNP was 12.7 years (Harmon 1982). The removal of human settlements prior to park establishment in 1934 and the onset of effective fire suppression circa 1940 reduced fire frequency dramatically; for the period 1940-1989, the mean fire return interval on xeric sites increased to > 500 years (Harmon 1982, J. Harrod, unpublished data). Between the 1930s and 1990s, mean density and basal area of canopy trees have doubled. Species of *Pinus* subgenus *Pinus*[2] and *Quercus* have declined, while more shade-tolerant species such as *Acer rubrum, Nyssa sylvatica,* and *Tsuga canadensis* have increased (Chapters 1, 2 this volume). Similar trends have been observed on xeric sites throughout the southern Appalachians (e.g. Ross et al. 1982, Williams and Johnson 1990, Bratton and Meier 1998). While several studies in southern Appalachian xeric forests have addressed effects of changing fire regimes on canopy structure and composition and short-term responses of understory vegetation to fire (Harmon 1980, Arthur et al. 1998,

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[2] We distinguish *Pinus* subg. *Pinus*, the relatively shade-intolerant, fire-resistant two and three-needled "yellow" pines, from the more shade-tolerant, fire-sensitive *Pinus strobus* (Burns and Honkala 1990, Harmon 1984, Little and Critchfield 1969).

Turrill 1998, Elliott et al. 1999), none have documented longer-term effects of fire regime on understory vegetation.

In 1977-78 I established permanent plots on recently burned sites in western GSMNP. The plots were resampled periodically between 1978 and 1995. I use these data to examine the first two decades of post-fire succession in detail, describing changes in the composition of the herb, shrub, seedling and sapling layers and in the composition and structure of the canopy. I also use plot data collected in 1977-78 and 1995 to describe structure and composition of stands occupying similar sites that have not burned since before 1940. These later-successional stands are used to extend the successional sequence beyond that observed directly in recently burned permanent plots. Finally, I use data from non-permanent plots sampled in the 1930s to reconstruct fire regime and post-fire succession in the early 20th century. By comparing recent and historical composition and structure, I seek to assess the effects of reduced fire frequency on stand and landscape composition, structure, and dynamics.

METHODS

Study area

The westernmost portion of Great Smoky Mountains National Park is a region of relatively low (262-940 m above sea level) but steep and highly dissected topography between the high peaks of the central Smokies and the Great Valley of eastern Tennessee. Bedrock is primarily Precambrian sandstone, siltstone, and shale (King et. al. 1968). Soils, mostly ultisols and inceptisols (Elder 1959), are acidic and infertile. The mean annual temperature in Gatlinburg, approximately 40 km northeast of the study area and at 442 m elevation, is 12.9

°C; mean annual precipitation is 1425 mm (Weather America 1996). Vegetation patterns vary along a topographic moisture gradient, with *Pinus* subg. *Pinus* and *Quercus* historically dominating xeric upper slopes and ridges (Whittaker 1956, Harmon 1980, Chapter 1 this volume). Fire-scar chronologies indicate that most xeric stands last burned between 1920 and 1949 (Harmon 1982). Additional information on vegetation, climate, geology, and disturbance history of the region can be found in Harmon (1980, 1982), Harmon et al. (1983), Pyle (1988), and Chapter 1(this volume).

Permanent plots

Between 1977 and 1985, staff of the National Park Service Uplands Field Research Laboratory sampled and permanently marked 410, 20 x 50 m plots in GSMNP. Of these, 108 were established in the western GSMNP study area between 1977 and 1979. Plot locations were chosen subjectively with the goal of capturing a range of site conditions and disturbance histories; plots include old agricultural fields and areas that burned in 1976 or 1977. The 20 x 50 m plots were subdivided into 5, 10 x 20 m subplots. Within each subplot, field crews recorded species and diameter at 1.37 m (dbh) to the nearest cm for all live and standing dead woody stems ≥ 0.5 cm dbh. On recently burned plots, trees that appeared to have died prior to the fire were distinguished from those that appeared to have been killed by the fire, allowing approximate reconstruction of the pre-fire stand. Stem counts and cover estimates were made for woody stems (tree seedlings and sprouts, shrubs, and vines) < 0.5 cm dbh in a series of five, 2 × 2 m quadrats distributed in a diagonal pattern within each subplot, yielding a total of 25 quadrats per plot. Cover of herbaceous species was estimated for 1 × 1 m quadrats located in the lower right corner of each seedling/shrub quadrat. Evidence of past disturbance, including fire, logging, and pine beetle (*Dendroctonus frontalis*) activity, was recorded. Years of past fires were determined, where possible, by sectioning fire scars. On sites that burned in 1976-77, mean depth of the duff (O2) layer was recorded, and percent canopy cover was measured using a spherical densiometer. Plot locations were marked on 1:24,000 topographic maps, and plot corners were monumented with tagged witness trees and iron bars.

I identified xeric plots in this data set using a digitally derived topographic moisture index that combined relative slope position, incident solar radiation, and local curvature; for details see Chapter 1(this volume). Xeric sites included east-, west-, and south- facing, moderately concave to highly convex upper slopes and ridges. The present study focuses on two groups of xeric plots with no history of past settlement or agricultural clearing. Ten plots were established in 1977 or 1978 in areas that burned in 1976 or 1977. Analysis of fire scar chronologies indicates that prior to the 1970s fires, these plots last burned in 1933 or 1942. Nine of these, including six that burned in fall 1976, two that burned in winter 1976, and one that burned in summer 1977, were sampled post-fire during the 1977 growing season. An additional plot was established in 1978 on a site that burned in the summer 1977 fire. In all ten plots, herbs and woody plants < 0.5 cm dbh were sampled in 1978, 1979, 1980, 1984, and diameters of woody stems ≥ 0.5 cm dbh were sampled in 1984. In 1995, woody stems ≥ 0.5 cm dbh and cover of herbs and woody plants < 0.5 cm dbh were sampled on six of the ten plots. No counts of stems < 0.5 cm dbh were made in 1995.

I also examined plots on topographically similar sites that have not burned since circa 1940. Seven such plots were established in 1977 or 1978 and resampled in 1995. Evidence of historical fire was found in all seven of these plots; the two for which fire dates could be established last burned in 1926. Site characteristics of the permanent plots used in this study are listed in Table 3.1.

1930s plots

Between 1935 and 1937, field crews sampled more than 1375, 20 x 40 m plots throughout GSMNP. Ninety-four of these plots were sampled in the western GSMNP study area in 1936 and 1937. Within plots, crews tallied live and dead trees of each species using the following diameter at breast height (dbh) classes: 10 to < 30 cm, 30 to < 60 cm, 60 to < 91 cm, and ≥ 91 cm. Stems smaller than 10 cm dbh were not tallied; however, crews did record the dominant species < 10 cm dbh in each of 100, 1 × 1 m quadrats per plot. Crews also recorded evidence of fire and logging, reporting, in some cases, the date of the most recent fire. MacKenzie and White (1998) provide additional information on this data set. I transcribed plot locations from early topographic maps to modern 1:24,000 USGS topographic quadrangles, digitized plot locations, and identified 28 plots in the western GSMNP study area that occupied xeric sites and had no history of past settlement or cultivation.

Analyses

I documented recent fire effects and post-fire succession on permanent plots using total densities of tree seedlings and sprouts (stems < 0.5 cm dbh), saplings (stems 0.5 - 10 cm dbh), and canopy trees (stems > 10 cm dbh), basal area of stems of tree species ≥ 0.5 cm dbh, and percent cover of woody shrubs, vines, and herbs. Species richness of woody shrubs, vines, and of herbs was documented at two spatial scales, that of individual quadrats (4 m^2 for

Table 3.1: Characteristics of permanent plots established in 1977-78 used in this study. For details on the derivation of digital topographic measures, see Chapter 1 (this volume).

Plot #	Elevation (m)	Slope position (0-100)	Slope (°)	Aspect (°)	Topographic moisture index (0-60)	Pine beetle damage in mid 1970s	Known fires	% basal area killed, 1970s fires	Postfire litter depth (mm)	Canopy cover (%)
Plots that burned in 1976-77										
10	599	88	9	139	12	Moderate	Summer 1977, 1933	25	6.8	44
16	720	96	11	152	6	Heavy	Fall 1976, 1933, 1909, 1905	84	0.9	18
18	734	97	11	126	7		Fall 1976, 1942, 1933, 1909	5	9.0	67
37	683	96	15	143	7	Light	Winter 1976, 1933	12	29.8	63
38	664	87	20	145	9	Heavy	Winter 1976, 1933	93	26.7	11
39	681	86	28	166	10	Heavy	Fall 1976, 1933, 1909, 1905	72	8.2	25
40	706	96	18	234	7		Fall 1976, 1933, 1909, 1905	4	27.0	86
41	707	85	29	134	10	Light	Fall 1976, 1942, 1933, 1909	13	5.8	50
42	682	87	26	117	15	Heavy	Fall 1976, 1942, 1933, 1909	57	4.7	53
94	612	89	7	225	10		Summer 1977, 1933	85	7.8	20
Plots that last burned before 1940										
6	606	96	5	131	12		1926, 1900			
9	596	91	18	169	6		1926, 1900			
45	636	94	12	212	7		No date, before 1940			
58	692	69	19	254	14		No date, before 1940			
70	514	92	18	104	11		No date, before 1940			
85	604	100	5	279	11		No date, before 1940			
88	597	87	18	124	12	Moderate	No date, before 1940			

shrubs and vines, 1 m^2 for herbs) and that of all 25 quadrats within a plot. To facilitate temporal comparisons, vegetation descriptions presented in text and tables include only the six burned and seven unburned plots sampled through 1995. Classification of species as trees, shrubs, woody vines, or herbs follows White (1982).

To examine effects of site and fire characteristics on vegetation response, I generated a matrix of Pearson correlation coefficients for the following parameters: elevation, topographic moisture index, percent of canopy trees killed by recent pine beetle activity, percent basal area killed by fire, post-fire percent canopy cover and litter depth, season of burn (coded as summer=1, fall=2, winter=3), density of *Pinus* subg. *Pinus* seedlings in 1980, density of *Pinus* subg. *Pinus* saplings in 1984, maximum cover of shrubs and woody vines over the period 1977-1984, and maximum cover of herbs over the same period. All ten plots that burned in 1976-1977 were used in the correlation analysis.

To document successional patterns in the early 20th century, I grouped the 1930s plots into the following time-since-fire categories: three to four years (seven plots), six to eight years (eight plots), 10 to 13 years (six plots), 17 to 20 years (three plots), and no date / no evidence of fire (four plots). I summarized basal area, canopy density and richness, and understory dominance for each of these successional classes. I then compared composition and structure along this successional chronosequence with that observed on recently burned permanent plots.

I used time-since-fire dates of the 1930s plots to estimate mean fire rotation in xeric stands in the early 20th century for comparison with previous estimates based on fire- scar data (Harmon 1982). Fire rotation is the time necessary for all stands or patches in a system to burn an average of one time; some elements may burn more than once, and others may not burn at all (White and Pickett 1985). Dates of past fire were recorded for 24 of the 28 plots. I subtracted the year last fire from the year of sampling (1936 or 1937) to obtain time-since-fire for these plots; values ranged from 3 to 20 years.

A maximum likelihood estimate of fire rotation, *b*, was calculated from the distribution of time-since-fire dates using a formula presented by Johnson and Gutsell (1994):

$$b = \frac{(a_r x_r)^{+} + \sum^{r} a_i x_i}{N}$$

where $(a_r x_r)^{+}$ is the time-since-fire age (x_r) beyond which time-since-fire was not recorded multiplied by the number of plots (a_r) for with no time-since-fire dates, *r* is the total number of observed time-since-fire ages, $a_i x_i$ is each time-since-fire age multiplied by the number of plots of that age, and *N* is the total number of plots. This approach assumes that time-since-fire dates follow a negative exponential distribution and thus that probability of fire is independent of time since previous fires. This assumption should be valid where fire occurrence is controlled more strongly by weather conditions and ignitions than by fuels. This appears to be the case in much of the southern Appalachians; fire scars, historical accounts, and observations of recent fire behavior indicate that fuels sufficient to carry a fire develop within 1-2 years after fire (Harmon 1982, Arthur et al. 1998), and year-to-year fluctuations in fire occurrence and size are strongly linked to annual variations in rainfall (Barden and Woods 1974, Harmon 1980, Sutherland et al 1995).

Because time-since-fire dates were not available for all plots, estimation of fire rotation also required an assumption concerning the maximum age at which fires could be detected and dated (Johnson and Gutsell 1994). To examine the sensitivity of my results to this assumption, I calculated fire rotation assuming that the time-since-fire distribution was truncated at 20 years, the maximum time-since-fire recorded in the 1930s data; I then repeated the calculations assuming that fires as old as 50 years could have been detected and dated. The 50-year assumption exceeds the maximum interval between fires (49 years) observed in fire scar chronologies from xeric pine forests in western GSMNP (Harmon 1982).

RESULTS

Post-fire succession on permanent plots

TREES: The pre-fire canopies of burned plots were dominated by *Pinus rigida, Pinus virginiana, Quercus coccinea,* and *Nyssa sylvatica* (Table 3.2). The most abundant saplings were *Nyssa, Pinus virginiana*, and *P. rigida* (Table 3.3). Basal area averaged 20.90 m^2/ha, canopy density 490 stems/ha, and sapling density 2921 stems/ha. Fires reduced mean basal area to 12.28 m^2/ha, canopy density to 285 stems/ha, and sapling density to 585 stems/ha.

Fire effects varied considerably between plots. Basal area killed ranged from 4 to 93%, post-fire litter depth from 0.9 to 29.8 mm, and post-fire canopy cover from 11 to 86%. Percent basal area killed showed a highly significant negative correlation with post-fire canopy cover, and both measures showed significant positive correlations with pre-fire pine beetle damage (Table 3.4). Post-fire litter depth was not significantly correlated with measures of canopy damage. However, litter depth did show a significant correlation with burn season; mean litter depth tended to be lower following summer burns and higher following winter burns.

Mortality patterns varied with species and fire severity; in all plots, mortality was concentrated on smaller stems. On plots on which fires killed $\geq$ 25% of basal area, 30 to 85% of canopy trees (stems > 10 cm dbh) and 87% to 99% of saplings (stems $\leq$ 10 cm dbh) were

Table 3.2: Mean densities (stems/ha) of canopy trees (> 10 cm dbh) in xeric permanent plots that burned in 1976-77 and in topographically similar plots that have not burned since before 1940

	Burned plots				Unburned controls	
Species	Pre-fire	1977-78	1984	1995	1977-78	1995
Acer rubrum	7	2	2	5	41	76
Carya glabra					13	7
Carya alba					6	3
Cornus florida					1	
Liriodendron tulipifera					1	1
Nyssa sylvatica	10	3	10	27	13	44
Oxydendrum arboreum	5	2	2	2	14	17
Pinus echinata	13	5	10	3	6	1
Pinus pungens	5	3	2	10	1	1
Pinus rigida	133	82	72	88	71	60
Pinus strobus	5			2	49	87
Pinus virginiana	137	68	37	328	131	137
Quercus alba				2	3	7
Quercus coccinea	132	95	95	85	54	46
Quercus marilandica	20	8	5	5	19	
Quercus prinus	15	13	13	10	113	106
Quercus rubra					1	1
Quercus velutina	8	7	8	8	40	13
Robinia pseudoacacia			2	7		
Sassafras albidum					1	1
Tsuga canadensis						24
Total	490	288	258	582	578	632

Table 3.3: Mean densities (stems/ha) of saplings (0.5 - 10 cm dbh) in xeric permanent plots that burned in 1976-77 and in topographically similar plots that have not burned since before 1940.

	Burned plots				Unburned controls	
Species	Pre-fire	1977-78	1984	1995	1977-78	1995
Acer pennsylvanicum					19	30
Acer rubrum	60	10	222	690	443	321
Amelanchier arborea				7		4
Betula lenta			2	3		
Carya glabra	7	2	2	3	21	7
Carya alba	5			2	41	4
Castanea dentata	5		3	7	7	
Cornus florida				3	120	101
Diospyros viginiana			17	27		4
Halesia carolina					1	
Ilex opaca			5	3		3
Liriodendron tulipifera					3	1
Magnolia fraseri						1
Nyssa sylvatica	890	298	680	843	569	394
Oxydendrum arboreum	95	30	183	490	84	46
Pinus echinata	13	3	3		7	
Pinus pungens	8	3	47	95	4	
Pinus rigida	273	58	220	1078	113	21
Pinus strobus	28	2	7	145	169	326
Pinus virginiana	785	77	1388	5568	260	160
Quercus alba	2	2	10	15	26	4
Quercus coccinea	140	55	205	303	46	30
Quercus marilandica	103	8	97	140	34	3
Quercus prinus	17	13	32	37	47	17
Quercus rubra	3	3		5	1	1
Quercus velutina	62	15	42	75	46	10
Robinia pseudoacacia	2		80	33		
Sassafras albidum	72	2	282	722	87	67
Tsuga canadensis	2			8	77	144
Total	2572	581	3527	10302	2225	1699

Table 3.4: Matrix of Pearson correlation coefficients and associated p-values for site and fire characteristics and measures of vegetation response for xeric plots in western GSMNP that burned in 1976-77. Sample size was 10 plots for all correlations except maximum shrub cover (n=8).

	Elevation	Topographic Moisture Index	Burn season	Pre-fire pine beetle damage	% basal area killed	Post-fire canopy opening	Post-fire litter depth	*Pinus* subg. *Pinus* seed- lings, 1980	Density *Pinus* subg. *Pinus* sap- lings, 1984	Maximum shrub cover 1977-1984	Maximum herb cover 1977-1984
Elevation	1.000	-0.509	0.516	0.042	-0.310	-0.358	0.031	0.077	0.193	0.176	-0.713
	p=0.000	0.133	0.127	0.907	0.384	0.309	0.932	0.834	0.592	0.677	0.021
Topographic Moisture Index	-0.509	1.000	-0.364	0.398	0.174	0.389	-0.384	0.710	-0.029	-0.500	0.388
	0.133	0.000	0.302	0.255	0.630	0.266	0.274	0.021	0.937	0.207	0.268
Burn season	0.516	-0.364	1.000	0.216	-0.028	-0.066	0.651	-0.312	-0.133	0.801	-0.361
	0.127	0.302	0.000	0.549	0.939	0.856	0.042	0.381	0.713	0.017	0.306
Pre-fire pine beetle damage	0.042	0.398	0.216	1.000	0.664	0.710	-0.276	0.358	0.594	0.068	0.240
	0.907	0.255	0.549	0.000	0.036	0.021	0.440	0.310	0.070	0.873	0.505
% basal area killed	-0.310	0.174	-0.028	0.664	1.000	0.935	-0.246	-0.115	0.526	0.281	0.795
	0.384	0.630	0.939	0.036	0.000	0.000	0.494	0.752	0.118	0.501	0.006
Post-fire canopy opening	-0.358	0.389	-0.066	0.710	0.935	1.000	-0.416	0.130	0.529	0.167	0.798
	0.309	0.266	0.856	0.021	0.000	0.000	0.232	0.720	0.116	0.693	0.006
Post-fire litter depth	0.031	-0.384	0.651	-0.276	-0.246	-0.416	1.000	-0.663	-0.595	0.763	-0.250
	0.932	0.274	0.042	0.440	0.494	0.232	0.000	0.037	0.070	0.028	0.487
Density *Pinus* subg. *Pinus* seedlings 1980	0.077	0.710	-0.312	0.358	-0.115	0.130	-0.663	1.000	0.252	-0.626	-0.069
	0.834	0.021	0.381	0.310	0.752	0.720	0.037	0.000	0.483	0.097	0.850
Density *Pinus* subg. *Pinus* saplings 1984	0.193	-0.029	-0.133	0.594	0.526	0.529	-0.595	0.252	1.000	-0.522	0.191
	0.592	0.937	0.713	0.070	0.118	0.116	0.070	0.483	0.000	0.185	0.598
Maximum shrub cover, 1977-1984	0.176	-0.500	0.801	0.068	0.281	0.167	0.763	-0.626	-0.522	1.000	0.094
	0.677	0.207	0.017	0.873	0.501	0.693	0.028	0.097	0.185	0.000	0.825
Maximum herb cover, 1977-1984	-0.713	0.388	-0.361	0.240	0.795	0.798	-0.250	-0.069	0.191	0.094	1.000
	0.021	0.268	0.306	0.505	0.006	0.006	0.487	0.850	0.598	0.825	0.000

killed. No species-specific patterns of canopy disturbance were evident on the sites of these severe fires; all species experienced relatively high mortality, and species dominant in the pre-fire canopy generally remained dominant in the more open post-fire canopy. The large majority of saplings that survived these severe fires were *Nyssa sylvatica, Pinus rigida,* and *P. virginiana*. On plots where fires killed < 25% of basal area, 0 to 7% of canopy trees and 29% to 60% of saplings were killed. The few large trees killed in these less severe fires were all *Quercus*. At sizes between 3 and 10 cm, species varied considerably in their fire resistance, with thick-barked species such as *Pinus rigida, Quercus primus,* and *Nyssa sylvatica* surviving better than thin-barked species such as *Acer rubrum* (Harmon 1980, 1984).

Tree regeneration following fire included both new seedlings and sprouts of individuals whose above-ground parts were damaged or killed by fire. The most important angiosperm taxa, including *Acer rubrum, Nyssa, Oxydendrum, Quercus coccinea*, and *Sassafras,* all sprouted extensively; the most consistent and vigorous sprouting was observed in individuals between 1 and 10 cm dbh. Limited sprouting was observed in the conifers *Pinus rigida* and *P. echinata.* The conifers *P. strobus, P. virginiana,* and *Tsuga canadensis* lack the ability to sprout (Harmon et al. 1983).

During the first through fourth growing seasons after fire, *Sassafras*, *Nyssa,* and *Quercus coccinea* remained the most abundant angiosperm trees in the seedling/sprout size class (Table 3.5). Density and cover of small *Pinus virginiana, P. rigida* and *P. pungens,* most of which arose from seeds that germinated after the fire, increased steadily throughout this period. By year four, mean total density of *Pinus* stems < 0.5 cm dbh exceeded 10,000 stems/ha. While *Pinus* subg. *Pinus* seedlings were difficult to identify to species when small, data from subsequent sampling suggests that > 90% of these were *P. virginiana.* Four

Table 3.5: Mean densities (in stems/ha) of seedlings and sprouts < 0.5 cm dbh of tree species in plots of differing successional age.

	Time since fire (years)					
	1	2	3	4	8	~50
Acer pensylvanicum						71
Acer rubrum	520	1400	1117	2033	3017	1857
Amelanchier arborea			33	67	67	57
Betula lenta				17	33	
Carya alba						71
Carya glabra	160	233	67	100	50	243
Carya ovata					17	
Castanea dentata	440	233	67	50	67	129
Cornus florida					33	2529
Diospyros virginiana		533	300	617	567	57
Fagus grandifolia					17	43
Ilex opaca	40	33				43
Juniperus virginiana				17		
Liriodendron tulipifera		33	133	100	83	
Magnolia fraseri	40		17		17	43
Nyssa sylvatica	16600	15533	7367	8950	4750	1614
Oxydendrum arboreum	2480	1600	2017	2500	6017	400
Paulownia tomentosa						
Pinus pungens	80			17	17	
Pinus rigida	360	1233	467	267	1167	143
Pinus spp.	240	867	950	7317		
Pinus strobus	40		33	33	200	1186
Pinus virginiana	680	1900	1583	2500	10350	943
Prunus serotina						
Quercus alba	320	100	50	167	117	14
Quercus coccinea	5800	4900	2650	2683	1650	2314
Quercus falcata						
Quercus marilandica	560	1667	983	733	367	371
Quercus prinus	80	267	133	150		1214
Quercus rubra	880	33				29
Quercus velutina	2240	1200	600	600	617	943
Robinia pseudoacacia	40	167	100	100	83	200
Sassafras albidum	22640	30033	16533	15017	10483	3543
Tsuga canadensis				67	83	114
Total	54240	61967	35200	44100	39867	18172

growing seasons after fire, densities of *Pinus* subg. *Pinus* showed significant negative correlations with post-fire litter depth but were uncorrelated with either canopy cover or basal area killed. Year 4 density of *Pinus* subg. *Pinus* also showed a significant positive correlation with topographic moisture index. In years 3 and 4, small seedlings of *Pinus strobus* and *Tsuga* appeared at low densities on a few plots.

Eight years after fire, many stems that established post-fire had grown to between 0.5 and 10 cm dbh. As a result, sapling densities on the most severely burned plots increased considerably and reached levels comparable to those in pre-fire stands. *Pinus virginiana* and *Nyssa sylvatica* dominated the sapling stratum. Eight years after fire, densities of *Pinus* subg. *Pinus* saplings showed marginally significant correlations with pre-fire pine beetle damage (p=0.07) and post-fire litter depth (p=0.07). Relative density of *Pinus* subg. *Pinus* saplings, expressed as an arcsine-transformed percentage of total sapling density, showed a significant negative correlation with litter depth (p=0.02) but no significant correlation with percent basal area killed or post-fire canopy cover. Seedlings of *Pinus strobus* and *Tsuga*, while still rare, continued to increase. On most plots, canopy density and basal area remained constant or showed modest increases relative to year one. On one plot (Plot 10), basal area and canopy density declined considerably from year one, apparently as a result of delayed mortality of large *Pinus* and *Quercus*. Canopy changes on other plots were relatively minor, reflecting growth and scattered mortality of individual trees.

Six burned plots were sampled in 1995, ~18 years after fire. Three plots (plots 10, 39, and 94) on which fires had reduced litter depth below 10 mm and killed 25% or more of basal area had developed into dense "dog hair" stands in which densities of saplings 0.5 to 10 cm dbh exceeded 10,000 stems/ha. The sapling layer on these sites was heavily dominated by

Pinus virginiana; other important species included *P. rigida, Nyssa, Sassafras,* and *Acer rubrum.* Substantial numbers of *P. virginiana* had grown to 10 to 15 cm dbh; as a result, mean density of canopy trees reached a level comparable to that on pre-fire plots. Basal area on these plots also showed large increases over year eight but remained considerably below pre-fire values. Plot 38, which experienced a winter fire that killed 93% of basal area but left a deep litter layer, remained fairly open. Its year 18 sapling density was about 6000 stems/ha; its basal area, at 10.55 m^2/ha, remained substantially below that of other plots. Sapling densities on plots 37 and 40, on which < 15% of basal area was killed and post-fire litter depth exceeded 20 mm, were considerably lower (< 3000 stems/ha) than those on sites of more severe fires. No tallies of stems < 0.5 cm dbh were made in year 18. However, mean cover of *Pinus virginiana, Sassafras,* and *Nyssa* < 0.5 cm dbh declined by 91, 64, and 63% respectively between years eight and 18; cover of *P. rigida, Oxydendrum, Acer rubrum, Quercus coccinea,* and *Q. velutina* also dropped by more than 20%.

Canopy and sapling strata of unburned plots sampled in 1977-78 generally resembled those of burned plots prior to fire, but had higher basal areas reflecting less extensive pine beetle damage. The species with highest basal areas were *Quercus prinus, Pinus virginiana, Quercus coccinea,* and *P. rigida.* The most abundant saplings were *Nyssa sylvatica, Acer rubrum,* and *Pinus virginiana. Quercus* species, though abundant both in the canopy and as seedlings, were poorly represented in the sapling layer. Mean total density of tree seedlings and sprouts < 0.5 cm dbh was one third to one half the mean values observed on recently burned plots in the first eight years after fire. Relative to burned sites, seedlings and saplings of *Pinus virginiana* and *P. rigida* were poorly represented on unburned sites. These species, which made up 65% of saplings and 29% of seedlings on 18-year-old burned sites, represented only 11% of saplings and 5% of seedlings in ~50-year-old unburned plots.

Between 1977-78 and 1995, canopy density and basal area on some unburned plots changed considerably; however, mean values remained relatively constant. Sapling densities declined in six of seven plots. Several *Quercus* and *Carya* species showed marked decreases in both sapling and canopy densities. Densities of saplings and small canopy trees of *Pinus virginiana* and *P. rigida* also decreased sharply, while densities of trees in most size classes larger than 15 cm remained stable or increased. Similar trends were evident in *Nyssa, Acer rubrum,* and *Sassafras;* sapling densities showed moderate declines while densities of canopy trees increased. Sapling and canopy densities of *Pinus strobus* and *Tsuga* both increased; for the first time, individuals of *Tsuga* exceeded 10 cm dbh.

No tallies of stems < 0.5 cm dbh were made in 1995. Total cover of tree seedlings and sprouts declined between 1977-78 and 1995; cover of *Sassafras, Cornus florida, Quercus coccinea, Acer rubrum, Nyssa, Quercus prinus,* the species that dominated the seedling/sprout stratum in 1977-78, all declined. Over this period, cover of small *Pinus strobus* and *Tsuga* increased.

WOODY SHRUBS AND VINES: Post-fire changes in woody shrubs and vines were less dramatic than those observed in trees or herbaceous species (Table 3.6). Shrub and vine cover rebounded rapidly, increasing from 14% the first year to 23% the second. (On one plot, plot 10, which was first sampled two weeks after fire in 1977, no shrub species were recorded in year one.) Mean shrub cover peaked at 36% in year eight before declining to 24% in year 18. Highest values for individual plots were recorded in years three through eight. Maximum shrub cover showed a significant positive correlation with post-fire litter depth and a

Table 3.6. Mean cover (%) of woody shrubs and vines in xeric permanent plots that burned in 1976-77 A76and in topographically similar plots that have not burned since before 1940.

	Burned plots						Unburned control plots	
Species	1977	1978	1979	1980	1984	1995	1977-78	1995
Chimaphila maculata	0.02	0.01	0.02	0.03	0.01	0.10	0.15	0.11
Epigaea repens	0.02	0.01	0.11	0.10	0.12	0.08	0.19	0.03
Gaultheria procumbens	0.18	0.35	0.65	0.71	1.34	0.40		
Gaylussacia baccata	4.48	5.68	6.27	5.62	7.98	7.13	0.87	0.09
Gaylussacia ursina	0.04	0.05	0.18	0.13	0.41	0.65	12.34	8.37
Kalmia latifolia	2.02	2.80	4.92	3.61	6.02	2.80	0.45	0.06
Lyonia ligustrina	0.19	0.12	0.45	0.17	0.23	0.17	0.03	0.01
Rhus copallinum	0.01	0.13	0.22	0.21	0.19	0.06		
Smilax glauca	1.07	1.71	1.87	1.45	1.20	0.85	0.79	0.51
Smilax rotundifolia	0.71	1.91	4.05	2.66	2.63	1.81	4.17	1.11
Vaccinium hirsutum	0.68	1.21	1.47	1.97	1.83	1.24	4.12	1.10
Vaccinium pallidum	3.80	7.81	10.53	9.41	12.33	7.38	21.04	7.45
Vaccinium stamineum	0.66	0.91	1.33	1.22	1.44	0.79	1.14	0.61
Other	0.09	0.15	0.07	0.22	0.19	0.32	0.57	0.41
Total cover	13.90	22.72	32.09	27.30	35.75	23.58	45.33	19.54
Mean species /4m^2 quadrat	2.74	2.73	2.75	3.11	3.27	3.83	2.98	3.08
Mean species / 25 quadrats	6.00	7.17	6.83	7.67	7.83	10.33	8.14	8.00

significant correlation with season (highest for winter burns) but was uncorrelated with percent basal area killed or canopy cover. Mean richness of shrub and woody vine species per 4 m^2 quadrat increased from 2.7 in year one to 3.8 in year 18; species per plot (e.g. per 25, 4 m^2 quadrats) increased from 6.0 to 10.3.

The woody shrub component was dominated by members of the family Ericaceae. Of these, *Gaylussacia baccata*, *Vaccinium pallidum*, and *Kalmia latifolia* remained most abundant throughout the first 18 years of post-fire succession; *V. stamineum* and *V. hirsutum* were also important on some plots. Dominant woody vines were *Smilax glauca* and *S. rotundifolia*. Cover of most shrub and vine species reached peak cover in years three through eight and declined by year 18.

On sites that had not burned since 1940, mean shrub and vine cover in 1977-78 was 45%, a value higher than that observed on burned plots during any year. In 1995, mean cover had declined to 19%. In both 1977-78 and 1995, number of species per 4 m^2 quadrat and number per plot (3.0 to 3.1 and 8.0 to 8.1 respectively) were lower than those observed in 18-year-old burned stands. *Gaylussacia baccata* and *Kalmia*, which were abundant on some burned plots, occurred at much lower levels in unburned stands. In contrast, *Gaylussacia ursina* was far more abundant on unburned than on burned sites. *Rhus copallinum*, a minor shrub on several burned plots, was absent entirely from unburned plots. All major woody shrub and vine species show marked decreases over the period 1977-78 to 1995.

HERBACEOUS PLANTS: Richness and cover of herbaceous species changed considerably over the first 18 years of post-fire succession. Mean herbaceous cover increased from 3% during the first growing season after fire to 15% the second year and remained between 21 and 24% in years three, four, and eight. Maximum herb cover showed a highly significant positive correlation with percent basal area killed and a highly significant negative correlation with canopy cover but was uncorrelated with post-fire litter depth. Maximum herb cover also showed a significant negative correlation with elevation. Eighteen years after fire, mean herbaceous cover had dropped to 4%.

Trends in fine-scale herb richness mirror those in cover. The mean number of herb species per 1 m^2 quadrat increased from 1.5 during the first growing season after fire to 2.5 the second. During the third, fourth, and eighth growing season after fire, mean richness remained between 2.8 and 3.0 species/m^2. By year 18, fine-scale richness dropped to 1.7 species/m^2, and several plots showed sharp drops in richness relative to year eight. On Plot 38, the canopy of which remained more open than that of other burned plots, fine scale richness in year 18 remained higher than that of other plots. Mean herbaceous richness at the whole-plot scale (e.g. species per 25, 1 m^2 quadrats) was 10.2 the first growing season after fire and remained between 12.3 and 13.5 in years two through 18.

Important herbaceous species on burned plots include several members of the families Asteraceae (*Aster surculosus, Coreopsis major, Erechtites hieracifolia, Gnaphalium obtusifolium*, and *Solidago odora),* Fabaceae (*Lespedeza hirta, L. repens,* and *Tephrosia virginiana*) and Poaceae *(Dichanthelium* spp., *Schizachyrium scoparium,* and *Sorghastrum nutans)* (Table 3.7), as well as *Lechea racemulosa racemosa* and *Pteridium aquilinum*. In the first growing season after fire, *Pteridium* dominated the relatively sparse herb layer. In year two, cover of *Erechtites* increased dramatically. *Erechtites* remained the dominant herb in year three, declining to very low levels in years four and eight before disappearing entirely in year 18. *Schizachyrium* increased steadily from the first through eighth year, becoming the most abundant herb in year four. *Schizachyrium* reached its greatest cover and dominance in

Table 3.7. Mean cover (%) of herbaceous plants in xeric permanent plots that burned in 1976-77 and in topographically similar plots that have not burned since before 1940.

	Burned plots						Unburned control plots	
Species	1977	1978	1979	1980	1984	1995	1977-78	1995
Aster solidagineus	0.01	0.10	0.10			0.07		
Aster spp.	0.01	0.03	0.21	0.10	0.21	0.04	0.06	0.03
Aster surculosus	0.17	0.60	1.08	0.65	0.95	0.26	0.03	0.05
Aureolaria laevigata	0.14	0.01			0.09	0.07	0.04	0.01
Aureolaria pectinata		0.03		0.11	0.42			
Baptisia tinctoria	0.02	0.05	0.17	0.09	0.19	0.08		
Conyza canadensis		0.05	0.55	0.27				
Coreopsis major	0.30	1.10	1.08	0.86	0.41	0.17	0.14	0.01
Dennstaedtia punctilobula			0.03	0.03	0.33			
Dichanthelium spp.	0.47	1.49	3.47	2.49	0.48	0.15	0.24	0.07
Erechtities hieraciifolia	0.02	3.14	4.97	0.03	0.05			
Galax urceolata	0.30	0.33	0.27	0.35	0.15	0.17	1.17	1.08
Gnaphalium obtusifolium	0.02	0.03	0.37	0.83	0.01			
Lechea racemulosa	0.22	0.71	0.45	0.37				
Lespediza hirta	0.02	0.13	0.33	0.50	1.45	0.04		
Lespediza repens	0.01		0.34	0.87	0.03			
Polygala curtissii	0.03	0.05	0.16	0.02	0.01			
Polystichum acrostichoides			0.01				0.23	0.03
Pteridium aquilinum	1.04	2.95	0.98	1.55	1.49	1.11	0.18	0.13
Schizachyrium scoparium	0.17	1.47	3.97	5.69	10.97	0.55	0.22	0.10
Solidago odora	0.07	1.20	2.24	2.86	1.91	0.25	0.05	
Sorghastrum nutans	0.16	0.17	1.52	1.19	0.87	0.12	0.05	0.04
Tephrosia virginiana	0.12	0.65	1.67	1.31	1.41	0.16	0.27	
Uvularia puberula	0.05	0.13	0.18	0.15	0.11	0.25	0.03	0.02
Other	0.08	0.14	0.07	0.19	0.17	0.21	0.54	0.32
Total cover	3.43	14.59	24.21	20.51	21.71	3.71	3.27	1.87
Mean species /1m^2 quadrat	1.50	2.52	2.96	2.80	2.79	1.85	1.06	0.85
Mean species / 25 quadrats	10.20	12.33	12.83	12.17	13.50	12.67	9.57	7.43

year eight, at which time its cover, at 11%, was more than five times that of *Solidago odora*, the next most abundant species. By year 18, *Schizachyrium* cover dropped to only 5% of its year eight value. In that year, *Pteridium* dominated the relatively sparse herbaceous layer.

With a few exceptions, the herbaceous species important in the first eighteen years of post fire succession were observed in plots by the first or second year after fire. However, species differed in the year in which they reached maximum cover; *Coreopsis*, *Lechea*, and *Pteridium* peaked in year two, *Aster surculosus*, *Dichanthelium*, *Erechtites*, *Sorghastrum*, and *Tephrosia* in year three, *Gnaphalium* and *Lespedeza repens* in year four, and *Schizachyrium* and *Lespedeza hirta* in year eight. With the exception of *Pteridium*, the species that dominated the herbaceous layer during the first decade after fire had declined to low levels or were absent entirely in 18-year-old stands.

On sites that had not burned since before 1940, herbaceous cover was low, decreasing from 3% in 1977-78 to 2% in 1995. During this period, herb cover on all seven unburned plots decreased. Mean herbaceous richness on these sites was also lower than on recently burned plots. Fine scale richness dropped from 1.1 species/m^2 in 1977-78 to 0.9/m^2 in 1995; species per 25, 1 m^2 quadrats decreased from 9.6 to 7.4. In 1977-78, the only herbaceous species with mean cover exceeding 1% was *Galax urceolata*. Several herb species abundant in burned plots, including *Tephrosia*, *Dichanthelium*, *Schizachyrium*, *Pteridium*, *Coreopsis*, *Solidago odora*, and *Aster surculosus*, were present at low levels in unburned stands. Others, including *Erechtites*, *Gnaphalium*, *Lechea*, and *Lespediza* spp., were absent from sample quadrats in unburned plots. Between 1977-78 and 1995, cover of most herb species decreased. *Dichanthelium* and *Coreopsis* showed particularly sharp declines, and *Tephrosia* and *Solidago odora* disappeared entirely.

Historical plot data

SUCCESSIONAL DYNAMICS: The chronosequence constructed using 1930s xeric plots failed to show clear successional trends in composition and structure. Neither basal area nor canopy density were significantly correlated with time since fire. Values of basal area and canopy density for plots three to 13 years old were within the range observed on more recent permanent plots of comparable successional age (Figure 3.1). However, the 1930s plots did not show clear increases basal area or canopy density with age. Density values for 17- to 20-year-old 1930s plots were considerably below those observed on 18-year-old permanent plots; densities and basal areas on plots with no recorded fire date were lower than those observed in stands that had not burned in 50 to 70 years.

Pinus virginiana, P. rigida, Quercus prinus, and *Q. coccinea* were important canopy trees throughout the 1930s chronosequence (Table 3.8). *Pinus strobus* and *Quercus alba* were also prominent in the canopy in some time-since-fire classes. Saplings of tree species dominated the understory quadrats; important species included *Pinus virginiana, P. rigida, Nyssa sylvatica, Acer rubrum, Quercus coccinea,* and *Q. velutina.* Shrub species were recorded as dominant on less than 10% of quadrats. The most important shrub was *Vaccinium pallidum;* other Ericaceae, including *Kalmia* and *Gaylussacia baccata,* were recorded at lower levels. The category “annual,” which apparently included all non-woody plants, was recorded as dominant on a few quadrats. In one of the four plots for which no fire date was recorded, the understory of 93 of 100 quadrats was described as “open,” with no species listed as dominant.

Table 3.8: Understory dominance and canopy density in 1930s plots of varying successional age. Due to rounding, understory dominance may not sum to 100%.

	Understory dominance (% of quadrats)					Canopy density (stems/ha)				
	3-4 yr	6-8 yr	10-13 yr	17-20 yr	no date	3-4 yr	6-8 yr	10-13 yr	17-20 yr	no date
Canopy trees										
Acer rubrum	6	14	9	7	5	9	8	6		9
Carya alba	6	2	5	2	9		2		8	19
Carya glabra	2	2	1	1		2				
Castanea dentata	7	4	3	3	5	3	12			
Cornus florida	2	2	3	1	3					
Diospyros virginiana				1						
Halesia carolina			1							
Nyssa sylvatica	10	6	8	12	7	2	2		16	
Oxydendrum arboreum	5	5	8	6	9				4	12
Pinus echinata	1	1				3	5			
Pinus pungens						2	3			
Pinus rigida	3	6	4	16	5	55	136	62	70	12
Pinus strobus	2	1	5		5	16	5	10		37
Pinus virginiana	12	7	12	18	4	61	100	74	61	40
Quercus alba	4	2	6	3	8	12	17	14		102
Quercus coccinea	5	8	8	7	8	17	15	23	57	34
Quercus marilandica		2				5				
Quercus prinus	5	6	6	4	1	17	11	37	20	12
Quercus rubra	3	3	3	6	2	7	14		8	3
Quercus velutina	8	8	8	1	3	16	5	6		25
Robinia pseudoacacia	2	2	1				3	4		
Sassafras albidum	3	4	3	3	1					
Shrubs and woody vines										
Ceanothus americanus					5					
Gaylussacia baccata	1									
Ilex montana			1							
Kalmia latifolia	3	5								
Leucothoe spp.		2								
Rhododendron maximum		3								
Smilax spp.			1							
Vaccinium arboreum			2							
Vaccinium pallidum	6	5		6						
Vaccinium spp.					1					
"Annual"	2		4	3						
"Open"					23					
Total	98	100	102	100	104	227	338	236	244	305

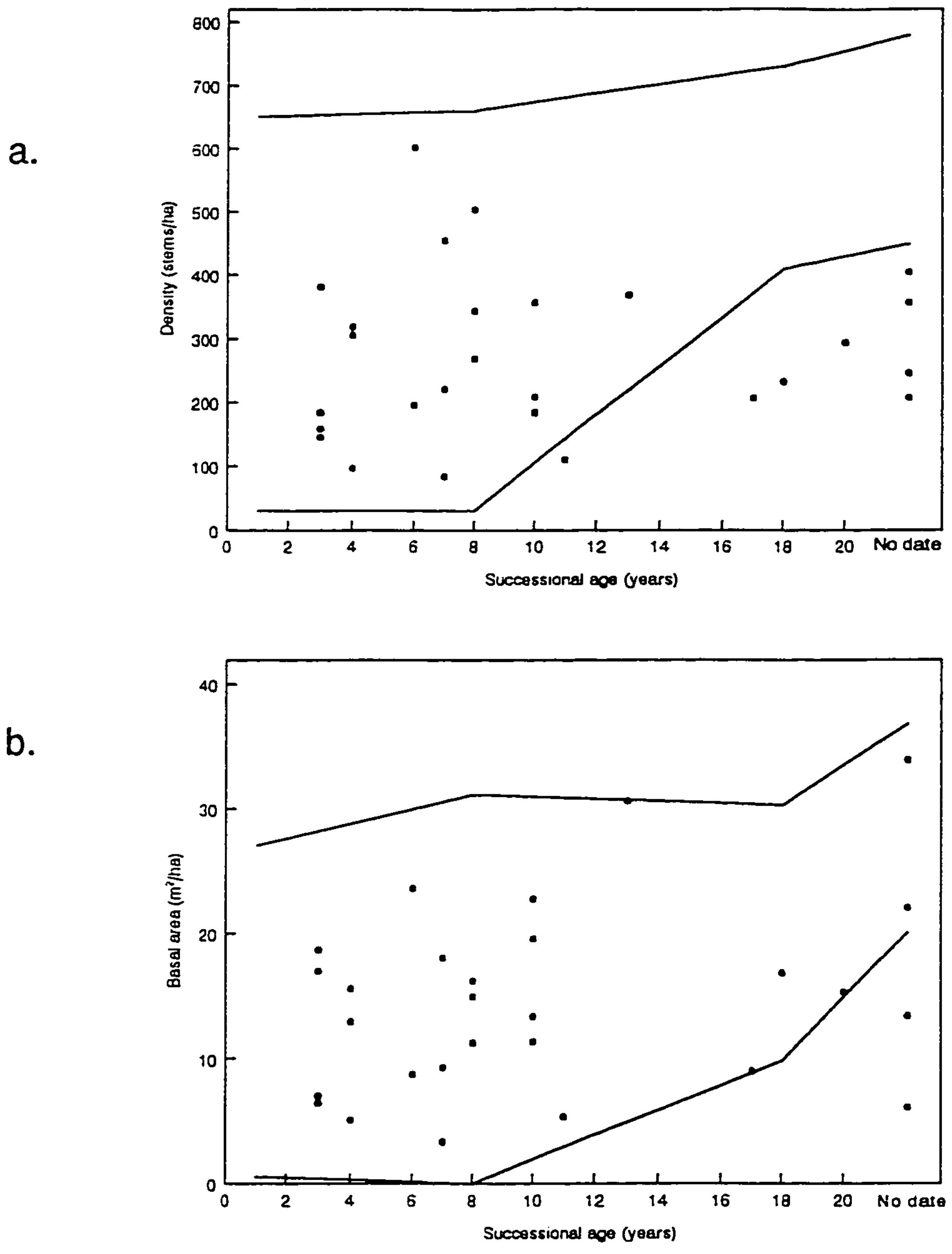


Figure 3.1. Density and basal area of 1930s plots of differing successional age (points). Lines represent maximum and minimum values observed in permanent plots sampled 1977-1995. 1930s plots for which no fire date was recorded were compared with permanent plots that have not burned since before 1940.

EARLY 20TH CENTURY FIRE REGIME: Time-since-fire dates between 3 to 20 years were recorded for 24 of the 28 plots sampled in the 1930s; no dates were reported for the other 4 plots. Fires were reported for most years between 1916 and 1933. Fifteen of the 28 plots burned within 10 years of sampling; most of these burned in 1926, 1928-30, or 1932-33. When I assumed that the time-since-fire distribution was truncated at 20 years (e.g. that dates of fires older than 20 years could not be determined), the maximum likelihood estimate of fire rotation based on the negative exponential model was 10.0 years. When I assumed that fires as old as 50 years could have been detected and dated, the negative exponential model yielded a mean fire rotation of 14.3 years.

DISCUSSION

Wildfire effects and short-term vegetation changes on xeric sites in western GSMNP are similar to those observed in other xeric southern Appalachian forests one to two years after wild or prescribed fires (Arthur et al. 1998, Turrill 1998, Elliott et al. 1999). Longer-term changes appear to follow the general pattern of succession after fire, logging, and agricultural abandonment in the southeastern US (e.g. Keever 1950, DeSelm and Clebsch 1990, Elliott et al. 1997). The first ~10 years after disturbance (the establishment phase; Peet and Christensen 1987) are characterized by open conditions, vigorous herb and shrub growth, and regeneration of both shade-tolerant and intolerant trees by seed and sprout. Within 10-20 years after disturbance, dense growth of young trees leads to closure of the canopy. The onset of this thinning or stem exclusion phase (Peet and Christensen 1987) coincides with dramatic declines in herbaceous cover and richness. Tree regeneration also drops sharply, and understory composition shifts toward species capable of establishment and growth under intense shade.

Variation in post-fire response between plots appears to reflect differences in site conditions, pre-fire composition and structure, fuel loads, and fire severity and season. Pine beetle outbreaks lead to heavy fuel accumulations (Nicholas and White 1984, Smith 1991) and thus to high-intensity fires that kill large numbers of canopy trees. Fire season affects litter depth, with greatest litter reduction occurring during summer and fall burns (Turrill 1998). Components of the vegetation respond individualistically to variation in fire characteristics. High light and low litter are widely recognized as necessary for regeneration of *Pinus* subg. *Pinus* (e.g. Barden and Woods 1976, Burns and Honkala 1990, Williams et al. 1990 but see Waldrop and Brose 1999). I found that *Pinus* subg. *Pinus* showed a negative correlation with litter depth and a marginal positive correlation with pre-fire pine beetle damage but was uncorrelated with measures of canopy opening per se. Shrub cover was highest on sites of winter burns, where deep litter remained after fire. Thus, burn season and its effects on litter depth may influence the outcome of competition between *Pinus* subg. *Pinus*, other tree species, and shrubs such as *Kalmia* (Vose et al. 1995). Herbaceous diversity appears to respond primarily to tree mortality and associated canopy opening. The correlation results presented in this study should be interpreted with caution, taking into account the relatively small sample size, the possibility of spatial and temporal autocorrelation among plots, and the likelihood of observing spurious but statistically significant correlations in large matrices (Rice 1989). The growing literature on experimental burns in xeric southern Appalachian forests (e.g. Turrill 1998, Elliott et al. 1999, Waldrop and Brose 1999) should allow more rigorous assessment of the effects of fire severity and season on vegetation response.

I compared vegetation on burned xeric plots with that on plots occupying topographically similar sites that had not burned in more than 50 years. In the 1970s, basal area and canopy densities on these unburned sites were similar to those of pre-fire burn plots but substantially higher than those observed following severe fires (Chapter 1 this volume). Total canopy density and basal area on unburned plots remained relatively constant between the 1970s and 1995. However, canopy composition shifted; densities of *Quercus* species declined, while densities of *Acer rubrum, Nyssa,* and *Pinus strobus* increased. Total sapling densities decreased on most plots. Mid-tolerant and intolerant species such as *Quercus* spp., *Carya* spp., *Pinus virginiana,* and *P. rigida* showed particularly sharp declines, while shade-tolerants such as *Nyssa* and *Acer rubrum* showed less dramatic decreases. Loss of canopy *Quercus* may be due, in part, to a severe regional drought in the mid 1980s (Clinton et al. 1993a). Declines in *Quercus* saplings may be linked to competition with saplings of more shade-tolerant species (Lorimer et al. 1994). Increasing sapling densities of *Pinus strobus* and *Tsuga canadensis* suggest continued recruitment of these species into the canopy (Chapter 2 this volume this volume). While mean shrub cover on unburned plots sampled in the 1970s was higher than that observed on burned plots, cover of all important shrub/vine species declined between the 1970s and 1995.

Mean cover and fine-scale richness of herbaceous species in unburned plots were sharply lower than those observed in burned plots in the first eight years after fire, and most of the herb species important in early post-fire succession were rare or absent in unburned plots. Total cover values for the families Asteraceae, Fabaceae, and Poaceae in stands than have not burned for > 50 years are one to two orders of magnitude lower than those observed in the first eight years after fire. On most unburned plots, herb cover and fine-scale richness declined between the 1970s and 1995.

Overall, total cover of seedlings/sprouts, shrubs, vines, and herbs on unburned plots decreased considerably between the 1970s and 1995. Estimates of vegetative cover may vary considerably between observers, and some of the differences I observed may reflect the fact that the 1970s and 1995 surveys were conducted by different individuals. Year-to-year fluctuations in climate and seed production and germination may also produce variation in seedling, shrub/vine, and herb cover. In contrast to cover estimates, tallies of stems 0.5 to 10 cm dbh are highly repeatable between observers; in addition, sapling densities are less sensitive than seedling densities to short-term variations in climate or recruitment. Sapling tallies indicate decreases in density comparable to, though less dramatic than, those observed in seedling/sprout cover and suggest that decreases in shrub, vine and herb cover are also real phenomena. Possible explanations for observed decreases in understory cover include decreases in understory light levels due to low light transmission by increasingly important shade-tolerant tree species (Canham et al. 1994) and heavy browsing by white-tailed deer (Whitney 1994).

The 1930s data indicate that xeric sites in western GSMNP supported a mosaic of open, early-successional areas and closed-canopy forests. Mean canopy density, basal area, and richness were similar to those of recently burned plots and lower than those of unburned sites sampled in the 1970s and 1990s (Chapter 1 this volume). *Pinus* subg. *Pinus* and *Quercus* made up the majority of canopy trees, and other species occurred at low densities. Regeneration of *Pinus, Quercus* and other tree species was widespread in the understory, ericaceous species were the most important shrubs, and herbaceous species dominated a few quadrats. I failed to detect clear successional trends in the 1930s data. One explanation for this result is that site-to-site variations in edaphic conditions, pre-fire vegetation, and fire behavior may have obscured successional trends. Many of the changes I observed following more recent burns were evident only because I could follow individual plots through time. In general, studies that employ space-for-time substitution do not appear to be as sensitive at detecting successional changes as permanent plot studies (Pickett 1989).

I did find some evidence suggesting that, while canopy densities on most recently burned permanent plots converged rapidly on those of unburned sites, the canopies of some 1930s plots remained considerably more open 17 to 20 years after fire. In addition, 1930s plots for which no fire date was recorded had lower basal areas and canopy densities than unburned plots sampled in the 1970s or 1995. These observations may represent an artifact of my limited sample size, the incorrect assessment of fire history by the 1930s researchers, or the inappropriateness of comparisons between 1930s plots with no fire dates and more recent unburned plots. Alternately, the observations may indicate a real change in successional dynamics. One possibility is that, in the early 20th century, vigorous growth of shrubs and herbs may have suppressed tree establishment and slowed rates of canopy closure. Another is that a history of chronic low-severity fires slowed canopy closure by limiting densities of stems < 10 cm dbh, the size class capable of most vigorous sprouting (Harmon 1984). A third possibility is that livestock grazing may have limited tree recruitment and maintained open structure in some xeric stands (Ayres and Ashe 1905).

The estimated fire rotation of 10-14 years, based on time-since-fire dates for the 1930s plots, agrees well with Harmon's (1982) estimate, based on fire-scar chronologies, of 12.7 years for the western Smokies and with other estimates of fire rotations for southern Appalachian pine stands (Sutherland et al. 1995). If I assume a mean fire rotation of 12.7

years, the negative exponential model (Johnson and van Wagner 1985, Johnson and Gutsell 1994) suggests that, at a typical moment in the early 20th century, more than 50% of xeric stands would have time-since-fire dates of 8 years or less. Seventy-five percent would have time-since-fire dates of 18 years or less, and only 2% would escape fire for more than 50 years. These calculations suggest that, in the early 20th century, most xeric sites were occupied by early-successional communities with relatively open canopies and sapling layers and high herbaceous richness and cover, and a smaller proportion were occupied by dense young stands in which understory light levels were greatly reduced and herb and shrub cover were low. The 1930s data, while not revealing clear successional trends, strongly support the conclusion that the early 20th century landscape was a mosaic of open, early successional patches and young thinning stands.

Fire behavior in the early 20th century may have differed considerably from that observed following several decades of fire suppression. While frequent fires would have limited accumulations of woody fuels, thick growth of grasses and ericaceous shrubs may have provided a highly flammable fuel bed. More open canopies would have allowed increased insolation and drying of the understory. Under such conditions, fires may have started more easily, spread more quickly, and reached larger size than those observed in recent decades (e.g. Barden and Woods 1973, Harmon et al. 1983).

Analyses of fire maps in the GSMNP geographic information database indicate that less than 10% of xeric forests in the western Smokies burned during the period 1940 to 1989 (J. Harrod, unpublished data). This change in fire regime has led to decreases in herbaceous cover and richness, poor regeneration by *Pinus* subg. *Pinus* and *Quercus* species, and the growth into increasingly dense canopies of shade-tolerant species historically rare on xeric sites. In many respects, effects of fire suppression on xeric forests in GSMNP parallel those observed in fire-suppressed *Pinus ponderosa* woodlands in the southwestern US (Covington and Moore 1994) and *Pinus palustris/Arista stricta* savannas in the southeastern coastal plain (Ware et al. 1993). A growing body of evidence suggests that the historical vegetation mosaic of the southeastern US included scattered open-canopy woodlands and prairies with grass and herb-rich understories on sites where fire, drought, or unusual edaphic conditions prevented the development of closed-canopy forest (e.g. Ware et al. 1993, Barden 1997). On xeric sites in the southern Appalachian mountains, fire appears to have been the principal factor preventing canopy closure. Because most fires were ignited by humans (Barden and Woods 1973), the open woodlands that occupied xeric sites prior to 1940 may represent components of a cultural landscape (Dunwiddie 1989) in which human activities created and maintained open vegetation structure and increased the richness and cover of herbaceous species.

Chapter 4:

Stand and landscape change in a protected area: western Great Smoky Mountains National Park 1936-1995

ABSTRACT

In western Great Smoky Mountains National Park (GSMNP), Tennessee, as in much of eastern North America, logging, agricultural clearing, and anthropogenic burning peaked in the mid 19th through early 20th centuries. Although land-use activities have declined since the early 20th century, atmospheric pollution and introduced insects and pathogens represent important ongoing human impacts. I examine the effects of changes in disturbance regime on stand and landscape-level vegetation patterns using plot data from 1936-37, 1977-79, and 1995-96. Specifically, I ask 1) have the site variables most strongly associated with landscape-level vegetation patterns remained constant through time, 2) what changes in vegetation composition and structure have occurred within groups of sites sharing similar environments and disturbance histories, and 3) have distributions of species along major environmental gradients changed through time?

I used non-metric multidimensional scaling (NMDS) in conjunction with digital terrain models to identify site variables most closely associated with compositional patterns in the 1930s, 1970s, and 1990s data sets. Length and relative position of environmental vectors were highly consistent across the three time periods. Compositional variation during each

time period was significantly correlated with soil texture, measures of local topography, and composite indices of topographic moisture.

Comparisons of 1930s and 1970s plot data indicate that highly significant increases in canopy density, richness, basal area and biomass occurred on mesic, intermediate, and xeric sites. *Castanea dentata* disappeared from the forest canopy, and the relative abundance of shade-tolerant species increased in all topographic moisture classes. Although the numbers of trees in most diameter classes increased, the largest absolute increases were among smaller trees (< 30 cm dbh). Several species largely restricted to mesic sites in the 1930s (*Acer rubrum, Liriodendron tulipifera, Rhododendron maximum, Tsuga canadensis)* had spread onto more xeric sites by the 1970s.

Between the 1970s and 1990s, basal area, biomass, and density of canopy trees remained relatively constant; significant decreases in sapling density and tree species richness occurred on mesic and intermediate sites. Relative abundance of shade-tolerant species continued to increase in all topographic moisture classes, and tree diameter distributions shifted toward larger size classes. Gradient distributions of several species contracted, *Oxydendrum arboreum* and *Pinus virginiana* toward xeric sites, *Cornus florida* and *Kalmia latifolia* toward intermediate sites, *Carya alba* and *Rhododendron maximum* toward mesic sites.

Changes in vegetation composition and structure in western GSMNP since the 1930s appear to reflect forest development and recovery following disturbance in the late 19th and early 20th centuries and ongoing disturbance by introduced pathogens. Observed changes in vegetation are consistent with current models of stand development (Bormann and Likens 1979, Oliver 1980). I conclude that historic anthropogenic disturbance profoundly altered both the structure of individual stands and the distribution of plant species across the landscape, and that future disturbances and environmental changes will interact with legacies of past land-use to produce ongoing changes in stand and landscape-level vegetation patterns.

INTRODUCTION

In ecosystems throughout the world, humans have altered primeval disturbance regimes, suppressing some forms of disturbance and introducing others. Documenting the effects of human modifications of disturbance regimes represents a central challenge in ecology (Lubchenco et al. 1991). Over the past century, many studies have examined the impacts of disturbances on vegetation composition, structure, and dynamics within individual stands and watersheds (reviewed in Peet 1992). In recent decades, researchers have devoted increased attention to landscape and regional interactions between vegetation, environment, and patterns of natural and anthropogenic disturbance (Turner 1989, Foster et al. 1998). In addition, the effects of changing land-use on ecosystem properties such as carbon storage have become subjects of increased attention (e.g. Harmon et al. 1990, Birdsey et al. 1993). The study of vegetation response to historical human activity provides a critical context in which to interpret effects of ongoing land-use and global atmospheric and climatic change (Christensen 1989, Foster et al. 1998).

In environmentally heterogeneous landscapes, frequency and intensity of natural disturbances and land-use activities often vary along the same topographic and edaphic gradients that appear to control distributions of plant species (Harmon et al. 1983, Foster 1992). Variation in disturbance regime along environmental gradients may play an important role in establishing and maintaining observed species distributions (Romme and Knight 1981).

Changes in disturbance regime may thus lead to changes in both the composition and structure of individual patches and in the distribution of species across landscapes (Harmon et al. 1983).

In Great Smoky Mountains National Park (GSMNP), North Carolina and Tennessee, as in much of eastern North America, logging, agricultural clearing, and anthropogenic burning peaked in the mid 19th through early 20th centuries (Christensen 1989, Williams 1989, Foster 1993, Foster et al. 1998). Although land-use activities have declined since the early 20th century, atmospheric pollution and introduced insects and pathogens represent important ongoing human impacts (SAMAB 1996, Sauer 1998). I seek to examine the effects of these changes in disturbance regime on stand and landscape-level vegetation patterns.

Forest composition in GSMNP varies strongly with topography, as do the distributions of major natural and anthropogenic disturbances (Whittaker 1956, Harmon et al. 1983, Pyle 1988). In addition, tree species exhibit highly individualistic responses to topography and disturbance (Whittaker 1956, Harmon 1984). In a previous study, I documented substantial changes in low-elevation xeric forests in western GSMNP since park establishment in the 1930s (Chapter 1 this volume). That study is among several that use long-term plot data to document vegetation changes within single stands or site types in the southern Appalachian Mountains (e.g. Della-Bianca 1983; Busing et al. 1988; Busing 1989, 1993). Whereas a few studies (e.g. Parker and Swank 1982, Phillips and Murdy 1985, Elliott et al. 1997) have documented multi-decade changes in watershed-level forest composition and structure following clearcutting on southern Appalachian sites, relatively little attention has been given to long-term changes in landscapes with more complex disturbance histories. In addition, the effects of changing disturbance regimes on vegetation-site relations and distributions of plant species along environmental gradients remain poorly understood (Foster et al. 1998).

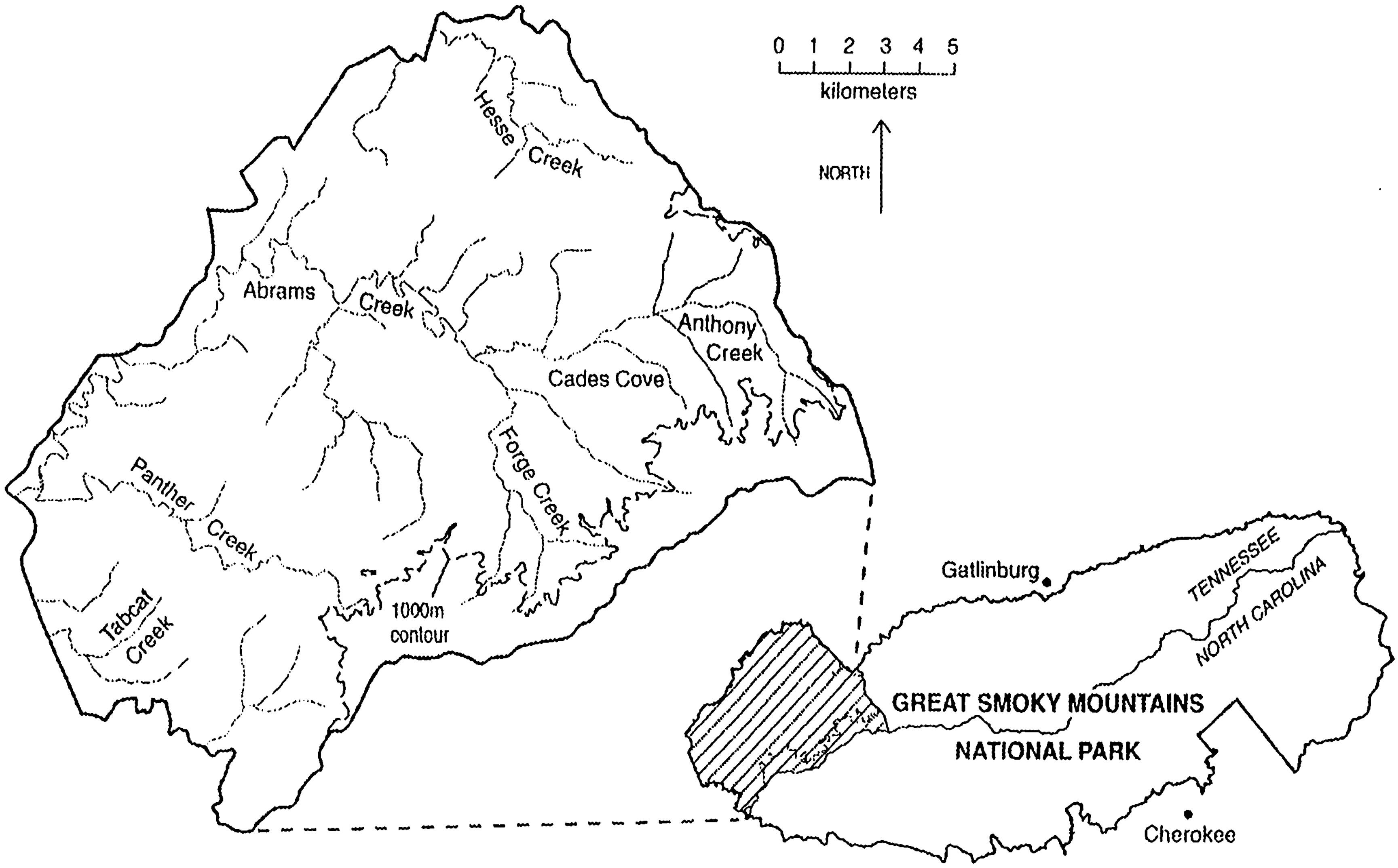
I examine changes in forests of western GSMNP using plot data from 1936-37, 1977-79, and 1995-96. Specifically, I ask 1) have the site variables most strongly associated with landscape-level vegetation patterns remained constant through time, 2) what changes in composition and structure have occurred within groups of sites sharing similar environments and disturbance histories, and 3) have distributions of species along major environmental gradients changed through time?

STUDY AREA

Plots used in this study are distributed across a 28,940 ha area comprised of three watersheds in western GSMNP (Figure 4.1). The northwestern portion of the study area, which includes the Panther Creek and Hesse Creek watersheds and the lower portion of the Abrams Creek watershed, is relatively low in elevation (~260-940 m) and is dominated by a series of southwest-northeast trending ridges and valleys. To the south and east, the land rises steeply to ~1500 m along State Line Ridge, the central crest of the Smokies. Only relatively low-elevation sites (≤ 1000 m elevation) are considered in the present study. Bedrock is primarily Precambrian sandstone, siltstone, and shale (King et. al. 1968). These strata are overthrust on Ordivician limestone, which is exposed in Cades Cove, a broad, gently rolling 1100 ha valley in the central portion of the study area. Outside the relatively fertile limestone areas, the soils, mostly ultisols and inceptisols (Elder 1959), are acidic and infertile. The mean annual temperature in Gatlinburg, approximately 30 km northeast of the study area and at 442 m elevation, is 12.9 °C; mean annual precipitation is 1425 mm (Weather America 1996).

Native Americans have been present in western GSMNP since at least 8000 years before present (Bass 1977). One the basis of pollen and charcoal from one sediment core,

Figure 4.1. Location of the study area in western Great Smoky Mountains National Park, Tennessee.



Delcourt and Delcourt (1997) conclude that Native Americans practiced deliberate burning in southern Appalachian forests beginning at least 4000 years ago. They suggest that Native American impacts were greatest on upper slopes and ridges, where fire was used to improve game habitat and berry crops and facilitate the gathering of acorns and nuts, and in floodplains and mesic coves, where fire was used to clear land for agriculture and settlement (Delcourt and Delcourt 1997).

European-American settlement began in the early 19th century (Dunn 1988) and was followed by the forced removal of the Cherokee in 1838. The European-American population of Cades Cove peaked twice, in the mid 19th and early 20th centuries, and was already declining when the US Department of the Interior began acquiring land for the proposed park in the 1920s (Shields 1981). Land-uses of European-American settlers included cultivation, grazing, hunting, nut and berry gathering, and small-scale timber extraction (Pyle 1988). Most of Cades Cove was cleared, and isolated agricultural fields and home sites were scattered throughout the northwestern portion of the study area, mostly in coves and valley bottoms and along lower slopes. Although much of Cades Cove was cultivated more or less continuously, a form of shifting agriculture known as "forest fallow" was practiced on more remote and marginal sites (Otto 1983). About 12% of the study area was cleared for settlement and agriculture at some point, though the actual area in cultivation at any one time was probably considerably lower.

Livestock, including cattle, sheep, goats, hogs, and horses, foraged in forests, abandoned fields, and the marshy meadows along the western end of Cades Cove. Settlers leased grazing rights to farmers from as far away as the Tennessee Valley, and every spring large herds of sheep and cattle were driven through Cades Cove to graze on high-elevation grassy balds along State Line Ridge (Dunn 1988). Settlers used fire to reasons similar to those of Native Americans: to clear land, improve grazing, increase berry yields, and facilitate gathering of nuts and other forest products. For the period 1856 to 1940, the mean fire rotation in xeric pine forests in western GSMNP was 12.7 years (Harmon 1982).

Settlers harvested forests for fuel and timber. Prior to about 1900, almost all the wood cut in the western Smokies was used locally (Ayres and Ashe 1905). In the first decade of the 20th century, portions of the Anthony Creek drainage on the southeast side of Cades Cove were selectively logged by a small, local operation that used portable sawmills and transported milled timber in wagons (Lambert 1958). Between 1908 and 1911, portions of the Hesse Creek Watershed were logged heavily using steam-powered skidders and locomotives (Schmidt and Hooks 1994).

GSMNP was officially established in 1934, and all logging activities in the western Smokies had ceased by 1940 (Pyle 1988). The removal of settlers, together with the implementation of effective fire control measures about 1940, led to a sharp decrease in fire frequency; for the period 1940-1989, the apparent mean fire rotation on xeric sites was > 500 years (Harmon 1982, J. Harrod, unpublished data). Agricultural activities also ceased, except in portions of Cades Cove where hay making and grazing have been continued to preserve the historical appearance of the landscape (Bratton et al. 1980).

In the 20th century, introduced fungal pathogens have caused extensive mortality of susceptible tree species. The chestnut blight (*Endothia parasitica*), a fungus of Asian origin, appeared in GSMNP about 1925. Between 1930 and 1940, the blight killed most canopy chestnuts in the park (Woods and Shanks 1959). Blight-infected *Castanea* died standing and often remained standing for several decades after their death. The dogwood anthracnose fungus, which first was first detected in the southern Appalachians in the late 1980s, has killed large numbers of *Cornus florida* (Daughtry and Hibben 1994, Wilds 1997). Major natural disturbances in the 20th century include severe droughts in 1925-26 and 1986-88, which caused extensive mortality of canopy oaks *(Quercus* spp.*)*, wind and ice storms, and outbreaks of the southern pine beetle *(Dendroctonus frontalis)*, which attacks mature individuals of some *Pinus* species (Hursh and Haasis 1931, Kuykendall 1978, Clinton et al. 1994). Botanical nomenclature follows Kartesz (1993).

METHODS

Forest conditions circa 1900

Ayres and Ashe's (1905) survey of the forests of the southern Appalachian region provides information on forest conditions in the western Smokies circa 1900. Ayres and Ashe traveled throughout the mountains of western North Carolina and eastern Tennessee, compiling statistics on forest composition and land use. They report data at the level of "districts" defined by watershed boundaries and other physiographic features (Figure 4.1). I tabulated their data on the four districts that contain portions of the western GSMNP study area. Ayres and Ashe's sampling methods were not recorded, and the accuracy of their data is not known; however, their data represent the only quantitative information on forest composition prior to GSMNP establishment.

1930s plots

Between 1935 and 1937, field crews under the supervision of GSMNP Assistant Forester F. H. Miller sampled approximately 1375, 20 × 40 m plots throughout GSMNP. 197

of these plots were sampled in the western GSMNP study area in 1936 and 1937 (MacKenzie and White 1998). Some plot locations were chosen randomly or spaced regularly along grids or transects; in other cases, plots were established non-randomly on ecotonal sites. Crews recorded plot locations on early topographic maps. I transcribed approximate plot locations to modern 1:24,000 USGS topographic quadrangles. Shape and location of some topographic features differed between the old and new maps; where discrepancies occurred, I attempted to transcribe plots to locations that matched original elevation, slope, aspect, and topographic position.

Within plots, the 1930s crews tallied live and dead trees of each species using the following diameter at breast height (dbh) classes: 10 to < 30 cm, 30 to < 60 cm, 60 to < 91 cm, and ≥ 91 cm. Stems smaller that 10 cm dbh were not tallied; however, crews did record the dominant woody species < 10 cm dbh in each of 100, 1 × 1 m quadrats per plot. The criteria used by the 1930s researchers to determine dominance in understory quadrats have not been preserved. Crews recorded evidence of fire and logging, reporting, in some cases, the date of the most recent fire.

Basal area estimates for 1930s plots were generated following MacKenzie (1998), who based his calculations on the geometric mean of the upper and lower limits of each diameter class and set the upper limit for the ≥ 91 cm size class at 122 cm. I estimated biomass of living stems ≥ 10 cm dbh from size-class geometric means using species-specific allometric equations in Busing et al. (1993); corrections for transformation bias were performed as recommended by Sprugel (1983). Additional equations for *Pinus echinata* and for the white oak group (*Quercus alba* and *Q. prinus)* were calculated by log-linear regression from data in Sollins and Anderson (1971). For species for which no allometric equations were available, I used equations for a member of the same subgenus, genus, or family. When no appropriate substitute existed, I used Busing et al.'s (1993) equation calculated from a mixture of deciduous species.

Permanent plots

Between 1977 and 1985, staff of the National Park Service (NPS) Uplands Field Research Laboratory sampled and permanently marked 410, 20 × 50 m plots in GSMNP. Of these, 254 were established in the western GSMNP study area between 1977 and 1979. Plot locations were chosen subjectively with the goal of capturing a range of site conditions and disturbance histories; plots include mature forests, former agricultural fields, and areas that had burned in 1976-77 prior to sampling. Plot locations do not correspond with those of the 1930s plots. The 20 × 50 m plots were subdivided into five, 10 × 20 m subplots. Within each subplot, field crews recorded species and dbh to the nearest centimeter for all live woody stems ≥ 0.5 cm dbh. Plot locations were marked on 1:24,000 topographic maps, and plot corners were monumented with tagged witness trees and iron bars. For 54 plots, samples of the A soil horizon were analyzed for soil texture [% sand, silt, and clay using the hydrometer methods of Bouyoucos (1963)] and pH (1:1 solution). In 1995 and 1996, I located and sampled vegetation in 123 of these plots following original methods. Texture and pH of A horizon soils were obtained for an additional 51 plots using procedures identical to those used in the 1970s. To maximize the number of plots with soils data, texture and pH values from the 1970s and 1990s are pooled in analyses below.

To control for effects of differences in sampling methodology between the 1930s and 1970s permanent plots, I processed the 1970s data to simulate 1930s methods. The 20 × 50 m plots were truncated to 20 × 40 m by the deletion of the last 10 × 20 m subplot. Stems < 10 cm dbh were excluded, and stems ≥ 10 cm were grouped into the size classes listed above. Henceforth, I refer to the data set composed of 1970s plots processed to simulate 1930s sampling methods as the "processed 1970s plots." Basal area and biomass estimates for the processed 1970s plots were calculated in a manner identical to that used for the 1930s plots, replacing actual dbh values with size-class geometric means.

Analyses

The locations of the 1930s, 1970s, and 1995 plots that fell within the study area were digitized using the ARC/INFO geographic information system (ESRI 1996). The NPS Twin Creeks Natural Resource Center provided the following digital coverages: elevation, slope, and aspect (all 30 m resolution), geology, generalized land-use history, and post-1930 fires (all 90 m resolution). All results presented in this study are for plots ≤ 1000 m elevation. I excluded from my analyses plots that were old agricultural fields and home sites and plots placed to assess impacts of backcountry campsites. 1970s plots that burned in 1976 or 1977 are discussed in detail elsewhere (Chapter 1 this volume, Chapter 3 this volume) and are not included in present analyses.

Additional terrain variables were derived from the digital elevation model. Curvature (CURV), a measure of local convexity or concavity, was generated using the ARC/INFO GRID module (ESRI 1996). Relative slope position (RSP; Skidmore 1990), which expresses downslope distance to the nearest cove or valley as a percentage of the total distance between valley and ridge, was calculated in GRID using algorithms developed by Wilds (1996); values range from 0 for valley bottoms to 100 for ridges and summits. Potential incident solar radiation (SOLRAD) for spring equinox (March 20) was estimated using the SOLARFLUX program (Rich et al. 1995). SOLARFLUX calculates insolation over the course of a day, taking into account shading effects of distant landforms as well as local slope and aspect. Relative hydrological inputs were estimated using a topographic convergence index (TCI) developed by Beven and Kirkby (1979). I also constructed two topographic moisture indices (TMI1 and TMI2) with which I attempted to model the combined effects of solar radiation and hydrologic flow on site moisture. TMI1 was calculated following Newell (1997). Values of SOLRAD, RSP, and CURV were re-scaled, with SOLRAD on a 30-point scale, RSP on a 20-point scale, and CURV on a 10-point scale. In each case, low values corresponded to xeric conditions (high solar radiation, ridgetop, convex topography) and high values corresponded to mesic conditions (low solar radiation, valley bottom, concave topography). TMI1 was then calculated as the sum of the three rescaled variables; possible values ranged between 0 and 60. TMI2 was constructed in a similar manner using SOLRAD and TCI, each on a 30 point scale.

I used non-metric multidimensional scaling (NMDS) to identify the site variables most closely associated with compositional patterns in the 1930s, processed and unprocessed 1970s, and 1990s data sets. NMDS is a technique for indirect gradient analysis in which plots are arranged in n-dimensional ordination space so that distance between plots corresponds as closely as possible with rank order of compositional dissimilarities. Tests using simulated data suggest that NMDS is better than other widely used ordination techniques at recovering underlying compositional gradients (Minchin 1987). I performed separate two, three, and four-dimensional NMDS ordinations, using basal area as a measure of abundance, on each of the three data sets using the DECODA software package (Minchin 1994). Data were standardized by species and sample totals, and Bray-Curtis distance was chosen as a robust measure of compositional dissimilarity (Faith et al. 1987). Other settings followed program defaults and recommendations in Minchin (1994). Relationships between ordination scores and site variables were examined using rotational correlation (Faith et al. 1989) as implemented by the vector fitting subroutine in DECODA. Rotational correlation seeks to identify the direction in ordination space that corresponds with maximum change in each site variable. Significance of correlations between site variables and ordination scores was then examined using a randomization test in which the strength of each observed correlation was compared with the strength of correlations produced using 1000 random combinations of actual ordination scores and site variables (Minchin 1994). Prior to vector fitting, aspect values were cosine-transformed and geology was coded as a binary variable (limestone vs. non-limestone).

In all four datasets (1930s, processed 1970s, unprocessed 1970s, and 1990s), patterns of compositional variation were significantly correlated with elevation, measures of local topography (TCI, RSP, SOLRAD, and CURV), and composite indices of topographic moisture (TMI1 and TMI2). In data sets for which soils data were available, percent sand and percent clay were also significant (see Results, below). These findings are consistent with previous gradient analyses of lower-elevation sites in the southern Appalachian Mountains (Whittaker 1956, Harmon 1980, Golden 1981, Callaway et al. 1987, Newell 1997).

TMI1 was available for all three data sets and was consistently among the variables most strongly correlated with vegetation patterns. In subsequent analyses, I classified plots into one of three topographic moisture classes: xeric (TMI1 $\leq$ 15), intermediate (15 $<$ TMI1 $\leq$ 30), or mesic (TMI1 $>$ 30). My approach to assessing changes within topographic moisture classes is an extension of that used by Harrod et al. (1998). On xeric sites, this approach has produced results highly consistent with dendrochronological studies (Chapter 2 this volume).

Structural and compositional changes between the 1930s and 1970s were documented by comparing each group of 1930s plots with 1970s plots in the same topographic moisture class, processed to simulate 1930s sampling methods. For the 1930s data set, sample sizes were 34 mesic plots, 62 intermediate plots, and 66 xeric plots. For the 1970s data set, sample sizes were 38 mesic plots, 50 intermediate plots, and 27 xeric plots. Multiple analysis of variance (MANOVA) using the Wilks' λ statistic revealed no significant differences in elevation, slope, cosine-transformed aspect, solar radiation, relative slope position, curvature, TCI, TMI1, TMI2, or geology within each topographic moisture class between the 1930s and 1970s plots (mesic sites: $p = 0.39$; intermediate sites: $p = 0.08$; xeric sites: $p = 0.84$). MANOVA and all subsequent statistical tests were performed using SAS 6.12 (SAS Institute 1996). The rejection level for all statistical tests was set *a priori* at $\alpha = 0.05$. Mann-Whitney tests were used to test for significant differences in total canopy density, basal area, biomass and richness within moisture classes over time. Because structural comparisons of 1930s with 1970s plots include only stems ≥ 10 cm dbh, I use the terms "canopy density" and "canopy richness" to describe stand attributes.

Direct comparisons of the abundance of saplings, woody shrubs and vines between the 1930s and 1970s plots were impeded by differences in sampling methodology. To provide a general assessment of understory trends, I compared 1930s quadrat dominance data with relative densities of stems ≤ 10 cm dbh in 1970s plots. I acknowledge that, because of the clumped nature of plant distributions and the fact that individuals can dominate small patches without exceeding dbh (and vice versa), the two methods (% quadrat dominance vs. relative stem density) may produce substantially different estimates of abundance. For that reason, understory comparisons between the 1930s and 1970s data sets should be interpreted with caution and are not evaluated statistically.

To examine broad compositional trends over this period, I assigned tree species to one of three shade-tolerance classes based on ratings in Baker (1949) and Burns and Honkala (1990): tolerant (including species ranked by these authors as "very tolerant"), mid-tolerant, and intolerant (including "very intolerant" species). I then compared the relative basal area and understory abundance of species in each tolerance class during each period.

Changes in the basal area of individual species within topographic moisture classes were examined using Mann-Whitney tests. I were unable to test the statistical significance of changes in species' distributions across topographic moisture classes between the 1930s and 1970s. For most species, basal area values deviated strongly from the normal distribution, ruling out the using of two-way analysis of variance (ANOVA), and I were unable to identify a suitable non-parametric equivalent. Nonetheless, the data suggest some striking trends, which I report without asserting statistical significance.

Changes between the 1970s and 1990s were documented using the subset of 1970s plots sampled in 1995-96. Sample sizes for this comparison were 26 mesic plots, 34 intermediate plots, and 11 xeric plots. MANOVA revealed no significant differences in site conditions between the 1970s plots resampled in the 1990s and those not resampled on either mesic or xeric sites (mesic sites: $p = 0.15$; xeric sites: $p = 0.35$). However, MANOVA did reveal a highly significant difference in site conditions between resampled and non-resampled plots on intermediate sites ($p=0.002$). This difference was due largely to the mean elevation of the non-resampled plots being approximately 140 m higher and the mean slope being approximately 5° steeper than those of the resampled plots. Ordination results suggest that neither of these factors strongly influence vegetation composition. Although the resampled plots may not be entirely representative of the 1970s data set as a whole, the use of only those plots sampled in both the 1970s and 1990s ensures that changes observed over that period are the result of vegetation dynamics rather than sampling bias.

For 1970s to 1990s comparisons, data were not processed to simulate 1930s sampling methods; rather, all subplots and all stems ≥ 0.5 cm dbh were included in the analyses. Wilcoxon signed rank tests were used to evaluate the significance of changes in total densities of canopy trees (> 10 cm dbh) and saplings (stems of tree species 0.5 cm to 10 cm dbh), total live basal area, biomass, and species richness within moisture classes over time. In addition, changes in relative abundance of shade-tolerant, mid-tolerant, and intolerant tree species were examined using χ^2 tests on raw stem tallies. Changes in basal area of species within topographic moisture classes were examined using Wilcoxon signed rank tests, and changes in tree and shrub distributions across the gradient were examined using χ^2 tests on raw stem tallies.

RESULTS

Forest conditions circa 1900

Forest composition at the beginning of the 20th century varied considerably between the four districts that contain portions of the study area. According to Ayres and Ashe (1905), the Cades Cove district, which includes the eastern portion of the study area, supported forests dominated by *Castanea dentata* and *Quercus prinus,* which together made up 50% of timber trees (Table 4.1). The Abrams Creek and Tennessee Gap districts, which make up most of the western portion of the study area, were dominated by *Pinus strobus* and assorted *Quercus* species. The xeric south-facing slope of Chilhowee Mountain was heavily dominated by *Pinus rigida* and *Quercus velutina*. Overall, the forests of western GSMNP appear to have been dominated by shade-intolerant and mid-tolerant species, particularly *Castanea dentata*, *Pinus* spp., and *Quercus* spp. Shade-tolerants such as *Acer* spp. and *Tsuga canadensis* made up less than 20% of trees.

Ayres and Ashe (1905, pp. 176-178) make several references to the frequency and effects of anthropogenic fire and grazing. Of the Abrams Creek district, they write, "Fires are very frequent. Many trees have been injured or killed, but no large areas are entirely deadened." In the Cades Cove district, "Fires are set whenever they will run, and the forest shows the effect of this practice. The brush is subdued; the timber is frequently scorched at the butt, often killed." In the Tennessee Gap district, "… on the ridges reproduction in very scant, owing to fire and grazing … little humus or litter is left." And on Chilhowee Mountain, "Many seedlings start up, but they are usually killed by fire and grazing. Under these conditions pine reproduces better than other species."

Gradient analyses

In all four data sets (1930s, processed 1970s, unprocessed 1970s, and 1990s), patterns of compositional variation were significantly correlated with elevation, measures of local topography (TCI, RSP, SOLRAD, and CURV), and composite indices of topographic moisture (TMI1 and TMI2) (Table 4.2). In data sets for which soils data were available, correlations with percent sand and percent clay were also significant. Ordinations of all data

Table 4.1. Forest conditions in western GSMNP circa 1900, based on data in Ayres and Ashe (1905). a) Area (in km^2) in forested and cleared land in each of the four districts. b) Forest composition (%). Species names represent my interpretation of common names.

a)	Abrams Creek	Cades Cove	Chilhowee Mountain	Tennessee Gap	Total
Forested	122.3	79.1	33.2	48.8	283.3
Cleared	5.0	18.3	1.2	0.6	25.2
Total	127.3	97.4	34.4	49.4	308.5

b)	Abrams Creek	Cades Cove	Chilhowee Mountain	Tennessee Gap	Area-weighted mean
Acer	2	6		2	3
Betula	2	4		2	2
Castanea	12	30	1		14
*Pinus rigida**	10		50	10	12
Pinus strobus	20	12		20	15
Quercus alba	5		5	3	3
Quercus coccinea	10		5		5
Quercus prinus	10	20	5	15	13
Quercus rubra	5		6	3	3
Quercus velutina	2	4	20	20	8
Tsuga canadensis	10	12		15	10
Others**	12	12	8	9	11
Total	100	100	100	100	100

* (probably includes *P. echinata, P. virginiana, P. pungens*)

** (includes *Carya, Halesia, Magnolia, Prunus, Liquidambar, Nyssa, Liriodendron,* and *Fraxinus*)

Table 4.2. Rotational correlations between three-dimensional NMDS ordination scores and environmental variables in the 1930s, processed and unprocessed 1970s, and 1990s data sets.

	1930s	processed 1970s	unprocessed 1970s	1990s
GIS variables				
Elevation	0.33 ***	0.40 ***	0.76 ***	0.77 ***
Slope	0.19 n.s.	0.16 n.s.	0.18 n.s.	0.31 n.s.
Aspect	0.15 n.s.	0.11 n.s.	0.09 n.s.	0.30 n.s.
TCI	0.40 ***	0.51 ***	0.54 ***	0.58 ***
RSP	0.54 ***	0.68 ***	0.69 ***	0.68 ***
SOLAR	0.46 ***	0.49 ***	0.55 ***	0.45 **
CONVEX	0.32 **	0.42 ***	0.47 ***	0.45 **
TMI1	0.62 ***	0.70 ***	0.71 ***	0.63 ***
TMI2	0.52 ***	0.60 ***	0.61 ***	0.56 ***
Limestone	0.09	0.26 n.s.	0.24 n.s.	0.23 n.s.
n	161	115	115	71
Soil variables				
% clay	---	0.67 ***	0.75 ***	0.79 ***
% silt	---	0.39 n.s.	0.35 n.s.	0.42 n.s.
% sand	---	0.64 ***	0.68 ***	0.70 ***
pH	---	0.25 n.s.	0.30 n.s.	0.61 ***
n		45	45	35

* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$
n.s. $p > 0.05$

sets produced two to three interpretable dimensions; for consistency, only three-dimensional ordinations are presented here.

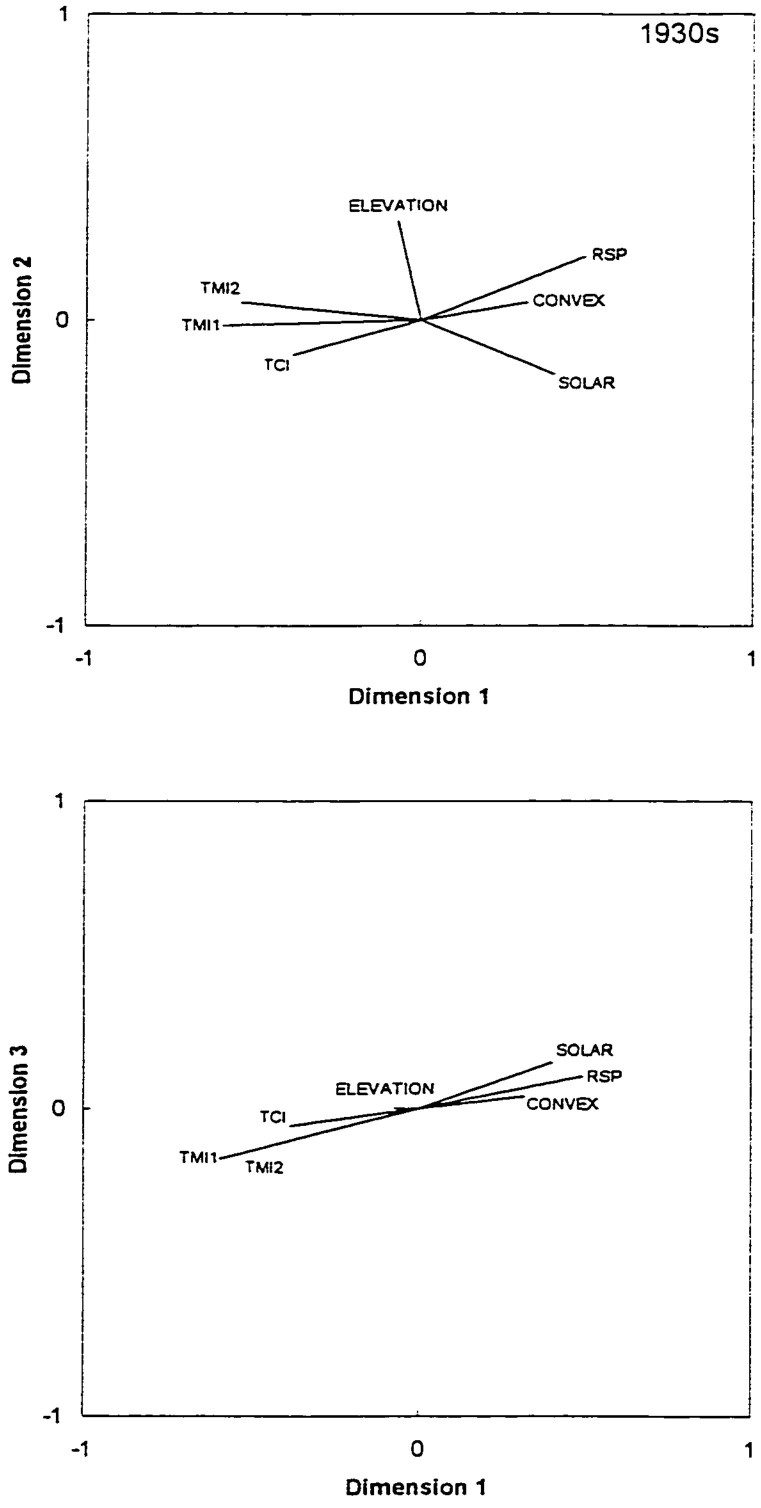
In the 1930s data set, the first ordination dimension appears to represent a topographic moisture gradient, from mesic, concave lower slopes (high TMI1, TMI2, TCI) to xeric convex upper slopes with high insolation (Figure 4.2a). A weaker elevation gradient appears along the second dimension, roughly orthogonal to the topographic moisture gradient. Most of the interpretable variation in the 1930s data appears to be captured in these two dimensions, and the third dimension adds little information.

The relative length and orientation of environmental vectors in the ordination of 1970s data processed to simulate 1930s sampling methods are very similar to those of the 1930s data (Figure 4.2b). In this data set, limited to trees ≥ 10 cm dbh, a strong gradient associated with topographic moisture appears along the first dimension. Variation in soil texture appears closely correlated with this moisture gradient, with sandier soils on mesic sites and higher clay content on xeric sites. As with the 1930s data, most interpretable variation in vegetation occurs along two major axes.

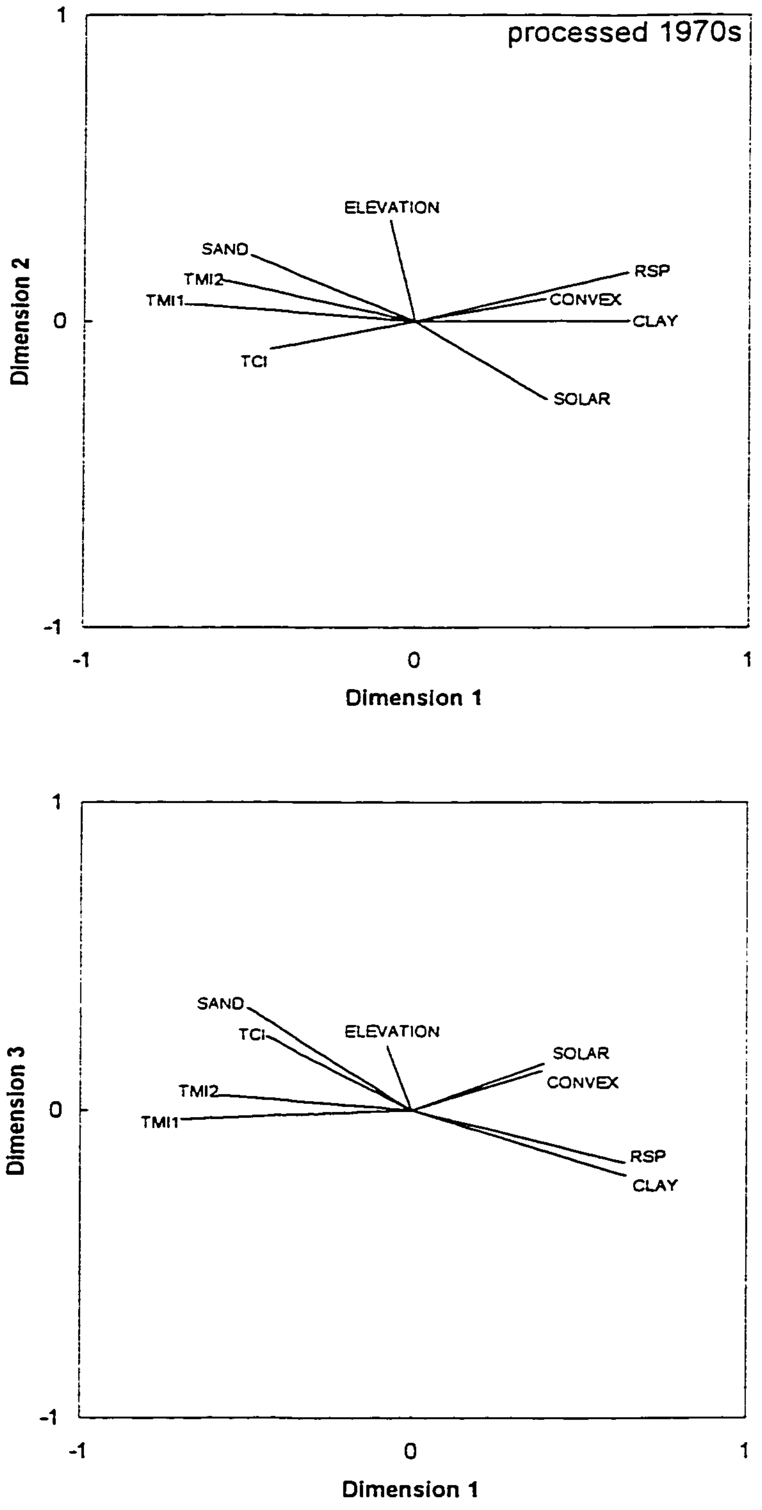
Ordinations of the unprocessed 1970s and 1990s data sets (which include all stems ≥ 0.5 cm dbh) indicate variation along three major gradients (Figure 4.2c, d). As in previous ordinations, a topographic moisture gradient is evident along the first dimension. In these data sets, the soil texture gradient runs obliquely to topographic moisture. The elevation gradient, running along the third dimension, appears much stronger than in the 1930s or processed 1970s data. The length and relative position of environmental vectors in the unprocessed 1970s and 1990s data sets appear quite similar.

Figure 4.2. Statistically significant relationships between site variables and three-dimensional NMDS ordination scores in the 1930s (a), processed (b) and unprocessed 1970s (c), and 1990s (d) data sets. Vectors indicate direction of maximum correlation between site variables and NMDS sample scores; vector lengths are equal to correlation coefficients.

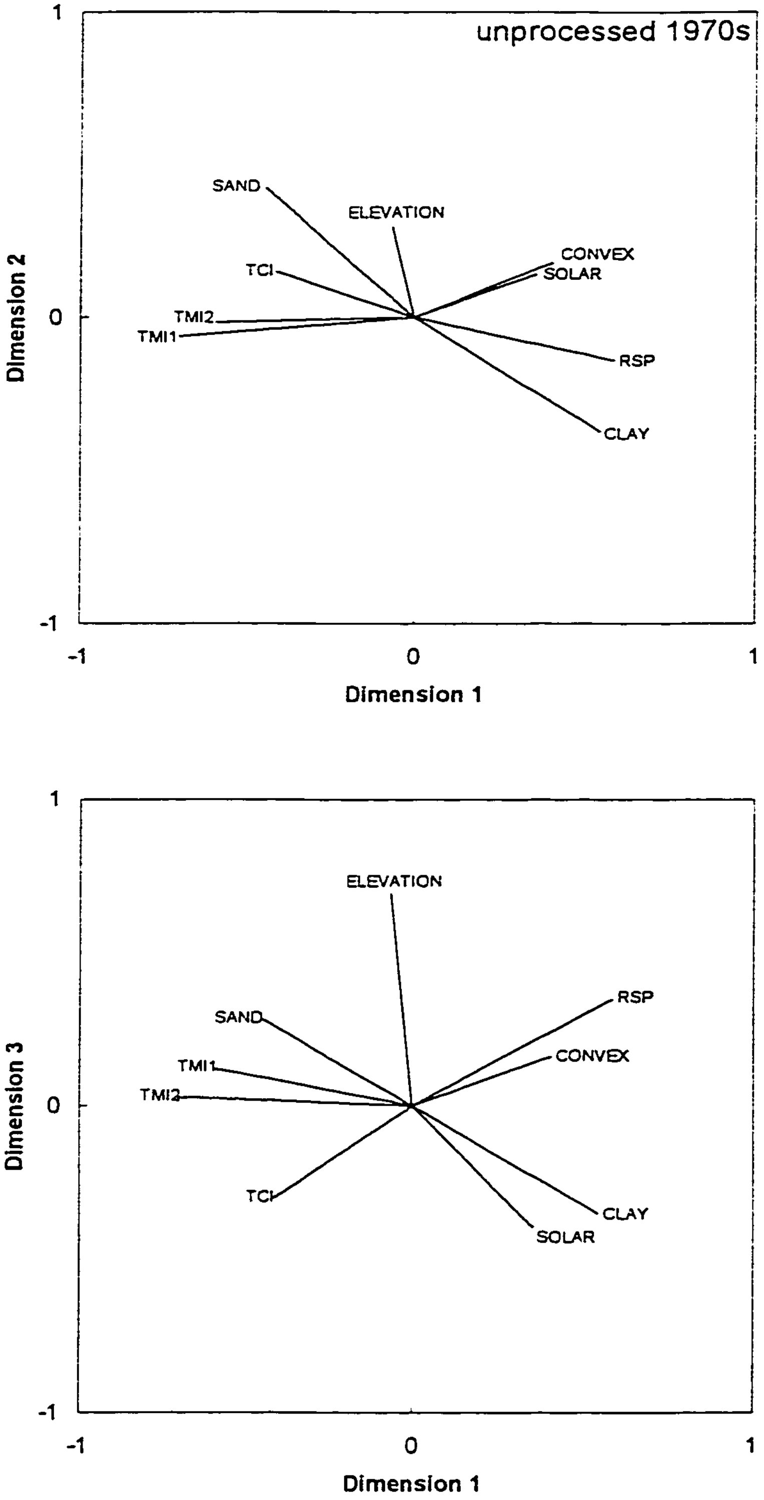
a.


1930s
ELEVATION
RSP
TMI2
CONVEX
TMI1
TCI
SOLAR
Dimension 2
Dimension 1
1
0
-1
-1
0
1
SOLAR
RSP
ELEVATION
CONVEX
TCI
TMI1
TMI2
Dimension 3
Dimension 1
1
0
-1
-1
0
1

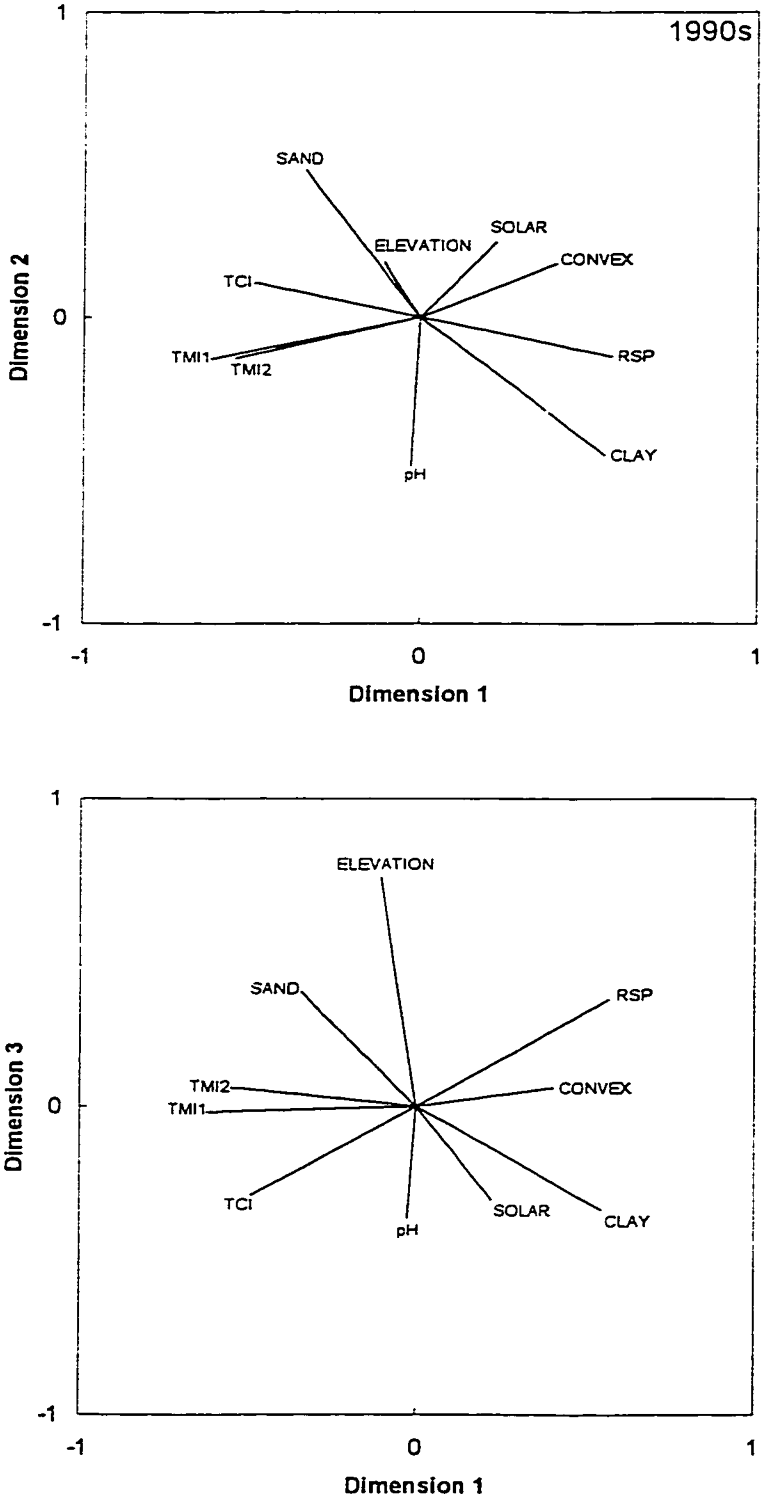
b.


processed 1970s
1
0
-1
Dimension 2
-1
0
1
Dimension 1
ELEVATION
SAND
TMI2
TMI1
TCI
RSP
CONVEX
CLAY
SOLAR
1
0
-1
Dimension 3
-1
0
1
Dimension 1
SAND
TCI
ELEVATION
TMI2
TMI1
SOLAR
CONVEX
RSP
CLAY

c.


unprocessed 1970s
SAND
ELEVATION
CONVEX
SOLAR
TCI
TMI2
TMI1
RSP
CLAY
Dimension 2
Dimension 1
1
0
-1
-1
0
1
ELEVATION
RSP
SAND
CONVEX
TMI1
TMI2
TCI
CLAY
SOLAR
Dimension 3
Dimension 1
1
0
-1
-1
0
1

d.


1990s
SAND
SOLAR
ELEVATION
CONVEX
TCI
TMI1
TMI2
RSP
CLAY
pH
Dimension 2
Dimension 1
1
0
-1
-1
0
1
ELEVATION
SAND
RSP
TMI2
TMI1
CONVEX
TCI
pH
SOLAR
CLAY
Dimension 3
Dimension 1
1
0
-1
-1
0
1

Forest conditions in the 1930s

Mean canopy density, basal area, biomass, and species richness of plots sampled in the 1930s were significantly lower than those of plots occupying similar sites sampled in the 1970s (Figure 4.3). In the 1930s, *Tsuga canadensis, Liriodendron tulipifera,* and *Quercus prinus* dominated the canopies of mesic sites; other important species included *Castanea dentata* and *Acer rubrum* (Tables 4.3, 4.4). Tree species most frequently dominating understory quadrats on mesic sites were *Acer rubrum, Cornus florida, Castanea dentata, Carya alba*, and *Oxydendrum arboreum*. On intermediate sites, important canopy species included *Pinus rigida, P. strobus, Quercus prinus, Q. alba, Tsuga canadensis,* and *Castanea dentata;* dominance of understory quadrats was shared by several species including *A. rubrum, Castanea dentata, Q. prinus, Q. coccinea, Carya alba,* and *P. rigida*. Xeric sites were dominated by *Pinus rigida, P. virginiana,* and *Quercus prinus*; these species, together with *Q. coccinea, Nyssa sylvatica, Acer rubrum, Oxydendrum,* and *Castanea* dominated understory quadrats.

As a group, shade-tolerant species such as *Tsuga* and *Acer rubrum* reached their greatest abundance (expressed as either proportion of total basal area and as percent dominance of understory quadrats) on mesic sites. The greatest abundance of mid-tolerant species such as *Quercus prinus, Castanea,* and *Pinus strobus* occurred on intermediate sites. Xeric sites supported the greatest proportion of shade-intolerant species. Whereas *Liriodendron* was the most abundant shade-intolerant on mesic sites, *Pinus rigida, P. virginiana,* and *Quercus coccinea* were the most abundant shade-intolerants on xeric sites. The shrub *Rhododendron maximum* was most abundant on mesic sites, where it dominated 20% of understory quadrats. *Kalmia latifolia,* the other important shrub, occurred at much

Figure 4.3. Canopy richness, density, basal area, and biomass of mesic, intermediate, and xeric sites sampled in the 1930s and 1970s.

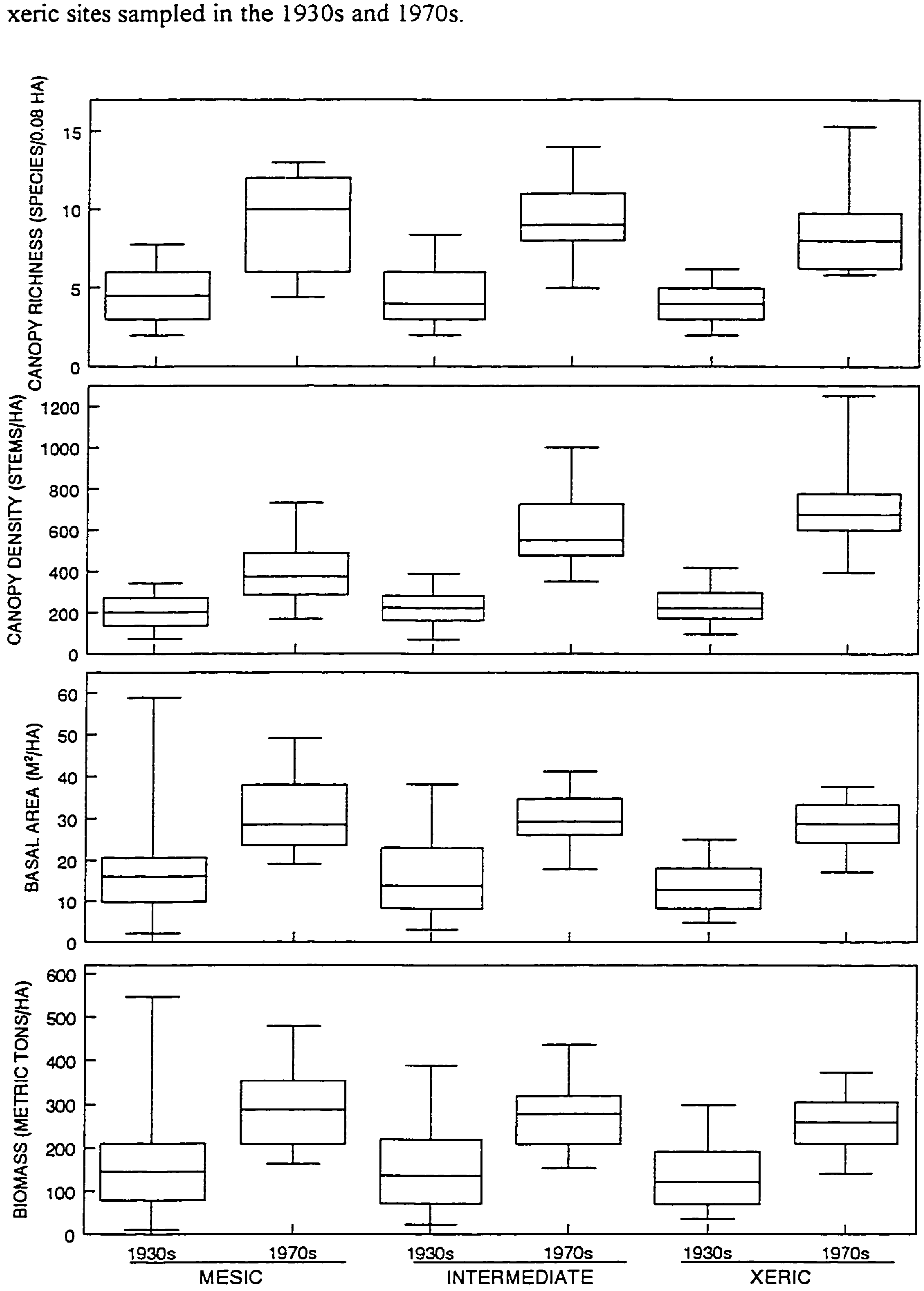


Table 4.3: Vegetation of 1930s and 1970s plots in western GSMNP. (a) Basal area (in m^2/ha) of tree species. Statistical significance of changes within topographic moisture classes was evaluated using Wilcoxon two-sample tests. (b) Total tree basal area by shade-tolerance class. (c) Relative abundance of treespecies in the understory (<10 cm dbh) by tolerance class. Due to rounding, columns may not sum to totals.

(a)		Basal area (m^2/ha)					
	Shade	Mesic		Intermediate		Xeric	
Species	tolerance	1930s	1970s	1930s	1970s	1930s	1970s
Acer rubrum	high	1.01	2.32 **	0.25	2.92 ***	0.13	1.21 ***
Acer saccharum	high	0.00	0.77 **	0.00	0.06	0.03	0.00
Aesculus flava	high	0.01	1.12 *	0.00	0.04	0.03	0.00
Betula lenta	low	0.04	0.94 ***	0.02	0.19 *	0.00	0.13 **
Carya alba	low	0.52	0.32	0.64	0.78	0.27	0.30
Carya glabra	medium	0.43	0.85	0.20	1.21 ***	0.04	0.30 *
Castanea dentata	medium	1.46	0.00 ***	1.23	0.00 ***	0.87	0.00 *
Cornus florida	high	0.01	0.47 ***	0.02	0.26 ***	0.00	0.02
Fagus grandifolia	high	0.54	0.69	0.07	0.01	0.00	0.00
Halesia carolina	high	0.00	2.33 ***	0.06	0.93 **	0.00	0.09 **
Liriodendron tulipifera	low	3.12	4.95 *	0.99	2.80 ***	0.00	0.12 *
Nyssa sylvatica	high	0.10	0.40	0.35	0.64 **	0.11	0.71 ***
Oxydendrum arboreum	high	0.15	0.41 *	0.12	1.05 ***	0.04	0.74 ***
Pinus pungens	low	0.00	0.00	0.02	0.96 **	0.07	1.70 ***
Pinus rigida	low	0.40	0.08	2.63	1.12 *	4.14	6.10
Pinus strobus	medium	1.00	0.89	1.93	1.67	0.72	1.28 ***
Pinus virginiana	low	0.29	0.48	0.93	0.84	2.75	5.42
Quercus alba	medium	0.82	0.85	1.02	0.68	0.82	0.90
Quercus coccinea	low	0.46	0.09	0.74	1.24	0.85	2.81 **
Quercus prinus	medium	2.04	1.40	1.88	5.93 ***	1.69	3.80 *
Quercus rubra	medium	0.96	1.05	0.54	1.16 **	0.40	1.17
Quercus velutina	medium	0.15	0.33	0.70	0.92	0.44	0.44
Robinia pseudoacacia	low	0.21	0.46	0.06	0.56 ***	0.08	0.12
Tilia americana	high	0.38	0.93	0.13	0.10	0.09	0.00
Tsuga canadensis	high	5.20	7.33 *	1.25	2.68 ***	0.01	0.54 ***
Other		0.25	1.71	0.50	1.14	0.11	0.52
Total		19.56	31.16 ***	16.29	29.88 ***	13.68	28.40 ***

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

(b)	Basal area (m^2/ha)					
	Mesic		Intermediate		Xeric	
	1930s	1970s	1930s	1970s	1930s	1970s
Total shade-tolerant	7.41	17.08	2.25	8.90	0.44	3.31
Total mid-tolerant	6.94	6.15	7.60	11.91	4.99	8.07
Total shade-intolerant	5.21	7.92	6.43	9.07	8.24	17.00
Total unassigned	0.00	0.02	0.00	0.01	0.00	0.02
Total	19.56	31.16	16.29	29.88	13.68	28.40

(c)	Relative abundance in understory (%)					
	Mesic		Intermediate		Xeric	
	1930s	1970s	1930s	1970s	1930s	1970s
Total shade-tolerant	44	82	32	75	27	52
Total mid-tolerant	30	7	36	11	28	14
Total shade-intolerant	24	7	31	11	45	33
Total unassigned	1	4	1	3	0	1
Total	100	100	100	100	100	100

Figure 4.4. Distribution of *Kalmia latifolia* and *Rhododendron maximum*. See text for details of frequency, dominance, and relative density calculations.

	1930s		1970s	
	Frequency (%)	Understory dominance (%)	Frequency (%)	Relative density (%)
Kalmia latifolia				
Mesic	41	4	18	2
Intermediate	39	6	42	26
Xeric	26	4	67	32
Rhododendron maximum				
Mesic	56	20	58	49
Intermediate	19	5	24	10
Xeric	3	<1	19	4

lower levels (4 - 6% dominance) and was distributed fairly evenly across the topographic moisture gradient. Non-significant trends toward increased canopy richness, basal area, and biomass and decreased canopy density occurred with increasing topographic moisture.

Considerable variation in composition and structure is evident in the 1930s data. For example, canopy density on mesic plots ranged from 49 to 346 stems/ha, basal area from 1.16 to 106.67 m^2/ha (the largest value observed on any site during any time period), biomass from 7.62 to 1110.75 Mg/ha, and canopy richness from 1 to 9 species/0.08 ha. On mesic sites, relative basal area of shade-tolerants ranged from 0 to 100%; mid-tolerants from 0 to 97%, and shade-intolerants from 0 to 100%. Intermediate and xeric sites showed comparable structural and composition variation.

The 1930s data provide evidence of widespread disturbance by fire, logging, and *Castanea* blight (Table 4.5). Past fires were reported on 86% of xeric plots, 82% of intermediate plots, and 62% of mesic plots; 66% of xeric plots burned during the period 1926-1936 alone. Evidence of past logging, mostly selective cutting, was reported on 15% of mesic plots, 11% of intermediate plots, and 9% of xeric plots. Living and standing dead *Castanea* are observed across all moisture classes at mean combined densities of 25-36 canopy stems/ha and combined basal areas of 2.1-3.2 m^2/ha.

Changes, 1930s to 1970s

Comparisons of 1930s and 1970s plot data indicate that highly significant increases in canopy density, richness, basal area and biomass occurred in all topographic moisture classes (Figure 4.3; $p < 0.001$ for all comparisons). The largest proportional increases in basal area

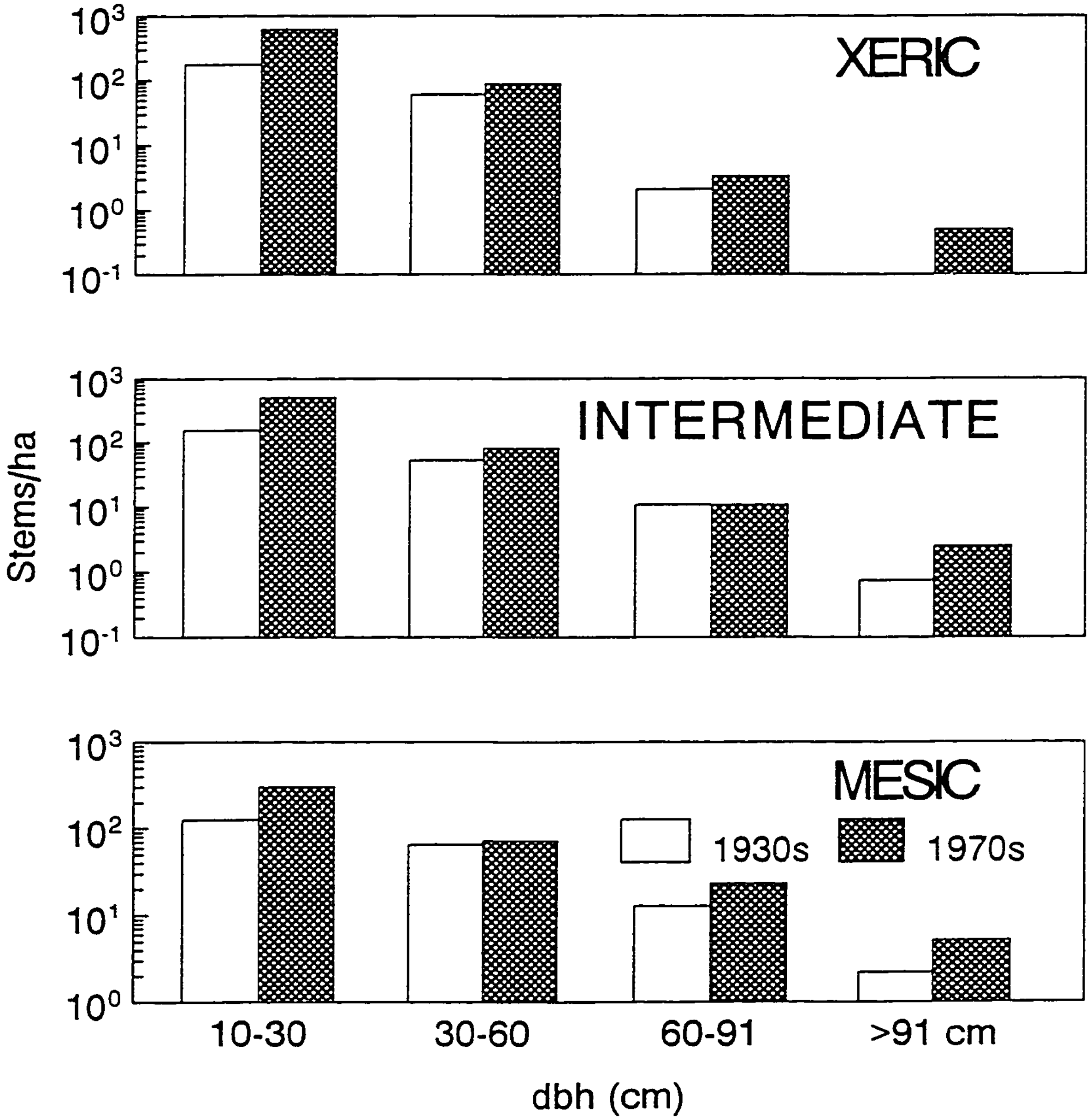
Table 4.5: Disturbances affecting 1930s plots in western GSMNP. a) Percent of plots burned, by year b) Percent plots with evidence of past logging c) Basal area of live and standing dead Castanea dentata. Due to rounding, columns may not sum to totals.

a) Year of last recorded burn (% of plots)	Mesic	Intermediate	Xeric
1931-36	0.0	11.3	18.2
1926-30	35.3	48.4	48.5
1921-26	5.9	4.8	4.5
1916-20	5.9	9.7	4.5
Burned, date unknown	14.7	8.1	10.6
No evidence of fire	38.2	17.7	13.6
Total	100.0	100.0	100.0
b) Logging (% of plots)			
Evidence of logging	14.7	11.3	9.1
No evidence of logging	85.3	88.7	90.9
Total	100.0	100.0	100.0
c) Mean basal area of *Castanea* (m^2/ha)			
Live	1.46	1.23	0.87
Dead	1.73	0.98	1.22
Total	3.19	2.21	2.09

and biomass occurred on xeric sites. As a result, variation in basal area and biomass across the topographic moisture gradient decreased relative to the 1970s.

Comparisons of size structure between the 1930s and 1970s indicate increases in the numbers of trees across most diameter classes (Figure 4.4). The largest absolute increases were in the smallest diameter class (10 to < 30 cm dbh). Large proportional increases were also observed in the ≥ 91 cm class, however, the actual number of trees involved was very small. On mesic sites, the large majority (> 75%) of the increase in small canopy trees was due to increases in the densities of shade-tolerant species, particularly *Tsuga canadensis, Halesia carolina, Acer rubrum, Aesculus flavia, Cornus florida,* and *Oxydendrum arboreum.* As a result, abundance of shade-tolerant species (expressed as a proportion of total basal area) increased from 38% in the 1930s to 53% in the 1970s. On intermediate sites, increases in the densities of shade-tolerants also accounted for the majority (56%) of the increase in 10 to < 30 cm stems, and relative basal area of shade-tolerants increased from 14 to 26%. Although numbers of small mid-tolerants (especially *Q. prinus* and *P. strobus)* and intolerants (especially *Liriodendron, P. virginiana,* and *Robinia pseudoacacia)* also showed strong increases, the relative abundance of these groups declined. On xeric sites, the majority (58%) of the increase in 10 - 30 cm stems was due to increases in the abundance of shade-intolerant species, especially *P. rigida* and *P. virginiana.* However, total density of 10-30 cm shade-tolerants showed a very strong proportional increase (> 1000%) on xeric sites; as a result, relative abundance of shade-tolerants (especially *A. rubrum, Nyssa sylvatica,* and *Oxydendrum*) increased from 3 to 12% of basal area, and relative abundance of mid-tolerant and intolerant species declined correspondingly. Comparisons of 1930s understory dominance and 1970s sapling relative densities suggest increased dominance of the sapling stratum by

Figure 4.4. Size structure of mesic, intermediate, and xeric sites sampled in the 1930s and 1970s.



shade-tolerant species at the expense of mid-tolerant and shade-intolerant species. In the 1970s, shade-tolerants continued to reach their greatest understory dominance on mesic sites but made up more than 50% of saplings in all topographic moisture classes. While mid-tolerant basal areas remained highest on intermediate sites in the 1970s, saplings of both mid-tolerant and shade-intolerant trees were most abundant on xeric sites.

Considerable structural variability within topographic moisture classes remained evident in the 1970s data. For example, on mesic sites, canopy density ranged from 138 to 1050 stems/ha, basal area from 16.60 to 61.98 m^2/ha, biomass from 129.52 to 682.37 Mg/ha, and canopy richness from 3 to 15 species/0.08 ha. Compositional variability also remained high, with relative canopy basal area of shade-tolerants ranging from 0 to 100%, mid-tolerants from 0 to 83%, and intolerants from 0 to 64%. However, very open stands (e.g. those with basal areas of < 10 m^2/ha), common in the 1930s, were nearly absent from the 1970s data.

Between the 1930s and 1970s, most tree species showed significant increases in basal area in one or more topographic moisture classes, and several species showed significant increases on all site types (Tables 4.3, 4.4). The only species showing significant decreases over this period were *Castanea dentata,* which disappeared from the canopy on all sites, and *Pinus rigida,* which decreased on intermediate sites. Shifts in the distributions along the topographic moisture gradient were most apparent in the trees *Acer rubrum, Liriodendron tulipifera, Pinus rigida,* and *Tsuga canadensis* and the shrubs *Kalmia latifolia* and *Rhododendron maximum*. In the 1930s, *Acer rubrum, Liriodendron tulipifera* and *Tsuga canadensis* were most abundant on mesic sites and were absent or present at much lower levels on intermediate and xeric sites. Between the 1930s and 1970s, frequency, basal area, and density of these species increased on all site types; however, proportional increases were much greater on intermediate and xeric sites than on mesic sites. Size class distributions for these species provide additional evidence of changes in tree distribution. In the 1970s, *Acer rubrum, Liriodendron* and *Tsuga* on mesic sites occur in both large and small size classes. On intermediate and especially on xeric sites, their size structures are skewed toward the smallest size class, suggesting relatively recent recruitment of these species on these sites. Between the 1930s and 1970s, the distributions of *Pinus rigida* and *Kalmia* appeared to shift toward xeric sites. *Rhododendron maximum,* which was largely restricted to mesic and intermediate sites in the 1930s, increased in frequency and abundance on xeric sites.

Changes, 1970s to 1990s

While comparisons of permanent plots sampled in the 1970s and 1990s indicate ongoing changes in forest composition and structure, these changes are generally less dramatic that those observed over the preceding four decades (Figure 4.5). Significant decreases in species richness (species of woody stems ≤ 0.5 cm dbh/0.1 ha) were observed on mesic and intermediate sites. These decreases amounted to about 10% or about 1.5-2.0 species/0.1 ha plot. Densities of saplings (stems 0.5 - 10 cm dbh) also showed significant decreases, amounting to 25-33% of stems, on mesic and intermediate sites. Densities of canopy trees showed no significant changes on any topographic moisture class; basal area and biomass showed small but statistically significant changes (increases of 6% for each parameter) on intermediate sites.

Between the 1970s and the 1990s, significant decreases in *Cornus florida* basal area occurred on all site types (Table 4.6). Basal areas of *Acer rubrum* and *Tsuga canadensis* increased significantly on intermediate and xeric sites, and *Oxydendrum arboreum* decreased

Figure 4.5. Canopy richness, sapling density, canopy density, basal area, and biomass of mesic, intermediate, and xeric permanent plots sampled in both the 1970s and 1990s.

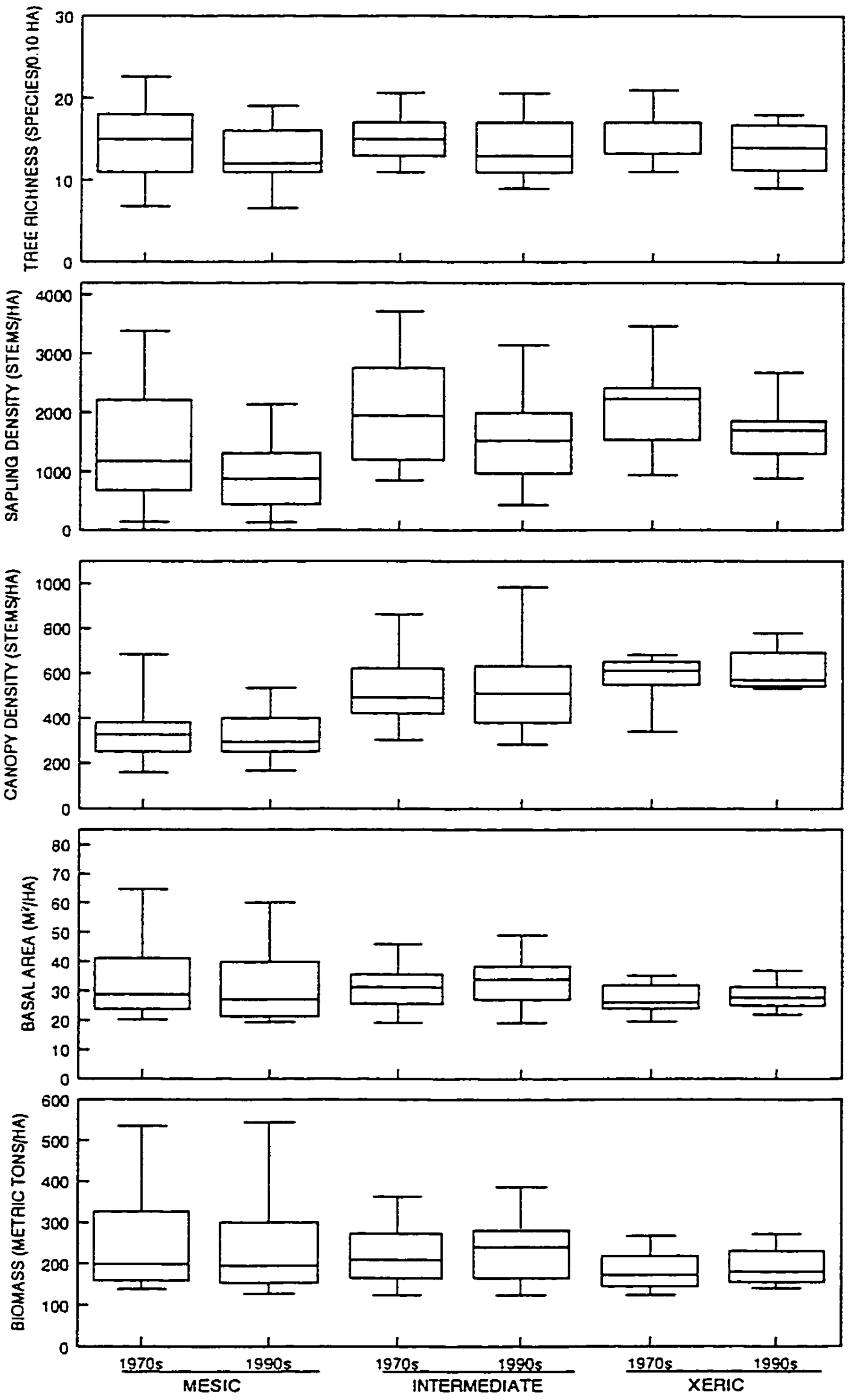


Table 4.6: (a) Basal area (in m^2/ha) by species for 1970s and 1990s permanent plots in western GSMNP. Statistical significance of changes in basal area within topographic moisture classes was evaluated using Wilcoxon signed rank tests. (b) Total basal area by shade-tolerance class.

(a)

	Mesic		Intermediate		Xeric	
Species	1970s	1990s	1970s	1990s	1970s	1990s
Acer rubrum	1.82	2.04	3.25	3.76 ***	1.93	2.58 ***
Acer saccharum	0.39	0.32	0.09	0.09	0.00	0.00
Aesculus flavia	1.22	1.04	0.03	0.03	0.00	0.00
Betula lenta	0.61	0.65	0.25	0.27	0.20	0.21
Carya alba	0.51	0.60	1.05	0.90	0.67	0.12 *
Carya glabra	0.99	0.82	1.35	1.04	0.16	0.12
Castanea dentata	0.00	0.00	0.00	0.00	0.00	0.00
Cornus florida	0.77	0.30 ***	0.53	0.31 ***	0.17	0.06 **
Fagus grandifolia	0.70	0.36	0.01	0.01	0.00	0.00
Halesia carolina	2.02	1.79	0.64	0.54	0.16	0.16
Liriodendron tulipifera	7.45	6.91	3.50	4.22 ***	0.47	0.62
Nyssa sylvatica	0.05	0.13	0.50	0.52 **	0.78	1.05
Oxydendrum arboreum	0.45	0.18 **	0.90	0.62 ***	0.50	0.29
Pinus pungens	0.00	0.00	0.18	0.11	0.03	0.03
Pinus rigida	0.07	0.03	0.57	0.37 *	2.47	2.43
Pinus strobus	0.57	1.03	2.28	2.85	2.87	3.51
Pinus virginiana	0.70	0.38	0.50	0.52	4.83	5.14
Quercus alba	1.17	1.18	0.71	0.70	1.97	1.80
Quercus coccinea	0.06	0.00	0.79	0.62	1.53	1.34
Quercus prinus	1.50	1.29	5.90	5.70	3.98	3.92
Quercus rubra	0.59	0.62	1.03	1.21	1.19	1.93
Quercus velutina	0.38	0.56	1.09	0.83	0.91	0.25 *
Robinia pseudoacacia	0.40	0.28	0.70	0.55	0.19	0.17
Tilia americana	1.46	1.58	0.00	0.00	0.00	0.00
Tsuga canadensis	8.40	9.14	4.04	6.16 ***	1.31	2.39 ***
Other	1.42	1.44	1.33	1.27	1.00	0.32
Total	33.71	32.67	31.19	33.17 *	27.32	28.45

* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

	Mesic		Intermediate		Xeric	
(b)	1970s	1990s	1970s	1990s	1970s	1990s
Total shade-tolerant	17.54	17.01	10.19	12.19	4.85	6.54
Total mid-tolerant	5.56	6.13	12.82	12.83	11.36	11.60
Total shade-intolerant	10.54	9.50	8.11	8.12	10.93	10.21
Total unassigned	0.07	0.03	0.08	0.03	0.18	0.10
Total	33.71	32.67	31.19	33.17	27.32	28.45

significantly on mesic and intermediate sites. *Liriodendron tulipifera* and *Nyssa sylvatica* also increased significantly on intermediate sites, while *Pinus rigida* decreased. On xeric sites, *Quercus velutina* and *Carya alba* also showed significant decreases in basal area.

Significant shifts in the relative abundance of stems in different shade-tolerance classes occurred between the 1970s and 1990s; similar trends were observed on all sites (Table 4.7). For canopy trees, declines in both absolute and relative densities of shade-intolerant and mid-tolerant species were accompanied by increases in both absolute and relative abundance of shade-tolerants. Absolute densities of saplings decreased over this period for all shade tolerance classes. The declines were generally sharpest for shade-intolerants and less severe for mid-tolerant and shade-tolerant species. As a result, the relative abundance of shade-tolerant saplings increased at the expense of less tolerant species. I did observe considerable variation in species responses within shade tolerance classes. For example, precipitous declines (70-80%) in total sapling densities of mid-tolerant *Quercus* species occurred on all topographic moisture classes; in contrast, sapling densities of the mid-tolerant *Pinus strobus* decreased only slightly on intermediate sites and increased on xeric sites.

Size structure also shifted between the 1970s to 1990s; again, patterns were broadly similar across topographic moisture classes (Figure 4.6). Overall densities of stems 0.5-10 and 11-20 cm dbh declined, while densities in most larger size classes remained constant or increased slightly. As classes, shade-intolerant and mid-tolerant species showed declines in numbers of stems 0.5-10 and 11-20 cm dbh accompanied by modest increases or decreases in numbers of stems in larger size classes. Numbers of shade-tolerant stems 0.5-10 cm dbh decreased, while numbers of shade-tolerants in most larger size classes increased.

Table 4.7. Changes in densities (stems/ha) of (a) saplings (0.5 - 10 cm dbh) and (b) canopy trees (> 10 cm dbh) in permanent plots sampled in the 1970s and 1990s, by shade-tolerance class. Chi-square tests were used to evaluate changes in relative abundance of stems of various size classes.

	Mesic		Intermediate		Xeric	
(a)	1970s	1990s	1970s	1990s	1970s	1990s
Total shade-tolerant	1158	837	1692	1326	1231	1070
Total mid-tolerant	98	52	213	150	304	285
Total shade-intolerant	120	46	104	53	505	256
Total unassigned	50	27	66	38	55	32
Total	1426	961	2075	1566	2094	1644
Chi-square significance	***		***		***	
Chi-square for species of known tolerance	***		***		***	

	Mesic		Intermediate		Xeric	
(b)	1970s	1990s	1970s	1990s	1970s	1990s
Total shade-tolerant	183	186	201	271	120	211
Total mid-tolerant	80	68	201	166	216	192
Total shade-intolerant	92	69	121	96	245	206
Total unassigned	1	0	1	0	5	3
Total	355	323	523	534	586	612
Chi-square for species of known tolerance	*		***		***	

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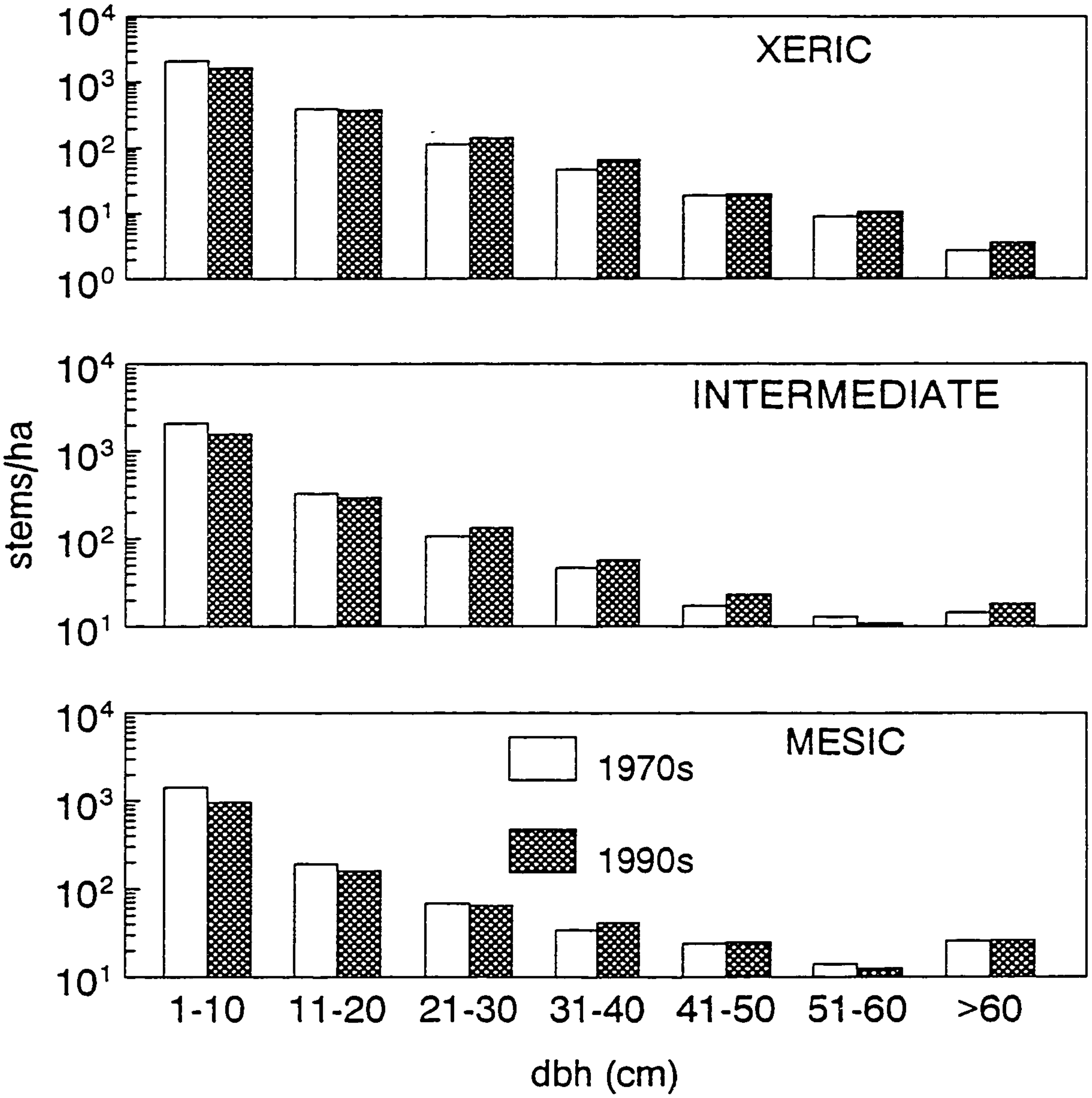
* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

Figure 4.6. Size structure of mesic, intermediate, and xeric permanent plots sampled in both the 1970s and 1990s.



Several tree species showed statistically significant shifts in distribution among topographic moisture classes (Table 4.8). Although densities of *Carya alba* declined on all sites, these decreases were proportionally largest on xeric sites and smallest on mesic sites. Decreases in *Cornus florida* density were greatest on mesic and xeric sites. Densities of *Liriodendron tulipifera* decreased sharply on mesic sites but increased considerably on intermediate sites. While densities of *Oxydendrum arboreum* and *Pinus virginiana* decreased on all site types, decreases for each species were proportionally largest on mesic sites and smallest on xeric sites. *Pinus strobus* densities decreased considerably on mesic sites and slightly on intermediate sites but increased on xeric sites. *Tsuga canadensis* increased on all site types; however, these increases were much larger on xeric than on intermediate or mesic sites. The shrubs *Kalmia latifolia* and *Rhododendron maximum* also showed statistically significant distributional shifts. For both species, densities of stems ≥ 0.5 cm dbh decreased on all site types; *Kalmia* became increasingly concentrated on intermediate sites, while *Rhododendron* shifted toward mesic sites.

Changes in tree species distributions appear to be driven primarily by changes in the densities of smaller stems. Analyses restricted to stems ≤ 10 cm dbh produce statistically significant results similar to those described above. When stems > 10 cm are considered, only the distributional changes in *Pinus virginiana* and *Tsuga canadensis* are statistically significant.

Table 4.8: Densities (stems $\geq$ 0.5 cm dbh/ha) of (a) tree species and (b) shrub and woody vine species for 1970s and 1990s permanent plots in western GSMNP. Statistical significance of changes in distributions across topographic moistureclasses was evaluated using chi-square tests on raw stem tallies.

	Mesic		Intermediate		Xeric		Change in
Species	1970s	1990s	1970s	1990s	1970s	1990s	distribution
(a) Tree species							
Acer rubrum	180	118	435	279	382	273	
Acer saccharum	40	33	6	4	1	1	
Aesculus flava	24	38	1	1	0	0	
Betula lenta	29	24	22	14	21	17	
Carya alba	21	14	44	21	54	11	**
Carya glabra	34	15	59	23	28	11	
Castanea dentata	4	1	6	8	6	1	
Cornus florida	397	118	405	173	83	22	***
Fagus grandifolia	10	7	3	2	1	1	
Halesia carolina	162	223	76	126	19	25	
Liriodendron tulipifera	55	31	33	42	8	6	***
Nyssa sylvatica	26	17	109	78	423	305	
Oxydendrum arboreum	50	17	113	59	88	72	***
Pinus pungens	0	0	4	2	4	1	
Pinus rigida	2	1	12	5	135	63	
Pinus strobus	52	32	146	142	231	327	***
Pinus virginiana	25	6	33	19	387	257	***
Quercus alba	15	10	25	13	57	29	
Quercus coccinea	0	0	16	12	60	48	
Quercus prinus	23	17	111	73	93	64	
Quercus rubra	15	7	28	16	14	16	
Quercus velutina	7	3	19	9	50	15	
Robinia pseudoacacia	6	4	14	9	5	3	
Tilia americana	33	26	1	0	0	0	
Tsuga canadensis	318	331	623	715	350	571	***
Other	249	189	256	255	182	120	
Tree total	1777	1282	2600	2100	2682	2259	
(b) Shrubs and woody vines							
Kalmia latifolia	29	8	415	342	398	180	***
Rhododendron maximum	1375	1177	360	261	381	225	***
Other	207	171	85	82	49	75	
Shrub/vine total	1611	1356	860	685	828	480	

* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

DISCUSSION

Historic land-use and disturbance regime

In the decades prior to the establishment of GSMNP in 1934, the western Smokies were subject to pervasive, chronic anthropogenic disturbance, including burning, grazing, logging, and chestnut blight. This pattern of historical disturbance appears to be characteristic of many currently forested areas in the southern Appalachian Mountains (Ayres and Ashe 1905, Phillips and Murdy 1985, Pyle 1988, USDA 1994, Bratton and Meier 1998). These disturbances profoundly influenced the structure and composition of forest stands and the distribution of species across the landscape. Changes observed since the 1930s reflect, to a large extent, recovery from disturbance in the late 19th and early 20th centuries.

Ayres and Ashe's (1905) survey, the 1930s plot data, and fire scar analyses (Harmon 1982) provide evidence for widespread anthropogenic fire in western GSMNP in the late 19th and early 20th centuries. In the southern Appalachians, most fires during the period of European American settlement (and, probably, most fires since the late Archaic Indian period) were anthropogenic in origin (Barden and Woods 1973, Harmon 1982, Delcourt and Delcourt 1997, Bratton and Meier 1998). Fire appears to have been an integral component of both Native American and European American land-use strategies, playing roles in agricultural clearing, improvement of habitat for game and livestock, and gathering of forest products.

Mortality from low-intensity fires is concentrated on stems < 10 cm dbh (Harmon 1984, Arthur et al. 1998, Turrill 1998). By selectively thinning the understory, low-intensity surface fires would have limited recruitment into the canopy and promoted dominance of fast-growing *Pinus* and *Quercus* species with thick, fire resistant bark and/or ability to sprout following top-kill. Frequent low-intensity fires may have also had more subtle effects; for example, trees scarred by low intensity fires are often more susceptible to damage by fungi, insects, and wind (Schowalter 1985, Matlack 1993). Less frequent high-intensity fires would have caused more extensive mortality of canopy trees and reductions in litter depth and allowed establishment of taxa such as shade-intolerant *Pinus* that require high light and low litter (Williams 1998). Fires in southern Appalachian forests also appear to increase cover of ericaceous shrubs and cover and fine-scale richness of herbaceous species, particularly grasses, composites, and legumes (Arthur et al. 1998, Turrill 1998, Chapter 3 this volume).

The chestnut blight also resulted in disturbance to stands across the topographic moisture gradient. The death of canopy *Castanea* was well underway at the time of the 1930s survey and was largely complete by the early 1940s (SAMAB 1996). Because most *Castanea* remained standing for a decade or more after their death, the sum of living and dead *Castanea* in the 1930s data can be used to estimate the magnitude of this disturbance to the forests of western GSMNP. As in other areas of the southern Appalachians, *Castanea* made up more than 75% of basal area in some stands (McCormick and Platt 1980, Stephenson 1986). In western GSMNP, the blight resulted in the removal of 14 to 16% of total canopy basal area on all topographic moisture classes. This estimate of *Castanea*'s pre-blight abundance is consistent with data in Ayres and Ashe (1905), who report that *Castanea* made up about 14% of timber trees in the districts encompassing western GSMNP but somewhat below estimates for the southern Appalachian region as a whole (Keever 1950, USDA 1994). It is possible that the 1930s data may underestimate the pre-blight density of *Castanea* because *Castanea* were cut in anticipation of the blight's arrival.

Grazing and logging also contributed to the milieu of chronic anthropogenic disturbance that shaped the forests of western GSMNP in the late 19th and early 20th centuries.

Although logging profoundly affected many southern Appalachian landscapes, its impact on western GSMNP appears to have been less important than those of fire and chestnut blight. The extent and impact of livestock grazing are difficult to quantify. Ayres and Ashe (1905) mention it on several occasions along with fire as a factor inhibiting forest growth. One effect of livestock may have been to favor *Pinus* species over more palatable angiosperms (Pyle 1988).

My data are generally consistent with assertions that fires were most frequent on xeric upper slopes and ridges and that logging was most frequent on mesic sites (Harmon 1982, Pyle 1988). However, their impacts, and that of chestnut blight, appear to have been more evenly distributed across the topographic moisture gradient than suggested by some previous studies (e. g. Harmon et al. 1983). In addition, the high degree of variability in forest composition and structure observed within topographic moisture classes suggests that disturbance occurrence and severity varied considerably from stand to stand. (Some of this variability is also an artifact of plot size; in southern Appalachian forests, estimates of stand attributes based on plots smaller than about 0.5 ha may deviate considerably from values based on larger plots; Busing et al. 1993, Busing and White 1993).

Stand composition and structure

The 1930s plots sample forest conditions in GSMNP immediately following park establishment in 1934. At that time, the era of logging, livestock grazing, and deliberate burning was coming to an end and the chestnut blight had nearly run its course. The western Smokies were a mosaic of open woodlands and young, developing stands interspersed with mature, closed-canopy forests. Values of canopy species richness, density, basal area, and biomass of live canopy trees were considerably lower that those observed during later periods.

Forest dynamics immediately following park establishment appear to have been dominated by the process of reorganization (Bormann and Likens 1979) initiated by the pulse of disturbance in the early 20th century. Reorganizing forests are characterized by open conditions, reduced competition, and establishment and rapid growth of both shade-tolerant and intolerant species. On most forested sites in the southern Appalachians, closure of the forest canopy typically occurs within 10-20 years after disturbance (Woods and Shanks 1959, Runkle 1982, Elliott et al. 1997, Chapter 1 this volume), suggesting that, in most stands in western GSMNP, the reorganization phase ended no later than 1960. In xeric stands, sharp drops in establishment of shade-intolerant *Pinus* and *Quercus* suggest that the reorganization phase may have ended as early as the mid-1940s (Chapter 2 this volume).

Mechanisms of canopy closure include lateral extension of established canopy trees and vertical growth of advance regeneration, sprouts, and seedlings originating after disturbance; the relative importance of these mechanisms varies with disturbance size and intensity and stand composition and structure (Woods and Shanks 1959, Runkle 1982, Phillips and Shure 1990). In general, lateral extension and advance regeneration tend to be more important in small gaps, and seedlings and sprouts more important in larger openings. Woods and Shanks (1959) argue that the dominant mechanism of canopy closure following chestnut blight thus varied between stands with the pre-blight abundance of *Castanea*. Harmon et al. (1983) suggest that, in the southern Appalachians, the relative importance of sprouting versus seedling establishment varies with stand composition and thus with position along the topographic moisture gradient, with sprouting most important on intermediate sites. Elliott et al. (1997) found that, whereas seedlings were the primarily source of regeneration following clearcutting on mesic sites, sprouts were most important on intermediate and xeric sites. Elliott et al. (1997) also found within-species variation in regeneration mechanism with topographic moisture. Among the species that increased in basal area from the 1930s to 1970s in western GSMNP were those whose modes of canopy recruitment include advance regeneration (e.g. *Tsuga, Halesia),* post-disturbance sprouting (e.g. *Quercus prinus*), and post-disturbance germination (e.g. *Pinus rigida),* suggesting that several mechanisms of canopy closure were important. Variation in the composition of new canopy recruits across the topographic moisture gradient generally mirrored the distribution of canopy and understory species in the 1930s; recruitment of shade-tolerants was most important on mesic sites, mid-tolerants on intermediate sites, and shade-intolerants on xeric sites.

Following canopy closure, developing stands would have entered the aggradation phase (Bormann and Likens 1979), with dynamics characterized by intense resource competition and rapid accumulation of biomass. Between the 1930s and 1970s, all topographic moisture classes in western GSMNP showed large increases (~50-100%) in basal area and biomass. My estimates include live aboveground woody biomass only; estimates of total change in biomass and carbon storage would likely be substantially higher if changes in soil organic matter and coarse woody debris resulting from decreased fire frequency and altered understory conditions were taken into account.

Although the forests of western GSMNP forests appear to have approached a near-steady state in terms of biomass by the 1970s, changes in composition and structure have continued. The relative abundance of shade-tolerant species increased from the 1930s to the 1970s and again from the 1970s to 1990s. These increases were most pronounced in the smaller size classes, consistent with the observation that although shade-intolerants are often well-represented in the canopies of aggrading forests, establishment of new individuals is limited to those species capable of survival and growth under low-light conditions (Oliver 1980). Because shade-tolerants cast deeper shade than early successional species (Canham et al. 1994), increases in the importance of shade-tolerant species may lead to ongoing reductions in understory light levels. Declines in sapling density between the 1970s and 1990s appear to reflect the process of competitive thinning characteristic of aggradation-phase forests (Peet and Christensen 1987).

While the general trend over the past 60 years has been toward increased importance of shade-tolerants, behavior of individual species has varied considerably. Factors other than competition have influenced compositional changes. Recent declines of *Cornus florida* are largely the result of the introduced dogwood anthracnose fungus (Daughtry and Hibben 1994, Wilds 1997). Declines in densities of shade-intolerant *Pinus* species were, in some cases, accelerated by the activities of the southern pine beetle (Kuykendall 1978*)*; losses of *Quercus* were accelerated by a severe regional drought in the mid 1980s (Clinton et al. 1993). High deer populations, especially around Cades Cove, may have driven some changes in forest composition, as they have in some northeastern forests (e.g. Whitney 1984, who reports that heavy deer browsing has favored shade-tolerant over intolerant species).

The general trends I observed in western GSMNP over the past sixty years are similar to those observed in other southern Appalachian forests subject to extensive anthropogenic disturbance. Phillips and Murdy (1985), Stephenson (1986), Clebsch and Busing 1989, Agrawal and Stephenson (1995), and Elliott et al. (1997) report rapid increases in basal area and biomass in the first few decades after disturbance, slower increases in ~50 year old stands, and increases in the importance of shade-tolerant species, particularly in the smaller size classes. The structural and compositional changes I observed on mesic sites that underwent chronic, diffuse disturbance appear intermediate between those in old-growth coves subjected to minimal anthropogenic disturbance other than chestnut blight (Busing 1989, 1993) and those in mesic secondary stands developing following agriculture or clearcutting, which are heavily dominated by *Liriodendron* (Della-Bianca 1983, Phillips and Murdy 1985, Clebsch and Busing 1989).

Several studies of changes on southern Appalachian sites with intermediate topographic moisture have focused on the role of chestnut blight. Taxa reported as the most important replacements for *Castanea* (*Quercus prinus, Q. rubra, Carya* spp., *Liriodendron,* and *Acer rubrum;* Keever 1953, Nelson 1955, Woods and Shanks 1959, McCormack and Platt 1980, Stephenson 1986) increased on intermediate sites in western GSMNP between the 1930s and 1970s. However, observed increases in basal area of these species greatly exceed estimates of the pre-blight basal area of *Castanea.* Recent trends include continued increases in the importance of shade-tolerant, fire-sensitive species such as *Tsuga* and declines in the importance of mid-tolerant and shade-intolerant taxa. I suggest that changes observed on intermediate sites in western GSMNP and throughout the southern Appalachians are best interpreted as the product of reduced fire frequency in conjunction with chestnut blight and historic logging. Fire and logging history may be important factors explaining local and regional variation in *Castanea* replacement (e.g. McCormack and Platt 1980).

Reduction in fire frequency appears to be the primary cause of changes on xeric sites (Chapter 2 this volume). Since the 1930s, xeric sites have developed from open-canopy woodlands dominated by fire-resistant, light-demanding *Pinus* and *Quercus* species to closed-canopy forests increasingly dominated by more fire-sensitive, shade-tolerant taxa (Chapter 1 this volume). Similar changes have occurred on xeric *Pinus-Quercus* forests throughout the southern Appalachians (e.g. Barden 1976, Ross et al. 1982, Williams and Johnson 1990, Bratton and Meier 1998). Changes in fire regime and canopy structure have led to substantial decreases in cover and fine-scale diversity of herbaceous species on xeric sites (Chapter 3 this volume).

Data from the Forest Service Forest Inventory and Analysis (FIA) for the North Carolina portion of the southern Appalachians allow assessment of regional trends in forest composition and structure. FIA data indicate steady increases in forest biomass over the period 1955-1990 (Cost 1975, Craver 1985, Johnson 1991); decreases in rates of biomass accumulation, if present, are less pronounced that those observed in western GSMNP. More detailed examination of FIA data for the period 1974-1990 indicates regional structural and compositional trends broadly similar to those observed in GSMNP over the same period: decreases in the abundance of *Quercus, Carya,* and shade-intolerant *Pinus* spp., increases in abundance of *Acer rubrum, Liriodendron tulipifera, Pinus strobus,* and *Tsuga canadensis,* and decreases in sapling densities accompanied by increases in densities of larger size classes. Overall, structural and compositional trends in western GSMNP are strikingly similar to those of the southern Appalachian region as a whole, especially considering that GSMNP has been protected since the 1930s, whereas much of the region has been subject to ongoing timber harvests.

Landscape-level vegetation patterns

My study echoes others in finding that anthropogenic disturbance has altered the landscape and regional distributions of plant species at time scales ranging from decades to centuries (e.g. Werner and Platt 1976, Parker and Swank 1982, Christensen and Peet 1984, Foster 1992, Elliott et al. 1997, Foster et al. 1998). Whereas studies in landscapes subject to extensive agricultural clearing (Christensen and Peet 1984, Foster et al. 1998) have concluded that anthropogenic disturbance may lead to the homogenization of vegetation and the weakening of relationships between vegetation and environment, my study suggests that the basic gradient structure of western GSMNP has remained stable from the 1930s to the 1990s. The overriding importance of the elevation, soil, and topographic moisture gradients has persisted despite large changes in stand structure and in the distribution of species across that gradient. Reasons for these differing results may include the presence of a very strong moisture gradient in the western Smokies versus more subtle climatic and edaphic gradients in Peet and Christensen's (1984) and Foster et al.'s (1998) study areas, the relatively diffuse nature of land-use in the western Smokies as compared to landscapes with more intensive agricultural activity, and the fact that the frequency of fire, the most important anthropogenic disturbance in the western Smokies, varied along the same environmental gradients most strongly correlated with vegetation patterns.

Distributions of several species have shifted markedly since GSMNP establishment. In the 1930s, canopy *Tsuga canadensis* and *Acer rubrum* were common on mesic sites but rare on intermediate and xeric sites. By the 1970s, these species had spread onto intermediate and xeric sites; *Tsuga*'s spread across the moisture gradient continued through the 1990s. These trends are consistent with the hypothesis that, prior to the 1930s, these species, which are sensitive to fire when small (Harmon 1984), were largely restricted to mesic sites where intervals between fires were long enough to allow individuals of these species to grow to fire-resistant size. Decreases in fire frequency following park establishment may have allowed these species to spread onto more xeric sites. *Tsuga* and *Acer rubrum* may represent examples of species that, although tolerant of a wide range of resource levels and conditions, may have been restricted to particular sites by disturbance (Romme and Knight 1981). Decreased fire frequency, together with the generally open condition of the canopy, may have also allowed *Rhododendron* to spread across the topographic moisture gradient between the 1930s and 1970s (Phillips and Murdy 1985). While fires may have restricted the distributions of shade-tolerant, fire-sensitive species, they apparently allowed relatively fire-resistant, shade-intolerant *Pinus* and *Quercus* species to establish on a range of sites (Williams 1998). Since the 1930s, the distribution of *Pinus rigida* has contracted toward more xeric sites.

Between the 1970s and 1990s, several species' distributions contracted, *Oxydendrum* and *Pinus virginiana* toward xeric sites, *Cornus florida* and *Kalmia* toward intermediate sites, *Carya alba* and *Rhododendron* toward mesic sites. Recent restrictions in these species' gradient breadths are apparently driven by competitive processes and may reflect succession towards conditions that would have existed in the absence of human activity. One exception may be *Cornus florida*, whose distribution changes appear to be largely due to high rates of anthracnose mortality on mesic sites (Wilds 1997).

Although I did not observe marked changes in the strength of species-environment relations, changes in species distributions are otherwise consistent with concept of competitive sorting (Peet 1992). According to this scenario, disturbances reduce competition, free resources, and allow species to establish on a wide range of sites. But as individuals grow and stand density and competition increase, species persist only on sites on which they are strong competitors. In general, observed changes in species' distributions were driven by changes in the abundance of saplings and small to medium-size trees. It is not surprising that the distributions of smaller individuals are more volatile than larger ones at the time scales considered in this study. On xeric sites, most trees that established since 1930 are still less that 30 cm dbh (Chapter 2 this volume). In addition, small stems in rapidly aggrading stands are subject to intense competitive stress and high levels of mortality (Peet and Christensen 1987). Variations in rate and timing of forest development along the topographic moisture gradient may be responsible for complex changes in distribution such as those observed in *Pinus strobus* and *Liriodendron.*

Forest dynamics in the 21st century

Changes in forest composition and structure that have occurred since GSMNP establishment will affect response to future disturbances. Effects of fire on modern xeric forests, which have not burned in several decades, may differ profoundly from effects on early 20th century stands subject to repeated, short-interval burns (Harmon 1984, Chapter 1 this volume). Extensive *Quercus* recruitment occurred following fire, chestnut blight, and logging early in the 20th century; since that time, abundance and vigor of *Quercus* regeneration have declined, apparently as the result of reduced fire frequency, canopy closure, and competition from more shade tolerant species in the understory (Abrams 1992, Lorimer et al. 1994, SAMAB 1996). More recent canopy disturbance in *Quercus*-dominated stands has generally resulted in little *Quercus* regeneration (Loftis 1983, Elliott et al. 1997). The arrival of the invasive European gypsy moth (*Lymantria dispar)* may contribute to the continuing decline of

Quercus spp., their preferred hosts (SAMAB 1996). The hemlock woolly adelgid (*Adelges tsugae)*, an invasive insect of Asian origin, is expanding its range in the southern Appalachians (SAMAB 1996). The adelgid infests *Tsuga canadensis*, causing mortality within five years of infestation; no resistance is known. The total abundance and gradient breadth of *Tsuga canadensis* in western GSMNP have increased steadily since the 1930s. My results suggest that the adelgid's impact as it invades western GSMNP in the late 20th or early 21st century will be greater than it would have been had it invaded at any time in the historical past. However, the rapid increases in stand density, basal area, and biomass observed following fire, chestnut blight, logging, and grazing in the early 20th century suggest that the forests of western GSMNP will respond vigorously to losses of *Quercus* and *Tsuga.* Future disturbance and climatic change will interact with the legacies of past land-use to produce ongoing changes in stand and landscape-level vegetation patterns.

Chapter 5:

Fire ecology of xeric pine-oak forests in the southern Appalachian mountains

Xeric pine-oak forests in the southern Appalachian Mountains present an enigma: a fire-maintained community in a region where lightning fires are infrequent, small, and generally of too low an intensity to regenerate component species (Barden and Woods 1973, Bratton and Meier 1998, Williams 1998). In the 19th and early 20th centuries, xeric forests experienced frequent, mostly anthropogenic fires. Since about 1940, fires have largely been suppressed (Harmon 1982, Ross et al. 1982, Sutherland 1995). This reduction in fire frequency and associated declines in fire-adapted species have prompted land managers to initiate prescribed burning programs (Vose et al. 1995, Turrill 1998, Elliott et al. 1999, Waldrop and Brose 1999).

Until recently, the fire ecology and successional dynamics of xeric forests were poorly understood (Schafale and Weakley 1990). Perhaps as a consequence of this lack of knowledge, attempts at restoring historical composition and structure and regenerating fire-dependent species have been only partially successful or have produced unexpected results (e.g. Turrill 1998, Waldrop and Brose 1999). Recent applications of prescribed fire, together with research on wildfire effects and historical fire regimes and vegetation patterns, have yielded new insights into the fire ecology of xeric pine-oak forests. In this paper, I review data on the characteristics of historic and prehistoric fire regimes, the ecological effects of fire, and recent changes in vegetation composition and structure. I then attempt to synthesize these data to produce an understanding of the historical dynamics of xeric forests and identify some of the gaps that remain in our understanding of this vegetation type.

Introduction to southern Appalachian pine-oak forests

The present discussion focuses on xeric pine-oak forests in the southern Appalachian Mountains, including the southern Blue Ridge and Ridge and Valley physiographic provinces of North and South Carolina, Virginia, Georgia, and Tennessee. Related vegetation types occur in the central Appalachians, the Cumberland Plateau, the mid-Atlantic coastal plain, and the Ozark highlands (Zobel 1969, Williams 1998). In the southern Appalachians, xeric pine-oak forests occur at low to mid elevations (~300-1500 m). Throughout most of the region, the forest type is largely restricted the driest and droughtiest positions in the landscape, including ridges, south- to west-facing upper slopes, and the margins of rocky outcrops. In the rugged interface between the Blue Ridge escarpment and the southern piedmont, the forest type may occur across a wider range of topographic positions (Newell 1997). Xeric pine-oak forests are more abundant in landscapes with extensive systems of contiguous, relatively low-elevation ridges, such as western Great Smoky Mountains National Park, than in areas of greater topographic relief (MacKenzie and White 1998). Soils are typically shallow, rocky ultisols and inceptisols with low nutrient status (Zobel 1969, Schafale and Weakley 1990, Newell 1997).

The vegetation of southern Appalachian xeric pine-oak forests has been described in numerous studies (e.g. Whittaker 1956; Racine 1966; Zobel 1969; Schafale and Weakley 1990; Groeschl et al. 1992; Newell 1997; Chapter 1 this volume, in review; Newell and Peet

1998; Turrill 1998; Williams 1998, Elliott et al. 1999); the most comprehensive and detailed floristic treatment is that of Newell (1997). The largest and oldest trees in most stands are yellow pines (*Pinus echinata, P. pungens, P. rigida,* and *P. virginiana*) and oaks (mostly *Quercus primus* and *Q. coccinea*, but also *Q. velutina, Q. falcata, Q. rubra, Q. alba, Q. stellata,* and *Q. marilandica*). *Acer rubrum, Nyssa sylvatica, Pinus strobus*, and *Sassafras albidum* are often common as small to medium-sized trees and saplings. The shrub layer is typically well developed and dominated by Ericads, particularly *Kalmia latifolia*, *Vaccinium* spp., and *Gaylussacia* spp. Common low shrubs and woody vines include *Epigaea repens, Galax urceolata, Gaultheria procumbens*, and *Smilax* spp. Herbaceous species are typically sparse; characteristic herbs include grasses (*Dichanthelium* spp., *Schizachyrium scoparium*), composites (*Aster* spp. *Coreopsis major, Solidago odora),* legumes (*Lespediza* spp., *Tephrosia virginiana)*, *Chimaphila maculata,* and *Pteridium aquilinum.*

Canopy composition and structure are highly variable (Whittaker 1956, Zobel 1969, Barden 1979, Newell 1997, Newell and Peet 1998, Williams 1998). Open slopes and broad ridges below 1000 m elevation typically support closed-canopy forests; canopy dominance ranges from nearly pure yellow pine or oak to mixtures of pines, oaks, and other species. Higher elevations, thinner soils, and more exposed sites often support open-canopy forests with scattered yellow pines and oaks (particularly *P. rigida* and *P. pungens)* and dense understories of *Kalmia*. On very thin-soiled sites such as the margins of rock outcrops, scattered *P. pungens* and *P. virginiana* may be interspersed with low-growing shrubs and herbs and stretches of bare rock and lichen.

Life history characteristics of several species typical of xeric pine-oak forests suggest evolution in the context of fire. Yellow pine species regenerate best under regimes of high light and relatively thin litter (Burns and Honkala 1990, Williams et al. 1990), and *Pinus pungens*, a southern Appalachian endemic, produces partially serotinous cones (Barden 1979). Yellow pine traits that promote survival following fire include high rates of bark production (particularly in *P. rigida)*, epicormic buds in *P. rigida*, and the formation of a basal crook that allows resprouting following top-kill in *P. echinata, P. rigida*, and possibly *P. pungens* (Zobel 1969, Harmon 1984, Burns and Honkala 1990).

The life history of southern Appalachian oak species also appears linked to fire (Van Lear 1990, Abrams 1992). Oaks possess relatively thick bark and resprout vigorously following repeated top-kill. Oak saplings require medium to high light levels and are sensitive to competition from canopy trees, shade-tolerant saplings, and shrubs; repeated low-intensity fires appear to favor oak regeneration by opening the canopy and reducing competing vegetation (Phillips and Murdy 1985; Loftis 1983, 1990; Van Lear 1990; Abrams 1992; Lorimer et al. 1994; SAMAB 1996). Fire appears to promote growth and reproduction of several other species found on xeric sites, including several herbaceous species and the endangered endemic shrub *Hudsonia montana* (Gross et al. 1998, Chapter 3 this volume).

Historic and prehistoric fire regimes

The fire rotation of xeric forests prior to European settlement remains a matter of speculation. Reconstructions of fire frequency are limited to the last ~150 years because few fire scarred trees predate the mid 19th century (Harmon 1982, Sutherland et al. 1995). Native American populations have been present in the southern Appalachian region at least the last 10,000 years (SAMAB 1996). Native Americans set fires to clear land, facilitate travel, improve game habitat, and promote desirable plant species. Pines and oaks were abundant at the time of first European settlement, making up 26% and 42% of witness trees respectively in an 1820 land lottery survey in northern Georgia (Bratton and Meier 1998). Limited paleoecological evidence suggests that fire frequency prior to European settlement was sufficient to maintain pine as a prominent component of the landscape, though perhaps at a level somewhat lower than that of postsettlement times. Delcourt and Delcourt (1997), examining sediments from a bog in western North Carolina, conclude that pine species have made up > 8% of terrestrial plant pollen since the late Archaic period (~ 4000 years before present), increasing to ~16% following European-American settlement circa 1830. They report that rates of charcoal accumulation appear roughly similar before and after 1830, and size-class distributions of charcoal particles suggest that throughout the study period, much or most of charcoal was the product of fires on the dry uplands surrounding the bog. Bog sediments from the Cherokee Nation in western North Carolina show an increase in charcoal corresponding to the arrival of the Cherokee between 1450 and 1600 AD and an additional increase in pine pollen following European settlement (Lynch and Clark 1996).

Fire frequencies in xeric forests have changed considerably over the past ~150 years, the time period covered by fire scar analyses. As a result of active fire suppression, most stands have not burned since the 1940s or 1950s; under current regimes, estimated fire return intervals in many landscapes are > 500 years (Harmon 1982, Sutherland et al. 1995, SAMAB 1996, Chapter 1 this volume, Newell and Peet 1998). Fire scars and written records indicate that fire frequency during the period of active European-American settlement (~1830-1940), was one to two orders of magnitude higher (Ross et al. 1982). During that period, settlers set fires to clear land, increase livestock forage and berry crops, and facilitate the gathering of chestnuts. Historical accounts indicate annual or semiannual burning in some heavily settled areas (Ayres and Ashe 1905, Lambert 1958). Estimates of landscape-level fire frequency for the 19th and early 20th centuries include 5-10 years for Linville Gorge, NC (Frantz and Sutter 1987), 9-11 years for a *Pinus pungens* stand in southwest Virginia (Sutherland et al. 1995), 10-14 years for pine-oak stands in eastern Tennessee (Harmon 1982, Chapter 3 this volume), and ~18 years for pine stands in western North Carolina (Barden 1976). Fire frequencies may have been particularly high between 1880 and 1920, when logging and agricultural activity peaked in the region (Bratton and Meier 1998, Williams 1998). The decrease in fire frequency after 1940 does not coincide with marked changes in fire-season drought severity (Sutherland et al. 1995) and appears due largely the removal of human settlements, the cessation of land-use activities, and the implementation of fire exclusion policies (Harmon 1982).

The temporal pattern of fires in xeric pine-oak forests remains unclear. Harmon (1984) and Chapter 3 (this volume) model landscape dynamics based on the assumption that probability of fire is independent of time since last fire, i.e. the distribution of time-since-fire dates follows a negative exponential distribution (Johnson and Van Wagner 1985). This assumption should be valid where fire occurrence is controlled more strongly by weather conditions and ignitions than by fuels. This appears to be the case in much of the southern Appalachians; fire scars, historical accounts, and observations of recent fire behavior indicate that fuels sufficient to carry a fire develop within 1-2 years after fire (Harmon 1982, Arthur et al. 1998). Year-to-year fluctuations in fire occurrence and size in the southern Appalachians are closely linked to annual variations in rainfall and humidity (Barden and Woods 1973, Harmon 1980, Sutherland et al. 1995). In contrast, Frost (1998) argues that cycles of fuel development should lead to a more regular fire cycle, with observed between-fire intervals clustering around the mean fire rotation. Under this scenario, the distribution of time-since-fire dates should follow a Weibull distribution (Johnson and Van Wagner 1985). A regular distribution of time-since-fire dates could also arise in areas where cultural practices resulted in burning at regular intervals. While the effects of time-since-fire on the likelihood of subsequent fires remains unclear, the history of fire and other disturbances may have a strong effect on fuel load and thus on fire intensity (see below).

Most fires observed since the onset of fire suppression have been small; the median size of both lightning and anthropogenic fires since 1940 is less than 1.0 ha, and mean sizes are 3.4 ha for lightning fires and 5.4 ha for anthropogenic fires (Barden and Woods 1973, Harmon 1982, Bratton and Meier 1998). The small size of recent southern Appalachian fires is in part a product of fire suppression. It also appears to reflect the highly dissected nature of the southern Appalachian terrain, in which xeric slopes and forests are interspersed with streams and mesic coves. Other factors limiting fire spread include the high rainfall and generally humid character of the region and the fact that lightning is generally associated with rain (Barden and Woods 1973). While fires are typically small, under drought conditions fires can reach very large size. Barden and Woods (1973) report fires during droughts in 1925 and 1952 that each burned > 10,000 ha. Several large wildfires occurred during a severe regional drought in 1988. During that summer, a wildfire in Shenandoah National Park burned 350 ha and continued for four weeks despite suppression efforts (Groeschl et al 1992).

Lightning ignitions appear to be relatively rare in most of the southern Appalachians. Estimates of annual rates of lightning ignitions include 4 per 100,000 ha for the Chattooga Watershed in the Southern Escarpment (Bratton and Meier 1998), 2.7 per 100,000 ha for the western Smokies (Harmon 1982), and 1.5 per 100,000 ha for the southern Appalachian region as a whole (Barden and Woods 1973). Records dating from the 1930s onward indicate that lightning fires account for 5-15% of ignitions and 4-15% of the total area burned (Barden and Woods 1973). While most lightning ignitions occur on ridges and peaks, anthropogenic fires tend to start at lower slope positions (Harmon et al. 1983, Bratton and Meier 1998).

Lightning and human-set fires differ in intensity and speed of movement. The large majority of lightning fires are relatively slow-moving, low-intensity surface fires. Eighty-five percent of lightning fires observed over the period 1960-1971 were "cool" surface fires that killed < 20% of canopy basal area (Barden and Woods 1973, 1976). Most of the remaining lightning fires were "hot" surface fires that removed 20-85% of the canopy. Only a very few lightning fires, located on extremely steep and xeric sites, were categorized as crown fires; these intense fires killed 85-100% of canopy trees. Age structure studies also suggest that stand-replacing fires have been historically rare; most pine and pine-oak stands show a multi-aged structure, with one or more large cohorts and scattered older trees. As Barden and Woods (1976) note, their 12-year study period did not include years of severe drought, which are associated with more extreme fire behavior. A lightning fire in Shenandoah National Park during the 1988 drought included extensive areas of crown fire in which overstory mortality approached 100% (Groeschl et al. 1992, 1993). Fires started by humans tend to move faster and reach higher intensities than do lightning fires. Because human ignitions are not linked to storm activity, they may occur during periods of lower humidity (Barden and Woods 1973). Starting at lower slope positions, they may reach high intensities as they move rapidly up slope. Seven percent of the human-caused fires observed by Barden and Woods were crown fires (1973, 1976).

Most fires the southern Appalachians occur during spring. More than 50% of the area burned by 20th century lightning fires burned in April and May; most of the remainder burned in June, July, and August (Barden and Woods 1973). Anthropogenic fires in the 20th century show two peaks, a large one in March and April, and a smaller one in October and November. Peaks in fire occurrence correspond to times when leaf litter is driest (Barden and Woods 1973). Year-to-year variations in both ignitions and total area burned are closely linked to variations in precipitation and humidity; the occurrence of major fires coincides closely with periods of spring and summer drought (Barden and Woods 1973, Harmon 1980, Sutherland et al. 1995).

Typical scorch heights range from < 2 m for lower-intensity surface fires, ~ 6 m for higher-intensity surface fires, to >15 m for crown fires (Turrill 1998, Waldrop and Brose 1999). Fire intensity appears to vary with woody fuel levels, climate, and season. Both dense growth of woody shrubs such as *Kalmia* and large fuel accumulations such as those that occur following southern pine beetle outbreaks may lead to increases in fire intensity (Harmon 1980, Nicholas and White 1984, Waldrop and Brose 1999, Chapter 3 this volume).

Fire effects

Damage to trees varies with tree species and size and fire characteristics (Barden and Woods 1976, Harmon 1984, Turrill 1998, Elliott et al. 1999, Waldrop and Brose 1999, Chapter 3 this volume). Top-kill following low-intensity surface fires is heavily concentrated on small stems and is minimal for stems > 15 cm dbh of all species. Mortality among smaller stems varies with species and size, with larger stems and thick-barked species such as yellow pines, oaks, and blackgum surviving better than thinner-barked species such as red maple, white pine, and hemlock (Harmon 1984). In addition to killing trees outright, fires may reduce tree vigor and structural strength by scorching foliage and scarring boles. Higher-intensity surface fires produce near complete mortality of small stems, more extensive scarring and scorching, and increased mortality in larger size classes; again, yellow pines and oaks appear to survive better than thinner-barked species of similar size. Crown fires tend to produce high and relatively indiscriminate mortality. Because mortality following low- to medium-intensity fires is concentrated on smaller stems, relative reductions in tree density are generally larger than reductions in basal area. Reductions in total stem numbers, together with size- and species- specific patterns of mortality, generally result in decreases in the species richness of the tree stratum (Chapter 1 this volume, Turrill 1998, Elliott et al. 1999).

Fires both consume fuels by combustion and create fuels by killing relatively non-flammable live trees (Van Lear 1996); as a result, fire effects on woody fuels appear highly variable. For example, a prescribed stand-replacement fire resulted in a 12% reduction in levels of downed coarse woody debris (downed wood $\geq$ 7.5 cm diameter), and an 80% reduction in smaller fuels but conversion of 30% of live tree basal area to dead snags (Elliott et al. 1999, Vose et al. 1999). While fuel reductions and overstory mortality were reported in different units (mass vs. basal area), comparison with estimates of live aboveground biomass for xeric forests (Chapter 4 this volume) suggest that the net result of that fire was a large increase in total dead fuels. Rates of downed fuel consumption are typically very high for fine fuels (< 7.5 cm diameter) but considerably lower for larger fuels (Swift et al. 1993). Net effects of fire on fuel levels will vary with stand structure and fire intensity. They will also vary with time since fire as newly killed fuels season and decay. In cases where high-intensity fires cause extensive canopy mortality, fuel loads may be elevated for several years after fire

(White 1987, Van Lear 1996). Lower-intensity surface fires, which kill few canopy trees, are more likely to result in a net reduction in fuel levels (Elliott et al. 1999, Vose et al. 1999).

Consumption of litter and duff does not appear to be strongly linked to woody fuel load or canopy mortality (Waldrop and Brose 1999, Chapter 3 this volume) but does appear to depend on the moisture content of the litter layer and thus on the season of the burn. In general, summer and fall fires appear to consume more litter and duff than winter and spring fires (Turrill 1998, Chapter 3 this volume). Reported levels of leaf litter consumption are on the order of 55-80 % for spring prescribed fires and ~96% for one fall prescribed burn (Swift et al. 1993, Vose et al. 1994, Turrill 1998). Humus consumption is typically lower; published values range from 0-10% for spring burns and 30-66% for fall burns (Swift et al. 1993, Vose et al. 1994, Turrill 1998). Again, wildfires during drought periods may produce more extreme effects; in large areas of the July 1988 wildfire in Shenandoah National Park, litter and duff were completely consumed (Groeschl et al. 1992, 1993). At fine spatial scales, fire effects on litter and duff can be quite patchy, with large variations occurring within the perimeter of a single fire.

Fires alter ecosystem nitrogen pools. A prescribed stand replacement fire reduced total nitrogen pools by ~15%, with largest losses occurring in small wood and litter components (Vose et al. 1999). These N losses were considerably smaller than the 33-61% losses observed on three similar sites subjected to fell-and-burn site preparation treatments (Vose and Swank 1993). In the 1988 wildfires in Shenandoah National Park, nitrogen losses were minimal in areas of low-intensity fire. However, high-intensity fires volatilized all forest floor N and ~35% of N in the top 10 cm of mineral soil (Groeschl et al. 1993). Fell-and-burn treatments resulted in increases in soil ammonium concentrations and net mineralization rates and thus in available soil nitrogen (Knoepp and Swank 1993). Although preliminary data show some trends toward increased nitrogen concentrations in soil and stream water following fell-and-burn treatments (Knoepp and Swank 1993), one prescribed stand-replacement fire resulted in no increase in stream N concentrations (Vose et al. 1999).

Fires also influence other ecosystem properties. Higher-intensity fires mineralize cations including calcium and potassium, increasing their concentrations in the mineral soil (Groeschl et al. 1993). However, total pools of these cations show little change (Vose et al. 1999). Fell-and-burn treatment treatments resulted in little minimal soil erosion and no off-site movement of soil (Swift et al. 1993). Other effects of fell-and-burn treatments include increases in soil temperature and moisture availability (Swift et al. 1993). Whether comparable effects occur following burn-only treatments remains unknown.

Vegetation response to fire

While fires cause extensive mortality of seedlings and saplings and consumption of most aboveground portions of shrubs and herbs, they also initiate growth and regeneration of the vegetation. Tree regeneration following fire occurs from sprouts of trees top-killed by fire and by establishment of newly germinated seeds. Recovery of shrubs and herbs occurs by resprouting of underground buds and germination of seeds either present in the seed bank or arriving post-fire. As a result, total understory cover and density in burned stands generally equals or exceed that of unburned stands within 1-2 years after fire (Arthur et al. 1998, Elliott et al 1999, Chapter 3 this volume).

Although fire characteristics do not appear to strongly influence the total post-fire density of small woody stems (Groeschl et al. 1992, Waldrop and Brose 1999), they do influence the relative abundance of yellow pines, other tree species, shrubs, and herbs. While some yellow pine species are capable of resprouting, the majority of yellow pine regeneration occurs from seeds that germinate in the first few years after fire. Studies indicate high variability in levels of yellow pine regeneration following fire, with post-burn regeneration ranging from minimal to very dense (Barden and Woods 1976; Groeschl et al. 1992, 1993; Turrill 1998; Elliott et al. 1999; Waldrop and Brose 1999; Chapter 3 this volume). Highly variable effects are often observed within the perimeter of a single fire. Canopy opening and increases in understory light levels appear to be major factors influencing yellow pine recruitment. Barden and Woods (1976) found minimal yellow pine regeneration on sites of surface fires that removed < 85% of the canopy and successful regeneration only on sites where crown fires removed > 85%. In contrast, Waldrop and Brose (1999), found highest levels of *P. pungens* regeneration on medium to low intensity fires, and lower levels in areas of higher fire intensity. Chapter 1 (this volume) observed generally good recruitment of yellow pines only on sites where fires removed > 25% of the canopy, but subsequent analysis (Chapter 3 this volume) revealed that yellow pine regeneration was more strongly correlated with reductions in litter depth than with canopy mortality.

Litter depth and type appear to be major factors in yellow pine regeneration. Williams and Johnson (1992) found that *P. pungens* seedlings in unburned stands are restricted to sites where litter depth is less than 40 mm and are generally associated with pine, rather than oak, litter. Groeschl et al. (1992) report highest densities of *P. pungens* and *P. rigida* seedlings on sites of high-intensity fires on which leaf litter was completely removed. Chapter 3 (this volume) found that successful *P. rigida* and *P. virginiana* regeneration was negatively correlated with post-burn litter depth and largely restricted to plots where mean litter depth was less than 10 mm. In contrast to other studies, Waldrop and Brose (1999) report high rates of establishment and growth for *P. pungens* in post-fire litter depths of up to 75 mm. While mineral soil is sometimes considered an ideal substrate for yellow pine regeneration, seedling survival may be actually higher in thin pine litter, where seedlings are protected from dessication (Williams et al. 1990). Dry weather and competition from hardwood sprouts and shrubs may cause high mortality and limit yellow pine recruitment on some sites.

Vigorous sprouting of red maple, sassafras, sourwood, blackgum, and scarlet oak is reported following most fires (Harmon 1980, Groeschl et al. 1992, Arthur et al. 1998, Chapter 1 this volume, Turrill 1998, Elliott et al. 1999). Stems less that 10 cm diameter tend to sprout most vigorously follow topkill (Harmon et al. 1983) In general, chestnut oak has regenerated poorly in areas burned after several decades without fire. This may be due, in part, to the fact that many chestnut oak populations are made up mostly of large individuals that suffer little mortality but are poor sprouters. It may also reflect the fact that oaks compete poorly with sprouts of other tree species and with shrubs (Phillips and Murdy 1985, Loftis 1990, Lorimer et al. 1994). Repeated fires do appear to increase the relative abundance of chestnut oak regeneration (Arthur et al. 1998). Regeneration of white pine and hemlock occurs from seed, beginning in the first few years after fire and continuing in later-successional stands (Chapter 2 this volume, Chapter 3 this volume).

Although several studies have documented vegetation response 1-2 years after fire, only a few have followed post-fire succession over longer periods. Five to ten years after most intense fires, large numbers of tree stems have grown to 1-10 cm dbh (Chapter 3 this volume). Most are sprouts of hardwoods top-killed by fire and seedlings of yellow pines and early successional hardwoods (e.g. black locust) that established in the first few years after fire. By 15-20 years after fire, growth of these saplings led to canopy closure on most sites. While basal area remains substantially lower than that of undisturbed stands, density of canopy trees (>10 cm dbh) in these aggrading stands generally equals or exceeds that of unburned stands by 20 years after fire. Severe fires that remove most or all the canopy will generally produce extremely dense "dog-hair" stands which gradually thin as saplings and small trees compete with each other. Following less severe fires, lateral extension of canopy trees may contribute to canopy closure and the demise of smaller stems.

By about 40 years after fire, basal area and biomass have increased to levels comparable to those in unburned stands (Chapter 1 this volume). In most stands, the aggradation and thinning phase (Borman and Likens 1979, Peet and Christensen 1987) continues for at least 40-60 years after major disturbance. During this phase, establishment of new trees is largely limited to mid-tolerant and shade-tolerant species, particularly white pine, red maple, blackgum, and hemlock (Chapters 2, 4 this volume). Further disturbance to the canopy by beetle outbreak, logging, drought, or ice damage releases this advanced regeneration. In the absence of additional fire, it appears that most xeric stands will develop towards closed-canopy forests largely dominated by relatively shade-tolerant species. In some cases, vigorous growth of shrubs, particularly mountain laurel, may suppress tree regeneration after fire; as a result, the forest canopy may remain open for several decades. Similar suppression of tree growth by mountain laurel may occur following other types of disturbance, including pine beetle outbreak.

Yellow pines become increasingly susceptible to pine beetle outbreaks with age; susceptibility also increases when trees are stressed by drought (White 1987). Droughts may also result in mortality of mature oaks, in part by increasing their susceptibility to native insects and fungi (Hursh and Haasis 1931, Clinton et al. 1993a, SAMAB 1996). While cycles of drought and fire may have played a role in the historic maintenance of pines and oaks on xeric sites, droughts during the period of fire suppression may have the surprising effect of accelerating replacement of yellow pines and oaks by species more characteristic of mesic sites.

Effects of fire on woody shrubs and vines are poorly understood. For example, studies that include pre- and post-burn data for the same plots indicate decreases in *Kalmia latifolia* cover for the first 1-2 years following prescribed fire (Turrill 1998, Elliott et al. 1999). Studies that compare burned areas with unburned reference sites produce more mixed results; some suggest increases in *Kalmia* cover with fire (Groeschl 1992, Chapter 3 this volume), others suggest decreases (Vose et al. 1994), and one suggests that *Kalmia* may increase after a single fire but decrease following repeated, short-interval fires (Arthur et al. 1998). Similarly variable fire effects have been reported for *Vaccinium* and *Gaylussacia* species (Arthur et al. 1998, Chapter 3 this volume). One explanation for these mixed results may be the patchy nature of most shrub distributions, which confounds comparisons between burned and unburned reference sites. Another may be the fact that shrub response is likely determined by two, somewhat independent, effects of fire: canopy opening and duff removal. Fires that cause extensive canopy opening but leave duff layer and shrub rootstocks largely intact may create ideal conditions for vigorous shrub growth. In contrast, fires that burn into the forest floor may kill shrub root stocks, thus limiting post-fire shrub growth. Chapter 3 (this volume) found that post-fire shrub cover was positively correlated with litter depth. A third factor is that total shrub cover may continue to increase through at least the third year after fire (Chapter 3 this volume), beyond the time frame considered by most published reports. A five-year demographic study of the endangered shrub *Hudsonia montana,* which grows on xeric sites around Linville Gorge, indicates that a fire frequency of 6-8 years would produce maximum population growth but that a fire frequency of 12-16 years would be adequate for its restoration and maintenance (Gross et al. 1998).

Studies are consistent in demonstrating an increase in herbaceous cover, richness and/or diversity in the first 1-2 years following fire relative to prefire conditions or unburned reference stands (Groeschl et al. 1992, Arthur et al. 1998, Turrill 1998, Elliott et al. 1999, Chapter 3 this volume). Post-fire increases in species richness occur at spatial scales ranging from 1 m^2 to several hectares (Clinton et al. 1993b, Chapter 3 this volume). Herbaceous richness and cover appear to be positively correlated with extent of canopy opening (Chapter 3 this volume) and may be higher following multiple fires than following a single fire (Arthur et al. 1998). Among the herbaceous species that increase after fire are several composites (*Aster* spp., *Coreopsis major, Erectities hieracifolia, Helianthus* spp., *Solidago odora*), grasses (*Dichanthelium spp., Schizachyrium scoparium, Sorghastrum nutans*), legumes (*Lespediza* spp., *Tephrosia virginiana)*, and the fern *Pteridium aquilinum.* Fire appears to stimulate the growth and flowering of some herbs that are present but declining in pre-fire stands (largely perennials such as *Schizachyrium* and *Solidago odora);* it also appears to promote the germination and establishment of some species not observed in unburned stands but present in the seed bank (including annuals such as *Erechtites* and perennials such as *Lespediza).* Few studies have examined herbaceous responses for more than 2 years after fire. Clinton et al. (1993b) report that 13 years after a site-preparation burn, herbaceous diversity and cover remained higher than that of an unburned reference stand. Chapter 3 (this volume) report changes in herbaceous communities over 18 years of post-fire succession, with dominance shifting from *Dichanthelium*, *Erechtites*, and *Pteridium* in the first three years after fire to *Solidago odora* and *Schizachyrium* in years four through 8. Herbaceous cover and richness peak three to eight years after fire, during which time herbaceous cover is 6-10 times higher and fine scale species richness was about 3 time higher than values in comparable unburned stands. Herbaceous richness and cover drop precipitately following canopy closure ~10-15 years after fire. In xeric stands that had not burned since before 1940, herbaceous richness and cover are very low and have declined over the last two decades.

Effects of reduced fire frequency

Analysis of stand age structures represents the primary tool for reconstructing vegetation changes in xeric pine-oak forests over the past one to two centuries. In some xeric stands, the large majority of trees that established before 1920 are yellow pines (Williams and Johnson 1990); in others, the oldest trees are a mixture of yellow pines and oaks, with an occasional blackgum (Ross et al. 1982, Bratton and Meier 1998, Chapter 2 this volume). Most yellow pine and oak populations show a multi-aged structure, with peaks in recruitment apparently corresponding to historical fires.

Considerable differences in demographic structure have been reported between yellow pine species and between study areas. *Pinus echinata* appears to be the longest lived of the southern Appalachian yellow pines; many individuals that established before 1800 are still extant. Two studies report a peak period of *P. echinata* and *P. rigida* recruitment between about 1850 and 1900 (Bratton and Meier 1998, Chapter 2 this volume); a third reports a peak in *P. rigida* recruitment between 1915 and 1930 (Ross et al. 1982). One *P. pungens* population in Virginia shows a peak of establishment between 1850 and 1870, and several show large peaks between 1920 and 1950 (Williams and Johnson 1990, Sutherland et al. 1995). In the western Smokies, the large majority of extant *Pinus virginiana* established between 1920 and 1945, and older trees are rare (Chapter 2 this volume).

In the 1920s and 1930s, widespread burning, grazing, logging and chestnut blight gave way to fire suppression and public land management, and extensive establishment of yellow pines and oaks occurred on many xeric sites (Ross et al. 1982, Williams and Johnson 1990, Sutherland et al. 1995, Chapter 1 this volume). This period also corresponds to the establishment of several shade-tolerant and/or fire sensitive species such as red maple, sourwood, hemlock, and white pine on many xeric sites. Until the mid 1940s, a relatively open canopy and limited litter accumulation apparently provided conditions favorable for establishment and rapid growth of yellow pines. On most sites, little yellow pine establishment has occurred since about 1950, and yellow pines are rare or absent in the sapling stratum (Barden 1976, Ross et al. 1982, Williams and Johnson 1990, Sutherland et al. 1995, Bratton and Meier 1998, Chapter 2 this volume).

Although several researchers have suggested that the exclusion of fire would lead to an increase in oak dominance in xeric forests (Whittaker 1956, Harmon 1980, White 1987, Williams and Johnson 1990, Williams 1998), age structure analyses indicate that few oaks that established after 1950 have recruited into the canopy (Ross et al. 1982, Bratton and Meier 1998, Chapter 2 this volume). Yellow pine and oak populations are made up largely of mature canopy trees > 60 years old and small suppressed individuals with low vigor and little ability to respond to subsequent release (Ross et al. 1982, Williams and Johnson 1990). In contrast, white pine, red maple, hemlock, and sourwood have continued to establish and grow into the canopy (Chapter 2 this volume).

Long-term plot data support the trends inferred from age-structure studies and provide additional evidence of structural and compositional change in xeric forests. A survey conducted just after the establishment of Great Smoky Mountains National Park in 1934 indicates that xeric sites supported a mosaic of open, early-successional areas and closed-canopy forests with median basal areas on the order of 12-15 m^2/ha (Chapter 1 this volume, Chapter 4 this volume). Yellow pines and oaks made up the majority of canopy trees, and other species occurred at low densities. In addition, yellow pine and oak saplings were widespread in the understory. Between the 1930s and 1970s, these forests developed into closed-canopy forests with median basal areas of 25-30 m^2/ha. This increase in basal area coincided with doubling of aboveground biomass. Densities of canopy yellow pines and oaks increased dramatically, as did densities of red maple, white pine, and hemlock, species once rare on xeric sites. Canopy richness increased as increasingly dense canopies were invaded by species formerly excluded by fire. By the 1970s, the sapling stratum was dominated by shade-tolerant trees.

Following rapid initial increases, overall canopy density, basal area, biomass, and richness on fire-suppressed sites remained nearly constant between the 1970s and 1990s. During this period, the relative density of shade-tolerant, fire-sensitive species such as red maple, white pine, and hemlock continued to increase at the expense of yellow pines and oaks, which are currently declining in the canopy and very scarce in the sapling layer. Similar changes have been reported in xeric pine-oak forests at Coweeta Hydrological Laboratory, where a severe drought in the mid 1980s and outbreaks of the southern pine beetle have contributed to extensive losses of yellow pines and oaks in the past two decades (Smith 1991, Clinton et al. 1993a).

On a small proportion of ultra-xeric sites with very thin soils, *Pinus* populations may persist indefinitely in the absence of fire (Whittaker 1956, Racine 1966, Zobel 1969). Barden (1977, 1988) describes an apparently self-maintaining population of *Pinus pungens* growing in pockets of soil around the edges of a granitic dome near Brevard, NC. Newell and Peet (1998) report that on the rocky bluffs surrounding Linville Gorge, NC, populations of *P. pungens* and *P. rigida* appear to be self- maintaining only on the most exposed sites, representing less than 25% of sampled plots in the xeric pine-oak forest class. No stands with self-maintaining yellow pine populations were sampled by Newell et al. (1997) the Joyce Kilmer-Slickrock Wilderness or in western Great Smoky Mountains National Park (Chapters 1, 2 this volume). The multi-sized, multi-aged structures of several pine stands once thought to represent such self-maintaining populations now appear to be the products of past fires (Barden 1976, Chapter 2 this volume). The distribution of self-maintaining yellow pine populations deserve further study, but it now appears that yellow pines can persist without fire over only a small portion of their present and historic range (Waldrop and Brose 1999).

Southern Appalachian pine-oak forests: historical dynamics and future prospects

The structure, composition, and dynamics of xeric pine-oak forests prior to widespread anthropogenic burning remain poorly understood. However, life-history characteristics of several species, including the endemics *Pinus pungens* and *Hudsonia montana,* clearly indicate evolution in the context of fire. Modern observations suggest that lightning fires are too infrequent and too low in intensity to maintain xeric pines and oaks on many of the sites they now occupy. Inferences about the early Holocene dynamics of xeric forests are complicated by possible changes in temperature, lightning and rainfall regimes

(White 1987). It is possible that these species evolved during a period when, due to climatic differences, the frequency of lightning fires was substantially higher than today. Another non-exclusive possibility is that xeric species were largely restricted to rocky, ultra-xeric sites where they could persist indefinitely in the absence of fire (e.g. Barden 1977, Williams 1998) and to the most fire-prone sites in the landscape. A third possibility is that severe regional droughts and pine beetle outbreaks occurring at intervals of several decades may have led to large, intense lightning fires that allowed episodic establishment of yellow pines on a wider range of xeric and subxeric sites (White 1987).

By about 4000 years ago, native Americans represented an important source of ignitions (Delcourt and Delcourt 1997). As during later periods, fire frequencies would have varied from place to place with population density, topographic position, and landscape structure and through time with changes in climate, population, and cultural practices. A mean fire rotation of 10-20 years may represent a reasonable "best guess" for most xeric pine-oak stands in the southern Appalachians prior to European settlement. In favored hunting grounds and areas adjacent to population centers, fires may have been set as frequently as once or twice a year, as they were in parts of southern New England (Cronon 1983).

Variations in fire frequency, season, fuel load, and weather would have resulted in considerable variation in forest composition and structure. Most fires were probably low-intensity surface fires occurring during the spring. Although these fires would have killed few canopy trees and removed little duff, they would have thinned the understory and culled small stems of fire-sensitive species. The principal effects of low-intensity fire may thus have been to limit recruitment into the canopy and promote the dominance yellow pines and oaks, species whose high rates of radial growth and bark production allow them to attain fire resistance rapidly (Harmon 1984). Variation in intervals between fires would have occasionally permitted fire-sensitive species to grow to fire-resistant size (Harmon 1982, 1984). Less frequent, higher-intensity fires would have occurred during periods of infrequent drought and in areas of heavy fuel accumulation. Intense summer and fall fires that burned off substantial litter may have led to extensive recruitment of yellow pines. Fires that killed large numbers of canopy trees without extensive litter removal may have led to stands dominated by oaks or to suppression of trees by vigorous growth of shrubs such as *Kalmia*. As a result of the mixed regime of frequent, low-intensity fires and infrequent high-intensity fires, much of the landscape would have been maintained as open-canopy, low-basal area woodland in which cover of grasses, composites, legumes, and other herbaceous species was high (Chapter 3 this volume).

The arrival of European settlers in the early 19th century appears to have corresponded with an additional increase in fire frequency (Lynch and Clark 1996, Delcourt and Delcourt 1997). Increases in fire frequency would have resulted in further decreases in basal area and biomass and increases in the relative abundance of yellow pines. Browsing by cattle and other livestock may have also limited tree regeneration and favored dominance of relatively unpalatable yellow pines (Ayres and Ashe 1905, Pyle 1988). The occurrence of fire and other anthropogenic disturbances probably peaked in the first few decades of the twentieth century.

Beginning about 1920, widespread land abandonment, the incorporation of land into national parks and forests, and active fire suppression resulted in a dramatic drop in fire frequency. As a result, most xeric stands have developed from open-canopy woodlands dominated by yellow pines and oaks to closed canopy forests with an increasing component of fire-sensitive, shade-tolerant species once rare on xeric sites and to corresponding declines in herbaceous cover and richness. On most sites, yellow pines and oaks have regenerated poorly since the 1940s. Droughts and pine beetle outbreaks in the 1970s and 1980s have led to extensive mortality of canopy trees (Smith 1991, Clinton et al. 1993a); sapling numbers have also continued to decline (Chapter 1 this volume). Additional droughts, pine beetle outbreaks, ice storms, and other disturbances may lead to rapid losses of remaining yellow pines and oaks from the canopy in the next few decades and their replacement by species such as white pine, red maple, and blackgum (Kuykendall 1978).

The presence of apparently fire-adapted endemics species such as *Pinus pungens* and *Hudsonia montana* on southern Appalachian xeric sites remains enigmatic. For at least the last 4000 years, humans appear to have been the major source of ignitions in the southern Appalachians. It appears likely that anthropogenic burning increased the relative abundance of yellow pines and oaks and allow these species to spread across a wider range of site types than they had previously occupied (Williams 1998). Two of the main effects of fire, opening the forest canopy and increasing herbaceous cover, were central the subsistence strategy of both Native American farmer/hunters and European farmer/pastoralists. Southern Appalachian forests may represent an example of a "cultural landscape" in which anthropogenic disturbance created and maintained open vegetation structure and increased the richness and cover of herbaceous species (e.g. Dunwiddie 1989).

In this context, 20th century fire suppression may be viewed not as the disruption of a natural fire regime but as the replacement of one human-controlled management system with another. The recent reintroduction of fire into these communities represents yet another anthropogenic disturbance regime, one whose goal is to increase populations of fire-adapted native species, restore pre-European forest conditions, and maintain or increase biological diversity on these sites.

The historic fire regime, characterized by variability in fire interval, ignition source, weather, and fuel loads, probably produced a wide range of stand structure and composition. Recent data on the relationships between fire characteristics and responses should allow managers to tailor fire prescriptions to achieve specific management goals. For example, a hot summer or fall fire that both opens that canopy and burns well into the duff may produce best regeneration of yellow pines, while a regime of winter or spring surface fires at relatively short intervals may favor chestnut oaks, and a winter or spring fire that kills much of the canopy but burns off minimal duff may produce greatest response from shrubs and perennial herbs. A long-term regime that includes a stochastic mix of low-intensity spring surface fires every 10-20 years with higher-intensity summer/fall fires occurring about once a century probably comes closest to the historical fire regime of the past 4000 years. Under such a regime, much of the landscape would be maintained as relatively open-canopy woodland in which yellow pines and oaks regenerate successfully and herbaceous richness and cover are high.

Knowledge of the fire ecology of southern Appalachians xeric forests has grown considerably in the past decade. However, prescribed fires continue to yield surprising and often conflicting results. We should continue to treat the reintroduction of fire into Appalachian forests as an experiment, evaluating the effects of different burn seasons, intervals, and intensities. This experimental approach, together with continued research into the historical development of these communities and the evolution of their component species, should continue to yield insights into the roles of historic and pre-historic fire in shaping the vegetation in eastern North America.

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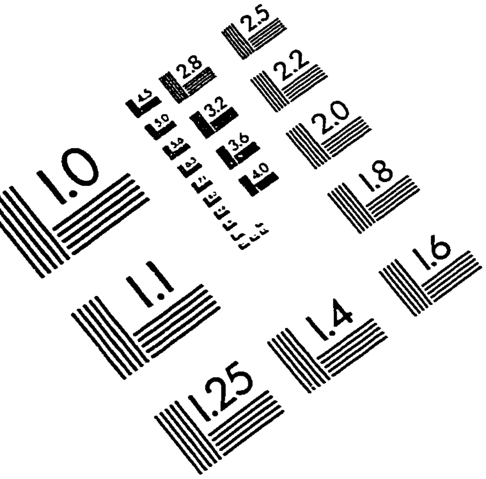
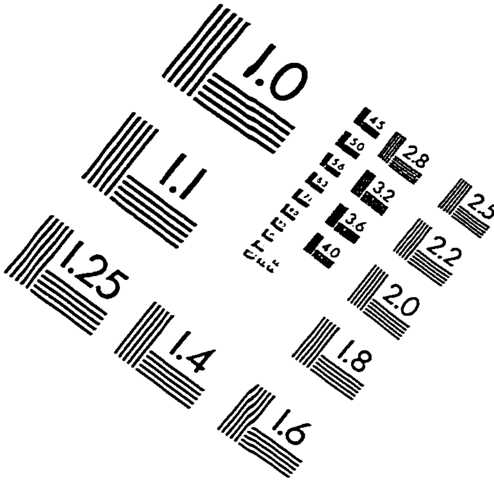
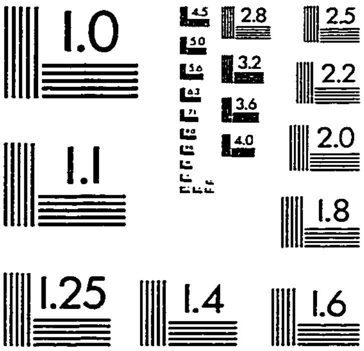
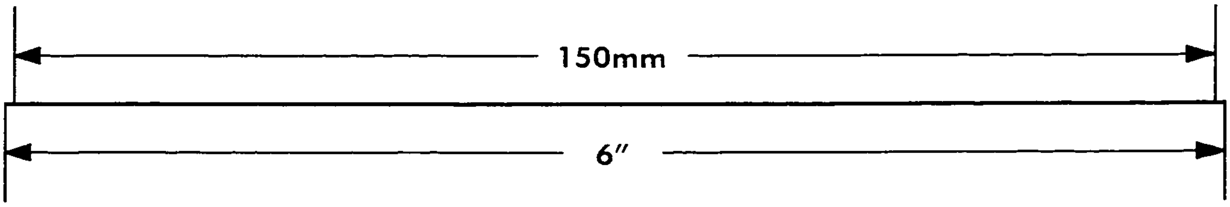
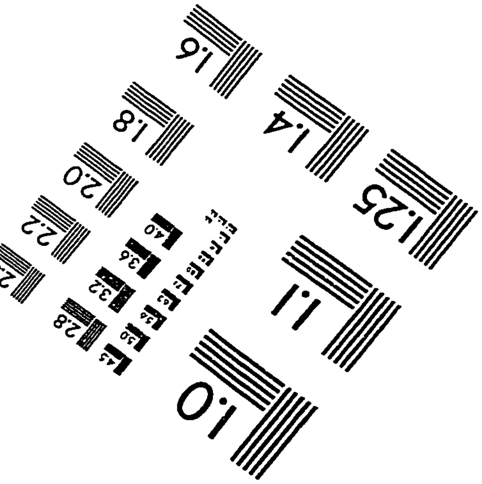
IMAGE EVALUATION TEST TARGET (QA-3)











APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989