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Changes in Xeric Forests in Western Great Smoky Mountains National Park, 1936–1995

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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.

INTRODUCTION

In the southern Appalachians, xeric slopes and ridges below 1,000 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

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* Nomenclature follows Kartesz (1994).

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. We 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 dominates 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).

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 1,425 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 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 8,000 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 opera-

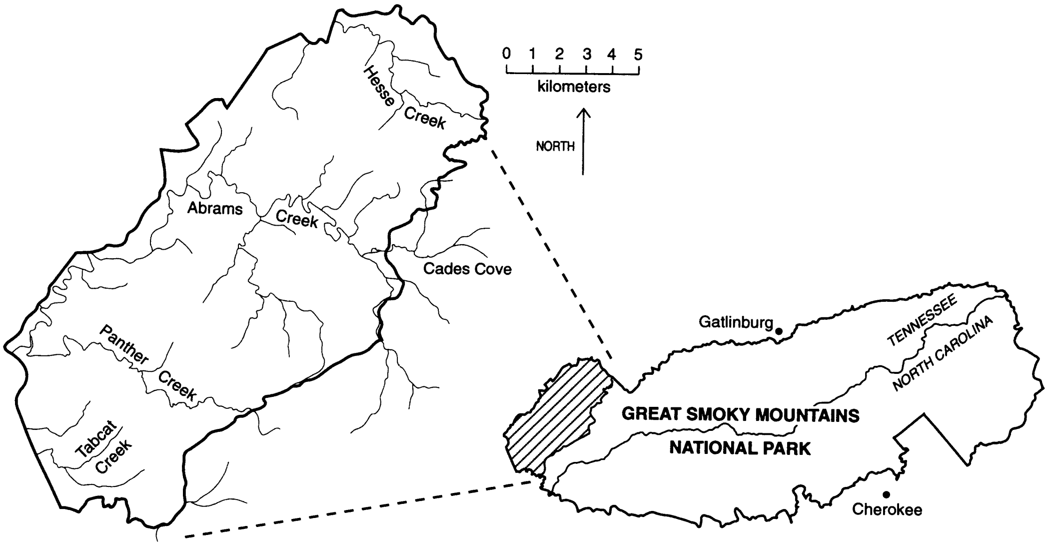

Figure 1. Location of study area in western Great Smoky Mountains National Park, Tennessee.

tions 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, unpubl. 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. We 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, we attempted to transcribe plots to locations that 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, with White 1998) 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 $\geq$1 cm dbh and for all standing dead trees $\geq$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, we located and sampled 72 of these plots following original methods.

Analyses

We 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 $\geq$10 cm were grouped into the size classes listed above. Because results presented in this paper represent only stems $\geq$10 cm dbh, we 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 $\geq$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; we 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 that 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 that had not burned since before 1940 were considered "fire-suppressed." Three Uplands plots that burned in the 1950s and three Miller plots and two Uplands plots that 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

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

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. We 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, we 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). Yellow pines, mostly *P. rigida* and *P. virginiana,* comprised 55% of canopy trees (Table 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 3).

Table 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

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 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 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 5). Oaks made up 40% of the canopy in the 1970s but only 27% in 1995; absolute densities of

Table 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 that 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		Fire-suppressed
	1930s	Pre	Post	Pre	Post	
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

four of six oak species declined. While factorial ANOVA revealed no statistically significant changes in total oak density, decreases (ranging from 8 to 70%) 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). 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.*

Table 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 × TIME (p = 0.0001)
Yellow pines	38 ± 14	420 ± 279	283 ± 202	363 ± 371	205 ± 195	186 ± 208	GROUP × 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)	2.11 ± 1.49^{a}	15.00 ± 3.56^{a}	23.10 ± 3.69^{b}	24.17 ± 6.27^{b}	25.90 ± 7.00^{b}	25.93 ± 5.35^{b}	GROUP (p = 0.0006) TIME (p = 0.005) GROUP × TIME (p = 0.0002)
Canopy richness (species/0.08 ha)	2.75 ± 1.26^{a}	6.25 ± 3.69	6.33 ± 1.53^{b}	6.33 ± 2.08	9.00 ± 2.00^{b}	8.71 ± 2.06	GROUP (p = 0.01) GROUP × TIME (p = 0.03)
n	4		3		7		

Table 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

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 2,800%). 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

We 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), we 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, unpubl. data). We found no significant environmental differences between any of the groups we compared. However, we limited our 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. We acknowledge that some of the observed differences between the Miller and Uplands plots may reflect differences in soil conditions. We 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, our inability to locate all the original Uplands plots may have subtly biased our results. Mean values of structural and compositional variables for the subset of Uplands plots that we 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 we found little recent change in yellow pine densities on the fire-suppressed plots we resampled, at least two plots we searched for but could not locate were in areas of heavy pine beetle infestation. It thus seems likely that we have underestimated losses of yellow pines from the canopy.

To make the Uplands and Miller data sets compatible, we 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 our 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, unpubl. data).

In spite of these limitations and potential biases, our 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, p. 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 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 probably contributed to high levels of canopy oak mortality (Clinton et al. 1993).

Regeneration failure appears to be another factor in declining oak densities. Our 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 we sampled, canopy densities of yellow pines have decreased only slightly over the past two decades. However, it seems likely that, for reasons discussed above, we 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, unpubl. 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* that are abundant in the understory. Periods of elevated pine beetle activity such as those that occurred 1954–58 and 1967–77 (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, we 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, we support the use of prescribed fire to restore and maintain patches of open forest dominated by yellow pines and oaks. However, our 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.

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