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Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites

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Abstract. We document post-fire succession on xeric sites in the southern Appalachian Mountains, USA and assess effects of 20th century reduction in fire frequency on vegetation structure and composition. Successional studies over 18 yr on permanent plots that had burned in 1976-1977 indicate that tree mortality and vegetation response varied with fuel load and fire season. In the first three years after fire, hardwood sprouts dominated tree regeneration. On sites where summer and autumn fires reduced litter depth to less than 1 cm, densities of shade-intolerant *Pinus* seedlings increased steadily over this period. 4 to 8 yr after fire, large numbers of newly established seedlings and sprouts 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. On similar sites that had not burned in more than 50 yr, regeneration of shade-intolerant *Pinus* spp. and mean cover and richness of herbs were considerably lower than those observed on recently burned plots. Reconstructions of landscape conditions based on observed post-fire succession and 20th century changes in fire regime suggest that reductions in fire frequency circa 1940 led to substantial changes in forest structure and decreases in cover and richness of herbaceous species.

Keywords: Fire regime; Litter; *Pinus* subgenus *Pinus;* Species richness; Xeric forest.

Abbreviation: GSMNP = Great Smoky Mountains National Park

Nomenclature: Kartesz (1994).

Introduction

In many areas of North America, the historical regime of frequent surface fires ignited by lightning and humans maintained open canopy woodlands dominated by fire-resistant trees (Ware et al. 1993; Covington & Moore 1994; Sparks et al. 1998). Understories in these communities often included a vigorous grass component and possessed high species richness, particularly at fine spatial scales (Peet et al. 1983). Reductions in fire frequency resulting from active fire suppression and changing land use patterns have led to substantial decreases in fire frequency, increases in stand density and declines in understorey richness and productivity (e.g. Ware et al. 1993; Covington & Moore 1994). In some ecosystems, 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. Covington & Moore 1994); in others, 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), Tennessee, 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 with a mean rotation of 12.7 yr (Harmon 1982); the majority of fires were probably ignited by humans (Barden & Woods 1973; Bratton & Meier 1998). The removal of human settlements prior to establishment of the park in 1934 and the onset of effective fire suppression circa 1940 increased mean fire rotation to over 500 yr (Harmon 1982). Between the 1930s and 1990s, mean density and basal area of canopy trees doubled, and light-demanding, fire-resistant taxa such as *Pinus* subgenus *Pinus*[1] and *Quercus* declined, while more shade-tolerant species such as *Acer rubrum* increased (Harrod et al. 1998; Harrod & White 1999). Similar trends have been reported throughout the southern Appalachian Mountains (e.g. Sutherland et al. 1995; Bratton & Meier 1998; Williams 1998). Although several studies have addressed effects of changing fire regimes on canopy structure and composition and documented short-term understorey responses to fire in southern Appalachian forests (Elliott et al. 1999; Waldrop & Brose 1999),

[1]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* (Little & Critchfield 1969; Harmon 1984; Burns & Honkala 1990). Since no confusion can arise in this paper, we will write *Pinus* hereafter.

none have documented longer-term effects of changing fire regimes on understorey vegetation. In the present study, we describe successional changes on xeric sites in western GSMNP that burned in 1976-1977 and compare vegetation in these burned stands to that of similar sites that have not burned since before 1940. We then use observations on recent post-fire succession in conjunction with data on historic fire regimes to assess the effects of reduced fire frequency on vegetation structure and diversity.

Methods

Study area

The westernmost portion of GSMNP is a region of relatively low (260 - 940 m a.s.l.) 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; soils, mostly ultisols and inceptisols, are acidic and infertile. The mean annual temperature in Gatlinburg, ca. 40 km NE of the study area and at 440 m a.s.l., is 12.9 °C; mean annual precipitation is 1425 mm. Vegetation patterns vary along a topographic moisture gradient, with *Pinus* subg. *Pinus* and *Quercus* historically dominating xeric upper slopes and ridges (Whittaker 1956; Harrod et al. 1998). 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 (1982), Harmon et al. (1983), Pyle (1988) and Harrod et al. (1998).

Fire effects and post-fire succession

Between 1977 and 1979, staff of the National Park Service Uplands Field Research Laboratory sampled and permanently marked 108 plots (20 m × 50 m) in western GSMNP. 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 plots were subdivided into five subplots (10 m × 20 m) within which field crews recorded species and diameter at 1.37 m (DBH) for all live and standing dead woody stems ≥ 0.5 cm DBH. On recently burned plots, trees that died prior to the fire were distinguished from those that were killed by the fire, allowing approximate reconstruction of the pre-fire stand (the wood of dead trees chars and burns in a fire, whereas the moist wood of live trees does not). 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 quadrats (2 m × 2 m) distributed in a diagonal pattern within each subplot, yielding a total of 25 quadrats per plot; cover of herbaceous species was estimated in 1 m × 1 m quadrats located in the lower right corner of each seedling/shrub quadrat. Evidence of past disturbance, including fire, logging and % canopy pines killed by recent pine beetle (*Dendroctonus frontalis*) activity, was recorded. Years of past fires were determined, where possible, by sectioning fire scars. On sites that burned in 1976-1977, mean depth of the duff layer was recorded and % canopy cover was measured using a spherical densiometer.

We identified xeric plots in this data set using a topographic moisture index (derived from a digital elevation model) that combines relative slope position,

Table 1. Characteristics of permanent plots established in 1977-1978 used in this study.

Plot #	Elevation (m)	Slope position (0-100)	Slope (°)	Aspect (°)	Topogr. moisture index (0-60)	Pine beetle damage in mid 1970s	Known fires	% basal area killed, 1970s fires	Postfire litter depth (cm)	Canopy cover (%)
Plots that burned in 1976-1977										
10	599	88	9	139	12	Moderate	Summer 1977, 1933	25	0.7	44
16	720	96	11	152	6	Heavy	Autumn 1976, 1933, 1909, 1905	84	0.1	18
18	734	97	11	126	7		Autumn 1976, 1942, 1933, 1909	5	0.9	67
37	683	96	15	143	7	Light	Winter 1976, 1933	12	3.0	63
38	664	87	20	145	9	Heavy	Winter 1976, 1933	93	2.7	11
39	681	86	28	166	10	Heavy	Autumn 1976, 1933, 1909, 1905	72	0.8	25
40	706	96	18	234	7		Autumn 1976, 1933, 1909, 1905	4	2.7	86
41	707	85	29	134	10	Light	Autumn 1976, 1942, 1933, 1909	13	0.6	50
42	682	87	26	117	15	Heavy	Autumn 1976, 1942, 1933, 1909	57	0.5	53
94	612	89	7	225	10		Summer 1977, 1933	85	0.8	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			

incident solar radiation and local curvature; for details see Harrod et al. (1998). Xeric sites identified using this index include 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 (Table 1). 10 plots were established in 1977 or 1978 in areas that burned in 1976 or 1977. Fire scar chronologies indicate that prior to the fires from the 1970s, these plots last burned in 1933 or 1942. Nine of these, including six that burned in the autumn of 1976, two that burned in winter 1976 and one that burned in summer 1977, were sampled post-fire during the 1977 growing season; a tenth plot was established in 1978 on a site that burned in the summer 1977 fire. In all 10 plots herbs and woody plants < 0.5 cm DBH were sampled in 1978, 1979, 1980 and 1984, 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 10 plots. No counts of stems < 0.5 cm DBH were made in 1995. We also examined plots on topographically similar sites that had not burned since before 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.

We 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. Densities of canopy trees observed over the period 1977-1995 are compared with previously published values for xeric plots in western GSMNP sampled between 1935 and 1937 (Harrod et al. 1998). Species richness of woody shrubs, vines and herbs was documented for individual quadrats (4 m^2 for shrubs and vines, 1 m^2 for herbs) and for all 25 quadrats within a plot combined. To facilitate temporal comparisons, vegetation descriptions presented below include only the six burned and seven unburned plots sampled through 1995. To examine effects of site and fire characteristics on vegetation response, we generated a matrix of Pearson correlation coefficients for the following parameters:

Elevation
Topographic moisture index
% recent pine beetle mortality
% basal area killed by fire
Post-fire % canopy opening (100-% canopy cover) and litter depth
Season of burn (coded as summer = 1, autumn = 2, winter = 3)
Density of *Pinus* seedlings in 1980
Density of *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 10 plots that burned in 1976-1977 were used in the correlation analysis.

Results

Tree mortality and regeneration

Fire effects varied considerably between plots, with basal area kill ranging from 4 to 93%, post-fire litter depth from less than 1 to 3 cm and post-fire canopy cover from 11 to 86%. Percent basal area killed showed a highly significant positive correlation with post-fire canopy opening, and both measures showed significant positive correlations with pre-fire pine beetle damage (Table 2). Post-fire litter depth was not significantly correlated with measures of canopy damage. However, litter depth did show a significant correlation with burn season, tending to be lower following summer burns and higher following winter burns.

Mean post-fire densities of live stems >10 cm DBH

Table 2. Matrix of Pearson correlation coefficients for site and fire characteristics and measures of vegetation response for xeric plots in western GSMNP that burned in 1976-1977. Sample size was 10 plots for all correlations except maximum shrub cover (n = 8). Bold coefficients were significantly different from zero (p < 0.05). *Pinus* = *Pinus* subgenus *Pinus*.

	Elevation	Topographic Moisture Index	Burn season	Pre-fire pine beetle damage	% basal area killed	Post-fire canopy opening	Post-fire litter depth	*Pinus* seedlings 1980	*Pinus* saplings 1984	Maximum shrub cover 1977-1984
Topographic Moisture Index	– 0.509									
Burn season	0.516	– 0.364								
Pre–fire pine beetle damage	0.042	0.398	0.216							
% basal area killed	– 0.310	0.174	– 0.028	**0.664**						
Post–fire canopy opening	– 0.358	0.389	– 0.066	**0.710**	**0.935**					
Post–fire litter depth	0.031	– 0.384	**0.651**	– 0.276	– 0.246	– 0.416				
Density *Pinus* seedlings 1980	0.077	**0.710**	– 0.312	0.358	– 0.115	0.130	**– 0.663**			
Density *Pinus* saplings 1984	0.193	– 0.029	– 0.133	0.594	0.526	0.529	– 0.595	0.252		
Maximum shrub cover, 1977–1984	0.176	– 0.500	**0.801**	0.068	0.281	0.167	**0.763**	– 0.626	– 0.522	
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

Table 3. Mean densities (stems/ha) of canopy trees (> 10 cm DBH; first number) and saplings (0.5 - 10 cm DBH; second number) in xeric permanent plots that burned in 1976-1977 and in topographically similar plots that have not burned since before 1940.

	Burned plots				Unburned controls	
Species	Pre-fire	1977-1978	1984	1995	1977-1978	1995
Acer rubrum	7/ 60	2/ 10	2/ 222	5/ 690	41/443	76/321
Carya spp.	—/ 12	—/ 2	—/ 2	—/ 5	19/ 62	10/ 11
Castanea dentata	—/ 5	—/ —	—/ 3	—/ 7	—/ 7	—/ —
Cornus florida	—/ —	—/ —	—/ —	—/ 3	—/120	—/101
Diospyros virginiana	—/ —	—/ —	—/ 17	—/ 27	—/ —	—/ 4
Nyssa sylvatica	10/890	3/298	10/ 680	27/ 843	13/569	44/394
Oxydendrum arboreum	5/ 95	2/ 30	2/ 183	2/ 490	14/ 84	17/ 46
Pinus echinata	13/ 13	5/ 3	10/ 3	3/ —	6/ 7	1/ —
Pinus pungens	5/ 8	3/ 3	2/ 47	10/ 95	1/ 4	1/ —
Pinus rigida	133/273	82/ 58	72/ 220	88/1078	71/113	60/ 21
Pinus strobus	5/ 28	—/ 2	—/ 7	2/ 145	49/169	87/326
Pinus virginiana	137/785	68/ 77	37/1388	328/5568	131/260	137/160
Quercus alba	—/ 2	—/ 2	—/ 10	—/ 15	3/ 26	7/ 4
Quercus coccinea	132/140	95/ 55	95/ 205	85/ 303	54/ 46	46/ 30
Quercus marilandica	20/103	8/ 8	5/ 97	5/ 140	19/ 34	—/ 3
Quercus prinus	15/ 17	13/ 13	13/ 32	10/ 37	113/ 47	106/ 17
Quercus velutina	8/ 62	7/ 15	8/ 42	8/ 75	40/ 46	13/ 10
Robinia pseudacacia	—/ 2	—/ —	2/ 80	7/ 33	—/ —	—/ —
Sassafras albidum	—/ 72	—/ 2	—/ 282	—/ 722	1/ 87	1/ 67
Tsuga canadensis	—/ 2	—/ —	—/ —	—/ 8	—/ 77	24/144
Other species	—/ 3	—/ 3	—/ 7	—/ 18	3/ 24	2/ 40
Total	490/2572	288/581	258/3527	582/10302	578/2225	632/1699

were similar to those of xeric plots sampled in the 1930s (Fig. 1). Mortality patterns varied with species and fire severity; in all plots, mortality was higher for smaller stems (Table 3). On plots in which fires killed ≥ 25% of basal area, 30 to 85% of canopy trees (stems > 10 cm DBH) and 87% to 99% of saplings (stems ≤ 10 cm DBH) were killed. No species-specific patterns of canopy disturbance were evident in these severe fires; all species experienced relatively high mortality, and species dominant in the pre-fire canopy remained dominant following fire. On plots in which fires killed < 25% of basal area, 0 to 7% of canopy trees and 29% to 60% of saplings were killed. At sizes between 3 and 10 cm DBH, species varied considerably in their fire resistance, with thick-barked species such as *Pinus rigida*, *Quercus prinus* and *Nyssa sylvatica* surviving better than thin-barked species such as *Acer rubrum* (Harmon 1984).

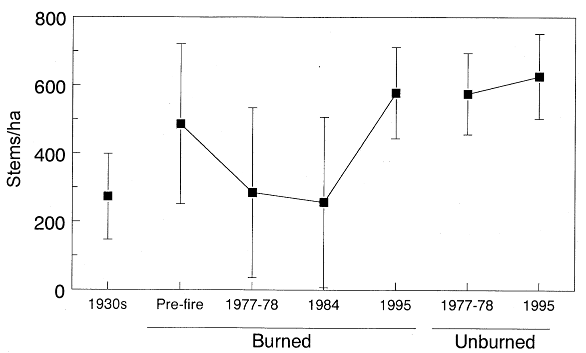

Fig. 1. Densities (stems/ha) of trees > 10 cm DBH in three sets of xeric plots: non-permanent sampled in the 1930s, permanent plots that burned in 1976-1977, and topographically similar plots that have not burned since before 1940. Points represent means; bars represent one standard deviation.

Tree regeneration following fire included both new seedlings and sprouts of individuals whose above-ground parts were damaged or killed by fire (Table 4). 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).

Four growing seasons after fire, densities of *Pinus* seedlings showed significant negative correlations with post-fire litter depth but were uncorrelated with either canopy opening or basal area killed. 8 yr after fire, many stems that established post-fire had grown to between 0.5 cm and 10 cm DBH, and sapling densities on the most severely burned plots had reached levels comparable to those in pre-fire stands. Densities of *Pinus* saplings showed marginally significant correlations with pre-fire pine beetle damage (p = 0.07) and post-fire litter depth (p = 0.07). On most plots, canopy density and basal area remained constant or increased modestly relative to year 1. On one plot (Plot 10), basal area and canopy density declined considerably, apparently as a result of delayed mortality of large *Pinus* and *Quercus* individuals.

In 1995, ca. 18 yr after fire, densities of canopy trees on most burned plots had increased to levels comparable to those of pre-fire stands. Three plots (10, 39 and 94) on which fires had reduced litter depth to less than 1 cm and killed ≥ 25% of basal area had developed into extremely dense stands dominated by small *P. virginiana*. While no

Table 4. Mean densities (in stems/ha) of seedlings and sprouts < 0.5 cm DBH of tree species 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
	1977	1978	1979	1980	1984	1977-78
Acer rubrum	520	1400	1117	2033	3017	1857
Carya spp.	160	233	67	100	67	314
Castanea dentata	440	233	67	50	67	129
Cornus florida					33	2529
Diospyros virginiana		533	300	617	567	57
Nyssa sylvatica	16600	15533	7367	8950	4750	1614
Oxydendrum arboreum	2480	1600	2017	2500	6017	400
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
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 pseudacacia	40	167	100	100	83	200
Sassafras albidum	22640	30033	16533	15017	10483	3543
Tsuga canadensis				67	83	114
Other	80	67	183	200	217	257
Total	54240	61967	35200	44100	39867	18172

tallies of stems < 0.5 cm DBH were made in year 18, mean cover of seedlings of the most important tree species declined sharply relative to year 8.

Canopy and sapling strata of unburned plots sampled in 1977-1978 generally resembled those of burned plots prior to fire, but had higher basal areas reflecting less extensive pine beetle damage. Mean total density of tree seedlings and sprouts < 0.5 cm DBH was substantially lower than values observed on recently burned plots in the first eight years after fire, and seedlings and saplings of *P. virginiana* and *P. rigida* were less abundant on unburned than on burned sites. While total canopy density and basal area on some unburned plots changed considerably between 1977-1978 and 1995, mean values remained relatively constant. Densities of saplings and small trees decreased in most plots, and densities of trees in most size classes >15 cm remained stable or increased. Major compositional trends on unburned plots included increases in the abundance of *Acer rubrum* and *Pinus strobus* in the canopy and declines of *Quercus* species, particularly in the sapling stratum.

Woody shrubs and vines

Shrub and vine cover re-established rapidly following fire, increasing from 14% the first year to 23% the second; it peaked at 36% in year 8 before declining to 24% in year 18 (Table 5). Maximum shrub cover showed a significant positive correlation with post-fire litter depth and a significant correlation with season (highest for winter burns) but was uncorrelated with percent basal area killed or canopy opening. Mean richness of shrub and woody vine species per 4 m^2 quadrat increased from 2.7 in year 1 to 3.8 in year 18; species per plot (e.g. per 25 4-m^2 quadrats) increased from 6.0 to 10.3 over the same period. The dominant woody shrubs were members of the *Ericaceae*, particularly *Gaylussacia baccata*, *Vaccinium pallidum* and *Kalmia latifolia.* Dominant woody vines were *Smilax glauca* and *S. rotundifolia.*

On sites that had not burned since 1940, mean shrub and vine cover in 1977-1978 was 45%, a value higher than that observed on burned plots in any year. In 1995, mean cover had declined to 19%. In both 1977-1978 and 1995, quadrat and plot-scale richness were within the range observed in 1 - 18 yr-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. Cover of all major woody shrub and vine species showed marked decreases over the period 1977-1978 to 1995.

Herbaceous plants

Mean herbaceous cover increased from 3% during the first growing season after fire to 15% in year 2 and remained between 21 and 24% in years 3, 4 and 8 (Fig. 2). Maximum herb cover showed a highly significant posi-

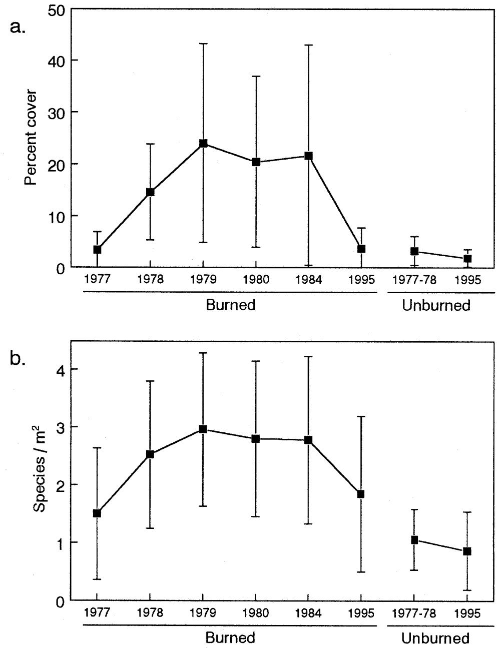

Fig. 2. Percent cover and fine-scale richness (species/m^2) of herbaceous plants in xeric permanent plots that burned in 1976-1977 and in topographically similar plots that have not burned since before 1940. Points represent means; bars represent one standard deviation.

tive correlation with basal area killed and a highly significant positive correlation with canopy opening but was uncorrelated with post-fire litter depth. 18 yr after fire, mean herbaceous cover had dropped to 4%. Trends in fine-scale herb richness generally mirror those in cover.

Important herbaceous species on burned plots include (Table 5):

Asteraceae: *Aster surculosus, Coreopsis major, Erechtites hieracifolia, Gnaphalium obtusifolium* and *Solidago odora*;
Fabaceae: *Lespedeza hirta, L. repens, Tephrosia virginiana*;
Poaceae: *Dichanthelium* spp., *Schizachyrium scoparium* and *Sorghastrum nutans*;
others: *Lechea racemosa* and *Pteridium aquilinum.*

With few exceptions, the herbaceous species important in the first 18 yr of post-fire succession were observed in plots by the first or second year after fire. Dominance of the herbaceous layer shifted from *Pteridium* in the first growing season after fire to *Erechtites* in years two and three to *Schizachyrium* in years 4 to 8. By year 18, *Schizachyrium* cover dropped to only 5% of its year-8 value and *Pteridium* again dominated the relatively sparse herbaceous layer.

On sites that had not burned since before 1940, herbaceous cover and richness were much lower than those observed on burned plots in the first decade after fire. The only herbaceous species with mean cover exceeding 1% was *Galax aphylla* and several herb species abundant in burned plots were absent from sample quadrats in unburned plots.

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 (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). 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.

Our stand-based successional data can be combined with data on fire history to yield fresh insights into the effects of changing fire regimes on southern Appalachian xeric forests. The distribution of landscape states under a given fire regime can be estimated using the negative exponential model (Johnson & Van Wagner 1985). Under the early 20th century fire rotation of 12.7 yr (Harmon 1982), more than 50% of xeric stands would have time-since-fire dates of eight years or less, ca. 25% of the landscape would be occupied by stands 8 - 18 yr old and only 2% of stands would escape fire for more than 50 yr. Under the late 20th century fire rotation of more than 500 yr, less than 2% of xeric sites would have time-since-fire dates of eight years or less and more than 90% of sites would be occupied by stands with time-since-fire dates of more than 50 yr. 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 that a smaller proportion were occupied by dense young stands in which understorey light levels were greatly reduced and herb and shrub cover were low. In contrast, the majority of xeric sites in the late 20th century landscape are occupied by mature, closed canopy stands in which herbaceous cover and richness are low.

Variation in post-fire response between plots appears to reflect differences in site conditions, pre-fire composition and structure, fuel loads, fire severity and season. Pine beetle outbreaks lead to heavy fuel accumulations (Nicholas & White 1984) 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 autumn burns. 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* (e.g. Barden & Woods 1976; Burns & Honkala 1990 but see Waldrop & Brose 1999). In our study, *Pinus* showed a negative

Table 5. Mean cover (%) of (a) shrubs and woody vines and (b) herbaceous plants in xeric permanent plots that burned in 1976-77 and in topographically similar plots that have not burned since before 1940.

(a) Shrubs and woody vines	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 species	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

(b) Herbs	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
Erechtites 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 species	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 / m^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

correlation with litter depth and a marginally 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*, 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. While our results are suggestive, the growing literature on experimental burns in xeric southern Appalachian forests (e.g. Elliott et al. 1999; Waldrop & Brose 1999) should allow more rigorous assessment of the effects of fire severity and season on vegetation response.

Our data also suggest that fire behaviour 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 shrubs may have provided a highly flammable fuel bed, and more open canopies would have allowed increased insolation and drying of the ground layer. Under such conditions, fires may have started more easily, spread more quickly and reached a larger size than those observed in recent decades (e.g. Barden & Woods 1973; Harmon et al. 1983).

In many respects, effects of reduction in fire frequency in on xeric forests in GSMNP parallel those observed in fire-suppressed *Pinus ponderosa* woodlands in the southwestern US (Covington & Moore

1994) and *Pinus palustris/Arista stricta* savannas in the southeastern coastal plain (Ware et al. 1993). Our study adds to a growing body of evidence that the historical vegetation mosaic of the southeastern US included scattered open-canopy woodlands and prairies with grass and herb-rich understories (e.g. Ware et al. 1993) on sites where natural or anthropogenic fire, drought or unusual edaphic conditions prevented the development of closed-canopy forest.

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References

Barden, L.S. & Woods, F.W. 1973. Characteristics of lightning fires in southern Appalachian forests. *Proc. Tall Timbers Fire Ecol. Conf.* 13: 345-361.

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

Bratton, S.P. & Meier, A.J. 1998. The recent vegetation disturbance history of the Chattooga River Watershed. *Castanea* 63: 372-381.

Burns, R.M. & Honkala, B.H. 1990. *Silvics of North America: Vol. 1, Conifers.* Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Covington, W.W. & Moore, M.M. 1994. Southwestern ponderosa pine forest structure: Changes since Euro-American settlement. *J. For.* 92: 39-47.

Elliott, K.J., Hendrick, R.L., Major, A.E., Vose, J.M. & Swank, W.T. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *For. Ecol. Manage.* 114: 199-213.

Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. *Bull. Torr. Bot. Club* 109: 74-79.

Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65: 796-802.

Harmon, M.E., Bratton, S.P. & White, P.S. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio* 55: 129-139.

Harrod, J.C. & White, R.D. 1999. Age structure and radial growth in xeric pine-oak forests in western Great Smoky Mountains National Park. *J. Torr. Bot. Soc.* 126: 139-146.

Harrod, J., White, P.S. & Harmon, M.E. 1998. Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995. *Castanea* 63: 346-360.

Johnson, E.A. & Van Wagner, C.E. 1985. The theory and use of two fire history models. *Can. J. For. Res.* 15:214-220.

Kartesz, J.T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, Vol. 2 – Thesaurus.* 2nd ed. Timber Press, Portland, OR.

Keever, C. 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecol. Monogr.* 20: 229-250.

Little, E.L. & Critchfield, W.B. 1969. *Subdivisions of the genus Pinus (pines).* USDA For. Serv. Misc. Publ. 1144, Washington, DC.

Nicholas, N.S. & White, P.S. 1984. *The effect of the southern pine beetle on fuel loading in yellow pine forests of Great Smoky Mountains National Park.* USDI, National Park Service, Southeast Regional Office Research/Resources Management Report SER-73.

Peet, R.K., Glenn-Lewin, D.C. & Wolf, J.W. 1983. Prediction of man's impact on plant species diversity: A challenge for vegetation science. In: Holzner, W., Werger, M.J.A. & Ikusima, I. (eds.) *Man's impact on vegetation*, pp. 41-50. Junk, Boston, MA.

Pyle, C. 1988. The type and extent of anthropogenic disturbance in the Great Smoky Mountains before National Park Service acquisition. *Castanea* 53: 183-196.

Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W. & Bukenhofer, G.A. 1999. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *J. Veg. Sci*. 9: 133-142.

Sutherland, E.K. et al. 1995. *Two centuries of fire in a southwestern Virginia Pinus pungens community.* In: Proceedings IUFRO Conference on inventory and management in the context of catastrophic events, June 21-24, 1993, University Park, PA.

Vose, J.M., Swank, W.T., Clinton, B. D., Hendrick, R.L. & Major, A.E. 1995. Using fire to restore pine/hardwood ecosystems in the southern Appalachians of North Carolina. In: Greenlee, J.M. (ed.) *Proceedings First conference of fire effects on rare and endangered species and habitats*, pp. 149-152. Int. Ass. of Wildland Fire, Fairfield, WA.

Waldrop, T.A. & Brose, P.H. 1999. A comparison of fire intensity levels for stand replacement of table mountain pine (*Pinus pungens* Lamb.). *For. Ecol. Manage.* 113: 155-166.

Ware, S, Frost, C. & Doerr, P.D. 1993. Southern mixed hardwood forest: The former longleaf pine forest. In: Martin, W.H., S.G. Boyce, & Echternacht, A.C. (eds.) *Biodiversity of the southeastern United States: Lowland terrestrial communities*, pp. 447-493. John Wiley & Sons, New York, NY.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.

Williams, C.E. 1998. History and status of table mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). *Nat. Areas J.* 17: 81-90.

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