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Age structure and radial growth in xeric pine-oak forests in western Great Smoky Mountains National Park¹

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HARROD, J. C. AND R. D. WHITE (Curriculum in Ecology, University of North Carolina, Chapel Hill, NC 27599-3275). Age structure and radial growth in xeric pine-oak forests in western Great Smoky Mountains National Park. *J. Torrey Bot. Soc.* 126:139–146. 1999.—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, we measured tree ages, diameters, and radial growth rates in four xeric *Pinus-Quercus* stands. Most trees in the present canopy (stems ≥ 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 ≥ 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.

Key words: xeric forests, *Pinus*, *Quercus*, fire regimes, age structure, southern Appalachian Mountains

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; Harrod et al. 1998). 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, we 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 (Harrod et al. 1998). 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*) and, to a lesser extent, *Quercus* species (mostly *Q. alba*, *Q. coccinea*, *Q. prinus*, *Q. rubra*, and *Q. velutina*). [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 and Critchfield

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1969; Harmon 1984; Burns and Honkala 1990). Botanical nomenclature follows Kartesz (1994).] 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, we examine data on tree ages and radial growth rates from four xeric stands. We ask whether dendrochronological data are consistent with our 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.

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; 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 (1980, 1982); Harmon et al. (1983); Pyle (1988); and Harrod et al. (1998).

We 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 Harrod et al. (1998). 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 Harrod et al. (1998). We established additional site selection criteria for the present study: 1. Because we were interested in the effects of reduced fire frequency, we excluded xeric sites that had burned since 1940. 2. To allow evaluation of earlier findings, we excluded sites within 100 m of plots used in previous studies. 3. To allow for 100 m point-quarter transects (see below), we excluded patches less than 120 m in length. 4. To ensure that each study site represented an independent sample of the landscape, we selected sites that were at least 500 m from each other and in separate patches of xeric habitat. To avoid bias in site location, we 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.

Our field methods resemble those used by Abrams and Downs (1990) to examine successional changes in Pennsylvania oak forests. In April 1998, we established a 100 m transect at each study site. At 20 m intervals along the transect, we 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. We 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. We 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, we 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. We used a similar procedure for hollow trees, except that we 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.

We employed two methods to estimate the

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

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, we calculated mean annual increments by decade. We 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 (Harrod et al. 1998).

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 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. virginiana* also exceeded 50 stems/ha. Total basal areas ranged from 33 to 49 m²/ha with a mean of 40 m²/ha. *Pinus echinata*, *P. strobus*, and *P. virginiana* were the basal area dominants, each contributing $>$ 6 m²/ha. Mean basal areas of *Acer rubrum*, *Pinus rigida*, *Quercus prinus*, and *Q. rubra* also exceeded 2 m²/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 (Fig. 1). *Pinus echinata* and *P. rigida* were represented entirely

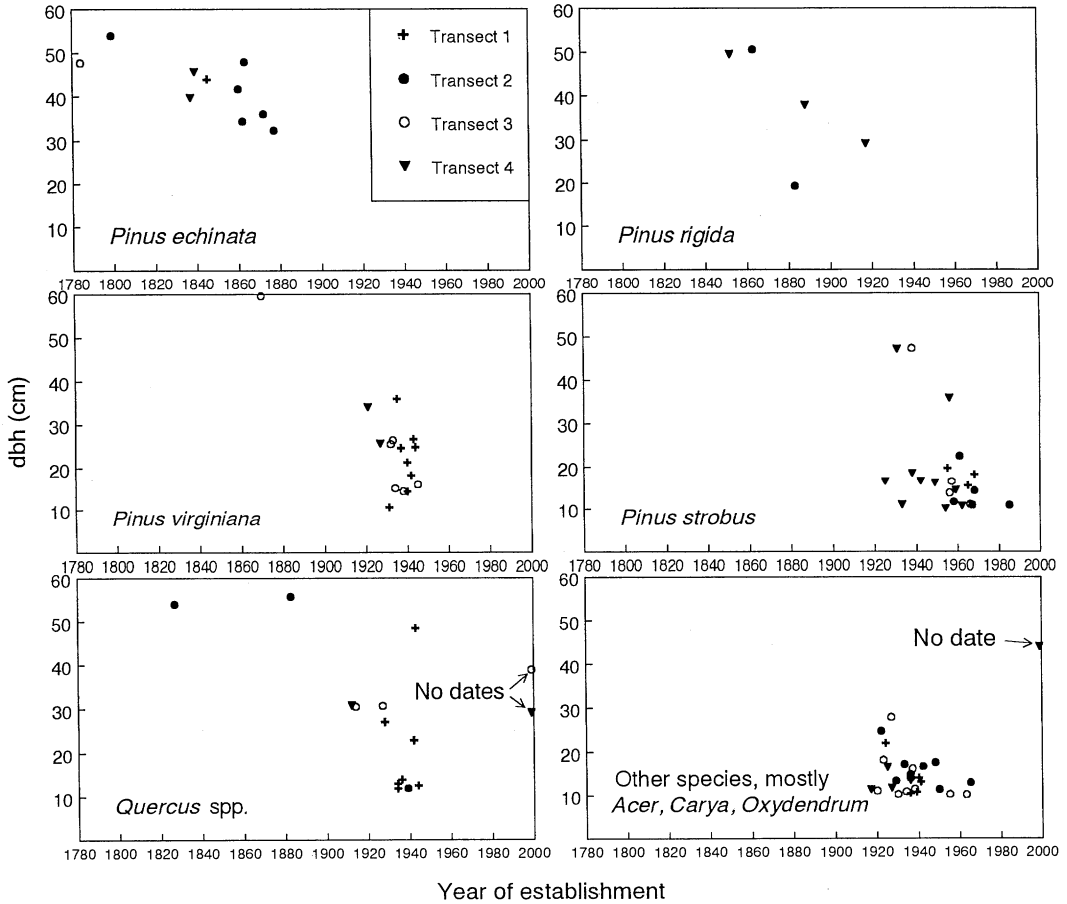


Fig. 1. Date of tree establishment vs. diameter at breast height (dbh) for canopy trees (stems ≥ 10 cm dbh).

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* subgenus *Pinus* species occurred from the late 18th through mid 20th centuries (Fig. 1). The oldest trees in each transect were *Pinus echinata* that established be-

fore 1850. Establishment 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.

Table 2. Numbers of canopy trees (stems ≥ 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.

Decade	<i>Pinus</i> subg. <i>Pinus</i>			<i>Quercus</i> spp.			<i>Pinus strobus</i>			Other			Total		
	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

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.

We 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. We observed 15 growth releases and 26 growth suppressions between the 1850s and 1980s (Table 2). Frequency of growth release (numbers of releases relative to number of 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 we observed no more than one suppression in any decade prior to 1960, we 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 (Harrod et al. 1998).

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, unpubl. 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; Harrod et al. 1998); 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). Our 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. Our 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.

Our 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 our study area, little *Quercus* regeneration has occurred since the mid 20th century. Densities of *Quercus* saplings have declined sharply in the past two decades (Harrod et al. 1998), and *Quercus* are now poorly represented in sapling size classes. Our 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.

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