RESEARCH ARTICLE

Disturbance Characteristics and Overstory Composition of an Old-Growth Shortleaf Pine (*Pinus echinata* Mill.) Forest in the Ozark Highlands, Missouri, USA.

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ABSTRACT: The Eck Memorial Natural Area is the largest old-growth shortleaf pine (*Pinus echinata* Mill.) forest in Missouri, USA. The objectives of this study were to characterize vegetation, examine historic and contemporary disturbances, and describe potential vegetation changes for this natural area. Shortleaf pine was the most important tree species at the site and had the highest single species basal area (8.1 m^2 ha^{-1}). Old-growth shortleaf pines averaged 230 years in age and ranged from approximately 120 to 325 years. Canopy gaps (≤ 6 years old) constituted 4% of the total area, and average expanded and actual gap sizes were 421 m^2 and 210 m^2, respectively. The uneven-aged structure of shortleaf pine suggests that the species has continually regenerated and recruited to the overstory despite the relatively low fire frequency of 44 years. Results of this study suggest that although canopy gaps are important in allowing understory trees to recruit to overstory positions, they are not likely the sole reason for the uneven-aged shortleaf pine structure. During the past century, pine regeneration and recruitment have decreased, possibly as a result of fire suppression. Without major changes in disturbance type and frequency, future forest composition probably will be dominated by hardwoods such as black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), and hickories (*Carya* Nutt. spp.)— species that were most successful in gap-phase replacement and regeneration.

Características de los Disturbios y Composición del Dosel en un Bosque Maduro de Pino de Hoja Corta (*Pinus echinata* Mill.*)* en las tierras altas de los Ozark, Missouri, USA.

RESUMEN: El área natural Eck Memorial, es el bosque maduro más grande de pino de hoja corta (*Pinus echinata* Mill.) en Missouri, USA. Los objetivos de este estudio fueron caracterizar la vegetación, examinar los disturbios históricos y contemporáneos, y describir los cambios potenciales de vegetación para esta área natural. El pino de hoja corta fue el árbol más importante en el sitio y tuvo el área basal mayor por especie (8.1 m^2 ha^{-1}). Los pinos de hoja corta maduros promediaron 230 años de edad y variaron de 120 a 325 años. Los gaps del dosel (≤ 6 años de antigüedad) constituyeron el 4% del área total, y promediaron una superficie, expandida y actual, de 421 m^2 y 210 m^2 respectivamente. La despareja estructura de edades de los pinos de hoja corta, sugieren que la especie se ha regenerado continuamente y se ha reclutado al dosel, aún con una baja frecuencia de fuego de 44 años. Los resultados de este estudio sugieren que aunque los gaps del dosel son importantes al permitir la incorporación de árboles al dosel, ellos no son posiblemente la única razón para la estructura despareja de edades de los pinos de hoja corta. Durante el último siglo, la regeneración y el reclutamiento de pinos ha disminuido, posiblemente como resultado de la supresión de fuegos. Sin cambios mayores en la frecuencia y tipo de disturbio, la composición futura del bosque probablemente esté dominada por maderas duras, tales como *Quercus velutina* Lam., *Quercus alba* L., y *Carya* Nutt. spp.—especies que fueron más exitosas en el remplazo y la regeneración de los gaps.

Index terms: disturbance, forest succession, Ozark Highlands, *Pinus echinata*, shortleaf pine

INTRODUCTION

The Ozark Highlands region of Missouri, USA, comprises the northern portion of the Interior Highlands, a larger physiographic region that also includes the Boston and Ouachita Mountains of Arkansas and Oklahoma. The Ozark Highlands region is part of an ancient uplifted plain that has been exposed to dissecting action of streams since the Pre-Cambrian period (Fletcher and McDermott 1957, Thom and Wilson 1983). Most of the region consists of contiguous hardwood forests, but variation in terrain and disturbance has led to the presence of savannas, glades, and prairies. Shortleaf pine (*Pinus echinata* Mill.), Missouri's only native pine species, is found in association with hardwoods throughout much of the region.

During the late nineteenth century, many ecologically important events occurred in the Ozark Highlands, altering the region's forest composition and structure. Eastern-based timber companies bought extensive areas of land and constructed sawmills in the region during the mid-1800s, and regionwide lumbering of shortleaf pine and hardwoods began soon thereafter (Hill 1949, Cunningham and Hauser 1989). As a result of lumbering and increased Euro-American settlement, factors influencing disturbance regimes of Ozark forests were altered. For example, the frequency of anthropogenic burning and populations of large ungulates such as bison (*Bison bison* Linnaeus) and elk (*Cervus elaphus* Linnaeus) were reduced.

The majority of commercially valuable timber of the region was cut between 1880 and 1920, ultimately producing an estimated 1.5 billion board feet of lumber (Schuchard and Kohler 1984). After the logging, shortleaf pine failed to regenerate, probably due to lack of seed trees and the effects of land-use practices both preceeding and following the lumbering era (Krusekopf et al. 1921, Cunningham and Hauser 1989, Guyette and Dey 1997). Annual burning to improve livestock grazing conditions further diminished shortleaf pine abundance, particularly regeneration, and favored vigorous-sprouting hardwood species (Record 1910, Cunningham and Hauser 1989). Moreover, free-range grazing by goats, sheep, and hogs promoted sprouting of less palatable hardwood vegetation such as oaks and hickories. Comparisons of early estimates of shortleaf pine abundance (Liming 1946) and current abundance (Hansen et al. 1992) suggest that up to 2 million ha of shortleaf pine were converted to primarily oak-dominated forests during the lumbering period of 1880–1920.

Prior to lumbering, extensive pine-dominated forests were located throughout the Ozark Highlands region (Stevens 1991, Batek et al. 1999). At the time of European settlement, shortleaf pine occurred on an estimated 2.7 million ha in Missouri (Liming 1946, Cunningham and Hauser 1989). Currently, shortleaf pine occurs on approximately 200,000 ha (Hansen et al. 1992). Following the lumber boom at the turn of the nineteenth century, species in the red oak group were most successful in replacing the original shortleaf pines (Cunningham and Hauser 1989). In the Ozark Highlands, black oak (*Quercus velutina* Lam.), scarlet oak (*Q. coccinea* Meunchh.), northern red oak (*Q. rubra* L.), and southern red oak (*Q. falcata* Michx.) are the dominant red oak group species, but white oak (*Q. alba* L.) and post oak (*Q. stellata* Wangenh.) are also common.

Structural changes in both uncut and second-growth Ozark forests probably have occurred as a result of fire exclusion. Fire suppression during the past half century has contributed to an increase in woody vegetation in fire-maintained communities such as savannas and glades (Beilmann and Brenner 1951a, Abrams 1992, Nelson 1997). The presettlement forest canopy structure of the Ozarks was commonly open, particularly in the uplands of the Springfield and Salem Plateaus (Schoolcraft 1821, Beilmann and Brenner 1951b, Thom and Wilson 1983, Iffrig and Nelson 1997) where frequent and intentional burning by Native Americans maintained fire-mediated communities such as prairies and savannas (Guyette and Cutter 1991, Cutter and Guyette 1994, Guyette 1995). Though rare in occurrence, remnant uncut and old second-growth shortleaf pine forests are undergoing successional changes due to fire suppression. There is considerable evidence that hardwood encroachment results from fire suppression in other old-growth pine communities throughout the southeastern United States (Fountain 1991, Masters et al. 1995, Gilliam and Platt 1999). Canopy gaps formed by wind, insects, and pathogens have become an increasingly important disturbance mechanism influencing forest vegetation and succession. Descriptions of disturbance mechanisms are necessary for evaluating successional theories, understanding community properties, and providing useful information to land managers (Pickett and Thompson 1978). Few investigations have documented the dynamics of canopy gaps in shortleaf pine forests, especially in the western portion of the species' range.

In this paper we describe the largest known old-growth shortleaf pine-oak forest of the Missouri Ozark Highlands region. Our objectives were to characterize the current woody vegetation of the site, examine the historic and contemporary disturbances affecting woody vegetation, and describe evidence of vegetation changes and forest developmental processes. In particular, we examined the importance of fire and canopy gap disturbances in the forest's historic and potential future development.

METHODS

Study Area

Eck Memorial Natural Area (ENA) is the largest old-growth shortleaf pine (*Pinus echinata* Mill.) forest in Missouri, USA. The natural area is located in the northwestern portion of the Ozark Highlands region in northwestern Texas County, Missouri (Figure 1). Texas County landscape is characterized by an ancient plateau; streams on the plateau's western border flow northward to the Missouri River and streams on its eastern border flow southeast to the Mississippi River. The study site is located in the Big Piney River Oak-Pine Woodland Forest Hills land type association of the Gasconade River Hills subsection of the Ozark Highlands section (Nigh et al. 2000).

According to Kramer et al. (1996), the ENA consists of 107 ha of old-growth and old, second-growth shortleaf pine, scarlet, black, and white oaks, and black (*Carya texana* Buckl.) and mockernut hickories (*Carya tomentosa* Nutt). Its natural features are represented in a dry-mesic forest with scattered Roubidoux sandstone outcrops occurring on the steepest slopes and overlaying the Gasconade dolomite chert residuum formation. Soils are primarily mesic Typic Paleudults and have a granular structure and contain large amounts of chert at the surface with a region of cherty silty clay loam at depths of 60 to 80 cm (Gilbert 1971).

Elevations in the ENA range from 250 to 360 m above sea level. The majority of the study area is located on southwest aspects immediately adjacent to the Big Piney River. Slopes range from 0% to 42% and the terrain is moderately dissected with broad to narrow ridgetops. Within the region, monthly average temperatures over the past 66 years ranged from –9.2° to 29.2° C, and average annual precipitation, primarily in the form of rain, is 155 cm, with monthly means ranging from 0.1 to 34 cm (National Climatic Data Center 2001).

General Land Office survey notes from 1834 describe the ENA landscape as "land

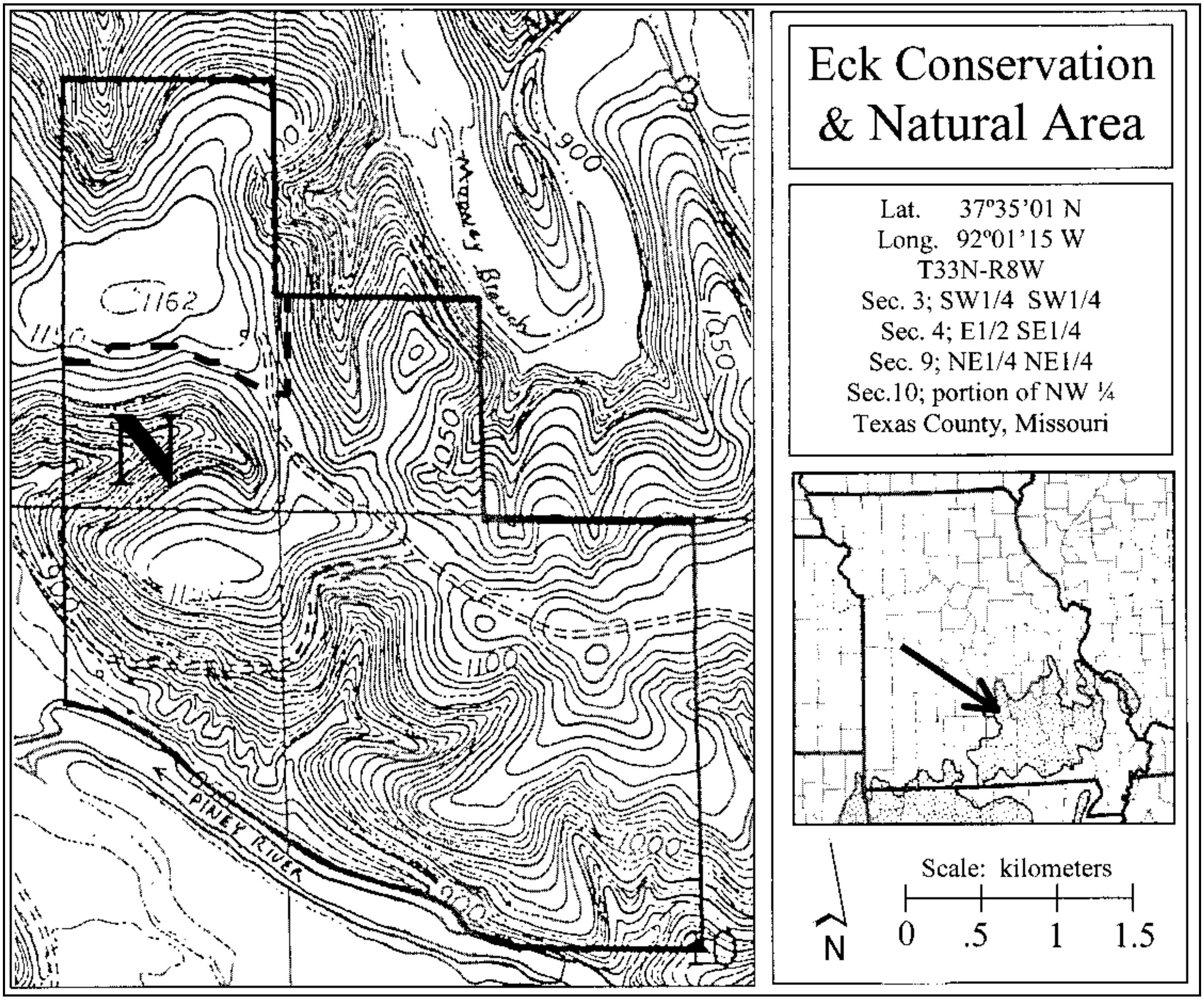

Figure 1. The Eck Memorial Natural Area is a 94.3-ha reserve (area below dashed line) within a larger (129.5-ha) conservation area managed by the Missouri Department of Conservation (total area outlined on map). It is located in the northwest portion (arrow) of the shortleaf pine range (darkened portion of Missouri state map).

thinly timbered with post oak and pine undergrowth oak and blackjack. Unfit for cultivation. Timber pine and oak; understory oak bushes. Hilly rocky land." Pine trees up to 86 cm diameter were the largest individuals, with 48- to 50-cm trees tallied most frequently. The area was once open range and undoubtedly was grazed by cattle or other livestock. Evidence of logging, probably during the late nineteenth century, exists in a small localized area in the southernmost portion of the natural area.

Sampling Methods

Overstory Composition and Canopy Gaps

During June and July 1999, we quantified overstory composition and evaluated the distribution and abundance of forest canopy gaps at ENA. Transects 50 m apart and extending to the study area boundary were used in locating all gaps and quantifying the overstory composition. Subsequent transects were walked parallel to the initial transect line until the entire study area was sampled. At every 75 to 100 paces (randomly determined) along transect lines we located 71 points to quantify the overstory structure and composition using the point-centered quarter method (Cottam and Curtis 1956). Only trees ≥ 25 cm diameter at breast heigh (dbh) were measured and considered as overstory trees.

Canopy gap sampling was conducted in accordance with guidelines established by Runkle (1992), with modification. Canopy gaps were sampled for the purposes of determining their disturbance characteristics (i.e., size, abundance, mode, and frequency of formation) and understanding the regeneration and recruitment of tree species occurring in canopy gaps, particularly shortleaf pine, a shade-intolerant species. Gaps were defined as openings in the canopy caused by the death of 1 to 10 trees and were considered only if their age was ≤ 6 years. In gaps > 6 years of age, canopy closure limited our ability to locate and age gaps accurately. Data collected at each gap included gap size, gap maker(s), gap age, woody species composition in the gap, topographic features, and adjacent forest composition. Gap size was determined using the area of an ellipse. Ellipse length was measured as the longest axis of the gap and width was measured as the longest axis perpendicular to the length. Both expanded and actual canopy gap sizes were measured. Expanded gap size was defined as the area bounded by the stems of the overstory trees surrounding the canopy opening and actual gap size was defined as the area of the canopy opening. We recorded the azimuth of the longest axis and made a sketch of the gap shape and orientation. A gap maker was defined as any tree ≥ 25 cm dbh whose death created the gap. The species, dbh, height, mode and agent of death, and direction of fall were recorded for each gap maker. Mode described how the gap maker tree(s) were affected by the disturbance agent, and the gap maker was classified as either standing dead, broken, or uprooted. Disturbance agents were classified as wind, lightning, damage (from a falling tree), or other (i.e., pathogen, senescence, insects, undetermined causes). Gap ages were determined using gap maker bud or leaf condition, release ages of saplings growing in gaps, recovery of stems damaged by the gap maker(s), release of adjacent canopy trees, and ages of seedlings occurring in the gaps. Basal cores were taken from at least one understory pine ≥ 1.3 m tall in each gap. Cores further aided in accurately determining gap age and were used to analyze shortleaf pine recruitment years, growth rates, and potential for recruitment to the overstory.

All woody stems ≥ 1.3 m tall occurring within the expanded gap area were considered to be in the understory layer and were identified and recorded in 2-cm dbh classes. Canopy gap replacement tree species were noted and measured for diameter and height. Replacement trees were the tallest individuals in the gap with at least 20% live crown ratio. The distance to the nearest pine seed tree, canopy heights, and height to the base of the canopy of trees adjacent to gaps were recorded because they are likely to influence regeneration.

All woody stems in the regeneration layer (< 1.3 m tall) of expanded gaps were inventoried by species in four 1-m^2 circular subplots located equidistant between gap center and the expanded gap edge in four cardinal directions. Only woody species were tallied within regeneration subplots. Topographic features of the gap were described by slope degree, aspect, and slope position and shape.

Fire History

Overstory pines were cored to determine age and, when possible, fire scarring frequency. Cores rather than wedges were removed because the destructive sampling is incompatible in a designated natural area. Core samples are a reliable technique for accurately dating fire scars and constructing fire or other disturbance histories (Sheppard et al. 1988). Two cores were taken from the upslope side of each tree, one from the base and one at ~~dbh~~breast height (1.3 m). We recorded the overstory tree's location within the natural area including the slope, aspect, and comments about the physical characteristics of the tree, soils, and fire scars. Sixty-four cores were taken from 32 living overstory shortleaf pine trees.

Table 1. Overstory composition of the Eck Natural Area, Missouri, USA. Relative importance values were calculated as the sum of a species relative density, relative dominance, and relative frequency divided by 3. Basal areas were generated from the point-centered quarter method. Tree species are listed by decreasing importance.

Species	Absolute Density (trees ha^{-1})	Relative Density	Relative Basal Area	Relative Frequency	Relative Imp. Value (RIV)	Basal Area (m^2 ha^{-1})
Pinus echinata Mill. shortleaf pine	71.0	34.9	32.8	27.0	31.6	8.1
Quercus velutina Lam. black oak	52.0	25.7	29.5	24.1	26.4	7.3
Quercus alba L. white oak	33.0	16.2	18.8	19.5	18.2	4.6
Quercus stellata Wangenh. post oak	18.0	8.8	7.0	10.3	8.7	1.7
Quercus rubra L. northern red oak	11.0	5.3	7.0	6.3	6.2	1.3
Carya tomentosa Nutt. mockernut hickory	8.0	3.5	2.4	5.2	3.7	0.6
Carya texana Buck black hickory	6.0	3.3	1.8	4.1	3.1	0.5
Juglans nigra L. black walnut	3.0	1.5	1.0	1.8	1.4	0.2
Juniperus virginiana L. eastern red-cedar	1.0	0.8	0.4	1.1	0.7	0.1
Total	203.0					24.4

Laboratory Procedures and Statistical Analysis

Relative overstory importance values were generated by summing relative density, relative frequency, and relative basal area by species and dividing the result by 3. Understory and regeneration class importance values were generated by summing relative densities and relative frequencies. Frequency distributions were created for overstory size and age classes, canopy gap makers, and understory stems. Growth rates of understory pines were derived from annual diameter increases. Simple linear regression was used to describe relationships between gap size and gap maker basal area.

In the lab, tree cores were mounted and sanded, and annual rings were measured using a stereomicroscope. If the pith was not represented in a core, the total number of rings was estimated using a derivation of a geometric equation developed by Duncan (1989): ENMR = $L^2/8h+h/2$, where *ENMR* equals the estimated number of missing rings, *h* equals the height of the last arc (ring), and *L* equals the length of that arc. Ring-width series from each sample were plotted and used for visual cross-dating (Stokes and Smiley 1968, Guyette and Cutter 1991). Annual ring width files were imported into COFECHA, a program used for determining the accuracy of both relative and absolute dating of the samples by correlation analysis (Grissino-Mayer et al. 1996). Periods of distinctive ring patterns (signature years) resulting from annual variations in climate were used to cross-date cores. Notable droughts occurred in the Ozark Highlands region during the years 1736, 1780, 1784, 1820, 1930s, and 1953-55 (Law and Gott 1987, Cook et al. 1999).

RESULTS

Forest Composition and Structure

The overstory composition primarily consisted of shortleaf pine, oak, and hickory species, and total stand basal area was 24.2 m^2 ha^{-1} (Table 1). Shortleaf pine was the most important species and had a basal area of 8.1 m^2 ha^{-1} and density of 71 trees

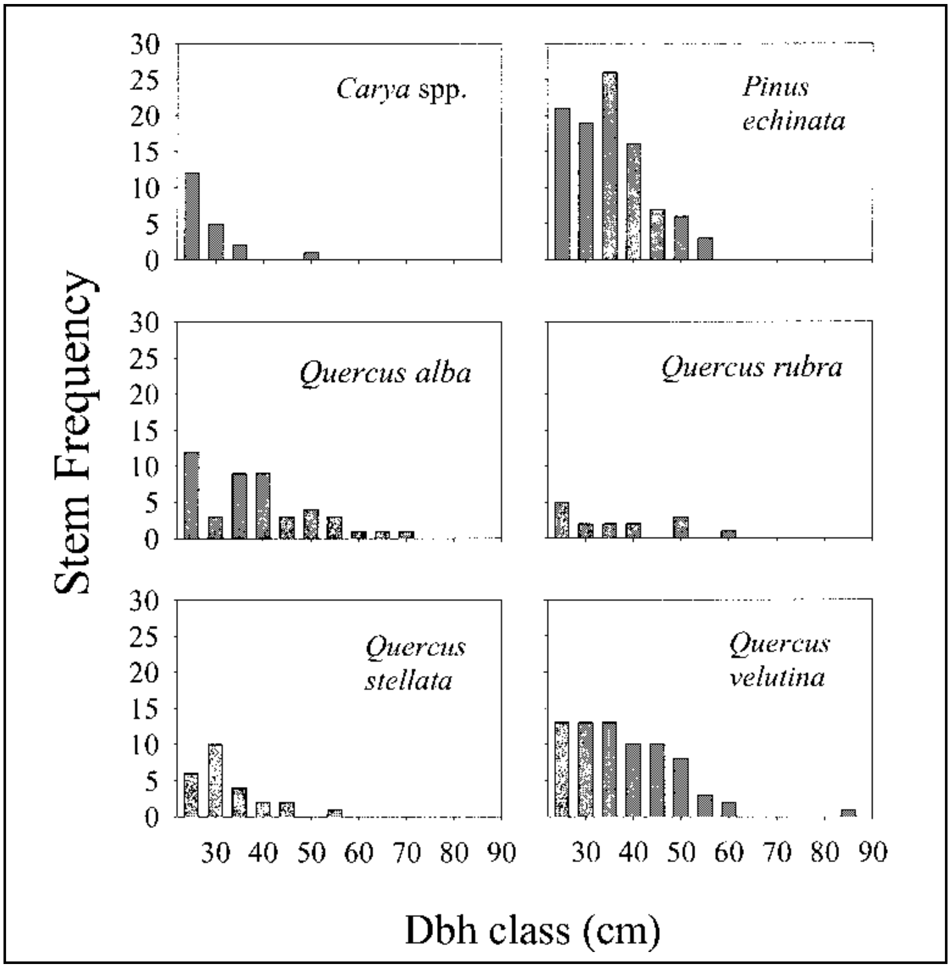

Figure 2. Diameter distributions for overstory trees at the Eck Natural Area, Missouri, USA. Overstory species distributions were derived from sampling using the point-centered quarter method (Cottam and Curtis 1956).

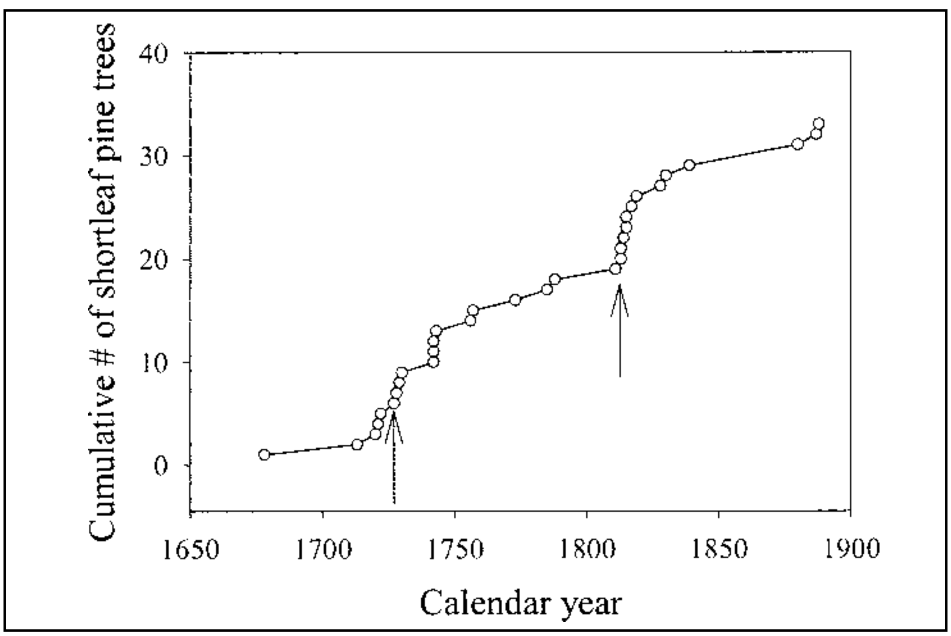

Figure 3. Cumulative distribution of pith dates of overstory shortleaf pines at the Eck Natural Area, Missouri, USA. Arrows denote periods of accelerated recruitment.

ha^{-1}. Black oak was the second most important species at the site (basal area = 7.3 m^2 ha^{-1}) and had the second greatest stem density with 52 trees ha^{-1}. The next three important overstory species were white oak, post oak, and northern red oak. Collectively, oak basal area was 14.9 m^2 ha^{-1}.

Black oak, northern red oak, white oak, and hickory species were most abundant in the 25- to 35-cm dbh classes (Figure 2). Shortleaf pine showed the greatest relative abundance of overstory individuals up to the 40 cm dbh class, above which black oak became the most abundant species. The largest individuals (≥ 55 cm dbh) were most frequently white oak with additional representation by northern red oak, black oak, and post oak. Overstory pines were up to 325 years old with the majority between 200 to 280 years (Figure 3). The youngest overstory pine sampled was 120 years old and 60 cm dbh; however, size is not a good predictor of age—the oldest individual was 40 cm dbh. Tree-ring dating of cores from overstory shortleaf pine individuals showed that continual regeneration and recruitment of shortleaf pine occurred from approximately 1675 to 1890 with pulses around 1730 and 1820 (Figure 3). Cores from overstory pines indicate that nearly all individuals grew under suppression/release conditions with up to three releases occurring before the tree reached the overstory position.

A total of 29 tree and shrub species were identified in the understory (≥ 1.3 m; Table 2). Blueberry (*Vaccinium* L. spp.), a small acidiphilic shrub, had the highest importance value in the understory layer. *Ulmus* L. spp. were the most important tree species followed by black oak, sassafras (*Sassafras albidum* [Nutt.] Nees), white oak, and hickory. Shortleaf pine ranked ninth of the 29 understory tree and shrub species. Sassafras and flowering dogwood (*Cornus florida* L.), species generally limited to the understory layer in mature forests of the Ozark Highlands, were also relatively high in importance.

Thirty-one woody species were identified in the regeneration layer (< 1.3 m; Table 2). Importance values were, on average, highest for those species restricted to the ground flora such as Virginia creeper (*Parthenocissus quinquefolia* [L.] Planch.), blueberry, and wild grape (*Vitis* L. spp.). Importance values of potential canopy tree species in the regeneration layer were greatest for black oak (18.1) followed by white oak (12.7), shortleaf pine (12.3), and hickories (8.2). Sassafras and flowering dogwood were also relatively important. Shortleaf pine ranked sixth in importance of the 31 regenerating species.

Table 2. Importance values based on the relative density and relative frequency of the most common species in the understory and regeneration layers at the Eck Natural Area, Missouri. Importance values were calculated per vegetation layer.

		Vegetation Layer	
	Species	**>1.3 m tall**	**<1.3 m tall**
Potential Overstory Trees	*Ulmus* spp.	23.1	7.0
	Quercus velutina	17.4	18.1
	Quercus alba	14.5	12.7
	Carya spp.	14.5	8.2
	Pinus echinata	9.6	12.3
	Quercus rubra	9.4	0.6
	Quercus stellata	5.7	1.9
	Nyssa sylvatica	5.5	1.0
	Fraxinus americana	2.0	0.9
	Juglans nigra	1.8	0.0
	Celtis occidentalis	1.4	0.6
	Acer rubrum	1.2	2.7
	Quercus marilandica	0.9	0.3
	Acer negundo	0.3	0.9
	Betula nigra	0.3	0.0
Understory Trees	*Sassafras albidum*	16.8	18.9
	Cornus florida	13.0	11.1
	Rhamnus caroliniana	10.1	2.5
	Juniperus virginiana	5.7	3.0
	Amelanchier arborea	3.9	0.6
	Morus spp.	2.1	0.3
	Diospyros virginiana	1.1	0.0
	Cercis canadensis	0.6	0.3
	Asimina triloba	0.3	0.0
	Lindera benzoin	0.3	0.0
	Prunus spp.	0.0	1.7
Woody Shrubs and Vines	*Parthenocissus quinquefolia*	0.0	38.0
	Vaccinium spp.	35.1	35.4
	Vitis spp.	0.0	10.8
	Rhus aromatica	1.7	3.2
	Toxicodendron radicans	0.0	2.0
	Symphoricarpus orbiculatus	0.3	1.9
	Smilax spp.	0.0	1.5
	Ribes spp.	0.0	0.9
	Viburnum spp.	1.4	0.4
	Rubus spp.	0.0	0.3
	Total	200.0	200.0

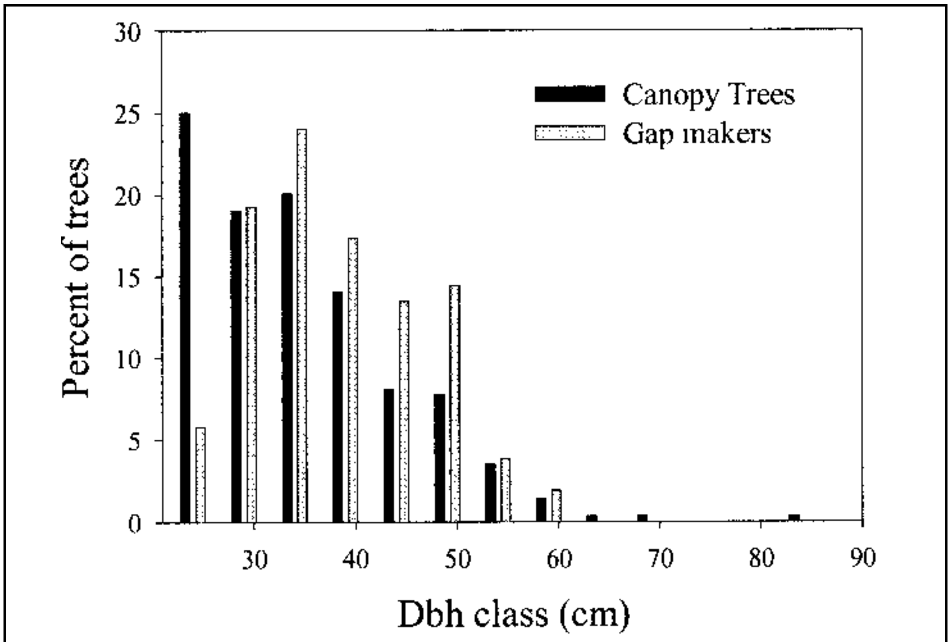

Figure 4. Percent of all canopy trees sampled at the Eck Natural Area, Missouri, USA, and those that were gap makers, by diameter class,.

Disturbance History

Canopy Gaps

Forty-six canopy gaps, created by a total of 112 trees, were located within the ENA. Overall, about 4% of the land area was in actual canopy gaps and 8% in expanded gaps. Mean expanded gap size (± SE) was 421 ± 7 m^2 and mean actual gap size was 210 ± 4 m^2. Expanded gap sizes ranged from 103 to 1583 m^2 with the smaller gaps most commonly represented by a single dead standing tree. Forty-three percent of gaps were formed by one tree, 33.3% by two to three trees, and 22.9% by four or more trees. The largest gap (1583 m^2) was formed by seven trees. Gap sizes were influenced not only by the number of gap makers but also by gap maker size. Gap maker basal area was significantly related to expanded gap size ($n = 113$, $r^2 = 0.55$, $P < 0.01$). Comparisons of size distributions for living canopy trees and gap makers showed that larger trees are more likely to become gap makers (Figure 4) and the percentage of trees becoming gap makers rapidly increases from the 25- to 35-cm dbh class.

Gaps were created by various combinations of canopy tree species and sizes (Table 3). Black oak accounted for 65% of the gap makers and shortleaf pine accounted for 23%. No other species contributed more than 3% trees to the gap maker total. Mean gap maker dbh was 41.0 cm and mean height was 19.1 m. Wind accounted for 89.4% of all identifiable modes of death, followed by other (4.8%), lightning (2.8%), and impact from another tree (2.8%). Modes of death were somewhat predictable given the high influence of wind as a disturbance agent. This was evidenced by 67% of the trees being uprooted, 25.5% broken at stump height, 3.8% partially uprooted, and 3.7% standing dead.

Fluctuations in yearly disturbance rates were evident. For example, six-year-old gaps constituted 39.6% of the gaps and 76.6% of the total area in gaps. Five-year-old gaps constituted 31.3% of gap total and 14.7% of the total area in gaps, and all younger gaps together made up 29.1% of gap total and 8.7% of the total area in gaps. Over the past six years, the average annual disturbance rate from canopy gaps was 1.3% of the area per year and has varied from 0.7% to 2.2%.

The average dbh of all trees recruiting from the understory to the canopy layer was 15.9 cm. Understory hickories, most oaks, and elms were most abundant in the smaller dbh classes with decreasing abundance as dbh size class increases (Figure 5). Shortleaf pine and post oak were most abundant in the 4-cm dbh class. The smallest size classes (0–4 cm) were dominated by hickories and white oak.

Pith dates of understory pines show that continual regeneration and recruitment occurred from 1935 to 1954 (Figure 6), but

Table 3. Frequency and size of gap makers at the Eck Natural Area, Missouri, USA. Values represent the percentage of canopy gaps with a given species as a gap maker and the diameter and heights by species.

Species	N	% of Gaps	Mean dbh (cm)	Range of dbh	Average height (m)	Range of heights
Carya spp.	3	6	31.7	28–35	17.3	15–19
Juglans nigra	2	4	35.5	31–40	17.5	16–19
Juniperus virginiana	1	2	22.0	—	13.0	—
Morus rubra	1	2	32.0	—	14.0	—
Pinus echinata	26	35	36.9	25–52	20.1	17–23
Quercus alba	2	4	39.9	38–41.8	16.3	12.6–20
Quercus rubra	2	4	36.7	33.9–39.4	18.6	17.2–20
Quercus stellata	2	4	33.2	26.4–40	17.0	—
Quercus velutina	74	71	44.1	25–64	19.3	16.6–23
Total	113					

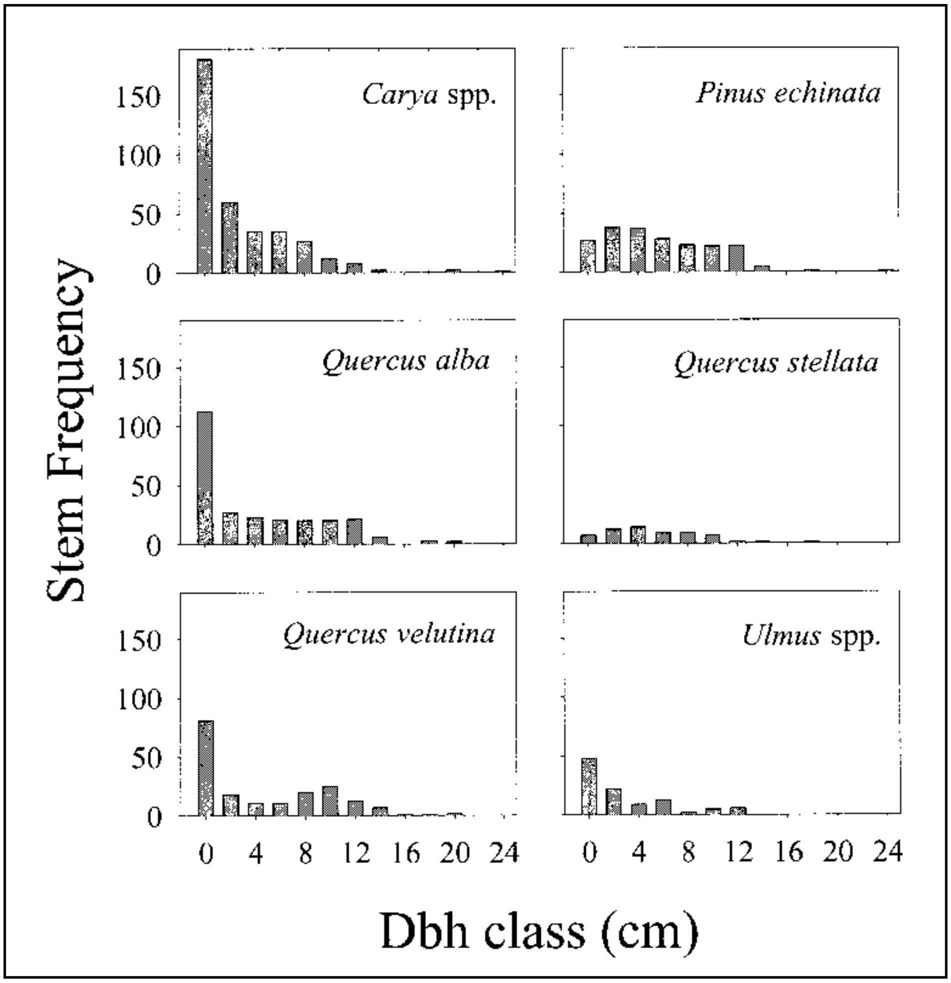

Figure 5. Diameter distributions of the six most abundant understory species (> 1.3 m in height) occurring in the expanded gap area at the Eck Natural Area, Missouri, USA.

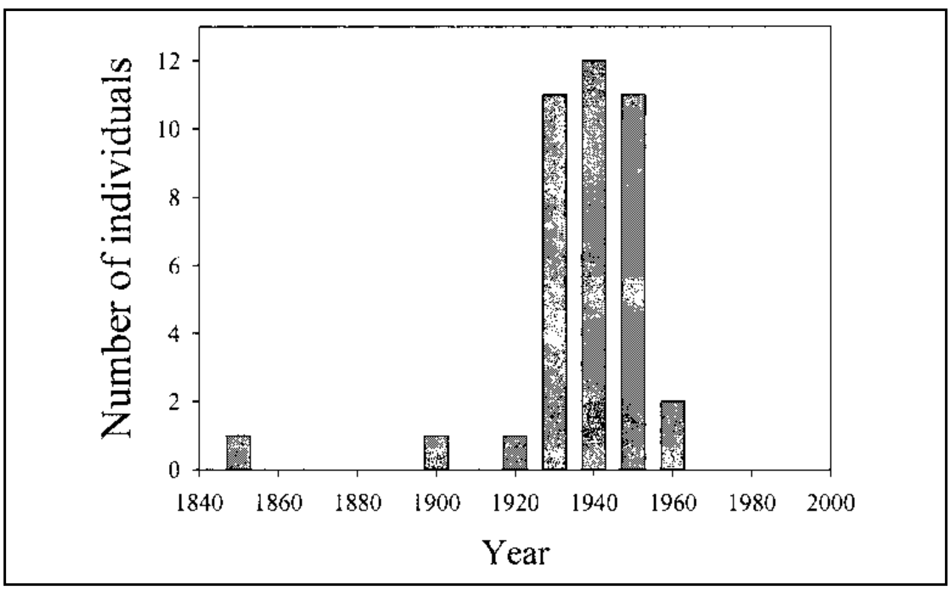

Figure 6. Estimated establishment dates of understory shortleaf pines occurring in gaps at the Eck Natural Area, Missouri, USA.

that no shortleaf pines have entered the understory layer since 1961. The average diameter and height of understory shortleaf pines that recruited into canopy gaps was 10.1 cm and 13.6 m, respectively. Average age of these trees was 55 $\pm$ 0.6 years and ranged from 38 to 80 years, with the exception of one 147-year-old tree. Annual growth rates of understory pines ranged from 0.05 to 8.58 mm $year^{-1}$ and the average growth rate was 1.14 mm $year^{-1}$.

Fire

Evidence of past fire was surprisingly scarce at the ENA when compared to other sites in the Ozark Highlands (Table 4). Six of the 64 trees sampled had fire scars, and the maximum number of fire scars on any tree was four. Fires occurred at the ENA on a mean return interval of approximately 44 years. Evidence of fire varied throughout the study area, with the southeastern portion of the area having less evidence of fire than the north. In the southern portion only three of the older pines had external evidence of fire scars. Only one of these trees had multiple scars (3), but these may not have been fire scars (rodent tooth marks on callus tissue wood). No old pine stumps or natural remnants were observed in the southern drainage.

The northern portion of the natural area had more evidence of fire, especially recent fires. Considerable charcoal was present at the base of several understory pines located at the head of the north drainage (N, Figure 1), and one pine stump in this area had multiple (4) fire scars. A fire scar from one of the understory pine trees, which appeared to be representative of this group, dated to 1942. One 179-year-old pine located in a rocky area on the south-facing rim of the north drainage had four distinct fire scars. The scar face was 1.4 m high and scars dated to 1837, 1871, 1879, and 1907.

DISCUSSION

Stand Development and Successional Theory

Based on severity and intensity, disturbances may accelerate, set back, or completely change successional pathways (Abrams and Scott 1989). In addition, landforms may influence successional pathways in forested communities by limiting the site potential and vegetation (Host et al. 1987). At the ENA, under current conditions of fire suppression, canopy gaps influence succession by favoring hardwood regeneration and reducing shortleaf pine abundance in both the understory and regeneration layers. It is probable that species with the greatest abundance in the understory, such as white oak, black oak, and hickories, will make up the overstory in the future.

Repeated recruitment of shortleaf pine, such as occurred approximately 100 to 300 years ago and evidenced by the overstory shortleaf pine age distribution at ENA, is indicative of repeated disturbances that allowed pines to regenerate and recruit to the overstory (Oliver and Larson 1996). Unexpectedly, past fire disturbances indicated by scars have no correspondence to historic periods of increased shortleaf pine establishment (Figure 3). Although we found little evidence of fire at the site (e.g., low number of scarred trees, of scars per tree, of natural pine snags [remnants], and absence of soil charcoal), it is possible that our fire history underestimated the evidence of fire due to the small size of the fire history sample (i.e., 6 of 64 trees sampled had fire scars). Past fire disturbances would have promoted shortleaf pine because they can result in decreased hardwood competition (Williamson and Black 1981) and reduced litter depth. Shortleaf pine is well adapted to fire, as characterized by its ability to sprout from axillary buds following top-kill.

It is unlikely that fires occurred more frequently than the 44-year interval that we recorded for the ENA. The relatively low fire frequency (Table 4) is supported by the small number of individual pine trees having fire scars. Furthermore, absence of old pine remnants (i.e., burned stumps and snags) throughout the area indicates that the current abundance of shortleaf pine may represent its maximum abundance at this site. Pine stumps can be preserved for long periods of time because they are saturated with terpenoid-rich oleoresin, which is zootoxic and phytotoxic, and therefore have slow decomposition rates (Harborne 1994). Preservation of pine remnants is related to the oleoresin content of the wood, and oleoresin saturation is a protective response following fire injury (Guyette and Dey 1997). It is expected, therefore, that fire-injured pines will persist longer than those that are not injured. The absence of preserved shortleaf pine stumps or snags, the low number of scarred overstory trees, and the high abundance of large, old northern red, white, and black oaks suggest that historically fires were not frequent or intense at the ENA site. It is possible that frequent, low-intensity fire would not scar trees; however, it is unlikely that the majority of fires were of low intensity given the area's steep, long slopes and exposure to wind.

Reasons for a long mean fire return interval at the ENA are speculative. The topographic variability of the surrounding landscape and presence of natural fire breaks may have reduced the potential for fires to enter the ENA. For example, the Big Piney River, nearby, may serve as a fire break, especially for fires moving eastward, the direction of prevailing winds. A low fire frequency on the east side of the river may be further evidence of a fire "shadow" effect, which has been documented for other Ozark sites (Batek et al. 1999). Batek et al. (1999) described a fire shadow effect as a decrease in the spread of fire due to some barrier—in this case, a river.

Three periods of high pine seedling establishment occurred around 1730, 1820 (Figure 4), and 1935 (Figure 6). These years roughly correspond to regional droughts (Law and Gott 1987, Cook et al. 1999). The loss of canopy cover during periods of drought may favor pine survival and regeneration by reducing growth and possibly causing mortality of hardwoods. Following release from competition, the number of seeds per shortleaf pine tree and number of seeds per cone can increase significantly (Phares and Rogers 1962; Yocum 1968, 1971). Thus, in pine-hardwood forests like the ENA, droughts may favor shortleaf pine over hardwoods. Furthermore, xeric site conditions (i.e., low precipitation, limited moisture absorption, high evapotranspiration rates) favor drought-tolerant species such as shortleaf pine. Therefore, site conditions may be important in controlling vegetation composition at the ENA. According to Murphy and Nowacki (1997), even in the absence

Table 4. Comparison of a sentinel shortleaf pine from the Eck Natural Area, Missouri, USA, with sentinel pines from other oak-pine areas in the Ozark Highlands region of Missouri and Arkansas (Guyette 1995). Sentinel pines are those that occupy sites high on the landscape, with steep slopes and long distances to the bottom of the valley, and low quantities of local ground fuels. Mean fire return interval is defined as the average period in years between subsequent fire events.

Site	# Scars	Period (year)	Mean fire Return Interval	Mean # of Scars per Tree	# of stumps with More than 100
Eck Natural Area, Texas Co., MO	4	1814–1993	44.8	<2	0
Mill Hollow, Shannon Co., MO	26	1719–1897	6.8	12	>100
Mill Creek, Carter Co., MO	43	1631–1871	5.6	32	>100
Blue Spring, Shannon Co., MO	27	1747–1887	5.2	12	>100
Mill Mountain, Shannon Co., MO	25	1702–1831	5.2	13	>100
Jerktail Mountain, Shannon Co., MO	29	1708–1911	7	13	>75
Trackler Moutain, Madison Co., MO	36	1710–1915	5.7	—	>50
Granny Gap, Pope Co., AR	26	1695–1915	8.5	9	<20
Lower Buffalo River, Marion Co., AR	31	1770–1967	6.4	—	—

of fire, successional changes of old-growth xeric pine and pine-oak woodlands may be restricted because these sites are infertile and dry.

In mature forests, tree species groups may have unique diameter distributions reflecting differences in understory tolerance, growth habitat, life history, and age structure (Shelton and Cain 1999). At the ENA the diameter distribution of hickories may be indicative of a recently altered disturbance regime, such as fire suppression, resulting in high abundance in the regeneration and understory layers but relatively low importance in the overstory. Low hickory abundance in the overstory could also be explained by drought—especially if drought conditions during the 1930s caused mortality of hickories. The transition to more shade-tolerant and fire-intolerant species is evident in the bell-shaped diameter distributions of shortleaf pine and post oak (Figure 5). Both of these species' diameter distributions include slightly lower numbers of individuals in smaller diameter classes compared to intermediate diameter classes, a pattern that indicates recently decreased recruitment. Similar results were found in mature pine-oak forests of Arkansas and Texas and were attributed to the shade intolerance of pines relative to oaks as well as fire suppression (Glitzenstein et al. 1986, Fountain and Sweeney 1987, Shelton and Cain 1999).

The presence of 49- to 80-year-old understory shortleaf pines filling gaps suggests that pines are capable of persisting in the understory long enough to be effective competitors in gap-phase replacement. Also, the release potential of shortleaf pine, relative to hardwoods, increases with the amount of overstory removal (Brinkman and Liming 1961). If trees adjacent to canopy gaps undergo repeated mortality due to predisposing factors of the gap (i.e., increased susceptibility of trees adjacent to the gap to wind and pathogens), the potential for repeated release of shortleaf pine is increased, assuming repeated gap formation at one location increases the recruitment potential of trees at that site. However, we found little evidence of repeated gap formation. Therefore, pines that were commonly found in the understory may have low success in reaching the overstory position.

Recruitment potential of trees to the overstory position is influenced by gap size and rate of closure. Brinkman and Liming (1961) found that young shortleaf pines grew faster than all associated species following overstory removal. Excluding results from studies of catastrophic storm events, gap sizes at the ENA are of median size compared to those reported from eastern deciduous and southeastern pine forests (e.g., Moore and Vankat 1986, Runkle 1990, Brockway and Outcalt 1998). Although no significant relationship was found between gap size and number of pines regenerating in the gap, the average number of pines per gap increased as the number of overstory pines adjacent to the gap increased. Therefore, the close proximity to a seed source is important for the establishment of shortleaf pines in gaps.

Compared to growth rates of open-grown and managed pine plantations, the understory growth rates of pines at the ENA resembled those characterized by suppressed growth (Brinkman and Smith 1968). On average Missouri sites, open-grown shortleaf pines reach 13.5–15 m height at 30 years and 0.3 m annual height growth increments are typical (Brinkman and Smith 1968). Understory pines at the ENA were found to be as old as 75 years with heights of 5 m. However, shortleaf pine can survive suppression for extended periods and still respond to release (Lawson 1990), and this suppression/ release growth, obvious in increment cores from understory individuals, was common for many overstory individuals as well.

A decrease in shortleaf pine regeneration at the site is likely to continue as hardwoods become more abundant in the overstory. Overstory replacement by hardwoods would cause a decrease in future shortleaf pine seed sources and an increase in litter accumulation rates. Grano (1949) found that pine regeneration was inversely related to litter depth and completely absent when litter depths exceeded 8 cm. Nevertheless, on xeric aspects where mesic hardwoods cannot establish or compete effectively, shortleaf pine may be maintained. In the Ozark Highlands, shortleaf pine seedling abundance is greatest on sites near the most xeric aspect (205°; Stambaugh 2001), and in the Boston Mountains of Arkansas the species achieves its highest site index near the same aspect (Graney and Ferguson 1971).

Conservation of Late-Successional Shortleaf Pine-Oak Forests

The ENA is an important example of a late-successional shortleaf pine-oak forest. It is one of the few intact stands of late-successional shortleaf pine forest in Missouri and thus provides rare information on growth and regeneration in an area undisturbed by logging. The low fire frequency contrasts with other Ozark pine sites that historically burned, prior to fire suppression efforts, every 1 to 15 years on average (Guyette and Cutter 1997). Although fire is typically important in maintaining early successional species such as shortleaf pine, we surmise that droughts may be important at this site for promoting shortleaf pine.

Spatial and temporal occurrence of gaps, as well as diverse vertical structure, provide a complex forest structure favored by many wildlife species (Meyer 1986, Haney and Lydic 1999). Snags and fallen logs from gaps are important components of forest ecosystems as they cycle nutrients and energy, provide habitat and food, serve as substrate for vascular plants and fungi, and influence rates of soil and water movement. Little is known about gap-phase regeneration in the Ozark Highlands region, especially in shortleaf pine forests. ~~However, the implications of further~~ Results from gap research [illegible] likely to become useful as many of the second-growth Ozark forests that resulted from the 1880–1920 logging era approach ages of understory reinitiation (Oliver and Larson 1996).

High red oak group mortality represented by gap makers at the ENA may be a result of regionwide oak decline that occurred throughout the 1980s (Law and Gott 1987, Jenkins 1992). Specifically, mortality of black oak was evident across the area and may be accounted for by the species' high abundance or the red oak group's relatively short longevity. Because of their importance in creating and recruiting into canopy gaps, black oak and other oaks will likely continue to be important in pine-oak forests of the Ozark Highlands.

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