Historic Shortleaf Pine (*Pinus echinata* Mill.) Abundance and Fire Frequency in a Mixed Oak - Pine Forest (MOFEP, Site 8)

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Abstract.—Historic and present day shortleaf pine (*Pinus echinata* Mill.) abundance was measured and compared using 84 plots along 16 transects in site 8 of the Missouri Ozark Forest Ecosystem Project. Remnant pine stumps were used to estimate historic pine density and to construct a dendrochronological record of fire frequency. There has been a 66-percent reduction in the relative abundance of pine from historic levels (circa 1900) within the study area. Present day pine abundance is only 21 percent of historic levels on slopes and only 25 percent of historic levels on ridges. Historic and present day pine abundance was not significantly different on toe slopes and in riparian areas. Elevation, slope, and aspect were significantly ($P < 0.05$) correlated with changes in pine abundance. Pine abundance was reduced at 60 percent of the plot locations, increased at 20 percent of the plots, and remained the same at 9 percent of the plots. Mean fire-free intervals were 6.3 years for the period 1701 to 1820 and 3.1 years for the period 1821 to 1900. Patterns in the change in pine abundance were consistent with changes in fire frequency and expected fire behavior at a landscape level. In some areas, such as riparian or road corridors, it was difficult to estimate historic pine abundance because of the disturbance of pine stumps and remnants.

Knowledge of historic shortleaf pine abundance and fire frequency in the oak-pine forests of the Ozarks has important implications for the ecology, regeneration, and perpetuation of this native forest cover. The different chemistry, anatomy, and physiology of gymnosperms adds to the diversity of Ozark forests and may have unknown ecological implications. In a mixed oak-pine forest, the crowns of shortleaf pine emerge above the hardwood canopy layer. Shortleaf pine crowns shade and shelter the surrounding forest in all seasons and provide the only canopy shelter from late fall to spring. The crowns of pines growing above the hardwoods add edge habitat to the surface of the forest canopy, changing its fractal dimensions. Kritz (1989) found that both the Cooper's (*Accipiter cooperi*) and the sharp-shinned hawks (*Accipiter striatus*) nest in conifer stands and trees in Missouri. Shortleaf pine was by far the most common choice by these accipiters for nesting trees. The removal of the shortleaf pine component from mixed oak-pine forest affects the canopy structure of the forest, the pyrodynamics and chemistry of the litter layer, as well as the composition of the herbaceous vegetation.

Surface fires dominate in mixed oak-pine forests. Pine litter is highly flammable because of its volatile high energy compounds, structure, and surface to volume ratio. Pine litter promotes the spread of light surface fires. Periodic surface fires in oak-pine forests result in fuel structures that reduce the likelihood of stand-replacing crown fires. Crown fires in mixed oak-pine forests are less common because hardwoods reduce the volatility of the vertical fuel structure. The discontinuous pine canopy also inhibits the spread of crown fires. Thus, shortleaf pine trees in oak-pine forests are less susceptible to crown injury and death than pine growing in pure stands. Consequently, pines may live longer in mixed oak-pine forests.

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Foresters and others have written about the loss of shortleaf pine (*Pinus echinata* Mill.) and the frequent occurrence of wildland fire in areas of the Ozarks following the nearly complete harvest of the species between the late 1800's and early 1900's (Cunningham and Hauser 1989, Galloway 1961, Krusekopf *et al.* 1921). Liming (1946) surveyed pine range data from "records and informed people ... and the general pine area by car and on foot." He determined the range of pine to be about 2,670,000 ha in the Missouri Ozark Highlands. By 1976, more detailed forest inventories showed that the pine and oak-pine types occurred on only 162,000 ha in the Missouri Ozarks (Essex and Spencer 1976). While qualitative losses of shortleaf pine from mixed oak-pine forests have been documented throughout its natural range in the United States, the degree of loss has not been quantified in relationship to site characteristics. Subjective judgements and selective memories of stands where shortleaf pine did not regenerate may have influenced the perception of how much pine was lost. Frequent wildland fires, extensive logging of shortleaf pine, and overgrazing from about 1880 to 1920 have been given as primary factors causing the loss of shortleaf pine throughout its natural range (Brinkman and Smith 1968, Cunningham and Hauser 1989, Fletcher and McDermott 1957, Law 1984, Liming 1946). Wildfire suppression, which began in the 1930's, favored the development of oak-dominated forests on sites that once had an abundance of pine.

This study compares the numbers of live shortleaf pine with estimated numbers of pine that grew about 100 years ago in site 8 of the Missouri Ozark Forest Ecosystem Project. Old pine stumps and remnants were used to develop a quantitative environmental history of changes in the abundance of shortleaf pine and to document the frequency of wildland fire. The specific objectives of the study were to:

1. Measure changes in shortleaf pine abundance,
2. Determine if there is any pattern to this change,
3. Quantify fire frequency and discuss its potential effects on changes in pine population,
4. Develop methods for comparing the current and historic population of shortleaf pine.

Although shortleaf pine is shade intolerant when mature, young seedlings are able to establish and survive for a time in a shaded understory (Baker 1992, Shelton 1995). Pine seedlings can survive under hardwood canopies for up to 30 years and still respond to release provided they receive sufficient light and moisture to maintain vigor (Brinkman and Rogers 1967, Brinkman and Smith 1968, Fris and Schmollinger 1984). This requires a low to moderately dense overstory (e.g., basal area <14 m^2/ha), a lack of understory hardwoods greater than about 2.5 cm in diameter at the base, and only moderate amounts of herbaceous vegetation (Baker 1992, Shelton and Baker 1992). These conditions characterized pine-oak forests in the 18th and 19th centuries.

Although their early growth is slow, shortleaf pine trees can outgrow most hardwood species in full sunlight if they establish before being overtopped by the hardwoods (Brinkman and Liming 1961). Once shortleaf pine overtops its competitors, it can maintain dominance to maturity (Baker 1992). Pine seedlings growing under dense shade in mature stands, or suppressed by dense oak sprout reproduction grow slowly and do not survive long. In fact, competition for light and moisture is a major cause of regeneration failure (Baker 1992). Initially, some shade benefits shortleaf pine seedlings by moderating environmental extremes and limiting the growth of competitors while the pines establish a root system. However, light levels (e.g., 25 percent of full sunlight) are too low for pine survival under fully stocked pine-oak stands that have a midstory of hardwoods (Shelton and Baker 1992). Although pines grow best in full sunlight, they can develop under moderately dense overstories (e.g., basal area 10 to 14 m^2/ha) where light levels are 55 percent of full sunlight when there is no midstory canopy. This shortleaf pine advance reproduction is competitive when released by overstory removal (Baker 1992, Shelton and Baker 1992).

Periodic light surface fires over long periods create the stand conditions that favor the establishment and development of shortleaf pine so that it can be recruited into the overstory when there is a major reduction in the overstory canopy. Shortleaf pine is well adapted to fire because bud clusters near the root collar produce sprouts when light surface fires kill the shoot. However, the ability to sprout declines with tree age and size, and mature pines or trees over 15 to 20 cm d.b.h. seldom, if ever, sprout (Brinkman and Rogers 1967, Lawson 1990).

The early logging history of the Missouri Ozarks followed patterns similar to those experienced in other eastern North American pine forests during European settlement. Large timber companies came to the Ozarks and began harvesting in the 1880's (Cunningham and Hauser 1989). Rivers and later railroads provided access throughout the natural range of shortleaf pine in Missouri. Any pine that met minimum specifications of a 12-in. diameter butt (Cunningham and Hauser 1989) was cut without regard for regeneration or the future forest (Record 1910). Many of the oaks and other hardwoods were left, producing a poor environment for pine regeneration. By 1910, 80 percent of the shortleaf pine forests in the Missouri Ozarks had been cut over, and most of the pine had been removed (Record 1910). The annual burning by settlers to improve range conditions and clear land, and the loss of seed-bearing pines resulted in few new pine seedlings becoming established. Similar patterns in settlement, land-use, fire history, and forest succession have been repeated throughout the pine forests of North America including the pine forests of the Ozark and Ouachita National Forests in Arkansas (Shelton and Baker 1992, Smith 1992) and the white and red pine forests in Ontario (Howe and White 1913).

The State of Missouri's once magnificent pine forests, after approximately 30 years of logging and European settlement, were summarized in 1910 by Samuel J. Record, Forest Assistant, Forest Service:

> "The forest resources of the state are being rapidly destroyed with no thought of their continuation. The shortleaf pine forests will soon be entirely cut over, with little opportunity for reproduction. The present methods of lumbering are very destructive and grub trees are rapidly taking the place of valuable timber. Forest fires are of too common occurrence and should be controlled."

Eventually fire control programs would be initiated in Missouri (circa 1930's) by State and Federal agencies, but not until after the shortleaf pine forests had been cut over and repeatedly burned and grazed. With fire control came a succession to hardwoods, primarily the oaks, on sites formerly occupied by shortleaf pine.

METHODS

The site 8 study area is about 335 ha and is located at the headwaters of an unnamed creek in the Pike Creek watershed within the Peck Ranch Wildlife Management Area in the southeast Missouri Ozarks. The study area is now dominated by oak species that are intermixed with some shortleaf pine. Surface fuels are predominantly hardwood leaf litter. The historic fire regime of the region surrounding the study site is one of frequent low-intensity fires resulting from anthropogenic ignitions (Guyette and Cutter 1997).

The presence of pine stumps was used in this study to reconstruct the number of trees per unit area. Shortleaf pine stumps and knots are preserved in the humid-continental climate of the Ozarks by their density and high oleoresin content. Injury by fire, felling, and mechanical stresses, such as wind, stimulates resin formation in the wood, preserving it for many decades. Preservation is, however, usually limited to larger stems because sapwood often decays much more rapidly than the resinous heartwood. Few pine stumps less than 15 cm in diameter were found. Thus, comparison of stumps to live trees is limited to those stems and stumps greater than 15 cm in diameter.

Transect starting points were chosen by a random selection of intervals, spaced at 0.16 km apart, along the access roads. Starting points were selected without replacement, so each point was used only once. At these locations, an azimuth was randomly selected from the set or range of compass points that transected the area from the road to a drainage. A total of 84 circular plots 30 m in diameter were then established every 100 paces along each transect (fig. 1). Sixteen transects were established in site 8. Stumps, and less often, knot traces were used to estimate the number of pines growing at the plots at the time of the first harvest. The remnants of shortleaf pine stumps were very distinctive and could be recognized easily by:

1. The presence of charred wood,
2. The growth of smooth white lichens on the light gray exterior of the wood,
3. A relatively smooth exterior,
4. Mosses at their base,
5. A ring of chert around the stump,
6. The resinous odor of the wood, and
7. The high density of the wood.

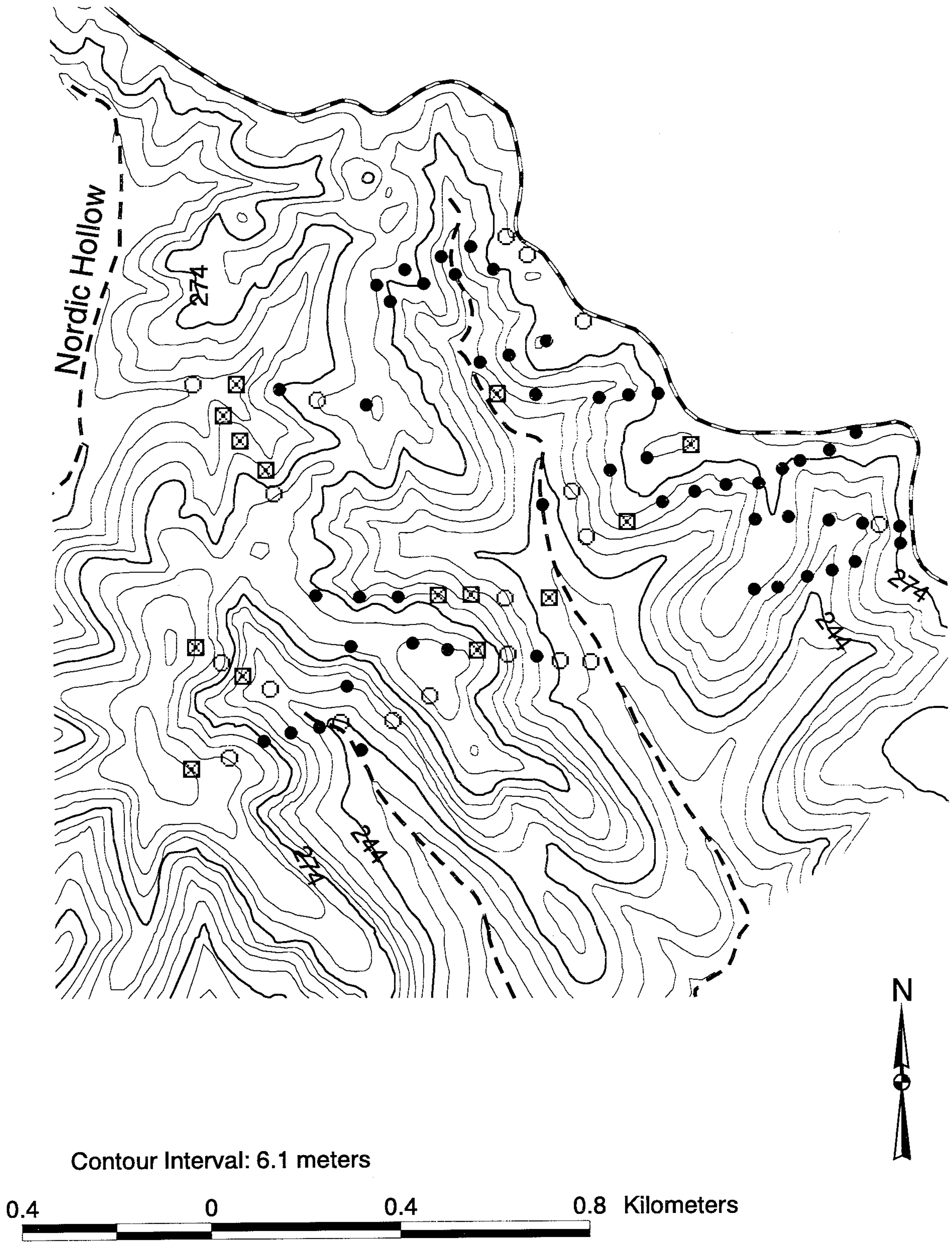

Figure 1.—*Map of study area with 16 transects, 84 sample sites, and changes in pine abundance. Empty circles indicate increased pine abundance, filled circles indicate decreased pine abundance, and circles with a slash indicate no change in pine abundance.*

Slope, aspect, and elevation were taken at each plot, and the number of pine stumps and live trees were counted. Elevation was measured with an altimeter and the aid of topographic maps. Plots were classified into one of four landscape types: (1) ridges, (2) slopes, (3) toe slopes, and (4) riparian areas.

Six fire-scarred cross sections of shortleaf pine remnants were collected in site 8. These cross sections were cut from the only stumps that had fire scars out of all the stumps observed along 5.1 km of transects. Four of the samples were located on south- and west-facing slopes, one on a ridge top, and one along a creek bottom. Compass orientation of the cross section, slope, and aspect were recorded for each sample, as was the location on a topographic map. Fire scars were identified by callus tissue, traumatic resin canals, charcoal, and cambial injury. All samples had charcoal present on the scarred exterior. Scars were dated to the first year of cambial injury.

Cross sections were surfaced with an electric hand planer with a sharp carbide blade. Where rings were very narrow or indistinct, the ring structure and cellular detail were revealed with sandpaper (220 to 600 grit), fine steel wool, or razor cuts. On each cross section, a radius (pith to bark ring series) was selected for measurement that had the (1) least amount of ring-width variability due to reaction wood, injury, or callus tissue, (2) maximum number of rings and (3) most year-to-year ring-width variance. Ring-width series from each sample were measured and plotted. Ring-width plots were used for visual cross-dating of growth patterns. Visual matching of ring-width patterns allows weighing of important *signature years* over years with low common variability between trees, an important environmental-biological process not considered in statistical correlation programs. Ring-width plots also aid greatly in identifying errors resulting from measurement and missing rings associated with injury or drought. The computer program COFECHA (Holmes *et al.* 1986) was used to ensure the accuracy of both relative and absolute dating of the samples by correlation analysis. Absolute dating of the pine remnants was accomplished by cross-dating with a ring-width chronology based on live shortleaf pine growing in Shannon County, Missouri (Guyette 1996a). The dates of the fire scars on the cross sections were identified and combined into a composite fire scar chronology that dated from 1656 to 1899. The computer program FHX2 was used to graph the fire chronology (Grissino-Mayer 1996).

RESULTS AND DISCUSSION

Shortleaf Pine Abundance

Overall change in pine abundance by landscape type in the study area was estimated by multiplying the area (hectares) of the landscape type by the mean density (stems/hectares) of pine stems or remnants (table 1). The number of stems or stumps was then summed for all landscape types. The overall result was (see table 1):

1. Estimated total number historic pine (> 15cm d.b.h.) = 17,143
2. Estimated total number present day pine (> 15cm d.b.h.) = 5,744.

Thus, present day pine abundance is about 34 percent of the historic level. This estimate excludes the four plantations that were sampled. If plantations are included, about 47 percent fewer shortleaf pines are growing now than in the past. Including data from plantations may bias the comparison of historic and present day pine because activities such as site preparation or fuelwood gathering may have removed many of the pine remnants.

The percentage of historic versus present day pine numbers (34 percent, excluding pine plantations) may be very conservative due to differences in the age, size, and stage of stand development of historic pines and pines now present. Shortleaf pine trees in the present day forest are less than 100 years old and rarely exceed 35 cm d.b.h. (Brookshire and Hauser 1993). Shortleaf pines in the historic forest attained ages of 250 to 300 years or more and were more than 70 cm d.b.h. If the existing population of pines were projected through with adjustments for growth and survival until they were similar in size and age to the historic pines, there would be fewer trees than observed in this study at this time. Thus, the 34-percent estimate (present day/historic) may actually underestimate the loss of pine.

The abundance of shortleaf pine declined most on the ridges and side slopes (table 1). Historic and current day pine abundances were similar on toe slopes. Riparian areas showed an insignificant increase ($P > 0.05$) in pine abundance over historic levels, possibly the result of pine

Table 1.—*Area, density, number of sites, and percent change for historic and present shortleaf pine abundances are given by landscape position. The density mean, range and standard deviation are given in stems (> 15 cm d.b.h.) per hectares. Following each landscape type the area is given (hectares). Ratio of current to historic density is: (total # current stems/total # historic stems)x100. Data for sums and totals are density times area. Data for ridges exclude plantations. T-values are given, and ** indicates that the historic and current abundance are significantly different (p < 0.01).*

Landscape position	Historic pine density				Current pine density				Plots	t-value	Current/ historic density
	Density	Range	SD	Total #	Density	Range	SD	Total #			
									n	*t*	*Percent*
Ridges (80)	53.6	0-113	40.4	4,279	11.1	0-28	12.6	886	14	3.75**	21
Slopes (223)	52.9	0-184	39.7	11,821	13.2	0-85	23.0	2,949	46	5.87**	25
Toe slopes (3)	45.7	0-85	28.4	122	45.7	0-99	30.7	122	13	0.00	100
Riparian (29)	32.3	14-57	22.7	921	62.7	14-113	42.0	1,787	7	1.68	194
Sums and % change				17,143				5,744	80		34
Sums and % change with plantations				17,381				9,239	84		53

seeding on abandoned agricultural fields along the streams.

The change in the abundance of shortleaf pine was significantly correlated with elevation, slope, and aspect (table 2). The loss of pine was greatest on slopes with a west or south aspect and least on slopes facing east or north, which may be a result of the greater historic abundance of pine on sites with south and west aspects, where the frequency of fires was greater on these hotter and drier aspects. There are fewer pine trees today than historically at higher elevations in the landscape. This may be due to increased fire intensity from the preheating of stems on upper slopes. Thus, sites with western aspects and moderate slopes (6 to 23 degrees) exhibited a strong correlation (r = -0.60, p < 0.001) among estimates of pine abundance and elevation. Fire was probably a major factor in reducing pine regeneration in relation to landscape type because it was likely to occur more frequently and burn at higher intensities on slopes and upper ridge tops than in riparian areas and along the toe of slopes. At the landscape level, moderate slopes facing south and west have less pine today than in historic times (fig. 1).

About 60 percent of the plots (fig. 2) measured showed a decrease in the number of shortleaf pine stems compared to historic abundance estimates from pine stumps. Of these plots, 41 percent occupied slope positions, 12 percent

Table 2.—*Correlation of plot variables with historic, present, and differences in pine density. Difference is the number of pines > 15cm d.b.h. presently growing on the plots minus the number of pine stumps. Correlations with aspect are for all sites with slopes between 6 and 23 degrees. Correlations (r) are with the natural log (ln) of slope. P-values are given with each correlation coefficient.*

Class	Elevation		Slope (ln)		Aspect	
	r	p-value	r	p-value	r	p-value
Historic	0.08	(0.510)	0.20	(0.080)	0.46	(0.0001)
Present day	-0.35	(0.002)	-0.26	(0.019)	0.17	(0.192)
Difference	-0.28	(0.013)	-0.32	(0.004)	-0.29	(0.021)

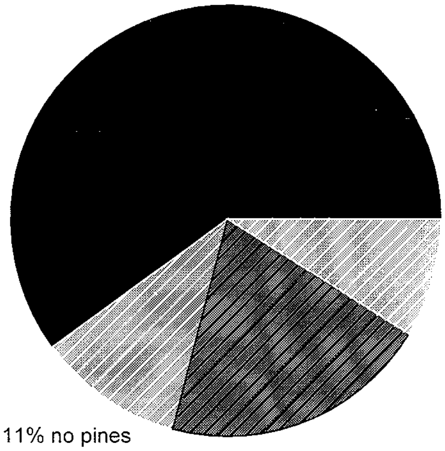

Figure 2.—*Percentage of sample sites showing increases, decreases, and no changes in pine abundance.*

occurred on ridge tops, 6 percent were on toe slopes, and 1 percent were in riparian areas. About 20 percent of the plots measured showed an increase in the number of shortleaf pine stems over estimates of historic abundance. Another 11 percent of the plots measured had no evidence of shortleaf pine growing on the plots during either the present or historic period. About 9 percent of the plots had a present day pine abundance similar to historic densities.

The density of both historic and present day pine on the sites was highly variable. Standard deviations (table 1) were large, about 30 stems per hectare overall. The sample of 84 plots (168 counts of historic and present day pine) was sufficient to detect overall changes in pine density since historic times, especially since the difference between historic and present day pine density was so large, about 40 stems per hectare for ridges and slopes. This number of plots yields overall estimates of mean historic and present day pine density that have better than a 95-percent probability of falling within plus or minus seven stems per hectare ($n=3.92*sd^2/L^2$, or $72=3.92*30^2/7^2$) (Snedecor and Cochran 1989). Comparisons of changes in pine density within and among various ecological land types in site 8 are less precise because of the high variability and relatively low sample size. For instance, on toe slopes, about 35 plots, instead of the measured 13 plots, would be needed for a 95-percent probability of the estimates being within plus or minus 10 stems per hectare ($n=3.92*sd^2/L^2$, or $35=3.92*30^2/10^2$) (Snedecor and Cochran 1989). Thus, there could be undetected differences on toe slopes. Although the standard deviations of density estimates for ecological land types are high, the large differences (about 32 stems per hectare) such as those between toe slopes and slopes for present day pine densities (table 1) allow the detection of differences even with low numbers of plots ($n=3.92*sd^2/L^2$, or $14=3.92*30^2/16^2$) (Snedecor and Cochran 1989).

The use of *ridge to drainage* transects has advantages and disadvantages for comparing present day and historic pine abundances. The *ridge to drainage* transects oversample the toe slopes and riparian areas because headwater locations have much more area in ridge and slopes than in riparian areas. This sample bias is, however, not a problem if accurate information on the area of these ecological land types is available and can be used for estimating the abundance of pine from estimated pine densities for each land type. On the other hand, an advantage to this method is that all land types get sampled with much less effort than is required by a random sampling scheme.

Fire Frequency

Although at least 1,000 pine stumps and remnants were observed along the transects, less than 10 had external and identifiable fire scars. This may be in part due to the relatively large size of the sample trees and their inherent ability to resist scarring. The low incidence of scarring may also be due to less sustained heat from a fine flash fuel matrix, such as might be provided by pine litter and grasses (fig. 4). Also, the moderate slopes of the area (fig. 1) may have decreased the likelihood of scarring by reducing slope-induced fire severity. Only four of the samples were cross-dated and used in constructing a fire chronology.

Fire-free intervals at Nordic Hollow (table 3, fig. 3) were comparable by historic period to fire-free intervals reconstructed for other fire histories in the Current River region. Fire-free intervals at nearby Stegall Mountain (8 km to the north) and Mill Creek (8 km to the northeast) were within one standard deviation of

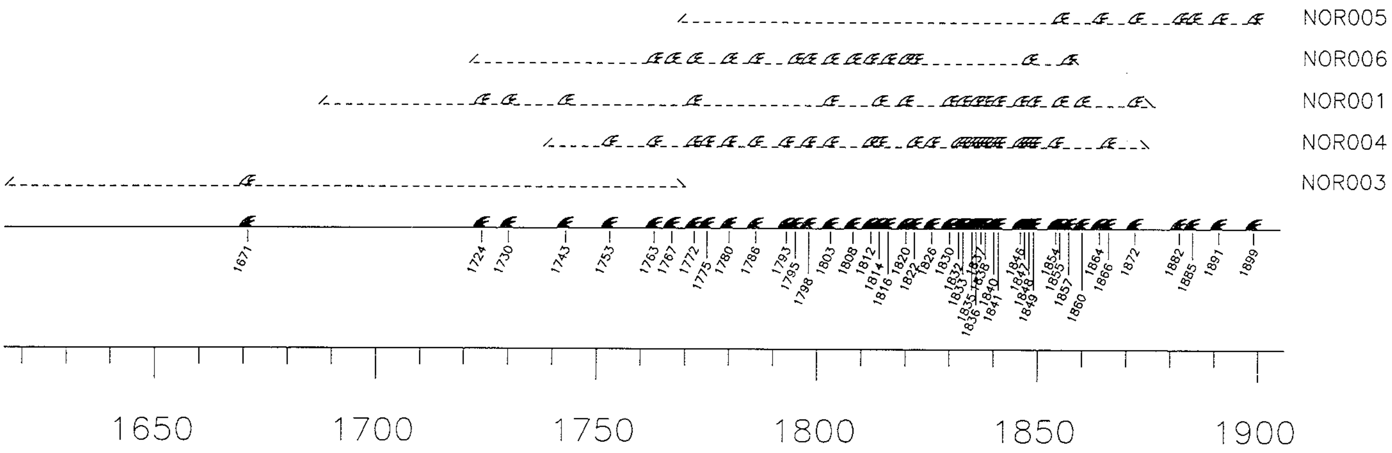

Figure 3.—*Fire scar dates from four stumps and their composite fire scar chronology for the study area. Note that for about 100 years before pine logging (circa 1900's) fires burned so frequently that they inhibited pine regeneration.*

Table 3.—*Means, ranges, and standard deviations for fire-free intervals at Nordic Hollow by historic period. There were insufficient data for the early period as well as for the period after 1900. The mean fire-free intervals for the Native American period (1701-1820) and the Euro-settlement period (1821-1900) are significantly different (t-statistic = 3.41, p > |t| = 0.002).*

Period	**Mean**	**Range**	**Standard deviation**
1701-1820	6.3	24 - 2	3.0
1821-1900	3.1	10 - 1	2.4

those at Nordic Hollow (site 8, MOFEP) (Guyette and Cutter 1997).

During the 1700's, several extensive fires burned over the Nordic Hollow (table 4). At Nordic Hollow, five of the 13 fire years in the 1700's were among the top 10 fire years in the Current River watershed (Guyette and Cutter 1997). The size and extent of these early fires indicate that they may have been severe (Guyette 1996b). Osage, Quapaw, Shawnee, and Delaware visited the Current River region (Stevens 1991). Between 1780 and 1820, a time of aboriginal immigration into the Current River region, the mean fire-free interval (MFI) was 6.3 years. For example, approximately

Table 4.—*Top 10 fire years during the 1700's in the Current River watershed (Guyette 1996b) ranked by area burned and compared to the percent of trees scarred for the same years in Nordic Hollow.*

Rank	**Year**	**Current River Area (km^2)**	**Nordic Hollow (% trees scarred)**
1	1780	1,109	50
2	1728	1,005	0
3	1777	924	0
4	1704	809	0
5	1753	623	25
6	1772	619	75
7	1795	607	50
8	1713	535	0
9	1757	440	0
10	1786	440	50

6,000 Cherokee were living in southeast Missouri and northeast Arkansas at the time (1803) of the Louisiana Purchase (Gilbert 1996). Their settlement in the region increased ignition sources and brought a tradition of burning from the aboriginal peoples of the southeastern United States (Hammett 1992).

Euro-American movement into this area began in the early 1800's. They settled in the Pike Creek watershed (< 5 km from the study site)

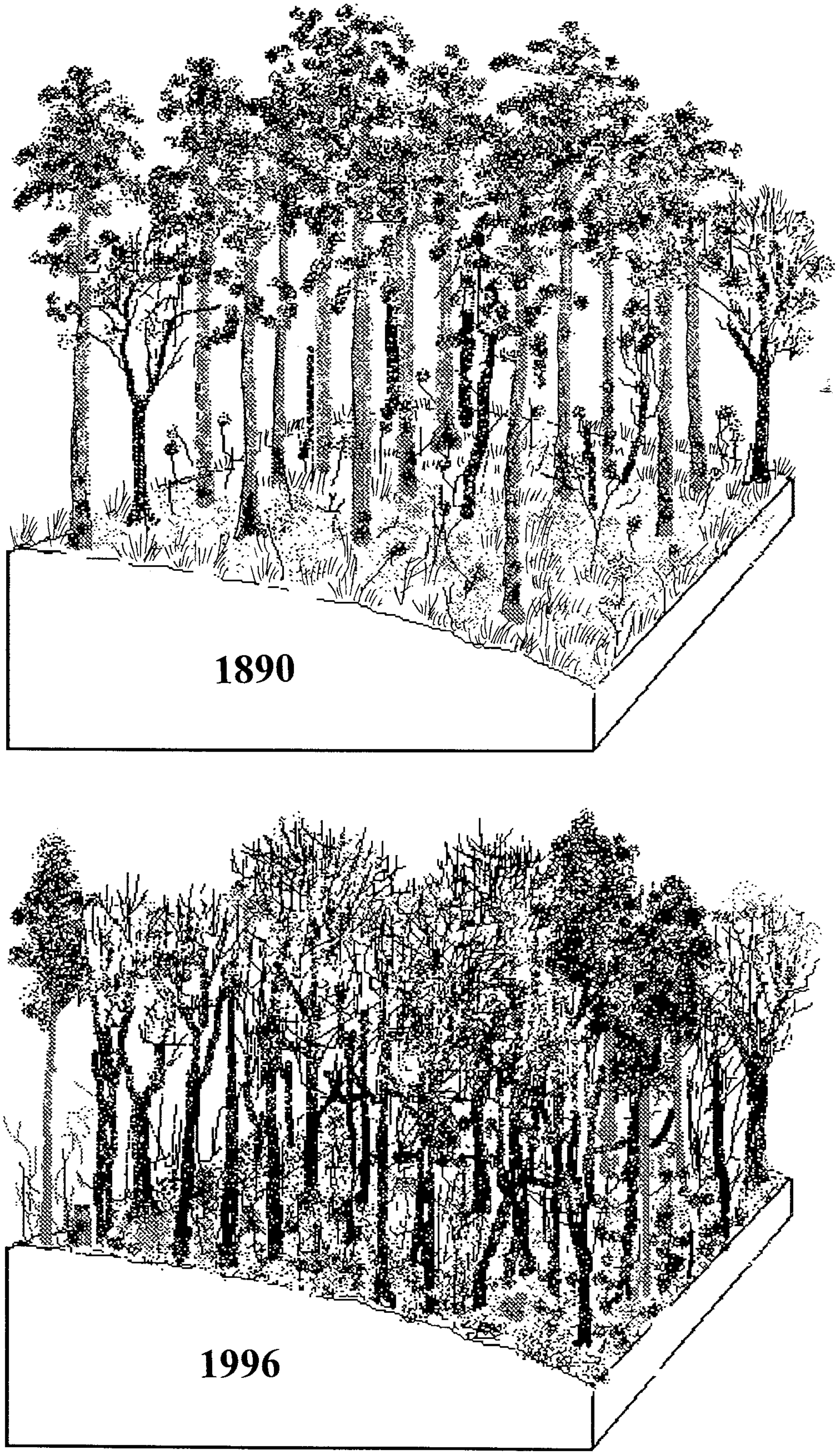

Figure 4.—*Artist concept of changes at site 8 over the last 100 years. Illustrated on a 0.25-ha section are changes of: 1. shortleaf pine to oak dominance, 2. canopy structure and density, 3. the surface fuels from pine litter and grasses to oak leaves, 4. the distribution of pine to lower landscape positions.*

between 1812 and 1860 (Stevens 1991). Settlement by Euro-Americans continued to increase throughout the 19th century, and their land-use practices drastically altered the character of the Ozark forest. Their use of fire to improve grazing conditions in the forests and to clear land for agriculture caused significant increases (P = 0.002) in fire frequency, resulting in an MFI of 3.1 years from 1821 to 1900. The extensive logging of shortleaf pine began in this area of Missouri in the late 1880's and peaked at the turn of the century; by 1920, much of the original pine forest had been harvested (Cunningham and Hauser 1989). No doubt, the frequent fires and heavy amounts of slash left by the loggers led to an increase in fire intensity that affected pine regeneration and thus, the nature of our modern day forests.

Fire and Pine Abundance

Four fire-related factors probably led to the present day density of shortleaf pine in site 8. These factors are consistent with the hypothesis that frequent fire had a negative effect on pine regeneration. They are:

1. Frequent fires during the 100 years (MFI = 3.1 years from 1821-1900) before the pine logging era, which eliminated or reduced advanced pine regeneration.
2. The removal of most, if not all, pines of seed bearing age by logging and intense slash fuel fires.
3. Continued frequent burning after pine logging inhibited pine recruitment.
4. Increased competition for light and nutrients from new sprouts of trees in the red oak group.

Before 1790, fires were frequent enough to promote regeneration of pine seedlings but not so frequent as to prevent recruitment of pine into the overstory. From 1701 to 1790, the MFI was 8.9 years, and it was common for individual fire-free intervals to be from 10 to 20 years. This disturbance regime favored the establishment of shortleaf pine and allowed recruitment of pine into the overstory. Fire improves seed bed conditions for shortleaf pine by reducing the depth of litter or by exposing mineral soil (Baker 1992). Although shortleaf pine does not require mineral soil for germination, seedling establishment decreased as leaf litter depths increased above 6 cm (Shelton and Wittwer 1992, Shelton 1995). Periodic surface fires also favor the development of young pines in the understory by controlling the subcanopy hardwoods, woody perennials, and herbaceous ground cover (Shelton and Baker 1992, Shelton 1995).

Growth of shortleaf pines beyond the seedling stage requires a fire-free period sufficiently long to permit the development of features that increase the resistance of pine to fire. Pines that are 4 to 5 m tall can survive low intensity fires (Baker 1992), and open-grown pines can reach heights of 11 to 12 m by age 25 on site indices between 16.7 and 18.3 m (Brinkman and Rogers 1967). Increasing the distance between the crown and ground reduces the probability that pines will experience crown scorch. Also, bark thickness increases as pines grow, which protects the cambium from heat injury caused by fire. Fires in the study area were frequent enough to maintain low fuel loadings and thus reduce the severity of subsequent fires. Fires were most likely low intensity surface fires in all but the driest years. Only five of the ten fires that occurred between 1701 and 1790 were hot enough to scar 50 percent or more of the pines sampled in this study (fig. 3). At the study site, individual fire-free intervals between 1701 and 1790 were long enough to allow shortleaf pine to grow beyond the seedling stage and develop the characteristics needed to survive fires of low to moderate intensity.

The open, parklike character of shortleaf pine-oak forests of the Ozarks in Missouri and Arkansas at the time of Euro-American settlement has been reported and is attributed to periodic burning (Buckner 1989). Early European settlers continued the aboriginal practice of woods burning but with increased frequency (fig. 3) (Pyne 1982, Sutherland 1997). This maintained and even enhanced the open nature of Ozark pine forests. At the beginning of the 20th century, these forests were severely cut over with low to moderate levels of overstory stocking, little or no undergrowth, and ground flora dominated by grasses (Cunningham and Hauser 1989, Record 1910).

Fire frequency increased as the area around the study site was settled by aboriginal peoples that had been pushed west from eastern regions of the United States and by Euro-American immigrants. Fires became more frequent from 1820 through 1900. The longest fire-free interval during this period was 10 years, which is probably an underestimate because dated fire scars were based on only one sample stump in the latter part of the record (1872-1899). Fires during this period were probably frequent enough to kill pine seedlings and sprouts, thus eliminating the recruitment of pines for about 100 years before the removal of mature pine from the stand by logging. Record (1910) surveyed the shortleaf pine forest region in Missouri during the early 1900's. In uncut mature pine stands in the Ozarks, he found that the surface fires that burned every year eliminated young pine from the understory and encouraged an undergrowth of *"inferior species"* (i.e., blackjack oak and post oak).

The pattern of change in pine abundance is consistent with a reduction in pine regeneration caused by fire in the various landscape types sampled in this study. Historically, riparian areas had fewer pines than slopes and ridges (table 1). Although pine numbers increased in riparian areas over historic times, the increase was not significant ($P > 0.05$). With lower densities of pines in riparian areas historically, slash fires would have been less intense. Today, pine abundance on toe slopes is similar to historic pine densities. Fire intensity and frequency are reduced on toe slopes by landscape position and surface fuels. Many toe slopes in the study area had a high percentage of rock cover, which would act to reduce fire temperatures, lower herbaceous fuel loading, and protect seedlings. Toe slopes are more mesic, and have greater fuel moisture and slower wind speeds, thus reducing fire intensity. Fire intensities are lower along toe slopes than in upper slope positions because there is no preheating of fuels from fires burning below. On the other hand, at upper slope and ridge sites, where pine abundance has decreased, preheating from the slopes below probably increased fire intensity and pine mortality. Wind speeds are also generally greater on both upper slope and ridge top sites, while fuel moisture tends to be low. Upper slopes and ridges have been found to have more frequent fires than sites at lower elevations in the landscape because fires spread more rapidly uphill (Guyette 1996b).

CONCLUSIONS

About 100 years after the removal of shortleaf pine from site 8, the present day numbers of shortleaf pine are 34 percent of the estimated historic (1890) population. Inclusion of shortleaf pine plantations reduces the overall loss in abundance of shortleaf pine to about 47 percent of historic levels. Data from plantations, however, may be seriously biased by stump removal.

Changes in the relative abundance of pine by slope position and aspect appear to be consistent with the dendrochronological fire history and landscape-level effects on fire behavior. The comparative numbers of pine were most affected along ridges and slopes where fire intensity would be greatest because of exposure to increased wind velocity and preheating of fuels and stems from downslope fire. Frequent burning following the near complete removal of merchantable-size shortleaf pine caused a reduction in pine regeneration on slopes and ridges. Early reports describe advance reproduction as minimal at the time of these early harvests due to the high frequency of burning in the preceding 100 years. Frequent post-harvest fires killed pine seedlings that may have been present or became established following harvest. The intensity of slash fires may have contributed to the reduction in the number of pole-size and other residual pines after harvest.

Current pine abundance on toe slopes and in riparian areas was not significantly ($P > 0.05$) different from historic populations. Although current pine numbers in riparian areas appeared to have increased, high variability, low numbers of sample plots, and possible bias from stump removal leave the change in pine populations in this ecological land type in question. The clearing of forests for agricultural purposes in riparian areas, followed by abandonment of fields and pastures, could have created favorable conditions for pine regeneration and development. The method of using pine remnants for estimating early pine populations is less reliable for areas that experienced high anthropogenic disturbances, such as riparian areas that may also have had low initial pine densities.

Differences in pine abundance were related to slope, elevation, and aspect. The relative abundance of pine was maintained on very steep, rocky slopes, but these sites were rare in the study area. This maintenance of pine numbers relative to earlier populations may be explained by the high percentage of rock cover and the low amount of surface fuel, which likely mitigated the adverse effects of frequent fires on pine regeneration on these sites. The loss of pine was greatest on south- and west-facing slopes at the higher elevations and least on low east- and north-facing slopes. The strongest correlation of comparative pine abundance with elevation occurred at plots with western aspects and moderate (6 to 23 degrees) slopes.

The use of pine remnants to estimate historic pine abundance provides a quantitative means of measuring changes in pine density with limitations imposed by anthropogenic disturbance of pine remnants. Although this study considered a limited area of the natural range of shortleaf pine and oak-pine forests of the Ozarks, we believe that it presents an approach that can be used to estimate pine abundance on a larger scale. It also provides a means of estimating historic levels of pine where early records cannot be found. Because of the limited scope of this study, it should not be applied to characterize the many changes in shortleaf pine abundance that have taken place across the Ozarks.

LITERATURE CITED

Baker, J.B. 1992. Natural regeneration of shortleaf pine. In: Brissette J.C.; Barnett, J.P., comps. Proceedings of the Shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 102-112.

Brinkman, K.A.; Liming, F.G. 1961. Oak and pine reproduction responds to overhead release. Journal of Forestry. 59: 341-346.

Brinkman, K.A.; Rogers, N.F. 1967. Timber management guide for shortleaf pine and oak-pine types in Missouri. Res. Pap. NC-19. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 15 p.

Brinkman, K.A.; Smith, R.C. 1968. Managing shortleaf pine in Missouri. Sta. Bull. 875. Columbia, MO: University of Missouri-Columbia, Agricultural Experiment Station. 35 p.

Brookshire, B.; Hauser, C. 1993. The Missouri Ozark Forest Ecosystem project: the effects of forest management on the forest ecosystem. In: Gillespie, Andrew R.; Parker, George R.; Pope, Phillip E.; Rink, George, eds. Proceedings, 9th Central hardwood forest conference; 1993 March 8-10; West Lafayette, IN. Gen. Tech. Rep. NC-161. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 289-307.

Buckner, E. 1989. Evolution of forest types in the Southeast. In: Waldrop, T.A., ed. Proceedings of Pine-hardwood mixtures: a symposium on the management and ecology of the type; 1989 April 18-19; Atlanta, GA. Gen. Tech. Rep. SE-58. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 27-33.

Cunningham, R.J.; Hauser, C. 1989. The decline of the Ozark Forest between 1880 and 1920. In: Waldrop, T.A., ed. Proceedings of Pine-hardwood mixtures: a symposium on the management and ecology of the type; 1989 April 18-19; Atlanta, GA. Gen. Tech. Rep. SE-58. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 34-37.

Essex, B.L.; Spencer, J.S. 1976. Timber in Missouri. Resour. Bull. NC-30. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 108 p.

Fletcher, P.W.; McDermott, R.E. 1957. Influence of geologic parent material and climate on distribution of shortleaf pine in Missouri. Res. Bull. 625. University of Missouri. 42 p.

Fris, F.; Schmollinger, M. 1984. Artificial reforestation of shortleaf pine - planting. In: Artificial reforestation of shortleaf pine: a Missouri seminar; 1984 May 9; Salem, MO. Rolla, MO: U.S. Department of Agriculture, Forest Service, Mark Twain National Forest: 73-87.

Galloway, J.A. 1961. John Barber White: lumberman. Columbia, MO: University of Missouri. 267 p. Ph.D. dissertation.

Gilbert, J. 1996. The trail of tears across Missouri. Columbia, MO: University of Missouri Press. 122 p.

Grissino-Mayer, H.D. 1996. Software for the analysis of fire history. Tucson, AZ: Laboratory of Tree-Ring Research, University of Arizona. 117 p.

Guyette, R. 1996a. Tree-ring data, Ontario and Missouri. International tree-ring data bank. IGBP PAGES/World Data Center-A for Paleoclimatology data contribution Series # 96-004. Boulder, CO: NOAA/NGDC Paleoclimatology Program.

Guyette, R.P. 1996b. A tree-ring history of wildland fire in the Current River watershed. Fire history report. Jefferson City, MO: Missouri Department of Conservation. 74 p.

Guyette, R.P.; Cutter, B.E. 1997. Fire history, population, and calcium availability in the Current River watershed. In: Pallardy, S.G.; Cecich, R.A.; Garrett, H.G.; Johnson, P.S., eds. Proceedings of the 11th Central hardwood conference; 1997 March 23-26; Columbia, MO. Gen. Tech. Rep. NC-188. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 354-372.

Hammett, J.E. 1992. Ethnohistory of aboriginal landscapes in the southeastern United States. Southern Indian Studies 41: 1-51.

Holmes, R.L.; Adams, R.K.; Fritts, H.C. 1986. Quality control of crossdating and measuring: a users manual for the program COFECHA. In: Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Tucson, AZ: Laboratory of Tree-Ring Research, University of Arizona: 41-49.

Howe, C.D.; White, J.H. 1913. Trent watershed survey. Toronto, ON: The Bryant Press. 156 p.

Kritz, K.J. 1989. Nesting ecology and nest site habitat of sharp-shinned and Cooper's Hawks in Missouri. Columbia, MO: University of Missouri. 84 p. M.S. thesis.

Krusekopf, H.H.; DeYoung, W.; Watkins, W.I.; Deardorff, C.E. 1921. Soil survey of Reynolds County, Missouri. Washington, DC: U.S. Department of Agriculture, Bureau of Soils. 30 p.

Law, J.R. 1984. The range of shortleaf pine in Missouri. In: Artificial reforestation of shortleaf pine: a Missouri seminar; 1984 May 9; Salem, MO. Rolla, MO: U.S. Department of Agriculture, Forest Service, Mark Twain National Forest: 1-8.

Lawson, E.R. 1990. Shortleaf pine. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: conifers. Agric. Handb. 654. Vol. 1. Washington, DC: U.S. Department of Agriculture, Forest Service: 316-326.

Liming, F.G. 1946. The range and distribution of shortleaf pine in Missouri. Tech. Pap. 106. Columbus, OH: U.S. Department of Agriculture, Forest Service, Central States Forest Experiment Station. 4 p.

Pyne, S.J. 1982. Fire in America. Princeton, NJ: Princeton University Press. 654 p.

Record, S.J. 1910. Forest conditions of the Ozark Region of Missouri. Bull. 89. Columbia, MO: Agricultural Experiment Station, University of Missouri. 280 p.

Shelton, M.G. 1995. Effects of seed production, seed bed condition, and overstory basal area on the establishment of shortleaf pine seedlings in the Ouachita Mountains. Res. Pap. SO-293. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 13 p.

Shelton, M.G.; Baker, J.B. 1992. Uneven-aged management of pine and pine-hardwood mixtures in the Ouachita Mountains. In: Brissette, J.C.; Barnett, J.P., comps. Proceedings of the Shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 217-224.

Shelton, M.G.; Wittwer, R.F. 1992. Effects of seed bed condition on natural shortleaf pine regeneration. In: Brissette, J.C.; Barnett, J.P., comps. Proceedings of the Shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 124-139.

Smith, O.D., Jr. 1992. Historical perspectives on regeneration in the Acadia and Ozark Mountains — the Ozark National Forest. In: Brissette, J.C.; Barnett, J.P., comps. Proceedings of the Shortleaf pine regeneration workshop; 1991 October 29-31; Little Rock, AR. Gen. Tech. Rep. SO-90. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 7-11.

Snedecor, G.W.; Cochran, W.G. 1989. Statistical methods. Ames, IA: Iowa State University Press. 503 p.

Stevens, D.L., Jr. 1991. A homeland and a hinterland the Current and Jacks Fork Riverways. Van Buren, MO: Historic Resource Study, Ozark National Scenic Riverways, National Park Service. 248 p.

Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. In: Pallardy, S.G.; Cecich, R.A.; Garrett, H.G.; Johnson, P.S., eds. Proceedings of the 11th Central hardwood conference; 1997 March 23-26; Columbia, MO. Gen. Tech. Rep. NC-188. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 172-183.