SUCCESSIONAL TRENDS OF SIX MATURE SHORTLEAF PINE FORESTS IN MISSOURI

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ABSTRACT.—Many of Missouri's mature oak-shortleaf pine (*Quercus-Pinus echinata*) forests are in a mid-transition stage characterized by partial pine overstory, limited pine recruitment, and minimal pine regeneration. Restoration of shortleaf pine communities at a large scale necessitates the understanding and management of natural regeneration. To understand late-successional conditions of shortleaf pine forests, we conducted a complete survey of woody vegetation and canopy openings at six uncut and old second-growth oak-pine stands in southeastern Missouri. A total of 121 canopy gaps were mapped and measured in terms of their size, age, and vegetation structure. Shortleaf pine was a common canopy replacement tree along with black oak (*Quercus velutina*), white oak (*Quercus alba*), and hickories (*Carya* spp.). The abundance of shortleaf pine appears to be diminishing, however, owing to the absence of shortleaf in understory and regeneration layers. The resulting forest probably will consist almost exclusively of hardwoods. Shortleaf pine regeneration in canopy openings was limited by aspect, seed source, and litter depth. In addition to their current conditions, information from these forests provides insight into the future development and management needs of younger oak-pine communities. In forests where regeneration and recruitment of shortleaf pine are lacking, restoration efforts require timely action because the overstory seed source is crucial to preserving the shortleaf pine component. These findings contribute to an understanding of shortleaf pine forests, and can ultimately determine restoration and management guidelines for shortleaf pine forests in the Missouri Ozarks.

INTRODUCTION

Although historic evidence suggests that oak-shortleaf pine (*Quercus-Pinus echinata* Mill.) forests of the Ozark region were strongly influenced, if not perpetuated, by recurring fires for at least 300 years prior to the 16th century (Masters and others 1995, Guyette and others 2002, Guyette and others 2006), contemporary policies and logistics often reduce the occurrence of burning. This situation is an important issue to the conservation of many fire adapted species, including shortleaf pine. In general, the disturbance regime of shortleaf pine forests has changed from one that included fire to one that primarily excludes fire and is represented by small-scale events (Stambaugh and others 2002) that result in canopy gap openings. In an attempt to understand the effects of these changes on species composition and forest succession, we examined canopy gap disturbances and forest stand dynamics of six representative uncut and old second-growth oak-shortleaf pine forests. Our objectives were to: 1) describe the current overstory composition, 2) characterize and quantify the frequency of canopy gap disturbances, and 3) identify trends in vegetation development within canopy gaps, specifically addressing the potential for shortleaf pine regeneration and recruitment to the overstory.

METHODS

Study Site Descriptions

Study sites were located throughout the Ozark Highlands region of southeastern Missouri in an area that occurs within the natural shortleaf pine range (Liming 1946). Investigations were conducted at the Eck Natural Area, Alley Spring, Indian Trails Conservation Area, Greer Spring, and two sites on the Mark Twain National Forest—one near the town of Bixby and another near Slabtown (Table 1). Detailed descriptions of study areas were presented in Stambaugh (2001). Study sites were selected non-randomly due to the limited availability of shortleaf pine forests exhibiting late-successional forest characteristics. Guidelines for selecting study sites were:

1. Average age of dominant overstory shortleaf pines > 100 years
2. Forested area greater than 10.1 hectares
3. A minimum of 25 percent overstory composition in shortleaf pine
4. No apparent anthropogenic disturbances, i.e., logging operations or prescribed burning
5. Some evidence of canopy gap disturbances, as reflected in a multi-structured canopy

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Data collection

Canopy gap sampling was conducted during 1999 and 2000 in accordance with guidelines established by Runkle (1992), with modification. All gaps were located by systematically traversing the study sites. Canopy gaps were defined as the opening in the overstory forest canopy caused by the death of 1-10 trees. All observed canopy gaps 6 years old and less were sampled; therefore the data represent a complete "inventory" of gaps for each site. For each gap, measurements taken included gap size, gap maker(s) (i.e., trees that formed the gap), gap age, woody species, litter depth, and trees adjacent to the canopy opening. Expanded gap size was measured as the distance across the length and width of the gap to and from the boles of the trees surrounding the gap. Gap size was determined using the area of an ellipse. Using these data, we calculated rotation interval by summing the entire area in gaps, and dividing by six (the number of years in which gaps were considered) to create an annual gap area. Annual gap area was then divided into the total area of the site to determine the rotation interval. Rotation interval represents the number of years required for the entire area to be replaced by canopy gaps (i.e., disturbance frequency).

Basal increment cores were taken from at least one understory shortleaf pine > 1.37 m in height in each gap. Increment cores from various trees within the canopy gap provided an accurate determination of gap age and were used in analyzing recruitment years, growth rates, and the potential for shortleaf pine recruitment to the overstory.

Vegetation Sampling

At randomly determined distances (between 150 and 300 m) along transects, the overstory was sampled using the point centered quarter method (Cottam and Curtis 1956). The nearest live tree to plot center that was > 25 cm diameter at breast height (DBH) was measured in each quadrant. The tree species, DBH (to the nearest 0.1 cm), and horizontal distance from plot center to the center of the stem (to the nearest 0.1 m) were recorded. Importance values were calculated by summing the relative density, frequency, and dominance values (i.e., basal area) for each tree species.

In canopy gaps all woody stems > 1.37 m in height occurring within the expanded gap area were considered to be in the understory; stems were identified by species and recorded in 2 cm diameter classes. The tallest individuals were considered the most probable gap replacements if the individual tree had at least 20 percent live crown ratio and was well positioned within the canopy opening. Replacement tree species were noted, and DBH measurements (to the nearest 0.1 cm) and height measurements (to the nearest 1 m) were made. If the replacement tree was a shortleaf pine, a basal core was taken to determine age and growth rate.

All woody stems < 1.37 m in height occurring within the expanded gap area were considered to be in the regeneration layer, and four 1-m^2 circular regeneration subplots were located equidistant between gap center and the expanded gap edge in the four cardinal directions. Within subplots all woody species were tallied. Additionally, a one-minute timed count was used to determine the number of pine seedlings occurring in both the southern and northern half of the expanded gap area in order to quantify pine regeneration in gaps. The average litter depth of subplots was measured (four measurements per subplot) to the nearest cm from the top of the O horizon to the top of the litter. The percentage of the forest floor covered in leaves, needles, and exposed area was estimated for the ground surface of the expanded gap area.

RESULTS AND DISCUSSION

Gap Dynamics and Canopy Gap Characteristics

Across all six sites, we identified 121 gaps, and the Eck Natural Area had the greatest number of canopy gaps of any site (n = 48) as well as the greatest mean gap size (table 1). The Alley Spring site had the greatest area in gaps (522 m^2 ha^{-1}). Gap sizes were normally distributed at the Eck Natural Area and gaps constituted 4.0 percent of the total area. Mean gap size was 421 m^2 and sizes ranged from 104 - 1583 m^2. Unlike other sites, the Eck Natural Area had a relatively high number of gaps > 500 m^2. Canopy gap ages showed increasing frequency from recent gaps to gaps 6 years old. The majority of the identified canopy gaps at Eck Natural Area were created during 1993 and 1994. At the Alley Spring site, 28 canopy gaps were identified, accounting for 5.2 percent of the total area. Mean gap size was 322 m^2 and sizes ranged from 105 to 847 m^2.

Indian Trails, Greer Spring and Bixby each had nearly the same area in gaps, although we identified 13, 9, and 9 gaps respectively from these three sites. Canopy gaps constituted 1.6 percent of the total forested area at Indian Trails, Greer Spring, and Bixby. At Indian Trail, mean expanded gap size was 247 m^2 and sizes ranged from 87 to 394 m^2. Mean expanded gap size for Greer Spring was 323 m^2 and sizes ranged from 261 to 419 m^2, therefore generally larger than at Indian Trail. At Bixby, mean expanded gap size was 241 m^2 and gap sizes were more variable than at any other site, ranging from 15 to 404 m^2.

Fourteen canopy gaps were identified from the Slabtown site, constituting 1.8 percent of the total area or 186 m^2 ha^{-1}. Mean expanded gap size was 148 m^2 and sizes ranged from 30 to 280 m^2. Despite its proximity to the Eck Natural Area (~4 km) the relative abundance of gaps from year to year showed no similarities between the two sites. Patterns of gap formation may be strongly autogenically controlled and influenced by local weather patterns.

Gap rotation ranged from 115 years to 385 years. Alley Spring site had the lowest value and thus would completely regenerate via gaps in 115 years. Eck Natural Area would regenerate in 152 years. Our estimates indicate that Slabtown would regenerate in 323 years, Greer Springs and Bixby in 377. Indian Trails has the most protracted turnover rate. Although calculated, rotation interval represents a theoretical successional timeframe. Variation in disturbance or stochastic events can alter the rotation interval. Since canopy gaps are evident for less than about 10 years in these sites, a decadal rotation interval recalculation would provide greater predictability of stand dynamics.

Table 1.—Study site characteristics, overstory composition, canopy gap replacement trees, and percentage of trees species regenerating in gaps.

Site	Eck NA	Alley Spring	IndianTrails	Greer Spring	Bixby	Slabtown
Area (ha)	50.8	17.2	19	18.3	13.6	11.1
Forest Age (~years)	320	200	125	120	160	150
Canopy gaps (n)	48	28	13	9	9	14
Area in gaps (m^2 ha^{-1})	405	522	156	159	159	186
Mean gap size (m^2)	421	322	247	323	241	148
Rotation interval (yrs)	152	115	385	377	377	323
Overstory species importance values						
Pinus echinata	94.7	93.3	210.1	65.5	71.9	93.3
Quercus velutina	79.3	37.6	37.7	58.2	39.7	82.3
Q. alba	54.5	70.2	32.5	57.2	68.4	57.3
Q. stellata	26.1	40.5	11.9	0	0	28.4
Q. rubra	18.6	0	7.8	0	0	10.1
Q. coccinea	0	22.3	0	34.8	116.2	0
Carya tomentosa	0	0	0	28.5	0	0
C. texana	0	0	0	0	3.8	0
Gap replacement trees: sum of trees in all gaps (total number of gaps)						
Pinus echinata	43 (19)	15 (10)	11 (5)	0 (0)	5 (4)	5 (3)
Quercus velutina	34 (24)	9 (9)	11 (7)	1 (1)	2 (2)	2 (2)
Q. alba	44 (22)	5 (4)	16 (9)	6 (6)	10 (7)	5 (5)
Q. stellata	5 (4)	2 (2)	0 (0)	1 (1)	0 (0)	0 (0)
Q. rubra	5 (4)	3 (2)	2 (1)	1 (1)	0 (0)	0 (0)
Q. coccinea	0 (0)	6 (5)	1 (1)	0 (0)	4 (4)	0 (0)
Carya spp.	31 (20)	10 (7)	0 (0)	3 (3)	0 (0)	10 (8)
Acer rubrum	1 (1)	0 (0)	2 (1)	0 (0)	0 (0)	0 (0)
Ulmus spp.	4 (2)	1 (1)	0 (0)	1 (1)	0 (0)	0 (0)
Percentage of regeneration by tree species in all gaps						
Pinus echinata	12.9	0	0	0	0	11
Quercus velutina	16.4	13.6	16.1	10.1	17.4	14.7
Q. alba	13.3	8.1	10.8	0	0	16.6
Q. stellata	0	0	17.2	0	0	0
Q. coccinea	0	0	0	0	12.8	0
Carya spp.	0	13.3	0	8.3	9.3	0
Acer rubrum	0	0	0	17.4	22.1	14.7
Sassafras albidum	19	20.4	8.6	10.1	16.3	15.3
Cornus florida	12.3	13.6	20.4	14.7	0	0
Prunus serotina	0	0	0	8.3	0	0

Vegetation Structure – Existing Overstory

The five most important overstory species at the Eck Natural Area site, in order of importance, were shortleaf pine, black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), post oak (*Q. stellata* Wangenh.), and northern red oak (*Q. rubra* L.) (Table 1). Although shortleaf pine made up almost 1/3 of the total importance values (IV), as a group, the oaks comprised the majority (IV = 59.5). The average DBH of overstory trees was 38.2 cm and the largest individual was a black oak at 89.0 cm DBH. The majority of the trees were between 26 and 40 cm DBH. Shortleaf pine was the most abundant species at the site followed by black oak. Shortleaf pine was the most abundant species in the 25 to 40 cm DBH class, and the largest individual was represented in the 55 cm DBH class.

The five most important overstory species at the Alley Spring site, in decreasing order of importance, were shortleaf pine, white oak, post oak, black oak, and scarlet oak (*Q. coccinea* Muenchh.) (Table 1). As with the Eck Natural Area site, shortleaf pine comprised almost 1/3 of the total importance values, but the oak group made up the majority of total IV. Average DBH of the overstory trees was 41.4 cm and the largest individual was a 75.0 cm DBH white oak. Shortleaf pine was the most abundant species at the site, followed by white oak was. The bell-shaped diameter distribution of shortleaf pine (Fig. 1) suggests that recent recruitment to the overstory is less than historical.

At Indian Trails, the overstory consisted only of shortleaf pine, black oak, white oak, post oak and northern red oak. Shortleaf pine was clearly dominant at the site comprising over 2/3 of the total overstory importance values, and black oak was second in abundance. Average size of the overstory trees was 40.7 cm DBH and the largest individual was a 60.8 cm DBH black oak. The most abundant species across all size classes was shortleaf pine and its diameter distribution was somewhat bell-shaped (Fig. 1) with its greatest abundance occurring in the 40 cm DBH class.

The five most important overstory species at the Greer Spring site, from most to least important, were shortleaf pine, black oak, white oak, scarlet oak, and mockernut hickory (*Carya tomentosa* [Poir.] Nutt.) (Table 1). Similar to the Eck Natural Area and Alley spring sites, shortleaf pine was the most important species, but oaks constituted a majority (IV = 50.1 percent). Average size of the overstory trees was 38.3 cm DBH and the largest individual was a white oak at 74.7 cm DBH. The bell-shaped overstory distribution of shortleaf pine was best represented by the 35 cm DBH class (Fig. 1).

Scarlet oak dominated the Bixby site and comprised over 1/3 of the total importance values (Table 1). Shortleaf pine, white oak, black oak, and black hickory followed in importance. As a group, oaks accounted for nearly 75 percent of IV totals. Average size of the overstory trees was 34.3 cm DBH and the largest individual was a 55.6 cm DBH white oak. Shortleaf pine had the highest abundance in the smallest DBH class (Fig. 1), and its abundance decreased sharply until the 40 cm DBH class, above which it was absent.

The five most important overstory species at the Slabtown site, listed from most to least important, were shortleaf pine, black oak, white oak, post oak, and northern red oak (Table 1). Similar to the Eck Natural Area, Alley spring, and Greer spring sites, shortleaf pine made up almost 1/3 of all importance values, however oaks made up the majority of all importance values (59.4 percent). Average size of the overstory trees was 35.1 cm DBH and the largest individual was a white oak at 61.7 cm DBH. Shortleaf pine was the most abundant species in the smallest size class and its diameter distribution resembled a reverse J-shape (Fig. 1).

Vegetation Structure – Canopy Gap Understory and Regeneration

Eck Natural Area

Shortleaf pine was the most abundant gap replacement tree species at the Eck Natural Area followed by white oak and black oak; however, black oak occurred in more canopy gaps than did any other species (Table 1). Other overstory trees that occurred in gaps included hickories (*Carya* spp.), black tupelo (*Nyssa sylvatica* Marsh.), post oak, and elm (*Ulmus* spp). Post oak and shortleaf pine both showed somewhat bell-shaped diameter distributions (Fig. 1), suggesting that levels of current recruitment to the overstory are reduced compared to historical levels. Shortleaf pine exhibited the greatest number of stems in the 2- to 12-cm DBH classes. White oak had the second highest abundance in the smallest diameter class of all other tree species. Both white oak and black oak showed an approximately 75 percent reduction in stem density from the 0- to 2-cm DBH class with stem density from the 2- to 12-cm DBH class was relatively consistent.

Regenerating tree species at the Eck Natural Area included sassafras (*Sassafras albidum* Nees and Eberm.), black oak, white oak, shortleaf pine, and flowering dogwood (*Cornus florida* L.) (Table 1). Sixteen other species accounted for the remaining 26.1 percent of the regeneration.

Pith dates of shortleaf pines occurring in canopy gaps at the Eck Natural Area site were concentrated around the years 1935 to 1950, an era following the Dust Bowl and corresponding with a significant reduction in state-wide wildland fire occurrences. Shortleaf pine establishment in gaps decreased gradually both prior to and following this period. Other than one individual, no pines dated prior to 1920 or after 1965. The average diameter and height of understory shortleaf pines that were recruiting to canopy openings was 10.1 cm DBH and 13.6 m, respectively.

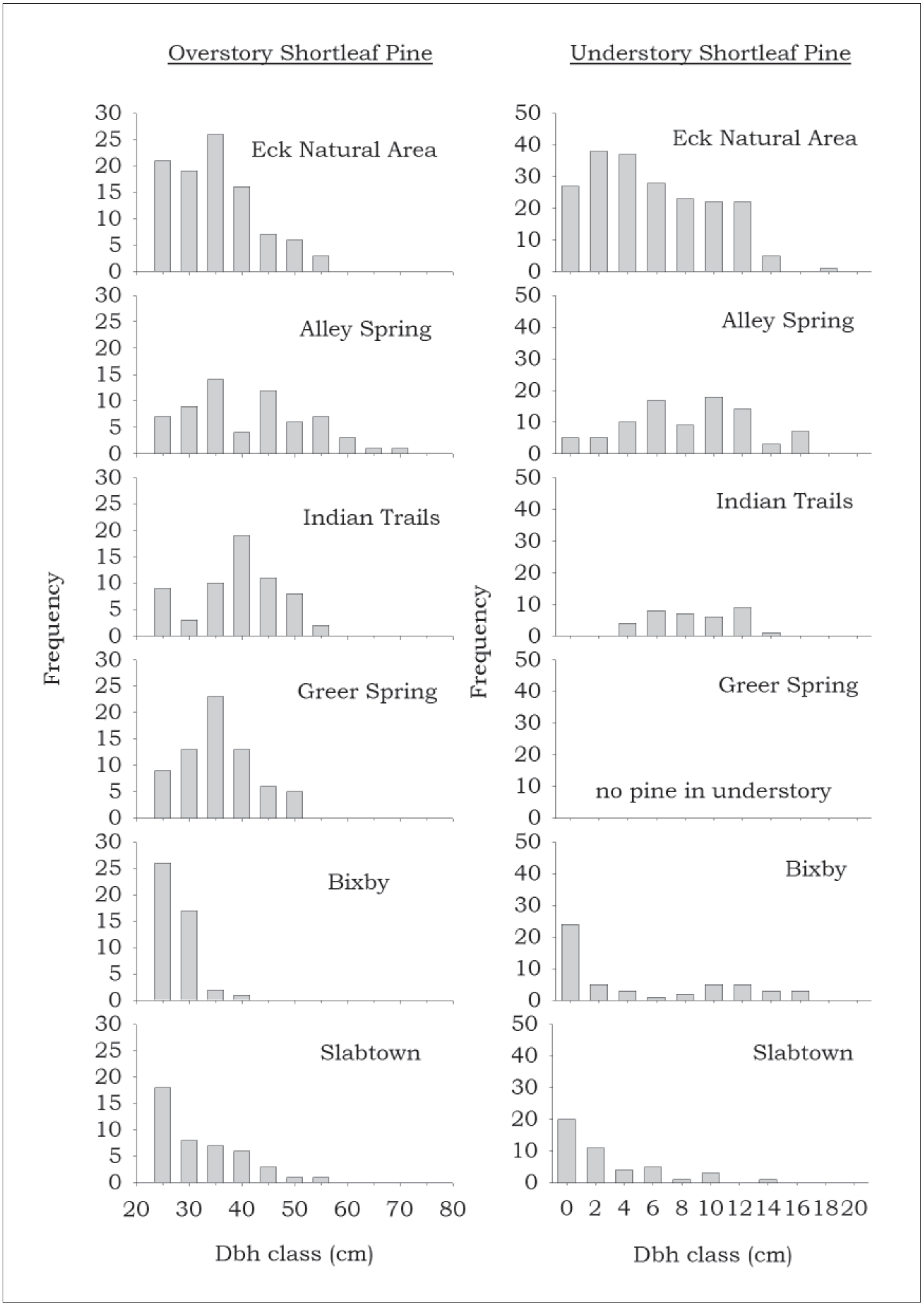

Figure 1.—Diameter distributions of shortleaf pine in the overstory (left column) and understory (right column) of the six study sites. DBH classes begin with the label value.

Average age of these trees was 59 years old and ranged from 38 to 80 years, with the exception of one individual at 147 years old. Twelve of 31 understory shortleaf pines cored showed a growth release due to canopy gap disturbances. Released trees occurred in canopy gap sizes that ranged from 200 to 700 m^2 in size.

Alley Spring

The most abundant species in the understory of canopy gaps of Alley Spring were hickories, black tupelo, shortleaf pine, white oak, scarlet oak, black oak, and elms. This is the same suite of species that was identified at the Eck Natural Area site but with the addition of scarlet oak. Similar to the Eck Natural Area site, shortleaf pine's abundance was characterized by a bell-shaped distribution. It was the most abundant gap replacement tree species, followed by hickories and black oak (Table 1). Shortleaf pine was also found in more gaps than any other species, though it was absent from the regeneration.

At Alley Spring, sassafras, flowering dogwood, black oak, hickories, and white oak (Table 1) were present as regeneration in gaps. Twenty-two other tree species accounted for the remaining 31 percent of regenerating tree species identified at Alley Spring.

Pith dates of shortleaf pines occurring in canopy gaps were most frequent during 1925 and 1935 and all understory pines sampled were established between 1915 and 1955. The bell-shaped diameter distribution (Fig. 1) and pith dates were similar to those from the Eck Natural Area, again suggesting a recent decrease in pine regeneration or successful recruitment to the understory. The average age of understory pines was 55 years and ranged from 31 to 84 years. Annual growth rates of understory pines ranged from 0.02 to 6.77 mm/yr and the average annual growth rate was 1.00 mm/yr, an extremely slow growth rate compared to its potential. Six of 24 understory shortleaf pines cored showed growth releases as result of the canopy opening and these trees occurred in gaps ranging from the 200 to 500 m^2.

Indian Trails

The most abundant tree species occurring in the understory of canopy gaps at the Indian Trails site were red maple (*Acer rubrum* L.), hickories, black tupelo, shortleaf pine, white oak, black oak, and post oak. Shortleaf pine and post oak diameter distributions were similar to those at the Eck Natural Area and Alley Spring sites. White oak and black oak showed bimodal distributions. Overall, black oak was the most common species found in canopy gaps at the Indian Trails site. Post oak, with a similar distribution to shortleaf pine, was represented by increasing abundance from the 0- to 10-cm DBH class with the majority of the stems occurred from the 6- to 10-cm DBH classes. White oak was the most abundant gap replacement tree species (n = 16) followed by shortleaf pine and black oak (n = 11) equally. White oak was found in more gaps than any other species followed by black oak and shortleaf pine (Table 1).

The most abundant regenerating tree species in canopy gaps at the Indian Trails site, listed from most to least abundant, were flowering dogwood, post oak, black oak, white oak, and sassafras (Table 1). Five other species comprised the remaining 26.9 percent of regenerating tree species identified. The diameter distribution of understory shortleaf pine was bell-shaped (Fig. 1) with no individuals recorded in the 0- to 6-cm DBH class.

Greer Spring

Shortleaf pine was absent as a gap replacement species in canopy gaps at Greer Spring. Red maple, sugar maple (*A. saccharum* Marsh.), hickories, black tupelo, white oak, northern red oak, and elm spp. were common. The dominance of mesic species such as red maple and sugar maple and the absence of shortleaf pine (Fig. 1) and post oak in canopy gaps distinguish this site from the others. Black tupelo showed the greatest abundance in the smallest diameter class; red maple and hickory had similar, yet smaller abundance. White oak was the most abundant gap replacement tree species followed by hickories.

The five most abundant regenerating tree species in canopy gaps at Greer Spring, listed from most to least abundant, were red maple, flowering dogwood, sassafras, black oak, and hickories and black cherry (Table 1). Twelve other species comprised the remaining 31.1 percent of the regenerating tree species.

Bixby

Red maple, hickories, black tupelo, shortleaf pine, white oak, scarlet oak, and black oak were the most commonly occurring species in canopy gaps at the Bixby site (Table 1). Shortleaf pine and white oak distributions were somewhat bimodal, both showed greatest abundance at the 0- and 6- to 10-cm DBH range. With the exception of species occurring only in the understory, red maple was the most abundant, followed by hickories and shortleaf pine. White oak and shortleaf pine were the only species represented in all DBH classes and they were the first and second most abundant species in diameter classes > 6 cm DBH. White oak was the most abundant gap replacement tree species, followed by shortleaf pine, scarlet oak, and black oak (Table 1).

The five most abundant regenerating tree species in canopy gaps at the Bixby site, listed from most to least abundant, were red maple, black oak, sassafras, scarlet oak, and hickories (Table 1). Five other species comprised the remaining 22.1 percent of regenerating tree species identified.

Pith dates of shortleaf pines occurring in canopy gaps of the Bixby site were most abundant in the 1940s, though only

10 trees were sampled from the understory layer because of the small number of gaps. Average age of shortleaf pines in the understory was 55 years. The abundance of pine regeneration was greatest between 1930 and 1940, as with the Eck Natural Area and Alley spring sites. No pith dates were represented prior to the 1930 class. Annual growth rates of understory shortleaf pines ranged from 0.03 to 3.66 mm/yr and the average annual growth rate was 0.96 mm/yr. Two of nine understory shortleaf pines cored showed growth releases as result of the canopy gap opening. Both trees were located in gaps with areas of 100 m^2.

Slabtown

The most abundant tree species occurring in the understory layer in canopy gaps at the Slabtown site were red maple, hickories, shortleaf pine, white oak, black jack oak, black oak, and elm species (Table 1). This site is the only one to include black jack oak among the seven most abundant overstory tree species occurring in the understory of gaps; its presence is indicative of a site with dry, sterile soils (Harlow and others 1991). Diameter distributions were somewhat similar for all species; and hickories, shortleaf pine, black jack oak, and elm species. were represented by a reverse J-shaped distribution. Hickories were the most abundant gap replacement species, followed equally by shortleaf pine and white oak (Table 1). Hickories were found in more gaps than were any other species (n = 8), followed by white oak (n = 5) and shortleaf pine (n = 3).

The five most abundant regenerating tree species in canopy gaps at the Slabtown site, from most to least abundant, were white oak, sassafras, black oak and red maple, and shortleaf pine. Thirteen other species comprised the remaining 27.7 percent of the regenerating tree species identified.

The greatest number of pith dates of shortleaf pines in canopy gaps at Slabtown occurred in the 1970 class. Average age of shortleaf pines in the understory of canopy gaps was 43 years. The oldest pith date was represented in the 1890 class and the youngest in the 1980 class. Pith dates occurring in the last 30 years were more common at the Slabtown site than at any other site. Pith dates of shortleaf pines at the Slabtown site were represented during the years of common regeneration at other sites (1930 to 1940); however, the greatest number was from 1960 to 1975. Annual growth rates of understory shortleaf pines ranged from 0.03 to 3.91 mm/yr and the average annual growth rate was 0.90 mm/yr. Two of 12 understory shortleaf pines cored showed growth releases as result of the canopy gap disturbance. Released understory shortleaf pines occurred in gaps with areas of 200 m^2.

Shortleaf Pine Regeneration

Shortleaf pine regeneration was absent from all canopy gaps at four of the six study sites. Despite the presence of shortleaf pine in the overstory, the two sites with shortleaf pine regeneration had a substantial component of black oak, white oak, and, in one case, red maple regeneration. Sassafras and flowering dogwood were abundant in the regeneration layer and likely imparted competitive effects (e.g., shading, resource competition) on shortleaf regeneration. Interestingly, several of these species (e.g., sassafras, flowering dogwood, red maple) are very fire intolerant and could be effectively reduced through prescribed burning.

Gap size is likely one of the most important variables controlling pine regeneration. We observed that the maximum number of shortleaf pine seedlings regenerating can increase by approximately eight times from smaller (e.g., 400 m^2) to larger (1700 m^2) canopy openings (Stambaugh and Muzika 2004). Larger gaps likely increase the potential for shortleaf pine regeneration because there is lowered leaf area, increased light, less leaf litter limiting seedling establishment, and increased temperatures at the forest floor that perhaps accelerate litter decomposition and minimize damping-off (Liming 1945). Certainly, an important consideration for regeneration is the presence of available seed trees. Seedling abundance in subplots increased with the number of overstory pines surrounding the canopy gap. The average number of pine seedlings increased by approximately three seedlings per 100 m^2 as the number of overstory shortleaf pine trees surrounding the gap increased from zero to one tree. Additionally, the average number of shortleaf pine seedlings per 100 m^2 increased by approximately nine seedlings as the number of overstory shortleaf pine trees surrounding the gap increased from two to three trees.

Shortleaf pine regeneration was highest near azimuth of 200 degrees (SSW) and decreased consistently as aspects deviated from 2000 (Fig. 2). The majority of shortleaf pine regeneration occurred on aspects between 150 to 2600 (e.g. south southwest to west), and no regeneration occurred between approximately 325 and 1100 (north northwest to northeast). Outlying regeneration data were fit to a third-order polynomial to show the potential bound of regeneration by aspect (Fig. 2).

Litter depth plays an important role in limiting shortleaf pine regeneration (Grano 1949). Shortleaf pine seedlings were found on litter depths of 0 to 6 cm and the greatest abundance of shortleaf pine regeneration was found on a litter depth of 2.5 cm (Fig. 3). The number of regenerating pine seedlings continually decreased as litter depth increased from 2.5 to 6 cm. No pine regeneration was found in subplots where litter depths exceeded 6 cm, and the type of litter was not found to be important.

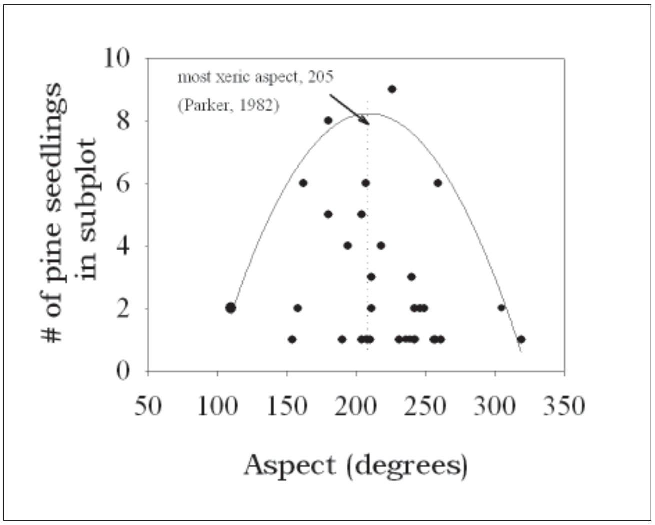

Figure 2.—Shortleaf pine seedling abundance and aspect of the subplots. Data are from all sites combined. The polynomial line was fit to outlying regeneration points to show the potential bound of regeneration across subplots.

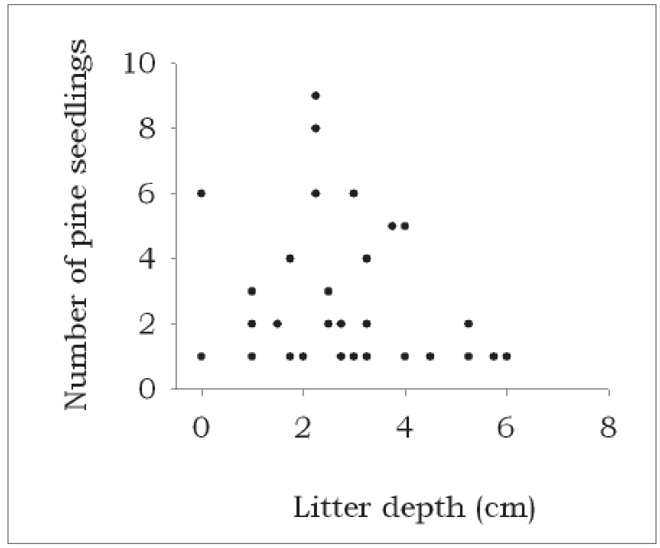

Figure 3.—Relationship between litter depth and shortleaf pine abundance in regeneration subplots. Data are from all sites; each point represents an individual subplot.

Shortleaf Pine Recruitment

The relationship between diameter and height was analyzed for shortleaf pines occurring in the understory layer of canopy gaps. For trees from all sites that were probable gap replacements, a positive linear relationship existed ($r^2 = 0.72$; $p < 0.01$). The size of gap-replacing trees was variable, depending on the size of all other competitors. For this reason the variability in trees sizes was large ranging from 1.7 to 24.9 cm DBH and from 2 to 17 m in height. Nongap-replacing trees showed a diameter-height relationship similar to gap-replacing trees up to about 10 cm DBH or 10 m in height. Few nongap-replacing pines were represented above this size.

Shortleaf has the potential to persist in the understory for long periods of time (e.g., 80+ years) (Stambaugh 2001). Many of these trees have weak epinastic control as result of a prolonged suppression beneath high shade (Oliver and Larson 1996) resulting in “crooked” or flat tops. Much of the understory shortleaf pine observed in canopy gaps originated between 1930 and 1955. An informal survey of many more understory pines throughout the Ozarks found similar periods of origin and growth form (Stambaugh, unpublished data). Not only was this period relatively dry, but it also corresponded with extensive burning. Ring-widths of shortleaf pine trees growing in gaps were about 1 mm/year on average. This rate is extremely slow compared to the potential rates of open-grown pines (i.e., ring-widths of 5 mm/year). Shortleaf pine trees showed growth increases in response to small (e.g., 200 m^2) canopy openings, which result from mortality of a single-tree. However, the duration of increased growth was not tracked and is likely short-term, particularly in smaller gap sizes.

CONCLUSIONS

This study describes the vegetative status of six pine forests that are in mid-transition towards being replaced by hardwoods. Overall, this study suggests that natural, noncatastrophic canopy gap disturbances are not sufficient to maintain an overstory composition of shortleaf pine. In general, canopy gap disturbances do not have the effects on the understory or regeneration layer needed for sustaining the processes of regeneration and recruitment of shortleaf pine to the overstory. Small-scale disturbances such as canopy gaps appear to support the transition to forests dominated by hardwood species, particularly black oak, white oak, and hickories. The forest stand dynamics of these forests are similar to a mature pine stand studied by Shelton and Cain (1999), in which pines were described as being rapidly replaced by shade-tolerant hardwoods. This transition in forest composition is relatively common throughout the Ozark Highlands and likely represents an effect of lowered disturbance frequency, primarily fire.

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