

A frontier shortleaf pine stand in the old-growth Cross Timbers of Oklahoma¹

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Abstract. We investigated an old-growth oak-shortleaf pine (*Pinus echinata*) stand of high ecological integrity in east-central Oklahoma located west of the continuous native distribution of shortleaf pine. With the exception of an abundance of shortleaf pine, the basal area (17.2 m²/ha), density (559.6 trees/ha), and species composition of this unmanaged stand is similar to other old hardwood forests in the Cross Timbers ecoregion. Tree-ring dating indicates that the oldest post oak (*Quercus stellata*) and shortleaf pine sampled in Shortleaf Canyon were 262 and 230 yr old, respectively. Dendrochronology indicated that drought-related disturbances contributed to several episodic pulses of natural regeneration of shortleaf pine at this site. Coupled with local historical documentation and regional paleoecological evidence, the absence of older pines at this isolated site suggests that *P. echinata* may have naturally colonized Shortleaf Canyon recently, perhaps during the last 250 yr.

Key words: Cross Timbers, old-growth, range expansion, shortleaf pine

Shortleaf pine (*Pinus echinata*) has the widest distribution of all the southern pines, covering approximately 1.14 million km² of the southeastern United States (Little 1971, Lawson 1990). Due to its wide distribution and high quality lumber, shortleaf pine has long been commercially prized. Not surprisingly, shortleaf has been heavily logged over its entire range (Mattoon 1915, Smith 1986). Lumbering was so intensive that by World War I it was estimated that original-growth shortleaf pine had been cut from 60% to 80% of its native range (Mattoon 1915). Large-scale commercial harvesting of the virgin shortleaf pine continued unabated along the western edge of the species range in the Ouachita Mountains of Arkansas and Oklahoma

into the early 1940s (Smith 1986). While second- and third-growth pine stands have replaced the original forest, shortleaf pine has declined appreciably over the last century (e.g., Oswalt 2012, Bragg in press), affecting many other species and ecosystems across the southeastern United States. For example, the decline of the red-cockaded woodpecker (*Picoides borealis*) across the western and northern portions of its range has been linked to the degradation and loss of the once common shortleaf pine-bluestem (*Schizachyrium* spp. and *Andropogon* spp.) habitat (Masters, Skeen, and Whitehead 1995; Hedrick *et al.* 2007).

Even after such intensive lumbering, the Ouachita Mountains region still contains multiple examples of old-growth shortleaf pine, including stands at Hot Springs National Park and Lake Winona Natural Area in Arkansas and the McCurtain County Wilderness Area in southeast Oklahoma. In east-central Oklahoma, a number of isolated stands of natural-origin shortleaf pine can be found well beyond the western edge of the species' contiguous distribution (Silker 1968, Little 1971, Lawson 1990). These mature pine stands tend to be small, ranging from approximately 4 ha to 40 ha, and are usually separated from one another by several kilometers. Most of these shortleaf pine "islands" are found on rugged terrain, often surrounded by old-growth oak-dominated forests. Given their presence in an old-growth hardwood matrix and the nature of the

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overstory pine in these outliers, it is likely that some of these shortleaf pine stands are themselves old-growth remnants.

Natural-origin shortleaf pine outliers offer a number of opportunities to understand this species' dynamics and biogeographical trends. Previous palynological work (*e.g.*, Henry, Butler, and Hall 1979; Albert and Wyckoff 1981; Hall 1982) suggests that the populations of southern pine species have been steadily aggrading in Oklahoma in recent centuries. However, their work was not able to determine if this was due to a gradual process or one of discrete and dramatic range expansion events. While most pine species are not known for wide seed dispersal, long distance colonization events are not without precedent. For example, Jackson *et al.* (2005) found evidence of such events for *Pinus edulis* in the Dutch John Mountains of Utah. Determining the origin of these outliers is useful because they may be very important for understanding both range expansion and species genetics (Hasse 1993, Willson 1993, Levin 2000). Given recent concerns about the genetic integrity of shortleaf pine (Tauer *et al.* 2012, Stewart *et al.* 2015), these isolated stands may have considerable scientific and conservation potential.

We evaluated a mature, unmanaged outlier of natural-origin shortleaf pine located on the western frontier of this species using historical records, contemporary field inventories, and dendrochronology. In addition to documenting the structure, composition, and age of this frontier shortleaf pine stand, we also consider the likelihood that this and similar outliers may represent a relatively recent range expansion of shortleaf pine.

Materials and Methods. STUDY AREA. The study site (Shortleaf Canyon) is located along the extreme western edge of the known distribution of shortleaf pine in northwestern McIntosh County, OK, near the confluence of the North Canadian River and Lake Eufaula (Fig. 1). Shortleaf Canyon is a privately owned tract of pine, hardwood, and some eastern redcedar (*Juniperus virginiana*) that was identified as a potential example of old growth based on preliminary tree-ring aging of several increment cores collected from the site. The current property owner states the stand has never been logged, and the possibility of at least some uncut old growth remaining is supported by the rugged, sparsely inhabited landscapes in and



FIG. 1. Location of Shortleaf Canyon in McIntosh County, Oklahoma. The gray shaded region is the natural distribution of shortleaf pine, according to Lawson (1990).

around Shortleaf Canyon. Bedrock in the region is of Pennsylvanian age, with sandstone escarpments commonly found where erosion has cut away the underlying, softer shale (Clark 1928, Bruner 1931). Steep hills (elevations varying from 189 to 290 m above sea level) broken by bluff lines and rock outcrops encompass two small upland drainages that converge in Shortleaf Canyon. Soils are dominated by the Endsaw-Hector association, which is composed of well-drained, slightly acidic, stony fine sandy loams low in natural fertility (Natural Resources Conservation Service [NRCS] 2009). Average yearly precipitation in the region is 114 cm (National Climatic Data Center [NCDC] 2002).

While there is little evidence of logging or agricultural land clearing across most of the study area today, this part of Oklahoma has had a long history of human occupation. Scores of prehistoric sites dating back 8,000 or more years before present have been documented in McIntosh County (Oklahoma Archeological Survey 2015). When European Americans first started exploring the area in the early 1800s, Shortleaf Canyon was primarily the territory of the Osage Indians, seminomadic hunter-gatherers who practiced some limited agriculture along major river bottoms (Foreman 1934). United States military expeditions crossed the Canadian River near Shortleaf Canyon in the early 1830s, but never established any forts along this part of the river (Agnew 1980, Dodge 2000). Creek Indians were removed to the vicinity between 1825 and 1836 and settled the land around Eufaula, OK, approximately 20 km from Shortleaf Canyon (Foreman 1934). General Land Office (GLO) land surveyors worked in the Shortleaf Canyon area in late 1895 and early 1896, and their plat map clearly shows a number of

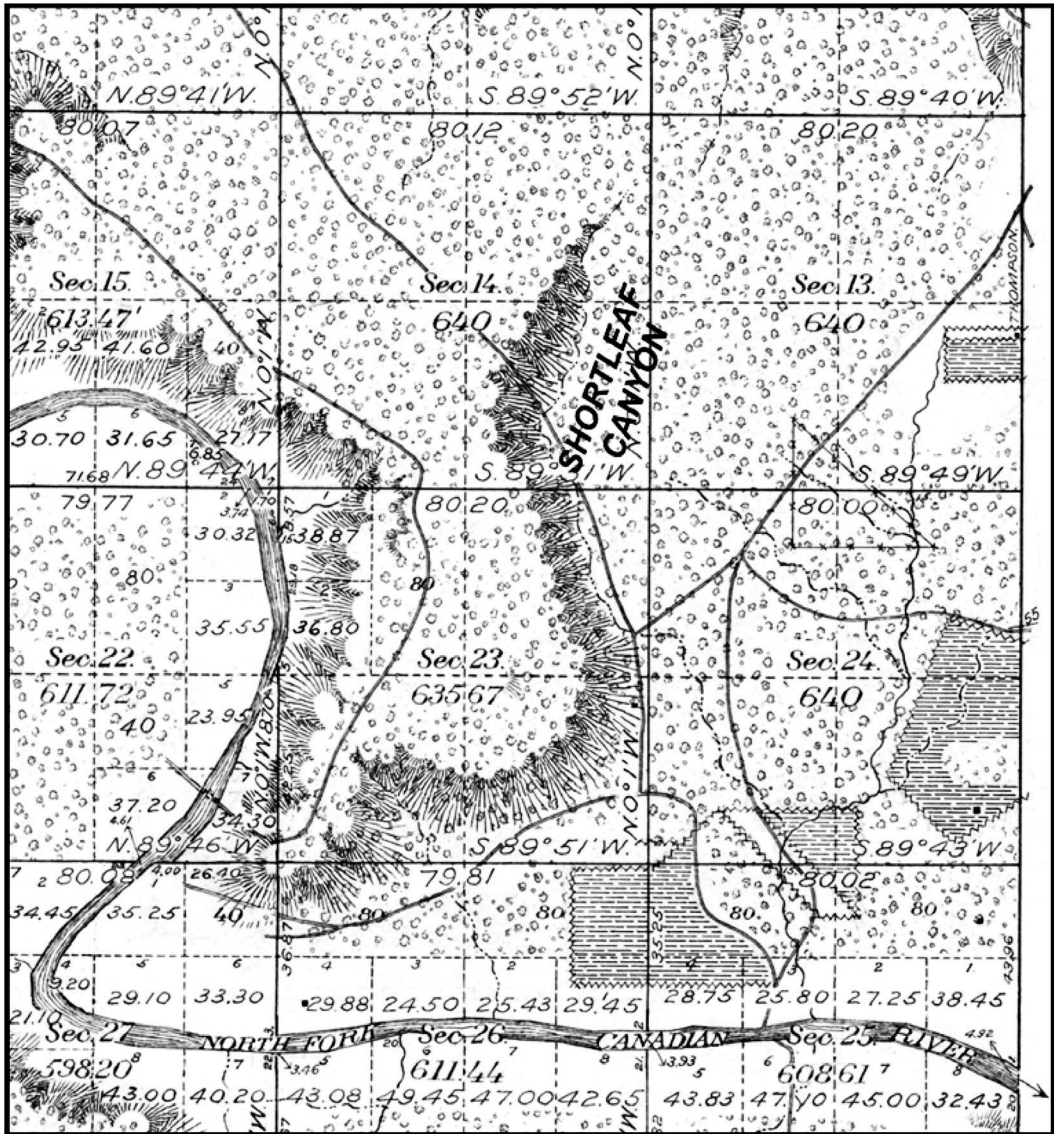


FIG. 2. A portion of the 1895–1896 GLO plat map of Township 11 North, Range 14 East of the Indian Meridian, Indian Territory, showing the sparse settlement noted by surveyors in the area around the study site.

historic roads and fields (Fig. 2). Portions of a long-abandoned road can still be observed in places along the western flank of Shortleaf Canyon, and we did encounter some old strings of barbed wire and a few old redcedar stumps near a modern road at the western edge of the site.

Most of the pine islands encountered in this region occur where the eastern oak-hickory forest gives way to the oak-dominated woodlands of the Cross Timbers. The Cross Timbers represents a transitional ecoregion along a pronounced precip-

itation gradient between the mesic deciduous forest to the east and the xeric grasslands of the southern Great Plains to the west (Bruner 1931, Dyksterhuis 1948, Rice and Penfound 1959, Stahle and Hehr 1984, Hoagland *et al.* 1999, Bragg *et al.* 2012). Post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) dominate the forests of the Cross Timbers (Rice and Penfound 1959, Risser and Rice 1971). Poor site conditions have contributed to the persistence of many large patches of old-growth Cross Timbers forest

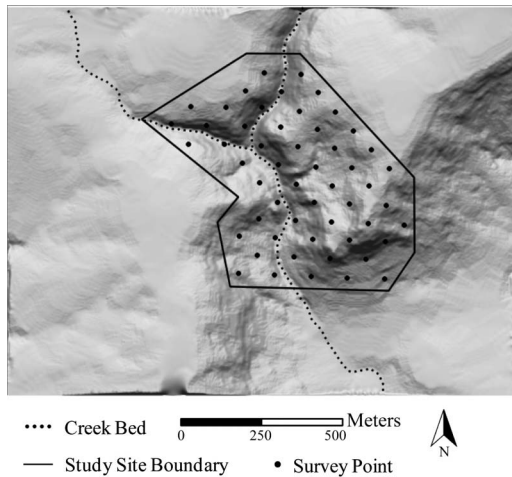


FIG. 3. Shaded relief map of the study area at Shortleaf Canyon derived from the 1:24,000 USGS topographic map and overlain with the final site boundary that was produced from a GPS survey. Sample points are shown on the 80×80 m grid layout.

throughout the region (Stahle and Hehr 1984, Stahle and Chaney 1994, Stahle 1996, Therrell and Stahle 1998). Due to the harsh environment, the trees of the Cross Timbers tend to be small in stature, slow growing, and produce low quality timber, which has discouraged large-scale logging operations, particularly along rough terrain similar to that found at Shortleaf Canyon (Dyksterhuis 1948, Silker 1968, Stahle and Hehr 1984, Clark *et al.* 2006).

VEGETATION SAMPLING. To define the approximately 40-ha study area at Shortleaf Canyon, we used a global positioning system (GPS) survey to map the part of the stand with canopy dominant shortleaf pine. The boundary of the GPS survey was then digitally overlain on a 1:24,000-scale topographic map using ArcMap® v. 9.2 (Esri, Redlands, CA) and an 80×80 m grid was oriented along the southeast-trending drainages, producing 54 field sampling points (Fig. 3). The exact location of each grid point was determined in ArcMap (Esri), exported to a waypoint table, and downloaded into a GPS receiver for field location. In the field, each grid point was marked with a stake and vegetation sampling was centered on those points in the summer of 2009.

We sampled both understory and overstory trees at Shortleaf Canyon. Overstory trees (stems with diameter at breast height [DBH] of at least 10 cm)

were sampled using a 10 Basal Area Factor (BAF) prism (variable radius plot, converted to metric units) to estimate stand-level species composition, stem density (trees/ha), and basal area (m^2/ha). Borderline trees in these variable radius plots were checked against a limiting distance table to determine if they should be included in the plot (Avery and Burkhart 2002). The understory trees were sampled with a 5.64-m radius (0.01-ha) circular plot centered on the sampling point. Understory trees were identified to species and placed into one of six size classes: A (stems 15–75 cm tall), B (75.1–135 cm tall), C (> 135 cm height and < 2.5 cm DBH), 1 (2.5–4.9 cm DBH), 2 (5.0–7.4 cm DBH), or 3 (7.5–9.9 cm DBH). Understory stem density (trees/ha) and basal area (m^2/ha for only those stems that had a DBH, using the DBH class midpoint) were then determined.

TREE AGE SAMPLING AND ANALYSIS. Increment cores were extracted from post oak and shortleaf pine in Shortleaf Canyon to obtain age data. Trees to be aged were randomly selected at each sample point by circling clockwise from north around the point marker and coring the first post oak, the first three understory pines, and the first three overstory pines encountered within a 35 m radius. Because three pines in the overstory or understory were not always present at each sample point, up to three extra trees in either category were sampled at later points to maintain an average of three per point. Pine was sampled more intensively than post oak because we were interested in the history of pine regeneration. Post oaks were sampled to document the age of the hardwood component at Shortleaf Canyon. Any particularly old looking trees of either species were also cored, but were kept as voucher trees apart from the random sample. Cross sections were also removed from any downed, dead (relict) pine wood encountered for age analysis.

All tree cores were sampled using a 5 mm Swedish increment borer. Both understory and overstory pines were cored or cut at approximately 20 cm above ground level so that tree age was sampled as close as possible to the actual emergence date of the stem, while cores were taken at breast height from the oaks for ease of sampling. Any understory pine that was too small to core was cut at the ground line and at 20 cm up the stem so that its cross section at both its base and 20 cm height could be aged.

All cores were dried, mounted, and then prepared for analysis by sanding with increasingly finer sandpaper until a highly polished surface was obtained. Cut pine seedlings were sanded at their base and at 20 cm height. Visual crossdating of the pine and oak cores based on tree ring widths was performed under a stereo zoom microscope following tree ring dating techniques outlined by Stokes and Smiley (1996). Oak cores were crossdated based on total ring width. Pine cores were crossdated based on the latewood width within each annual ring, which has been reported to have stronger matching than total ring width (Schulman 1942, Cleaveland 1975). For those pine increment cores close to (but lacking) the pith, a simple ocular estimation of the number of missing rings was made to approximate the pith date (Clark and Hallgren 2004).

Once crossdated, a subsample of 40 shortleaf pine cores taken from Shortleaf Canyon and 14 additional shortleaf pine cores (all chosen for their old age) sampled previously from other nearby pine outliers by the University of Arkansas Tree-Ring Laboratory (UATRL) was measured for earlywood (EW), latewood (LW), and total ring (TR) width using a stage micrometer and a precision of 0.001 mm. All ring width measurements were submitted to the program COFECHA (Holmes 1983, Grissino-Mayer 2001) for quality control over dating and measurement accuracy and to the program ARSTAN (Cook 1985) for detrending and standardization of the ring width time series and for computation of the mean index chronologies for EW, LW, and TR width.

To examine shortleaf pine regeneration patterns, the emergence dates of age-sampled overstory pines were estimated. Only reliably aged pines were used to evaluate pine emergence patterns; cores of hollow or punky trees or cores that were too far from pith to estimate were excluded from this analysis, resulting in an age estimation sample of 134 overstory pine trees. First, we estimated the average time it took for pine seedlings to grow to 20 cm tall by differencing the ring counts on each cut pine seedling between the ground-line cut and 20 cm height. Next, a confidence classification of "strong" (easily identifiable ring boundaries), "average" (identifiable ring boundaries with limited amounts of reaction wood or false rings), or "poor" (difficult boundary identification due to extensive reaction wood or false rings) was assigned to each of these seedlings based on the

certainty of the ring count. A ring count difference for stems that received a confidence classification of strong or average (50 in total) was then averaged and rounded to the nearest whole number as an estimate of the number of years it takes a newly emerged seedling to grow to 20 cm tall at Shortleaf Canyon. Finally, this value was then added to all cores with a pith date to estimate when the pine germinated or resprouted.

Results. TREE COMPOSITION AND STRUCTURE. Prism sampling at Shortleaf Canyon tallied 404 overstory trees from 10 taxa (Table 1). The average overstory stand basal area totaled 17.2 m²/ha from 559.7 trees/ha. Post, blackjack, and black oak (*Quercus velutina*) accounted for over 80% of all overstory trees and over 75% of stand basal area, while shortleaf pine comprised only 7.2% and 12.6%, respectively. Most of the hardwood stems in Shortleaf Canyon were small, with DBH < 30 cm (Fig. 4). Although Shortleaf Canyon was not densely stocked with shortleaf pine or black oak, they tended to be some of the largest and most prominent members of the overstory. For example, the largest shortleaf pine and black oak encountered were 56.2 cm and 56.8 cm DBH, respectively. While the pine canopies are visually impressive, they are confined to the steepest terrain at the site, and Shortleaf Canyon is an overwhelmingly oak-dominated forest (Fig. 5).

Four additional tree species were encountered only in the understory: winged elm (*Ulmus alata*), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), and black cherry (*Prunus serotina*). The understory of Shortleaf Canyon had a density of 12,065 trees/ha and a basal area of 1.5 m²/ha (Table 2). The vast majority of understory stems (96.4%) occurred in the three smallest size classes, with 78.1% of all understory stems falling in the smallest class. However, most species were represented in all understory size classes. Many of the smallest individuals in this stand are likely sprouts from top-killed hardwoods, and may actually be rootstocks that are years to decades old, rather than recent germinants (Clark and Hallgren 2003).

Post oak and blackjack oak dominated the understory, although in this stratum they combined for only 50.9% of the density and 53.1% of the basal area (Table 2). Shortleaf pine was also less common in the understory, making up only 2.9% of the relative density and 2.7% of the relative

Table 1. Estimated density and basal area values of the overstory tree component in the Shortleaf Canyon study area.

Species	Absolute density (stems/ha)	Absolute basal area (m ² /ha)	Relative density (%)	Relative basal area (%)
Post oak (<i>Quercus stellata</i>)	239.7	7.4	42.8	42.8
Blackjack oak (<i>Quercus marilandica</i>)	171.6	3.6	30.7	20.8
Shortleaf pine (<i>Pinus echinata</i>)	40.1	2.2	7.2	12.6
Black oak (<i>Quercus velutina</i>)	37.9	2.0	6.8	11.9
Hickory ^a (<i>Carya</i> spp.)	37.5	1.0	6.7	5.7
Shumard oak (<i>Quercus shumardii</i>)	12.0	0.6	2.1	3.5
Winged elm (<i>Ulmus alata</i>)	10.2	0.1	1.8	0.7
Eastern redcedar (<i>Juniperus virginiana</i>)	7.9	0.2	1.4	1.2
White ash (<i>Fraxinus americana</i>)	2.2	0.1	0.4	0.5
American elm (<i>Ulmus americana</i>)	0.6	0.04	0.1	0.2
Totals	559.7	17.2	100.0	100.0

^a At Shortleaf Canyon, most hickory is *Carya texana*, with some *Carya tomentosa* mixed in (species were not distinguished in the field). Flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), and black cherry (*Prunus serotina*) were only found in the understory.

basal area, and much like the overstory pine, tended to be confined to the steepest terrain (Fig. 5). The prominence of winged elm increased the most, to 16.1% of the relative density and 15.9% of the relative basal area. Although woody shrubs were not part of our understory sample, huckleberry (*Vaccinium arboreum*) was widespread and extremely dense in some areas, and winged sumac (*Rhus copallinum*) was also common.

AGE STRUCTURE. Age data at Shortleaf Canyon were collected on 58 overstory post oaks (54 randomly sampled and 4 voucher trees), 160 overstory shortleaf pines, and 158 understory shortleaf pines (80 cored, 78 cut). Four relict pine logs were also sampled. The minimum post oak age was 37 yr and the maximum age was 262 yr (Fig. 6). The mean age of the sampled oaks was 114 yr, with a standard deviation of 62 yr, and 13.8% were 200+ yr old. The 160 cross-dated overstory shortleaf pines ranged in age from a minimum of 11 yr to a maximum of 163 yr (Fig. 6). Mean overstory pine age was 79 yr, with a standard deviation of 47 yr, and 6.9% of overstory pines were 150+ yr old. Additionally, a shortleaf pine previously sampled (in 1999) at this site by the UATRL was 230 yr old at breast height when collected. This tree was not found during our field sampling and is likely hollow now (or dead); however, this older core sample is still available for analysis. Only one relict pine log successfully crossdated, and had a pith date of 1867 and a death date of 1990.

Understory pine ages ranged from a minimum of 1 yr to a maximum of 44 yr. Mean age for all

158 understory pine samples was 11.8 yr, with a standard deviation of 10.2 yr. Four pines were over 40 yr old but still had not attained a DBH of 10 cm, and 17.8% of understory pines were 20+ yr old. On average, 1.8 yr (range: 0–6 yr, median = 1 yr) were required by the 50 cut seedlings and saplings to reach 20 cm height. Thus, a value of 2 yr was added to the age of the 134 overstory pine trees that included pith or had an estimated pith date, and is considered the “emergence” date of the tree. Several pines emerged in the 1840s and 1850s, and large pulses of pine emergence occurred in the 1870s and the 1960s (Fig. 7). An interesting age gap in the overstory is also noticeable in Fig. 7; very few pines that may have established between 1920 and 1960 remain.

Correlation analysis of the shortleaf pine LW measurements confirms the strong visual cross-dating based on LW width, with an average correlation between series (RBAR) among radii of 0.576 (Cook 1985, Cook *et al.* 2007). The average correlation among EW and TR width measurements is lower at RBAR = 0.403 and 0.493, respectively. In all three cases, these RBAR statistics were computed based on only one core per tree. Multiple periods of below-average ring width are evident in the latewood chronology shown in Fig. 7. Most prominent is one period of extreme growth suppression in the 1950s, coinciding with a significant regional drought over the southern Great Plains (Stahle and Cleaveland 1988, Herweijer *et al.* 2007). Correlation analyses between the LW width chronology and monthly precipitation and temperature data from east-

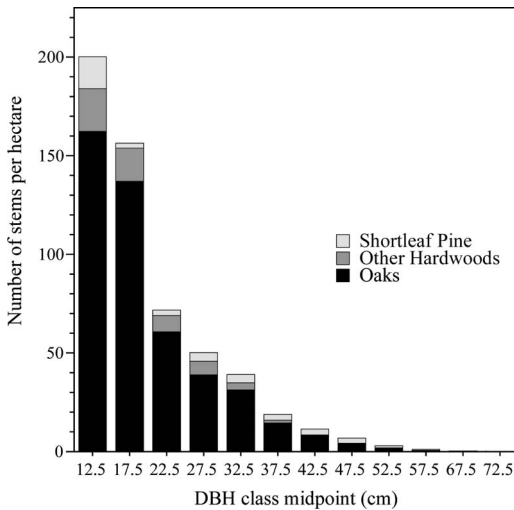


FIG. 4. Diameter class distribution of all species tallied in the overstory. Post oak, blackjack oak, and black oak dominate the study site.

central Oklahoma indicate that LW growth is positively correlated with precipitation and negatively correlated with temperature from June through September for the period 1895 to 2008 (Cerny 2010). These correlations are significant ($P < 0.05$) and confirm the climate sensitivity of shortleaf pine radial growth near the western limits of its range, as first documented by Schulman (1942) in western Arkansas.

Finally, the spatial distribution of pine emergence dates was mapped to examine the potential colonization and subsequent proliferation of pine at Shortleaf Canyon (Fig. 8). The oldest pine tree known from Shortleaf Canyon (sampled in 1999 by the UATRL) was found near the southern edge of the study area (see the X marked on the map for 1850 in Fig. 8). The oldest trees located during the present randomized survey date to the 1840s and 1850s (Fig. 8). All of these trees are located on steep, rocky terrain where natural breaks in the hardwood canopy occur and may have been the founders of the pine population at Shortleaf Canyon. By 1870, shortleaf pine trees were established at numerous sample points along the steepest terrain in Shortleaf Canyon, and pine regeneration has continued to the present.

Discussion. With the exception of the shortleaf pine component, the structure of the overstory at Shortleaf Canyon is similar to other xeric oak-dominated stands of the Cross Timbers (Bruner

1931, Duck and Fletcher 1945, Rice and Penfound 1959, Kuchler 1964). The basal area and tree density found at Shortleaf Canyon resemble those reported by Peppers (2004) at 16 sites in Texas and by Clark (2003) at three sampling locations in the Keystone Ancient Forest Preserve in Oklahoma. The primary difference between these other old-growth Cross Timber stands and Shortleaf Canyon is the persistent, multiaged shortleaf pine component (see also Taylor 1965, Jones and Bowles 2012).

Some of the original evidence that pines at Shortleaf Canyon likely predate widespread European American settlement came from the GLO records that mentioned pine along several of the section lines in the area. Furthermore, visual cues of old trees in the stand were quite apparent (e.g., twisted trunks, flattened crowns and crown die-back, relatively smooth bark, stout limbs, exposure of the root collar, and extensive heart rot; Pederson 2010). The tree-ring data confirmed the visual markers of an old pine component at Shortleaf Canyon. Our data also indicated multiaged oak and pine populations at Shortleaf Canyon, including distinct pine cohorts of approximately 50-, 105-, and 140-yr-old trees. The upper pine age range of 230 to 240 yr seems to mark the original appearance of shortleaf at this location. While it is possible that the oldest pines were removed by lumbering during the early 20th century, it seems unlikely that this rugged, remote location would have been commercially logged.

In addition to the old-growth nature of this oak-pine stand, the lack of significant anthropogenic disturbance within the stand and a minimal encroachment of native *Juniperus* suggest that a high degree of ecological integrity remains in the rugged and poorly accessible confines of Shortleaf Canyon. Eastern redcedar comprises only 1.4% of the overstory and 1.0% of the understory densities (Table 1, 2), and is limited to fire-protected rock outcrops at Shortleaf Canyon. These fire-sheltered sites are part of the historic ecological distribution of eastern redcedar in the nonriparian forests of the Cross Timbers ecoregion (Bidwell *et al.* 2009, Edmondson 2010). Eastern redcedar sampled on similar outcrops near Shortleaf Canyon routinely reach ages greater than 250 yr (Edmondson 2010), suggesting that ancient eastern redcedar may also be present at Shortleaf Canyon (none were sampled for this project). The scarce distribution of *Juniperus* at Shortleaf Canyon is significant,

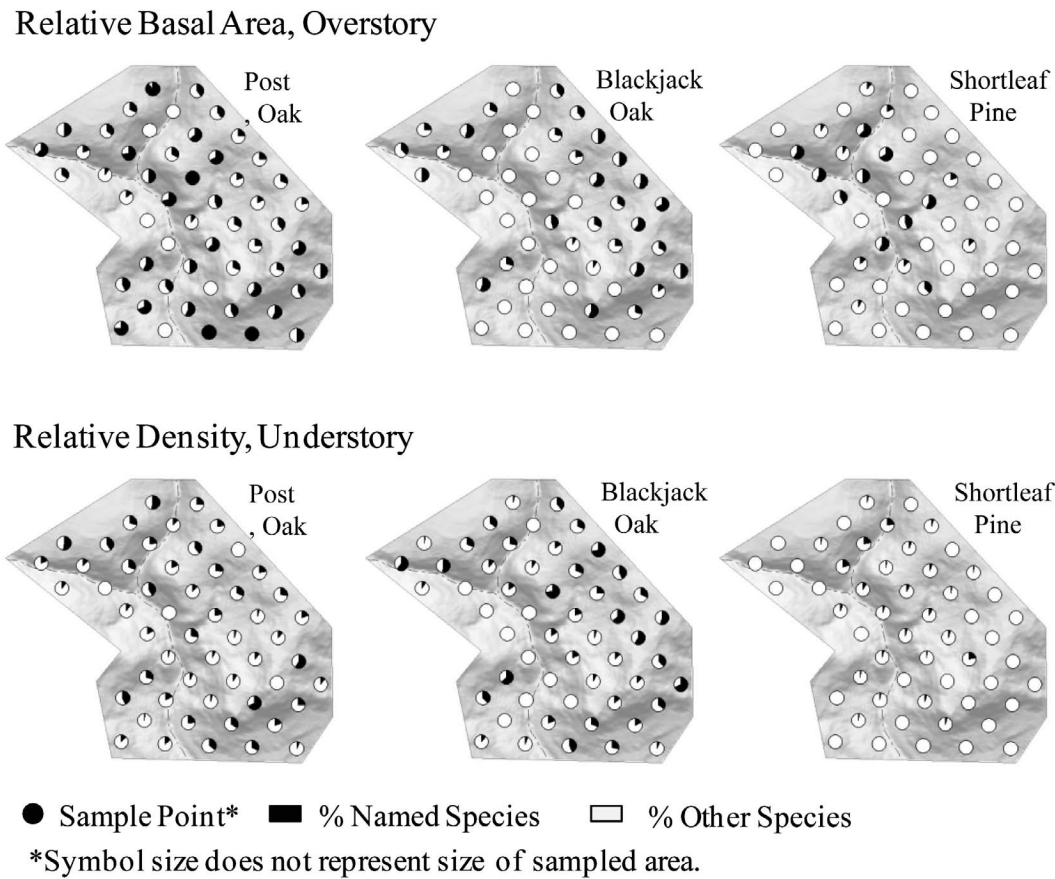


FIG. 5. These maps display the spatial distribution of species dominance as quantified by overstory basal area and understory density. Note that overstory pine only predominates along the steep upland ridges where it is able to compete with the surrounding hardwood canopy. Understory pine density shows a similar but less pronounced pattern.

because eastern redcedar and Ashe juniper (*Juniperus ashei*) have expanded across Oklahoma (including McIntosh County) at a rate of greater than 110,000 ha per year during recent decades (Bidwell *et al.* 2009). Immediately outside of Shortleaf Canyon, young redcedar are widespread along roads, in pastures, and in the abandoned farmland and disturbed woodlands, in some areas occurring as thick stands. However, our study site has not yet experienced this invasion.

THE PERSISTENCE OF SHORTLEAF PINE IN THIS FRONTIER OUTLIER. A hardwood-dominated canopy and the prevalence of hardwoods in the understory should not favor the long-term persistence of pine at Shortleaf Canyon (Stahle *et al.* 1985, Masters *et al.* 1995), particularly if it experienced logging pressure. However, shortleaf pine has successfully reproduced in this forest matrix since

at least the 1780s. Two notable periods of pronounced pine emergence (evidenced by surviving trees) occurred between 1860 and 1880, and again from 1960 until 1990; other minor recruitment events also contributed to the present canopy (Fig. 7). The often sparse, patchy hardwood canopy created in part by the rough topography of Shortleaf Canyon may permit a low level of pine regeneration and recruitment into the overstory. However, the episodic pulses of regeneration driven by decadal patterns in drought and wetness and influenced by stand-level disturbances such as fire, windthrow, or ice storms may ultimately be responsible for the long-term persistence of shortleaf pine at the site (Jones and Bowles 2012). Brown (2006) documented similar climate-mediated episodic recruitment patterns in an analysis of ponderosa pine

Table 2. Estimated understory species composition of the Shortleaf Canyon study area.

Species	Stems per hectare by size class						Density (stems/ha)	BA ^a (m ² /ha)	Relative	
	A	B	C	1	2	3			Density (%)	BA (%)
Post oak (<i>Quercus stellata</i>)	2,413.0	211.1	66.7	18.5	38.9	50.0	2,798.1	0.44	23.2	30.3
Blackjack oak (<i>Quercus marilandica</i>)	2,851.9	300.0	197.4	31.5	24.1	29.6	3,344.4	0.30	27.7	20.2
Shortleaf pine (<i>Pinus echinata</i>)	294.4	27.8	18.5	3.7	3.7	3.7	351.9	0.04	2.9	2.7
Black oak (<i>Quercus velutina</i>)	1,185.2	175.9	142.6	27.8	13.0	3.7	1,548.1	0.11	12.8	7.4
Hickory (<i>Carya</i> spp.)	903.7	203.7	166.7	31.5	22.2	24.1	1,351.9	0.26	11.2	18.1
Shumard oak (<i>Quercus shumardii</i>)	150.0	75.9	66.7	3.7	3.7	1.9	301.9	0.03	2.5	2.4
Eastern redcedar (<i>Juniperus virginiana</i>)	105.6	11.1	3.7	—	—	—	120.4	—	1.0	0.03
Winged elm (<i>Ulmus alata</i>)	1,264.8	307.4	285.2	50.0	22.2	13.0	1,942.6	0.23	16.1	15.9
White ash (<i>Fraxinus americana</i>)	13.0	3.7	5.6	—	1.9	—	24.1	0.01	0.2	0.4
Dogwood (<i>Cornus florida</i>)	187.0	11.1	13.0	1.9	5.6	1.9	220.4	0.03	1.8	2.1
Sassafras (<i>Sassafras albidum</i>)	42.6	1.9	7.4	3.7	—	—	55.6	0.01	0.5	0.3
Black cherry (<i>Prunus serotina</i>)	5.6	—	—	—	—	—	5.6	—	0.05	—
Totals	9,417	1,330	883	172	135	128	12,065	1.5 ^c	100 ^c	100 ^c

^a Class divisions are as follows: A = 15–75 cm tall, B = 75.1–135 cm tall, C > 135 cm height and <2.5 cm DBH, 1 = 2.5–4.9 cm DBH, 2 = 5.0–7.4 cm DBH, 3 = 7.5–9.9 cm DBH.

^b BA = basal area.

^c Any error in summation is due to rounding.

(*Pinus ponderosa* var. *scopulorum*) in the Black Hills of Wyoming and South Dakota.

A comparison of shortleaf pine emergence history to the latewood width chronology from Shortleaf Canyon and the tree-ring reconstructed summer Palmer Drought Severity Index (PDSI; June, July, August average) supports this theory (Fig. 7). The two most significant regional droughts observed in the Oklahoma tree-ring reconstructed PDSI occurred during the 1850s and the 1950s, events that have been confirmed in historical descriptions as well as other dendro-chronological research (Stahle and Cleveland 1988, Cook *et al.* 2004). The Shortleaf Canyon latewood chronology clearly shows the severe 1950s drought, which was the lowest period of radial growth in the well-replicated portion of the 230-yr chronology (Fig. 7). While the 1850s drought was also severe across the region, it did not impact the Shortleaf Canyon pine latewood chronology as dramatically. This may be due to a low sample size at Shortleaf Canyon covering this period or differences in the seasonal response of the post oak chronologies that dominate the Oklahoma reconstructions of summer PDSI, which emphasize late spring and early summer conditions (Cook *et al.* 2004). The 1850s to 1860s and the 1950s droughts were each followed by wet periods, both of which correspond to a pulse in pine regeneration at Shortleaf Canyon (Blasing, Stahle, and Duvick 1988; Stahle and Cleaveland 1988; NCDC 2010).

Given their apparent correspondence, it is likely that the transition from prolonged drought to wet conditions favored both the radial growth and regeneration of shortleaf pine. Periodic mortality of the hardwoods brought on by drought (or other disturbances such as fire, wind, or ice) would improve conditions for pine regeneration. For example, regional droughts produce stand-level stress and decrease the ability of the more mesic hardwood species to regenerate. Droughts can also spur more frequent and damaging fires in the Cross Timbers region (*e.g.*, Stambaugh *et al.* 2009), favoring tree species capable of tolerating surface burns and/or adapted to regenerate following this disturbance event. Unlike most pines, young shortleaf pines can also resprout from suppressed buds on their root collars, and thus are capable of taking advantage of a top-killing fire to exploit resources released by the disturbance (Mattoon 1915, Lawson 1990).

Although a fire chronology was not developed at Shortleaf Canyon, evidence for repeated recent fire is apparent on the numerous “cat-face” burn scars found on trees across the site. The xeric oak forests of eastern Oklahoma have a well-documented history of frequent surface fires, as noted by Clark (2003) and DeSantis, Hallgren, and Stahle (2010). This history likely represents a combination of recurrent droughts and the past use of fire by Native Americans and European American settlers to manipulate regional landscapes (Guyette and Spetich 2003, Stambaugh *et*

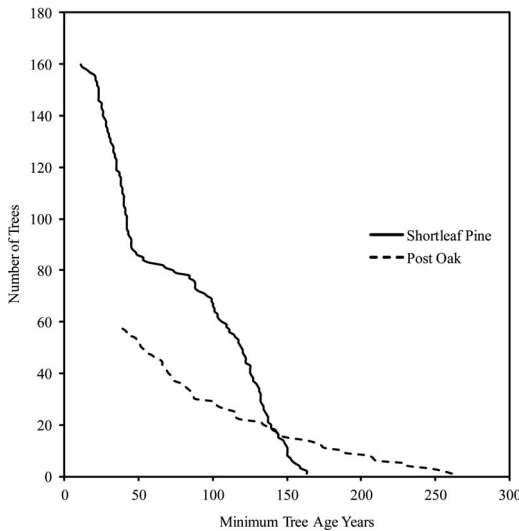


FIG. 6. Age distribution of overstory post oak and shortleaf pine. While not pronounced, both species demonstrate the “reverse J” structure that is characteristic of uneven aged forest stands.

al. 2009). Once shortleaf pine established at Shortleaf Canyon, the disturbance regimes helped perpetuate the population through episodic recruitment for which the long-lived, fire-tolerant shortleaf was well adapted. Persistence of shortleaf pine outliers in other margins of the species range has also been attributed to the interaction of various disturbance events that help to regulate both competition from species with higher shade tolerance and the availability of suitable regeneration sites (Jones and Bowles 2012).

PINE COLONIZATION AT SHORTLEAF CANYON—A POSSIBLE EXAMPLE OF RANGE EXPANSION. While the combination of rugged topography, decadal drought and pluvial events, and frequent fire may explain the persistence of pine at Shortleaf Canyon during the past 230 yr, the mechanism facilitating the arrival of pine is less clear. Evidence (presented below) suggests it is unlikely that Shortleaf Canyon represents a disjunct remnant of a previously continuous distribution. Rather, we contend that a long-distance dispersal and colonization event, which has been documented to play an important role in the range expansion of other tree species (*e.g.*, Willson 1993, Levin 2000, Jackson *et al.* 2005), is likely the best explanation. The multi-kilometer gaps between pine islands on the frontier of shortleaf pine’s range are hardly insurmountable barriers for natural seed dispersal given that

loblolly pine (*Pinus taeda*) seeds, very similar in their nature to shortleaf, have been documented to be dispersed 30 km or more via long-distance uplifting (Williams *et al.* 2006). Such long distance wind-born seed dispersal is quite possible in the severe wind events common to Oklahoma. The timing of this range expansion is also uncertain. Although we lack pollen data for the Shortleaf Canyon vicinity, palynological work elsewhere in eastern Oklahoma has found evidence of southern pine pollen increases over the last 500 to 1,000 yr, perhaps corresponding to increased aridity of the region during this period (Henry *et al.* 1979, Albert and Wyckoff 1981, Hall 1982). To support our hypothesis that the frontier shortleaf pine stand at Shortleaf Canyon represents an example of a potential (if incremental) range expansion event in the mid to late 18th century, we present the following inferences based on available evidence.

First, shortleaf pine has a documented longevity of 350–400 yr (Mattoon 1915; Stahle *et al.* 1985, Guyette, Muzika, and Voelker 2007), and may be capable of “longevity under adversity” (*sensu* Schulman 1954) as reported for many tree species growing under chronically stressful site conditions. Growing conditions in this part of Oklahoma are stressful for all tree species due to frequent droughts, hot summers, and poor, rocky soils. While it is possible that the longevity of shortleaf pine is much lower in the xeric regions of Oklahoma than is reported elsewhere for the species, shortleaf older than 350 yr have been found in other parts of southeastern Oklahoma (Stahle *et al.* 1985). Tree-ring data from the vicinity of Shortleaf Canyon have documented post oaks more than 300 yr old and eastern redcedar over 600 yr old (Stahle *et al.* 1985; Edmondson 2010). Therefore, it seems logical that if a self-replacing population of shortleaf pine had been present at this site for longer than 250 yr, some older trees should remain.

Second, no evidence of historical lumbering can be seen at Shortleaf Canyon. We found no sudden growth releases in the tree ring record to suggest a major disturbance such as logging, nor did we encounter any other physical evidence of harvesting activities such as abandoned equipment, cut stumps, or felled logs. In fact, we found very little old, dead pine wood. This is notable because the resinous wood of shortleaf pine is highly decay resistant (Stambaugh and Guyette 2006), especially in arid environments, and stumps, boles, and

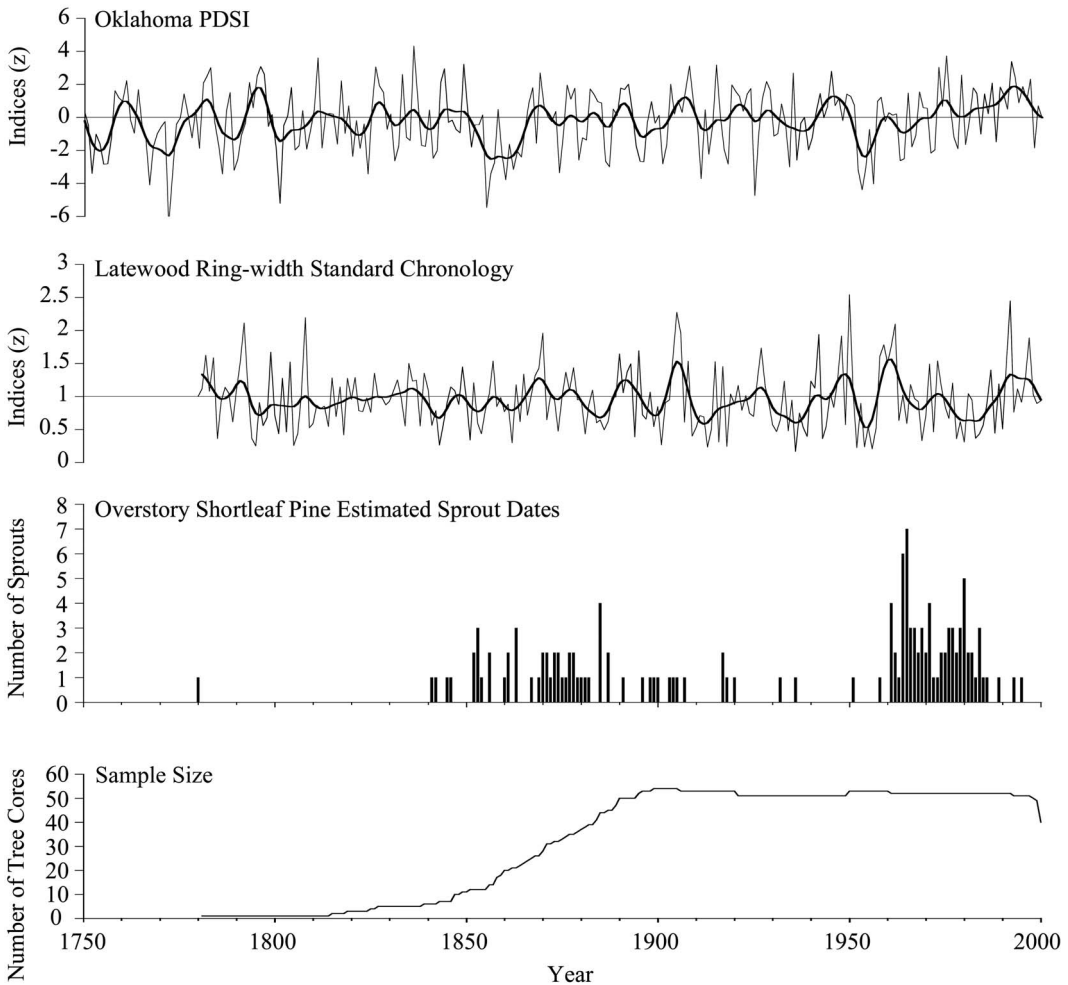


FIG. 7. Comparison of the tree-ring reconstructed summer Palmer Drought Severity Index (Cook *et al.* 2004) averaged from the two nearest Oklahoma grid points, the latewood width standard chronology from Shortleaf Canyon, the number of shortleaf pine to emerge each year at Shortleaf Canyon, and the sample size of cores used to create the latewood chronology. The oldest pine shown on the panel of estimated sprout dates was collected by the University of Arkansas Tree-Ring Laboratory during a prior visit to the site. Because this tree was cored at breast height (with an inner range date of 1780) it is not considered an “emergence” age estimate.

even branches often persist in sheltered locations for many decades when present. For example, Guyette and Spetich (2003) and Guyette *et al.* (2007) used shortleaf pine stumps from trees cut many decades prior to extend tree-ring chronologies of this species back into the 18th century in the Arkansas and Missouri Ozarks. Given that the one datable pine log we found at Shortleaf Canyon was still very sound almost two decades after it died, we know that relict wood can be preserved at the site. Though the absence of relict wood could possibly be attributed to loss via burning, the abundance of rock outcrops, talus, bluffs, and other

sheltered locations in the vicinity should have provided numerous locations for at least some additional dead pine wood to have escaped consumption, even with a presumably high fire frequency at Shortleaf Canyon. Our inability to find any live trees, cut stumps, or relict pine wood older than 230–240 yr was telling.

Third, although we know that the human history of this region goes back many thousands of years, it is highly unlikely that people played a direct role in the establishment of the mature pines at Shortleaf Canyon. The oldest pines at this site date back to the time when the Osage Indians controlled this territory,

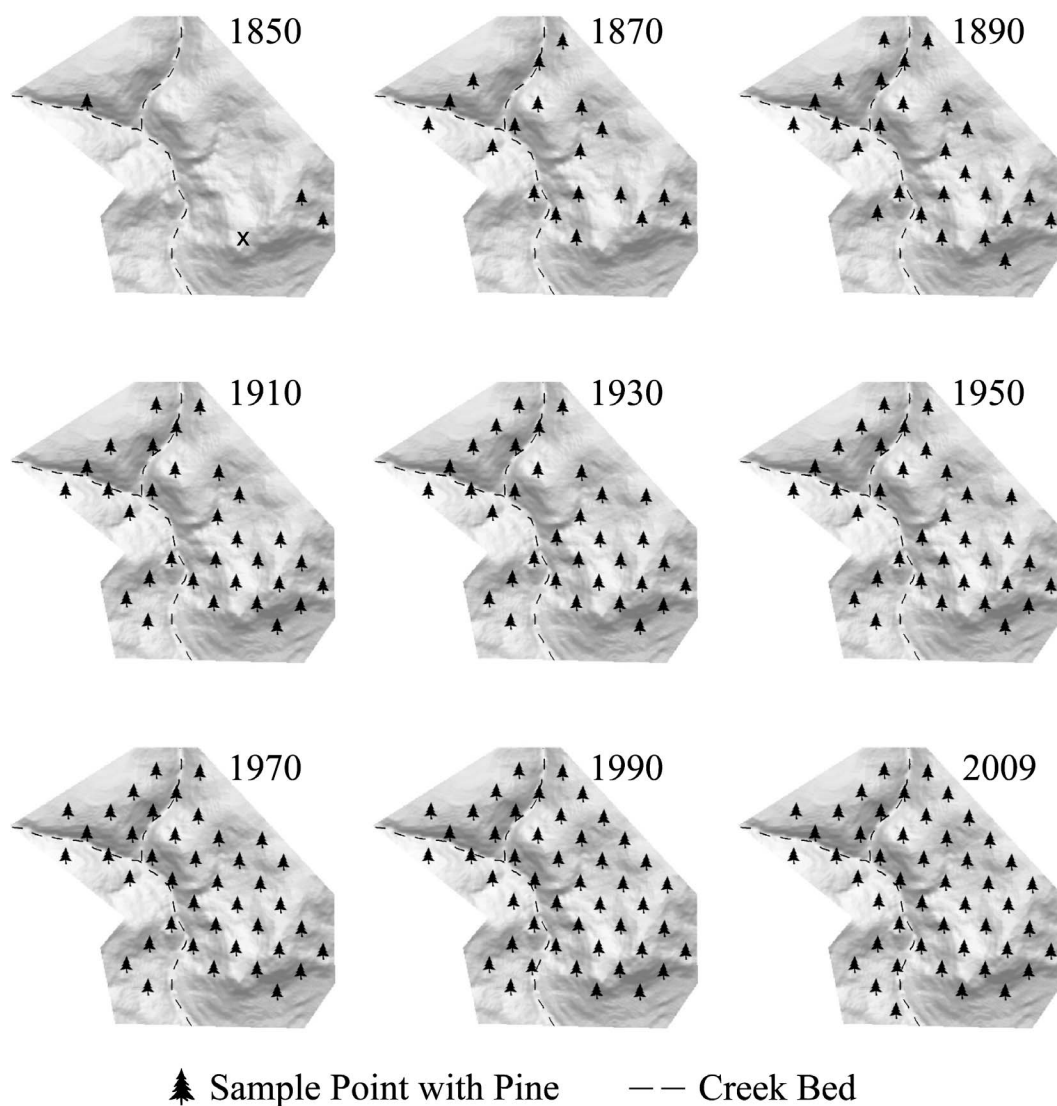


FIG. 8. These maps depict the age and location of living shortleaf pine at Shortleaf Canyon. Only the 134 age-estimated pines were used for this mapping. The sample points represented by the tree symbols indicate that at least one shortleaf pine was encountered within 35 m of the sample point that emerged before the corresponding year. The X on the 1850 map refers to the oldest pine found at the study site, which was cored in 1999 by the University of Arkansas Tree-Ring Laboratory and had an inner ring date of 1780.

and there is no evidence that they planted shortleaf pine at this remote, rugged site. However, Native Americans and early European American settlers used fire to achieve desired vegetative conditions (Guyette, Spetich, and Stambaugh 2006; DeSantis *et al.* 2010), which may have led to improved regeneration conditions for the shortleaf pine and thus increased their abundance at Shortleaf Canyon.

Finally, evidence from other nearby pine islands does not support a long history of shortleaf pine in

the surrounding landscape. Core samples collected by the UATRL from two other pine islands within 5 km of our site indicate that the oldest pines at those sites dated to the early 19th century (D.W. Stahle unpublished data). The scarcity of shortleaf pine witness trees used by the GLO surveyors in the area further suggests that the population of pine was small and likely young during the late 1890s and therefore was not suitable for widespread use as witness trees (Cerny 2010). In southeastern

Oklahoma, GLO surveyors commonly used pine trees to witness corners (Masters, Kreiter, and Gregory 2007), making it unlikely that they would have biased their selection against pine in this area.

Conclusions. Shortleaf Canyon is an old-growth oak-pine forest stand of high ecological integrity evidenced by its abundant old trees, lack of major anthropogenic disturbance, and absence of invasive species. The site is located along an ecotone that follows a strong precipitation gradient causing the eastern oak-hickory forest to give way to the Cross Timbers ecoregion. Aside from the presence of shortleaf pine, stand composition is similar to other examples of remnant old-growth Cross Timbers forests.

Although it is possible that Shortleaf Canyon represents a remnant population of an older pine population that once had a broader distribution, we contend that the study site represents a recent westward expansion of shortleaf pine into the Cross Timbers ecoregion, perhaps within the last 250 yr. Tree-age data, absence of historic lumbering (e.g., cut stumps, sudden growth release), and historical documentation collected for this study support the hypothesis that pine arrived at the site during the mid to late 18th century and subsequently expanded to occupy its current distribution across the study area (Fig. 8). Once established on the steep terrain under a sparse and patchy hardwood canopy, decadal drought, wildfire, and subsequent wet periods appear to have favored the persistence of pine in an otherwise hardwood-dominated landscape.

The timing and mechanism that facilitated the establishment of *Pinus echinata* at Shortleaf Canyon remain uncertain. However, the possibility of a recent range expansion is further supported by similar stand characteristics and tree ages observed at several nearby pine islands located along the rugged terrain common to this stretch of the North Canadian River. While pine seeds are not normally dispersed over long distances, the regular occurrence of severe wind events in eastern Oklahoma provides a plausible mechanism to the hypothesis of a long distance colonization event due to wind-borne dispersal of seeds.

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