FIRE CHRONOLOGY AND WINDSTORM EFFECTS ON PERSISTENCE OF A DISJUNCT OAK-SHORTLEAF PINE COMMUNITY

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Abstract.—We investigated effects of a human-altered fire regime and wind storms on persistence of disjunct oak-shortleaf pine vegetation occurring along 5.5 km of xeric habitat on the east bluffs of the Mississippi River in Union County, IL. In 2009, we resampled vegetation transects established in seven stands in 1954 and obtained 26 cross sections containing fire scars from pines downed by windstorms in 2008 and 2009. These scars revealed 81 years with fires between 1767-1991. Only presettlement fire years corresponded with drought conditions indicated by the Palmer Drought Severity Index. After settlement, fire return intervals measured within stands increased significantly from 4.55 years during the prelogging era (1825-1875) to 8.19 years during the postlogging era (after 1935). After 1975, only one wildfire and two of three management fires were detected. Pine recruitment and the percentage of scarred trees, a proxy for fire intensity, peaked during the prelogging era when both pine and oak recruitment were also positively correlated with fire frequency. Shortleaf pine (*Pinus echinata* Mill.), black oak (*Quercus velutina* Lam.), and post oak (*Quercus* stellate Wangenh.) were codominant in 1954, but by 2008, pine had become subdominant to black oak, and post oak had declined significantly. The 2008-2009 windstorms apparently compensated for recent fire exclusion by selective removal of black oak, allowing pine to regain codominance. At this site, longevity of shortleaf pine coupled with periodic canopy disturbance and favorable fire history appear to have been critical factors maintaining this species in optimum xeric habitat. However, unless fire processes are restored, post oak and other shade-intolerant species may disappear, and shade-tolerant woody species recently established in the understory may further influence future canopy composition.

INTRODUCTION

Fire and windstorms were two of the most important disturbance processes affecting composition and structure of presettlement forests (e.g., Frelich and Lorimer 1991, Peterson and Pickett 1995, Schulte and Mladenoff 2005). Postsettlement fire suppression has significantly altered oak forests by reducing oak regeneration and allowing establishment of fire-intolerant woody vegetation; however, this effect may be moderated on drier habitats (Abrams 1992). As a result, understanding how human-altered fire regimes and their interactions with other disturbances affect long-term vegetation change is critical for management of disturbance-dependent woody plant communities. To resolve this need, managers often seek information on fire history dynamics and reference stand conditions to develop management and restoration goals (Stambaugh and Guyette 2006, Swetnam and others 1999). Fire chronologies determined from tree rings and fire scars can reveal historic fire regimes that have maintained fire-dependent woody plant communities and can help set management strategies to maintain this vegetation (Wolf 2004). For example, Midwest fire chronologies for oaks have revealed comparatively long fire return intervals associated with landscape-scale fires before and during early settlement, followed by a shift toward more localized fire occurrences and fire suppression (reviewed in McClain and others 2010). Likewise, in the Missouri Ozarks, shortleaf pine (see Appendix I for nomenclature and common names) fire scars indicate that presettlement fires occurred during years of extreme drought, while more frequent postsettlement fires, as well as fire protection, mask the influence of drought (Engbring and others 2008, Stambaugh and Guyette 2006).

Severe windstorms alter stand structure by reducing basal area and increasing canopy openness (Hanson and Lorimer 2007). They range from narrow tornado paths or downbursts to wide-scale straight-line winds or derechos (Peterson 2000). Impacts correlate with wind speed and vulnerability due to topographic relief and range in scale from small gaps that are captured by advance regeneration of shade-tolerant species to stand-wide disturbances that may reset or advance successional stages, depending upon understory vegetation (Arevolo and others 2000, Canham and others 2000, Dunn and others 1993, Peterson 2000, Peterson and Pickett 1995, Van Couwenberghe and others 2010). Canopy disturbance return times may occur within the life span of a tree cohort in northern hardwood forests (Frelich and Lorimer 1991) as well as in the Missouri Ozark forests (Rebertus and Meier 2001). Under such disturbance regimes, variability in canopy species susceptibility to windthrow, as well as storm season, can determine their relative abundance in stand composition (Arevalo and others 2000, Fumiko and others 2006, Peterson 2000).

In this paper, we develop a fire chronology for disjunct oak-shortleaf pine vegetation in southwest Illinois. We correlate oak and pine recruitment with fire frequency and compare long-term vegetation change between 1954-2008 with short term change following windstorms in 2008 and in 2009. Our goal was to understand long-term vegetation change in relation to exogenous disturbance processes and to provide management recommendations to help sustain this vegetation. We asked the following research questions:

1) What are the chronology and characteristics of fire, and have they changed during presettlement, prelogging (1825-1975), logging (1876-1935), and postlogging eras?
2) How have pine and oak recruitment interacted with fire history over time?
3) How have canopy and sub-canopy vegetation structure and composition changed since 1954?
4) How did windstorms alter canopy structure and affect species persistence?

Because of its fire-dependence, we expected that pine dominance and reproduction would decline with reduced fire frequency, but that this effect would be moderated by xeric habitat conditions.

STUDY SPECIES AND STUDY AREA

Shortleaf pine is characteristic of the fire-adapted vegetation of the Missouri Ozark Plateau, which extends into Illinois along 5.5 km of southwest facing limestone bluffs of the Mississippi River at the LaRue-Pine Hills Forest Service Research Natural Area, Union County, IL (Fig. 1). We hereafter refer to the study area as Pine Hills. Shortleaf pine stands occupy cherty soils on convex slopes dissected by ravines; this xeric habitat averages 57 percent slope, with 21 percent canopy openness, 79 percent ground cover by litter, and 21 percent exposed mineral soil or moss (Jones and Bowles 2010). Shortleaf pines were recorded at Pine Hills by the U.S. Public Land Survey in 1810 and were sampled by Shake (1956), Suchecki (1987), and Jones (2003). In a dendrochronological analysis of shortleaf pine tree cores from Pine Hills, Jones (2003) indicated that most of the older trees established following major disturbance in 1811-12 and attributed episodic releases in the 1900s to tree harvest, natural canopy disturbance, and favorable precipitation. Both Suchecki (1987) and Jones (2003) projected the shortleaf pine population to decline with continued fire-protection. Concern for shortleaf pine population viability prompted this investigation (Jones and Bowles 2010).

Figure 1.—Distribution of shortleaf pine in southeastern North America, indicated by shading. Source: (http://esp.cr.usgs.gov/data/atlas/little/). Arrow indicates location (circled) of disjunct stands at Pine Hills.

Variation in fire frequency is critical for maintenance of shortleaf pine. In Missouri, pine seedlings establish with 1-4 year fire return intervals but require 8-15 year fire-free intervals for survival (Stambaugh and Muzika 2007). Adult pines are fire-resistant, but record fires by developing characteristic callus tissue over injured cambium, allowing development of fire chronologies (e.g., Stambaugh and Guyette 2006). Shortleaf pine occurs with black oak, post oak, and blackjack oak at Pine Hills, as well as in dry forests and savannas in the Missouri Ozarks (Kabrick and others 2004). Post oak, a member of the white oak group, is shade intolerant (Stransky 1990) and fire tolerant (Johnson and Risser 1975). It occupies fire-maintained savanna and woodland in the Cross Timbers (Stambaugh and others 2009) and appears to be declining in southern Illinois due to succession following fire protection (McClain at al. 2010). Blackjack oak, a member of the black oak group, also tends to be shade intolerant and may occupy an earlier-successional niche than post oak (DeSantis and others 2010, Fumiko and others 2006).

European settlement began at Pine Hills during the 1820s, followed by the initiation of a logging era in the mid 1870s, and acquisition as a Forest Service natural area between 1934-1937. The 1908 Union County plat book shows five saw mills within 1 mile of Pine Hills and six property owners of the seven shortleaf pine stands sampled for this study. The 1929 county plat indicates that ownership of these stands was halved within 21 years. Annual fall fires in the late 1800s and early 1900s reportedly did little damage to large trees at Pine Hills (Krause 1985). Nevertheless, concern for damage from frequent forest fires in this area lead to increasingly greater fire protection in southern Illinois (Miller 1920), thereby reducing the extent of fire coverage. For example, although an average of one fire per year was reported from the Pine Hills area between 1936 and 1968, they occurred mostly along roads and railroads (Suchecki 1987). The Shawnee National Forest conducted prescribed burns in 1989, 1991, and 1993.

Seven shortleaf pine stands at Pine Hills sampled in 1954 by Shake (1956) established that canopy importance was shared by shortleaf pine, post oak, black oak, and blackjack oak, with *Vaccinnium* and *Rhododendron* species in the shrub layer. In 2009, we resampled transects mapped by Shake (1956). This sampling followed 2008 and 2009 windstorms that downed both pine and oak canopy trees. Most pines were uprooted, while oaks were broken off near their bases. The 2008 storm may have been 80-130 km/hr straight-line winds that were associated with the 5-6 February Super Tuesday Tornado outbreak (CIMSS 2008). The 2009 storm was a cyclonic derecho with peak 145-160 km/hr winds that crossed eastern Missouri and southern Illinois on 8 May (Brown 2009, CIMSS 2009). The 2009 storm had far greater impact on Pine Hills than did the 2008 storm (M. Jones, personal observation).

METHODS

Data Collection and Processing

To develop a fire chronology, we used a chain saw to obtain 58 cross sections from the bases of pines downed by windstorms and from previously cut pine stumps. Downed pines were unavailable in one stand. We also extracted cores to pith from 71 standing shortleaf pine and 28 oaks representing 10 cm size classes in sampling plots. All samples were sanded with progressively finer grades of sandpaper (1200 minimum grit) to reveal annual rings and fire scars. Twenty-six of the cross sections contained 113 fire scars and were used to develop a stand fire chronology. Following Stambaugh and Guyette (2006), a radius of each cross section with the least variability due to fire scarring was used for measurement, and plots of ring-width series were used for visual cross-dating of "signature years" and for locating missing or false rings. Once dating was completed, series accuracy was verified on the COFECHA program (Grissino-Mayer 2001a) and combined into a master stand chronology represented by a standardized ring-width index using the ARSTAN program (http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html). FHX2 software (Grissino-Meyer 2001b) was used to graph fire scars, and to calculate fire intervals for each series, the percentage of scarred trees for each year of a fire occurrence, and Jaccard and Yule similarity indices of fire synchroneity among stands. Linear distances among stand midpoints were measured at a horizontal scale on a 7.5' USGS quadrangle map and ranged from 0.25-5 km, averaging 1.93 km in a pair-wise matrix.

Transect locations were mapped by Shake (1956) on the Wolf Lake, Illinois 7.5' USGS quadrangle. These transects were digitized onto a digital elevation model of the Wolf Lake quadrangle, from which Global Positioning System (GPS) positions were retrieved for field locations. The initial small mapping scale prevented precise relocation of transects, and our data represent random samples of stands over time. We sampled trees using the original point-center-quarter (PCQ) method (N = 210 points), as well as 0.025 ha tree plots (N = 56) in which were nested 0.001 ha sapling and 1-m^2 juvenile plots. PCQ tree sampling included the identity and diameter of the nearest tree (>10 cm d.b.h.) in each quadrant, including both standing trees and those toppled by the 2008 and 2009 windstorms. The nearest live saplings (2.54-10 cm d.b.h.) were also recorded in each quadrant. Plot sampling included trees >10 cm d.b.h. in 0.025 ha plots, saplings >1 m high and > 2.54-10 cm d.b.h. in 0.001 ha plots, and juvenile trees <1 m high in 1-m^2 plots. All windthrown trees originating within sample plots were sampled to reconstruct pre-storm (2008) stand structures. Following Shake (1956), PCQ data were used to calculate relative density and relative basal area (BA) for 2.5-25.4 and >25.4 d.b.h. size classes. Pre- and post-storm plot samples were used to calculate basal area and dominance (relative basal area) for each stand. Average 2008-2009 density was also calculated for trees, saplings, and juvenile tree species.

Statistical Procedures

What are the chronology and characteristics of fire, and have they changed during presettlement, prelogging, logging, and postlogging eras?

Superposed Epoch Analyses (SEA) was used on FHX2 software (Grissino-Meyer 2001a) to test whether fire years were associated with years of extreme drought during the presettlement, prelogging, logging, and postlogging eras. Proxy climate data were Palmer Drought Severity Indices (PDSI) from Grid 112 for southeast Missouri (Cook and others 2004); data were bootstrapped for 1000 simulations to derive 99 percent and 95 percent confidence intervals for normal drought conditions and were compared for each of the 5 years proceeding and 4 years following the year assigned to a fire scar. We used regression analysis to test whether stand ring-width indices had significant linear relationships with local 1901-2009 precipitation and temperatures in years t and t-1 for fall, winter, spring, and summer months. Data were obtained for Anna, IL from the Illinois State Climatologist Office and Illinois State Water Survey (Illinois State Water Survey 2012).

A Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test whether mean fire return intervals differed among eras. For this test, fire return intervals were measured within stands. Stands were not included in a factorial test because all stands were not represented by fire intervals within each era. A separate Kruskal-Wallis test was used to compare fire return intervals among stands. A Kruskal-Wallis one-way analysis of variance was also used to test whether the mean percentage of fire scarred trees (a proxy for fire intensity) differed among eras. Regression analysis was used to test whether significant linear relationships occurred between stand distance and fire synchroneity between stands, as measured by the Jaccard and Yule indices. This test was applied within eras.

How have pine and oak recruitment interacted with fire history over time?

Regression analysis was used to test whether significant linear relationships occurred between both pine and oak recruitment numbers and decadal fire frequency calculated in a sliding 10-year window (following Stambaugh and Guyette 2006) within eras. For this test, we based recruitment on trees aged from cores taken from sample plots and lagged fire by one decade to accommodate growth to d.b.h. in xeric habitat. The sample size for oaks was limited by availability of cores to pith because heart-rot was common among black oaks.

How have canopy and sub-canopy vegetation structure and composition changed since 1954?

Shake (1956) provided relative basal area and relative density data for each stand, which required converting modern data to relative values in order to test for significant temporal changes in these categories. Repeated measures analysis of variance (RMANOVA) was used to test whether relative basal area and relative density of trees > 10 cm d.b.h. changed between 1954 and 2008 (pre-storm), using the 7 stands as replicates. These tests were applied at the species level to shortleaf pine, white oak, blackjack oak, post oak, black oak, and hickory, as well as a single group representing subordinate species that were poorly represented as canopy trees. For each stand, Shake also provided tallies of tree species stem numbers in 2.5-25.4 cm and in >25.4 cm size classes. We converted these data to stand point sample densities for each species by dividing species tallies by the number of plots in each stand. They were analyzed by RMANOVA to test whether species point density changed between 1954-2008 (pre-storm) within size classes. This provided a validation of changes in relative density. We also used linear regression to test whether 0.025 ha plot density of post oak, which declined significantly, was related to canopy openness (measured with a digital camera and hemispherical lens, Jones and Bowles 2010) and whether its basal area was inversely related to that of black oak, the dominant canopy species.

How did windstorms alter canopy structure and affect species persistence?

To assess the 2008 and 2009 storm impacts on tree species density, we used RMANOVA to test whether significant temporal change occurred in basal area and relative basal area (dominance) of dominant tree species, as well as other subordinate species treated as a single group.

RESULTS

Chronology of Fire and Tree Growth

Cross sections from 25 windthrown trees contained 110 fire scars, while a single cross-dated stump cross section contained 3 scars, resulting in 113 scars dating between 1767 and 1993 on 26 trees (Fig. 2). Seasonality of presettlement fire scars was difficult to assess because of poor conditions of the cross sections. However, the majority of scars occurred during the dormant season, indicating most fires were between September-March. The total number of years during which fires were detected included 6 years in the presettlement era (1767-1825), 22 years in the prelogging era (1826-1875), 31 in the logging era (1876-1935) years, and 22 in the postlogging era. After 1975, only one wildfire and two of three management fires were detected, and no fires were

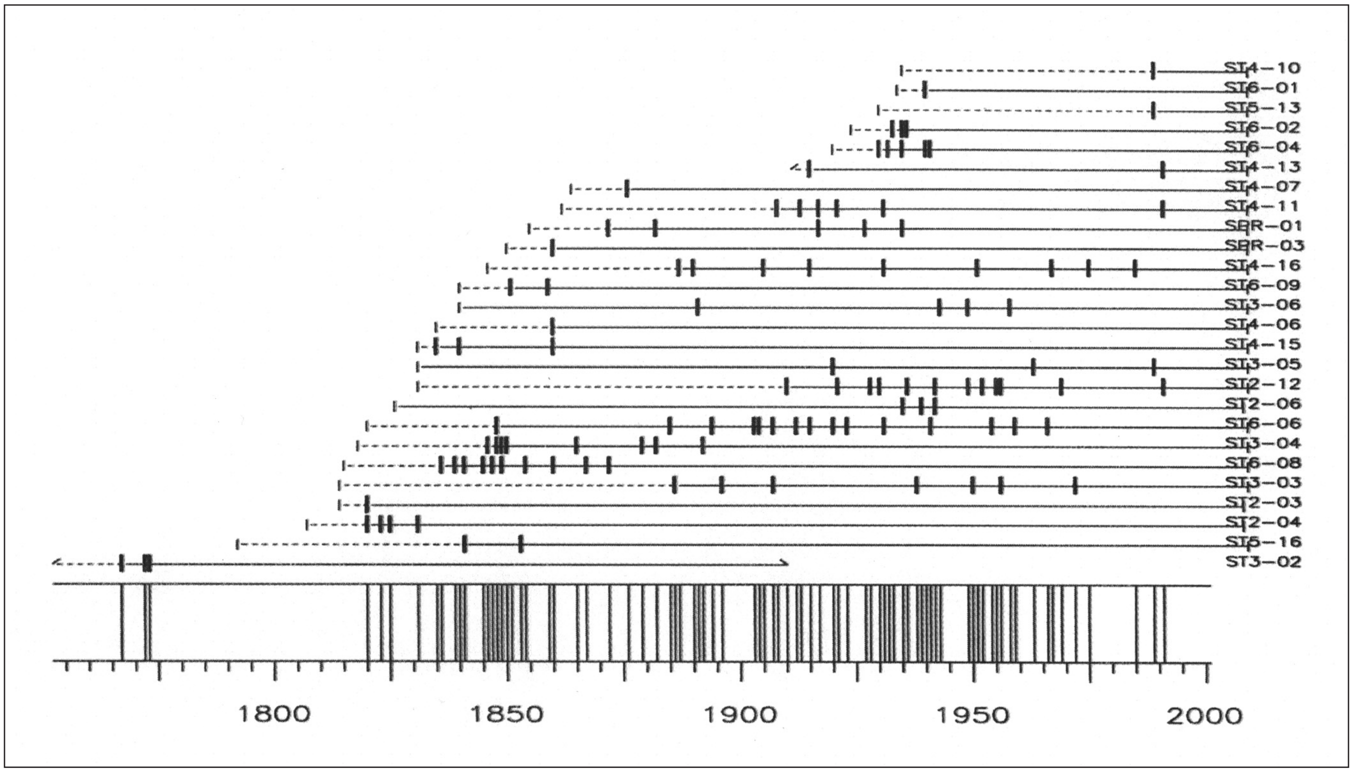

Figure 2.—Fire chronology of shortleaf pine at Pine Hills. Vertical bars represent fire scars on cross sections from 25 windthrown trees and a single cross-dated stump between 1767-1993. Vertical axis indicates stand and tree numbers.

recorded after 1993. At the landscape level, fires were recorded about every 2 years between 1820 and 1975. Fire-return intervals measured within stands increased significantly over time, averaging 4.55 (+1.1 se) years in the prelogging era, 6.57 (+1.2 se) years in the logging era and 8.19 (+1.5 se) years in the postlogging era (Fig. 3). These intervals also varied significantly (Chi-square = 13.06, P = 0.011) among stands, ranging from 3.7 (0.58 se) to 16.7 (8.69 se) years. The percentage of fire-scarred trees, indicating fire intensity, was greater during the prelogging era (Fig. 3). Within eras, there was no significant relationship between distance among stands and fire synchroneity. SEA indicated that fires during the presettlement era occurred during significant dry years, as indicated by the Palmer Drought Severity Index (Fig. 4). No significant relationships occurred between dry or wet years and fire during the postsettlement, logging, or postlogging eras. The standardized ring-width chronology was significantly positively correlated ($r^2 = 0.145$, $P < 0.001$) with summer precipitation and negatively correlated ($r^2 = 0.259$, $P < 0.001$) with summer temperature. There were no significant correlations with other seasonal precipitation or temperature variables, nor with any variables in the previous year.

Shortleaf pine and oak establishment based on plot-sampled tree cores were recorded from 1810-1970 (Fig. 5). The greatest percentage of pine recruitment occurred during the prelogging era when it was significantly positively correlated with decadal fire frequency (Fig. 6). Pine recruitment tended ($P < 0.07$) to be negatively correlated with fire frequency during the logging era and positively correlated during the postlogging era. Pine recruitment also underwent a moderate increase during the early decades of the postlogging era. Oak recruitment also was positively correlated with fire frequency during the prelogging era. However, a greater percentage of oak recruitment occurred during the last decade of the logging era and continued into the early postlogging era, when it was marginally ($P < 0.07$) correlated with fire frequency. Among oaks, white oak recruitment predominated during the prelogging era, black oak and blackjack oak predominated during the logging era, and white oak and black oak predominated during the postlogging eras (Fig. 5). Post oak recruitment was represented by single occurrences during the prelogging and logging eras.

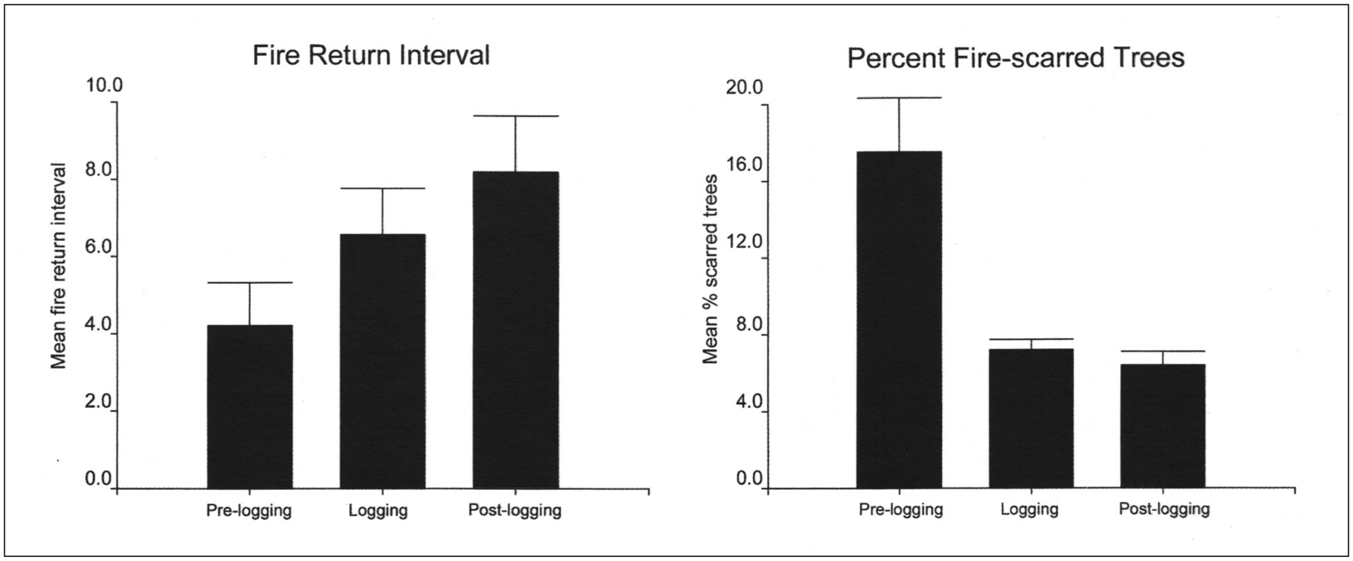

Figure 3.—Relationship between mean (+se) fire return interval and mean (+se) percentage of fire-scarred trees across eras at Pine Hills. Fire return interval: Chi-square = 6.15, P = 0.046. Sample size: Prelogging (N = 19), Logging (N = 30), Postlogging (N = 21). Percentage of fire-scarred trees: Chi-square = 31.56, P < 0.001. Sample size: Prelogging (N = 23), Logging (N = 30), Postlogging (N = 26).

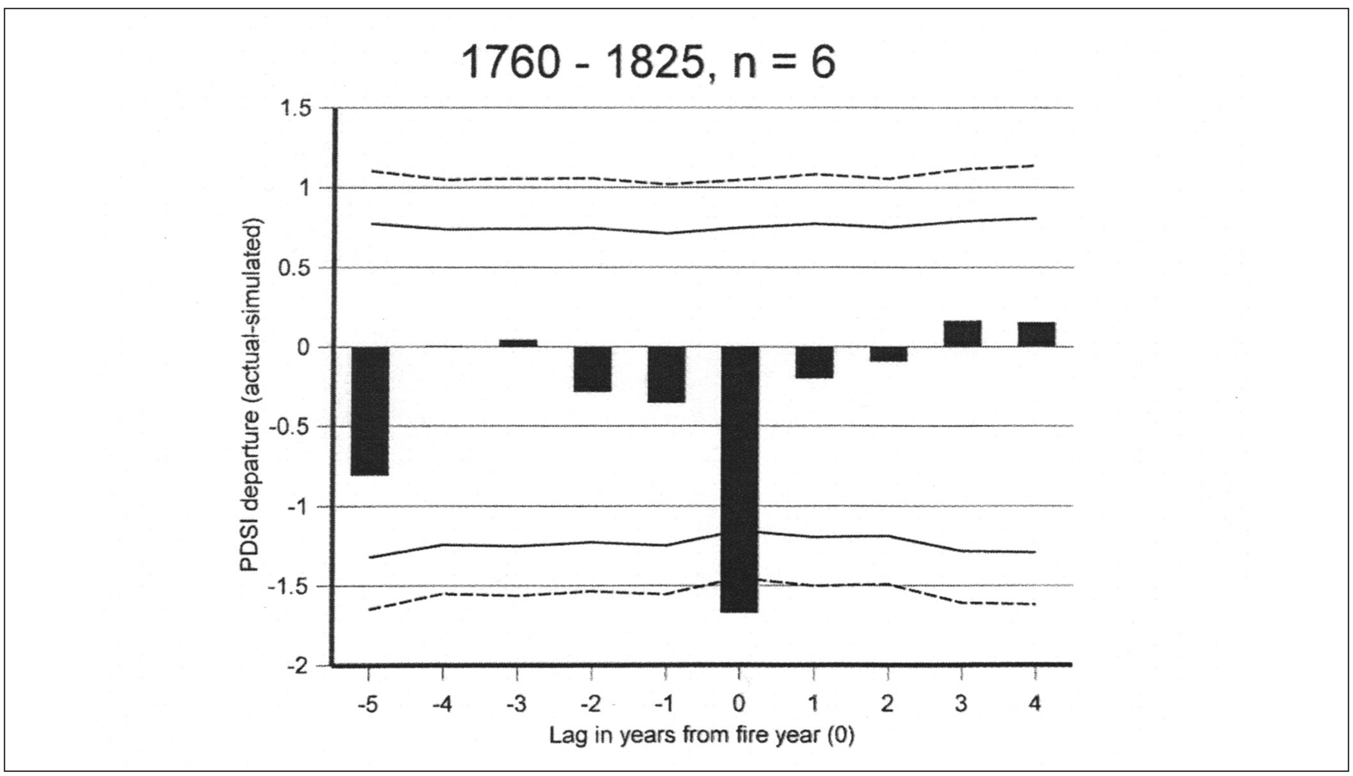

Figure 4.—Superposed epoch analysis (SEA) during the presettlement era at Pine Hills. Horizontal axis represents lag in years from fire year (0). Bars represent deviation from normal drought conditions based on 1000 simulations. Solid and dashed lines are 95 and 99 percent confidence intervals, respectively.

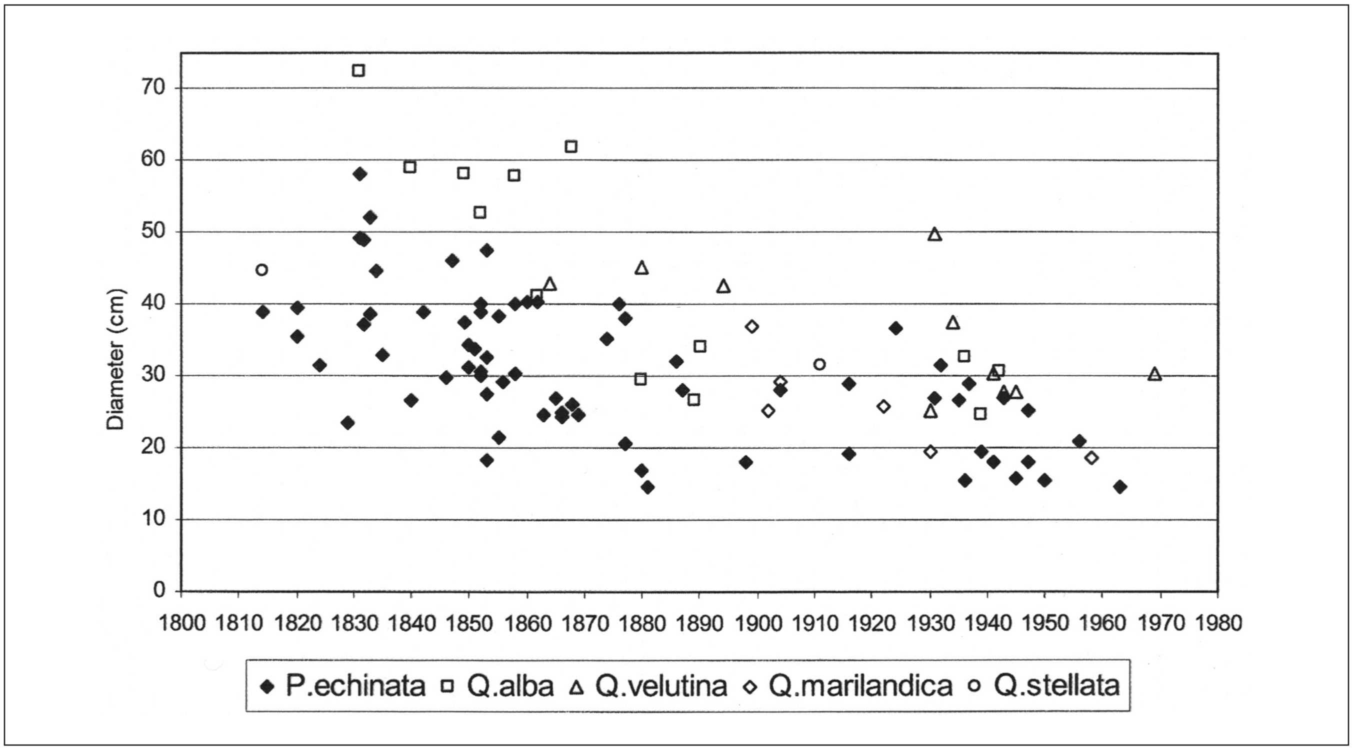

Figure 5.—Recruitment chronology and age-diameter relationships for shortleaf pine ($r^2 = 0.293$, P = < 0.001) and oak species ($r^2 = 0.610$, $P < 0.001$) at Pine Hills.

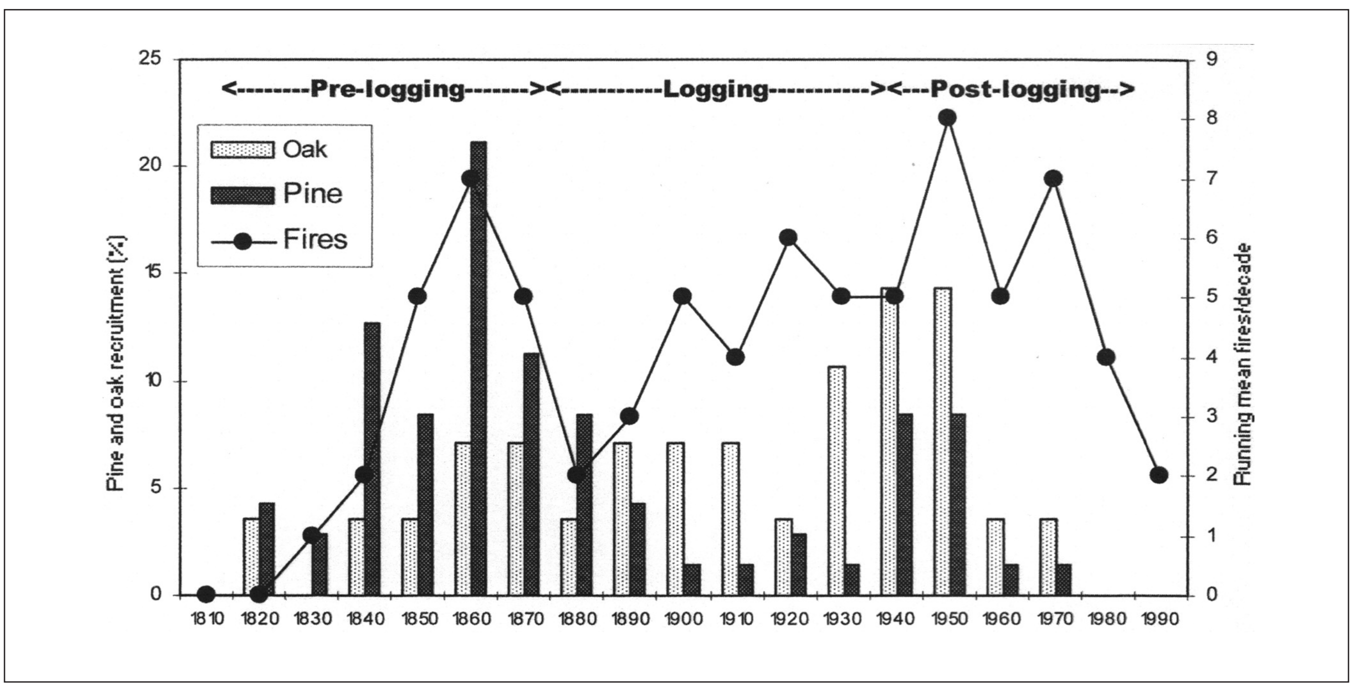

Figure 6.—Decadal relationship between running mean fires/decade and recruitment of shortleaf pine and oak at Pine Hills. Years represent end of decade. Fires are lagged 1-decade. Correlations: Prelogging (pine r = 0.869, P = 0.005; oak r = 0.832, P = 0.01); Logging (pine r = -0.83, P = 0.066; oak r = 0.211, P = 0.689); Postlogging (pine r = 0.788, P = 0.063); oak r = 0.788, P = 0.0625).

Structural and Compositional Change

By 2008, there were significant declines in relative BA and relative density of post oak and an increase in these measures for the group of subordinate species, including elm, sassafras, service berry, tulip tree, red maple, flowering dogwood, ironwood, white ash and American beach (Fig. 7, Appendix I). The most abundant of these species were subdominant with white oak, black oak, and shortleaf pine in juvenile and sapling size classes (Appendix I). Post oak also declined significantly in density in the 2.5-25.4 cm and > 25.4 cm size classes (Fig. 8). This change was accompanied by significant increases in white oak and other subordinate species in the 2.5-25.4 cm size class. In 2009, post oak density had a significant positive linear relationship with canopy openness ($r^2 = 0.5546$, P = 0.0022), and its basal area had a significant negative relationship with that of black oak ($r^2 = 0.2337$, P = 0.0264).

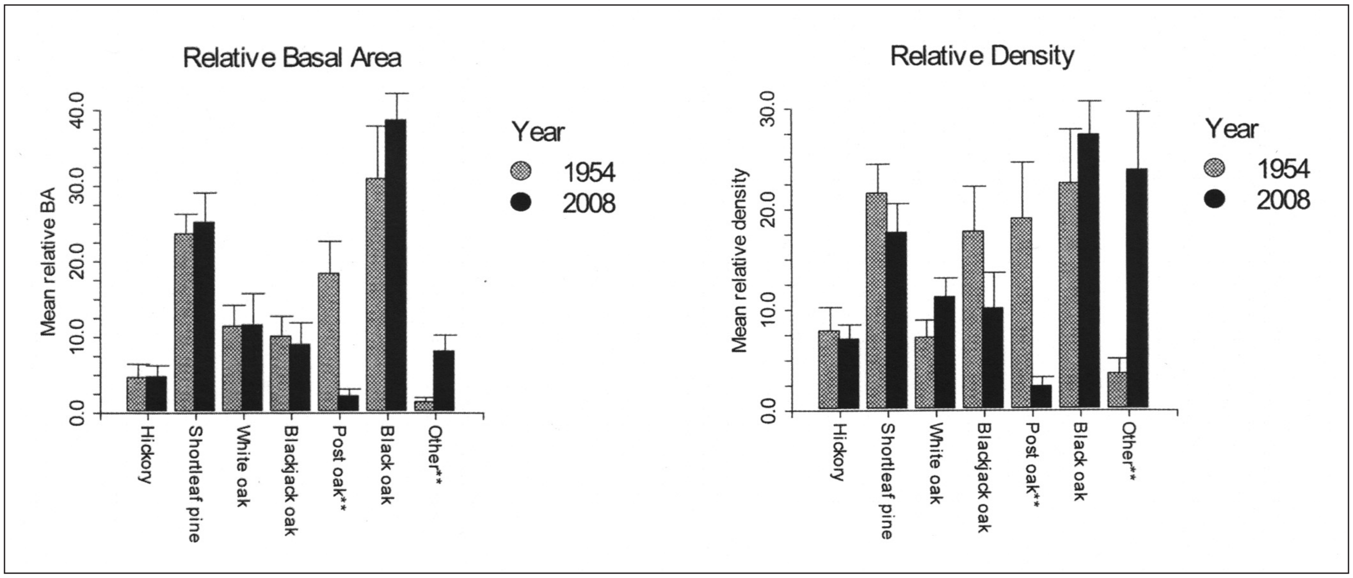

Figure 7.—Temporal change in tree species mean (+se) relative basal area (BA) and relative density at Pine Hills. Relative BA: post oak (F = 23.61, P = 0.0028), other (F = 14.78, P = 0.0086). Relative density: post oak (F = 18.26, P = 0.0052), other (P = 15.84, P= 0.0073).

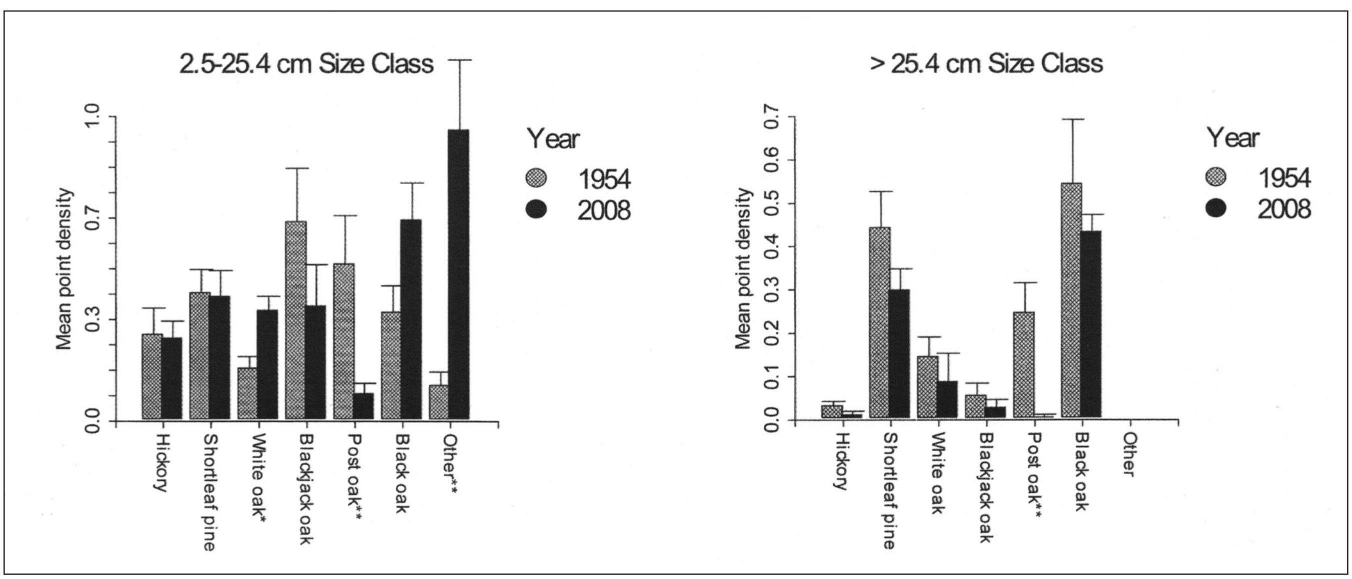

Figure 8.—Temporal change in species mean (+se) sample point density by size class at Pine Hills. 2.5-25.4 cm size class: white oak (F = 11.38, P = 0.0150), post oak (P = 11.90, P = 0.0016), other (F = 18.73, P = 0.0049); >25.4 size class: post oak (F = 29.32, P = 0.0016).

Before the windstorms, black oak had become the single dominant tree with subdominance by shortleaf pine and white oak and minor representation by blackjack oak and post oak (Fig. 9). Windstorm damage caused significant declines in BA of black oak and, to a lesser degree, shortleaf pine (Fig. 9). Because of the greater reduction of black oak BA, the storm damage resulted in increased relative BA (dominance) of hickory and shortleaf pine (Fig. 9).

DISCUSSION

Chronology and Change in the Fire Regime

At Pine Hills, average stand level fire return intervals increased from 4.55 years during the prelogging era to 8.19 years during the postlogging era. These intervals fall within the ranges reported for other Midwest oak-dominated stands with human ignition sources (McClain and others 2010) and indicate a strong human influence on the Pine Hills fire regime. The low fire synchroneity and high variability in fire return intervals among stands is probably due to spatially independent ignitions, as well as the site's dissected topography, which would reduce the landscape spread of fire. Indeed, the maximum number of stands with recorded wild fires during single years was three stands, which occurred only during 1860 and 1935. Ignitions also may have been independent of ownership by the early 1930s, when the seven stands had only three landowners. Cultural conditions may strongly affect fire return intervals. Wolf (2004) and McClain (2010) report three-decade fire return intervals during the mid to late 1800s in southeastern Wisconsin and in southern Illinois, and indicate that they correspond to periods of accelerated settlement and fire protection in the forest-prairie transition region. Although the increasing fire return intervals at Pine Hills support these findings, the absence of extended periods without fire indicates either more frequent ignitions or more moderate levels of fire suppression. The continuation of burning until about 1975 parallels results from the Ozark Wilderness of the Missouri Ozarks, where fires may have been set in protest against federal acquisition (Stambaugh and Guyette 2006). Similar actions could have taken place at Pine Hills after it was acquired as a Forest Service natural area.

Although our presettlement sample depth was limited to two trees, the lower fire frequency during this period is not inconsistent with other Midwest

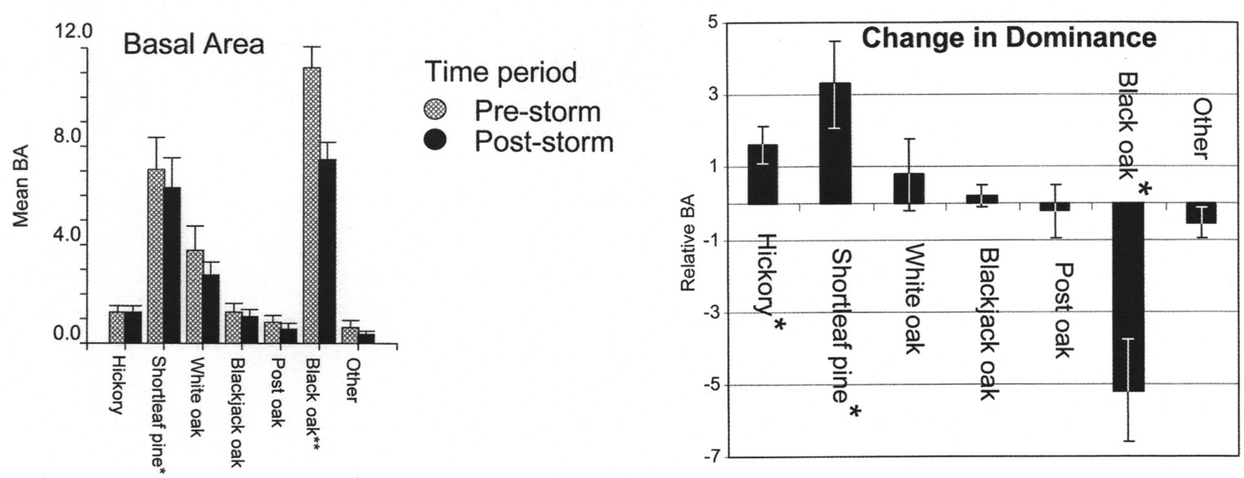

Figure 9.—Species mean (+se) pre- and post-storm basal area, and post-storm change in relative basal area (dominance) at Pine Hills. BA: shortleaf pine (F = 6.10, P = 0.0485), black oak (F = 30.51, P = 0.0015). Dominance: hickory (F = 10.34, P = 0.0183), shortleaf pine (P = 7.57, P = 0.0332), black oak (F = 13.7, P = 0.01).

studies (e.g., McClain and others 2010), which would suggest that less frequent fires characterized this period at Pine Hills. Our data also support findings of Stambaugh and Guyette (2006) that less frequent fires in the presettlement era corresponded to extreme drought conditions, while greater fire frequency during the postsettlement era masked the effects of drought on fire occurrence. Infrequent drought-driven fires may have been comparatively intense due to fuel accumulation between fire years and greater flammability during drought conditions. The occurrence of a greater percentage of scarred trees, a proxy for greater fire intensity, during the prelogging (1825-1875) era also suggests that high intensity fires would have continued through this era. The composition, structure and fuel loads of forests during this period also would have been more similar to presettlement conditions than to those that developed during the logging period. Increasing fire suppression during the 1900s may have contributed to less frequent burning as well as lower percentages of scarred trees.

Tree Recruitment and Interaction with Fire

The greater recruitment of shortleaf pine during the prelogging era, its positive correlation with decadal fire frequency, and the greater percentage of scarred trees during that era suggest that fire has had a strong positive influence on population dynamics of shortleaf pine at Pine Hills. Shortleaf pine seedling establishment requires 1-4 year fire return intervals, and 8-15 fire return intervals for subsequent survival and development (Stambaugh and Muzika 2007). At Pine Hills, temporal variation in fire return intervals falls within that range, and interactions with spatially variable topography and fuel loads may have facilitated pine regeneration and population maintenance. Nevertheless, the lower percentage of scarred trees during the logging and postlogging eras may indicate that reduced pine recruitment during these eras resulted from lower fire intensity. Slash from logging is often attributed to causing greater fuel loads and greater fire intensity, but no data are available on the intensity of logging in pine stands and the levels of fuels that might have accumulated. Although oak recruitment also had a positive relationship with fire frequency during the prelogging era, it had greater recruitment during the late logging era, as well as the early postlogging era. This process could have been enhanced by sprouts from cut stumps following logging, as well as large canopy gaps that would have persisted for a decade or more following logging. The lower recruitment of both oak and pine in the latter part of the postlogging era appears to correspond to decreasing fire frequency during that era.

Compositional Change and Compensatory Effects of Windthrow

Xeric habitats have been suggested to be resistant to successional replacement of oaks (Abrams 1992). However, long-term data have demonstrated successional change in western post oak-blackjack oak forests (DeSantis and others 2010). Likewise, our data suggest that reduced fire frequency and intensity has lead to replacement of post oak and shortleaf pine by black oak, with increased advance regeneration of shade-tolerant species. Canopy closure may be a strong causal factor in decline of post oak because of its shade intolerance (Stransky 1990), and has been suggested as a cause of post oak decline in southern Illinois (McClain at al. 2010). At Pine Hills, the positive relationship between post oak density and canopy openness and the negative relationship between post oak and black oak basal area suggest that post oak may be declining due to competition for canopy light caused by increasing canopy closure from black oak. The greater resilience of blackjack oak, white oak, and black oak may result from species specific adaptations to different habitat conditions. Blackjack oak may be adapted to more xeric or open early-successional habitat, which would allow it to persist in a comparatively narrow habitat range at Pine Hills where other species are less competitive. Black oak and white oak tend to have greater shade tolerance than blackjack oak (Dey 2003), and appear to tolerate a greater range of overlapping soil moisture conditions. This would promote their survivorship across a wider habitat range under more dynamic canopy conditions.

If fire protection continues, the increases in smaller size classes of shade-tolerant species may provide the basis for eventual successional replacement by many of these species, as they comprise well over 50 percent of the advance regeneration in oak-pine stands at Pine Hills. Similar successional change in other systems has been linked with fire protection. In Oklahoma, sapling densities of winged elm increased while densities of post oak and blackjack oak decreased (DeSantis and others 2010). Red maple is shade tolerant and fire sensitive and is currently expanding in eastern forests (Abrams 1998, Green and others 2010, McDonald and others 2002). Flowering dogwood and sassafras also colonize old fields in southwest Illinois but may not persist with succession (Ashby and Weaver 1970). Work is needed to understand whether restoring fire processes can prevent additional seedling establishment and canopy replacement by shade-tolerant species and also prevent competition by these species from excluding both pine and oaks seedlings.

Interactions between fire and windstorms have probably been important historic factors maintaining shortleaf pine at Pine Hills (Jones 2003). Our data suggest that in the recent absence of fire, the 2008 and 2009 windstorm effects have been compensatory, as they restored the former codominance of shortleaf pine with black oak (Shake 1956). Seasonality of windthrow was also critical, as the 2009 growing season storm selectively removed greater oak than pine basal area. This apparently resulted because broadleaf oak crowns are more vulnerable to windthrow than are needle-leaf pine crowns. Such stochastic exogenous disturbance processes may be important factors operating in combination with longevity of shortleaf pine and presence of optimum habitat in maintaining this disjunct pine population. The steep slopes and exposed soil at this site probably facilitated seedling germination during the presettlement fire regime and may have reduced local fuel loads and allowed seedling establishment during more frequent postsettlement fires. Although projection of increased storm damage is problematic (Peterson 2000), climate change models predict greater frequencies of severe storms (National Assessments Synthesis Team 2004) which could continue to favor shortleaf pine over hardwoods. However, as the windstorms had no direct effect on sapling or juvenile tree species, successional processes involving advance regeneration may determine future canopy composition (Peterson 2000). The size class distribution of shortleaf pine indicates that pine advance regeneration is present, and more work is needed to determine whether pine will access canopy openings created by windthrow.

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APPENDIX

Species nomenclature and stems/ha for tree species in juvenile (<1 m high), sapling (>1 m, 2.54-10 cm d.b.h), and tree (>10 cm d.b.h.) size classes at Larue-Pine Hills Natural Area, ranked by juvenile density. Densities represent averages of pre- and post- 2008-2009 storm data.

Scientific name	Common name	Juvenile	Sapling	Tree
Ulmus sp. L.	Elm	5826.19	553.23	12.36
Quercus alba L.	White oak	2127.72	220.31	62.81
Sassafras albidum (Nutt.) Nees.	Sassafras	2117.30	470.96	7.32
Quercus velutina Lam.	Black oak	2036.37	307.38	141.20
Amelanchier arborea (Michx. f.) Fern.	Service berry	1714.12	159.58	2.90
Liriodendron tulipifera L.	Tulip tree	1654.14	0.00	0.41
Acer rubrum L.	Red maple	1531.75	95.92	2.94
Pinus echinata Mill.	Shortleaf pine	1475.31	228.56	120.31
Quercus marilandica Muenchh.	Blackjack oak	1164.06	119.93	50.94
Cornus florida L.	Flowering dogwood	931.96	354.52	8.17
Ulmus rubra Muhl.	Red elm	864.66	14.29	0.00
Carya glabra (Mill.) Sweet.	Pignut hickory	747.71	148.02	21.17
Diospyros virginiana L.	Persimmon	294.97	24.85	7.33
Carya ovata (Mill.) K. Koch.	Shagbark hickory	168.94	24.87	0.00
Ostrya virginiana (Mill.) K. Koch.	Ironwood	144.23	43.65	0.00
Fraxinus Americana L.	White ash	134.71	20.41	0.00
Fagus grandifolia Ehrh.	American beech	112.44	37.70	0.00
Prunus serotina Ehrh.	Black cherry	75.19	0.00	0.00
Quercus stellata Wangenh.	Post oak	64.94	14.29	19.43
Carya sp Nutt.	Hickory	59.52	0.00	0.00
Juniperus virginiana L.	Red cedar	59.52	0.00	0.00
Quercus rubra L.	Red oak	8.93	65.56	7.20
Carya texana Buckl.	Black hickory	4.46	37.68	17.61
Carya ovalis (Wangenh.) Sarg.	Sweet pignut hickory	0	0	8.51
Cercis canadensis L.	Redbud	0.00	10.20	0.00