# THE HISTORICAL ECOLOGY OF FIRE, CLIMATE, AND THE DECLINE OF SHORTLEAF PINE IN THE MISSOURI OZARKS

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**ABSTRACT.**—We review studies that have shown reductions in the abundance of shortleaf pine (*Pinus echinata* Mill.) during the last century in the Ozark Highlands. These studies indicate that pine abundance is currently 15 to 53 percent of the pine abundance levels before major logging activity and fire suppression, activities dating from the mid- to late 19th century. Evidence of pine loss comes from General Land Office notes, the presence of pine remnants, and historical documentation that described pine forests. Selective removal of pine, followed by intense hardwood competition, reduced shortleaf pine abundance in the Ozarks over the past century. In addition, very short fire intervals (< 3 years) before and after logging reduced advanced pine regeneration. More recently (1940-2006), long fire intervals caused by fire suppression have contributed to a long-term decline in pine abundance. Under continuing fire suppression, vegetation dynamic models predict a decline in abundance that will stabilize in about 200 years. Additional, more recent threats to recruitment and maintenance of shortleaf pine populations may include global warming-induced insect outbreaks.

## THE ABUNDANCE AND LOSS OF SHORTLEAF PINE

Estimates of shortleaf pine occurrence and loss in Ozark forests come from several quantitative and qualitative sources, and are best presented in the context of the contemporary forest. Among the most recent studies, Voelker (2004) measured the diameter and age class distribution (Fig. 1) of oak and pine in the Current River Hill subsection of Missouri (Nigh and Shroeder 2002), and determined their current relative abundance. Shortleaf pine has a greater frequency in older age classes due to its greater maximum age relative to red oaks. The age class distribution of pine on these 1200 randomly chosen plots indicates that about 15 percent of the shortleaf pine in this region is over 90 years in age. Only two studies have evaluated the age structure of successional forests of the Ozarks left after the exploitation period, both of which were based in single stands in order to test silvicultural definitions of even-aged versus multi-aged forests (Loewenstein and others 2000; Shelton and Murphy 1990). It is common knowledge that many of the mature oak-pine stands are relatively even aged, but knowledge of the actual age distributions across the landscape is lacking.

The most recent forest inventory data indicate that the shortleaf pine forest type occurs on approximately 72,000 hectares or 1 percent of the forested land in Missouri (Moser and others 2006). Historically, shortleaf pine was estimated to have covered 2.7 million hectares in Missouri (Fletcher and McDermott 1957). Using landuse-landcover maps and comparing these with General Land Office (GLO) survey notes, Hamilton's (2003) analysis indicated that forests with a shortleaf pine component currently occupy about 36 percent of the landscape that was originally described as shortleaf pine forest in the Current and Eleven Point rivers region. An estimate by Cunningham and Hauser (1989) states that shortleaf pine forest types currently occur on approximately 162,000 hectares in Missouri. Despite considerable range in data describing current distribution, several studies have documented that the abundance of shortleaf pine in the Missouri Ozarks has diminished (Table 1). Batek and others (1999) quantified GLO note data in the Current River watershed of the Missouri Ozarks and identified 53 percent of the landscape as having supported a shortleaf pine component. Guyette and Dey (1997) documented the loss of pine by quantifying long-lasting pitch filled pine remnants such as stumps, snags and pine knots, and comparing that to current overstory composition. Additionally, Voelker (2004) found that the red oak group, primarily black oak (*Quercus velutina*) and scarlet oak (*Q. coccinea*) replaced the original shortleaf pine forest in the Ozark Highlands as evidenced by current distribution patterns of black and scarlet oak relative to occurrence of identifiable shortleaf pine remnants. The current diameter distribution of overstory shortleaf pines consists of a preponderance of small size classes, in contrast with the estimated historic distribution of shortleaf pine in the plots sampled in the Current River Hills Subsection (Fig. 2).

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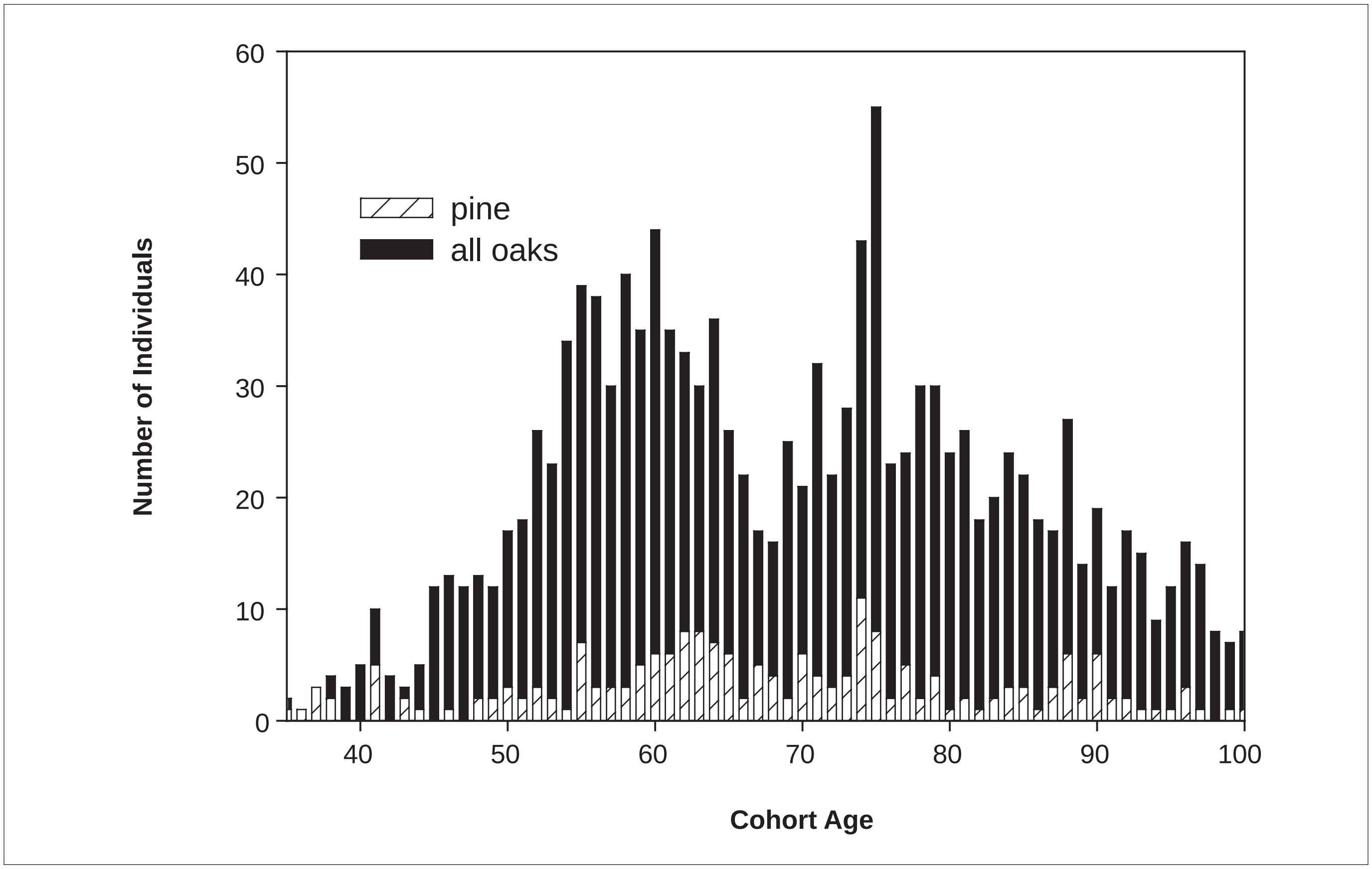


**Figure 1.**—The age class distribution of pine and upland scarlet and black oaks in the Current River Hill subsection of the Ozark Highlands of Missouri (Voelker 2004).

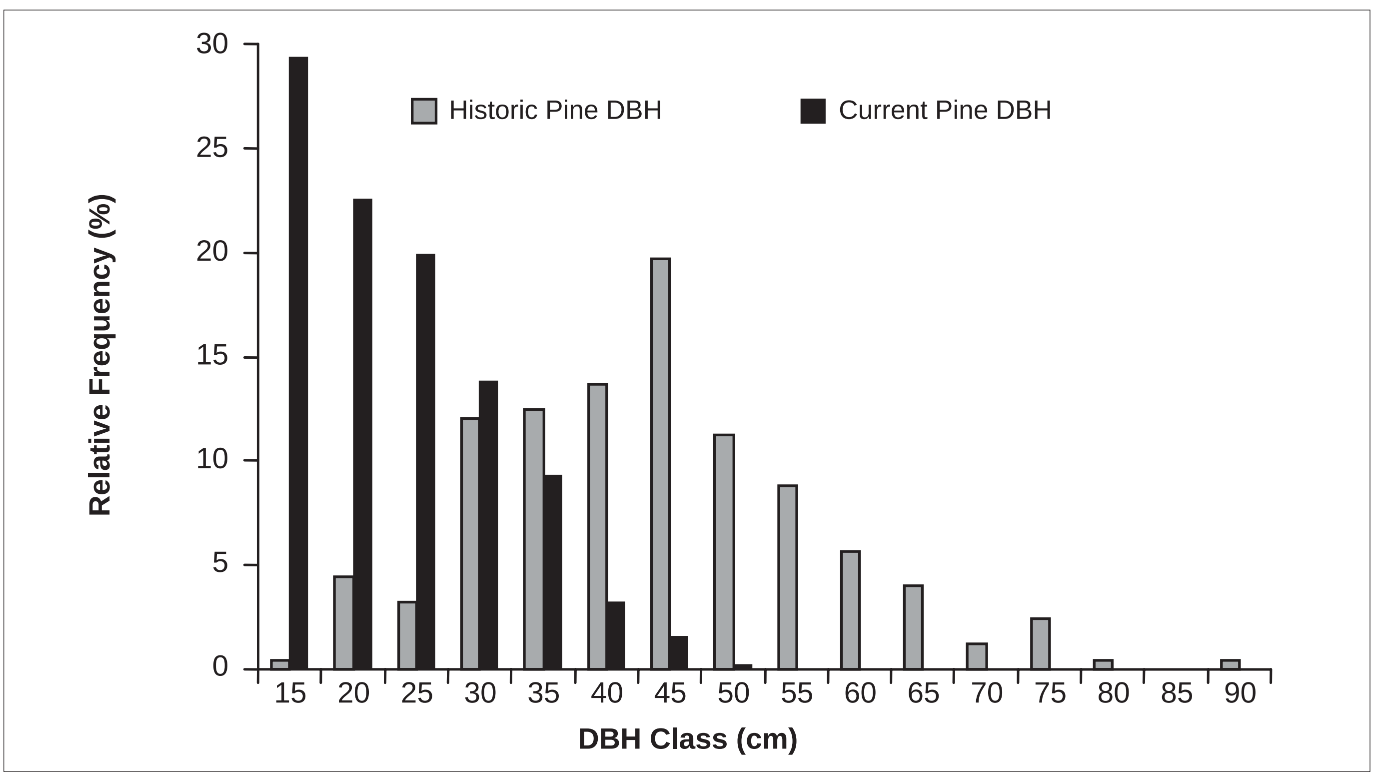


**Figure 2.**—Current and Historic Diameter Distributions of Shortleaf Pines on MOFEP Site 8. The historic diameter distribution was recreated by measuring diameter at root collar of all remaining pine stumps on plots at MOFEP site 8 and converting them to DBH from a linear regression model relating diameter at root collar to DBH (Voelker 2004).

**Table 1.**—Studies and estimates of shortleaf pine loss in the Missouri Ozarks. The percent of historic condition is the quantity of pine or pine forest pre-logging[a] divided by a post-logging quantity times 100. MOFEP 8 is on the Peck Ranch Conservation area near Van Buren, Missouri. Integrated moisture index (IMI)[b] and land use land cover (LULC) present indices of pine abundance.

| Measure | Scale | Location | Historic | Current and future | Percent of historic conditions | Source |
|---|---|---|---|---|---|---|
| Area | Ozark oak pine forests | Missouri Ozarks | 1.1 million ha[2] | 0.17 million ha | 15% | Cunningham and Hauser (1989) |
| Stem density, no plantations | 335 ha | MOFEP 8 SE MO | 17,143 stems $ha^{-1}$ | 5,744 stems $ha^{-1}$ | 34% | Guyette & Dey (1997) |
| Stem density with plantations | 335 ha | MOFEP 8 SE MO | 17,381 stems $ha^{-1}$ | 9,239 stems $ha^{-1}$ | 53% | Guyette & Dey (1997) |
| Spatial occurrence | 29,000 $km^2$ | Oak-pine region of MO | 47 % (IMI) | 9.6 % (LULC) | 20%[c] | Hamilton (2003) |
| Wood volume | 2 ac cut over oak-pine forest | Reynolds Co. MO. | 11.4 $m^4$ | 1.5 $m^3$ | 13% | Record (1910) |
| Predicted % of landscape with pine | century model estimate[d] | Oak-hickory pine forests | 60% (with fire) | 10% (with no fire) | 17% | Guyette and others (2004) |
| Basal area | 335 ha | MOFEP 8 ridge tops | 2.3 $m^2$ $ha^{-1}$ | 0.83 $m^2$ $ha^{-1}$ | 35% | Voelker (2004) |
| Mean | | | | | 22% without plantations | |

[a]IMI was developed by Iverson and others (1997) and used by Hamilton (2003) to evaluate Ozark shortleaf pine occurrence relative to simulated historic occurrence.
[b]The historic area of forests with pine is from Liming (1946) and is adjusted from 1.7 million ha by 0.53 (Batek and others 1999) to 2.3 and from 1 million ha by 0.20 to 194,250 ha and summed.
[c]Estimate is calculated based on approximate scales and areas used in this analysis.
[d]VDDT modeling results of percent of landscape with a pine component.

Given all estimates (Table 1), the present abundance of shortleaf pine in the Missouri Ozarks is probably between 20 and 50 percent of the abundance immediately prior to the mid 19th century. Much of the accumulated evidence suggests that about 50 to 80 percent of Missouri forests with a substantial pine component have such a dramatically different species composition such that shortleaf pine no longer dominates. Moreover, some of the “loss” can be attributed to a distinct loss of forested land through conversion and shifts in land use. Depending on the parameter used, losses of shortleaf pine can be considered approximately 15-20 percent of the area once occupied by forests dominated by shortleaf pine, while basal area was calculated to have been reduced by 35 percent in the past 150 years.

The reduction in shortleaf pine abundance can be attributed hypothetically to the removal of seed source by logging and a fire regime with fire intervals too frequent for optimum pine recruitment. Overall, fire frequency and logging resulted in the removal of seed and advanced pine regeneration. For roughly 80 years prior to extensive logging of the pine resource (1880 to 1920), very frequent fires occurred in this shortleaf pine-dominated forest type of the Ozarks (Mean fire interval [MFI] < 3 years, Guyette and others 2002). The recurrent fire removed small diameter advanced pine regeneration. Logging, especially selective pine logging, removed seed sources. Selective pine logging in mixed oak pine stands was particularly important in favoring succession to hardwoods. Frequent fire (MFI < 3 years) inhibited seedling survival, since a vigorously conditioned layer of oak root grubs outcompeted pine seedlings for light and nutrients. Finally, and more recently, fire suppression has promoted closure of canopy gaps, build-up of a deep litter layer, which all but eliminates bare mineral soil necessary for epigeous germination of pine seeds (Baker 1992, Stambaugh 2001).

The historic fire frequency (1880 to 1920), in conjunction with xeric sites in higher landscape positions such as upper slope or ridges, may have increased the advantage of pines once they were in larger diameter classes. Large pines have a suite of characteristics that convey advantages over most oaks and other hardwoods in the Ozarks. They have thick, insulating bark, resistance to rot induced by fire scars, resistance to drought conditions, longer available growing season (pines can photosynthesize later in the fall and earlier in the spring than deciduous hardwoods in temperate climates), and considerable longevity of 250 years or more. However, establishment of pine is limited by the proximity and timing of seed source as well as the potential seedbed conditions (Grano 1949, Lawson 1990, Cain 1991, Shelton and Cain 2000, Stambaugh 2001).

## The Influence of Site on Shortleaf Pine Abundance

In the southeast Missouri Ozarks, Liming (1946), Fletcher and McDermott (1957), Batek and others (1999), and Voelker (2004) considered soils and bedrock stratigraphy, specifically residuum over the Roubidoux formation, to be the most important factor influencing the pre-settlement extent of shortleaf pine on the landscape scale. A number of mechanisms working at multiple scales, however, can select for the success of pines and other tree species at any site, i.e., neighborhood effects. Neighborhood effects are defined here as those influences in which the rate or probability of change depends on the condition or behavior of sites surrounding the site of interest. For example, local disturbance history, or the last time a site burned (as well as its intensity and magnitude), has a complex interaction with prior and present species composition, which in turn is influenced by edaphic factors. For example, the relation of the site on the landscape to elevation, site quality, shape of the landform, and local topography all must be considered at the appropriate spatial scale. Moreover, the dynamics of neighborhood effects, as mediated by the canopy, may be significant at a smaller scale. The landscape to elevation ratio can be up to 100,000 $m^2$, whereas the scale of influence of site quality or local topography could be as small as 10 $m^2$.

Shortleaf pine remnants are the only direct evidence indicating the extent of pine dominance in forest structure before the exploitation era of logging. Using remnant stumps, and estimating the pre-logging relative occupation of a site by shortleaf pine, Voelker (2004) found that soils derived from the Roubidoux formation have more stumps than other geologic strata (Fig. 3), indicating that historically this soil-pine relationship was important.

However, geologic strata are also correlated with slope position and elevation, or percent of local relief. The Roubidoux was disproportionately associated with upper landscape positions (Voelker 2004). At a certain scale relative topographic position may influence the presence of pines due to its relationship with fire frequency and topographic roughness (Guyette and Dey 1997). The interrelationship between parent material, topographic position, and pine remnants is complex, and cannot be easily disentangled.

There is no definitive explanation for what constitutes a “pine site.” Xeric, exposed conditions on rocky, acid soils lead to consistently high evapotranspirative demand and water-stress in which shortleaf pine becomes more competitive with the hardwoods in the Ozarks. Shortleaf pine competes better with oaks on xeric sites, yet it is strongly associated with soils of lower base saturation in the Missouri Ozarks (Nigh and Schroeder 2002) and appears to be found exclusively on sites with acidic soil. Although there is no quantitative data clearly show this pattern, ecological evidence and strong anecdotal evidence support the local and edaphic site association with shortleaf pine in the Ozarks.

## Radial Variability in Shortleaf Pine Growth

Shortleaf pine growth rates vary greatly in time and space. Radial growth rates between trees range widely, from as low as 100 rings per 2.5 cm (0.25 mm per year) to higher than 3 rings per cm (8 mm per year). The oldest, slow-growing small trees are found on sandstone outcrops with little soil volume while some of the fastest growing shortleaf pines grow in deep, acid, and variable depth soils derived from sandstone, chert, and igneous bedrocks. The relationship

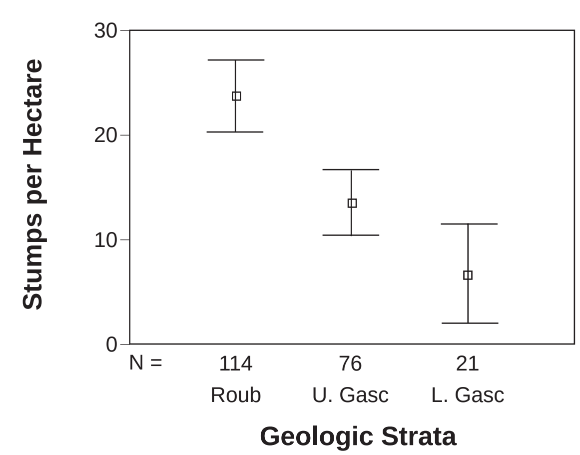


**Figure 3.**—The abundance of pine remnants (mean and 95 percent confidence intervals) on different geologic strata in the Current River Hill subsection. Geologic strata are Roubidoux, Upper Gasconade, and Lower Gasconade (from Voelker 2004).

between the diameter of shortleaf pine and age is strong (Voelker 2004), but only for young trees (Fig. 4). For trees over 100 years, diameter was not significantly related to age (Fig. 5). Additionally, tree-ring width series of shortleaf pine often show large abrupt changes in growth within a tree. Abrupt, frequent, and persistent growth reductions in shortleaf pine growth suggest that these evergreens are particularly vulnerable to canopy disturbances, especially when tree age is greater than 100 years. Canopy openings resulting from fire, climate, or wind result in radial growth declines, and likely mortality. When trees are less than 100 years, however, canopy openings provide opportunities for trees to respond competitively, and radial growth, as well as height growth in many cases, increases in response to canopy openings of varying sizes, regardless of cause. Recruitment and patterns of stand development of shortleaf pine, therefore, are strongly influenced by dominant cohort age and ability to respond to canopy openings.

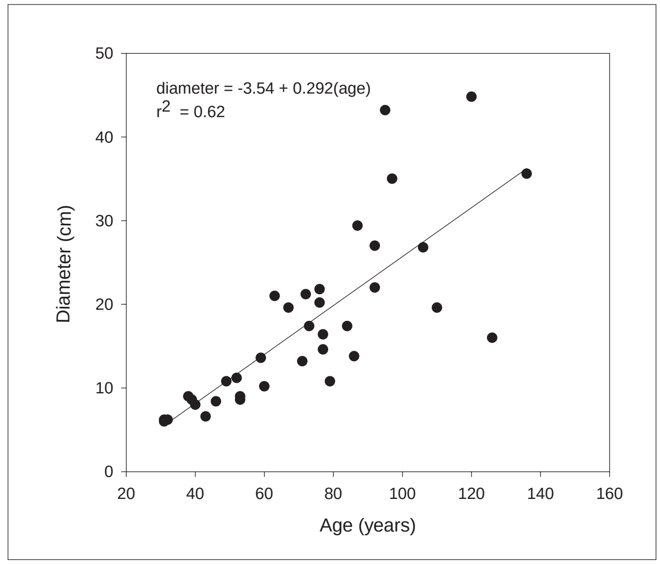


**Figure 4.**—The relationship between tree age and diameter for shortleaf pine trees less than about 100 years in age (unpublished data, Guyette and Stambaugh).

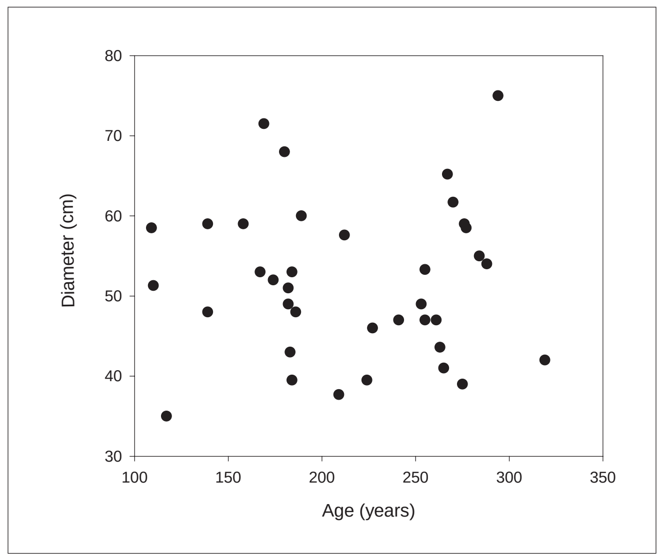


**Figure 5.**—The relationship between tree age and diameter for shortleaf pine trees greater than about 100 years in age (unpublished data, Guyette and Stambaugh).

## Shortleaf Climate Response and Climate Change

The relationship between drought and temperature and the growth of shortleaf pine has been documented by Stambaugh and Guyette (2004). When winter temperatures are favorable, evergreen trees such as eastern redcedar and shortleaf pine can photosynthesize, and thus demonstrate a physiological—and competitive—advantage over deciduous trees. With increasing winter temperature, and possibly accompanying drying in summers, forest evergreens such as shortleaf pine may express a growth advantage. Thus, shortleaf pines, unlike many deciduous tree species, may be able to compensate for hot dry summers if conditions provide for warmer winters with more soil moisture.

Higher concentrations of atmospheric $CO_2$ are thought to have fertilization effects on shortleaf pine, which consequently shows an increased growth rate. Although deciduous trees may capitalize on increases in $CO_2$ during the summer, pines would benefit from higher $CO_2$ in winter as well as summer. Voelker and others (2006) used an extensive tree ring data set from the Ozarks to demonstrate an increase in pine and oak growth that is hypothesized to be the result of putative $CO_2$ fertilization. This study and another (Stambaugh and Guyette 2004) showed increased growth rates, especially for younger pines, over the last century. These findings have substantial implications for tree growth of a younger cohort of shortleaf pine (Fig. 2), specifically that the growth rates may be increasing.

## Shortleaf Pine Growth and Climate Cycles

The growth of shortleaf pine has been shown to be cyclical and related to bi-decadal oscillations in climate (Stambaugh and Guyette 2004). This cyclical growth response can be further quantified by dating abrupt growth reductions in shortleaf pine ring-width series. We used 68 late successional shortleaf pines from near the Current and Big Piney Rivers to examine growth reductions associated with climate (Fig. 6). We calculated abrupt growth declines as 10-year exponentially weighted growth means divided by the prior 10-year weighted growth means. Abrupt growth reductions in shortleaf pine occurred on a bi-decadal frequency (Fig. 6). This cycle is broken by a 35-year hiatus in the 300-year-long record of abrupt growth reductions circa 1784 to 1820. The most extreme clustering of growth reductions usually approximately coincided with extreme drought years. Additionally, there were 14 years over the

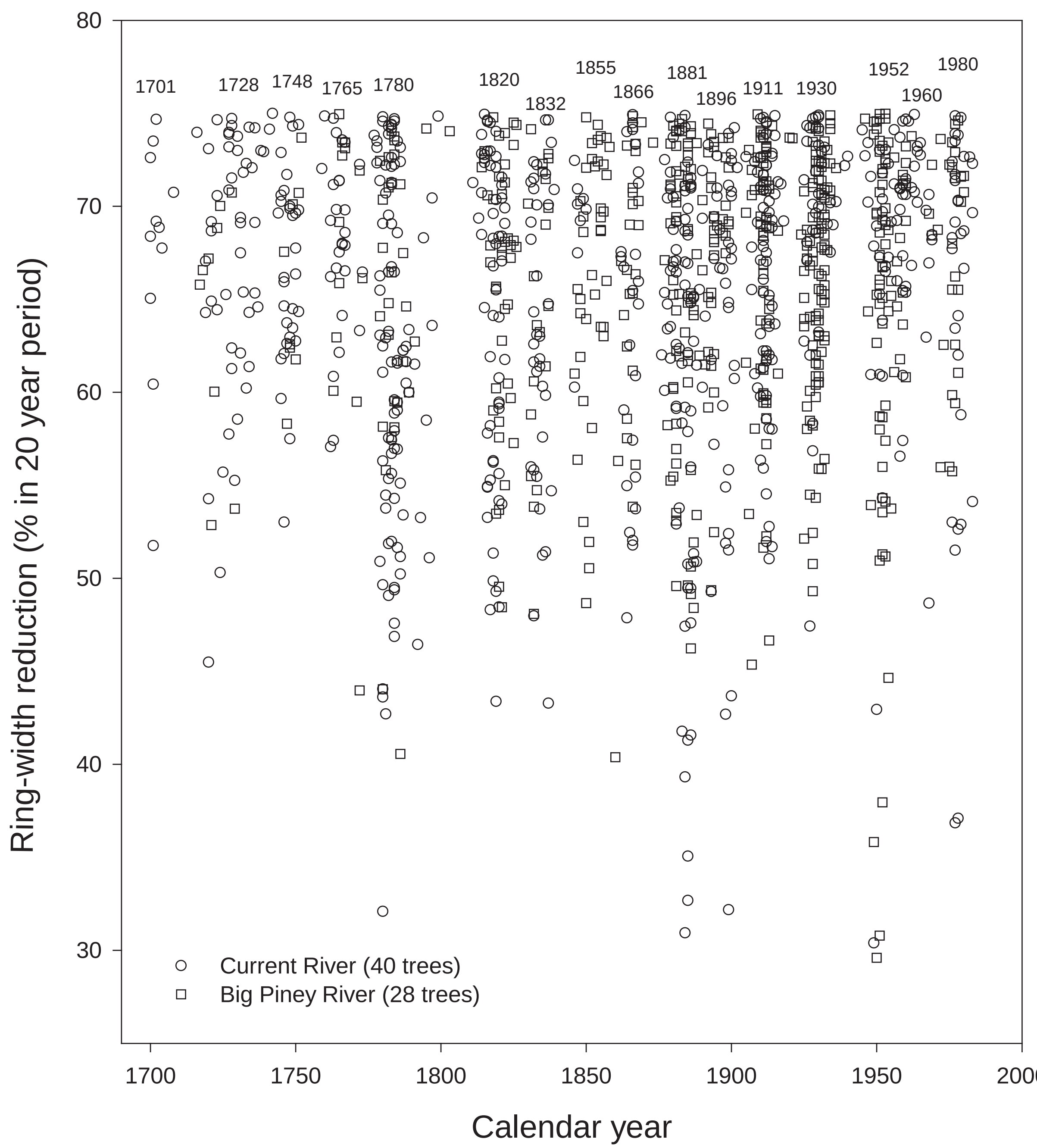


**Figure 6.**—The date and magnitude of ring-width reductions greater than 75 percent at two shortleaf pine sites in the Missouri Ozarks. Ring width reductions are calculated as the ring-width mean for 10 years before each date divided by the ring width mean after that date (unpublished data, Guyette and others).

last 300 years (Fig. 7) in which more than 30 percent of the trees had abrupt growth suppressions (> 25 percent growth reduction). These years tended to be drought years and drought transitions, but winter weather, snow, and early or late freezing events may be responsible for some of these growth setbacks.

In the context of stand development of shortleaf-dominated forests in the Ozarks, patterns of response to climate likely played a significant role. Although we cannot exclude the importance of a range of climate effects, there is a strong association of development and growth with drought years (Guyette and others 2006a). Drought years also co-occur with fires, which may also result in regeneration events and recruitment potential. Growth reduction events that influence the overstory may conincide with development events in the understory.

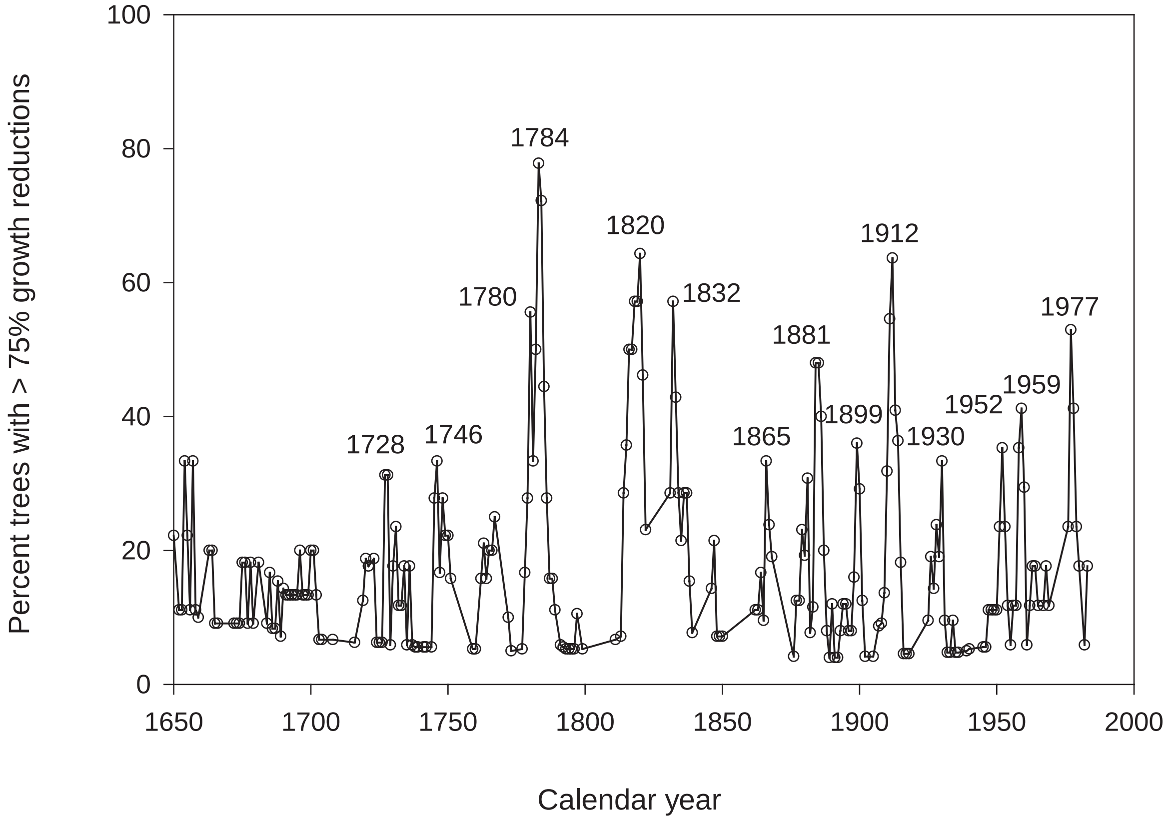


**Figure 7.**—The percent of shortleaf pine trees with abrupt growth declines over the last 350 years (unpublished data, Guyette and others).

## Dendroecological Inferences on Historical Stand Development

The rings of the well preserved wood of shortleaf pine have been used to study climate variations, the growth response of the species to sites and events, and wildland fires. Thousands of dated fire scars on shortleaf pine trees, cut stumps, and natural snags have led to a detailed, and quantitative understanding of Ozark fire history (Batek and others 1999, Guyette and others 2002, Stambaugh and others 2005, Guyette and others 2006a). Through the use of fire scars, we have dated fire occurrence since the 1500s in the Missouri Ozarks. Fire scars have been cross-dated on the thousands of well preserved pine stumps that have survived logging and fire. These scars, combined with those on natural remnants and living pines in the Ozarks, have led to a greater understanding of Ozark fire regimes. This knowledge in turn has helped us understand how humans, climate, and fire have interacted to produce the contemporary distribution and structure of Ozark oak and pine forests (Guyette and others 2002).

In Missouri, there is dendrochronological evidence for both even-aged and mixed-age shortleaf pine regeneration (Stambaugh and others 2002). Canopy dominants at two late successional, old-growth shortleaf pine forests (Highway 19 Virgin Pine Forest [HVP] and the Eck Natural Area [ECK]) illustrate even-aged and mixed-age regeneration (Fig. 8). A historically relevant question may focus on which type of regeneration predominated. Data from the ECK site suggest that small and large disturbances to the canopy allowed both mixed-age and even-aged regeneration, leading to shortleaf pine cohorts within a stand. Data from HVP suggest that very few events gave rise to regeneration at this site, creating essentially an even-aged forest. Both small- and large-scale disturbance events were probably important in the Ozarks, and there may be no consistent interpretation of how ecological site conditions relate to disturbance. The HVP and ECK are in similar, albeit not identical, ecological landtypes, however the association of Roubidoux strata is more evident at ECK. The difference in the effects of scale of disturbance may simply relate to fire interval and intensity. Above all, it is important to understand that fire

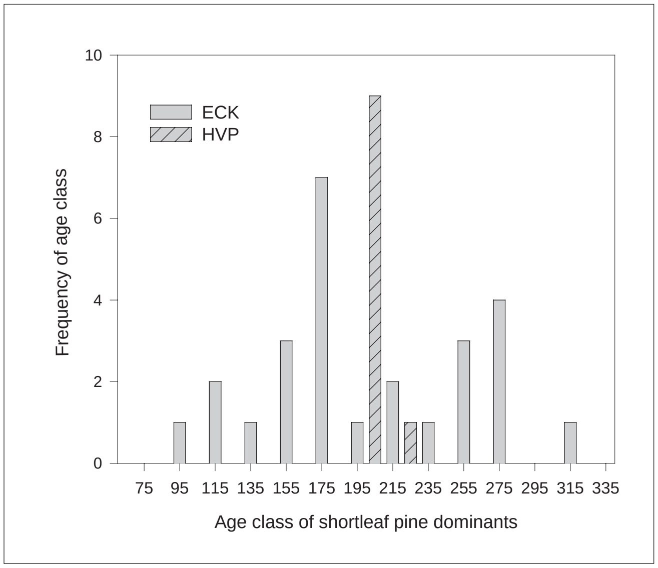


**Figure 8.**—Frequency distribution of pith dates at 1.3 m on shortleaf pine canopy dominates at the Eck Conservation Area (ECK) (solid bars) and the Highway 19 Virgin Pine Natural Area (HVP) (diagonally filled bars) (Stambaugh and others 2002).

contributes to stand initiation through stand replacing events and also results in mixed age classes of shortleaf pine through small-scale, perhaps surface fires.

Some support for the role of fire in shortleaf pine recruitment comes from fire history studies. Evidence suggests that the Ozarks had very frequent rotation intervals for large-scale fires (Guyette and others 2006b). Between 1748 and 1810 fire scars in Arkansas and Missouri indicate that over 310 percent of the landscape burned in 60 years. This yields a rotation interval of about 20 years for very large fires that occurred under moderate or severe drought conditions. In other words, an area the size of the Ozarks (129,500 $km^2$) burned about every 20 years. Unlike the typical characterization of Ozark fire regimes as having frequent low intensity surface fires, this landscape had fires that occurred over large sections of the Ozarks during moderate to extreme drought years. Because of the strong association between fire size and severity, these fires probably caused many small (1 to 10 hectare) stand-replacement events in the rough and broken topography of the Ozarks.

Given the large area of the Ozarks under consideration, the types of fires occurring between 1748 and 1810 were highly variable and likely dictated by topography as well as climate (Guyette and others 2002). The frequency of fire was in part attributable to the discontinuous nature of fuel, varying by landform and landscape position. Moreover, a steep, highly dissected landscape lends itself to small-scale events because fires are not perpetuated in topographically complex areas.

## FUTURE ISSUES AND THREATS

The restoration potential for shortleaf pine in part resides in selecting the appropriate site and providing necessary conditions for regeneration, recruitment, and development given the current forest condition. Successional trends in extant Ozark forests, even in the absence of management, suggest only limited potential for pine regeneration and recruitment into the overstory. Following extensive logging of the shortleaf pine resource, scarlet oak and black oak quickly regenerated many sites. These 90- to 120-year-old cohorts of oak have experienced decline since the 1980s, supported by ring-width studies from the Missouri Ozarks that have shown a pattern of a protracted decrease in growth increment, ending in the death of the tree (Dwyer et al. 1995, Jenkins and Pallardy 1995, Pederson 1998, Voelker 2004). By examining site conditions and shortleaf pine remnants, we have established that sites previously dominated by shortleaf pine often have the greatest dieback and mortality (Voelker 2004, Voelker and others 2007). This situation was particularly true on exposed slopes and ridges. Characterizing these sites by species composition and structure, we found that the successional trends indicate that without major disturbance, white oak, not shortleaf pine, will gradually replace much of the recent red oak dominance within the historic shortleaf pine range in Missouri (Voelker and others 2007).

In recreating historic shortleaf pine distribution using remnants, we found that many of the areas with the greatest number of shortleaf pine remnants also have the greatest amount of shortleaf pine in basal area, although many of the individuals are small and may not develop into the overstory. Appropriate management of these stands, then, can promote existing, developing shortleaf pine. An overall directive toward a greater composition of longer-lived, drought resistant species, shortleaf pine and white oak, is suggested and is already in place on some public lands. A specific and prerequisite consideration for the regeneration and success of shortleaf pine would include prescribed burning or some kind of site preparation that disturbs and reduces the litter layer (Grano 1949, Stambaugh 2001). Increasing the overall vigor of the shortleaf pine and shortleaf pine-oak forests of the Ozarks will surely require a flexible combination of even-aged and uneven-aged silvicultural techniques for the local site conditions and levels of advance regeneration present. Unless silvicultural regimes change drastically, shortleaf pine's inability to establish and compete with oaks following cutting, will quickly account for its displacement as a significant overstory presence in the Ozarks (Stambaugh 2001).

Despite the current presence of scarlet oak and black oak in the Ozarks, these oaks historically were probably limited by frequent fire on many sites (Batek and others 1999). It is hypothesized, however, that some of the same exogenous and endogenous factors (e.g., *Armillaria*, xeric conditions, drought, and longevity of pines versus red oaks) which selected against oaks in pre-settlement times may also select against red oaks currently on pine sites. As an example, Bruhn and others (2000) indicated that *Armillaria* root disease is present in almost every case of red oak mortality.

Owing to the relative scarcity of extensive stands of shortleaf pine, little is known about pests of shortleaf pine, nor has there been much opportunity to examine them in the Ozarks. Admittedly, the challenges are greater for restoring rather than protecting the shortleaf pine resource. However, as shortleaf pine stands develop, it will be critical to understand and evaluate the role of biotic challenges to the species and forests. Such concerns could include southern pine beetle (*Dendroctonus frontalis*), the most damaging insect in eastern pine forests. Southern pine beetle outbreaks have increased recently and spread into previously uninfested territory, such as the southern Appalachians, a phenomenon explained in part by climatic conditions (Ungerer and others 1999). Other beetles occurring in the Ozarks and for which shortleaf pine serves as a host are small southern pine engraver (*Ips avulsus*) and black turpentine beetle (*Dendroctonus terebrans*). Additional pests include insects that target regeneration, e.g., pine webworm (*Pococera robustella*), a defoliating caterpillar known to occur in the Ozarks. Annosum root disease (*Heterobasidion annosum*) and littleleaf disease (*Phytophthora cinnamomi*) are persistent diseases of shortleaf pine in the southern United States.

The potential interaction of climate change and insect and pest population relative to increasing shortleaf pine on the landscape must be considered when managing and promoting shortleaf pine. Similarly, the importance of a comprehensive understanding of the role of climate in determining fire frequency and severity requires further investigation to improve models describing fire occurrence and consequence across the Ozark landscape.

## CONCLUSION

Dendroecological approaches describing shortleaf pine growth, climate response, and fire history provide a long-term perspective on this species' development, success, and sustainability in the Ozarks. We have developed an understanding of shortleaf pine life history traits, particularly regarding growth and age relationship, and the role of fire in influencing stand initiation and development. Shortleaf pine trees can live for more than 350 years, but such ages are rare. As with most tree species, shortleaf pine growth is negatively affected by drought, but unlike other deciduous Ozark hardwoods, the growth may be increased by winter warming. Shortleaf pine growth can be as little as 20 rings per cm or as great as 1 ring per cm. Radial pine growth exhibits a 22-year cycle that is tied to drought and solar cycles. Although global warming may favor shortleaf pine, fire history in oak-pine forests shows that litter accumulation, dense canopies, and hardwood sprouting continue to be impediments for recruitment and successful regeneration.

Historic shortleaf pine distribution was associated with parent material, fires, and climate. Parent material, soil residuum, and landscape position all seem to play a role in explaining historic shortleaf distribution across the landscape. We corroborated older findings by close examination and analysis of shortleaf pine remnants. An extensive size class/age class distribution revealed that most contemporary shortleaf pine have developed within the last 80 years.

Abundance of shortleaf pine has resulted from large drought-driven mixed severity fires in the Ozarks occurring every 10-20 yrs. Both multiple and single cohort development of shortleaf pine occurred in the Ozarks. We have shown that the remnant late-successional shortleaf pine forests in the Missouri Ozarks have developed from a mixed disturbance regime. Therefore, a consistent or uniform management approach may not satisfactorily reestablish shortleaf pine communities. Such findings support earlier research such as Brinkman and Liming (1961) and Brinkman and Smith (1968).

Shortleaf pine growth setbacks occur frequently in the Ozarks, as evidenced by the dendrochronological record of radial growth patterns. Climatic conditions, such as drought, and canopy opening disturbance, including fire, disease, insects, or windthrow, can influence radial growth. However, the growth response strongly relates to tree age, and a general threshold of about 100 years indicates the species age when the tree may either respond positively, or be vulnerable to damage or abiotic conditions. This vulnerability is expressed by growth losses and an overall lack of response occurring in general in trees more than 100 years old.

Challenges include proper management, restoration of site conditions, and re-establishment of missing seed source. Although the pine plains supported areas of nearly 100 percent shortleaf pine, much of the Ozarks supported a pre-settlement mixed pine-oak forest, particularly in the topographically complex landscape of the river hills and breaks. The ecological benefits of increased overstory diversity in Ozark forests are manifold; therefore, promotion of shortleaf pine in oak-dominated landscapes addresses concerns of sustainability and ecological integrity. Mixed oak-pine forests create a diverse successional, structural, and habitat conditions in Ozarks forests. Attributes such as canopy cover, wood chemistry and life history help explain shortleaf pine's unique ecological role in oak-pine forests. Evergreen canopies provide nesting sites, roosting, and primary productivity in the winter and early spring. Toxic oleoresins preserve wood and cavities for long periods of time relative to other woody debris. Shortleaf pines may be less susceptible to crown fires and insect attacks in mixed oak-pine stands than in pure pine stands or plantations.

Shortleaf pine components of oak-hickory-pine forests are predicted to diminish without fire by a coarse-scale, state transition model (Guyette et al. 2004). These models are validated with Ozark fire history data (Shlisky and others 2005) and indicate that without fire, forests with a shortleaf pine component will occupy less than 10 percent of the landscape within a few centuries. Thus, in the absence of intervention, forests with a shortleaf pine component, which once covered more than 53 percent of parts of the Ozark landscape (Batek and others 1999) may be confined to 10 percent of the landscapes. Those few sites are characterized by xeric condition and soils with low base saturation. The silvicultural and ecological challenges of restoring the mixed pine-oak forests require attention, time, and evaluation.

## ACKNOWLEDGMENT

The authors would like to thank D.C. Dey and M.C. Stambaugh for their support and work on numerous shortleaf pine projects that have contributed to this work.

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