IS THERE EVIDENCE OF MESOPHICATION OF OAK FORESTS IN THE MISSOURI OZARKS?

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Abstract.—Many studies on oak-dominated forests of the Central Hardwood region (CHR) have reported increasing abundance of fire-sensitive species and poor recruitment of oak (*Quercus* spp.) in the absence of frequent fire. However, most of these studies were conducted in the eastern and central CHR, and the assumption that similar dynamics occur in the western CHR has not been fully substantiated. We investigated forest dynamics in relatively undisturbed, mature oak-hickory forests of the Missouri Ozarks during a 15-year period (1995-2010). Data for this study were from untreated sites (controls) of the Missouri Ozark Forest Ecosystem Project (MOFEP) that have not experienced wildfire or harvesting for over a half century. In order to evaluate the influence of site quality on compositional dynamics, we selected a subset of permanent plots found on four ecological land types (ELTs) spanning a range of site qualities. The density of maple (*Acer* spp.) seedlings (<1.5-inch diameter at breast height [d.b.h.]) increased on nearly all ELTs over the 15 year period. As of 2010, maples were the most abundant species in the seedling layer on higher quality ELTs, while oaks and hickories (*Carya* spp.) were a major component of the seedling layer of lower quality ELTs. However, oaks and hickories were a major component of the sapling (1.5- to 4.5-inch d.b.h.) layer of all ELTs, while maple was a minor component. In contrast to the understory dynamics, the oak-dominated overstories (≥4.5-inch d.b.h.) of all ELTs remained largely unchanged from 1995 to 2010. These findings supported four working hypotheses: (1) upland forests of the Missouri Ozarks are in early stages of mesophication where fire has been excluded for at least 50 years; (2) mesophication in the western CHR is occurring at a slower rate than in eastern portions of the CHR; (3) mesophication is slowest on xeric, south-facing slopes; and (4) the predominance of low quality soils and frequent drought in the Ozarks will limit these forests from reaching late stages of mesophication, particularly on xeric sites.

INTRODUCTION

There is mounting evidence that oak dominance in the Central Hardwood region (CHR) is unsustainable under prevailing disturbance regimes. Research on oak-dominated forests since the mid-20th century has indicated a potential shift in composition to more shade-tolerant tree species (Abrams et al. 1997, DeSantis et al. 2010, Christensen 1977, Glitzenstein et al. 1990, Lorimer 1984, Monk 1961, Nowacki et al. 1990, Richards et al. 1995). In particular, many studies have noted increasing abundance of fire-sensitive species coincident with diminishing or no recruitment of oak. These findings along with historical records, evidence from paleoecological and dendrochronological investigations, and knowledge of oak ecology have led to the widely held position that loss of oak dominance is linked to fire suppression (Abrams 1992).

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The loss of oak dominance has implications for other ecosystem components. Aside from direct and indirect effects on wildlife species through trophic interactions, successional replacement of oak species will likely also cause changes in understory microenvironment (light, temperature, humidity, soil moisture). In turn, alteration in the understory microenvironment may affect future forest vegetation. The mesophication hypothesis states that long-term fire suppression in communities of fire-tolerant species leads not only to successional replacement by fire-sensitive species, but that the microenvironment continually changes to favor fire-sensitive species and deteriorates for fire-tolerant species during the replacement process (Nowacki and Abrams 2008).

There is growing consensus that widespread mesophication is occurring throughout the CHR (Arthur et al. 2012, Nowacki and Abrams 2008). However, most of these studies have come from the eastern and central portions of the CHR, and the assumption that similar dynamics occur in the western CHR has not been fully substantiated. Recent research indicates that oak-dominated ecosystems at the extreme western edge of CHR are transitioning to opportunistic species in the absence of fire (Burton et al. 2010, DeSantis et al. 2010, Thomas and Hoagland 2011). Past research on forest succession in Missouri has revealed inconsistencies when generalizing trends at the state level. Pallardy et al. (1988) observed reductions in oak sapling densities accompanied by increases in sugar maple (*Acer saccharum*) saplings over 14 years. In another study, sugar maple regeneration was found to be abundant wherever a seed source was present, while oak regeneration was largely relegated to xeric sites despite a ubiquitous seed source (Nigh et al. 1985). However, these studies were focused on succession in the mesic Missouri River Hills where maple is prolific (Nigh et al. 1985, Pallardy et al. 1988) or in stands intentionally selected based on the presence of sugar maple (Nigh et al. 1985). There is evidence that mesophication may not proceed as quickly in the xeric Ozarks Highlands of Missouri as in other portions of the state or the CHR, a pattern consistent with how mesophication is predicted to proceed on xeric sites (Nowacki and Abrams 2008). Shifley et al. (1995) observed low abundance of maple in xeric forests of the Missouri Ozarks, which they contrasted with findings of increasing maple further east. However, a more recent study of long-term, large-scale compositional changes in the Missouri Ozarks detected both an increase in density and expansion of fire-sensitive species onto xeric, fire-prone sites currently dominated by oak species (Hanberry et al. 2012, Hanberry et al. 2014).

The objective of this study was to determine if oak-dominated upland forests of the Missouri Ozark Highlands are shifting to fire-sensitive species where fire has been excluded. Although the process of mesophication involves changes in multiple, inter-related factors that lead to reduced flammability of historically fire-maintained plant communities, compositional shifts to fire-sensitive species provide an early indication of mesophication. In the Missouri Ozarks, the major fire-sensitive species capable of replacing oak as a canopy component are red maple (*Acer rubrum*) and sugar maple. Therefore, we were mainly interested in assessing whether the abundance of maple was increasing relative to oak across a site quality gradient. Since the probability of oak self-replacement is inversely proportional to site quality and maples are typically associated with mesic sites (Johnson et al. 2009), we also postulated that the understory abundance of maple would be greater and that of oaks would be lower as site quality increased.

METHODS

Study Sites

This study used data collected as part of the Missouri Ozark Forest Ecosystem Project (MOFEP). MOFEP was initiated in 1989 by the Missouri Department of Conservation (MDC) as a long-term, large-scale experiment investigating the ecological impacts of even-aged, uneven-aged, and no-harvest management on Missouri Ozark forests. MOFEP sites are located on MDC land and occur mostly in the Current River Oak Forest Breaks and Current River Oak-Pine Woodland Hills land type associations (Kabrick et al. 2000). MOFEP's nine study sites are operational compartments that range in size from 776 to 1,275 acres and are representative of the scale of MDC forest management on state land in the Ozarks. At the start of the experiment, these sites were dominated by mature, relatively undisturbed forest and were largely free of manipulation for at least 40 years. See Brookshire and Shifley (1997) for more details on the MOFEP experiment.

Data for this study came from three untreated control sites of the MOFEP experiment. These sites have not experienced wildfire or harvesting for over a half century and, therefore, are well suited for assessing the consequences of fire exclusion on succession in oak-dominated forests of the Missouri Ozarks.

Analytical Approach

Data from permanent sample plots were used to assess changes in tree species abundance over the 15-year period from 1995 to 2010. Woody vegetation on MOFEP was monitored using nested fixed-area plots: trees ≥4.5-inch d.b.h. in 0.5-acre plots (henceforth referred to as overstory); stems 1.5- to 4.4-inch d.b.h. in four 0.05-acre plots (saplings); stems 3.3 feet tall and up to 1.4-inch d.b.h. in four 0.01-acre plots (large seedling); and stems <3.3 feet tall in sixteen 0.00025-acre plots (small seedling). Stems counts per plot of overstory, sapling, large seedling, and small seedling size classes were converted to trees per acre (TPA) prior to the analysis. Basal area (BA) measured in square feet per acre was included for assessing overstory change

The following nine taxonomic groups were included in this study: (1) red oak (*Quercus coccinea*, *Q. marilandica*, *Q. rubra*, *Q shumardii*, and *Q. velutina*); (2) white oak (*Quercus alba*, *Q. muehlenbergii*, and *Q. stellata*); (3) hickory (*Carya glabra*, *C. texana*, and *C. tomentosa*); (4) shortleaf pine (*Pinus echinata*); (5) blackgum (*Nyssa sylvatica*); (6) sassafras (*Sassafras albidum*); (7) flowering dogwood (*Cornus florida*); (8) maple (*Acer rubrum* and *A. saccharum*); and (9) other species (*Celtis* spp., *Diospyros virginiana*, *Juglans nigra*, *Morus* spp., *Prunus serotina*, *Ulmus* spp., and others).

We selected permanent sample plots spanning a site quality gradient to assess the influence of site quality on compositional dynamics. MOFEP permanent sample plots were originally stratified within each site according to ecological land types (ELT) as delineated based on variation in slope position and aspect (Brookshire and Shifley 1997). We selected plots occurring on four ELTs common to MOFEP sites (Table 1). ELTs 3 and 5 occur at upper and lower positions, respectively, on south-facing slopes (i.e., exposed slopes), while ELTs 4 and 6 are found at upper and lower positions on north-facing slopes (i.e., protected slopes). According to site index, these four ELTs can be arranged in order of increasing site quality as follows: ELT 3<ELT 5<ELT 4<ELT 6 with site index (SI_{50}) = 65, 69, 72, and 75, respectively, based on black oak at base age 50. Although these

Table 1.—Description of ecological land types (ELT) used in this study as part of the Missouri Ozark forest ecosystem project (MOFEP) experiment

ELT	Slope aspect	Slope position	Base saturation	Site index$_{50}$ (feet)	Extent in MOFEP study area (%)
3	135-314°	Upper backslope	Low	65[a]	21
5	135-314°	Lower backslope	Moderate	69	10
4	315-134°	Upper backslope	Low	72	18
6	315-134°	Lower backslope	Moderate	75	9

[a] Site index is based on black oak at base age 50, and ELTs are arranged in order of increasing site quality. Table modified from Kabrick et al. (2008b).

ELTs are more common to MOFEP sites relative to others, ELTs 5 and 6 each represent about 10 percent of MOFEP study sites.

In order to assess compositional changes between two sampling years, 1995 and 2010 densities of each taxonomic group by size class were analyzed by analysis of variance (ANOVA) using a randomized complete block design with repeated measures. For ANOVA models, ELT was included as a fixed effect and site was used as a blocking factor (random effect). Since our main interest was in assessing changes in abundance in relation to site quality, we used contrasts to compare densities between years by species and size class individually for each ELT. ANOVA models and contrasts were run using PROC MIXED (SAS 9.2, SAS Institute Inc., Cary, NC). Statistical significance was assessed at α=0.05.

RESULTS

Overstory

On upper, south-facing slopes (ELT 3), red oak overstory density was significantly lower in 2010 (50 TPA) than 1995 (68 TPA) (Fig. 1A). The density of overstory white oak, on the other hand, was significantly greater in 2010, increasing from 41 to 52 TPA. The densities of blackgum and dogwood were also significantly greater in 2010, but each made up only a fraction of total overstory density in both years. White oak overstory BA was significantly greater in 2010, and red oak BA was substantially larger than that of other species (Fig. 2A).

The density of overstory red oak on lower, south-facing slopes (ELT 5) was significantly lower in 2010 (Fig. 3A), dropping from 65 to 41 TPA. As a result of this decrease, white oak was the most abundant taxon in the overstory in 2010 (52 TPA). There were no differences detected in overstory BA between years (Fig. 2B). Based on BA, red oak was the most dominant overstory taxa in both years (>43 square feet per acre).

The density of red oak overstory trees on upper, north-facing slopes (ELT 4) was significantly lower in 2010, whereas maple and blackgum densities were significantly greater after 15 years (Fig. 4A). However, both maple and blackgum comprised only a minor component of total overstory density. White oak replaced red oak as the most abundant overstory tree by 2010. No significant changes in BA were detected over the 15 years where the overstory remained dominated by oak and hickory species (Fig. 2C).

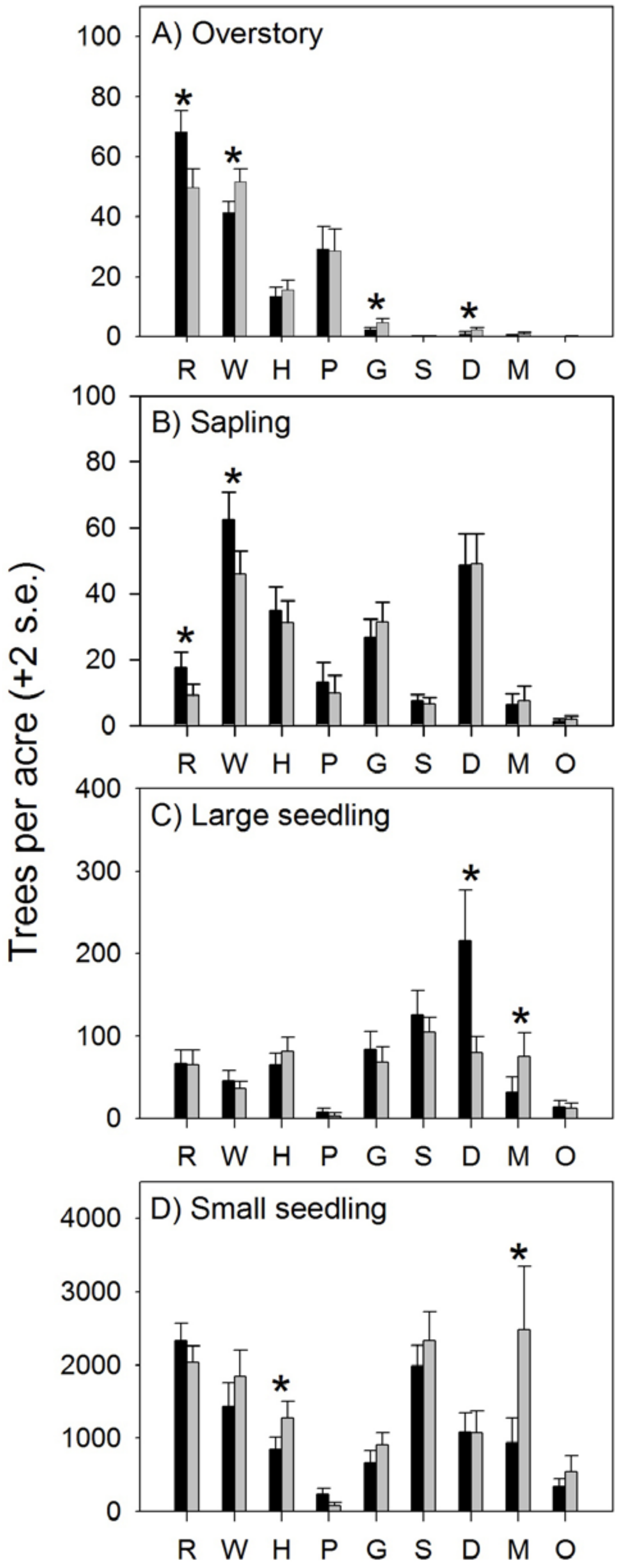

Figure 1.—Mean number of trees per acre (± 2 standard errors) in 1995 (black bars) and 2010 (gray bars) for (A) overstory, (B) sapling, (C) large seedling, and (D) small seedling size classes on ELT 3 in untreated control sites of the Missouri Ozark Forest Ecosystem Project. Abbreviations are: R=red oak, W=white oak, H=hickory, P=shortleaf pine, G=blackgum, S=sassafras, D=dogwood, M=maple and O=other species. Asterisk indicates a significant difference between years for a taxonomic group within size class ($p<0.05$).

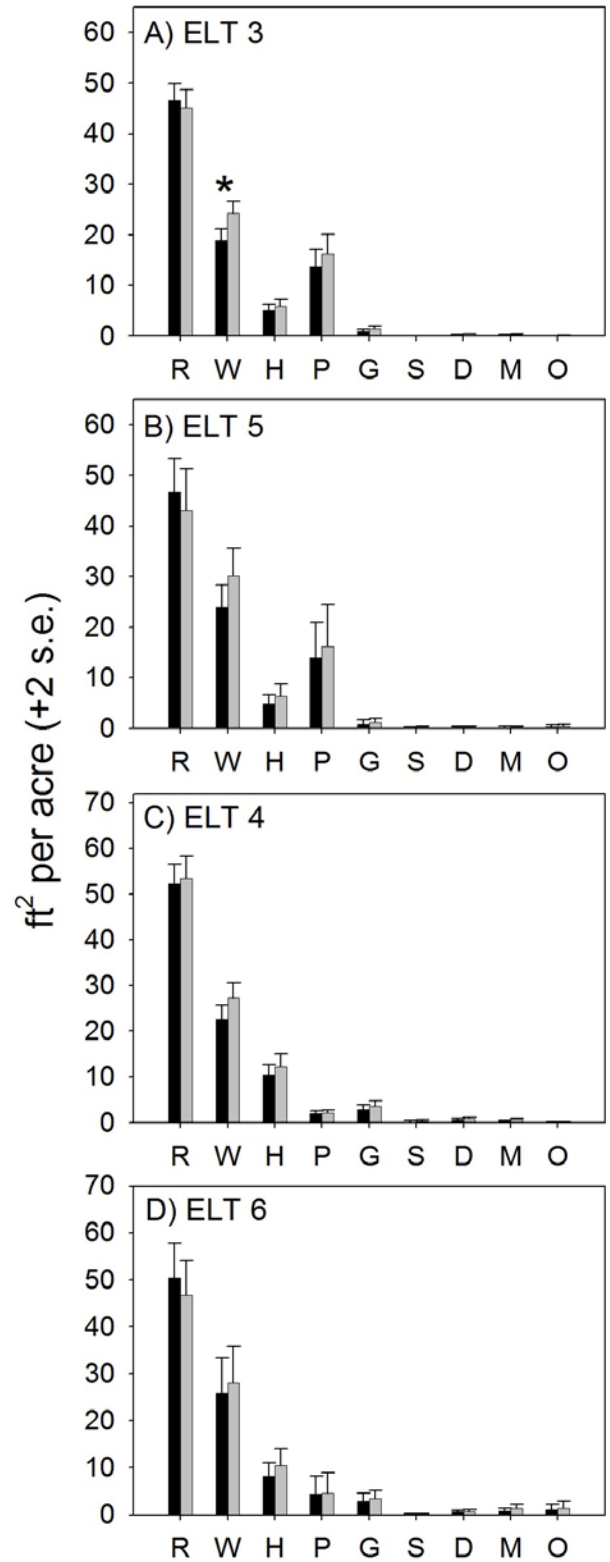

Figure 2.— Mean basal area (±2 standard errors) in 1995 (black bars) and 2010 (gray bars) for overstory taxa on different ecological land types (ELT) in the untreated control sites of the Missouri Ozark Forest Ecosystem Project: (A) ELT 3, (B) ELT 5, (C) ELT 4, and (D) ELT 6. Abbreviations are: R=red oak, W=white oak, H=hickory, P=shortleaf pine, G=blackgum, S=sassafras, D=dogwood, M=maple and O=other. Asterisk indicates a significant difference between years for a taxonomic group within size class ($p<0.05$).

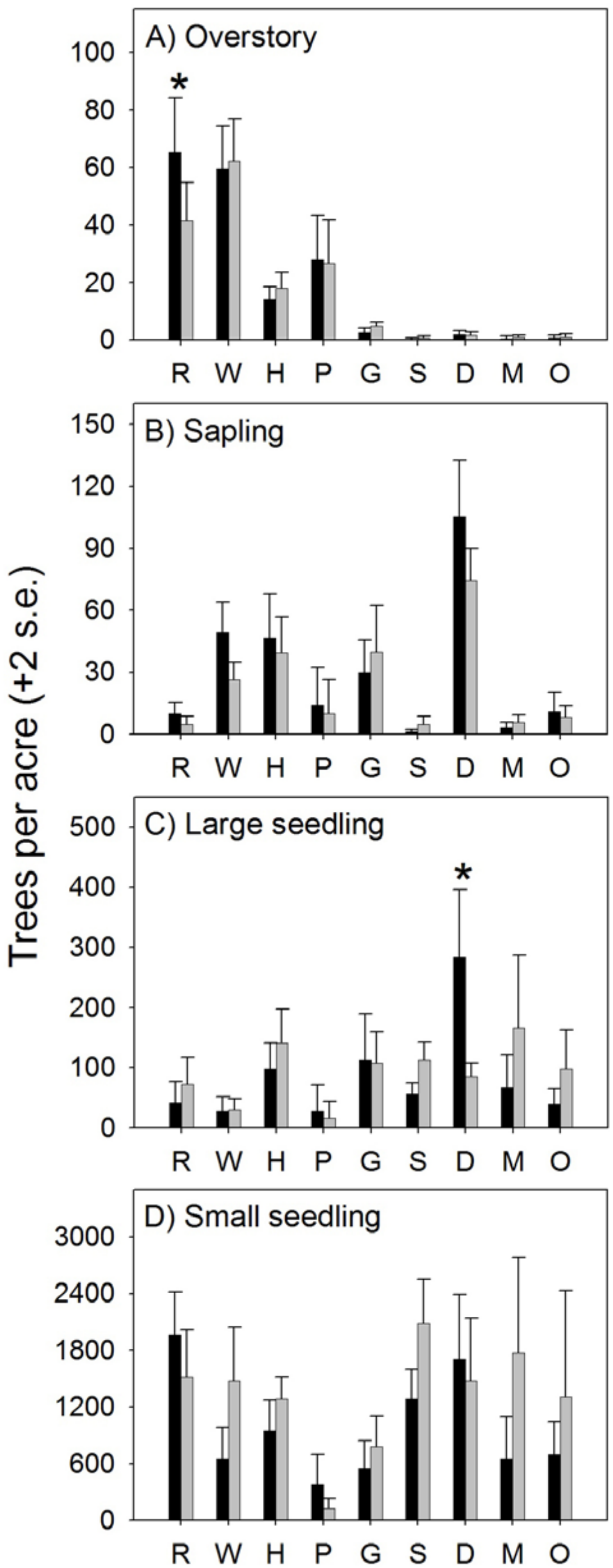

Figure 3.— Mean number of trees per acre in 1995 (black bars) and 2010 (gray bars) for (A) overstory, (B) sapling, (C) large seedling, and (D) small seedling size classes on ELT 5 in untreated control sites of Missouri Ozark Forest Ecosystem Project. Abbreviations are: R=red oak, W=white oak, H=hickory, P=shortleaf pine, G=blackgum, S=sassafras, D=dogwood, M=maple and O=other species. Asterisk indicates a significant difference between years for a taxonomic group within size class (p<0.05).

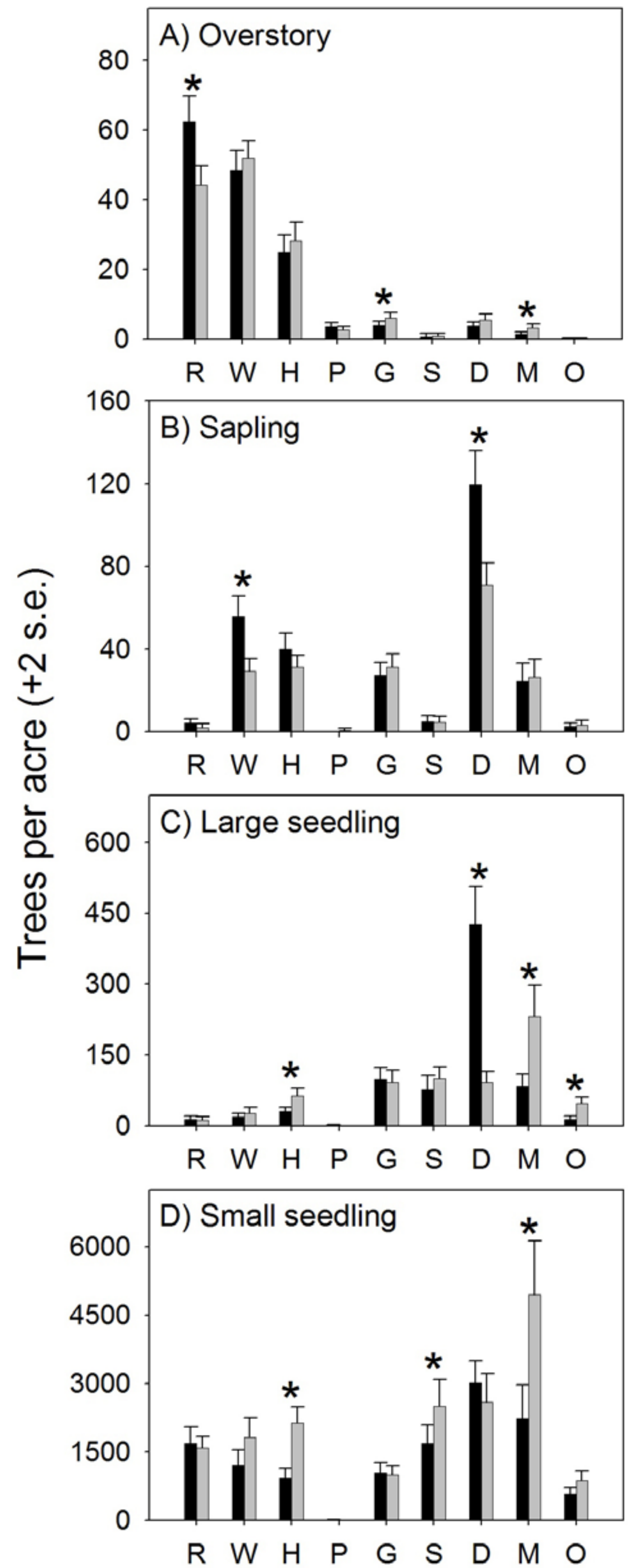

Figure 4.— Mean number of trees per acre in 1995 (black bars) and 2010 (gray bars) for (A) overstory, (B) sapling, (C) large seedling, and (D) small seedling size classes on ecological ELT 4 in untreated control sites of the Missouri Ozark Forest Ecosystem Project. Abbreviations are: R=red oak, W=white oak, H=hickory, P=shortleaf pine, G=blackgum, S=sassafras, D=dogwood, M=maple and O=other species. Asterisk indicates a significant difference between years for a taxonomic group within size class (p<0.05).

On lower, north-facing slopes (ELT 6), red oak overstory density was significantly lower in 2010 (Fig. 5A). Although not statistically significant, the density of white oak overstory trees were nominally lower and hickory was nominally greater in 2010. White oak was the most abundant overstory taxon in both years. Red oak was the second most abundant in 1995, whereas hickory density was slightly greater than red oak by 2010. Red oak and white oak were the dominant taxa according to BA (Fig. 2D).

Sapling

White oak was the most abundant species group of the sapling layer on ELT 3 in 1995 (Fig. 1B). Red oak and white oak sapling densities were significantly lower in 2010 than in 1995, dropping from a mean of 18 to 9 TPA and 62 to 46 TPA, respectively. Despite this significant decrease, the relative density of white oak saplings was still high in 2010. Dogwood was the most abundant species in the sapling size class in 2010. Maple sapling density was less than 10 TPA in both periods.

No differences were detected between years for any taxa in the sapling class on ELT 5 (Fig. 3B). However, there were notable numerical decreases in density over the 15 years. White oak and dogwood sapling densities were nominally lower in 2010. Dogwood remained the most abundant taxon in the sapling layer despite the large decrease in mean density.

Dogwood was the most abundant sapling on ELT 4 in 1995 (119 TPA; Fig. 4B) and maintained this status in 2010 despite a large reduction in density (71 TPA). Sapling densities of white oak were significantly lower in 2010. On ELT 4, white oak sapling density declined by nearly 50 percent over the 15-year period (56 vs. 29 TPA). Red oak was a minor component of the sapling layer. Maple sapling density changed little over the 15 years but was comparable to that of oak saplings by 2010.

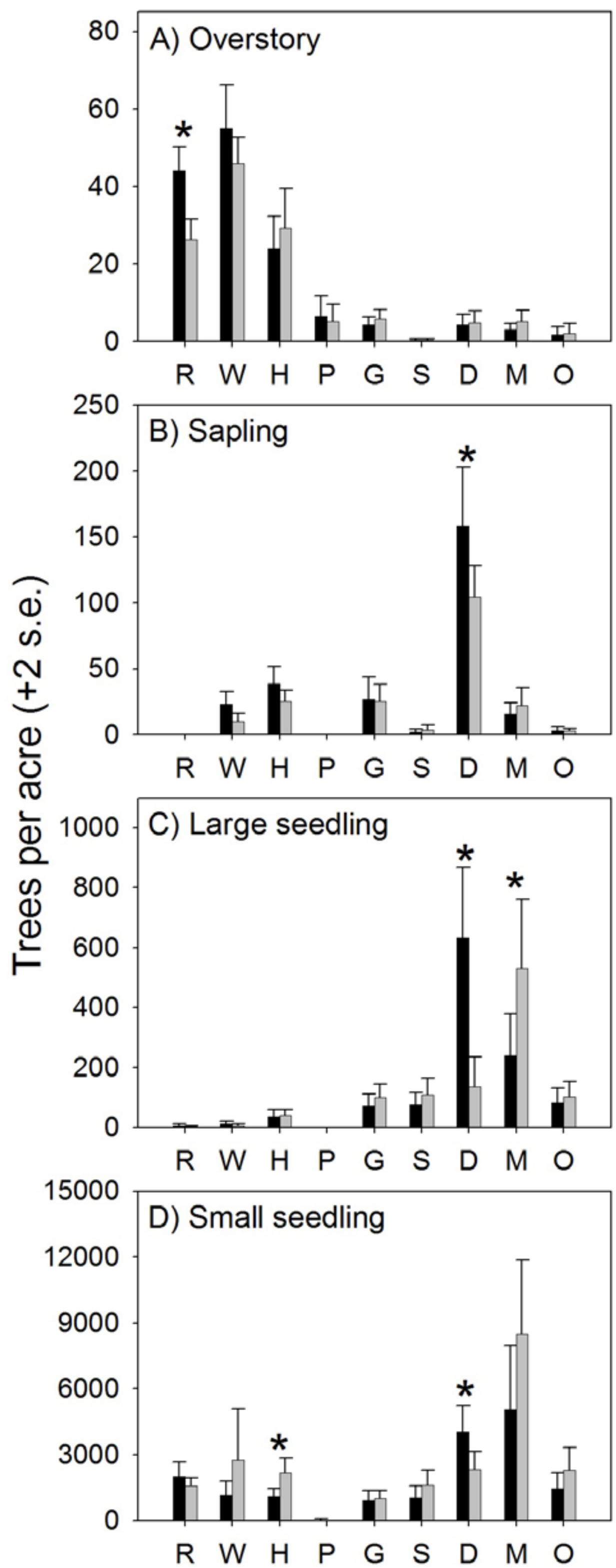

Figure 5.— Mean number of trees per acre in 1995 (black bars) and 2010 (gray bars) for (A) overstory, (B) sapling,(C) large seedling, and (D) small seedling size classes on ELT 6 in untreated control sites of Missouri Ozark Forest Ecosystem Project. Abbreviations are: R=red oak, W=white oak, H=hickory, P=shortleaf pine, G=blackgum, S=sassafras, D=dogwood, M=maple and O=other species. Asterisk indicates a significant difference between years for a taxonomic group within size class (p<0.05).

Dogwood was the most abundant sapling at both sampling periods on ELT 6, although it was significantly lower in 2010 (158 and 104 TPA; Fig. 5B). The mean densities of white oak and hickory saplings were nominally lower in 2010, whereas mean density of maple saplings increased slightly. No red oak saplings occurred in plots in either sampling period.

Large Seedlings

On ELT 3, dogwood was the most abundant taxon of large seedlings in 1995 (Fig. 1C). However, dogwood density was significantly lower in 2010 than 1995, dropping from a mean of 215 TPA to 80 TPA. In contrast, maple density was significantly greater in 2010, doubling over the 15-year period (31 vs. 75 TPA). Mean densities of red and white oaks showed very little change, making up only a small proportion of large seedlings. By 2010, sassafras was the most abundant taxon.

Dogwood was the most abundant taxon of large seedlings on ELT 5 in 1995 (283 TPA; Fig. 3C). However, the density of large dogwood seedlings was significantly lower by 2010 (85 TPA). Although not significant, mean densities of several taxa in the large seedling class were nominally greater in 2010 than 1995; most notable were increases in maple and other species. Red oak density also showed a sizeable increase over 15 years (42 vs. 73 TPA), whereas white oak density remained largely unchanged. Both oak species groups were a minor component of large seedlings in both years. By 2010, maple was the most abundant large seedling (167 TPA).

The number of large dogwood seedlings decreased significantly over the 15-year period on ELT 4 (427 vs. 93 TPA; Fig. 4C). Large seedling densities of maple, hickory, and other species were significantly greater in 2010 than in 1995, with maple being the most abundant taxon after 15 years (231 TPA). The oaks only made up a small fraction of large seedlings (<30 TPA).

There was a significant decrease in large dogwood seedlings on ELT 6 (Fig. 5C). The large decline in dogwood was offset by an increase in maple density, which was significantly greater in 2010 (239 vs. 532 TPA). As of 2010, maple was the most abundant large seedling. Both oak species groups made up a minor fraction of large seedlings (<11 TPA).

Small Seedlings

On ELT 3, small maple and hickory seedling densities were significantly greater in 2010 than 1995 (Fig. 1D). The density of small maple seedlings was 2.5 times greater after 15 years (2,482 vs. 939 TPA). Maple went from the fifth most abundant in 1995 to most abundant species group of the small seedling size class in 2010. Although no difference was detected between years, red oak density was nominally lower in 2010 while white oak density was greater after 15 years. Small sassafras seedling density remained high over the 15-year period (1,985 and 2,336 TPA in 1995 and 2010, respectively).

There were no significant differences in small seedling density detected between years on ELT 5 (Fig. 3D). Red oak was the most abundant species group in the small seedling class in 1995 (1,960 TPA). Although not significant, mean densities of white oak, sassafras, maple, and other species were considerably greater in 2010. Sassafras was the most abundant taxon by 2010 (2,087 TPA).

On ELT 4, densities of small hickory, sassafras, and maple seedlings were significantly greater in 2010 (Fig. 4D). Dogwood was the most abundant taxon in the small seedling class in 1995 (3,005 TPA). By 2010, maple was the most abundant (4,944 TPA) and had substantially greater density than other taxa. Although not significant, mean density of small white oak seedlings was nominally greater in 2010.

The density of small hickory seedlings was significantly greater in 2010 on ELT 6, whereas the density of dogwood was significantly lower (Fig. 5D). Mean densities of maple and white oak were nominally greater in 2010. Mean density of small maple seedlings increased from 5,058 to 8,484 TPA over 15 years, whereas mean density of small white oak (1,150 to 2,759 TPA) and hickory (1,104 to 2,284 TPA) more than doubled.

DISCUSSION

Mesophication is a process of shifting forest composition from fire-adapted to fire-sensitive species under fire exclusion (Nowacki and Abrams 2008). Maples are the most common mesophytic, fire-sensitive species in the Missouri Ozarks, and therefore we postulated that increasing abundance of maple species would provide early evidence of mesophication in this region. Our study showed that maple seedling densities (small and large seedlings) consistently increased across a gradient of site quality. Furthermore, maple was a major component of the seedling layer on all ELTs by 2010 and was among the most common taxa on better quality sites. Sites used for this study have not been burned in at least a half century suggesting that the observed increase in maple regeneration densities could be an early indicator of mesophication in Ozark upland forests.

The process of mesophication starts with the establishment of shade-tolerant, fire-sensitive species followed by their recruitment into larger size classes. Maple seedlings were relatively abundant by 2010, whereas maple sapling density still remained low. This pattern suggests that mesophication may be in an early stage at these sites. Historically, maple was relegated to less fire-prone sites in the Ozarks, such as mesic toe slopes, upland waterways, or rocky sites with shallow soil, but has expanded into adjacent uplands over the last two centuries along with other fire-sensitive species (Hanberry et al. 2012). Frequent, intense drought experienced in the Ozarks could also limit recruitment of non-oak species, such as maple (Johnson et al. 2009, Kabrick et al. 2008b, Nigh et al. 1985). Maple sapling densities were up to nine times greater on protected slope ELTs compared to those on exposed slopes suggesting stronger recruitment limitation on drier, south-facing slopes in this study.

Another potential outcome of mesophication is displacement of fire-tolerant species by fire-sensitive species in the understory. Oak, hickory, and shortleaf pine are the primary fire-tolerant tree species groups of the Missouri Ozarks. Although there were no significant differences detected for oak seedling density, numerical differences in mean density suggested that white oak tended to increase and red oak tended to decline over the study period. This difference between oak species groups is likely related to the greater shade tolerance of white oak (Johnson et al. 2009). Hickories, which are slightly more shade tolerant than are many of the oaks (Burns and Honkala 1990), increased in all seedling layers over the 15-year period, and increases were significant on nearly all ELTs. Shortleaf pine comprised only a small fraction of the seedling layers and, when present, densities declined. The low abundance of shortleaf pine regeneration in these mature, relatively undisturbed forests is mainly due to this species' low tolerance of shade and requirement of exposed mineral soil for seedling establishment (Lawson 1990). These findings suggest that not all fire-tolerant species regeneration is decreasing because of mesophication, but rather some decreases in regeneration abundance are simply due to limited availability of light and suitable seedbeds.

A low relative density of large oak advance regeneration compared to shade-tolerant species has been cited as an indicator of an oak-dominated forest undergoing successional replacement by fire-sensitive species (Abrams and Downs 1990, Abrams et al. 1997). Nowacki and Abrams (1992) refer to this as an oak sapling bottleneck. In this study, large seedlings and saplings were considered large advance regeneration. Relative to oak, large maple seedlings were more abundant on all ELTs except ELT 3 where oaks had a numerical advantage in both the large seedling and the sapling layers. ELT 3 is the most xeric of the ELTs considered in this study. This finding is consistent with our current knowledge of Ozark forests; specifically, that oaks are more resilient against non-oak displacement on drier sites compared to mesic sites (Johnson et al. 2009). However, sapling densities of oak and hickory decreased on all ELTs over 15 years, whereas maple sapling density was nominally greater by 2010.

The overstories of all ELTs remained dominated by oak and hickory species over the 15-year period, with pine a major component on south-facing sites (ELT 3 and ELT 5). However, red oak density significantly decreased on all ELTs, while BA nominally decreased. This reduction in red oak density was likely the result of oak decline, a widespread disease complex impacting mainly species of the red oak group, particularly black and scarlet oak (Kabrick et al. 2008a, Voelker et al. 2008). Along with this ubiquitous decrease in red oak were increases in the abundance of white oak in the overstories on all ELTs. White oak is less susceptible to decline than the red oak group. Using the same study sites, Shifley et al. (2006) observed that red oaks experienced three and a half times the mortality rate of white oaks. The high abundance of mature red oak species at these sites suggests that oak decline will continue to reduce the abundance of red oak and provide recruitment opportunities for white oak. Red oak decline could also release shade-tolerant, fire-sensitive species and facilitate their recruitment, thereby accelerating succession (Abrams and Nowacki 1992), and possibly mesophication, of these and similar Ozark forests.

There were several other notable trends that came out of this study. Perhaps the most conspicuous were the large declines in dogwood abundance, which was most evident on north-facing slopes (ELT 4 and ELT 6). Oswalt et al. (2012) observed significant range-wide declines in dogwood populations estimated from U.S. Forest Service Forest Inventory and Analysis data. The authors largely attributed the decline to mortality caused by the nonnative fungus *Discula destructiva* (dogwood anthracnose) but also cited increasing forest density, drought, and competition with shade-tolerant tree species, such as sugar maple, as other possible causes. Dogwood anthracnose is not considered a major issue in Missouri at this time[2], so the declines we observed were likely related to stress associated with drought and competition. Since dogwood is a major understory competitor in the Ozarks (Dey et al. 1996), dogwood decline would create recruitment opportunities for oak and non-oak species alike. Over the 15-year period of our study, sassafras developed into a major component of the regeneration layers on several ELTs, particularly on ELT 3 where it was the most abundant species in the small and large

[2] Wright, S. 2014. Personal communication. Forest Pathologist, Missouri Department of Conservation, 3500 E. Gans Road, Columbia, MO 65201.

regeneration classes. Although sassafras is considered shade intolerant (Griggs 1990), sassafras is often a part of the advance regeneration layer of oak-hickory forests in the Missouri Ozarks (Grabner 2000, Hartman and Heumann 2003, Shifley et al. 2000). The density of the other species group, composed of an ecologically diverse collection of species (including mesophytes), also tended to increase in regeneration layers. Several of these species are capable of developing into large overstory trees and, therefore, could potentially compete with oak and hickory for overstory positions. In particular, black cherry (*Prinus serotina*) is often locally dominant during early stand development following clearcutting in the Ozarks, yet it is conspicuously absent from mature stands. Frequent and intense drought likely limits the development of black cherry in Ozark upland forests.

CONCLUSIONS

The Ozarks are known for supporting a higher proportion of oak and hickory species than other forested areas of the CHR, even in the midst of fire suppression (Johnson et al. 2009). The unique combination of climate, soil quality, site conditions, and forest composition has led some to postulate that the oak-hickory forest type is successionally stable in the Ozarks (Pallardy 1995). However, there is evidence that mesophytic species, particularly maples, are not only capable of replacing oak overstory trees in the Ozarks but that this process is already underway (Hanberry et al. 2012, Hanberry et al. 2014, Nigh et al. 1985). We documented increases in maple abundance in the understories of upland Ozark forests over a 15-year period. During this same period, the densities of oak and hickory regeneration tended to increase, but their relative abundance was lower than that of maples by 2010 on all but the driest sites. Maple saplings and overstory trees, on the other hand, were a minor component of these forests, while oak and hickory dominated large size classes. The findings presented here along with findings of other recent studies (Hanberry et al. 2012, Hanberry et al 2014) suggest these and similar upland forests in the Missouri Ozarks could be in early stages of mesophication where fire has been excluded for at least 50 years, that this process may be occurring at a slower rate than in eastern and central parts of the CHR, and that the rate of mesophication is slowest on xeric, south-facing slopes. It also could be plausible that the predominance of low quality soils and frequent drought in the Ozarks will hinder these forests from experiencing much mesophication. This conclusion is consistent with research out of Oklahoma on sites that were more xeric than the ones considered in this study (Burton et al. 2010, DeSantis et al. 2010, Thomas and Hoagland 2011). However, since our findings are based on only 15 years of stand dynamics, which represents just 15-20 percent of a typical even-aged forest rotation (80-100 years), our conclusions are preliminary at this time and are best treated as working hypotheses. Continued monitoring and future analysis will be necessary for testing and refining our working hypotheses regarding successional status of Ozark forests under fire exclusion.

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LITERATURE CITED

Abrams M.D. 1992. **Fire and the development of oak forests.** BioScience. 42: 346-353.

Abrams M.D.; Downs, J.A. 1990. **Successional replacement of old-growth white oak by mixed-mesophytic hardwoods in southwest Pennsylvania.** Canadian Journal of Forest Research. 20: 1864-1870.

Abrams, M.D.; Nowacki, G.J. 1992. **Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania.** Bulletin of the Torrey Botanical Club. 119: 19-28.

Abrams M.D.; Orwig, D.A.; Dockry, M.J. 1997. **Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, USA.** Canadian Journal of Forest Research. 27: 994-1002.

Arthur M.A.; Alexander, H.D.; Dey, D.C.; Schweitzer, C.J.; Loftis, D.L. 2012. **Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States.** Journal of Forestry. 110: 257-266.

Brookshire, B.L.; Shifley, S.R., eds. 1997. **Proceedings of the Missouri Ozark forest ecosystem project symposium: an experimental approach to landscape research.** Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 378 p.

Burns, R.M.; Honkala B.H., tech. coords. 1990. **Silvics of North America: 2. Hardwoods.** Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.

Burton, J.A.; Hallgren, S.W.; Palmer, M.W. 2010. **Fire frequency affects structure and composition of xeric forests of eastern Oklahoma.** Natural Areas Journal. 30: 370-379.

Christensen, N.L. 1977. **Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina.** American Midland Naturalist. 97: 176-188.

DeSantis, R.D.; Hallgren, S.W.; Lynch, T.B.; Burton, J.A.; Palmer, M.W. 2010. **Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA.** Journal of Vegetation Science. 21: 606-615.

Dey, D.C.; Johnson, P.S.; Garrett, H.E. 1996. **Modeling the regeneration of oak stands in the Missouri Ozark Highlands.** Canadian Journal of Forest Research. 26: 573-583.

Glitzenstein J.C.; Canham, C.D.; McDonnell, M.J.; Streng, D.R. 1990. **Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York.** Bulletin of the Torrey Botanical Club. 117: 106-122.

Grabner, J.K. 2000. **Ground layer vegetation in the Missouri Ozark forest ecosystem project: pre-treatment species composition, richness, and diversity.** In: Shifley, S.R.; Brookshire, B.L., eds. Missouri Ozarks forest ecosystem project: site history, landforms, woody and herbaceous data, down wood, and inventory methods for the landscape experiment. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 107-121.

Griggs, M.M. 1990. **Sassafras**. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: 2. Hardwoods. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 773-777.

Hanberry B.B.; Dey, D.C.; He, H.S. 2012. **Regime shifts and weakened environmental gradients in open oak and pine ecosystems.** PLoS ONE. 7(7): e41337. DOI: 10.1371/journal.pone.0041337.

Hanberry, B.B.; Kabrick, J.M.; He, H.S. 2014. **Densification and state transition across the Missouri Ozarks landscape.** Ecosystems. 17: 66-81.

Hartman, G.W.; Heumann, B. 2003. **Prescribed fire effects in the Ozarks of Missouri: the Chilton Creek project 1996-2001**. In: Proceedings of the second international wildland fire ecology and fire management congress. Boston, MA: American Meteorological Society: 2B.8.

Johnson, P.S.; Shifley, S.R.; Rogers, R.. 2009. **The ecology and silviculture of oaks.** New York, NY: CABI Publishing. 503 p.

Kabrick, J.M.; Dey, D.C.; Jensen, R.G.; Wallendorf, M. 2008a. **The role of environmental factors in oak decline and mortality in the Ozark Highlands.** Forest Ecology and Management. 255: 1409-1417.

Kabrick, J.M.; Meinert, D.; Nigh, T.A.; Gorlinsky, B.J. 2000**. Physical environment of the Missouri Ozarks forest ecosystem project sites.** In: Shifley, S.R.; Brookshire, B.L., eds. Missouri Ozarks forest ecosystem project: site history, landforms, woody and herbaceous data, down wood, and inventory methods for the landscape experiment. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 41-70.

Kabrick, J.M.; Zenner, E.K.; Dey, D.C.; Gwaze, D.; Jensen, R.G. 2008b. **Using ecological land types to examine landscape-scale oak regeneration dynamics.** Forest Ecology and Management. 255: 3051-3062.

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

Lorimer, C.G. 1984. **Development of the red maple understory in northeastern oak forests.** Forest Science. 30: 3-22.

Monk, C.D. 1961. **The vegetation of the William L. Hutcheson Memorial Forest, New Jersey.** Bulletin of the Torrey Botanical Club. 88: 156-166.

Nigh, T.A.; Pallardy, S.G.; Garrett, H.E. 1985. **Sugar maple-environment relationships in the river hills and central Ozark Mountains of Missouri.** American Midland Naturalist. 114(2): 235-251.

Nowacki G.J.; Abrams, M.D. 1992. **Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania.** Canadian Journal of Forest Research. 22: 790-800.

Nowacki G.J.; Abrams, M.D. 2008. **The demise of fire and "mesophication" of forests in the eastern United States.** BioScience. 58: 123-138.

Nowacki, G.J.; Abrams, M.D.; Lorimer, C.G. 1990. **Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin.** Forest Science. 36: 276-292.

Oswalt, C.M; Oswalt, S.N.; Woodall, C.W. 2012. **An assessment of flowering dogwood (*Cornus florida* L.) decline in the eastern United States.** Open Journal of Forestry. 2(2): 41-53.

Pallardy, S.G. 1995. **Vegetation analysis, environmental relationships, and potential successional trends in the Missouri forest ecosystem project.** In: Gottschalk, K.W.; Fosbroke, S.L., eds. Proceedings of the 10th Central Hardwood Forest conference. Gen. Tech. Rep. NE-197. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 551-562.

Pallardy S.G.; Nigh, T.A.; Garrett, H.E. 1988. **Changes in forest composition in central Missouri: 1968-1982.** American Midland Naturalist. 120(2): 380-390.

Richards, R.H.; Shifley, S.R.; Rebertus, A.J.; Chaplin, S.J. 1995. **Characteristics and dynamics of an upland Missouri old-growth forest.** In: Gottschalk, K.W.; Fosbroke, S.L., eds. Proceedings of the 10th Central Hardwood Forest conference. Gen. Tech. Rep. NE-197. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 11-22.

Shifley, S.R.; Fan, Z.; Kabrick, J.M.; Jensen R.G. 2006. **Oak mortality risk factors and mortality estimation.** Forest Ecology Management. 229: 16-26.

Shifley, R.S., Roovers, L.M., Brookshire, B.L. 1995. **Structural and compositional differences between old-growth and mature second-growth forests in the Missouri Ozarks.** In: Gottschalk, K.W.; Fosbroke, S.L., eds. Proceedings of the 10th Central Hardwood Forest conference. Gen. Tech. Rep. NE-197. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 23-36.

Shifley, R.S.; Roovers, L.M.; Jensen, R.G.; Larsen, D.R. 2000. **Composition and structure of woody forest vegetation in the Missouri Ozark forest ecosystem project.** In: Shifley, S.R.; Brookshire, B.L., eds. Missouri Ozarks Forest Ecosystem Project: site history, landforms, woody and herbaceous data, down wood, and inventory methods for the landscape experiment. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 71-106.

Thomas, R.E.; Hoagland, B.W. 2011. **The changing forests of central Oklahoma: a look at the composition of the Cross Timbers prior to Euro-American settlement, in the 1950s, and today.** Oklahoma Native Plant Record. 11: 61-74.

Voelker, S.L.; Muzika, R.M.; Guyette, R.P. 2008. **Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks.** Forest Science. 54(1): 8-20.