The history of widespread decrease in oak dominance exemplified in a grassland–forest landscape

Brice B. Hanberry a,⁎, Daniel C. Dey b, Hong S. He a,1

a University of Missouri, 203 Natural Resources Building, Columbia, MO 65211, USA
b USDA Forest Service, Northern Research Station, University of Missouri, 202 Natural Resources Building, Columbia, MO 65211, USA

HIGHLIGHTS

• Oak establishment is decreasing and open oak ecosystems are remnants.
• We demonstrate loss of open oak ecosystems across a grassland–forest landscape.
• Oaks decreased from 62% of historical composition to 30% of current composition.
• Current forest densities were two times greater than historical densities.
• Prescribed fire with silvicultural methods may help establish oak.

ARTICLE INFO

Article history:
Received 29 October 2013
Received in revised form 14 January 2014
Accepted 15 January 2014
Available online xxxx

Keywords:
Fire suppression
Historical forest
Land use
Oak restoration
Savanna
Woodland

ABSTRACT

Regionally-distinctive open oak forest ecosystems have been replaced either by intensive agriculture and grazing fields or by denser forests throughout eastern North America and Europe. To quantify changes in tree communities and density in the Missouri Plains, a grassland–forest landscape, we used historical surveys from 1815 to 1864 and current surveys from 2004 to 2008. To estimate density for historical communities, we used the Morisita plotless density estimator and applied corrections for surveyor bias. To estimate density for current forests, we used Random Forests, an ensemble regression tree method, to predict densities from known values at plots using terrain and soil predictors. Oak species decreased from 62% of historical composition to 30% of current composition and black and white oaks historically were dominant species across 93% of the landscape and currently were dominant species across 42% of the landscape. Current forest density was approximately two times greater than historical densities, demonstrating loss of savanna and woodlands and transition to dense forest structure. Average tree diameters were smaller than in the past, but mean basal area and stocking remained similar over time because of the increase in density in current forests. Nevertheless, there were spatial differences; basal area and stocking decreased along rivers and increased away from rivers. Oak species are being replaced by other species in the Missouri Plains, similar to replacement throughout the range of Quercus. Long-term commitment to combinations of prescribed burning and silvicultural prescriptions in more xeric sites may be necessary for oak recruitment. Restoration of open oak ecosystems is a time-sensitive issue because restoration will become increasingly costly as oaks are lost from the overstory and the surrounding matrix becomes dominated by non-oak species.

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1. Introduction

In eastern forests of the United States, a wave of widespread and intensive timber harvesting occurred over a relatively short period (e.g., 1800 to 1920) following Euro-American settlement in North America. Extensive harvest promoted oak regeneration in predominantly oak forested ecosystems through release of advance regeneration and stump sprouts (Williams, 1989; Aldrich et al., 2005). The regional scale of forest disturbance resets the age distribution and structure of oak forest ecosystems to dense oak forests by initiating oak regeneration as forests were harvested. Subsequently, suppression of fire in North America changed the disturbance regime to small-scale disturbances, which has promoted the shift to fire-sensitive species in forests of various successional stages at a large scale (Nowacki and Abrams, 2008; Hanberry et al., 2012a). Due to changes in land use, oak recruitment failure and decreasing dominance are occurring throughout eastern North American forests and worldwide (Watt, 1919; Thadami and Ashton, 1995; Humphrey and Swaine, 1997; Niklasson et al., 2002; Svenning, 2002; Li and Ma, 2003; Hofmeister et al., 2004; Götmark et al., 2005; Pulido and Díaz, 2005; Strandberg et al., 2005; von Oheimb and Brunet, 2007; Zavaleta et al., 2007; Hédl et al., 2010; Altman et al., 2013). As a consequence, some light-demanding herbaceous plants,
and associated wildlife, saproxylic insects, epiphytes, and fungi of open oak ecosystems are declining along with oaks (McShea et al., 2007; Rogers et al., 2008; Lindblad and Foster, 2010). Oaks, a foundation genus, provide open forested structure, which has become an increasingly rare vegetation type, resulting in biodiversity changes to species that succeed under intensive land use or in closed forests.

The Missouri Plains, in the central United States, are part of the prairie peninsula (Transeau, 1935), a grassland extension into eastern broadleaf forests, where a mosaic of prairies, savannas, woodlands, and forests historically intermingled in patterns influenced by the interaction of soils, topography, and fire disturbances (Nigh and Schroeder, 2002). Prairies were present on flat plains and broad ridges exposed to annual or near-annual fires, oak savannas and woodlands occurred where topographic roughness or wetlands extended fire-free periods to probably at least 5 years, and forests were common on lower and rough slopes and near wetlands including stream networks protected from fire (Nigh and Schroeder, 2002). Stambaugh et al. (2006) reported a mean fire interval of 6.6 years before substantial Euro-American settlement around 1820 in the loess hills of northwestern Missouri. A fire regime that was frequent but not annual favored fire-tolerant oak species and the open structure of savannas and woodlands (Bond et al., 2005). Oak savannas and woodlands had open or simple canopies and fire removed midstories, permitting sufficient light to reach the ground to support a diverse ground cover of forbs and grasses (Nuzzo, 1986).

During the past 150 years, human culture and land use have changed in the Missouri Plains. The final transfer of Osage lands in Missouri by treaty to the US government in 1825 (Rollings, 1992) represented a historical shift in land ownership from Native American to European occupation and use. Stambaugh et al. (2006) observed that the mean fire interval decreased to 1.6 years during initial Euro-American settlement (1825–1850). The use of fire as a tool was continued by Euro-American settlers; in fact, fires were more frequent during initial Euro-American settlement. However, increased development and human densities led to fire suppression by the 1920s. Since the 1950s, wildfires have become rare and average about 4 ha in size during non-drought years in the Missouri Plains region (Westin, 1992). Agricultural development rapidly increased in the midwestern US, including Missouri, as corn and wheat farming developed between 1850 and 1910 (Ramankutty and Foley, 1999). Prairies, savannas, and woodlands of the Missouri Plains were converted to pasture and crop fields (Schroeder, 1981; Ramankutty and Foley, 1999). Later, farm abandonment that occurred during 1930 to 1990 initiated old field succession (Ramankutty and Foley, 1999).

Today, less than 1% of the original savannas in the midwestern prairie peninsula region remain due to conversion to intensive and extensive agriculture and grazing or rapid transition to (relatively) closed canopy forests following fire suppression (Nuzzo, 1986). Although oak forests still dominate xeric sites, oaks are declining on higher quality sites throughout eastern North America and communities are shifting to a range of fire-sensitive species that once were confined to sites protected from fire (Nowacki and Abrams, 2008; Fralish and McArdle, 2009; Hanberry et al., 2012a). Current forest densities and composition show less variation along large scale ecological gradients than in the past due largely to fire suppression and land use events such as exploitative logging and the conversion of forestlands to agriculture and subsequent agricultural abandonment; however, at small scales logging and land abandonment may produce a very high contrasting structure and composition (e.g., edges; Williams, 1989; Hanberry et al., 2012a, 2014).

Although there is a conceptual process of how eastern forests have changed over the past 100 to 150 years (Williams, 1989), there is little quantitative research on historical forest conditions and how they have changed in current times in the Missouri prairie peninsula region. To quantify historical forests, we used General Land Office (GLO) records from the Missouri Plains as a reference for historical forest communities and densities immediately before Euro-American settlement. To determine long term and large scale changes, we compared historical values to current forest communities and densities from USDA Forest Inventory and Analysis (FIA). In addition to the provision of 1) historical ranges of structural values and 2) large scale forest change over time, we present management approaches to address widespread decrease of oak dominance in the eastern United States that may be useful in other regions with oak dominance declines.

2. Methods

2.1. Ecological units

The Missouri Plains cover about 8 million ha and are located in the northwestern part of Missouri (Fig. 1). The Missouri Plains are composed of two ecological sections, the Osage and Till Plains, and further divided into ecological subsections by climate, soils, topography, vegetation, and then divided into land types, such as hills or plains (Nigh and Schroeder, 2002; Fig. 2). We used ecological units, composed of ecological subsections divided into land types, to provide a detailed spatial range of communities and densities across the landscape.

2.2. Community rules

We grouped some tree species into the following categories primarily because of genus-only identification in the GLO surveys: ashes (Fraxinus americana, Fraxinus pennsylvanica); cherries (Prunus spp.); elms (Ulmus alata, Ulmus americana, Ulmus rubra); hickories (Carya cordiformis, Carya glabra, Carya laciniosa, Carya ovata, perhaps Carya texana and Carya tomentosa); maples (primarily Acer saccharum, Acer negundo, Acer saccharinum); red oaks (Quercus rubra, Quercus falcata, Quercus coccinea); walnuts (Juglans nigra, Juglans cinerea); cottonwoods and willows (Populus spp., Salix spp.); and mulberry and locusts (Morus rubra, Robinia pseudoacacia, Celdisita triacanthos).

To determine community composition, we set a threshold of ≥200 trees per ecological unit, resulting in a total of 14 units that met that threshold during each time period (Appendix A). To be classed as a dominant species in a community, percent composition (of species) had to be ≥10% per ecological unit in order to limit communities to no more than 6 species/species groups and yet have species representation. The order of tree species reported within a community was based on descending mean percent composition for all GLO trees to make comparisons more straightforward. For example, black oak had the overall greatest percent composition across all ecoregions and was therefore the first species listed where it exceeded >10% in composition.

2.3. Current surveys and forest density

Every five years, the USDA Forest Inventory and Analysis program surveys long-term forest plots located about every 2400 ha across the country. Each plot contains four 7.31 m radius subplots, configured as a central subplot surrounded by three outer subplots. We used data from the latest complete cycle of 2004 to 2008. We selected live trees with a diameter ≥12.7 cm to correspond with diameters present in GLO surveys; additionally, smaller diameter trees are surveyed in a fraction of each subplot. We selected plots that were 100% forestland, which FIA defines as land at least 1 acre in area and 120 ft wide with at least 10% cover by live trees of any size, “including land that formerly had such tree cover and that will continue to have forest use”, and contained at least two trees to exclude some plots that were harvested recently. We calculated trees per hectare using the supplied FIA expansion factor of 6.02 (i.e., one tree represents the inverse of the plot area in acres; 1 / (4 • 0.042)), and summed the values for each plot.

To predict total density from discrete plots to a continuous surface, and ultimately comparable to historical densities, we used Random Forests regression trees (Breiman, 2001; Cutler et al., 2007) with the
Random Forest package (Liaw and Wiener, 2002) in R statistical software (R Development Core team 2010). We selected 21 predictor variables representing a combination of SSURGO (Soil Survey Geographic) soil and physiographic variables, topographic variables from DEM (digital elevation model), and subsection and geology variables, contained within SSURGO soil polygons (mean polygon area of 23 ha) as spatial units. The predictor variables were a comprehensive set of attributes that influenced tree densities. The 12 soil variables included landform type (bottomlands, protected backslope, exposed backslope, and uplands), parent material kind (e.g., alluvium, colluvium, residuum),

Fig. 1. The two ecological sections of the Missouri Plains. Gray shading shows historical forested extent of the Missouri Plains.

Fig. 2. Ecological subsections (numbered and shaded; Nigh and Schroeder, 2002) of the Osage Plains (OP) and Till Plains (TP) of Missouri, with outlined land types, where there are a sufficient number of large diameter trees (DBH ≥ 12.7 cm) to compare historical and current forests. Land types are shaded in panel.
drainage class (very poorly drained to excessively drained), taxonomic order, and flooding frequency. We also used depth (cm) to either the bottom of the soil profile or soil restriction. We calculated mean water holding capacity (cm/cm), pH, base saturation (sum of bases/effective cation exchange capacity), organic matter (%), clay (%), and sand (%) to the depth and then weighted the values by the percent of each soil series in a soil map unit, or a collection of soil polygons with similar properties. From a 30 m DEM (digital elevation model), we calculated seven variables: elevation (m), slope (%), transformed aspect (1 + sin(aspect // 180 × π + 0.79); Beers et al., 1966), solar radiation, topographic roughness (Sappington et al., 2007), wetness convergence, and topographic position index (T. Dilts, http://arcscripts.esri.com). We then calculated the mean value for each variable by prediction zones (mean area of 800 ha) that were soil map units of soil polygons with similar soil characteristics divided into smaller extents by land type association within ecological subsections and geology. The prediction zones were the prediction spatial unit that matched soil and topography values using a smaller ecological area than the soil map units, which shared the same soil values, albeit in discontinuous soil polygons. We also joined ecological subsections and bedrock geology designations to each individual polygon.

We compared the predicted density estimates to observed densities at the FIA plots (about 46 trees ha\(^{-1}\)) historically were the dominant species in all but one of the 14 ecological units where there were enough FIA trees to make comparisons (see Appendix B for density and composition of GLO trees for other ecological units). Black oak was no longer a dominant species in any of the current communities throughout the Osage and Till Plains sections. Fire-tolerant oaks (i.e., dominant species of upland forests, as opposed to for example, pine or oak) were no longer compositionally dominant in eight of the 14 ecological units of subsection and land type. White oak maintained its compositional dominance in only five ecological units. Bur oak (Quercus macrocarpa) and blackjack oak (Quercus marilandica) were dominant species in historical communities but were no longer dominant. Osage-orange densities. Using a rank-based method (sensu, Hanberry et al., 2012b) we calculated two density estimates: (1) a low value using spatial pattern correction and assuming a mean tree rank of 1.4, and (2) a mean value using no spatial pattern correction and assuming a mean tree rank of 1.8. Using a complementary bias method, we found the frequencies by ecological unit for quadrant location, quadrant configuration, and azimuth and we compared species and five diameter classes to line trees, which were recorded when surveyors encountered these trees along section lines, presumably with less bias than trees selected at survey points. We corrected for non-random frequencies by determining the adjustment quotient based on frequencies in regression equations (Hanberry et al., 2012b). We calculated a mean value and a high value, using the high value from the spatial pattern correction. We also set a maximum high value of the value corrected for an unvarying rank of 2 (varying rank of about 2.8).

We then averaged the two mean values and retained the low value (from the rank-based method) and high value (from the bias method). To equilibrate the density estimates from points with two trees and points with three trees, we took into account the type of survey point (density estimates from survey points with three trees are more accurate than points with two trees) and total number of points for each type of point (density estimates become more accurate with more points). We multiplied the count of points with three trees by two, giving twice the weight of points with two trees. We then multiplied each density estimate by a weight of the number of points over the total number of points and summed the two values.

2.5. Diameter, basal area, and percent stocking

The GLO surveyors selected trees of medium diameter that were healthy (White, 1983) and historical diameter distributions of trees may differ from diameters recorded in GLO surveys (Bouldin, 2010; Rheinhardt and Mladenoff, 2010). Nonetheless, we used GLO data to compare historical and contemporary forest structure for trees ≥12.7 cm DBH (diameter at breast height). For basal area estimates, we used the quadratic mean diameter (square root of the mean DBH\(^2\)) to calculate the arithmetic mean tree basal area and multiplied this by the number of trees per ha. We also calculated percent stocking (Gingrich, 1967), a measure of relative growing space occupancy that accounts for the number of trees per ha, tree diameter, and total basal area. A stocking percent of 60 represents the threshold between open and closed canopies and 100 represents average maximum growing space that a stand of trees can occupy but because we included only trees ≥12.7 cm DBH, stocking estimates were not expected to approach 100%. We estimated overall stocking by calculating the stocking contribution of the tree of arithmetic mean diameter and multiplying this by the number of trees per ha.

3. Results

3.1. Communities

No communities currently were the same as in the past (Table 1). Black oak (Quercus velutina) and white oak (Quercus alba) historically were the dominant species in all but one of the 14 ecological units where there were enough FIA trees to make comparisons (see Appendix B for density and composition of GLO trees for other ecological units). Black oak was no longer a dominant species in any of the current communities throughout the Osage and central dissected Till Plains sections. Fire-tolerant oaks (i.e., dominant species of upland forests, as opposed to for example, pine or oak) were no longer compositionally dominant in eight of the 14 ecological units of subsection and land type. White oak maintained its compositional dominance in only five ecological units. Bur oak (Quercus macrocarpa) and blackjack oak (Quercus marilandica) were dominant species in historical communities but were no longer dominant. Osage-orange
Communities and estimated mean densities (Dens; trees ha$^{-1}$), with low (Lo) and high (Hi) values of historical (GLO) and current (FIA) forests by ecological unit (subsection and land type).

<table>
<thead>
<tr>
<th>Ecological unit</th>
<th>GLO community$^1$</th>
<th>FIA community$^1$</th>
<th>GLO Dens Lo Hi</th>
<th>FIA Dens Lo Hi</th>
<th>Density increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>OP1 prairie plains</td>
<td>BO-WO-Hi-PO</td>
<td>El-Ma-OO</td>
<td>190 112 226</td>
<td>362 316 409</td>
<td>1.91</td>
</tr>
<tr>
<td>OP1 prairie/savanna dissected plains</td>
<td>BO-WO-Hi-PO</td>
<td>El-M-L-OO</td>
<td>115 63 146</td>
<td>360 120 401</td>
<td>3.12</td>
</tr>
<tr>
<td>OP2 prairie/savanna dissected plains</td>
<td>BO-HI-PO-BjO</td>
<td>PO</td>
<td>102 69 109</td>
<td>277 253 300</td>
<td>2.71</td>
</tr>
<tr>
<td>TP3 prairie plains</td>
<td>BO-WO-Hi</td>
<td>Ma-M-L-OO-Ha</td>
<td>90 52 108</td>
<td>331 312 350</td>
<td>3.67</td>
</tr>
<tr>
<td>TP3 woodland/forest breaks</td>
<td>BO-WO-El</td>
<td>Hi-El-M-L-Ha</td>
<td>190 107 237</td>
<td>318 296 341</td>
<td>1.67</td>
</tr>
<tr>
<td>TP4 prairie plains</td>
<td>BO-El-BuO-RO</td>
<td>El-M-L-Wa-Ha</td>
<td>94 49 123</td>
<td>322 297 347</td>
<td>3.43</td>
</tr>
<tr>
<td>TP4 woodland/forest hills</td>
<td>BO-WO-Hi-El-BuO-PO</td>
<td>Hi-El-M-L-OO</td>
<td>113 74 124</td>
<td>315 294 335</td>
<td>2.78</td>
</tr>
<tr>
<td>TP5 woodland/forest hills</td>
<td>BO-WO-Hi-El-BuO</td>
<td>WO-Hi-El-M_L</td>
<td>181 105 220</td>
<td>314 291 337</td>
<td>1.73</td>
</tr>
<tr>
<td>TP5 prairie/woodland hills</td>
<td>BO-WO-Hi</td>
<td>WO-El-PO</td>
<td>117 72 135</td>
<td>335 292 378</td>
<td>2.87</td>
</tr>
<tr>
<td>TP5 woodland/forest hills</td>
<td>BO-WO-BuO</td>
<td>WO-Hi</td>
<td>169 104 195</td>
<td>334 299 369</td>
<td>1.98</td>
</tr>
<tr>
<td>TP6 prairie plains</td>
<td>BO-WO-Hi</td>
<td>WO-Hi</td>
<td>122 72 144</td>
<td>282 252 312</td>
<td>2.32</td>
</tr>
<tr>
<td>TP6 prairie/woodland dissected plains</td>
<td>BO-WO-Hi</td>
<td>WO-Hi</td>
<td>133 69 173</td>
<td>275 244 306</td>
<td>2.06</td>
</tr>
<tr>
<td>TP7 prairie/woodland dissected plains</td>
<td>BO-WO-Hi</td>
<td>WO-Hi</td>
<td>259 153 314</td>
<td>281 241 321</td>
<td>1.08</td>
</tr>
<tr>
<td>TPB woodland/forest hills</td>
<td>BO-BO</td>
<td>WO-Hi</td>
<td>205 99 282</td>
<td>301 269 332</td>
<td>1.46</td>
</tr>
</tbody>
</table>

$^1$ BO = black oak (Quercus velutina); BuO = bur oak (Quercus macrocarpa); PO = pin oak (Quercus palustris); WO = white oak (Quercus alba); PO = post oak (Quercus stellata); BjO = blackjack oak (Quercus marilandica); Hi = hickories (Carya cordiformis, Carya glabra, Carya laciniosa, Carya ovata, Carya texana, Carya tomentosa); Ma = maples (primarily Acer saccharum, Acer negundo, Acer saccharinum); El = elms (Ulmus alata, Ulmus americana, Ulmus rubra); OO = Osage-orange (Maclura pomifera); M_L = mulberry and locust (Morus rubra, Robinia pseudoacacia, Celtis texana); Ha = hackberry (Celtis occidentalis); Wa = walnuts (juglans nigra, Juglans cinerea)

(Maclura pomifera), mulberry and locusts, maples, hackberry (Celtis occidentalis) and walnuts have become new dominant species (>10% of species composition) in current forests. Elms, maples, Osage-orange, mulberry and locusts, hackberry, and walnuts have replaced black oak and white oak. With the loss of black and white oaks, hickories have become relatively more dominant, but hickories also were displaced as a dominant species in six ecological units.

About 71% of all tree stems were represented by the dominant species of GLO communities but only 43% of all tree stems were represented in FIA communities. In the GLO surveys (DBH $\geq$ 12.7 cm), about 62% of species were oaks, in FIA surveys (DBH $\geq$ 12.7 cm), about 30% of species were oaks, and in FIA surveys for trees <12.7 cm, 13% of species were oak.

3.2. Structure

Historical forest densities averaged about 150 trees ha$^{-1}$ (DBH $\geq$ 12.7 cm), ranging from a mean low of 85 to a mean high of 180 trees ha$^{-1}$ (Table 1, Fig. 3). Current forest densities average about 315 trees ha$^{-1}$ and range from a mean of 280 to 345 trees ha$^{-1}$, about 2 times greater than historical densities on average. Twelve of the 14 ecological units had high historical densities that were lower than the low current densities. Historical tree densities were most similar to current densities only in the northeastern portion of Missouri. Density was significantly different between time intervals ($p = 0.0001$, Wilcoxon signed rank test; Proc Univariate, SAS software, version 9.1, Cary, North Carolina, USA).

Fig. 3. Current density as a fraction of historical density (trees DBH $\geq$ 12.7 cm) in the Missouri Plains.
Basal area historically averaged 18.7 m² ha⁻¹ (8.1 to 31.9 m² ha⁻¹), but has since decreased to an average of 16.3 m² ha⁻¹ (14.8 to 17.9 m² ha⁻¹) in current forests of the Osage and Till Plains sections (Table 2). Despite greater tree densities in current forests, average basal area is lower today because tree diameters are smaller than in the GLO surveys. However, spatial changes in basal area were distinctive, with overall decreases along riparian networks (e.g., the Missouri River along subsection TP3 and the Mississippi River along subsections TP7 and 8; Fig. 2) and increases generally in historically less forested areas, including the Osage Plains (Figs. 1 and 4). Due to spatial conflicts in change, basal area was not significantly different between time intervals (based on the Wilcoxon signed rank test).

Similarly to basal area, average stocking has remained relatively stable from the GLO (54%) to the FIA (55%) surveys. Average stocking among the ecological units was more varied (24 to 93%) in the historical survey than it is today (43 to 67%). Although trees today are smaller in diameter they occur in more dense forests than previously and this has resulted in similar levels of stocking of trees ≥ 12.7 cm DBH. Also similar to basal area, decreases occurred along riparian networks and increases occurred in most upland areas. Due to spatial conflicts in change, stocking was not significantly different between time intervals (based on the Wilcoxon signed rank test).

4. Discussion

4.1. Compositional changes

Current community composition is substantially different than it was in the early to mid-19th century, probably related to fire suppression and land use. Fire-tolerant oaks decreased from historical widespread dominance after fire suppression permitted fire-sensitive species to grow in woodland and forest understories (Pallardy et al., 1988; Westin, 1992; Stambaugh et al., 2006). Black and/or white oaks historically were dominant across 93% of the landscape while these species currently were dominant across 42% of the landscape, based on the area of ecological units where the species were dominant. The greatest changes in composition have been the loss of black oak species as a dominant species, dominance of white oak currently limited to forests on the more topographically dissected areas that are less suited to agriculture, and decline of minor oak species such as bur oak and blackjack oak. White oak is more shade-tolerant than black oak species and has been able to persist somewhat better under the changing disturbance regimes, maintaining its dominance primarily in woodland and forest hills ecological units (see Table 1). White oaks can be long-lived, i.e., dominant mature oaks today established 100 years ago or longer when fire was still part of the disturbance regime. Thus, there is uncertainty in this era of fire suppression whether white oak can be sustained at present stocking levels into the future under current management and disturbance regimes.

Oak forested ecosystems were cleared for agriculture, and subsequently a percentage was abandoned to old field succession because of declining crop production after severe soil erosion, drought, or poor farming practices (e.g., Bazzaz, 1968). When farm fields and pastures were abandoned in the plains, they were reforested by fire-sensitive and colonizing elms, maples, Osage-orange, mulberry, locusts, hackberry, and walnuts, which have doubled in compositional dominance since the mid-1800s (Hanberry et al., 2014, Table 1). These pioneer species have multiple adaptations that promote their establishment in abandoned fields. Osage-oranges, mulberry, locusts and walnuts are shade-intolerant, grow vigorously in open conditions, produce seed at early ages, and seed dispersal is aided by animals (Burns and Honkala, 1990). These species are well-suited to colonize overgrazed pastures with eroded soils that are abandoned after agricultural use. They are common in fencerows and along field borders, which facilitated the delivery of seed to recently abandoned fields, and the establishment of seedlings in advance of pasture abandonment. Osage-orange was planted widely near agricultural fields to produce fence posts, which facilitated the spread of its seed. Hackberry, elms, and maples tend to develop under established trees. These species produce good seed crops nearly yearly starting from a relatively early age and have seed that is wind-borne or disseminated by animals.

4.2. Structural changes

The study area lies within the historical eastern tallgrass prairie—broadleaf forest transition area described by Transeau (1935), where fire, modified by topography, soils and human population, determined vegetation structure, composition and distribution of prairies, savannas, woodlands and forests (Anderson, 1983; Stambaugh and Guyette, 2008). Schroeder (1981) estimated that prairies covered from 50% to 80% of the land area for most counties in the study area based on analysis of GLO survey data; however, surveyors were able to record trees at densities that indicated open forested ecosystems throughout most of the Missouri Plains (Fig. 1). We estimated overall historical mean basal area (for trees ≥ 12.7 cm DBH) to be greater than the thresholds commonly used to define savannas (e.g., < 7 m² ha⁻¹; MTNF, 2005). Nonetheless, the low values of historical basal area were within the range typical of savanna structure, whereas the greater values were

Table 2

Mean diameter, basal area, and stocking of historical (GLO) and current (FA) forests by ecological unit (subsection and land type). Diameter at breast height (DBH) is in cm, basal area (BA) is m² ha⁻¹ and stocking (Stock) is in percent.
representative of denser floodplain forests. For example, Dollar et al. (1992) inventoried floodplain forests in northern Missouri and reported an average density of 27 m² ha⁻¹ in basal area with some stands achieving 85 m² ha⁻¹ for trees >6.6 cm DBH.

Because of the variation intrinsic to historical landscapes, mean structural values for the entire ecological section or for an ecological unit were not very representative compared to the range of values. Firebreaks provided by stream networks and wetlands helped determine tree presence, structure, and composition in the plains (see Fig. 1) and riparian forests contained denser forests with a greater composition of fire-sensitive species. Therefore, dense forests of riparian or near-riparian species probably occurred alongside closed oak woodlands, which likewise graded into open woodlands, savannas, and prairies within most ecological units. Many of the small streams and wetlands have been filled or drained, so that some of the historical features that influenced forest composition and structure disappeared.

Historically, there was greater variability in the range of average structural values among ecological units than during the current period. Gradients in topography, water and rock firebreaks, and soils influenced fire return intervals, which in turn produced great variation in forest structure (Schroeder, 1981; Anderson, 1983). Even though overall current basal area and stocking were similar to historical structure because increases in tree density have offset reductions in tree diameters, historical basal area and stocking varied with environmental gradients. Therefore, basal area and stocking decreased compared to historical values along the Missouri and Mississippi rivers and major tributaries and basal area and stocking increased compared to historical values in subsections where the historical fire regime removed trees (Fig. 4).

Fig. 4. Current basal area (a) and stocking (b) as a fraction of historical basal area and stocking (trees DBH ≥ 12.7 cm) in the Missouri Plains (all subsections and landforms with current data included).
Structural estimates would be greater in current forests, which have multiple midstory layers, with inclusion of trees ∼ 12.7 cm in diameter, but in savannas and woodlands, trees in the 2 to 12 cm diameter class would have been largely eliminated and relegated to be sprouts by fires every 6 to 7 years in the Native American period (Stambaugh et al., 2006; Arthur et al., 2012).

Prairie and savanna communities have been eliminated from the landscape either by conversion to agriculture or transition to forests (Nuzzo, 1986). Current forest density was approximately two times greater than historical densities, demonstrating loss of savanna and woodlands and transition to dense forest structure. The typical transition following fire suppression is for prairies to be invaded by trees and for savannas and woodlands to become closed forests over several decades (Cottam, 1949; Grimm, 1984; Heikens and Robertson, 1994). Soils and climate in the prairie peninsula are capable of supporting tree growth and thus, forested ecosystems develop in the absence of fire. Current forest structure in the plains, although similar to values reported by Stambaugh et al. (2006), was lower than values for current fully-stocked mature forests in the state (Pallardy et al., 1988), which indicated that forests may be recovering from cycles of clearing for agriculture followed by agricultural abandonment.

4.3. Ecological considerations

With continued changes in land use, whether fire suppression or changes in land use intensity, non-oak species are expected to continue replacing oaks in the overstory (Abrams, 1998, 2003; Fei and Steiner, 2009). Oak forests are converting primarily to broadleaf forests composed of a variety of species in the eastern United States (Nowacki and Abrams, 2008) and Europe (Humphrey and Swaine, 1997; Niklasson et al., 2002; Svenning, 2002; Hofmeister et al., 2004; Strandberg et al., 2005; von Oheimb and Brunet, 2007; Hédl et al., 2010). Where land use is intensive and trees are removed frequently for agriculture and grazing, as in the Missouri Plains, non-oak species tend to be early-successional species tolerant of exposure, and sometimes planted for fencerows and landscaping purposes. Where land use is for residential and forestry purposes, non-oak species tend to be mid-successional species with greater shade tolerance; red maple in particular has increased in composition in the eastern US (Nowacki and Abrams, 2008; Fei and Steiner, 2009). In both land use scenarios, and even where oaks remain dominant, trees are present at greater densities than historical open oak forested ecosystems.

Foundation species are dominant species that define ecosystems and support biological communities (Dayton, 1972). Open oak-dominated ecosystem covered part of the central eastern United States for thousands of years and provided light and structure to associated herbaceous plants and animals. Herbaceous species present in oak savannas and open woodlands have declined due to decreased available light at the ground from increased tree density (Rogers et al., 2008). A combination of loss of open structure, herbaceous ground story, and light contributes to declines in animals dependent on oak ecosystems (McShea et al., 2007; Lindbladh and Foster, 2010).

Where oak species still remain dominant in forests throughout their worldwide distribution, there are reports of recruitment failure and thus, sustaining or increasing levels of oak stocking is problematic throughout its range (Watt, 1919; Thadami and Ashton, 1995; Li Ma, 2003; Götzmark et al., 2005; Pulido and Díaz, 2005; Zavaleta et al., 2007; Altman et al., 2013). Restoration of open oak ecosystems is an urgent issue because oak recruitment potential declines as forests transition to non-oak species. In healthy mature oak forests, acorn production is periodically sufficient to establish a population of oak seedlings in the understory. Sustaining oak stocking then currently is more of a problem of recruitment of oak advance reproduction into the overstory; recruitment often is limited due to weak competitiveness in heavily shaded understories (Franklin et al., 2003; Alexander et al., 2008; Iverson et al., 2008a; Holzmueller et al., 2011).

Identification of sites that have the greatest potential for restoration is important to efficiently use limited budget and staff resources. Priority sites should contain an oak overstory with the potential to establish oak advance regeneration, or pine forests that are converting to oak; across the Missouri Plains landscape, the ecological units that still contain dominant white oak and post oak should be targeted for restoration. In addition, not all sites have the same potential for restoration due to different disturbance and land use histories, degree of soil erosion, problems with invasive species and other factors that limit the potential or complicate the ability to achieve quality ecosystems inexpensively. For example, regenerating and sustaining oaks on xeric sites is easier than more productive sites, which may have more intact native ground flora than mesic sites that were converted to agricultural use. If restoring woodlands and savannas is the goal, then an assessment of the potential to recover ground flora diversity can aid in site selection. Size of restoration project area, its connectivity to other restoration properties, and landscape objectives for restored natural communities should be considered. Restoration is expensive and often involves treating vegetation that does not produce any marketable commodities, and hence, revenues. Agency and landowner budgets are limited, as are government cost-share and tax incentive programs.

4.4. Management approaches

Combinations of prescribed burning and timber harvesting or stand thinning are proving promising for oak restoration in the eastern United States (Brose et al., 1999; Franklin et al., 2003; Alexander et al., 2008; Hutchinson et al., 2008; Povak et al., 2008). Single prescribed fire effects on hardwood regeneration can persist for up to 10 years especially when the fire is medium to high intensity and done in the early spring when the leaves of competitors are just expanding and oaks are still dormant (Brose, 2010). Additional reductions in stand density may be needed to maintain sufficient light for oak seedling growth. However, reducing stand density to encourage oak sprouts and saplings also promotes non-oak species and necessitates their control. A series of prescribed fires is effective in controlling small diameter (< 15 cm DBH) competitors that are less tolerant of burns than oaks, which allocate resources to underground reserves for continued re-sprouting (Brose et al., 2013).

Oak reproduction establishment and development to competitive status is a process that may require 10 to 30 years (Arthur et al., 1998; Iverson et al., 2008a; Waldrop et al., 2008; Holzmueller et al., 2011; Brose et al., 2013). It takes years for small oak seedlings to build competitive root systems and high overstory density and shade prolongs the development of root mass (Brose, 2008). One set of disturbances (e.g., thinning followed by two prescribed burns, or several prescribed fires followed by group selection harvesting) may be enough to improve oak regeneration potential and dominance, but probably will not be enough to ensure oak recruitment into the overstory in the long-term or to achieve savanna or woodland structural reference conditions in the short-term (Waldrop et al., 2008; Hutchinson et al., 2012). Open oak forests developed from disturbances repeated over hundreds or thousands of years that produced a predominantly oak matrix, unlike current forests which provide a steady supply of non-oak propagules. Thus, long-term commitments to active management will be needed to restore and sustain oak savannas, woodlands and forests within an increasingly non-oak matrix. The time required to plan and manage the oak regeneration process is challenging due to changing staff, brief land ownership tenure, vacillating agency directives, and uncertain budgets.

Integration of prescribed fire with other traditional silvicultural methods to regenerate oak, to sustain oak stocking at maturity, or to restore savanna/woodland structure is a relatively new endeavor. Multiple types of treatments can be arranged in any number of various sequences and timings. Vegetation responses may differ in various silvicultural systems across a diversity of ecological units throughout the
eastern United States. Therefore, monitoring and research projects to assess treatment effectiveness should be designed using an ecological framework (Dey et al., 2009) and used to inform adaptive management after assessing the success of oak regeneration and development, or achievement of natural community desired future conditions (Yaussey et al., 2008). Meta-analyses such as Brose et al. (2013) are invaluable for understanding what appears to be confusing or inconsistent results from prescribed fire and regeneration experiments.

5. Conclusions

Similar to the fate of oak throughout the world, composition of oaks has decreased substantially in the Missouri Plains since the mid-1800s. Black and white oak historically were dominant across 93% of the landscape while these species currently were dominant across 42% of the landscape. The decline of oak dominance was accompanied by loss of open ecosystems either through conversion to agriculture or transition to closed, dense forests, similarly to other regions. The former landscape contained a continuum of prairie, savanna, woodland, and forest. In contrast, the current landscape contains agricultural crops, tall fescue pastures, or dense forests, generally the size of small woodlots and sometimes in the form of field rows.

Our research has provided much needed quantitative metrics describing historical composition and structure in a spatially explicit way within an ecological framework. These findings provide quantitative targets that may help managers define the desired future conditions in restoration. By comparison to current forest inventories, we have been able to demonstrate change in composition and structure over a large extent and location of changes in composition and structure helps to determine the amount of deviation from historical conditions, which may be used to identify priority areas for restoration, set restoration targets, design restoration prescriptions, and assess costs.

Loss of oak is expected to continue under current management practices and trends in land use, even though species distribution projections of climate change scenarios indicate that oak will be favored over its competitors (McKenney et al., 2007; Iverson et al., 2008b). The fate of oak and presence of diverse natural communities across the landscape are dependent largely upon human action at local scales and public policy and cooperation at landscape and regional scales, a daunting task given that most of the land is privately owned. However, active, purposeful management is needed to reverse the densification process that contributed to the loss of savannas and woodlands, and that continues to favor the replacement of oak by fire-sensitive species. The unfavorable economics of restoration currently limits efforts. Innovative silvicultural prescriptions are being developed in the eastern United States that combine fire with other practices to sustain oak in forested settings, or that regulate woody structure and favor ground flora typical of savannas and woodlands. The key to successful restoration of oak ecosystems will include the social adoption of needed silvicultural prescriptions, development of new markets that are able to use currently unmerchantable biomass, and identification of priority areas for restoration that collectively meet landscape and regional conservation goals. Land in the six ecological units that contain dominant white or post oak probably will require the fewest resources to restore. The Missouri Plains is a landscape critical for agricultural production in the midwestern United States. However, regional planning and land use policies that provide for restoration of natural communities and sustaining oak on the landscape are needed.

Conflict of interest

The authors have approved the final article and have no conflicts of interest. Funding was provided by the National Fire Plan of the USDA Forest Service, Northern Research Station; however, the work was completed without any contact with the sponsoring agency. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix A. Area and number of trees by ecological unit of ecological subsection and land type

<table>
<thead>
<tr>
<th>Ecological unit</th>
<th>Area (ha)</th>
<th>GLO tree count</th>
<th>FA tree count</th>
</tr>
</thead>
<tbody>
<tr>
<td>OP1 prairie plains</td>
<td>350,589</td>
<td>1288</td>
<td>550</td>
</tr>
<tr>
<td>OP1 prairie/savanna dissected plains</td>
<td>552,413</td>
<td>5445</td>
<td>950</td>
</tr>
<tr>
<td>OP2 prairie/savanna dissected plains</td>
<td>209,007</td>
<td>2416</td>
<td>487</td>
</tr>
<tr>
<td>TP1 prairie plains</td>
<td>245,013</td>
<td>1408</td>
<td>221</td>
</tr>
<tr>
<td>TP3 woodland/forest breaks</td>
<td>272,700</td>
<td>8026</td>
<td>453</td>
</tr>
<tr>
<td>TP4 prairie plains</td>
<td>248,941</td>
<td>893</td>
<td>226</td>
</tr>
<tr>
<td>TP4 prairie/woodland hills</td>
<td>880,173</td>
<td>11,996</td>
<td>973</td>
</tr>
<tr>
<td>TP4 woodland/forest hills</td>
<td>265,485</td>
<td>7958</td>
<td>317</td>
</tr>
<tr>
<td>TP5 prairie/hills</td>
<td>227,054</td>
<td>4438</td>
<td>337</td>
</tr>
<tr>
<td>TP5 woodland/forest hills</td>
<td>403,417</td>
<td>11,211</td>
<td>959</td>
</tr>
<tr>
<td>TP6 prairie plains</td>
<td>908,629</td>
<td>8892</td>
<td>1135</td>
</tr>
<tr>
<td>TP6 prairie/woodland dissected plains</td>
<td>133,780</td>
<td>3905</td>
<td>247</td>
</tr>
<tr>
<td>TP7 prairie/woodland dissected plains</td>
<td>277,134</td>
<td>6634</td>
<td>576</td>
</tr>
<tr>
<td>TP8 woodland/forest hills</td>
<td>508,817</td>
<td>13,456</td>
<td>1426</td>
</tr>
</tbody>
</table>

Appendix B. Communities and densities for historical forests by ecological unit (subsection and land type) where there were <200 trees for current forests

<table>
<thead>
<tr>
<th>Ecological unit</th>
<th>Density</th>
<th>Low</th>
<th>High</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>TP1 alluvial plains</td>
<td>122</td>
<td>68</td>
<td>153</td>
<td>BO-HI-El</td>
</tr>
<tr>
<td>TP2 alluvial plains</td>
<td>138</td>
<td>83</td>
<td>164</td>
<td>HI-El-BuO-PiO</td>
</tr>
<tr>
<td>TP2 prairie plains</td>
<td>99</td>
<td>59</td>
<td>119</td>
<td>BO-HI-PO-BJo</td>
</tr>
<tr>
<td>TP3 prairie plains</td>
<td>214</td>
<td>119</td>
<td>269</td>
<td>El-C_W</td>
</tr>
<tr>
<td>TP3 prairie plains</td>
<td>62</td>
<td>35</td>
<td>76</td>
<td>BO-HI-El-BuO</td>
</tr>
<tr>
<td>TP3 alluvial plains</td>
<td>328</td>
<td>185</td>
<td>402</td>
<td>El-C_W-Ma</td>
</tr>
<tr>
<td>TP4 alluvial plains</td>
<td>84</td>
<td>49</td>
<td>102</td>
<td>BO-HI-El-BuO</td>
</tr>
<tr>
<td>TP4 prairie plains</td>
<td>193</td>
<td>121</td>
<td>219</td>
<td>BO-WO-El</td>
</tr>
<tr>
<td>TP4 alluvial plains</td>
<td>209</td>
<td>120</td>
<td>254</td>
<td>HI-El-BuO-PiO</td>
</tr>
<tr>
<td>TP4 low prairie plains</td>
<td>133</td>
<td>70</td>
<td>173</td>
<td>BO-WO-HI-BuO-PiO</td>
</tr>
<tr>
<td>TP5 alluvial plains</td>
<td>154</td>
<td>76</td>
<td>207</td>
<td>BO-HI-El-PiO</td>
</tr>
<tr>
<td>TP7 prairie plains</td>
<td>130</td>
<td>77</td>
<td>155</td>
<td>BO-WO-HI-El-BuO-PiO</td>
</tr>
<tr>
<td>TP8 prairie/woodland hills</td>
<td>200</td>
<td>116</td>
<td>241</td>
<td>BO-WO-PiO</td>
</tr>
<tr>
<td>TP9 alluvial plains</td>
<td>221</td>
<td>113</td>
<td>293</td>
<td>BO-Ei-Ma</td>
</tr>
</tbody>
</table>

BO = black oak (Quercus velutina); BuO = bur oak (Quercus macrocarpa); PiO = pin oak (Quercus palustris); WO = white oak (Quercus alba); PO = post oak (Quercus stellata); HI = hickories (Carya cordiformis, Carya glabra, Carya laciniosa), Carya ovata, Carya texana, Carya tomentosa); Ma = maples (Acer saccharum, Acer negundo, Acer saccharinum); El = elms (Ulmus alata, Ulmus americana, Ulmus rubra); PiO = pin oak (Quercus palustris); WO = white oak (Quercus alba); PO = post oak (Quercus stellata); HI = hickories (Carya cordiformis, Carya glabra, Carya laciniosa), Carya ovata, Carya texana, Carya tomentosa); Ma = maples (Acer saccharum, Acer negundo, Acer saccharinum); El = elms (Ulmus alata, Ulmus americana, Ulmus rubra); and C_W = cottonwood and willow (Populus spp., Salix spp.).

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