ARTICLE IN PRESS

Forest Ecology and Management xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

How can prescribed burning and harvesting restore shortleaf pine-oak woodland at the landscape scale in central United States? Modeling joint effects of harvest and fire regimes

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ARTICLE INFO

Keywords:
Pinus echinata
Quercus
Woodland
Ecological restoration
Modeling
Landscape scale
LANDIS PRO

ABSTRACT

Historical fire regimes in the central United States maintained open-canopy shortleaf pine-oak woodlands on xeric sites. Following large-scale harvest and fire suppression, those woodlands grew denser with more continuous canopy cover, and they gained mesic species at the expense of shortleaf pine. There is high interest in restoring shortleaf pine-oak woodlands; most have been converted to other forest types but those that remain are valued for high stand-scale and landscape-scale diversity. Prior stand-scale studies suggest that prescribed burning and harvesting could be effective for restoring pine-oak woodlands. However, previous short-term, stand-scale studies provided little insight into long-term, landscape-scale outcomes. To estimate outcomes of alternative restoration treatments on future species composition and forest structure, we employed an integrated field and modeling approach to simulate effects of prescribed burning and harvesting on the restoration of shortleaf pine-oak woodland composition and structure in the Mark Twain National Forest for a 100-year period. Six scenarios were modeled: no management, burn only, harvest only, and a combination of harvest with burns treatments followed by fire-free intervals of differing starting times or durations to facilitate regeneration recruitment. Both no management and prescribed burn only scenarios cannot restore current forest to historical woodland condition (i.e., 40–80% percent canopy cover or less than 55% stocking); however, scenarios including harvest can restore current forest to woodland condition in late 2020s. Under a no management scenario, total basal area would increase to a maximum around 31 $m^2 ha^{-1}$, and white oak group remained the most dominant species group throughout the simulation. Under the burn only treatment, total basal area was not reduced substantially as compared to that under no management scenario, however, there were small increases in the basal area and density of shortleaf pine. All of the treatments that included a combination of burning and harvesting reduced total basal area, which fluctuated around 13 $m^2 ha^{-1}$ throughout the simulation than those under no management and prescribed only scenarios. The simulations suggested that shortleaf pine would become the most dominant group, followed by white, red oak groups, and other species with combined prescribed burning and harvesting. When coupled with harvest, the prescribed burning regime affected species composition: increasing the number of burns increased the basal area and density of shortleaf pine and decreased the basal area and density of white oak group species.

1. Introduction

Historical fire regimes in xeric region of the central U.S. Central Hardwood Forest were characterized by low-severity yet frequent ground fires and periodic intense crown fires (Dey and Hartman, 2005; Stambaugh and Guyette, 2006). This disturbance regime led to subregions that were historically dominated by fire-resistant shortleaf pine (*Pinus echinata* Mill.), where they grew in pure stands and with other hardwood species such as oaks (*Quercus* spp.) (Nowacki and Abrams, 2008; Hanberry et al., 2012). By limiting successful establishment of fire-sensitive species as well as many pine and oak seedlings, the historical fire regime maintained the widespread pine-oak woodland dominated by large trees without a continuous canopy (Fralish and McArdle, 2009). Pine-oak woodlands serve as critical habitat for several

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http://dx.doi.org/10.1016/j.foreco.2017.07.040
Received 28 April 2017; Received in revised form 13 July 2017; Accepted 24 July 2017
0378-1127/

threatened species, e.g., the federally listed endangered red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot) (Hedrick et al., 2007).

Past harvest practices and large-scale fire suppression resulted in substantial changes in forest composition and structure in pine-oak woodlands in the central U.S. and most notably in the Ozark Highlands. From 1880s to 1920s, shortleaf pine was exploitatively harvested, which caused loss of mature trees and reduced seed sources (Olson and Olson, 2016). Effective, regional fire suppression starting in the 1940s, favored regeneration of tree species that are more shade-tolerant and fire-sensitive than shortleaf pine, (e.g., red maple, *Acer rubrum* L.), resulting in loss of pine and pine-oak woodlands (Hanberry et al., 2014). Some of the current forests in the central U.S. either have an understory dominated by fire-sensitive species, or have already transitioned to more mesic forests dominated by species which were not historically competitive (Fralish and McArdle, 2009). In the Missouri Ozark Highlands, the shortleaf pine forest has been reduced by 90% relative to its former extent, and frequently has been replaced by closed-canopy oak forests that are marginally suited to the xeric sites formerly occupied by pine. In addition to forest composition changes, there are also changes in forest structure. One of the most significant changes is forest densification, which refers to the phenomenon of increases in the density, basal area, stocking level, or canopy cover of trees (Hanberry et al., 2014). Thus, historical dominance of shortleaf pine in the central U.S. decreased, and pine-oak woodland has shrunk in acreages. Not only may such forest regime shift disrupt historical forest community relationship, but also alter long-established environment-species interactions (Amatangelo et al., 2011).

There is growing interest in restoration of pine-oak woodlands given their ecological significance and capacity to mitigate oak decline (Blizzard et al., 2007; Clabo et al., 2016). In 2009, the Collaborative Forest Landscape Restoration Program (CFLRP) was established to encourage collaborative, science-based ecosystem restoration on or around national forests lands in the United States (USDA, 2016). Within the CFLRP, the Missouri Pine-Oak Woodlands Restoration Project was established to restore pine-oak woodland on a portion of the Mark Twain National Forest in the Missouri Ozarks subregion of the Central Hardwood Forest. Goals of this project include reestablishment of landscape dominated by fire-adapted pine-oak woodlands with structure, composition and function similar to those of remnant pine-oak communities at landscape scale (USDA, 2016).

Past restoration studies employing prescribed burning and harvesting have yielded early success in restoring pine-oak woodlands (e.g., Olson and Olson, 2016; Rimer, 2004; Tuttle and Houf, 2007b). However, prescribed burning alone has had limited effect in changing forest composition or structure. For instance, during a 14-year field experiment, a few prescribed burns (without other treatments such as harvest) were not effective in increasing number of shortleaf pine seedlings or saplings, nor did they create an open-canopy woodland condition (Olson and Olson, 2016). Harvest has been suggested as necessary to substantially reduce basal area and canopy cover, create a characteristic woodland stand structure, and to establish and recruit shortleaf pine by reducing competition from hardwood species and increasing light intensity in the understory (Elliott and Vose, 2005; Olson and Olson, 2016). Prescribed burning and harvesting in combination are more effective in changing species composition (shortleaf pine was more favored) of pine-oak woodland than prescribed burn alone (e.g., Olson and Olson, 2016). However, few studies have examined the effects of different fire regimes, combined with harvest, on changes in species composition. Since shortleaf pine is more fire-resistant than oak species in the Ozarks, it is expected that frequent prescribed burning with harvesting would favor shortleaf pine over oaks. However, it is unknown how alternative fire and harvest regimes in combination might affect the future species composition and stand structure for stands and landscapes where restoration of oak-pine woodlands is desired.

Because most field-based restoration studies have been carried out at relatively small spatial (typically for stands) and temporal (typically a few years to less than 2 decades) scales, the results of which are only beginning to shed light on anticipated long-term changes in composition and structure at the landscape scale. Thus, in this study we employed an integrated field and modeling approach to answer the question: How can prescribed burn and harvest help restore shortleaf pine-oak woodlands on Missouri Ozark landscapes in the next 100 years? Specifically, we addressed the following questions: (1) Can frequent prescribed burn that mimics historic fire regime over long-term restore pine-oak woodland? (2) Is harvest necessary in restoration of pine-oak woodland? (3) Do different prescribe fire regimes in combination with harvesting result in landscapes with different compositions of shortleaf pine and oaks?

2. Materials and methods

2.1. Study area

The study area was jointly identified by several federal and state agencies, as well as conservation groups as a priority area for pine-oak woodland restoration. It contains the highest known concentration of restorable pine-oak woodlands, and known occurrences of species of conservation concern (Mark Twain National Forest, 2011). The study area covers 31,000 ha in Mark Twain National Forest in southern Missouri between 36.76° and 37.05 °N, and 90.51° and 91.39 °W. It has been allocated into 120 prescribed burn units with an average size of

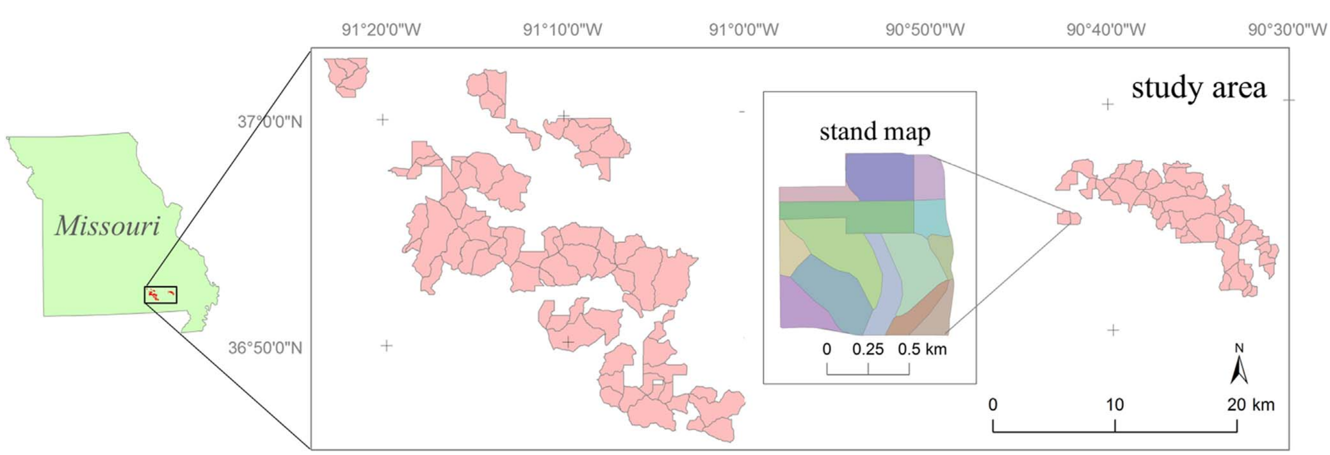

Fig. 1. Location of study area in southeastern Missouri, United States. The study area consists of 120 prescribed burn units (pink polygons), and each prescribed burn unit is divided into multiple forest stands (shown here with an example). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

258 ha each (ranging from 42 to 1144 ha) (Fig. 1). Most of the study area lies in a moderately dissected upland plain associated with the Roubidoux Formation, and average relief is less than 30 m. Soils are generally loamy to sandy and low in soluble bases such as calcium (Nigh and Schroeder, 2002). Climate is humid continental with long hot summers and cool winters. Mean annual temperature is around 13 °C, and mean annual precipitation is around 1115 mm (Brandt et al., 2014). Historically, fire was an important disturbance to maintain open pine-oak woodlands in the study area, however, understory vegetation has become more dense than the historic conditions (Nigh and Schroeder, 2002; Guyette and Dey, 1997). At landscape scale, current average basal area is approximately 11 m^2 ha^{-1}; average tree density is approximately 924 trees ha^{-1}, and average biomass density is approximately 65 Mg ha^{-1}. Common tree species belong to four major species groups: (1) pine: shortleaf pine (*Pinus echinata* Mill.); (2) white oak groups: white oak (*Quercus alba* L.), and post oak (*Q. stellata* Wangenh.); (3) red oak groups: black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), and northern red oak (*Q. rubra* L.); (4) others: sugar maple (*Acer saccharum* Marshall), red maple (*A. rubrum* L.), mockernut hickory (*Carya tomentosa* Sarg.), eastern red cedar (*Juniperus virginiana* L.), and black cherry (*Prunus serotina* Ehrh.).

2.2. Current and planned restoration management

Personnel of the Mark Twain National Forest have been using prescribed burning and harvesting to restore pine-oak woodland in the study area (Mark Twain National Forest, 2011). Currently, the prescribed burns occur on rotation of 3–5 years, emulating the mean historic (1701–1900) fire return intervals between 3.1 and 6.3 years (Guyette and Dey, 1997). Ground crews can generally burn smaller units within one day; helicopter ignition usually is employed for larger units or multiple adjacent units with the burn completed in one to three days (Mark Twain National Forest, 2011). In addition to the current frequent burn regime, there are also long-term plans to elongate the fire-free intervals to approximately 20 years to allow the next generation of overstory trees to become established and grow large enough to survive subsequent fires. Harvest is largely regulated by basal area, when stands reach an upper threshold of approximately 16 m^2 ha^{-1} they are thinned to a lower threshold of approximately 7 m^2 ha^{-1}. Thinning-from-below is utilized to keep larger trees on the landscape. Harvesting favors retention of long-lived shortleaf pines and white oaks. The priority order for species to harvest is the "other" group, the red oak group, the white oak group, and shortleaf pine. During fiscal years 2011–2015, harvest was projected to yield approximately 12,500 m^3 of sawtimber and approximately 260,000 metric tons of biomass (Mark Twain National Forest, 2011). The harvest rotation interval is approximately 15 years.

2.3. LANDIS PRO model and parameterization

As a spatially explicit forest landscape model, LANDIS PRO can operate at large spatial scales (10^6–10^8 ha) and long temporal scales (10^2–10^3 years). LANDIS PRO divides landscape into a grid system of cells with user-defined spatial resolutions (ranging from 30 to 500 m). This model can simultaneously simulate individual-species demography (birth, growth, and mortality), stand dynamics within each cell (e.g., competition due to different levels of shade tolerance among species), and landscape processes (e.g., seed dispersal and fire spread) across the landscape (Wang et al., 2014a; Fraser et al., 2013). Within each cell, LANDIS PRO tracks density and age for each species age cohort within each cell. Initial density and age of trees are derived from forest inventory data, and diameter at breast height (dbh) for each age cohort is subsequently updated according to prescribed age-dbh relationships, which can vary by land types (Wang et al., 2014a). Simulations were initialized using Landscape Builder (Dijak, 2013) based on 1187 plots from stand plot data, which were collected in the early 2010s, located in and around the study area. The landscape was modeled at a 90 × 90 m cell size. Eleven most common tree species in four species groups were included (see Section 2.1. for complete name list). Parameterizations of forest growth and succession followed those of Wang et al. (2016) and Wang et al. (2015).

LANDIS PRO is an effective tool to study long-term simultaneous effects of different types of disturbances (e.g., harvest, fire) at landscape scale. The harvest module of LANDIS PRO can readily simulate harvest removals that are regulated by residual stand basal area, residual stocking percent, or proportion of the stand treated (in the case of group selection harvest). For basal area regulation users specify the threshold stand basal area necessary to initiate a harvest and a target residual basal area for each stand. When the basal area of a stand reaches the threshold necessary for harvest, the harvest algorithm removes trees until reaching the residual target. Harvest can be done by species group in ascending or descending order of tree size (Fraser et al., 2013). Parameterization of harvest practices followed those of Fraser et al. (2013). The LANDIS PRO fuel module simulates common fuel treatment practices including prescribed burning, coarse fuel load reduction, or both by tracking changes in fine and coarse fuel loads. For modeled prescribed burns, users can specify how fine and coarse fuel loads change after each burn as well as the burning frequency. In LANDIS PRO, the effect of prescribed burn is equivalent to that of a surface fire, and the probability of tree mortality is related to both dbh and species-specific fire tolerance classes (He et al., 2004; He and Mladenoff, 1999). Fuel loading reductions were parameterized from field studies in the Missouri Ozarks (Ghilardi, 2016) (Table 1). Mortality rates due to prescribed burn were adapted from He et al. (2012), He et al. (2011). Such rates are assigned for each of five fire tolerance classes, and they are a function of tree diameter at breast height.

2.4. Model calibration and validation

Much of model calibration and validation has been done in previous studies; readers can refer to specific studies for further details. For calibration and validation of forest growth/succession, we used Forest Inventory and Analysis (FIA) data, which is the national forest inventory dataset in the United States (USDA, 2011). In order to utilize FIA data for both calibration and validation, we used a data splitting approach: 50% of the FIA plots from the 1980s to 2010s were used for model calibration, and the other 50% of the FIA plots were used for short-term model validation. Specifically, tree density, basal area, and aboveground carbon density of different species groups were used for calibration and validation. Discrepancies between model predictions and FIA data at the landscape scale were relatively small: both mean error and relative root mean square error were less than 10% (Wang et al., 2014b; Jin et al., 2017). When simulations of clearcut, intermediate release thinning, and fuel reduction thinning at the stand scale

Table 1
Reductions of fine fuel (1-, 10-h fuels and litters) and coarse fuel (100- and 1000-h fuels) due to one-time prescribed burn based on field studies in Ghilardi (2016). Corresponding range of fuel density (kg m^{-2}) for each fuel loading class can be found in Shang et al. (2007).

Fine fuel loading class before prescribed burn	Fuel loading class				
	Low	Medium-low	Medium	Medium-high	High
Fine fuel loading class after prescribed burn	Low	Low	Low	Low	Low
Coarse fuel loading class before prescribed burn	Low	Medium-low	Medium	Medium-high	High
Coarse fuel loading class after prescribed burn	Low	Medium-low	Medium-low	Medium	High

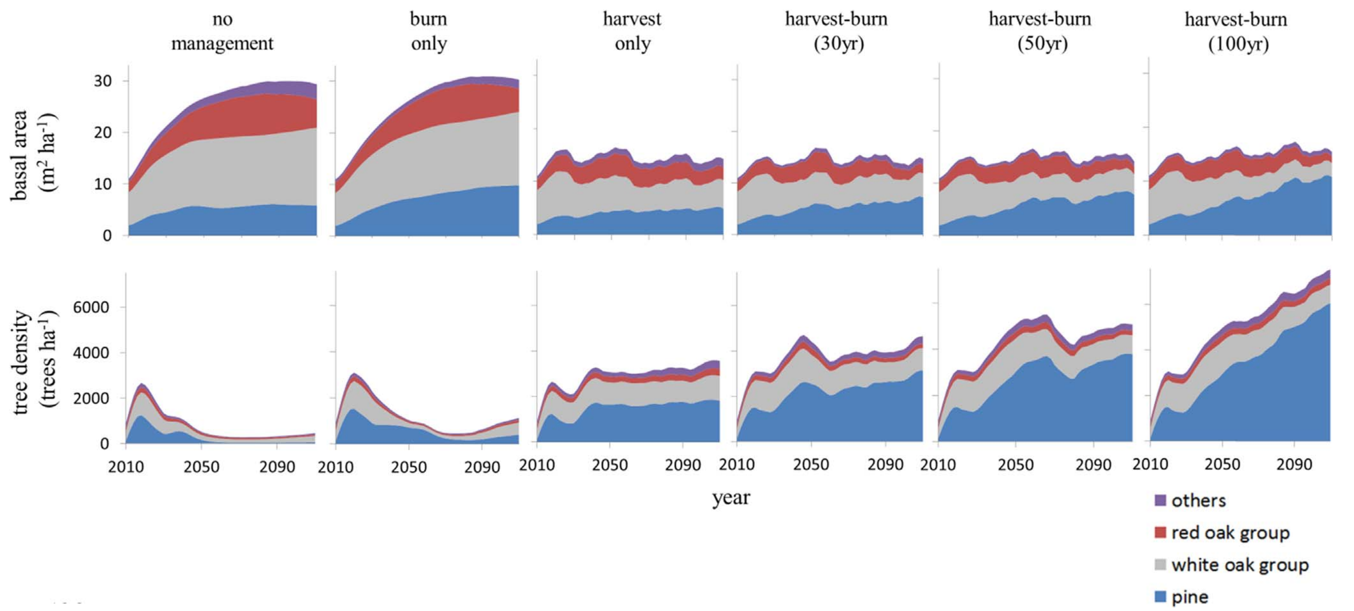

Fig. 2. Landscape-averaged basal area and tree density of four species groups (pine, white oak groups, red oak groups, and others) under six scenarios [no management, burn only, harvest only, harvest-burn (30 yr), harvest-burn (50 yr), harvest-burn (100 yr)] over 100-year simulation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were compared with field studies, changes in basal area, tree density, and quadratic mean diameter were found to be in agreement (Fraser et al., 2013). For validation of mortality rates due to prescribed burning, model predictions of mortality rates of common species in the study area were compared field studies in the Missouri Ozarks (Kinkead, 2013), and model predictions were similar to mortality rates from those of field studies. Specifically, average mortality rates after single burn from model prediction and field studies of trees with diameter at breast height less than 12 cm were 37% and 44%, respectively; and average mortality rates from model predictions and field studies of trees with diameter at breast height greater than 12 cm were 10% and 15%, respectively.

2.5. Design of simulation experiments

Simulation experiments examined a range of harvest and burning treatment alternatives that encompassed current and planned management for the landscape. The six included scenarios are: no management, burn only, harvest only, harvest-burn (30 yr), harvest-burn (50 yr), and harvest-burn (100 yr). All simulations run from 2010 to 2110 under current climate, with a time step of two years. In the *no management* scenario, forest dynamics were solely dependent on forest growth and succession. In the *burn only* scenario, half the study area will be burned in the first two years of simulation; in the next two years the other half will be burned, and so on. Thus, each stand in the study area will be burned every four years throughout the simulation. In the *harvest only scenario*, thinning-from-below is applied to hold basal area between 7 and 16 $m^2 ha^{-1}$. From the beginning of simulation, approximately 1/5 of the total study area will be assessed for harvest every two years with harvesting implemented if basal area exceeds16 $m^2 ha^{-1}$. Harvest priorities were assigned to four species groups in a descending order: others, red oak group, white oak group, and pine. Within a given group, trees with the smallest dbh will be harvested first. Every 16 years, the same harvest area will be evaluated again for harvest using the same criteria mentioned above. In the burn and harvest combination treatments, we examined three different scenarios. In the *burn-harvest* (30 yr) scenario, stands were burned every 4 years for the first 30 years (2010–2040), then each stand will be burned every 20 years to encourage regeneration until the end of the simulation; the harvest regime was the same as in the *harvest only* scenario. In the *burn-harvest* (50 yr) scenario, stands were burned every 4 years for the first 50 years (2010–2060), then stand burned every 20 years until the end of simulation; harvest regime was the same as the *harvest only* scenario. In the *harvest-burn* (100 yr) scenario, stands were burned every 4 years during the 100-year simulation period and harvested using the same basal area thresholds in the *harvest only* scenario. The simulation was conducted five times to identify the probable variation in outcome; however, since the variation was extremely low, we only included results from one simulation.

2.6. Data analysis

Simulated variables included basal area and tree density by four species groups and 10-year age classes. To assess whether each management scenario can restore current forest to historical woodland condition, percent canopy cover was calculated based on simulated basal area and tree density of all four species groups (Rogers, 1982), and compared to the historical percent canopy cover (40–80%) of woodland in the study area (Ladd et al., 2007). Only trees with a dbh larger than 12.7 cm (5 in.) were included for percent canopy cover calculation (Rogers, 1982).

3. Results

3.1. Basal area by species

In the no management scenario, total basal area increased from 11 $m^2 ha^{-1}$ in 2010 to 30 $m^2 ha^{-1}$ around 2080. Basal areas of all 11 species increased from 2010 to 2110 except for eastern red cedar. In terms of percent basal area, at the beginning of simulation, white oak group was the most dominant group, followed by the red oak group, shortleaf pine, and other species; at the end of simulation, the white oak group remained the most dominant, followed by pine, red oak group, and other species. White oak remained the most dominant species throughout the simulation. Basal area of shortleaf pine increased from 2 $m^2 ha^{-1}$ in 2010 to 6 $m^2 ha^{-1}$ in 2110, and percent basal area increased from 18% to 20% (Fig. 2).

In the burn only scenario, total basal area rose steadily from 11 $m^2 ha^{-1}$ in 2010 to 31 $m^2 ha^{-1}$ around 2072. White oak remained the most dominant species throughout the simulation. However, basal area and percent basal area of shortleaf pine were both greater than in the no management scenario throughout the simulation. At the end of the simulation, basal area and percent basal area of shortleaf pine were 10 m^2 ha^{-1} and 32%, respectively (Fig. 2).

In scenarios including harvest [harvest only, harvest-burn (30 yr), harvest-burn (50 yr), and harvest-burn (100 yr)], total basal area fluctuated around 13 m^2 ha^{-1} throughout the simulation due to periodic harvests that maintained stand basal area between 7 and 16 m^2 ha^{-1}. At the end of the simulation, pine was the most dominant group, followed by the white oak group, red oak group, and other species. Longer periods with fire repeated on a 4-year interval resulted in greater shortleaf pine basal area at the end of the simulation: basal area of shortleaf pine increased from 6 m^2 ha^{-1} (harvest only) to 11 m^2 ha^{-1} (harvest with most burn), and the corresponding percent basal area increased from 43% to 71%, respectively. Meanwhile, basal area and percent basal area of white oak group decreased at the end of simulation with more burns: basal area decreased from 5 m^2 ha^{-1} (harvest only) to 2 m^2 ha^{-1} (harvest with most burn), and percent basal area decreased from 34% to 16% (Fig. 2).

3.2. Tree density by species

In both no management and burn only scenarios, tree densities showed similar patterns: tree per ha increased rapidly from 2010 (924 trees ha^{-1}) to a peak around 2020 (2665 and 3094 trees ha^{-1}, respectively). After the peaks, tree densities steadily declined to the lowest point in the entire simulation period around year 2070 (281 and 449 trees ha^{-1}, respectively), and the gradually increased from 2080 to 2110. However, tree density in the burn only scenario was higher than that in the no management scenario throughout the simulation. The increased tree density in the prescribed burn only scenario was principally contributed by increases in the number of shortleaf pines and white oaks (Fig. 2).

In scenarios including harvest (harvest only, and the three harvest-burn combinations), tree densities generally increased throughout the simulations, despite some fluctuations associated with harvest events. With more burning, greater tree densities were predicted at the end of simulation: tree densities increased from 688 tree ha^{-1} (harvest only) to 1134 tree ha^{-1} (burn-harvest scenario). Higher densities of shortleaf pine were also associated with more burns: pine densities increased from 361 tree ha^{-1} (harvest only) to 962 tree ha^{-1} [harvest-burn (100 yr)] at the end of simulation. However, densities of species in the white oak group decreased with more burns: at the end of simulation, densities dropped from 231 tree ha^{-1} (harvest only) to 91 tree ha^{-1} [harvest-burn (100 yr)] (Fig. 2).

3.3. Basal area and tree density by age class

In terms of basal area by age class over time, no management and burn only scenarios shared similar pattern. At the beginning of simulation, the peak of the age-class distribution fell around 30–50 years old, and this peak shifted toward the older age classes during the simulation; at the end of simulation, age peak fell between 130–150 years old. In both scenarios, the rate of regenerations was low. Prescribed burn had little effect on basal areas of older age classes; however, with prescribed burning, there was more shortleaf pine regeneration and less in the white oak group and other species group. Scenarios including harvest (harvest only, and the three harvest-burn combinations) shared a similar pattern: height of age peak was reduced due to harvest, there were more regenerations than those under the no management and burn only scenarios. There was greater shortleaf pines regeneration with more burns throughout the simulations (Fig. 3).

Patterns of tree densities were similar under no management and prescribed burn only scenarios. However, with prescribed burning, there were more young trees (< 30 years) throughout the simulation, and there were more shortleaf pines in both young and adult (> 30 years) age classes (Figs. 4 and 5). In the four scenarios that included harvest, there were substantially more young trees than for scenarios that excluded harvest. With more burning, there were higher numbers of young trees and more shortleaf pines, but fewer white oaks. For trees older than 30 years, total tree density in a given age class did not change markedly for alternative burn regimes, however, there were more shortleaf pines and fewer white oaks with more burns (Figs. 4 and 5).

3.4. Percent canopy cover

Current percent canopy cover over the landscape was 88%. Under both no management and prescribed burn only scenarios, percent canopy cover steadily increased to 100% in early 2030s and remained 100% thereafter throughout the simulation period. This suggested that either no management or prescribed burn only can restore current forest to woodland condition. Under all four scenarios including harvest, percent canopy cover decreased from 88% to 80% (upper limit of historical woodland condition) in late 2020s, after which percent canopy cover remained in the woodland condition (40–80%). Despite different prescribed burn regimes in these four scenarios including harvest, trajectories of percent canopy cover were highly similar (Fig. 6).

4. Discussion

4.1. Can prescribed burning alone restore woodland structure and composition?

This study shows the effects of prescribed burning and harvesting on pine-oak woodland restoration in terms of forest composition and structure at the landscape scale in the Missouri Ozarks. Although the mortality rates due to fire vary among species, the mortality rate generally decreases with increasing stem diameter in a given species (e.g., He et al., 2011; Dey and Hartman, 2005). Since fire-induced mortality occurs largely in trees with small diameters, mortality of overstory trees is not substantially affected by fire, although boles of overstory trees may become fire-scarred. Thus overstory structure (tree density and basal area) in the first 40 years (2010–2050) showed relatively little change under the burn-only scenario compared to those under the no-management scenario (Fig. 3). A field study of longleaf pine ecosystem in southern Georgia, USA also found that periodic prescribed burn of more than 40 years had few effects on the composition and structure of overstory trees (Brockway and Lewis, 1997).

On the other hand, litter accumulation can be a substantial barrier to germination of shortleaf pine seeds. Stambaugh and Muzika (2007) reported that shortleaf pine seedlings can only be found on litter less than 6 cm deep, and most seedlings were limited to litter less than 2.5 cm deep. Fires reduce leaf litter, so germination of shortleaf pine seeds is negatively related to the length of time since last fire (Ferguson, 1958). In the Ozarks, forest litter accumulates to an equilibrium maximum in approximately 12 years after last fire (Stambaugh et al., 2006), and it is not uncommon for current Ozarks shortleaf pine communities to accumulate litter due to decades of fire suppression to such depth that shortleaf pine regeneration is largely precluded (Stambaugh et al., 2007). Prescribed burning reduces forest litter depth, thus germination of shortleaf pine seeds can be facilitated. In addition to establishment of seedlings, shortleaf pine is known to resprout after topkill, but sprouting ability declines with increasing tree size.

Shortleaf pine has relatively thick bark, and is more fire-resistant than other tree species in the study area. Thus, after 60 years of periodic prescribed burning the proportion of shortleaf pines increased in the midstory due to its lower rate of fire-induced mortality rate (Figs. 3 and 5). Although few shortleaf pine sites have been periodically burned for more than 50 years to evaluate long-term prescribed burning impacts on shortleaf pine dynamics, historic records dating back to pre-

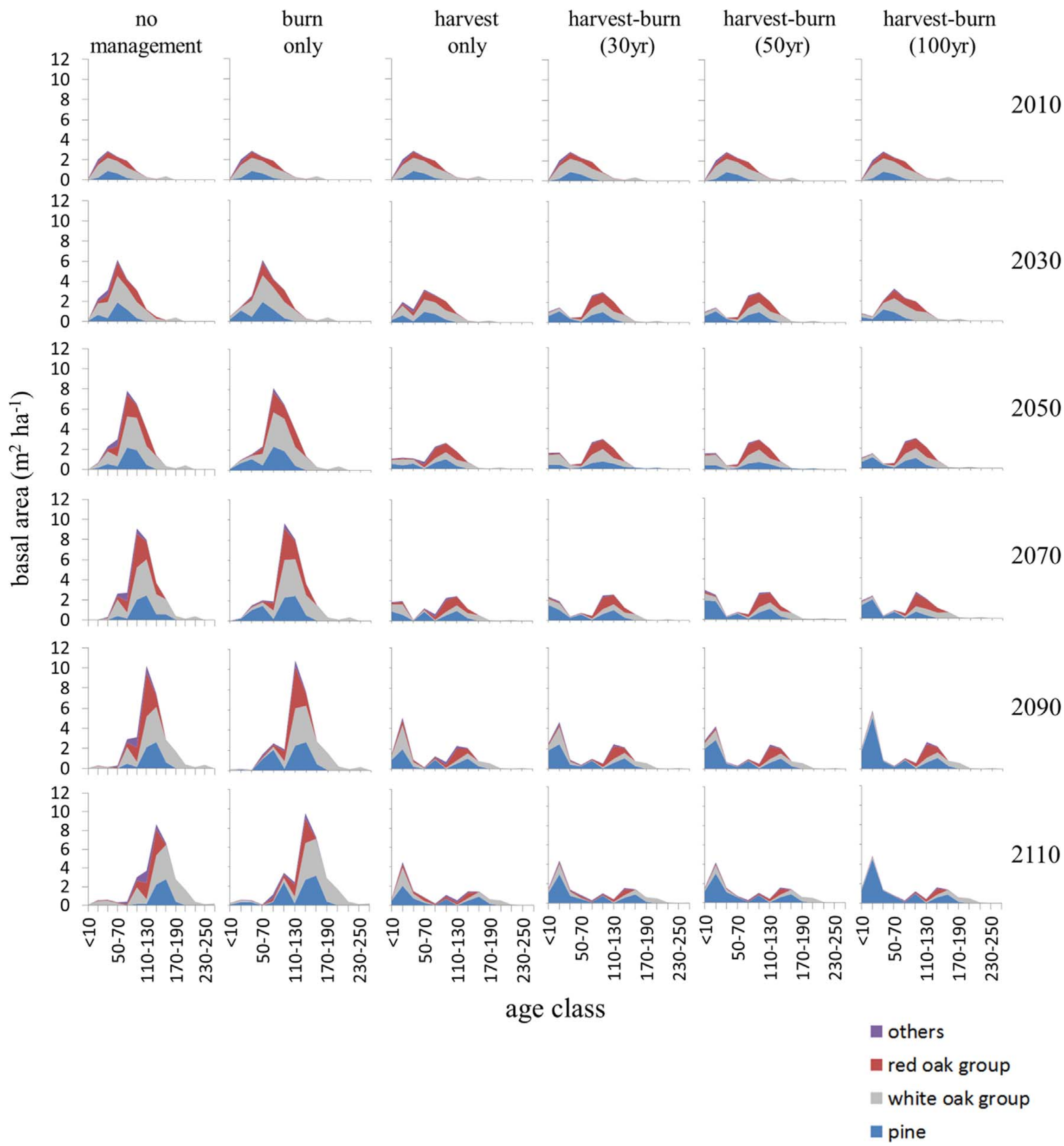

Fig. 3. Basal area by age class of four species groups (pine, white oak groups, red oak groups, and others) under six scenarios [no management, burn only, harvest only, harvest-burn (30 yr), harvest-burn (50 yr), harvest-burn (100 yr)] over 100-year simulation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

settlement era (early 19th century) in the Ozarks suggest that regional dominance of shortleaf pine resulted from frequent fire disturbances that favor pine regeneration and survival (Stambaugh et al., 2007). Although the pre-settlement historic fire regime apparently maintained an open-canopy woodland condition without timber harvesting (Fralish and McArdle, 2009), restoration of current close-canopy pine-oak forests to a woodland or savannah conditions appears to require harvesting or other disturbances in addition to fire.

4.2. Promotion of shortleaf pine by harvest

Our simulations suggest that harvest will reduce overall tree density in the overstory throughout the 100-year simulation period. Shortleaf pine has the lowest harvest priority in this study, so our modeled harvest scenarios specifically favor shortleaf pine. Although both shortleaf pine and oaks are known to resprout after being topkilled, oak species generally resprout more vigorously and can suppress shortleaf pine because the latter is more shade-intolerant (Tuttle and Houf, 2007a). Harvesting can help release shortleaf pines from suppression by oak sprouts. In addition, gaps created by harvest can favor establishment of shortleaf pine seedlings due to improved light condition and exposed soil to improve seedling establishment. Canopy gap size is found to be positively related to the density of shortleaf pine seedlings, which increases by approximately eight times from smaller (e.g., 400 m^2) to larger (e.g., 1700 m^2) gaps (Stambaugh and Muzika, 2004).

4.3. Combining prescribed burn and harvest to restore woodland

When prescribed burning and harvesting are combined, scenarios with most burning facilitated shortleaf pine the most, while scenarios with least burning had more white oaks. Combined prescribed burn and harvest can facilitate regeneration through improved light condition at the forest floor, reduced litter depth, and greater soil nitrogen concentration immediately after burn (DeLuca and Zouhar, 2000).

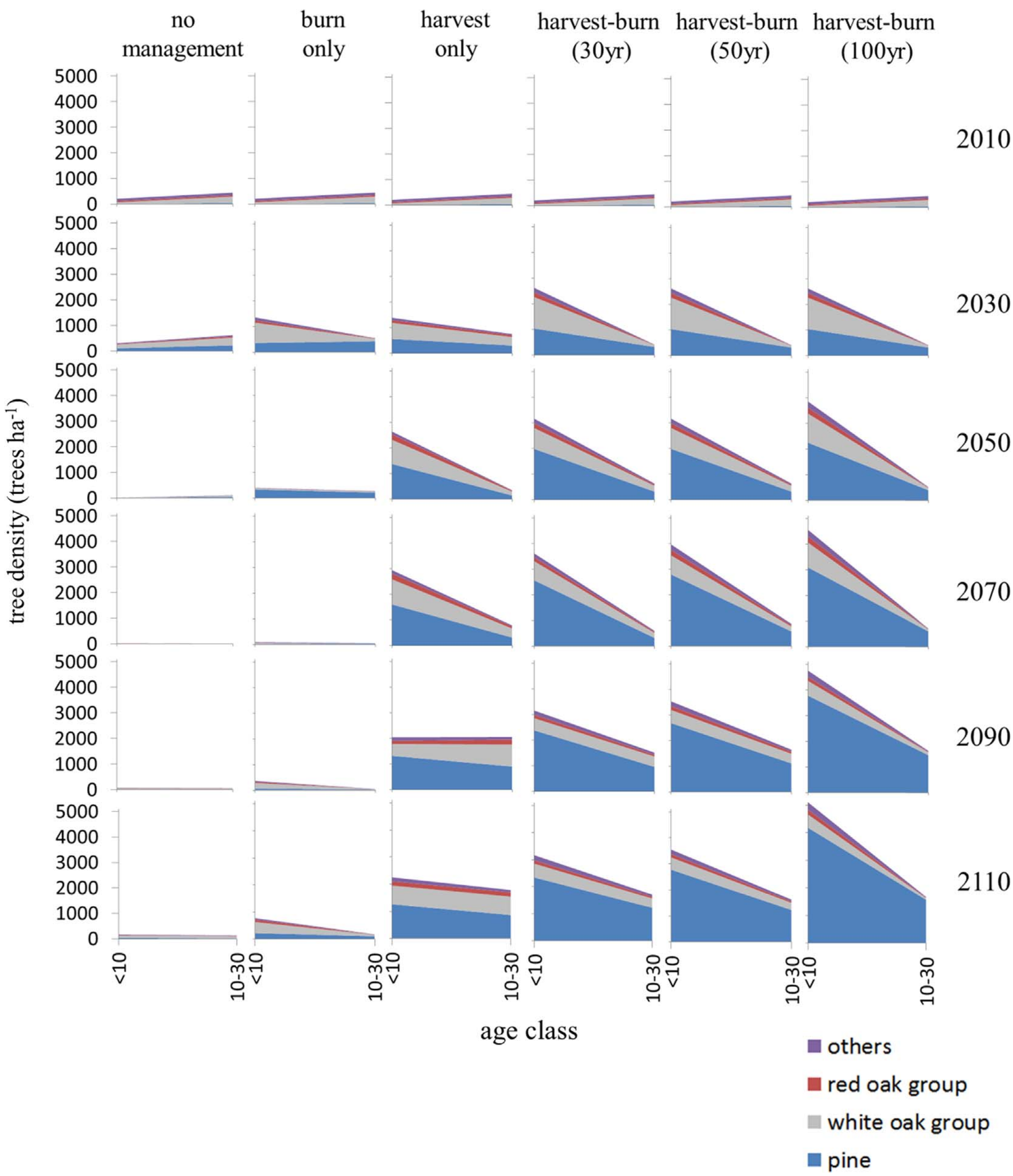

Fig. 4. Tree density of young trees (< 30 years) by age class of four species groups (pine, white oak groups, red oak groups, and others) under six scenarios [no management, burn only, harvest only, harvest-burn (30 yr), harvest-burn (50 yr), harvest-burn (100 yr)] over 100-year simulation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Densities of young trees (younger than 30 years, including seedlings and sprouts) of all four species groups were much greater under the combined harvest and burn scenarios than the other three scenarios. Since shortleaf pine is the most fire-resistant species in the study area, harvest with more burning would kill fewer shortleaf pines than other less fire-resistant hardwood species and reduce more competition from the latter. Thus shortleaf pine was most favored under the scenario that combined harvesting and the most burning. With less burning, survival of all other species increased. The white oak group had the lowest harvest priority among the hardwoods and was favored by scenarios with less burning. In this modeling study, the forest stands to be burned in a given years are fixed. In other words, locations of prescribed fires in a given year do not consider forest structure and composition or harvest regime. However, stands to be harvested are selected when they reach a basal area threshold. Specific locations and the spatial configuration of harvests are dependent on dynamic interactions among forest structure and composition, as well as effects of prescribed burning. Locations and spatial configuration of a given harvest event could also affect those of the next harvest event. Successful restoration is expected to diversify age structure in woodland communities, rather than create an even-aged structure. A curve somewhat similar to reverse J age distribution (although percentage of young trees should be less than that in a typical reverse J) should be expected.

4.4. Implications for landscape-scale management

Results from this landscape-scale modeling study suggest that prescribed burning alone, even over long periods cannot effectively restore dominance of shortleaf pine nor create a woodland tree structure from current closed-canopy forests. Tree mortality associated with prescribed burning is concentrated in small trees. Large overstory trees, which account for a substantial portion of basal area at both stand and landscape scales, rarely die from prescribed burning alone. Thus, the total basal area per hectare for prescribed burning alone was close to that

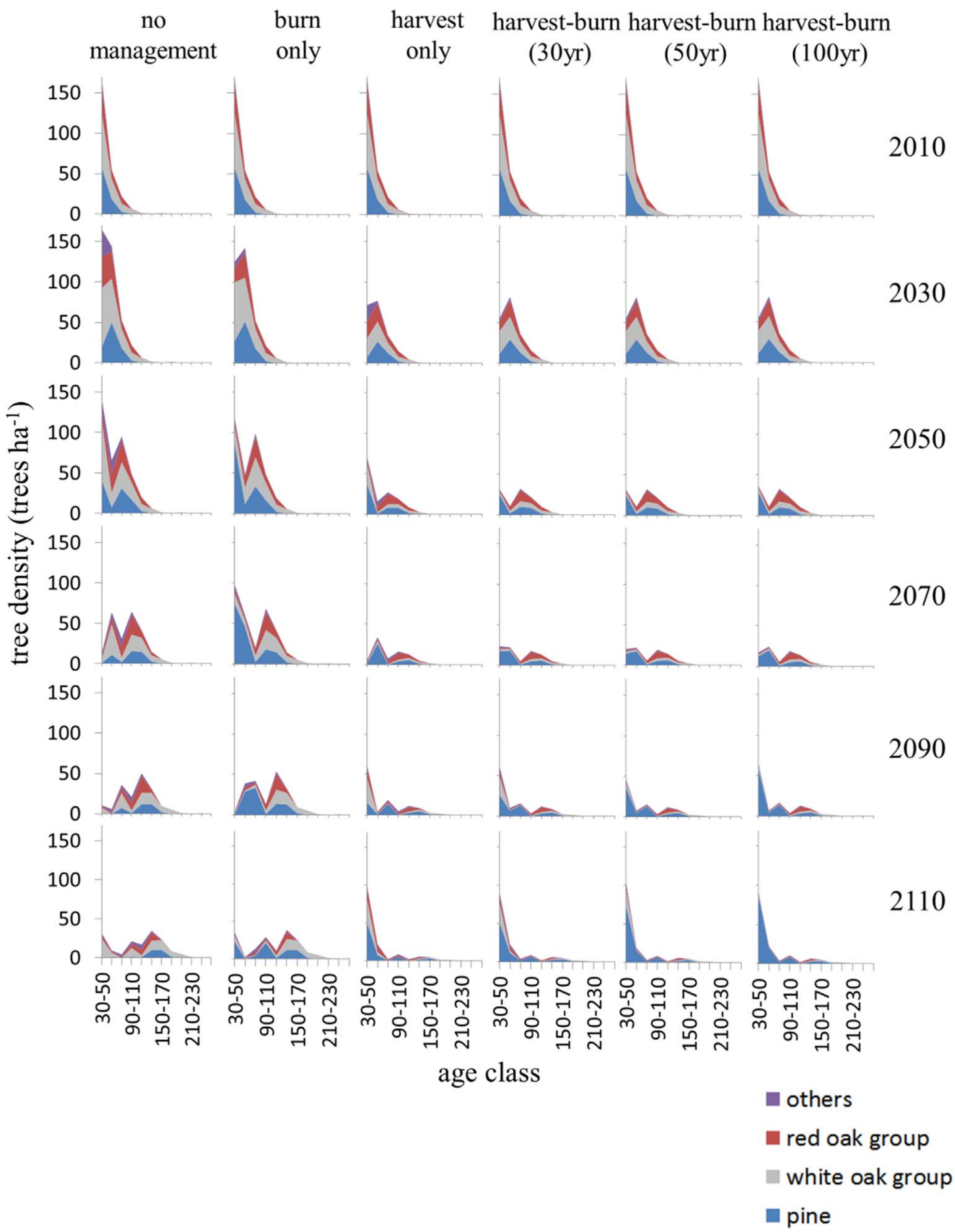

Fig. 5. Tree density of adult trees (≥30 years) by age class of four species groups (pine, white oak groups, red oak groups, and others) under six scenarios [no management, burn only, harvest only, harvest-burn (30 yr), harvest-burn (50 yr), harvest-burn (100 yr)] over 100-year simulation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

under the no management scenario, and current closed canopy remained intact. In this study, the shortest fire interval was set to 4 years, which is the average interval of planned prescribed burning in the CFLRP management plan. With helicopter-assisted broadcast burn and field crew efforts, it would be logistically feasible for approximately quarter of the study area (~7500 ha) to be burned, on average, annually. Harvest alone can reduce basal area compared to that under the no management and burn only scenarios. Since harvest preferences

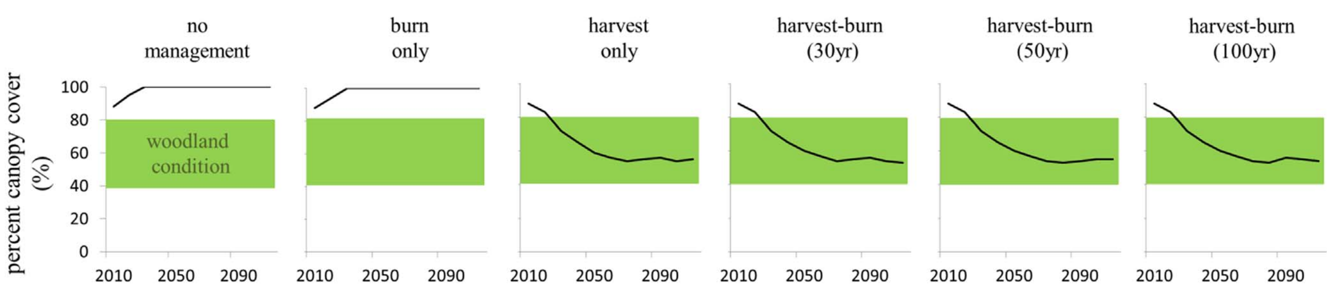

Fig. 6. Projected percent canopy cover change over time under six management scenarios over 100-year simulation period. Historically, percent canopy cover of woodland in the study area ranged from 40% to 80%.

were given to hardwood species, the percent of shortleaf pine in terms of basal area can slowly increase over time. Harvest can be more labor-intensive than prescribed burn on a per-unit-area basis at the landscape scale. Even though our study area is located in National Forest, private contractors, in addition to Forest Service staff, may be contracted to assist landscape-scale harvest.

With combined prescribed burn and harvest, the total basal area had a similar pattern over time as that under harvest only scenario. However, shortleaf pine became more dominant with more burns, and the proportion of white oak would increase with less burning. Under the combined prescribed burn and harvest scenarios, harvest regime can be affected by prescribed burning in two important ways: (1) total volumes to be harvested could be reduced. On one hand, this can lower work load; on the other hand, financial return from timber sales may be reduced. (2) Locations of stands to be harvested may differ from those under harvest only scenario. Higher spatial heterogeneity of forest has potential to mitigate disease/insect outbreak and oak decline (Clabo et al., 2016), and may also increase forest resilience to other disturbances (Churchill et al., 2013; Turner et al., 2013). Restoration of pine-oak woodland at the landscape scale can be a challenging task subject to uncertainty; this modeling study provided possible outcomes of using prescribed burning and harvesting. We expect results of this study can help policy makers and forest managers, along with considerations of financial cost and economic benefit, trade-offs among ecosystem services and functions, as well as specific restoration objectives such as wildlife conservation, to plan and implement pine-oak woodland restoration at the landscape scale.

4.5. Limitations

Long-term effects of prescribed burning and harvesting on shortleaf pine woodland restoration were the focus of this study; we did not simulate other silvicultural practice, such as planting of shortleaf pine seedlings to facilitate regeneration. In the Ozark Highlands, shortleaf pine seedling planting often is done after harvesting to ensure adequate reproduction. However, since our study area has both hardwood, especially oak species, and shortleaf pine, even if a small number of shortleaf pine seedlings planted after harvesting hardwood species would likely be suppressed by hardwood sprouts (Guldin, 2007). In the study area, periodic harvest and/or prescribed burn may still be needed even with seedling planting to help restore pine-oak woodland.

We also purposely did not include climate change scenarios in our simulations. Climate in the study area is projected to warm up in the 21st century under multiple climate change projections, e.g., Hadley-A1fi, GFDL-A1fi, and PCM-B1 (Schneiderman et al., 2015). How climate change affects tree species, especially shortleaf pine in this case, could also be of interest to forest managers. Biomass of shortleaf pine in our study area is generally projected to increase under three climate change scenarios mentioned above compared to that under current climate by a process-based model (Schneiderman et al., 2015). And a species distribution models predict that importance value of shortleaf pine increase under all three climate change scenarios (Prasad et al., 2007-ongoing). Thus, climate change is likely to benefit shortleaf pine in our study area, which can be advantageous to long-term pine-oak woodland restoration. In this study, we assumed that there will be no substantial land use change given the study area is located within a U.S. National Forest. We did not include effects of immigration of loblolly pine (*Pinus taeda* L.) (Schneiderman et al., 2015), disease/insect outbreak, pollution, CO_2 enrichment or nitrogen deposition.

Acknowledgement

Funding for this research was provided by Forest Service Research Joint Venture Agreement 12-JV-11242311-091 ("The Forecasting Landscape Change under Savannah and Woodland Restoration in Mixed Forest Ownerships") with the United States Department of Agriculture Northern Research Station, and the University of Missouri GIS Mission Enhancement Program. We appreciate generous support of inventory data and technique advisory from the Mark Twain National Forest. Casey Ghilardi and Benjamin Knapp supplied fuel load data used for model parameterization. David Larsen provided valuable comments. We also thank editors and one anonymous reviewer for their constructive comments that helped improve this manuscript.

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