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Dynamics of a temperate deciduous forest under landscape-scale management: Implications for adaptability to climate change ☆

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ABSTRACT

Landscape forest management is an approach to meeting diverse objectives that collectively span multiple spatial scales. It is critical that we understand the long-term effects of landscape management on the structure and composition of forest tree communities to ensure that these practices are sustainable. Furthermore, it is increasingly important to also consider effects of our management within the context of anticipated environmental changes, especially future climate. This study investigated two decades of tree community dynamics within a long-term, landscape-scale management experiment located in a temperate deciduous forest in southeastern Missouri, USA. This experiment tests three alternative landscape management systems: even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM). Specifically, we evaluated effects of landscape management alternatives on: (1) structural and compositional dynamics of the tree communities and (2) adaptability of the tree communities to projected climate change. Changes in the abundance of dominant species under these landscape management systems suggested a prevailing successional trend on these relatively xeric, oak-dominated landscapes. In the overstory layer, there was a decrease in the abundance of red oak species (Section *Lobatae*), mainly black oak (*Quercus velutina* Lam.) and scarlet oak (*Quercus coccinea* Muenchh.), and an increase in white oak (*Quercus alba* L.) suggesting a shift to white oak dominance is underway. In the midstory and understory layers, flowering dogwood (*Cornus florida* L.) abundance declined substantially, while maples (*Acer* spp. L.) and several minor species increased. Declines in shortleaf pine populations indicated that regeneration harvesting is not regenerating this species. Experiment-wide changes in tree community composition suggest that adaptability to projected future climate may have increased over the first two decades of the MOFEP experiment under all management systems and that diverse management objectives can be realized through active management, including adaptation to climate change. However, future research is needed to test this working hypothesis and to more fully evaluate the impacts of silviculture treatments within the context of projected climate.

1. Introduction

Forests are increasingly managed to meet multiple objectives designed to address a diverse set of ecological, social, and commodity goals (Gustafsson et al., 2012). These objectives can include conservation of biodiversity, natural community restoration, sustaining timber production, aesthetics, improving forest health, and climate change adaptation. In some cases, the objectives for a given land holding may require an approach capable of addressing desired conditions at sub-stand to landscape scales. Landscape management (i.e., management of an area composed of many stands) is one approach to integrating objectives across a wider range of scales (Hunter, 1999; Crow, 2008). For example, landscape management using even-aged and uneven-aged systems is being applied on public land in the Missouri Ozarks for conserving biodiversity, improving wildlife habitat, enhancing forest health, and sustaining timber production (Olson et al., 2015). Although these forms of even-aged and uneven-aged management can theoretically sustain a particular landscape structure, less is known about how they affect tree community composition and the adaptability of forests to future environmental conditions at the landscape scale.

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Climate change is regarded as one of the most challenging issues confronting forest management (Crow, 2008; D'Amato et al., 2011). Although there are many uncertainties regarding future climate change and its impact on forests, the consensus is that many forests will likely experience pronounced changes in climate over the next century (Park et al., 2014). Collaborative, multi-agency initiatives have started to promote an understanding of potential climate change impacts on forests and how to address climate change proactively through management (e.g., Climate Change Response Framework Projects in the United States). Efforts such as these depend on the knowledge gained from scientific investigations to help inform decisions on the adoption of management strategies for adapting to climate change.

There is considerable interest in management approaches that enhance the ability of forests to recover rapidly after disruptions induced by climate change (i.e., resilience) and to adapt to future climatic conditions and other perturbations (i.e., adaptive capacity) (Keenan, 2012; Park et al., 2014; Subramanian et al., 2016). Research on increasing resilience to environmental stresses related to climate change has addressed the efficacy of managing stand density (Cescatti and Piutti, 1998; Laurent et al., 2003; Magruder et al., 2013), managing species composition (Cortini et al., 2011; Buma and Wessman, 2013), and utilizing site preparation and vegetation control practices (Cortini et al., 2011). Investigations on the role of silviculture for enhancing adaptive capacity have focused mainly on increasing compositional and structural diversity at stand- to landscape-scales, which is hypothesized to promote a greater range of potential responses to future uncertainty (i.e., enhance response diversity) (Puettmann et al., 2008). An area that has received less attention is how contemporary forest management impacts adaptability to projected changes in climate.

The Ozark Highlands support forest and woodland natural communities that contribute to the ecological and socio-economic well-being of the region. Therefore, effects of anthropogenic climate change on Ozark ecosystems are potentially far-reaching. The Missouri portion of the Ozarks was included in a recent climate change vulnerability assessment for ecosystems of the Central Hardwood Region (Brandt et al., 2014). This effort used a model-based approach to compare recent abundances of tree species with their future abundances projected under two alternative climate change scenarios. Climate projections for the Missouri Ozarks from the periods of 1971–2000 to 2070–2099 indicated a 1–4 °C increase in mean annual temperature, while projected changes in mean annual precipitation were highly variable, ranging from a decrease of 15 cm to an increase of 5 cm. Simulated changes in the abundance of tree species in the Missouri Ozarks were variable with some species increasing, others decreasing, and some showing no change. Assessments such as this one provide resource managers with information on potential species' response to climate change that can be factored into management decisions. The next step in assessing climate change impacts for regions like the Missouri Ozarks is to evaluate the influence of alternative management regimes on the adaptability of forest communities to projected future climate.

The Missouri Ozark Forest Ecosystem Project (MOFEP) afforded a rare opportunity to examine the effects of landscape-scale management on forest dynamics and to assess management impacts on adaptation to climate change. MOFEP is a century-long, landscape-scale forest management experiment designed to evaluate the cumulative effects of even-aged, uneven-aged, and no-harvest management systems on the flora and fauna of upland oak ecosystems. The objectives of this investigation were to evaluate the effects of alternative landscape-scale forest management systems on: (1) structural and compositional dynamics of Missouri Ozark forests and (2) adaptability of the Missouri Ozark tree communities to projected climate change.

2. Material and methods

2.1. Study site and experimental design

Three management systems were initiated as treatments of the MOFEP experiment: even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM). The management systems are applied to MOFEP in the same manner as operationally applied by the Missouri Department of Conservation (MDC) on other managed public lands in the southeast Missouri Ozarks. The MOFEP experiment is located on two MDC-administered Conservation Areas in southeastern Missouri. All MOFEP sites fall within the Current River Ecological Subsection of the Ozark Highlands Section (Nigh and Schroeder, 2002). MOFEP sites are underlain mainly by Ordovician dolomites and sandstones (Meinert et al., 1997). Soils are highly weathered Ultisols and Alfisols derived mainly within loess, hillslope sediments, residuum, and gravelly alluvial parent material (Meinert et al., 1997). For nearly a quarter century, the MOFEP experiment has been a platform for multi-agency, collaborative research on managed forests (Knapp et al., 2014).

The MOFEP experiment employs a randomized complete block design (RCBD) that includes three blocks, with each management system randomly assigned to one of three experimental units per block (n = 9). MOFEP units range in size from 314 to 516 ha. Each MOFEP unit is an administrative compartment (hereafter 'site') composed of 44–82 stands, each ranging from 0.2 to 62 ha.

Silvicultural practices under EAM and UAM systems of the MOFEP experiment were first implemented from May 1996 to May 1997. The management cycle of both systems starts with a pre-treatment inventory of a site that is accomplished by inventorying each stand individually. This information is used to prescribe appropriate silviculture practices to each stand that also considers management impacts at the site level. Under MOFEP's EAM system, approximately 12% of the site is regenerated by clearcutting of mature stands every 15 years. Thinning is also applied as an intermediate treatment under EAM. Under MOFEP's UAM system, stands are treated with a combination of single-tree and group selection that tends size classes, similar to the BDq method, on the same 15-year cycle as the EAM system. Approximately 10% of each site was reserved as old growth under both systems prior to the first treatment entry. To date, there have been two treatment entries on MOFEP sites (1996–97 and 2011–12). See Brookshire et al. (1997) and Knapp et al. (2014) for more information about treatment implementation of the MOFEP experiment.

2.2. Woody vegetation monitoring

A network of 648 permanent sampling stations, with 70–76 sampling stations per site, is used to monitor forest vegetation on the MOFEP experiment. Since MOFEP sites are topographically and edaphically heterogeneous, sampling stations were strategically placed to capture topoedaphic variation within each MOFEP site using a stratified random sampling approach. Each station consists of a nested array of fixed-area plots designed to sample vegetation across size classes. Species, diameter at breast height (DBH), and condition (e.g., live or dead, crown class, etc.) of all woody stems $\geqslant$11.4 cm DBH are recorded within a 0.2-ha fixed-radius plot at each sampling station. The species and DBH of all live woody stems from 3.8 to 11.3 cm DBH are recorded within four, 0.02-ha fixed-radius plots located a fixed distance from the center of the 0.2-ha plot in the four cardinal directions. Nested within each 0.02-ha plot is a 0.004-ha fixed-radius plot for tallying live woody stems from 1 m tall to 3.7 cm DBH. This investigation used tree data collected over 18 years (1995–2013) on MOFEP's 0.2, 0.02, and 0.004-ha permanent plots (hereafter referred to as large, medium, and small size classes, respectively). Data from six inventories were included in this study: 1995 (pre-treatment), 1998 (post-first harvest), 2002, 2006, 2010, and 2013 (post-second harvest).

2.3. Analytical approach

2.3.1. Structural and compositional dynamics

The changes in basal area (BA; m^2 ha^{-1}) and stem density (trees ha^{-1}) from pre-treatment levels were used as response variables for assessing effects of MOFEP treatments on forest structure and tree community dynamics. Basal area was calculated by summing large and medium tree size classes. Stem density was calculated separately for large, medium, and small strata. The pre-treatment value was subtracted from the value of each post-treatment inventory individually to provide an estimate of change. Management impacts were assessed for twelve species and groups: total (all species combined), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.), post oak (*Quercus stellata* Wangenh.), hickories (*Carya* spp. Nutt.), shortleaf pine (*Pinus echinata* Mill.), blackgum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.), maples (*Acer* spp. L.), sassafras (*Sassafras albidum* (Nutt.) Nees), and other species. The other species group was composed of tree species of lower abundance, including blackjack oak (*Quercus marilandica* Muenchh.), northern red oak (*Quercus rubra* L.), chinquapin oak (*Quercus muehlenbergii* Engelm.), black cherry (*Prunus serotina* Ehrh.), black walnut (*Juglans nigra* L.), elms (*Ulmus* spp. L.), ashes (*Fraxinus* spp. L.), and eastern redcedar (*Juniperus virginiana* L.). Since MOFEP harvest treatments impact a portion of a site in each entry and this study covers only the first and second treatment entries, site level estimates were calculated from sampling stations in both harvested and unharvested stands within each actively managed sites, which captured the response at the larger, site level.

Repeated measures analysis of variance (ANOVA) for a randomized complete block design was used to test for effects of MOFEP treatments, inventory year, and the interaction of treatment and year on each variable by species group. ANOVA models were run using Proc Mixed in SAS 9.2 (SAS Institute Inc., 2002) with MOFEP treatment and inventory year specified as fixed effects and block and interactions between block and the fixed factors treated as random effects. Model residuals were checked for normality and equal variance. When distributional assumptions were violated, a power transformation was applied. Statistical significance was assessed at $\alpha = 0.05$. Fisher's least significant difference was used for comparing levels of significant fixed effects from ANOVA models, which was also performed in SAS 9.2.

2.3.2. Adaptability to projected climate change

Species' importance values (IV) were calculated at the site level for each of the six inventories and calculated separately for large, medium, and small tree strata. For large and medium classes, IVs were calculated as the mean of two measures: relative basal area and relative stem density. For the small stratum, only the relative stem density was used. Finally, site-level IVs were averaged by treatment for each inventory year.

Indices were used to assess the impact of MOFEP's landscape-scale management treatments on forest adaptability to projected climate change. Three indices were derived from multiplying species' IV by three species-specific weighting factors, then summing the three weighted IVs individually. Two of the species' weighting factors came from a separate modeling effort of the Central Hardwoods Climate Change Response Framework Project (Brandt et al., 2014). This effort used the model DISTRIB, a component of the Tree Atlas toolset (Iverson et al., 2008), to model and compare recent and future IVs of tree species for a three state area, which included a separate analysis for southern Missouri. Recent IVs were modeled based on estimates of suitable habitat for the period from 1961 to 1990. The projections of future IVs used in this study were predicted from potential suitable habitat for the period from 2070 to 2099 under two climate change projections representing alternative carbon emissions scenarios: (1) a low emissions scenario (Parallel Climate Model; Washington et al., 2000) and (2) a high emissions scenario (Geophysical Fluid Dynamics Laboratory; Delworth et al., 2006) (see Iverson et al. (2008) and chapters 4 and 5 of Brandt et al. (2014) for more information on the use of these models). The future to current IV ratio of each species under both low and high emissions scenarios were used as species-specific weighting factors for deriving a compatibility index (CI) for a low emissions future (CI_{LE}) and a high emissions future (CI_{HE}). A third index, called the adaptability index (AI), was calculated using species-specific adaptability scores as weighting factors. Adaptability scores were developed from multiple factors, called modifying factors, designed to capture potential adaptability of species to climate change that cannot be fully captured by the DISTRIB model (Matthews et al., 2011). Modifying factors incorporate information on species' traits, such as competition for light and edaphic specificity, and responses to stress and disturbance, including drought, pests, and fire, based on a literature review. Each modifying factor was weighted to account for confidence in the literature-based information and relevance to climate change. Unlike low emissions and high emissions weights, the weights based on adaptability scores are not specific to southern Missouri, since modifying factors were derived for a species across its entire range. CIs and AIs were calculated separately for large, medium, and small strata by inventory year for each MOFEP site. These site-level indices were averaged to derive a value for each treatment. CI and AI values were compared descriptively among and within treatments.

3. Results

3.1. 18-years of forest dynamics

Pre-treatment total BA was comparable among management systems prior to the first harvest entry (Fig. 1). Total BA in landscapes managed by EAM and UAM systems decreased immediately following both harvest entries, with a nominally lower BA following the second entry than the first. Mean separation results for the significant treatment by year interaction for total BA showed that BA was greater in NHM than in EAM and UAM in all years except 2010 (Fig. 1), one year before the second entry. This pattern suggests that BA under both active management systems nearly caught up with the BA of NHM landscapes during the 15-year period between first and second harvest entries.

For black oak and scarlet oak, reductions in BA following the first and second harvest were greater in EAM and UAM sites than NHM sites (Fig. 2A and B). There was a steady decline in black oak BA from 2002 to 2010 under NHM, while black oak BA was more stable under EAM and UAM during the same period. In contrast, scarlet oak BA increased under harvest management and remained fairly stable under NHM between harvests. Large stem densities of black oak and scarlet oak declined under all management systems (Fig. 3A and B). Reductions in large tree densities of both species were greater immediately after harvesting in UAM sites compared to NHM sites. White oak BA and large tree density also declined sharply after harvesting, while white oak abundance increased steadily under NHM (Figs. 2C and 3C). White oak rebounded rapidly and exceeded pre-treatment BA under active management by 2010. Following the second harvest, the

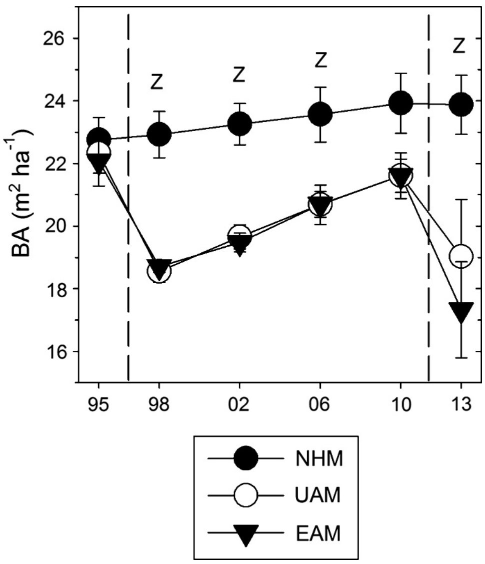

Fig. 1. Dynamics of mean basal area ($m^2\,ha^{-1}$; trees $\geqslant$3.8 cm DBH) of all tree species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in basal area between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD (α = 0.05). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

reduction in white oak BA and large tree density was greater under EAM than under the other systems. Despite this reduction in EAM sites, white oak was the dominant species, based on BA and large stem density, under all management systems by 2013. The BA of post oak and hickory species (Fig. 2D and E) and large tree density of hickories (Fig. 3E) also declined immediately after harvests but recovered to pre-treatment levels by 2010. Much like white oak, hickory BA and large tree density in unharvested sites increased over the study period. There was an experiment-wide decline in the density of large post oaks (Fig. 3D and Table 1).

Shortleaf pine BA increased experiment-wide (Fig. 2F and Table 1), while large stem density declined (Fig. 3F and Table 1), suggesting the basal area increase is mainly due to growth on existing trees rather than ingrowth. Further, medium stem density remained below 15 trees ha^{-1} under EAM and NHM and less than 8 trees ha^{-1} under UAM over the 18-year period (Fig. 4F). There was also an experiment-wide trend in small pine density with density increasing shortly after the first entry and later declining for the remainder of the study period, with 2013 being the lowest year (Fig. 5F and Table 1).

Increases in the density of small white oak stems in EAM and UAM sites were greater than changes under NHM over most of the 14 years between harvests (Fig. 5C). The density of small hickory stems also increased after the first harvest, especially under UAM (Fig. 5E). Although white oak and hickories in the medium size class of actively managed sites declined immediately after the first harvest (Fig. 4C and E), significant reductions were not detected until after the second entry and only under EAM (Fig. 6A and B). White oak steadily declined in the medium size class of NHM sites over the post-treatment period. However, ingrowth of white oak and hickory into the medium size class appeared to help slow the decline

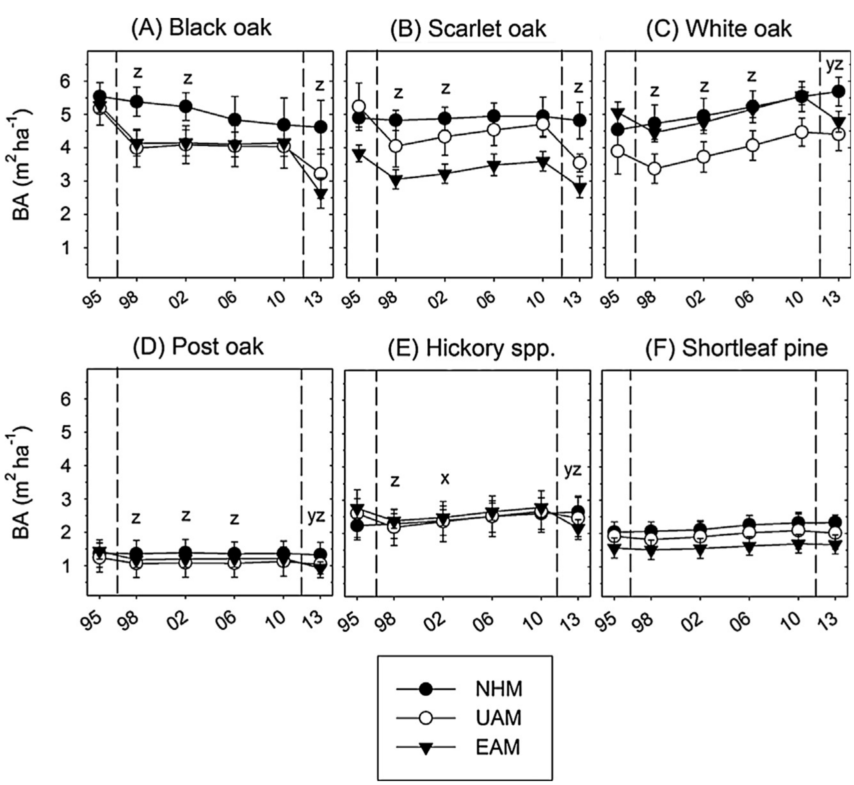

Fig. 2. Dynamics of mean basal area ($m^2\,ha^{-1}$; trees $\geqslant$3.8 cm DBH) of main overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in basal area between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD (α = 0.05). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

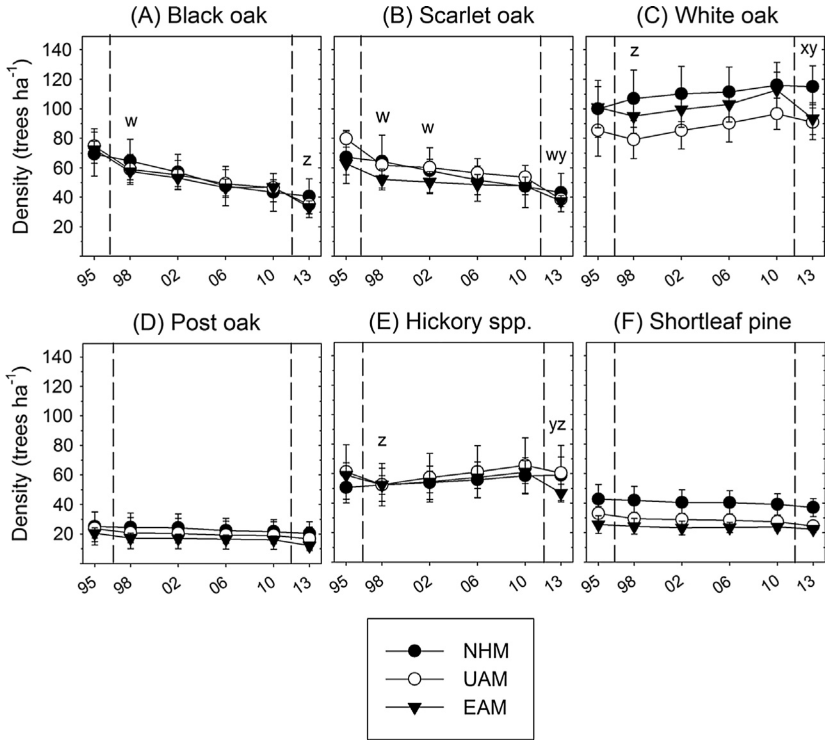

Fig. 3. Dynamics of mean large tree density (trees ha^{-1}; trees $\geqslant$11.4 cm DBH) of the main overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in large tree density between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD (α = 0.05). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

Table 1
Mean change in basal area and tree density for post-treatment years (i.e., post-treatment minus pre-treatment) across MOFEP management systems for species' responses with a significant year effect. Letters denote comparisons among years and are based on the results of Fisher's Protected LSD (α = 0.05). Means within a row with the same letter are not significantly different. Values in parentheses are equal to 1 SE.

Response variable and species	1998	2002	2006	2010	2013
Basal area					
Shortleaf pine	-0.05^{c} (0.07)	0.01^{bc} (0.08)	0.13^{ab} (0.13)	0.19^{a} (0.16)	0.16^{ab} (0.16)
Large tree density					
Post oak	-2^{a} (2)	-3^{a} (2)	-4^{ab} (2)	-4^{ab} (3)	-7^{b} (4)
Shortleaf pine	-2^{a} (2)	-3^{ab} (2)	-3^{ab} (4)	-3^{ab} (5)	-6^{b} (6)
Medium tree density					
Maple spp.	-2^{c} (2)	1^{b} (2)	5^{a} (2)	7^{a} (3)	7^{a} (4)
Other	1^{b} (3)	4^{b} (6)	17^{a} (17)	18^{a} (16)	19^{a} (17)
Small tree density					
Black oak	8^{b} (20)	24^{ab} (22)	44^{a} (17)	48^{a} (17)	26^{b} (14)
Scarlet oak	18^{ab} (16)	34^{a} (23)	4^{b} (13)	2^{b} (10)	25^{ab} (24)
Shortleaf pine	-1^{ab} (1)	3^{a} (5)	2^{ab} (6)	-1^{ab} (4)	-4^{b} (3)
Maple spp.	31^{c} (22)	157^{b} (94)	227^{a} (115)	227^{a} (103)	265^{a} (109)

between harvests under EAM. Experiment-wide, the density of small black oak stems increased between harvests (Fig. 5A and Table 1), while changes in the density of small scarlet oaks was more variable (Fig. 5B and Table 1). In the medium size class, black oak density increased under EAM compared to the other treatments (Fig. 4A) and scarlet oak density declined under UAM yet remained steady under EAM (Fig. 4B).

The densities of medium blackgum and dogwood on actively managed sites dropped immediately after the first harvest, followed by a recovery (Fig. 7A and B). By 2010, the increase in medium-sized blackgum on EAM sites was greater than changes on UAM and NHM sites. Experiment-wide, the densities of medium and small maple stems increased, but the gain was only an average of 7 trees ha^{-1} (SE = 4 trees ha^{-1}) in the medium stratum (Fig. 7C and Table 1) compared to 265 trees ha^{-1} (SE = 109 trees ha^{-1}) in the small size class (Fig. 8C and Table 1). The increase in medium sassafras density in EAM sites was greater than changes under the other management systems (Fig. 7D). The other species, a diverse group composed of mainly hardwood species, increased in the medium size class of all MOFEP sites (Table 1), but this trend was largely due to increases under EAM (Fig. 7E). Blackgum (Fig. 8A), sassafras (Fig. 8D), and other species (Fig. 8E) increased in the small size class of actively managed landscapes shortly after the first treatment followed by a decline. It is likely that these declines are at least partly due to recruitment into the medium size class.

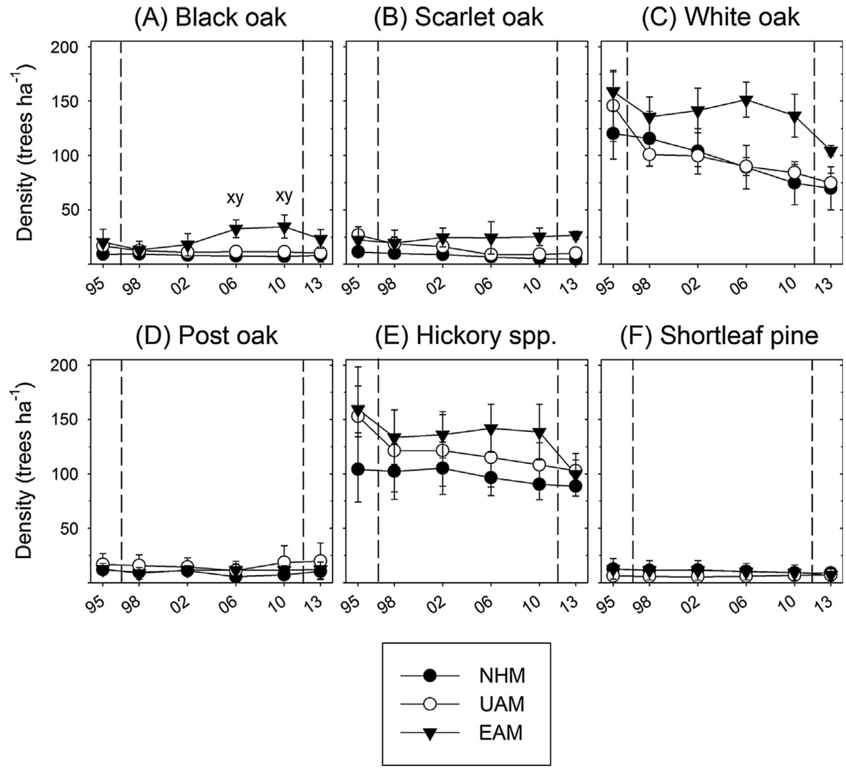

Fig. 4. Dynamics of mean medium tree density (trees ha^{-1}; 3.8–11.3 cm DBH) of the main overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in medium tree density between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD (α = 0.05). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

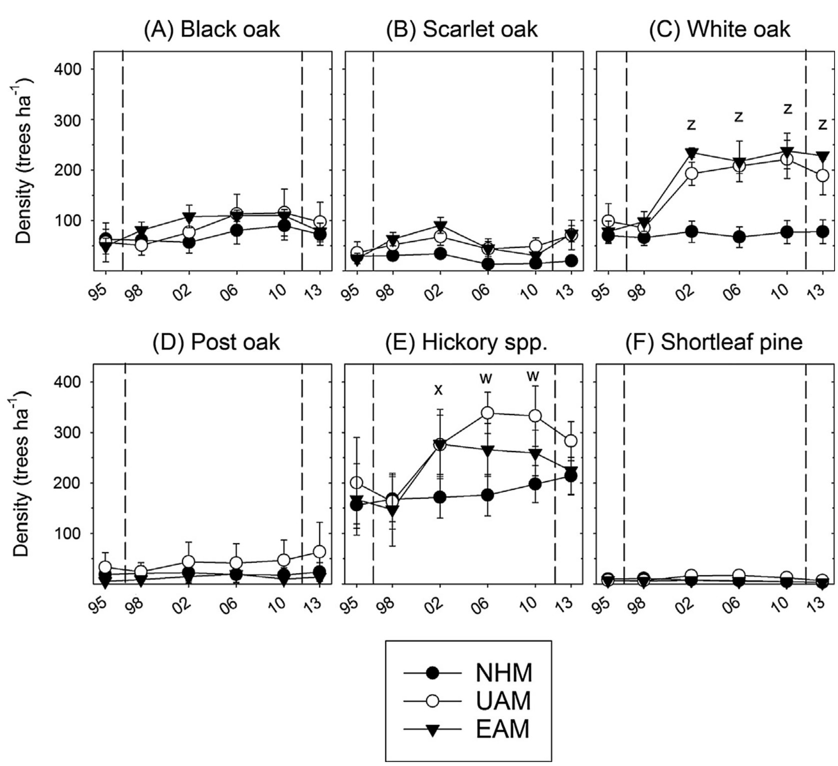

Fig. 5. Dynamics of mean small tree density (trees ha^{-1}; trees >1 m tall and <3.8 cm DBH) of the main overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in small tree density between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD (α = 0.05). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

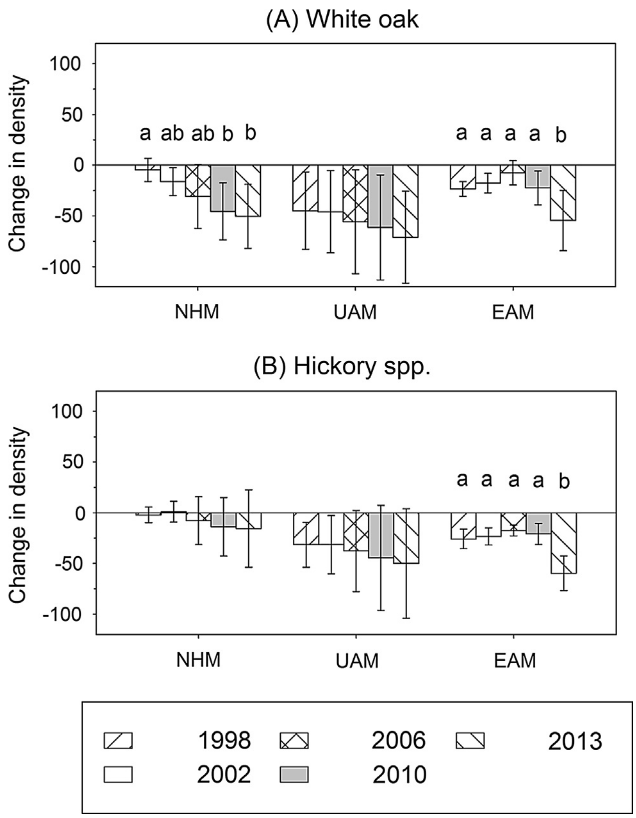

Fig. 6. Mean change in medium tree density (trees ha^{-1}; 3.8–11.3 cm DBH) of (A) white oak and (B) hickory spp. between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over a 15-year period of the MOFEP experiment from one year after the first harvest (1998) to one year after the second harvest (2013). Letters denote comparisons of years within the three management systems and are based on the results of Fisher's Protected LSD ($\alpha = 0.05$). Means with the same letter are not significantly different. Error bars are equal to 1 SE.

The densities of flowering dogwood in the medium and small size strata of MOFEP declined over the 18-year study period (Figs. 7B and 8B). Declines ranged from 189 trees ha^{-1} (SE = 92 trees ha^{-1}; UAM) to 615 trees ha^{-1} (SE = 197 trees ha^{-1}; NHM) in the small size class, while the loss of medium dogwood ranged from 84 trees ha^{-1} (SE = 12 trees ha^{-1}; NHM) to 105 trees ha^{-1} (SE = 21 trees ha^{-1}; UAM). The rate of decline was fairly constant under NHM compared to the actively managed sites. Immediate reductions in small and medium densities of dogwood after the 1996 harvest were followed by rebounds, especially in the small size class of actively managed sites. The slight rebound in medium-sized dogwood on EAM sites lagged behind the small class, suggesting a pulse of recruitment under EAM.

3.2. Impacts of management systems on adaptation to future climate

Compatibility and adaptability indices generally increased under all management systems and, in most cases, increases were greater than zero based on 95% confidence intervals (Fig. 9). CI confidence intervals for the large size class of EAM and UAM treatments did not include zero, suggesting an increase in the compatibility of large tree composition with habitat changes under both climate projections (Fig. 9A and B). AI confidence intervals for the large size class did not include zero, indicating an increase in the adaptability of the large tree class in all treatments (Fig. 9C). In the medium size class, CI confidence intervals did not include zero, suggesting an increase in compatibility under all management systems (Fig. 9D and E). Mean AI for the medium size class was negative for UAM and EAM treatments and positive for NHM, but confidence intervals included zero suggesting no change (Fig. 9F). In the small size class, confidence intervals for both CI_{LE} and CI_{HE} of the NHM treatment and CI_{HE} of the UAM treatment did not include zero, indicating an increase in compatibility of small tree composition, but not in sites under EAM or for UAM under the low emissions scenario (Fig. 9G and H). AI confidence intervals in the small class of all management systems did not include zero, indicating an experiment-wide increase in the

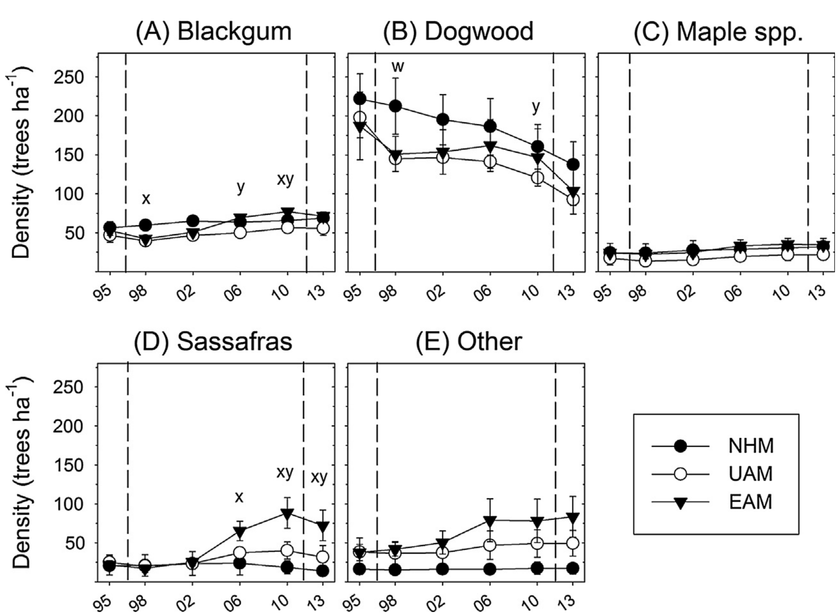

Fig. 7. Dynamics of mean medium tree density (trees ha^{-1}; 3.8–11.3 cm DBH) of the minor overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013). Letters denote comparisons of differences in medium tree density between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD ($\alpha = 0.05$). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

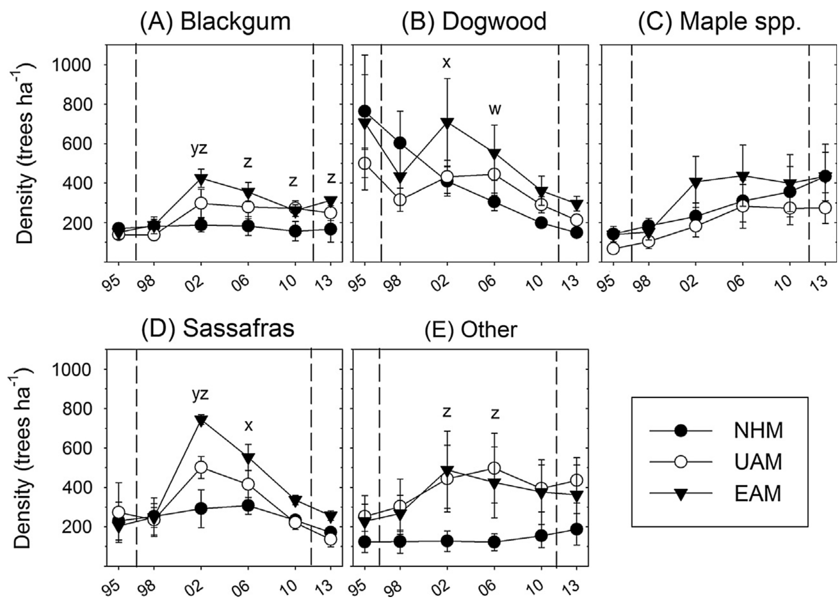

Fig. 8. Dynamics of mean small tree density (trees ha^{-1}; trees >1 m tall and <3.8 cm DBH) of the minor overstory species within sites treated with even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) over an 18-year period of the MOFEP experiment from pre-treatment (1995) to one year after the second harvest (2013) Letters denote comparisons of differences in small tree density between pre-treatment and post-treatment years (i.e., post-treatment minus pre-treatment) among the three management systems and are based on the results of Fisher's Protected LSD ($\alpha = 0.05$). Specifically, w is UAM ≠ NHM, x is EAM ≠ NHM, y is UAM ≠ EAM, and z is UAM & EAM ≠ NHM. Error bars are equal to 1 SE. Vertical dashed lines represent the two harvest treatments (1996–97 and 2011–12).

adaptability of the small tree class (Fig. 9I). Although overlapping confidence intervals suggest that indices did not differ between management systems, increases in mean CI_{LE} and CI_{HE} of medium and large size classes were nominally greater under active management than NHM and large tree AI of NHM and UAM were nominally greater than EAM, while increases in small tree CI and AI values were nominally greater under NHM than active management. Mean change in CI_{HE} values were of greater magnitude than CI_{LE} values.

4. Discussion

4.1. Dynamics of Ozark forests under landscape management

The first two decades of forest dynamics on the MOFEP experiment show the early effects of transforming mature, unmanaged forest into actively managed landscapes. As expected, total BA of sites under active management dropped immediately after harvesting. However, BA under both EAM and UAM rebounded nearly to the level of the NHM landscapes during the 15-year period between first and second harvest entries. Rebounds in total BA between harvests were likely due to both the increasing size of uncut overstory trees and the effectiveness of active management in initiating younger age classes and stimulating ingrowth. Forested landscapes of the Ozark Highlands generally support mixed hardwood stands often with a large component of senescent red oak species (Section *Lobatae*) (Spetich et al., 2016). Harvesting may be particularly effective in reducing the extent of stands at higher risk of oak decline in Ozark landscapes (Wang et al., 2013). By accelerating the replacement of senescent age classes by younger, more vigorous age classes, active management should enhance forest health in these landscapes. Diversifying landscape structure through active management should also benefit some wildlife species associated with younger stands (EAM) or stands with a multi-aged structure (UAM) (Morris et al., 2013) and could also help to boost the adaptability of forest vegetation to climate change (Crow, 2008).

Dynamics of black oak, scarlet oak, and white oak, the dominant overstory species of MOFEP sites, suggest a prevailing overstory compositional shift on these oak-dominated landscapes. Black oak and scarlet oak, both red oak species, generally decreased while white oak increased in the overstory across the MOFEP experiment. This shift in overstory composition is part of a successional trend facilitated by oak decline, an age-related disease complex that disproportionately affects mature red oak species and causes widespread mortality in deciduous forests of eastern North America (Shifley et al., 2006; Kabrick et al., 2008a). Black oak and scarlet oak are both acutely vulnerable to oak decline (Shifley et al., 2006; Fan et al., 2008). For example, Fan et al. (2011) observed that 65% and 73% of black oak and scarlet oak, respectively, survived during a 16-year period on MOFEP sites, while white oak survival was 92% during the same period. A management strategy in landscapes with extensive oak decline is to preferentially harvest senescent red oaks that will likely succumb to decline, while retaining white oak species (Section *Quercus*) (Wang et al., 2013). Our results suggest that this strategy is effective at capturing mortality of black and scarlet oaks through harvesting, as we generally observed similar reductions of these species in the overstory of NHM sites and harvested sites. As a result of the mortality in NHM and the harvesting in EAM and UAM, white oak was the dominant species of the large size class under all management systems by 2013 (Appendix).

The regeneration and recruitment of oak species is a main objective of landscape management on public land in the Missouri Ozarks. Our results suggest recruitment of black oak in EAM sites, with a slight increase in density in the medium size class at the landscape scale. Kabrick et al. (2008b) found greater density of red oak species regenerating in MOFEP clearcuts after the 1996 harvest than the other treatments, including selection methods and unharvested stands. Fan et al. (2015) concluded that clearcutting favored red oak species over white oak species on MOFEP. The concentration of red oak recruitment in clearcuts is expected since red oak species are relatively shade intolerant (Burns and Honkala, 1990) and have a height growth advantage over co-occurring tree

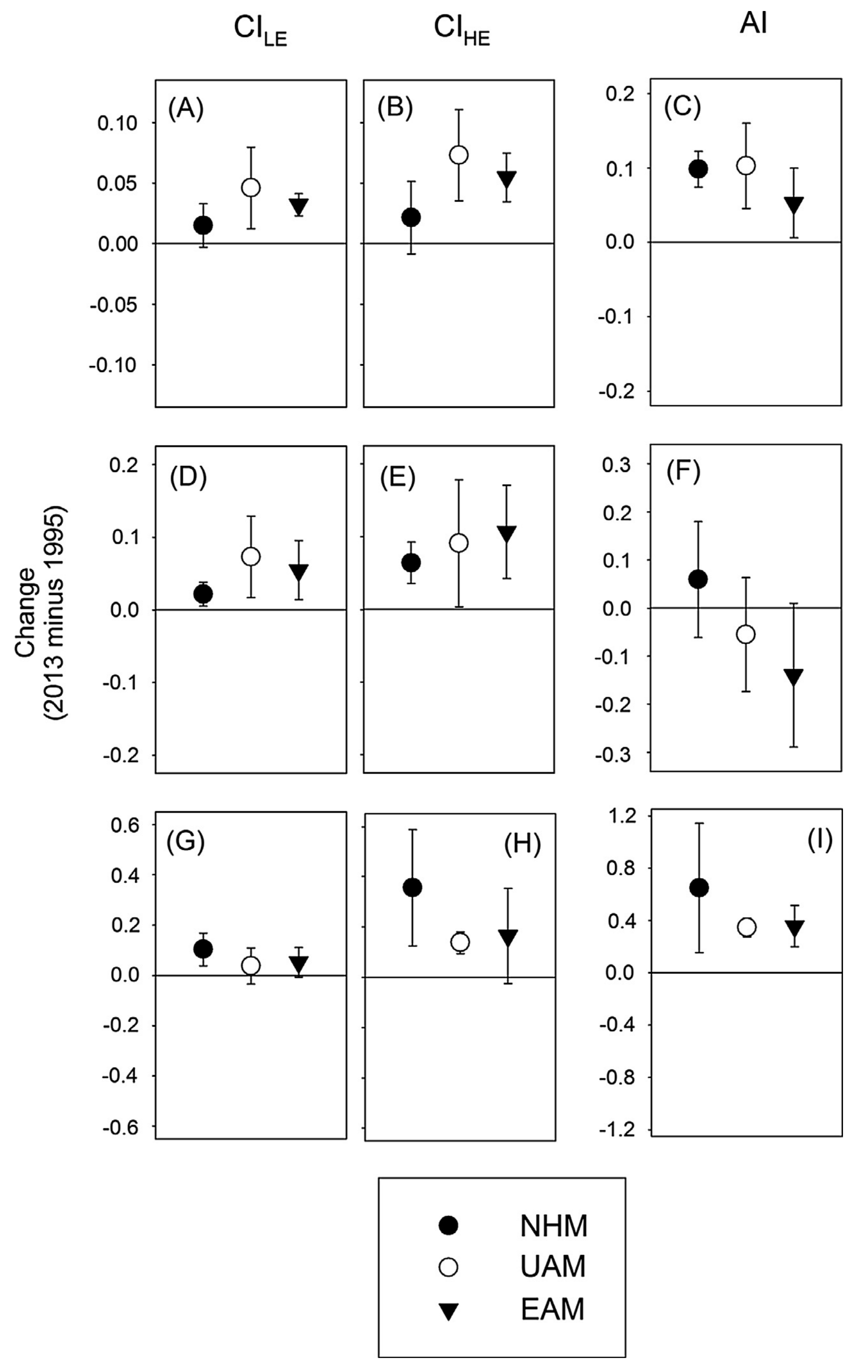

Fig. 9. Change in mean compatibility index (CI) and adaptability index (AI) from pre-treatment (1995) to one year after the second harvest (2013) (i.e., 2013 minus 1995) for large (A–C), medium (D–F), and small (G–I) size classes of trees of even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) treatments of the MOFEP experiment under a low emissions projection (CI_{LE}; A, D, & G), a high emissions projection (CI_{HE}; B, E, & H), and adaptability scores (AI; C, F, & I). Error bars represent 95% confidence intervals.

species under more open conditions (Vickers et al., 2014). Collectively, these findings suggest that EAM is fostering at least some red oak recruitment that is likely localized to clearcut stands. Our results also show that white oak and hickories were able to recruit new stems into the small and medium size class under both EAM and UAM systems. Previous research on MOFEP found that white oak regeneration increased in clearcuts as well as stands treated with both group openings and single-tree selection in the decade following the first harvest (Kabrick et al., 2008b). Recruitment of white oak and hickory species under UAM is not surprising given the greater shade tolerance of both species (Burns and Honkala, 1990) and lower abundance of shade tolerant competitors on these fairly xeric landscapes compared to more mesic forests of the Central Hardwood Region (Johnson et al., 2009).

Several species that were minor components of the large size class were major components of the smaller size classes and have increased in importance experiment-wide. The first harvest stimulated the recruitment of blackgum, dogwood, maple species, sassafras, and other species, which was most evident under EAM. This is likely an effect of clearcutting, which on average was applied to just over 10% of EAM sites in 1996 (Knapp et al., 2014). In the Central Hardwood Region, stand-replacing disturbances, like clearcutting, can initiate new stands composed of diverse tree species associated with different stages of secondary succession, similar to Egler's (1954) initial floristic composition model of succession (Johnson et al., 2009). The simultaneous recruitment of these minor overstory species along with the dominant oaks and hickories in EAM sites supports this pattern of secondary succession. UAM also triggered a recruitment pulse of the minor overstory species, especially the other species group. This taxonomically diverse group consists of species with regeneration responses ranging from opportunistic to more conservative with respect to site conditions and disturbance. The UAM treatment in 1996, which combined both single-tree selection and the creation of group openings, was applied extensively to UAM landscapes (applied to 57% of the site on average; Knapp et al., 2014). The strong regeneration response of the other species group seen at the landscape level could be associated with the extensive, mixed-severity disturbance caused by UAM, which impacted a wide range of sites within these topoedaphically heterogeneous landscapes.

The density of small and medium maple stems increased experiment-wide and, by 2013, red maple had the highest importance value of tree species in the small size class under all management systems (Appendix). In numerous studies on temperate deciduous forests of eastern North America there have been reported increases in the importance of maples species where fire has been excluded (Abrams, 1998; Hanberry et al., 2012; Olson et al., 2014). Historically, frequent fire maintained drier, more open-canopied woodlands throughout the Ozarks (Ladd, 1991; Hanberry et al., 2014), which favored species that were better adapted to surviving fire and tolerating drought, including shortleaf pine and upland oak species. There is mounting evidence that maple species, especially red maple, are expanding into upland forests of the Missouri Ozarks in the absence of fire (Hanberry et al., 2012; Olson et al., 2014). Since MOFEP sites have not experienced widespread burning since the mid-20th century (Guyette and Larsen, 2000), our results provide additional evidence for increasing maple importance in the absence of fire. However, this increase in maple importance occurred mainly in the small size class (i.e., understory layer) and maples have remained a minor component of both the medium and large size classes (i.e., midstory and overstory layers, respectively). The virtual absence of maple species in the overstory could be a legacy of historic drought and fire on the relatively xeric, oak-dominated landscapes of the Missouri Ozarks (Johnson et al., 2009). Continued monitoring of the tree community at MOEFP will determine if this increase in maple species regeneration leads to advancement into the overstory.

Densities of flowering dogwood declined precipitously on MOFEP sites over the 18-year study period. Several studies have observed declines in dogwood occurring locally and range-wide (Hiers and Evans, 1997; Schwegman et al., 1998; Williams and Moriarity, 1999; McEwan et al., 2000; Oswalt et al., 2012; Olson et al., 2014). Oswalt et al. (2012) largely attributed the decline in dogwood to mortality caused by the nonnative fungus *Discula destructiva* (dogwood anthracnose) but also cited increasing forest density, drought, and competition with shade-tolerant tree species as other possible causes. Since dogwood anthracnose is not considered a major issue in the southeastern Missouri Ozarks at this time (Simeon Wright, Personal Communication), the declines we observed were likely related more to removal by cutting treatments and stress associated with drought and competition.

The results of this study suggest shortleaf pine populations at MOFEP are in decline. This trend is consistent with the decline in shortleaf pine populations observed throughout the species' geographic range (Oswalt, 2012; South and Harper, 2016). The loss of shortleaf pine in the Missouri Ozarks has been associated with a shift in ecosystem states from open-canopied woodlands to closed-canopy forests that started over a century ago beginning with exploitative timber harvesting and extensive annual burning (Kabrick et al., 2008a) followed by fire suppression (Hanberry et al., 2012, 2014) that favored the proliferation of oaks and other hardwoods. Our results indicated virtually no shortleaf pines in the small and medium size classes across the MOFEP landscape. Since our results apply only to site-level averages, we are unable to determine the effect of the stand-level treatments (e.g., clearcutting and selection cutting) on shortleaf pine regeneration. However, data from the MOFEP study indicated that regeneration cutting alone is insufficient for regenerating shortleaf pine (Jensen and Kabrick, 2008). Poor shortleaf pine regeneration could be related to several factors, including the mistiming of the treatment with an adequate seed supply (Gwaze and Johanson, 2007), low density and limited dispersion of seed trees (Dovciak et al., 2003), lack of a suitable seedbed (Dovciak et al., 2003; Stambaugh and Muzika, 2007), and intense ground layer competition (Dovciak et al., 2003). Based on the time frame of this study, it is still too early to conclude on the effectiveness of the regeneration cuttings implemented in the second entry.

4.2. Landscape management and adaptability of Ozark forests

It is increasingly important to understand the potential consequences of our management decisions in the context of future climate (Park et al., 2014). We used the compatibility index (CI) and adaptability index (AI) as an initial step in assessing the impacts of landscape management on the adaptability of Missouri Ozark forests to future environmental change. Our results show that CI and AI generally increased across management systems. This suggests that experiment-wide forest dynamics on the MOFEP experiment over the 18 years covered by this study may have produced tree communities that are better adapted to future climate than they were at the start, including tree communities of unharvested sites.

Changes in CI of EAM and UAM treatments suggested an increase in the compatibility of large tree composition with climate projections for sites under active management, while results for AI indicated an increase in the adaptability of the large tree class in all treatments. Decreases in the dominant overstory red oak species, mainly black oak and scarlet oak, could partly explain increases in CI and AI of the large size class. Scarlet oak abundance is projected to experience large decreases under both emissions scenarios and both red oak species have moderate adaptability (Brandt et al., 2014). This could also help to explain relatively larger increases in CI and AI values under active management where mature red oaks were preferentially harvested. Shortleaf pine and white oak were preferentially retained in harvested stands of the MOFEP experiment and the importance of these species increased in the large size classes of sites under active management (Appendix). Shortleaf pine abundance is projected to increase under the climate change scenarios considered in this study, while white oak has a relatively high adaptability rating (Brandt et al., 2014). Therefore, increases in large tree CI and AI could also be related to increases in the importance of shortleaf pine and white oak, especially under active management. This suggests a management strategy of removing black oak and scarlet oak and retaining shortleaf pine and white oak could enhance the adaptability of Missouri Ozark forests to future climate.

CI of the medium size class increased under both emissions scenarios in all management systems indicating that compatibility of midstory tree composition with future climate projections increased across the MOFEP experiment. These increases in CI appear to be linked with decreasing importance of dogwood and white oak and increasing importance of maple species, especially red maple (Appendix). The abundances of both dogwood and white oak are projected to decrease under these future climate projections, while red maple is projected to increase (Brandt et al., 2014). Only nominal changes in AI were detected, suggesting that adaptability of the midstory layer of MOFEP sites was not affected by management. Nominal decreases in AI under EAM and UAM could also be associated with decreases in the importance of dogwood and white oak, since both species have moderate to high adaptability scores (Brandt et al., 2014). Since red maple has a high adaptability, the nominal increase in AI under NHM could also be due to the larger increase in red maple importance in unharvested sites.

In the small size class, the compatibility of tree composition with projected climate increased for both scenarios under NHM and the high emissions scenario under UAM but did not change under EAM. Increases in the importance of small red maple and decreases in small dogwood importance could help to explain these increases in CI (Appendix). Since the increase in red maple abundance is projected to be greater under high emissions than low emissions (Brandt et al., 2014), the large increase in red maple importance in the understory of unharvested MOFEP sites could explain nominally greater CI_{HE} under NHM than active management. This increase in red maple importance could also help explain the relatively large increase in AI of the NHM treatment. However, AI increased under all management systems, suggesting an experiment-wide increase in the adaptability of small tree layer over the two decades covered in this study.

5. Conclusions

Our study indicated that experiment-wide declines or shifts in dominant species are occurring in response to EAM, UAM, and NHM systems and that these shifts have important implications for forest adaptability to future climate change. Although we found evidence that the dominance of red oak species is decreasing on these sites, there is evidence that EAM stimulated red oak recruitment. Additionally, increases in white oak abundance could help to offset the loss of red oak and maintain a significant oak component. Hickories also increased in importance across the MOFEP experiment. These findings suggest that the benefits of oak and associated species for timber and hard mast production can be maintained under a range of management systems but that red oak species may not be a major component of future forests. The common red oak species are projected to not benefit from future changes in climate, so declines in these species could increase stand-level adaptability to climate change. However, red oak species are foundational components of these forests and an important economic resource. Therefore, efforts should be undertaken to sustain red oak species recruitment.

Shortleaf pine is considered better adapted to habitat changes associated with projected future climate than many of its associates (Brandt et al., 2014). Therefore, increasing the abundance of shortleaf pine not only would help to address conservation concerns for this species but could also enhance the adaptability of these forests to climate change. Our results showed that silvicultural treatments applied in 1996 failed to regenerate shortleaf pine. This finding suggests that overstory removal alone may not be enough to foster shortleaf pine regeneration and that additional treatments may be necessary. More research is needed to determine silvicultural practices for increasing shortleaf pine regeneration success.

Multiple lines of evidence suggest that the importance of maples and other minor species is increasing in the understory and midstory layers of these oak-dominated landscapes. Since several of the species are considered well-adapted to future climate change, particularly red maple (Brandt et al., 2014), increases in these groups may help to enhance adaptability to future climate. However, contradictory to this assertion, it has also been hypothesized that the low importance of these species in the current overstory suggests that chronic drought stress on these inherently drought-prone landscapes limits their development and generally favors oak species in the long term (Kabrick et al., 2008b; Olson et al., 2014; Fan et al., 2015). Future monitoring will help to elucidate the fate of red maple and other minor species on these sites.

Experiment-wide increases in CI and AI values observed in this study suggest that the adaptability of this forest to projected climate change may have increased over the first two decades of the MOFEP experiment under all management systems. However, silvicultural practices under both EAM and UAM facilitates the replacement of older age classes by younger classes and provides opportunities to manage stand density, both of which can enhance the resilience of these forests to climate change. Active management was able to capture some of the heavier anticipated mortality of overstory red oak species between harvests, especially black oak. Therefore, an additional benefit of active management is the ability to capture volume losses from elevated mortality caused by red oak decline. Therefore, active management is preferable to passive management for meeting diverse objectives, including timber production and climate change adaptation.

Future evaluations are needed to test the impacts of management on climate change adaptation, especially as new science-based information on tree response to projected climate becomes available. Examining the responses observed at the stand level within these or other managed landscapes will help to more fully evaluate the impacts of silviculture practices on both tree community dynamics and climate change adaptation.

Acknowledgements

We thank everyone who has contributed to the MOFEP experiment since its inception over 25 years ago. We give special thanks to Randy Jensen for managing many aspects of the project, including the collection of all of the tree community data used in this study. We also thank Sherry Gao (Biometrician, Missouri Dept. of Conservation) for providing statistical advice. Finally, we thank the Missouri Department of Conservation for its continued support of the MOFEP experiment and providing access to this data.

Appendix A

Weights and importance values (IV) for the top 22 tree species according to IV. Weights are for a low emissions scenario (LE), a high emissions scenario (HE), and adaptability scores (AS), which come from a separate effort by Brandt et al. (2014). IV for pretreatment and the most recent post-treatment years (1995 and 2013, respectively) were means calculated separately for each of the three management systems (NHM, UAM, and EAM) and by size class (large, medium, and small)

	Weights			Large						Medium						Small					
				NHM		UAM		EAM		NHM		UAM		EAM		NHM		UAM		EAM	
Spp.[a]	LE	HE	AS	95	13	95	13	95	13	95	13	95	13	95	13	95	13	95	13	95	13
Acru[b]	1.4	2.19	8.5	<1	1	<1	<1	<1	1	3	6	1	3	3	4	8	27	4	11	8	16
Acsa[b]	0.75	0.06	5.8	<1	<1	<1	<1	<1	<1	<1	1	1	1	<1	1	<1	<1	<1	1	<1	1
Cagl[b]	0.6	0.91	4.7	3	5	5	6	4	5	6	7	10	10	10	7	2	3	3	4	2	3
Cate[b]	1.15	0.87	4.1	5	5	3	4	4	4	4	7	4	7	5	5	3	6	4	5	4	3
Cato[b]	1.09	1.13	5.4	2	4	4	5	5	5	7	6	7	5	7	4	3	5	4	4	5	3
Ceoc[c]	0.91	0.81	5.7	<1	<1	<1	<1	0	0	<1	<1	<1	<1	<1	<1	1	4	2	5	1	2
Ceca[c]	0.76	0.76	4.9	<1	<1	<1	<1	<1	<1	1	1	<1	2	<1	1	1	2	3	3	2	2
Cofl[b]	0.96	0.62	5	1	1	1	1	1	1	33	27	26	18	24	14	42	9	29	10	34	12
Fram[b]	0.85	0.69	2.7	<1	<1	<1	1	<1	<1	<1	1	1	1	<1	1	3	4	2	4	2	4
Juvi[c]	0.88	0.64	3.9	<1	1	<1	1	<1	<1	<1	<1	<1	1	<1	<1	<1	<1	<1	1	<1	<1
Nysy[b]	1.42	1.06	5.9	2	3	2	2	2	2	9	14	6	10	7	10	10	11	8	11	8	13
Piec[b]	2.2	2.4	3.6	10	10	9	10	7	9	2	2	1	1	2	1	1	<1	<1	<1	<1	<1
Prse[b]	1.01	1.08	3	<1	<1	<1	<1	<1	1	<1	<1	<	1	<1	4	<1	1	<1	1	1	1
Qual[b]	0.77	0.49	6.1	22	28	19	27	25	31	22	17	22	17	24	19	4	5	5	9	4	10
Quco[b]	0.5	0.34	4.6	20	17	24	17	18	16	2	1	5	2	3	5	2	1	2	3	2	3
Qumu[c]	0.93	0.48	4.8	1	1	1	1	1	1	<1	<1	1	1	1	1	<1	<1	<1	<1	<1	<1
Qush[d]	4.9	14	5.8	<1	<1	<1	<1	0	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Qust[b]	1.09	1.29	5.7	7	6	6	6	6	5	2	2	3	5	2	2	1	2	2	3	<1	1
Quve[b]	0.97	0.73	4.9	23	16	23	15	23	14	2	2	3	2	3	4	4	5	3	5	3	3
Saal[b]	0.79	0.68	4.2	<1	<1	<1	<1	<1	<1	3	3	4	5	3	9	13	11	15	6	12	11
Ulal[b]	3.75	4.93	3.6	<1	<1	<1	<1	<1	<1	1	1	1	2	2	3	<1	1	3	2	3	3
Ulru[c]	0.49	0.43	4.8	<1	<1	<1	<1	<1	1	<1	<1	1	2	1	1	1	<1	5	3	2	1

[a] Species abbreviations are: Acru, Acer rubrum (red maple); Acsa, Acer saccharum (sugar maple); Cagl, Carya glabra (pignut hickory); Cate, Carya texana (black hickory); Cato, Carya tomentosa (mockernut hickory); Ceoc, Celtis occidentalis (hackberry); Ceca, Cercis canadensis (eastern redbud); Cofl, C. florida (flowering dogwood); Fram, Fraxinus americana (white ash); Juvi, J. virginiana (eastern redcedar); Nysy, Nyssa sylvatica (blackgum); Piec, P. echinata (shortleaf pine); Prse, P. serotina (black cherry); Qual, Q. alba (white oak); Quco, Q. coccinea (scarlet oak); Qumu, Quercus Muehlenbergii (chinkapin oak); Qush, Quercus shumardii (Shumard oak); Qust, Quercus stellata (post oak); Quve, Q. velutina (black oak); Saal, Sassafra albidum (sassafras); Ulal, Ulmus alata (winged elm); Ulru, Ulmus rubra (slippery elm).

[b] DISTRIB model results were of high reliability so reliability weight was 1.

[c] DISTRIB model results were of moderate reliability so reliability weight was 0.75.

[d] DISTRIB model results were of low reliability so reliability weight was 0.5.

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